Introduction

Standing dead trees (snags) serve a variety of ecosystem functions, including participating in carbon and nutrient cycles (Kurz and Apps, 1993; Howard et al., 2004) and serving as habitat (Harmon et al., 2004; Smith et al., 2008). As snags fall, they become downed dead wood, fulfilling other habitat and nutrient- and carbon-cycling roles (Everett et al., 1999; Harmon et al., 2004; Storaunet, 2004). Given that snags generally decay more slowly than downed dead wood (Boulanger and Sirois, 2006; Zielonka, 2006), snag dynamics influence landscape-level dead wood dynamics. Snag dynamics must be understood in order to manage and report landscape-level dead wood abundance (Garber et al., 2005).

Although Newfoundland forest management guidelines emphasize retention of snags for wildlife habitat, primarily for woodpeckers (Picoides species) (Smith et al., 2008), dead wood abundance has the potential to affect forest management for a range of other species and forest values. Downed dead wood and snags have been hypothesized to be important as den sites, subnivean shelter, access to small prey and vertical escape cover for American marten (Martes Americana), a threatened species in Newfoundland (Thompson and Harestad, 1994; Forsey et al., 1995). American marten in the north-eastern US prefer forests with larger downed logs (large-end diameter; mean ± SE = 21 ± 0.8 cm) and snag volumes of >10 m³ ha⁻¹ (Payer and Harrison, 2002). Dead wood abundance in managed forests has been linked to the abundance of small mammals and birds in Labrador black spruce (Picea mariana (Mill.) B.S.P.); Simon et al., 2000). Northern long-eared (Myotis septentrionalis) and little brown (Myotis lucifugus) bats, whose range includes Newfoundland, roost in cavities common in dead trees. Although, in New Brunswick, males of these species are known to roost in trees with diameter at breast height (d.b.h.; 1.3 m) <20 cm (Broders and Forbes, 2004), their preferences for roosting habitat in Newfoundland are unknown. Understanding the role of dead wood in biogeochemical cycles is becoming increasingly important (Harmon et al., 2004). As a signatory to the United Nations Framework Convention on Climate Change (United Nations Framework Convention on Climate Change, 2009), Canada must report and account for total ecosystem carbon stocks and stock changes in the managed forest. Dead wood forms an important yet relatively poorly documented forest carbon stock that is strongly impacted by forest management (Krankina and Harmon, 1994; Moroni, 2006).

Summary

Dead-tree (snag) density (stems per hectare), diameter, species distribution and input rate were examined in Newfoundland boreal forests dominated by black spruce (Picea mariana (Mill.) B.S.P.) and balsam fir (Abies balsamea (L.) Mill.). Examinations were based on permanent sample plot data. Total snag densities were higher in fir than spruce and were densest in 40- to 59-year-old stands of both species. Densities of >9 cm diameter at breast height (d.b.h.; 1.3 m, hereafter all dimensions are dbh) snags and live trees and larger live and dead trees (>19 cm stems) were also higher in fir than spruce. Fir also generated more larger snags at a younger age than spruce. Precommercial thinning reduced snag densities, virtually eliminating >9 cm snags from 37- to 48-year-old forests. Disturbance regime had a minor impact on snag densities in >40-year-old forests. The annual rate of >9 cm snag production in >60-year-old forests was <1.6 and <1.2 per cent of live trees per year in fir and spruce, respectively. The annual rate of live >9 cm tree fall down in >60-year-old forests was <0.6 and <0.9 per cent in fir- and spruce-dominated forests, respectively.
Studies of dead wood in Newfoundland have focused on old growth (Thompson et al., 2003) and post-harvest (Sturtevant et al., 1997; Setterington et al., 2000; Smith et al., 2008, 2009) balsam fir-dominated forests largely examined in western Newfoundland. McCarthy and Weetman (2007) examined live tree and snag dynamics in a chronosequence of balsam fir on NL’s west coast regenerating following insect outbreak only. Moroni (2006) compared dead wood in naturally and anthropogenically disturbed balsam fir and black spruce, expanding the study area to central Newfoundland but in limited age classes. To increase confidence in our ability to describe and manage dead wood dynamics for current and potential future needs, more intensive examinations of dead wood abundance in both balsam fir- and black spruce-dominated forests are required from all developmental stages, regions and disturbance histories.

The dynamics of small-diameter dead wood that is characteristic of boreal forests of Newfoundland (Moroni, 2006) has different temporal dynamics than forests with longer lived larger diameter trees, such as those occurring in western and southern North America where woody debris dynamics have been studied and documented for decades (Harmon et al., 2004). In contrast, the boreal forests of eastern North America and the circumpolar northern boreal are an enormous region that has attracted less attention, where forests dominated by short-lived small-diameter trees are common (Ahti et al., 1968; Hämet-Ahti et al., 1974; Ecoregions Working Group, 1989).

The Newfoundland Forest Service collects data on snags from roughly 1000 permanent sample plots (PSPs) located in black spruce- and balsam fir-dominated forests across Newfoundland. The PSPs are located in forests encompassing the full range of developmental stages, regions (Meades and Moores, 1994) and disturbance regimes. PSPs are scheduled for remeasurement every 4–5 years, at which time individual live trees are tagged and remeasured, allowing rates of snag recruitment and live-tree fall down to be estimated. The Newfoundland PSP snag dataset provides an opportunity to increase our understanding of snag structure and dynamics in small-treed boreal forests such as the black spruce- and balsam fir-dominated forests common to Newfoundland.

Here, we examine the Newfoundland PSP dataset to (1) determine and compare snag structure in Newfoundland balsam fir and black spruce forests, describing (a) d.b.h. distributions and (b) species compositions; (2) determine the impact on snag densities attributable to (a) disturbance at origin (stand-initiating disturbance) and (b) precommercial thinning (PCT); (3) determine what variables measured in PSPs are related to snag density (stems per hectare) and (4) determine the rate at which live trees fall down or become snags and which variables measured in PSPs are related to these rates.

Materials and methods

Site description and selection

Newfoundland is divided into four regions: central, western, northern (northern peninsula) and eastern (Newfoundland Department of Forest Resources and Agrifoods, 1998). The northern region is cooler than the other three, resulting in slower forest growth rates and lower yields (Newfoundland and Labrador Department of Natural Resources, unpublished data). The eastern region has the coldest summers and the warmest winters, but is more exposed, especially to high winds that stunt forest growth and limit productive forests to sheltered regions. Balsam fir (fir) is the climax tree species throughout most of Newfoundland, but its distribution is concentrated in western and northern Newfoundland. This is largely because of prevailing, moisture-laden westerly winds from the Gulf of St Lawrence that bring 1.0–1.5 m of precipitation to Newfoundland’s west coast, reducing the occurrence of fire. In contrast, central Newfoundland is characterized by an inland quasi-continental climate with warm dry summers that result in a high fire danger; regular burning has led to the establishment of extensive stands of black spruce (spruce; Wilton and Evans, 1974) in this region.

Harvesting is the major anthropogenic disturbance in Newfoundland, with ~17 500 ha clear-cut annually, roughly half in fir and half in spruce (Newfoundland Department of Forest Resources and Agrifoods, 1998). Since 1976, >74 000 ha of Newfoundland fir have been precommercially thinned. Rates of precommercial thinning were recently reported to be 2650 ha year⁻¹ (Moroni, 2006). The major natural disturbances in Newfoundland are fire in spruce (Wilton and Evans, 1974) and insect outbreaks in fir. Between 1997 and 2007, for example, fires have burned an average of 1088 ha year⁻¹, including 428 ha year⁻¹ of mostly spruce-dominated productive forest (E. Earle, personal communication). Spruce budworm (Choristoneura fumiferana (Clemens)) outbreaks between 1971 and 1979 killed 23 per cent of the island’s merchantable tree volume (Hudak and Raske, 1981), and hemlock looper (Lambdina fiscellaria (Guénée)) defoliated 73.6 million ha, killing 33 000 ha between 1983 and 1995 (Hudak, 1996).

In 1985, the Newfoundland Forest Service implemented an PSP programme to provide growth data for calibration and validation of stand growth projection models. The initial focus was predominantly on immature stand types in natural and managed forests throughout Newfoundland. In 1992, the programme was expanded to include stands in all developmental stages (regenerating, immature, semi-mature, mature and overmature), with ~1000 PSPs currently established in natural and managed stands of all developmental stages and scheduled for remeasurement every 4–5 years. During remeasurements, individual live trees and some dead trees were relocated, allowing changes in status from live to dead or live to downed to be detected between measurements. In 1996, a subplot was added to PSP plots. Within PSPs established or remeasured after 1996, dead trees not previously measured during earlier PSP measurement cycles were included in the PSP subplot. With the addition of the PSP subplot, all dead trees within PSPs were measured enabling total snag structures to be estimated.

The expanded PSP programme was designed to examine the major softwood-producing stand types in Newfoundland. Each stand type was ranked for sampling based on relative importance to commercial timber supply and level

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of financial investment. For example, precommercially thinned stands received a very high sampling priority because they contribute significantly to wood supply and have received substantial financial investment.

Stand types were stratified into sampling units based on variables related to stand development by summarizing forest inventory and silviculture stand records. Allocation of plots within sampling units was based on two main criteria: the sampling priority assigned to the stand type and the inherent variability within each sampling unit. Stands were selected from a list of potential PSP locations to ensure they were characteristic of the targeted stand type, well distributed across the ecoregions (Meades and Moores, 1994) and not scheduled for management treatment in the near term (Vanguard Forest Management Services, 1992). Selected stands were verified by field crews, and if suitable, plots were established, ensuring that they fell wholly within the targeted forest type. Established plots avoided regions with large gaps, clusters of non-target species and poorly stocked regions of forest polygons.

For this study, a snag was considered to be a self-supporting dead tree. Dead trees in PSPs tallied as snags were defined as standing intact with or without broken tops in PSP plots and subplots. All other PSP dead-tree classifications were considered downed dead wood, including leaning dead trees. It was not possible to determine if leaning dead trees were self-supporting. Based on discussions with Newfoundland and Labrador Forest Service staff, most leaning dead trees tallied were unlikely to be self-supporting and were considered downed.

Sample plot demarcation and snag identification

Following site validation, a path was marked on a bearing from an easily located landmark to the selected stand. PSPs form a rectangle, with four corner posts labelled A–D (Figure 1). Corner A is established in the targeted forest at the stand end of the marked path. Facing into the plot, away from the landmark in the direction of the marked path, Corner D is located 14.00 m on a bearing 90° to the right of Corner A. Corners B and C are located on the bearing of the path away from the landmark from Corners A and D, respectively, at a distance, or plot length, depending on the examined stand type and density. Plot length of mature and overmature stands was 28.57 m, creating 0.04-ha plots. Immature and semi-mature stand plot length was determined by the plot length required to tag a minimum of 75 trees that met minimum tagging criteria; however, plot size was restricted to seven standard plot sizes ranging from 0.002 to 0.1 ha. If, at remeasurement, a plot no longer contained a minimum of 75 trees, it was enlarged. Minimum tagging criteria varied by stand development stage. For mature and overmature stands, trees with d.b.h. ≥ 8.0 cm were tagged. The d.b.h. of tagged-trees drops with declining stand age until the stand contains the smallest trees considered for tagging, which exceed 1.3 m in height. This variable tagging threshold was developed as a practical response to dealing with the wide variability in tree density associated with typical stand development (Newfoundland Forest Service, unpublished data). All dead trees within the mature and overmature PSPs at the time of plot establishment that met minimum tagging criteria, had no green cambium and retained at least two-thirds of their original height with branches largely intact were tagged and measured for snag species and d.b.h. to the nearest centimetre.

In 1996, a subplot was added to the PSP plot within which all dead trees, both standing and fallen, that were never tagged and measured in the original PSP sampling were tallied. The subplot is rectangular, with a length equivalent to the centre line between Corners A and C; it is 4-m wide, 2 m either side of the centre line (Figure 1). Stems were counted if the midpoint of the standing stem was within the subplot. Untagged snags were tallied in 1–8.99, 9–18.99, 19–24.99 and >25 cm d.b.h. size classes, limiting the reporting of total PSP snag d.b.h. distributions to these classes. The species of untagged snags was not recorded. Because untagged snags could not be relocated and reassessed during later PSP remeasurements, estimates of average stand snag longevity and fall rate could not be made. All data describing snag structure (d.b.h. and species distributions) were based on the first PSP remeasurement or PSP establishment measurements.
that occurred after the 1996 inclusion of the PSP subplot. The rate of snag recruitment or live-tree fall down was based on changes in individual tagged and relocated tree status between PSP establishment measurements and the first remeasurement, including PSPs established from inception of the programme in 1985 and beyond.

Statistical analyses

In each PSP, the species or species group with the greatest live basal area was designated as the stand type. Only spruce and fir stand types were represented by sufficient PSPs to warrant analysis. In addition, PSP measurements where silvicultural intervention or disturbances had occurred following plot establishment were excluded from examination; stands of all disturbance-at-origin types were combined for analysis, unless otherwise stated. Data presented here are based on ≥9 cm stems only.

Snag density

To avoid autocorrelation, descriptions of snag density, diameter and species distribution by age class and d.b.h. class, as well as the examination of relationships between snag density and other variables collected during PSP measurements, were restricted to data collected from the first PSP measurement, which incorporated data from the PSP plot and subplot. When examining the PSP dataset for potential predictors of snag density, the natural logarithm of snag density (ln(snag density + 1)) was used as the dependent variable to achieve normality and homogenize the variance of the residuals. The transformation also has the desired effect of producing only positive predictions. Predictors of snag density were determined using the Generalized Linear Model (GLM procedure) in SAS version 9.1.3 (SAS Institute Inc., Cary, NC, 2007), with stand type, origin and region as fixed qualitative variables and dbh, stand age, (stand age)², live basal area, live ≥9 cm tree density and elevation as quantitative variables. The basal area of live trees ≥9 cm is proportional to the product of live-tree density and dbh². Quadratic terms were included because various authors have noted non-linear temporal trends in snag densities with stand development, from U-shaped (Hély et al., 2000) to inverse U-shaped (Moorman et al., 1999). Backward elimination was used to eliminate variables not statistically significant at α = 0.05. There were no departures from the assumption of homogenous variance.

Snag dynamics

Examinations of snag dynamics were restricted to tagged trees. To avoid autocorrelation, snag dynamics were determined between the first and second PSP plot measurement. Snag input rate was determined from changes in tagged-tree status between live and snag. Live-tree fall down rate was determined from changes in tagged-tree status between live and downed wood. It was assumed that trees that were live at one measurement and woody debris at the next were fallen down and did not go through a snag phase between live and woody debris.

The input rate of live trees to snags per year was estimated as follows:

\[
\text{rateL2S}_{t+1} = \frac{\text{Live2Snag}_{t+1}}{\text{Live}_{t+1} \cdot (t2 - t1) + 1},
\]

where Live2Snag is the number of live trees that become snags between time t1 and t2; Live_{t+1} is the number of trees live at time t1.

The rate at which live trees fall down was estimated as follows:

\[
\text{rateL2D}_{t+1} = \frac{\text{Live2Debris}_{t+1}}{\text{Live}_{t+1} \cdot (t2 - t1) + 1},
\]

where Live2Debris is the number of live trees that fell down between time t1 and t2; Live_{t+1} is the number of live trees at time t1.

Similar to snag density, snag input and fall down rates were analysed using the GLM procedure of SAS version 9.1.3 with stand type, origin and region as fixed qualitative variables and dbh, stand age, (stand age)², live basal area, live ≥9 cm tree density and elevation as quantitative variables. The transformed ln(rate + 1) was required to normalize the residuals. There were no departures from the assumption of homogenous variance.

Results

We examined snag and live-tree structure in 290 unthinned fir-dominated PSPs and 288 spruce-dominated PSPs (Table 1). The impact of PCT was examined in 476 thinned PSPs, 232 regenerating following clear-cutting and 244 not previously clear-cut (Table 2). Snag dynamics were based on data from 316 PSPs in spruce-dominated forests and 301 PSPs in fir-dominated forests. The distribution of PSPs varied with age class and between disturbance histories in fir- and spruce-dominated forests. The allocation of PSPs biased harvested fir-dominated forests aged 20–60 years (Table 1). There were more PSPs of harvest origin in >60-year-old fir-dominated forests than in spruce-dominated forests. In spruce-dominated forests, PSPs are biased towards 20- to 60-year-old stands of harvest and fire origin, as well as 80- to 99-year-old harvest-origin stands. Neither forest type has many PSPs in <20-year-old stands or in >100-year-old stands. In addition, PSPs in stands of natural disturbance origin (fire and insect) are more abundant in >60-year-old stands, whereas there are none in <40-year-old stands.

Snag density (snags per hectare) by diameter class

Snag density reported in this manuscript is always stems per hectare and should not be confused with wood density. Snag density in fir-dominated forests was significantly higher than in spruce-dominated forests for total snags (P < 0.0001) and ≥9 cm snags (P = 0.0008). Snag density in fir- and spruce-dominated forests, in all age classes, was dominated...
Table 1: Snag density and number of PSPs examined when determining snag structure and snag dynamics in Newfoundland balsam fir- and black spruce-dominated forests

<table>
<thead>
<tr>
<th>Age class (years)</th>
<th>0–19</th>
<th>20–39</th>
<th>40–59</th>
<th>60–79</th>
<th>80–99</th>
<th>110–119</th>
<th>120–139</th>
<th>140+</th>
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<tbody>
<tr>
<td>Total snag density</td>
<td>Fir</td>
<td>1250</td>
<td>6805</td>
<td>7234</td>
<td>3915</td>
<td>2472</td>
<td>1218</td>
<td>807</td>
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<tr>
<td></td>
<td>Spruce</td>
<td>220</td>
<td>2051</td>
<td>1967</td>
<td>991</td>
<td>1627</td>
<td>1217</td>
<td>982</td>
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<tr>
<td>Snag dynamics</td>
<td>Fir</td>
<td>8</td>
<td>100</td>
<td>72</td>
<td>38</td>
<td>20</td>
<td>14</td>
<td>10</td>
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<tr>
<td></td>
<td>Spruce</td>
<td>7</td>
<td>93</td>
<td>60</td>
<td>49</td>
<td>57</td>
<td>14</td>
<td>7</td>
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<td>Snag structure</td>
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<td>84</td>
<td>82</td>
<td>46</td>
<td>30</td>
<td>10</td>
<td>20</td>
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<td></td>
<td>Spruce</td>
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<td>76</td>
<td>39</td>
<td>61</td>
<td>15</td>
<td>10</td>
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<td>Harvest origin</td>
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<td>80</td>
<td>74</td>
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<td>2</td>
<td>8</td>
<td>9</td>
<td>6</td>
<td>15</td>
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<tr>
<td>Insect origin</td>
<td>Fir</td>
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<td>0</td>
<td>3</td>
<td>13</td>
<td>3</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>6</td>
<td>3</td>
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</table>

Table 2: Total snags per hectare and number of PSPs examined in thinned and unthinned balsam fir-dominated stands

<table>
<thead>
<tr>
<th>Age (years)*</th>
<th>25</th>
<th>30</th>
<th>35</th>
<th>40</th>
<th>45</th>
<th>50</th>
</tr>
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<tbody>
<tr>
<td>(Total snags ha(^{-1}))</td>
<td>Unthinned</td>
<td>4543</td>
<td>6415</td>
<td>5703</td>
<td>6131</td>
<td>8210</td>
</tr>
<tr>
<td></td>
<td>Thinned</td>
<td>534</td>
<td>811</td>
<td>850</td>
<td>720</td>
<td>1538</td>
</tr>
<tr>
<td>Number of PSPs examined</td>
<td>Unthinned</td>
<td>25</td>
<td>30</td>
<td>35</td>
<td>40</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>Thinned</td>
<td>14</td>
<td>30</td>
<td>56</td>
<td>52</td>
<td>43</td>
</tr>
<tr>
<td>Harvested and thinned</td>
<td>14</td>
<td>30</td>
<td>54</td>
<td>47</td>
<td>40</td>
<td>47</td>
</tr>
</tbody>
</table>

* Midpoint of 5-year age classes.
ForESTrY

Figure 2. Density of >9 cm d.b.h. snags by diameter class (cm) and age class in (a) balsam fir- and (b) black spruce-dominated forests. Bars are +S.E. of mean for total snag densities. Note difference in y-axis scale.

In spruce-dominated forests, snags were more evenly distributed over a limited range of d.b.h. classes.

In both fir- and spruce-dominated forests, a large proportion of total snags (data not shown) and >9 cm snags (Figure 5) were untagged trees measured in the subplot where snag species were not identified. Not surprisingly, >9 cm snags identified in fir- and spruce-dominated forests were dominated by snags of these dominant species. A larger proportion of tagged snags were not the dominant species in spruce-dominated forests than in fir-dominated forests.

The d.b.h. distribution of live trees in fir-dominated forests was positively skewed at young ages, becoming less skewed with age (Figure 3). The diameter of snags in both fir- and spruce-dominated forests peaks at approximately the same d.b.h. class as live trees. The d.b.h. distribution of live trees in spruce-dominated forests remains strongly positively skewed regardless of age, and the d.b.h. distribution of spruce snags is relatively flat between age classes (Figure 4). The tree-size term ddbh² was statistically significant in predicting fir snag density but not spruce snag density. The negative relationship between >9 cm d.b.h. snag density in fir-dominated forests and ddbh² is indicative of an inverse U-shaped relationship between tree size and snag density. As fir-dominated forests aged, they contained fewer but larger live trees, yet total snag density decreased quickly after the highs in the 40–59 years age class. Thus, total snag densities in fir-dominated forests were negatively correlated with >9 cm live-tree ddbh².

In forests dominated by fir and spruce, snag density increases with stand age until forests were 80–99 years old. Also, for both species, stand age and (stand age)² were predictors of snag density. The negative relationship between >9 cm d.b.h. snag density and (stand age)² is indicative of a negative U-shaped relationship between age and snag density. For fir-dominated forests, stand-originating disturbance was a significant predictor of snag density, where forests of insect origin generally contained more snags than forests regenerating from all other disturbance types.

In spruce-dominated forests, live basal area and live-stem density were statistically significant predictors of snag density. The negative coefficient associated with live-stem density in spruce-dominated forests is counterintuitive. The simple correlation between density of >9 cm spruce snags and live > 9 cm tree density is positive and significant ($P < 0.0001$). Basal area is strongly positively correlated with >9 cm spruce snag density and highly positively correlated with live spruce density ($r^2 = 0.86711$, $P < 0.0001$). Given basal area was in the model and likely accounted for much of the positive effect of density, the addition of live >9 cm spruce density to the model likely captures some sort of tree-size effect, where the higher the live spruce density, the smaller the average stem size.
Precommercially thinned stands contained fewer snags than unthinned stands, regardless of whether they originated following clear-cut harvesting or other stand-originating disturbances (Figure 6). Most interestingly, thinning substantially reduced the density of >9 cm snags in several age classes to <1, whereas unthinned stands maintained a high density of >9 cm snags in all age classes.

No significant differences in snag density with disturbance at origin were detected in spruce-dominated forests for total (data not shown) or >9 cm snags (Figure 7). In fir-dominated forests, the only difference was that the density of >9 cm snags was higher in stands originating following insect outbreak than in stands of harvest, unknown or natural origin.
Snag dynamics

Rates at which live tagged trees became snags (snag input) were <1.6 per cent year\(^{-1}\) in fir-dominated forests and <1.2 per cent in spruce-dominated forests (Figure 8). In fir-dominated forests, relatively high rates of snag input in 0- to 20-year-old stands dropped as stands aged to 20–39 years of age, after which there was a trend of increasing rates until stands exceeded 60 years in age. In spruce-dominated forests, snag input rates gradually increased with stand age. In fir-dominated forests, snag input rates were positively correlated with \(\text{dbh}\)_d (Table 3) but negatively with \(\text{dbh}\)_c indicating an inverse U-shaped distribution of snag input rates with \(\text{dbh}\)_d. Differences between regions in snag input rates within fir-dominated forests were evident, where input rates by
region were eastern > all other regions. In spruce-dominated forests, snag input rates were positively correlated with elevation only. Rates of tagged live-tree fall down were ≤0.57 per cent of live trees per year in fir-dominated forests and ≤0.82 per cent of live trees per year in spruce-dominated forests. Live-tree fall down in fir-dominated forests was positively correlated with dbh only. In spruce-dominated forests, live-tree fall down was positively correlated with stand age and negatively correlated with dbh but positively with $2dbh$ indicating an inverse U-shaped distribution of live-tree fall down with live-tree density. Live-tree fall down in spruce-dominated forests was also more frequent in the eastern region than all other regions.

Discussion

Snag densities and patterns in snag densities observed in Newfoundland boreal forests were similar to findings of others. Snag densities in this study were similar to those reported by others for fir- and spruce-dominated forests or boreal forests composed of these species and others of similar dimensions (Greif and Archibold, 2000; Ferguson and Elkie, 2003; Moroni, 2006; Taylor and MacLean, 2007). Total snag densities in all age classes of fir- and spruce-dominated forests were dominated by smaller <9 cm snags (Figure 2) and were positively correlated with live-stem densities (Table 3) as observed elsewhere (McCarthy and Weetman, 2007). Snag mean diameter and the range in diameters of snags recruited from regeneration increased with regeneration age (Figures 3 and 4), as expected (Lee et al., 1997), but were more pronounced in fir-dominated forests than in spruce-dominated forests. The inverse U-shaped distribution of >9 cm snags with stand age observed in this study for both fir- and spruce-dominated forests was also similar to observations elsewhere (Lee, 1998; Greif and Archibold, 2000).

Not surprisingly, the tree size term $dbh^2$ predicted >9 cm snag density in fir-dominated forests, as a large amount of self-thinning occurs in fir throughout its lifespan (Piene, 1981). The negative relationship between >9 cm d.b.h. snag density in fir-dominated forests and $dbh^2$ is indicative of an inverse U-shaped relationship between tree size and snag frequency, where there are low amounts of >9 cm snags produced in young forests where trees tend to be smaller and in older forests due to lower stem densities resulting from long periods of self-thinning.

Total snag density as well as the density of live ≥9 cm trees in live fir-dominated forests ($P < 0.0012$) was negatively correlated with elevation, indicating the stem density of fir forests decreased with elevation. Decreasing stem densities with elevation are likely associated with increased exposure that comes with elevation. Total snag densities in spruce- and fir-dominated forests were higher in central Newfoundland than in other regions. However, the PSPs
do not indicate higher densities of >9 cm live trees in central Newfoundland, indicating this relationship is associated with the density of <8 cm trees. Why the density of <9 cm snags would be higher in central Newfoundland is unknown and requires further study.

Initial snag abundance is heavily influenced by the legacy of the last stand-replacing disturbance (Krankina and Harmon, 1994). Immediately following natural disturbances, large snag densities are expected (Moroni, 2006). However, in the small-diameter-treed boreal forests of Newfoundland and Labrador, almost all snags are expected to have fallen within 30–40 years of disturbance (Moroni, 2006; Smith et al., 2008, 2009; Hagemann et al., 2009). No PSPs were established in <40-year-old naturally disturbed stands (Table 1). With PSPs only established in >40-year-old naturally disturbed stands, differences in

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**Figure 6.** Density of >9 cm d.b.h. snags by diameter class (cm) and age class in (a) unthinned balsam fir, (b) harvested and thinned balsam fir-dominated forests, and (c) thinned balsam fir. Ages shown are the midpoint of 5-year age classes. Bars are ±S.E. of mean for total snag densities within age class. Note the differences in y-axis scale.
Snag densities among PSPs in forests of different disturbance at origin are likely due to differences in snag production during regeneration. The only detected impact of disturbance history on snag density in this study was in fir-dominated stands, where stands of insect origin contained more >9 cm snags than those of harvest origin (Figure 7). Stands originating from insect outbreak may contain denser snags because insect outbreaks often leave some residual live trees that act as seed sources, increasing the density of regeneration. Both residual trees and additional regeneration are future sources of snags. In addition, ground disturbance in harvested stands may have reduced the density of regeneration and resultant snags (Piene, 1981).

Snag recruitment in regenerating stands is influenced by the regenerating species (Eid and Tuhus, 2001; Vanderwel et al., 2006; Taylor and MacLean, 2007), with differences in snag density between fir and spruce being observed in this study (Figure 7). Snags generated from insect outbreak may contain denser snags because insect outbreaks often leave some residual live trees that act as seed sources, increasing the density of regeneration. Both residual trees and additional regeneration are future sources of snags. In addition, ground disturbance in harvested stands may have reduced the density of regeneration and resultant snags (Piene, 1981).

Snag recruitment in regenerating stands is influenced by the regenerating species (Eid and Tuhus, 2001; Vanderwel et al., 2006; Taylor and MacLean, 2007), with differences in snag density between fir and spruce being observed in this study. Initially, small-diameter snags result from self-thinning (Neitro et al., 1985). Balsam fir and black spruce self-thin gradually, decreasing the density of live stems to <3000 stems ha\(^{-1}\) at maturity through the death of less competitive trees (McCarthy and Weetman, 2007), as observed in this study (Figure 2). Self-thinning generated larger numbers of snags in balsam fir than black spruce-dominated forests (Figure 2), as observed elsewhere (Karsh et al., 1994; Bégin et al., 2001; Pothier, 2002) due to very large initial stem densities in balsam fir (Table 1), also observed elsewhere (McArthur, 1965; Karsh et al., 1994; Moroni et al., 2005).

Although 2–13 per cent of stems in mature (>60-year-old) spruce-dominated forests were snags, which is typical of many forests (Hunter, 1990), fir-dominated forests contained larger proportions of snags, with 17–26 per cent of stems as snags in >60-year-old fir-dominated forests.

Self-thinning continued in mature stands, where 0.5–1.5 per cent year\(^{-1}\) of >9 cm live merchantable stems in fir- and spruce-dominated forests aged ≥60 years were lost to self-thinning and then senescence in overmature stands (Figure 8). The mortality rates of >9 cm live trees in >60-year-old fir- and spruce-dominated forests were similar to mortality rates of live trees in gap-driven hardwood systems (Mosseler et al., 2003; Siccama et al., 2007) but less than losses...
of >10 cm trees in aspen (Populus spp.)-dominated mid-boreal forests (Lee, 1998). Rates of >9 cm d.b.h. tree fall down in fir- and spruce-dominated forests were less than rates of thinning in both fir- and spruce-dominated forests (Figure 8). Not surprisingly, in spruce-dominated forests rates of fall down were higher in more exposed elevated locations and in the windy eastern region.

Precommercial thinning of fir is common outside of Newfoundland. For example, 92,000 ha of fir had been precommercially thinned in Quebec by 1998 (Pothier, 2002), and the impact of thinning on snag dynamics there is expected to be similar to dynamics in Newfoundland. Precommercial thinning reduced snag densities in fir-dominated forests (Table 2) as expected (Raulier et al., 2003), including the density of large d.b.h. snags (>9, >19 and >25 cm snags; Figure 6). Thinned stands are not yet old enough to determine how long snag densities will be suppressed, but the impact is likely to last until senescence generates large amounts of snags when stands are >80–100 years of age (Moroni, 2006). Although snag densities in thinned stands were similar to those previously reported in post-harvest sites in Newfoundland (Smith et al., 2008, 2009), unthinned stands contained far more snags. Based on snag densities encountered in this study, it is likely that 15- to 50-year-old post-harvest sites examined by Smith et al. (2008, 2009) were thinned. However, based on Smith et al. (2009), >9 cm snags in <37.5-year-old PSPs were likely inherited from the previous rotation or resulted from the death of residual live trees following harvesting.

Fir-dominated forest live-tree d.b.h. distributions in this study were similar to McCarthy and Weetman’s (2007) observations in western Newfoundland, where few trees had d.b.h. >45 cm. Newfoundland forest management guidelines require ≥10 snags ha⁻¹ be retained on the landscape for habitat, primarily for woodpeckers (Picidae spp.; Smith et al., 2008). Woodpeckers are important primary cavity nesters in Newfoundland (Setterington et al., 2000), excavating new cavities in both live trees and snags each breeding season, thus providing habitat for non-excavating secondary cavity nesters (Martin et al., 2004; Remm et al., 2006). Woodpeckers select larger d.b.h. snags to support their nests (Swallow and Gutierrez, 1986); in western Newfoundland, >20 cm snags in fir-dominated forests are more likely to be selected by woodpeckers for cavity excavation and some species are reported to prefer >30 cm d.b.h. snags (Setterington et al., 2000; Smith et al., 2008). Larger snags are commonly reported to be most significant for wildlife (Setterington
### SNAG FREQUENCY, DIAMETER AND SPECIES DISTRIBUTION

**Table 3:** Statistically significant correlates with total and >9 cm snag density with P-value and coefficient

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Balsam fir</th>
<th>Black spruce</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coefficient</td>
<td>P-value</td>
</tr>
<tr>
<td>Snag structure</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snag density (total)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>8.490</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Live ≥9 cm density</td>
<td>5.271 × 10⁻⁴</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Live ≥9 cm dbh&lt;sub&gt;q&lt;/sub&gt;</td>
<td>-7.596 × 10⁻²</td>
<td>0.0022</td>
</tr>
<tr>
<td>Region</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Elevation</td>
<td>-2.973 × 10⁻³</td>
<td>0.0001</td>
</tr>
<tr>
<td>Snag density (&gt;9 cm d.b.h.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-8.723</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Stand age</td>
<td>1.015 × 10⁻¹</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Stand age&lt;sup&gt;2&lt;/sup&gt;</td>
<td>-4.198 × 10⁻⁴</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Live ≥9 cm basal area</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Live ≥9 cm density</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Live ≥9 cm dbh&lt;sub&gt;q&lt;/sub&gt;</td>
<td>1.0486</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>dbh&lt;sub&gt;q&lt;/sub&gt; ≥9 cm</td>
<td>-2.942 × 10⁻²</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Origin</td>
<td>na</td>
<td>0.02†</td>
</tr>
<tr>
<td>Snag dynamics</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snag recruitment (includes fall down)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-3.689 × 10⁻²</td>
<td>0.0005</td>
</tr>
<tr>
<td>Elevation</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>dbh&lt;sub&gt;q&lt;/sub&gt;</td>
<td>4.712 × 10⁻¹</td>
<td>0.0005</td>
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<tr>
<td>Elevation&lt;sup&gt;2&lt;/sup&gt;</td>
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<tr>
<td>Region</td>
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<td>0.202‡</td>
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<tr>
<td>Snag falldown (excluding fall down)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-1.219 × 10⁻²</td>
<td>0.3865</td>
</tr>
<tr>
<td>Stand age</td>
<td>4.285 × 10⁻⁴</td>
<td>0.0024</td>
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<tr>
<td>Stand age&lt;sup&gt;2&lt;/sup&gt;</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Live ≥9 cm density</td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>

Regional or disturbance-at-origin-specific coefficients indicated below must be used. Coefficient is zero for default region or disturbance at origin. ns, not significant; na, not applicable.

* (Central > other regions); coefficients for other regions when compared with default central region; eastern -1.370, northern 2.916 and western -8.534 × 10⁻¹.

† (Insect > other disturbances at origin); coefficient for other disturbance at origin when compared with default insect origin; fire -1.093, harvest -1.6981, natural -1.183 and unknown -8.623 × 10⁻¹.

‡ (Eastern > other regions); coefficient for other regions when compared with default eastern region; central 7.049 × 10⁻³, northern -7.704.919 × 10⁻⁵ and western -7.596 × 10⁻³.

In addition to larger snags potentially being most significant for pine marten (*Martes americana atrata*; Payer and Harrison, 2002), boreal owls (*Aegolius funereus*; secondary cavity nesters present in Newfoundland) preferentially select cavities in >30 cm live or dead trees (Hayward and Hayward, 1993; Imbeau et al., 2001). Live and dead trees of these dimensions are far more common in fir-dominated PSPs than in spruce-dominated PSPs (Figure 3). Hence, the preservation of older fir-dominated forests is likely to have a greater positive impact on primary and secondary cavity nesters and potentially on a wider variety of species than the preservation of older spruce-dominated forests. However, some woodpecker species are most frequently reported in spruce (*Picea* spp.) and pine (*Pinus* spp.; Bock and Bock, 1974); thus, the preservation of old spruce forests should not be ignored.

Densities of >9 cm snags dropped below 10 snags ha⁻¹ in thinned stands 37.5-52.5 years following harvest in this study. However, PSPs from unthinned fir-dominated forests indicate that maintaining more than ten >9 cm snags throughout the full rotation can be expected if fir-dominated forests are not thinned. Unthinned fir-dominated forests begin to generate >19 and >25 cm d.b.h. snags when ~40 years of age (Figure 6), even in unthinned stands of harvest origin that contain few residual live trees for snag recruitment. Thus, leaving regions of fir unthinned would greatly improve wildlife habitat availability in balsam fir-dominated forests. Thinning balsam fir to hasten the production of merchantable stems is common in Newfoundland and elsewhere (e.g. Pothier, 2002). In unthinned post-harvest balsam fir landscapes, there will likely be a period with few or no >19 cm snags between the time when residual snags of these dimensions fall and regeneration...
produces such snags. Large snags may be protected or created on post-harvest landscapes (Smith et al., 2008), and leaving clumps of trees in clear-cuts may provide a future source of large snags, bridging the gap in >20 cm snag densities that occurs under current harvest regimes.

Smith et al. (2008, 2009) encountered a larger component of birch (Betula spp.) snags in fir-dominated stands than the PSPs record. These birch snags commonly attained large d.b.h. and appeared to stand for longer periods than snags of other species. Birch snags may have been more abundant than suggested in Figure 5 but recorded in the subplot where snag species are not identified. In addition, smaller diameter snags stand for shorter periods than larger snags (Bull, 1983; Wood, 1995; Garber et al., 2005) and generate less downed dead wood when they collapse, which decomposes faster than larger dead wood (Foster and Lang, 1982; Berg, 1984). Thus, in Newfoundland, dead wood abundance and associated habitat and stocks of carbon and nutrients in spruce-dominated forests are likely to be lower and more transient on the landscape than in fir-dominated forests.

As snag dynamics appear to be related to tree dimensions rather than climate, in particular temperature and moisture regimes (Harmon et al., 2000; Hagemann et al., 2009), the abundance and dynamics of snags and dead wood in Newfoundland and Labrador share many similarities with other forests composed of small-dimension trees (Moroni, 2006; Hagemann et al., 2009; Smith et al., 2009). Such forests—especially coniferous ones—which occur over an enormous area in the boreal (Ahti et al., 1968; Hämet-Ahti et al., 1974; Ecoregions Working Group, 1989) as well as in cooler elevated regions south of the boreal (Clark et al., 1998; Zielonka and Niklasson, 2001), will likely have similar snag dynamics to those of this study. Within North America, our findings are likely to be most applicable to balsam fir and black spruce across much of their range. Balsam fir extends its range west to Alberta and is present in many of the north-eastern US states. Black spruce ranges in a broad band from northern Massachusetts and northern Labrador in the east, west to the Alaskan coast (Burns and Honkala, 1990).

**Conclusions**

Balsam fir and black spruce forests are composed of small-diameter trees that produce small-diameter snags, and spruce-dominated forests are composed of smaller diameter ranges of both live and dead trees than fir-dominated forests. Although >19 cm snags do occur in both spruce- and fir-dominated forests, they only become abundant in >60-year-old fir and >80-year-old spruce, beyond the ~60-year rotation length for these species in Newfoundland. Precommercially thinning fir virtually eliminates the generation of >9 cm snags in <52.5-year-old regeneration and likely for longer periods. Thus, where large-dimension snags and woody debris are desirable (e.g. in habitat for primary and secondary cavity nesters and for the Newfoundland marten), old growth must be maintained on the landscape, potentially favouring older fir than spruce, and precommercial thinning of balsam fir should be avoided.

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**Conflict of Interest Statement**

None declared.

**References**


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