RESEARCH ARTICLE

Coarse Woody Debris in a Southern Appalachian Spruce-fir Forest of the Great Smoky Mountains National Park

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ABSTRACT: Spruce-fir forests in the southern Appalachian Mountains receive high atmospheric nitrogen inputs and have high nitrate levels in soil solution and streamwater. High levels of excess nitrogen have been associated with reduced tree vigor. Additionally, the balsam woolly adelgid (*Adelges piceae* Ratz.) has killed the majority of endemic Fraser fir [*Abies fraseri* (Pursh) Poir.] trees, resulting in large amounts of coarse woody debris. As part of a biogeochemical study in the Great Smoky Mountains National Park, coarse woody debris was sampled to determine volume, mass, change in density, and change in concentration and content of carbon and nitrogen over the decomposition process. Dead wood volume was highly variable across the watershed, ranging from 4.5 m^3 ha^{-1} to 306.8 m^3 ha^{-1} for standing boles and from 21.2 m^3 ha^{-1} to 402.7 m^3 ha^{-1} for down boles. Wood density decreased significantly for all three major overstory species [red spruce (*Picea rubens* Sarg.), yellow birch (*Betula alleghaniensis* Britt.), and Fraser fir] by approximately 60%, from slightly decayed boles to boles in advanced decay. Standing and down dead biomass averaged 39.4 Mg ha^{-1} and 33.8 Mg ha^{-1}, respectively. Carbon concentrations remained relatively constant and were approximately 47% for all decay classes and all species. Nitrogen concentrations increased sharply between live wood and highly decayed wood. The nitrogen content in live wood, compared to wood in advanced decay, increased by 40% to 118% for the species tested. At the watershed level, live bole wood contained 108.4 kg ha^{-1} of nitrogen, and dead bole wood contained 101.5 kg ha^{-1}. Total carbon in live and dead bole wood averaged 93.8 Mg ha^{-1} and 34.9 Mg ha^{-1}, respectively. The magnitude of coarse woody debris in this system is among the highest reported in the literature for the eastern United States, emphasizing the high degree of disturbance that has taken place in this ecosystem.

Index terms: *Abies fraseri, Adelges piceae,* balsam woolly adelgid, biomass, coarse woody debris, disturbance, Fraser fir, mortality, nitrogen saturation, *Picea rubens,* red spruce

INTRODUCTION

The most extensive old-growth southern Appalachian red spruce (*Picea rubens* Sarg.) – Fraser fir [*Abies fraseri* (Pursh) Poir.] forests occur in the Great Smoky Mountains National Park (GRSM) in North Carolina and Tennessee, where approximately 19,666 ha of this vegetation type is found (74% of the total spruce-fir forest in the southern Appalachians) (Dull et al. 1988). Historically, these high-elevation spruce-fir forests have largely escaped logging and fire (Harmon et al. 1983; Pyle and Schafale 1988). Throughout the southern Appalachians, the Fraser fir, which is endemic to the area, has been decimated by a non-native pest, the balsam woolly adelgid (also known as balsam woolly aphid) (*Adelges piceae* Ratz.) (Eagar 1978; Nicholas et al. 1992a). The infestation has resulted in large patches of dead fir trees in areas of pure fir stands and small patches of dead fir where it is co-dominant with spruce. Episodic events or stand replacement disturbances, such as insect infestations and changing environmental conditions, can contribute large amounts of coarse woody debris (CWD) to the forest floor and have a substantial impact on the nutrient cycling in affected areas. Several studies of CWD in spruce-fir forests have been conducted in the Northeastern United States (Lambert et al. 1980; Foster and Lang 1982), the Rocky Mountains (Arthur and Fahey 1990; Laiho and Prescott 1999), and sub-boreal and boreal Canadian forests (Sturtevant et al. 1997; Clark et al. 1998; Hely et al. 2000; Pedlar et al. 2002; Harper et al. 2003). However, few have concentrated on the spruce-fir ecosystem of the southern Appalachians (Nicholas and White 1985).

In addition to elevated levels of mortality, caused by the balsam woolly adelgid, there is evidence that some mature high elevation spruce-fir forests in the southeastern United States may be nitrogen saturated (Lovett 1992; Van Miegroet et al. 1992; Nodvin et al. 1995). These forests receive high levels of atmospheric nitrogen inputs (28 kg ha^{-1} yr^{-1}) and have high nitrate levels in soil solution (10-20 kg ha^{-1} yr^{-1}) and stream water (15 kg ha^{-1} yr^{-1}) (Johnson et al. 1991; Joslin and Wolfe 1992; Nodvin et al. 1995). When nitrogen losses begin to equal or exceed inputs, a system is said to be nitrogen saturated (Ågren and Bosatta 1988; Aber et al. 1989). Impacts to individual trees and stands include decreased foliar calcium, reduced tree growth, increased tree mortality rates, and reduced root growth (Joslin and Wolfe 1992; McNulty and Aber 1993; Joslin and Wolfe 1994; Aber et al. 1998; Boggs et al. 2005). These impacts are accomplished primarily through the leaching of cations from foliage and soil and through nitrate-mediated aluminum mobilization, which interferes with cation uptake and causes soil acidification and water quality deterioration (Ågren and Bosatta 1988; Johnson et al. 1991; Joslin et al. 1992; Garten and Van Miegroet 1994; Aber et al. 1998). Several factors predispose forested watersheds to nitrogen saturation, including chronically high rates of nitrogen deposition, advanced stand age, and the presence of large pools of soil nitrogen (Stoddard 1994).

Forest nutrient cycling and nutrient availability, especially in areas experiencing multiple stressors, cannot be fully understood without considering the CWD component, as it accounts for a significant store of biomass and nutrients within an ecosystem (Harmon et al. 1987; Keenan et al. 1993). CWD may also be a sink for nutrients, especially nitrogen, during portions of the decay process (Grier 1978; Edmonds and Marra 1999). As wood decays, the carbon to nitrogen (C/N) ratio decreases; respiration and leaching cause the proportion of carbon to decrease, while nitrogen immobilization during initial stages of decay causes the proportion of nitrogen to increase (Schlesinger 1991). This increase in nitrogen is of particular importance in areas of high nitrogen deposition and high amounts of CWD, because the dead wood may be a temporary sink for nitrogen and have an effect on nitrogen saturation. Assessing the role of CWD as a sink for nitrogen is complicated by the fact that changes in nitrogen concentration are affected by changes in wood density as the wood decays, both of which tend to be species and ecosystem specific. Determination of this potential is also confounded by the heterogeneity of CWD within a stand.

A nutrient cycling study was initiated in 1991 in a 17.4 ha spruce-fir forest watershed in the Great Smoky Mountains National Park. Species composition, stand structure, streamwater and soil water chemistry, as well as nitrogen and sulfur deposition have been monitored to understand the different components of nutrient cycling within a nitrogen saturated watershed (Johnson et al. 1991; Johnson et al. 1992; Nodvin et al. 1995; Shubzda et al. 1995; Pauley et al. 1996). Information regarding the dynamics and distribution of CWD from a study of this scale lends insight into how it interacts with other watershed issues. The objectives of this study were to determine: (l) the magnitude and spatial variability in CWD across a small watershed; (2) the wood density at different stages of decay for the three major overstory species [red spruce, yellow birch (*Betula alleghaniensis* Britt.), and Fraser fir]; and (3) the concentration and density-adjusted content of carbon and nitrogen of dead wood in order to estimate nutrient storage in the CWD component of a southern Appalachian spruce-fir ecosystem.

METHODS

Study Area

The spruce-fir forests of the GRSM range in elevation from 1500 m to 2000 m (Nicholas 1992). The area receives an average of 210 cm precipitation per year. Temperatures range from –11 °C to 8 °C in the winter and from 12 °C to 25 °C in the summer (1979-1990 data courtesy of GRSM).

The 17.4 ha Noland Divide Watershed (NDW) (35°34'N 83°29'W) is located on the upper reach of Noland Creek in the GRSM (Figure 1). The elevation of NDW ranges from 1676 m to 1921 m. Overstory vegetation is dominated by red spruce, yellow birch, and Fraser fir, which account for 64%, 14%, and 19% of the basal area, respectively. Typical mid-story species include mountain maple (*Acer spicatum* Lam.), mountain ash (*Sorbus americana* Marsh.), pin cherry (*Prunus pensylvanica* L. f.), and downy serviceberry [*Amelanchier arborea* (Michx. f.) Fern.] (Pauley et al. 1996). Basal area averages 39.6 m^2 ha^{-1} for live trees and 19.6 m^2 ha^{-1} for standing dead trees (Pauley et al. 1996). In 2000, the average age of overstory trees was 184 years. The oldest spruce was just over 400 years old, and the oldest fir was 90 years old (Creed et al. 2004b).

Soils in the spruce-fir zone tend to be highly acidic with relatively low base saturation (Fernandez 1992). In the watershed, the soils are Inceptisols classified as Dystrochrepts or Haplumbrepts (Johnson et al. 1991; Van Miegroet et al. 1993). They have a silt loam to sandy loam texture and are generally shallow throughout the watershed (< 50 cm depth to bedrock) (Van Miegroet et al. 2001).

Field and laboratory techniques

In 1993, fifty 20-m x 20-m plots (0.04 ha) were established systematically along nine elevation bands ranging from 1700 m to 1911 m in the NDW (Figure 1). All live and standing dead trees ≥ 5.0 cm diameter at breast height (dbh) were measured. Pauley et al. (1996) describes live species composition and stand structure within NDW.

In 1994, down CWD was mapped and identified by species in each of the 50 plots within at least two randomly chosen 10-m x 10-m subplots. Length, diameter at each end, and diameter at the midpoint, were recorded for all down boles. Down CWD was defined as woody material ≥ 10 cm in diameter at the large end and ≥ 1.54 m in length (Nicholas 1994). This is roughly comparable to the 7.6 cm diameter, 100-hour-plus size class used by Nicholas and White (1985). Decay classes were defined as follows: (1) class I: slightly decayed (penetration of a 0.5 cm diameter metal rod into the wood < 0.5 cm); (2) class II: moderately decayed (penetration to the center of the bole); and (3) class III: advanced decay (penetration through the bole). Decay classification follows methods used by Lambert et al. (1980), Bingham and Sawyer (1988), and Clark et al. (1998). Percentage of bark coverage, heartwood and sapwood sponginess, and presence of leaves and twigs were also determined (Nicholas 1994). Total height was measured on all standing dead trees. Species not identifiable in the field were sampled and identified in the laboratory. Time and cause of death of standing and down dead trees were not determined.

Wood samples were taken from the three major overstory species (red spruce, Fraser

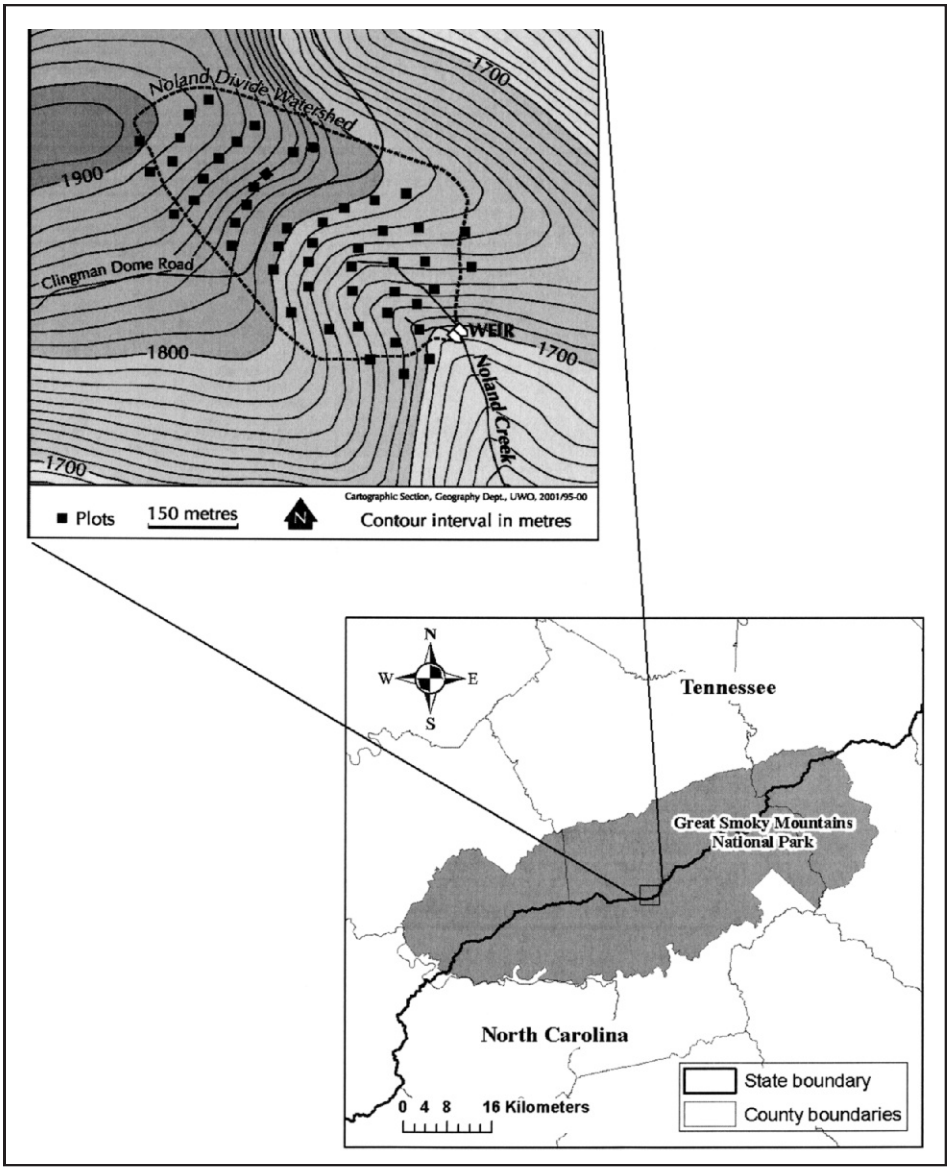

Figure 1. The Great Smoky Mountains National Park and location of Noland Divide Watershed study site.

fir, and yellow birch). Bark was not included in the study, because it constitutes a minor fraction of the dry mass of most boles. In addition, Fraser fir tends to lose bark very soon after death (only about 20% of down boles had bark). Cross-sections were taken from down CWD. Increment cores were taken from live trees of each species. For standing dead boles, either a wedge was taken without felling the tree or a cylinder of wood of known volume was removed using a brace and 1.9 cm diameter drill bit. An earlier evaluation of the data indicated that the brace and bit method and the wedge method were not significantly different for sound boles (J. Shen, unpubl. data). All samples were wrapped in aluminum foil and placed in plastic bags for transportation.

Samples for nutrient analysis were weighed, dried at 70 °C to constant weight, and ground in a Wiley mill to pass through a fine mesh screen. Nitrogen and carbon concentrations were determined with a Leco CNS 2000 apparatus (Leco Corp., St. Joseph, MI) (carbon via an infrared cell, and nitrogen via a thermal conductivity cell). Due to the variability in decay class II boles and the higher level of subjectivity involved when assigning this decay rating, only live trees and decay class I and III boles were tested for nutrient concentrations.

Wood density samples were weighed and volume determined by water displacement. Samples were then dried at 70 °C to constant weight. Wood density was obtained by dividing the dry weight of a sample by its fresh displacement volume.

Data analysis

Volume of logs was calculated using the formula for a frustum of a cone (the part of the cone that is left when the top is removed parallel to the base),

$$Volume = (L/3)*(A_l + \mathrm{sqrt}(A_l)(A_s) + A_s)$$

(Husch et al. 1972)

where L is the length of the log, A_l and A_s are cross-sectional areas of the log at the point where the large and small diameters were measured. The volume of standing dead trees was calculated as the volume of a paraboloid (a slightly convex or rounded cone),

$$Volume = ½*A_b*Ht$$

(Husch et al. 1972)

where A_b is the cross sectional area of the base calculated using diameter taken at breast height, and Ht is the height of the tree. Biomass of dead wood was calculated by multiplying the bole volume by the mean wood density for the appropriate species and decay class. The magnitude of carbon and nitrogen pools contained in standing and down wood was estimated by multiplying the biomass of the wood by the appropriate mean nutrient concentration. Nitrogen and carbon concentrations for decay class II boles were estimated by species based on live and decay class I and III data using the general linear model (GLM) procedure in SAS (SAS Institute 1990). Resulting decay class II nutrient values were found to be comparable to published values (Arthur and Fahey 1990; Creed at al. 2004a).

Main effects of independent variables were examined with separate analysis of variance (ANOVA) tests using the GLM procedure in SAS. For reporting purposes, three elevation classes were defined as 1700-1756 m (low) (n = 19 plots), 1783-1834 m (medium) (n = 19 plots), and 1865-1911 m (high) (n = 12 plots). Tukey's multiple range test was used to determine if differences existed for dependent variables among species and decay classes. Variables judged to be non-normal (at the 0.01 level), via a Shapiro-Wilks test, were square root transformed for comparisons between classifications and to test for significant independent variables. All tests were considered significant at the 0.05 alpha level.

RESULTS

Stand structure and CWD characterization

Within the NDW, 42% of all standing trees (≥ 5.0 cm dbh) were dead. For the three major overstory species, 70% of standing Fraser fir trees were dead, while only 16% of standing red spruce and 11% of standing yellow birch were dead. Collectively, 15% percent of the other species (mountain maple, mountain ash, pin cherry, and downy serviceberry) were dead.

Stem density of live trees in the NDW averaged 761 stems ha^{-1}, while standing and down CWD averaged 559.5 stems ha^{-1} and 692.1 boles ha^{-1}, respectively (Table 1). Fraser fir accounted for 82% of all standing dead trees and 61% of all down dead boles. For Fraser fir, standing dead trees (max dbh = 60.9 cm) tended to be larger than live trees (max dbh = 34.5 cm), with down dead boles being the largest (max dbh = 82.0 cm) (Figure 2). Red spruce however, had a more even diameter distribution. Diameter distributions of down Fraser fir boles also varied between decay classes. The average diameter for decay class I Fraser fir boles was 18.2 cm (8.8 S.D.), while average diameters for decay class II and III down boles were successively larger, 21.8 cm (10.7 S.D.), 26.7 cm (15.8 S.D.), respectively. There were significantly more decay class I and II Fraser fir boles ha^{-1} than yellow birch and red spruce ($p < 0.0001$) (Figure 3). Additionally, there were significantly more decay class II boles than decay class I and III for both red spruce and Fraser fir ($p < 0.0001$) (Figure 3).

Basal area of live trees averaged 39.6 m^2 ha^{-1} (Table 1). Red spruce accounted for 77% of the live basal area, while yellow birch, Fraser fir, and other species accounted for 18.6%, 2.6%, and 1.7%, respectively. Basal area of standing dead averaged 18.5 m^2 ha^{-1}. In contrast to the live basal area, Fraser fir accounted for 55.1% of standing dead and red spruce 37.8%. Yellow birch accounted for only 5.4% of the standing dead basal area.

Volume

Volume of live trees, standing dead CWD, and down dead CWD was highly variable between plots. Live volume ranged from 145.6 m^3 ha^{-1} to 839.5 m^3 ha^{-1} and averaged 460.6 m^3 ha^{-1} (Table 1). Standing dead volume ranged from 4.5 m^3 ha^{-1} to 306.8 m^3 ha^{-1} (average = 116.7 m^3 ha^{-1}), and down dead volume ranged from 21.2 m^3 ha^{-1} to 402.7 m^3 ha^{-1} (average = 158.8 m^3 ha^{-1}) (Table 1). Red spruce and Fraser fir each accounted for just over 45% of standing and down dead volume in the NDW. Although volume of down CWD tended to decrease with an increase in elevation, and that of standing dead increased, the total volume of CWD was nearly equal for each elevation class (Figure 4). These differences were not significant. Volume of live, standing dead, and down dead Fraser fir, as well as volume of live yellow birch, varied significantly with elevation. In general, live Fraser fir increased from 1.0 m^3 ha^{-1} at elevations < 1865 m to 11.8 m^3 ha^{-1} at elevations ≥ 1865 m. In contrast, live yellow birch volume decreased from 115.0 m^3 ha^{-1} at elevations < 1783 m to 7.7 m^3 ha^{-1} at elevations ≥ 1865 m. Volume of standing dead fir averaged 37.4 m^3 ha^{-1} at low, 62.2 m^3 ha^{-1} at medium, and 83.1 m^3 ha^{-1} at high elevations. Down dead fir averaged 97.5 m^3 ha^{-1} at low, 67.4 m^3 ha^{-1} at medium, and 46.8 m^3 ha^{-1} at high elevations.

Wood density and biomass

To estimate mass of CWD in the NDW, we first determined the wood density of the three principle species by decay class. Density decreased by approximately 60% from decay class I to decay class III and was highly variable within classes (Table 2). An ANOVA on square-root transformed wood density values indicated a highly significant species ($p = 0.0004$) and decay class ($p = 0.0001$) effect for standing and down boles (Table 3). For both Fraser fir and red spruce, density averaged approximately 0.34 g cm^{-3} for standing dead decay class I, and decreased to 0.13 g cm^{-3} for down dead decay class III. Density of yellow birch averaged 0.45 g cm^{-3} in standing dead decay class I and 0.18 g cm^{-3} in down dead decay class III.

Live biomass averaged 201.5 Mg ha^{-1}, and ranged from 62.2 Mg ha^{-1} to 353.5 Mg ha^{-1} (Table 1). Down CWD biomass for all species averaged 33.8 Mg ha^{-1} (min = 4.9 Mg ha^{-1}, max = 89.9 Mg ha^{-1}). Standing dead contributed an additional 39.4 Mg ha^{-1} (min = 1.5 Mg ha^{-1}, max = 102.0 Mg ha^{-1}) for a total of 73.2 Mg ha^{-1} of dead biomass (min = 20.9 Mg ha^{-1}, max = 124.2 Mg ha^{-1}), and 274.7 Mg ha^{-1} of total biomass (min = 158.5 Mg ha^{-1}, max = 441.5 Mg ha^{-1}) (Table 1).

Carbon and Nitrogen

To estimate watershed-level nutrients in CWD, we first determined carbon and nitrogen concentrations for the three principle species by decay class. The carbon concentration averaged 47% for all three species in live wood, and increased slightly, although significantly, to 49% in decay class III wood (Table 2). An analysis of variance also showed a significant species effect (Table 3). For all conditions of wood tested except down decay class III, the percentage of carbon in Fraser fir was significantly higher than the percentage of carbon in yellow birch. Decay class II boles were estimated as having an average of 47% carbon. Density-adjusted carbon content decreased significantly from 169 kg m^{-3} in live wood to 65 kg m^{-3} in down decay class III wood for Fraser fir, a 61%

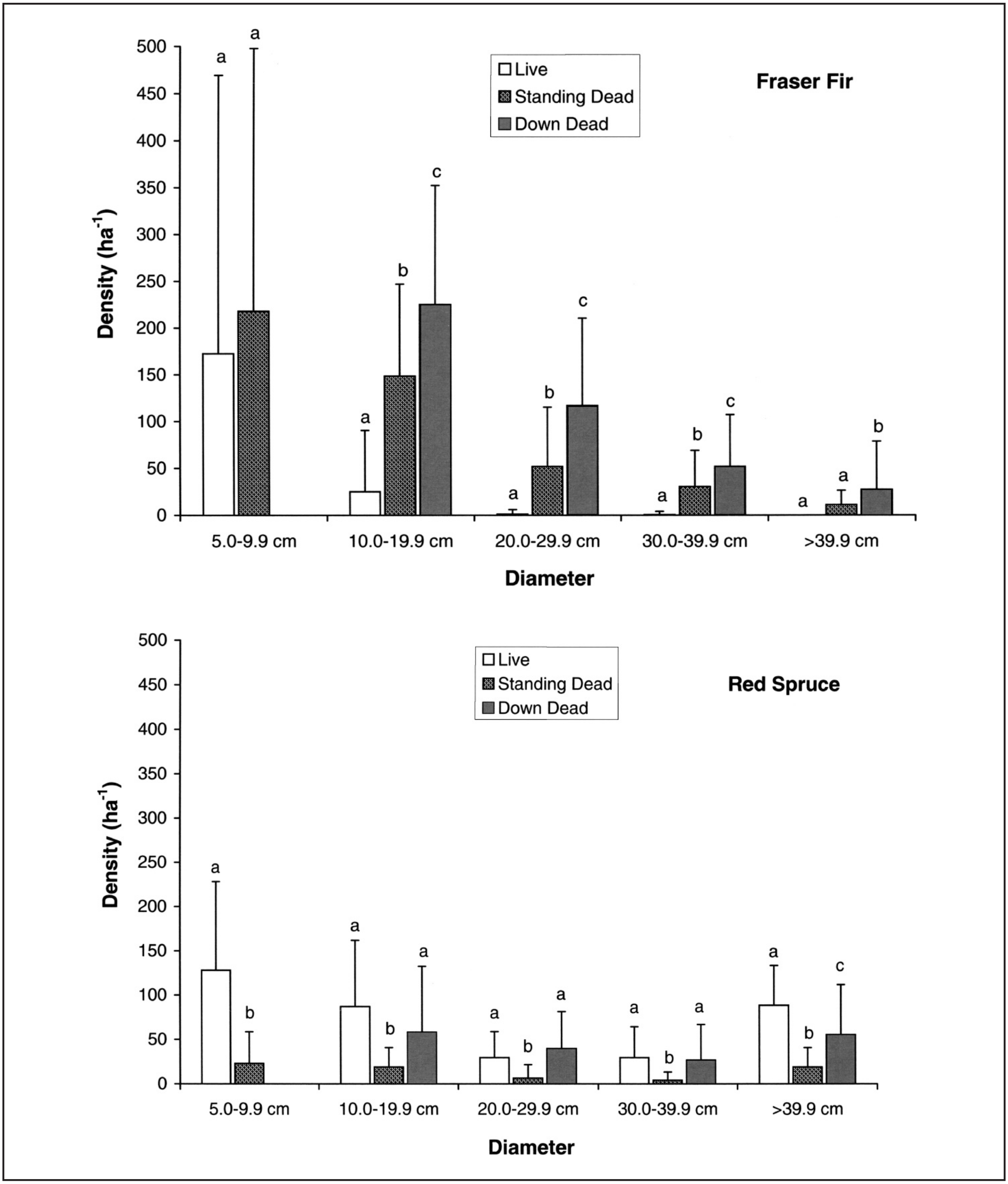

Figure 2. Density by diameter class for Fraser fir and red spruce NDW, GRSM, 1994 (n = 50 plots). Live and standing dead includes trees ≥ 5.0 cm dbh. Down dead includes boles ≥ 10.0 cm diameter at the large end. Sample statistics are the mean and standard deviation. Bar values within the same species and diameter class with the same letter are not significantly different (α = 0.05) based on Tukey's studentized range test.

Table 1. Stem density, basal area, volume, and biomass by species in the NDW, GRSM, 1994 (n = 50 plots). Sample statistics are the mean and the standard deviation in parentheses.

		Live[a]	Standing Dead[a]	Down Dead[b]
Stem Density			stems ha^{-1}	
	Fraser Fir	199.0 (354.1)	460.0 (363.8)	422.4 (184.0)
	Red Spruce	362.5 (156.9)	71.5 (54.9)	180.8 (129.6)
	Yellow Birch	135.0 (147.2)	16.5 (26.5)	52.8 (73.4)
	Other[c]	64.5 (79.1)	11.5 (20.3)	36.0 (63.5)
All species		761.0 (350.3)	559.5 (389.2)	692.1 (204.4)
Basal Area			m^2 ha^{-1}	
	Fraser fir	1.0 (2.0)	10.2 (6.3)	–
	Red Spruce	30.6 (13.1)	7.0 (7.5)	–
	Yellow Birch	7.4 (9.4)	1.0 (2.2)	–
	Other	0.7 (1.0)	0.3 (1.0)	–
All species		39.6 (11.8)	18.5 (10.5)	–
Volume			m^3 ha^{-1}	
	Fraser Fir	3.5 (7.6)	57.8 (41.8)	73.9 (61.0)
	Red Spruce	385.4 (184.0)	53.7 (70.5)	72.8 (66.7)
	Yellow Birch	67.6 (91.2)	4.5 (12.5)	8.8 (16.8)
	Other	4.2 (6.7)	0.7 (2.3)	3.4 (6.7)
All species		460.6 (166.0)	116.7 (82.0)	158.8 (94.0)
Biomass			Mg ha^{-1}	
	Fraser Fir	1.3 (2.8)	18.2 (13.5)	15.9 (12.5)
	Red Spruce	165.7 (79.1)	19.1 (24.6)	14.8 (13.6)
	Yellow Birch	34.5 (46.6)	2.1 (5.7)	3.1 (6.0)
All species		201.5 (72.4)	39.4 (28.0)	33.8 (20.4)

[a] Stems ≥ 5.0 cm dbh

[b] Boles ≥ 10.0 cm in diameter at large end

[c] Other includes: mountain maple, mountain ash, pin cherry, and downy serviceberry

– = no value for cell

change. Carbon content in red spruce and yellow birch also decreased significantly from live wood to down decay class III wood (200 kg m^{-3} to 70 kg m^{-3} for red spruce and 236 kg m^{-3} to 104 kg m^{-3} for yellow birch) (Table 2).

Significant increases in nitrogen concentration between live and decay class III were recorded for all species (Table 2). Nitrogen concentrations increased an average of 304% for Fraser fir, 502% for red spruce, and 483% for yellow birch. There was a significant effect of species, decay class, and the interaction of species and decay class on percent nitrogen (Table 3). For red spruce and Fraser fir combined, wood density explained approximately 50% of the variation in percent nitrogen ($p < 0.0001$) (Figure 5). All three species were significantly different from each other for live wood (Table 2). In decay class III wood, Fraser fir and red spruce did not differ significantly, but both were different from yellow birch. Nitrogen concentrations were always highest in yellow birch, followed by Fraser fir and red spruce. Density-adjusted nitrogen content increased, although not significantly, from 268.6 g m^{-3} in live wood to 380.3 g m^{-3} in down decay class III wood for Fraser fir, a 41% change. For red spruce, nitrogen content increased significantly from 187.8 g m^{-3} to 353.5 g m^{-3}, an 88% change. For yellow birch, nitrogen increased significantly from 512.2 g m^{-3} to 1118.7 g m^{-3}, a 118% change (Table 2).

The C/N ratio showed a steady decline over decay class. Initial C/N ratios for live wood were highest in red spruce (1113), followed by Fraser fir (654), and yellow birch (467) (Table 2). Ratios for decay class III samples averaged 245 for red spruce, 259 for Fraser fir, and 101 for yellow birch. An analysis of variance on square root transformed C/N ratios showed significant effects of species ($p = 0.0001$), decay class ($p = 0.0001$), and the interaction of species and decay class ($p = 0.0001$).

The estimates for wood density, nitrogen content, and carbon content were used to calculate total nitrogen and carbon in bole wood at the watershed level. Live bole wood within the NDW contained an estimated 108.4 kg ha^{-1} of nitrogen, with 67% of this in the red spruce component (Table 4). Dead wood contained another 101.5 kg ha^{-1} of nitrogen, or 48% of the total (209.9 kg ha^{-1}). Standing and down CWD each constituted about one-half of the 101.5 kg ha^{-1} of nitrogen. When total nitrogen in foliage (182 kg ha^{-1}), bark (106.8 kg ha^{-1}), and branch wood (90.8 kg ha^{-1}) was included (Barker et al. 2002), CWD accounted for 17% of the total (589.8 kg ha^{-1}) (Table 5). Fraser fir accounted for 8.7%, red spruce 6.9%, and yellow birch 1.6% of the total.

DISCUSSION

The percentage of standing trees that were dead in NDW (42%) was within the range

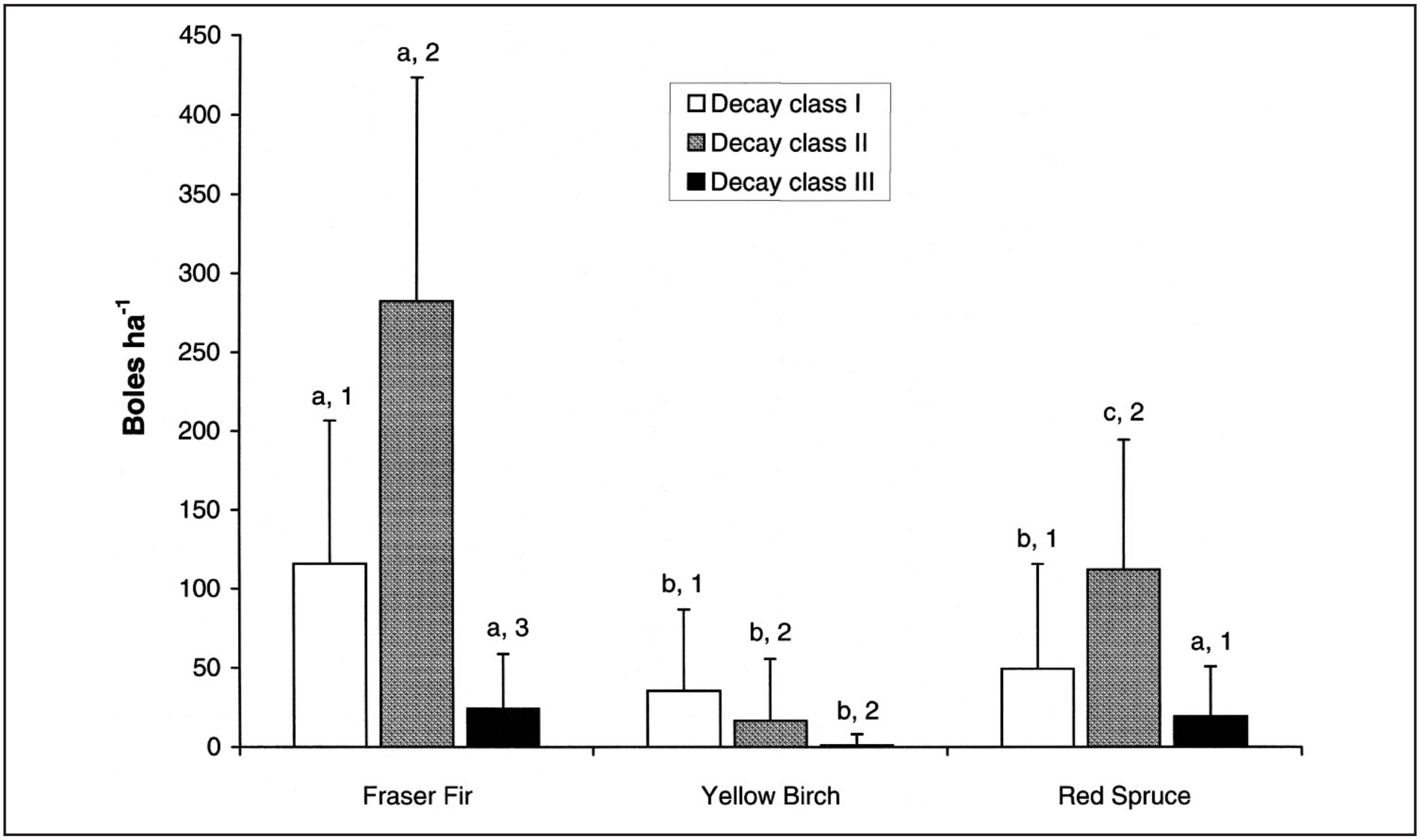

Figure 3. Stem density of down CWD by species and decay class NDW, GRSM, 1994 (n = 50 plots). Sample statistics are the mean and standard deviation. Bar values within the same decay class with the same letter are not significantly different; bar values within the same species with the same number are not significantly different (α = 0.05) based on Tukey's studentized range test.

reported for spruce-fir stands from the Black Mountains in North Carolina, where between 19% and 54% of all stems were dead (Nicholas et al. 1992a). The percentage dead in NDW exceeded the range of 5% to 36% of standing dead trees for a second growth northern hardwood stand in the Northeast (Tritton and Siccama 1990). This underscores the high degree of disturbance that has taken place in this ecosystem. Basal area for live (14.9 to 67.5 m^2 ha^{-1}) and standing dead (1.2 to 42.9 m^2 ha^{-1}) for the current study was slightly more variable than basal area for live (23.8 m^2 ha^{-1} to 46.8 m^2 ha^{-1}) and standing dead trees (9.2 m^2 ha^{-1} to 29.2 m^2 ha^{-1}) in other southern Appalachian spruce-fir forests (Nicholas et al. 1992a).

The uneven diameter distribution observed for Fraser fir in this study is due to the adelgid infestation that has killed the majority of large mature Fraser fir trees. Small fir trees typically have smooth bark and are somewhat more resistant to the adelgid than larger more mature trees, which have developed fissured bark (Eagar 1984). Historically, Fraser fir trees typically attained diameters of at least 50 cm (Eagar 1978).

Volume of down CWD in this study (158.8 m^3 ha^{-1}) was comparable to CWD in other mid and high elevation spruce-fir stands that were infested by the adelgid 3 to 17 years prior to measurement (146.9 m^3 ha^{-1} to 186.0 m^3 ha^{-1}) (Nicholas and White 1985). Down CWD in this study was also somewhat comparable to that reported from other old growth stands in the GRSM (134.3 m^3 ha^{-1}) (Webster and Jenkins 2005). However, snag density reported by Webster and Jenkins (2005) (56.4 stems ha^{-1} to 126.8 stems ha^{-1}) was substantially lower than that for this study (560 stems ha^{-1}). The differences could be attributed in part to their sampling only standing dead trees that were $\geq$ 10.0 cm dbh, while the present study had a minimum of 5.0 cm dbh. Primarily, however, the differences are most likely due to the high number of dead trees killed by the adelgid.

Decreasing wood density with increasing decay class has been noted by other researchers (Erickson et al. 1985; Arthur and Fahey 1990; Alban and Pastor 1993; Busse 1994). In addition, the wood density values obtained in this study are comparable to those in other spruce-fir studies. In the White Mountains of New Hampshire, red spruce wood density dropped from 0.43 g cm^{-3} in fresh boles to 0.13 g cm^{-3} in highly decayed boles (Foster and Lang 1982). In that same study, balsam fir [*Abies balsamea* (L.) Mill.] wood density dropped from 0.33 g cm^{-3} in fresh boles to 0.19 g cm^{-3} in highly decayed boles. For both red spruce and Fraser fir, in the current study, wood density dropped from 0.34 g cm^{-3} in decay class I wood to 0.13 g cm^{-3} in decay class III wood. Wood density in boles from a Rocky Mountain Engelmann spruce – subalpine fir [*Picea engelmannii* Parry – *Abies lasiocarpa* (Hook.) Nutt.]

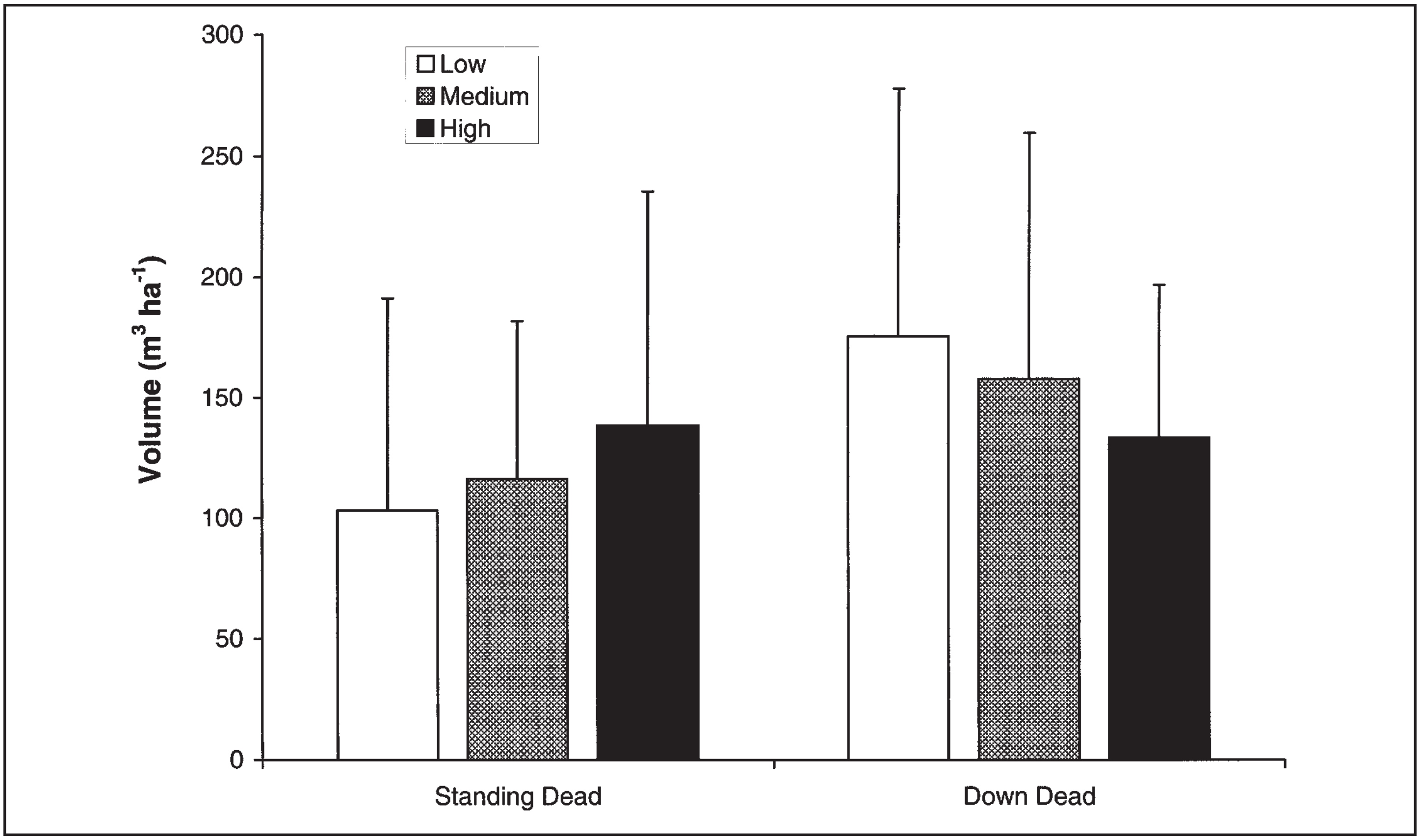

Figure 4. Volume of CWD by elevation class (no significant differences) (low = 1700-1756 m (n = 19 plots); medium = 1783-1834 m (n = 19 plots); high = 1865-1911 m (n = 12 plots)) NDW, GRSM, 1994. Sample statistics are the mean and standard deviation.

forest decreased from 0.31 g cm^{-3} (decay class I) to 0.17 g cm^{-3} (decay class V) (Arthur and Fahey 1990).

Biomass of CWD typically ranges from 10 to 511 Mg ha^{-1} for various temperate forested ecosystems and accounts for 1.3% to 45.1% of the total aboveground biomass (Harmon et al. 1986). CWD in the NDW accounted for 27% of the total biomass (not including woody species < 5.0 cm dbh or fine woody debris) and ranged from 20.9 Mg ha^{-1} to 124.2 Mg ha^{-1}. The percentage of total biomass that was dead was highly variable by species. Ninety-six percent of the total biomass of Fraser fir was in the CWD component. In contrast, 17% of total red spruce biomass was CWD.

Results from our nitrogen analyses indicate that nitrogen concentration increases with decay, as does nitrogen content, although to a lesser degree. This phenomenon has been documented by others and may be indicative of external nitrogen sources, such as throughfall, nitrogen fixation, and litter fall (Foster and Lang 1982; Sollins et al. 1987; Arthur and Fahey 1990; Alban and Pastor 1993; Busse 1994; Brown et al. 1996; Krankina et al. 1999).

The C/N ratios for Fraser fir (live = 654, decay class III = 259) were very similar to those reported for balsam fir in New Hampshire (live = 714, down dead = 208) (Foster and Lang 1982). Given that our C/N ratio for red spruce decay class III (245) was higher than that reported by Foster and Lang (1982) for the same species (71), our decay class III samples may not reflect the most highly decayed wood in the watershed. Additionally, the relatively high C/N ratios of decay class III wood, as compared to soil (typically 8 to 15), may be indicative of net nitrogen immobilization (McNulty and Aber 1993; Brady and Weil 1996).

In this study, CWD accounted for 101.5 kg ha^{-1} of nitrogen, which was 17% of the total (589.8 kg ha^{-1}). This was comparable to a spruce-fir forest in Colorado, where CWD accounted for 91 kg ha^{-1} of nitrogen, which was 18% of the total (507 kg ha^{-1}). However, when forest floor and belowground nitrogen was taken into consideration, CWD only accounted for 7% of the total (1,355 kg ha^{-1}) (Arthur and Fahey 1990).

Within the NDW, total carbon in live and dead bole wood averaged 128.7 Mg ha^{-1}, of which 34.9 Mg ha^{-1} was the dead portion. In contrast to watershed nitrogen, where CWD made up 48% of the total contained in bole wood, CWD only constituted 27% of the total carbon. This percentage would undoubtedly be lower if foliage, bark, and branch wood were included in the total estimate. In a balsam fir forest, the majority of carbon was in the soil and forest floor, and down CWD only accounted for 3% of the total carbon contained in various detrital components (Lang et al. 1981).

Table 2. Summary of wood density, nitrogen, carbon, and C/N ratios for live, standing dead, and down dead trees by species and decay class in the NDW, GRSM, 1994. Sample statistics are the mean and the standard deviation in parentheses.

Species	Condition	Decay Class	n	Density (g cm^{-3})	n[b]	%N	N (g m^{-3})	%C	C (kg m^{-3})	C/N
Fraser Fir	Live	–	–	0.36[a]	17	0.075a (0.02)	269a (55)	47.0a (1.5)	169a (5)	654a (132)
	Standing Dead	1	27	0.337a (0.09)	27	0.116a (0.06)	390a (187)	48.2a,b (1.7)	162a (6)	493a (185)
		2	25	0.296a (0.08)	–	0.166[c]	–	47.9[c]	–	
	Down Dead	1	14	0.293a (0.07)	33	0.108a (0.06)	317a (167)	47.6a,b (1.5)	141b (18)	553a (245)
		2	28	0.208b (0.07)	–	0.166[c]	–	47.9[c]	–	
		3	15	0.130c (0.04)	13	0.303b (0.21)	380a (223)	48.6b (2.5)	65c (17)	259b (176)
Red Spruce	Live	–	–	0.43[a]	29	0.044a (0.008)	188a (34)	46.6a (0.6)	200a (3)	1113a (274)
	Standing Dead	1	12	0.336a (0.12)	27	0.083a,b (0.03)	262a,b (82)	47.6a,b (2.3)	153b (30)	629b (184)
		2	7	0.383a (0.05)	–	0.135[c]	–	47.7[c]	–	
	Down Dead	1	5	0.314a,b (0.10)	16	0.111b (0.08)	355b (254)	47.4a,b (1.3)	155b (20)	579b (271)
		2	13	0.193b,c (0.05)	–	0.135[c]	–	47.7[c]	–	
		3	7	0.126c (0.02)	10	0.265c (0.14)	353b (165)	49.0b (3.2)	70c (23)	245c (146)
Yellow Birch	Live	–	7	0.511a (0.05)	23	0.100a (0.01)	512a (64)	46.2a (0.87)	236a (4)	467a (55)
	Standing Dead	1	10	0.452a (0.15)	18	0.136a (0.06)	576a (219)	46.3a (2.0)	205b (48)	396a (143)
		2	7	0.481a (0.11)	–	0.274[c]	–	47.2[c]	–	
	Down Dead	1	17	0.388a,b (0.10)	20	0.160a (0.10)	586a (348)	46.6a (1.4)	175b (36)	362b (136)
		2	13	0.293b,c (0.10)	–	0.274[c]	–	47.2[c]	–	
		3	5	0.181c (0.13)	6	0.583b (0.25)	1118b (414)	49.3b (2.0)	104c (46)	101c (49)

NOTE: Values within the same species followed by the same letter are not significantly different ($\alpha = 0.05$) based on Tukey's studentized range test for contrasts among means.

[a] Values are taken from Foster and Lang (1982) for balsam fir and red spruce.

[b] Values for this n apply to %N, N (g m^{-3}), %C, C (kg m^{-3}) and C/N.

[c] Values estimated via the GLM procedure in SAS.

– = no value for cell

Table 3. Analysis of variance for the main effects of species (Fraser fir, red spruce, yellow birch), decay class for density (standing dead – I, II; down dead – I, II, III), for percent nitrogen, and percent carbon (live, standing dead – I, down dead – I, III), and the interaction of species and decay class, in the NDW, GRSM, 1994 (n = 50 plots).

	Density ($g\ cm^{-3}$)[a]			Nitrogen (%)[a]			Carbon (%)		
Source	df	F value	Pr > F	df	F value	Pr > F	df	F value	Pr > F
Species	2	8.3	0.0004	2	8.5	0.0005	2	4.5	0.012
Decay Class	4	19.8	0.0001	3	47	0.0001	3	8.1	0.0001
Species * Decay Class	8	1.3	0.2586	6	3.6	0.0023	6	2	0.072

[a] Square-root transformed

CONCLUSIONS

Values for wood density, nitrogen concentration and content, as well as C/N ratios, were highly variable within decay classes, pointing to possible limitations of the use of decay class as a predictor of stage of decay. Daniels et al. (1997) found that decay class had a weak relationship with time since tree death for *Thuja plicata* (Donn ex D. Don *in* Lamb.) in a hemlock forest of southwestern coastal British Columbia, indicating that using time since death, rather than decay class, may better predict nutrient concentrations and content within decaying wood. Creed et al. (2004b) also found this to be true for wood density of red spruce and Fraser fir. However, none of the techniques tested could explain more than 53% of the variation in wood density. In contrast, Naesset (1999) found that decay class correlated well with wood density. That we found wood density to explain approximately 50% of the variation in percent nitrogen suggests that a more accurate measurement of wood density might better predict decay stage and, therefore, percent nitrogen, than decay class. Ultimately, this would mean better estimates of nitrogen at the watershed level.

Besides an increase in the amount of CWD, impacts to this ecosystem from the balsam

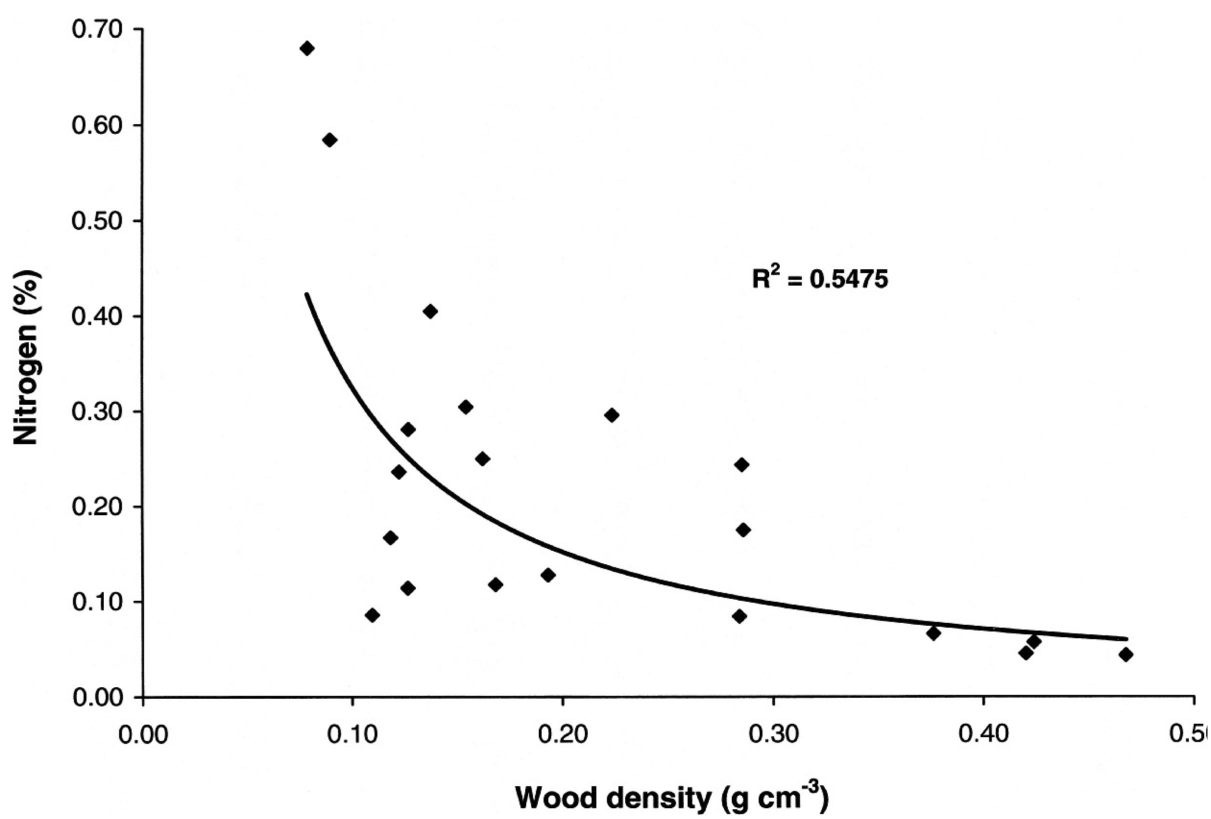

Figure 5. Relationship of percent nitrogen to wood density for decay class I and III down boles, red spruce and Fraser fir combined NDW, GRSM, 1994.

Table 4. Carbon and nitrogen pools for Fraser fir, red spruce, and yellow birch in the NDW, GRSM, 1994 (n = 50 plots). Sample statistics are the mean and the standard deviation in parentheses.

	Live	Standing Dead	Down Dead
Fraser Fir			
Nitrogen (kg ha^{-1})	0.94 (2.06)	25.70 (17.94)	25.51 (21.54)
Carbon (Mg ha^{-1})	0.59 (1.29)	8.75 (6.50)	7.62 (5.97)
Red Spruce			
Nitrogen (kg ha^{-1})	72.91 (34.81)	20.13 (25.46)	20.66 (18.59)
Carbon (Mg ha^{-1})	77.22 (36.86)	9.08 (11.71)	7.06 (6.50)
Yellow Birch			
Nitrogen (kg ha^{-1})	34.52 (46.58)	3.48 (8.47)	6.02 (11.56)
Carbon (Mg ha^{-1})	15.95 (21.52)	0.96 (2.62)	1.46 (2.81)
All[a]			
Nitrogen (kg ha^{-1})	108.37 (44.27)	49.31 (31.71)	52.20 (32.22)
Carbon (Mg ha^{-1})	93.76 (33.70)	18.79 (13.35)	16.14 (9.74)

[a] All refers to the summation of values for Fraser fir, red spruce, and yellow birch, only.

Table 5. Nitrogen pools in the NDW, GRSM, 1994 (n = 50 plots).

	Nitrogen (kg ha^{-1})	% of Total
Live Tissue		
Foliage	182.3[a]	31
Branch	90.8[a]	15
Bark	106.8[a]	18
Bole	108.4	18
Total Live	488.3	83
Dead Wood[b]		
Standing	49.31	8
Down	52.2	9
Total CWD	101.5	17
Grand Total	589.8	100

[a] From Barker et al. (2002)

[b] Only includes values for Fraser fir, red spruce, and yellow birch

woolly adelgid have resulted in a dense stand of regeneration of spruce and fir trees where canopy gaps exist (Witter and Ragenovich 1986; Nicholas et al. 1992b). These seedlings and saplings provide a sink for nitrogen, because plant nitrogen uptake depends on the vigor and successional stage of the forest (Fenn et al. 1998; Barker et al. 2002). Rapidly growing young trees depend more on the soil for nitrogen and are more effective at retaining nitrogen in plant biomass than older trees (Fenn et al. 1998). Between 1993 and 1998, nitrogen in live fir trees, in the NDW, increased from 7.8 kg ha^{-1} to 15.2 kg ha^{-1}, a 96% increase over a 5-year period (Barker et al. 2002). While net immobilization likely occurred in dead wood, this study found only a slight increase in nitrogen content over decay classes for Fraser fir and for red spruce boles. Due to the fact that nitrogen content in yellow birch increased more than in the other species (118% compared to 41% for Fraser fir), yellow birch boles were substantial sinks for nitrogen, which may be of greater significance in ecosystems with a higher proportion of this species.

An investigation into whether CWD was acting as a net sink or source for nitrogen at any given time during the decay process resulted in estimates for a critical C/N value for the major species in each decay class (Creed et al. 2004b). According to those critical C/N ratios, the majority of boles in the NDW were acting as sinks for nitrogen. Given that most logs were above the critical C/N ratio and the dense stand of regeneration that exists, there may be a temporary, albeit small, offset of nitrogen saturation in the NDW. The high degree of spatial heterogeneity of CWD may result in plot to plot differences in this offset; however, it is unknown what effect this variability would have at the watershed level. In the absence of another pulse to the system, once the majority of the CWD decays (18 years for 50% and 75 years for 95% of dead red spruce and Fraser fir; A. Rose, unpubl. data), uptake by regeneration may have slowed, and any benefits to the system from the offset of nitrogen will no longer be apparent.

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