To the Graduate Council:

I am submitting herewith a thesis written by Anita Kristine Rose entitled "Coarse Woody Debris and Nutrient Dynamics in a Southern Appalachian Spruce-Fir Forest." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

Niki S. Nicholas, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the council:

Associate Vice Chancellor and
Dean of the Graduate School

COARSE WOODY DEBRIS AND NUTRIENT DYNAMICS IN A SOUTHERN APPALACHIAN SPRUCE-FIR FOREST

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Anita Kristine Rose

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ABSTRACT

Spruce-fir forests in the southern Appalachian mountains have been hypothesized to be in the latter stages of nitrogen saturation. These forests receive high atmospheric nitrogen inputs and show high nitrate levels in soil solution and streamwater. The invasion of the balsam woolly adelgid (*Adelges piceae* Ratz.) in the late 1970s killed the majority of endemic Fraser fir (*Abies fraseri* (Pursh) Poir.) trees, resulting in large amounts of coarse woody debris. In an effort to quantify nitrogen cycling in spruce-fir ecosystems, the 17.4 ha Noland Divide Watershed in the Great Smoky Mountains National Park has been intensively studied since the mid 1980s. Permanent plots (20 x 20 m) were used to determine the volume and biomass of down and standing dead wood in this watershed. Red spruce (*Picea rubens* Sarg.), Fraser fir, and yellow birch (*Betula alleghaniensis* Britt.) boles were sampled to determine decay rates, change in density, change in concentration and content of carbon and nitrogen over the decomposition process, and the extent to which dead wood was acting as a sink for nitrogen.

Dead wood volume was highly variable across the watershed, ranging from 5 m^3/ha to 307 m^3/ha for standing boles, and from 25 m^3/ha to 400 m^3/ha for down boles. The average total volume of coarse woody debris in this watershed exceeded averages typical of other forest types in the Great Smoky Mountains. Annual decay rate constants (k) for slightly decayed down boles were 0.029, 0.036, and 0.217 for Fraser fir, red spruce, and yellow birch, respectively, indicating that up to 100 years may be necessary for the complete disappearance of most of the dead wood in this ecosystem. Decay rate constants changed markedly between decay classes. For all decay classes considered

together, *k*-values were 0.051, 0.062, and 0.097 for Fraser fir, red spruce, and yellow birch, respectively. The projected time for the disappearance of wood of all decay classes combined was 59 years for Fraser fir, 48 years for red spruce, and 31 years for yellow birch. Density decreased significantly for all three species by approximately 70% from live tissue to highly decayed wood. Carbon concentrations remained fairly stable at approximately 47% for all decay classes and all species. Nitrogen concentrations increased sharply between moderately decayed wood and highly decayed wood. Average nitrogen content on a unit volume basis increased by approximately 35% (270 g/m^3 to 368 g/m^3), 75% (189 g/m^3 to 330 g/m^3), and 95% (547 g/m^3 to 1055 g/m^3) in live tissue to decay class III wood for Fraser fir, red spruce, and yellow birch, respectively.

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1. INTRODUCTION

Despite the fact that nitrogen is often the most common limiting nutrient in terrestrial ecosystems, there is increasing evidence that some mature high elevation red spruce (*Picea rubens* Sarg.) - Fraser fir (*Abies fraseri* (Pursh) Poir.) forests in the southeastern United States may be nitrogen saturated (Lovett 1992, Van Miegroet et al. 1992a; Nodvin et al. 1995). These forests receive high levels of atmospheric nitrogen inputs (~ 27 kg/ha/yr) and have high nitrate levels in soil solution and stream water (~ 15 kg/ha/yr NO_3-N) (Nodvin et al. 1995). When nitrogen losses begin to equal or exceed inputs, a system is said to be nitrogen saturated (Agren and Bosatta 1988). High nitrate levels have been implicated in forest nutritional imbalances, soil acidification, and water quality deterioration (Joslin and Wolfe 1992, 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). (For a description of the nitrogen cycle and nitrogen saturation see Appendices 1 and 2).

In addition to excess nitrogen in the system, the southern Appalachian spruce - fir ecosystem has been severely impacted by an exotic pest, the balsam woolly adelgid (BWA). The BWA has decimated populations of mature Fraser fir trees throughout the southern Appalachians, which has resulted in a large number of dead trees (Eagar 1978, Nicholas et al. 1992a). The insect infestation has created both large disturbance patches (in areas of pure fir stands) and small disturbance patches where fir is co-dominant with spruce. This thinning of the canopy in spruce-fir stands may have implications for health

of the associated red spruce. Spruce trees may now be more susceptible to windthrow, or other disturbances (Nicholas et al. 1992a). Often windthrow is a major source of coarse woody debris (CWD), especially in spruce-fir forests, due to shallow rooting and ridge top exposure. Episodic events or stand replacement disturbances, such as insect infestation and changing environmental conditions, can create large amounts of CWD and have a substantial impact on the nutrient cycling in the affected area. Few CWD studies have been concentrated in spruce-fir ecosystems (Foster and Lang 1982, Arthur and Fahey 1990, Sturtevant et al. 1997, Clark et al. 1998), and even fewer have focused on the spruce-fir ecosystem of the southern Appalachians (Nicholas and White 1985). (For a description of the southern Appalachian spruce-fir forest see Appendix 3).

The importance of CWD, especially in managed forests, has only been recently realized. Forest nutrient cycling and nutrient availability cannot be fully understood without considering the CWD component, as it can account for a significant store of biomass and nutrients within an ecosystem (Harmon et al. 1987, Keenan et al. 1993). Decomposition leads to the release of carbon dioxide, water, and nutrients, and to the production of stable organic compounds known as humus (Schlesinger 1991). Prior to this release, CWD may serve as a sink for nutrients, especially nitrogen, during part of the decay process (Grier 1978, Edmonds and Marra 1999). Nadelhoffer et al. (1995) found decomposing litter to be a sink for nitrate additions in a nitrate fertilization study. As wood decays, the carbon/nitrogen (C : N) ratio decreases. Respiration and leaching cause the amount of carbon to decrease, while nitrogen immobilization during initial stages of decay causes the amount of nitrogen to increase. This increase in nitrogen may

result from fungal retention of the original nutrients in the wood, or fungal translocation of nutrients from throughfall, litter fall, and the underlying forest floor (Merrill and Cowling 1966, Stark 1972, Grier 1978). Fixation by bacteria may be another mechanism for an increase in nitrogen concentration, as has been found in wood of some coniferous species (Seidler et al. 1972, Larsen et al. 1978). (For a description of decomposition see Appendix 4).

Since 1991, a watershed scale nutrient cycling study has been conducted in a 17.4 ha spruce-fir forest in the Great Smoky Mountains National Park. Species composition, stand structure, streamwater chemistry, and nitrogen deposition have been closely monitored to understand the different components of nitrogen cycling within nitrogen saturated forests on a watershed scale (Johnson et al. 1991, Nodvin et al. 1995, Shubzda et al. 1995, Pauley et al. 1996). To fully comprehend these intricacies, an understanding of the dynamics and distribution of CWD within the watershed is vital. If CWD does act as a sink for nitrogen throughout the decay process it may serve to partially offset the nitrogen saturation that is occurring in the spruce-fir forest of the southern Appalachians. The objectives of this study were to characterize and quantify dead wood biomass levels, determine C : N ratio dynamics, examine decay rates in the southern Appalachian spruce-fir ecosystem, and consider these factors in light of the nitrogen saturation occurring in this changing ecosystem.

2. STUDY AREA & METHODS

Study Area

The most extensive old-growth southern Appalachian spruce-fir forests occur in the Great Smoky Mountains National Park (GRSM), North Carolina and Tennessee, where approximately 3700 ha of this vegetation type is found (74% of the total spruce-fir forest in the southern Appalachians) (Dull et al. 1988). Spruce-fir of the GRSM ranges in elevation from about 1500 m to 2000 m (Nicholas 1992). This area receives an average of 210 cm precipitation per year. Temperature lows in the winter range from 8° to 11°C and highs in the summer range from 12°C to 25°C (1979-1990 data courtesy of GRSM). Soils in the spruce-fir zone tend to be highly acidic with relatively low pH values and low base saturation (Fernandez 1992).

Study site 1. The main study site for this project is the 17.4 hectare Noland Divide Watershed (NDW) (35°34'N 83°29'W), on the upper reach of Noland Creek in the GRSM. The elevation of NDW ranges from 1676 m to 1921 m. This watershed is underlain by the Thunderhead Sandstone of the Great Smoky Group, a thick-bedded feldspathic sandstone quartzite and conglomerate interbedded with gray slate and phyllite. The soils are primarily shallow Inceptisols formed from bedrock or colluvium (Johnson et al. 1991).

This study site was chosen because of ongoing intensive nutrient cycling and watershed monitoring studies. In the 1980s, the Integrated Forest Study (IFS) established one of its monitoring sites at NDW at 1740 m; since then the NDW has been continuously monitored for precipitation and throughfall, with additional monitoring of

stream hydrology, stream chemistry, stand structure, and soil nutrient distributions (Johnson et al. 1992, Nodvin et al. 1995, Shubzda et al. 1995, Pauley et al. 1996). This watershed appears to have no history of commercial logging and fire (Pyle 1984).

Study site 2. In 1984 a series of 66 permanent plots were installed across the Clingmans Dome area in the spruce-fir forest of the GRSM as part of the National Acid Precipitation Assessment Program (NAPAP) Forest Response Program (Nicholas et al. 1992a, Nicholas et al. 1992b). Twenty of these plots, ranging in elevation from 1524 m to 1980 m, are concentrated in the Newfound Gap - Clingmans Dome area, and were originally measured for CWD in 1984.

Methods

Plot establishment and CWD quantification. In 1993, fifty 20 x 20 m plots (0.04 ha) were established in the Noland Divide Watershed (Study Site 1) at eight elevational intervals of 30 m (100 ft), starting at 1700 m and separated by at least 30 m along the contour (Figure 1). Most (86%) of the plots were on slopes of 17-31°, and most (74%) faced 90-180° azimuth (Pauley et al. 1996). Within each plot, all live and standing dead stems of at least 5.0 cm diameter at 1.37 m height were mapped, identified to species, and measured for diameter at 1.37 m. For a description of live species composition and stand structure within NDW, see Pauley et al. (1996).

In 1994, downed CWD was mapped and identified to species in each of the fifty plots within at least two 10 x 10 m subplots. Length, and diameter at each end and in the middle, was recorded for all down boles. For this study, CWD was defined as woody material greater than about 10 cm in diameter at the large end and at least 1.54 m

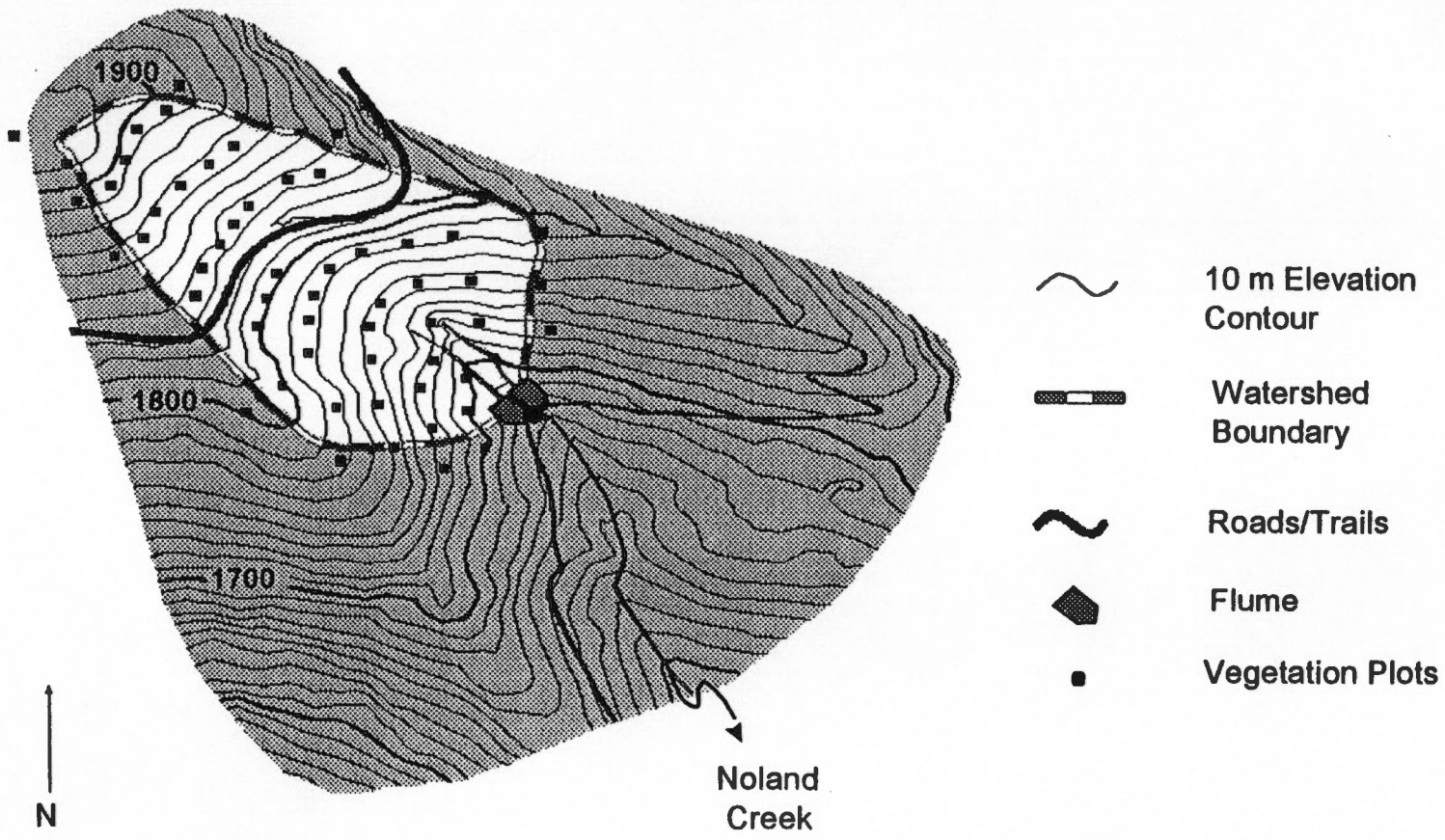

Figure 1. The Noland Divide Watershed of GRSM.

in length. This is roughly comparable to the 7.6 cm diameter, 100-hour-plus lag-time fuel size class used for fuel inventories (Brown 1974, Nicholas and White 1985). Decay class was determined by inserting a chaining pin, 0.5 cm in diameter, into each bole at several points along its length (similar to methods used by Lambert et al. 1980, Bingham and Sawyer 1988, and Clark et al. 1998). For this study, decay classes were defined as slightly decayed (penetration of the metal rod into the wood <0.5 cm - decay class I), moderately decayed (penetration 0.5 cm to the center of the bole - decay class II), and advanced decay (penetration through the bole - decay class III). Percentage of bark coverage, heartwood/sapwood sponginess, and presence of leaves and twigs were also determined. All standing dead trees were measured for height. Samples of unknown species were collected and identified in the laboratory.

Nutrient analysis. In 1995, the NDW plots were sampled for CWD nutrient analysis. Two hundred and fifty wood samples (excluding bark) were taken from the three major overstory species (red spruce, Fraser fir, and yellow birch (*Betula alleghaniensis* Britt.)). Representative samples for each of the three species were taken from the following categories: 'live', 'standing dead decay class I', 'down dead decay class I', and 'down dead decay class III'. Samples for down boles in decay class I and III were taken by removing a 5 cm cross-section using a hand saw. Cores were taken from live trees of each species. For standing dead boles, a wedge was taken without felling the tree, or a core removed using a brace and 1.9 cm bit drill. The brace and bit drill method excavated a cylinder of wood of known volume. Samples were wrapped in foil for transportation to the laboratory. Decay class II boles were not sampled due to

the variability in these types of boles and the higher level of subjectivity involved when assigning this decay rating. Additional samples were taken from nearby NAPAP plots to make up for species samples not found in the original NDW sampling plots.

Samples for nutrient analysis were weighed, dried at 70° C to constant weight, and ground on a Wiley mill. Nitrogen and carbon concentrations were determined with a Leco CNS 2000 (Leco Corp., St. Joseph, MI) (carbon via an infrared cell, and nitrogen via a thermal conductivity cell).

Density and moisture content. To evaluate how density changes with decay class, 5 cm cross-section samples were obtained for downed CWD in all three decay classes from NDW and NAPAP plots. A brace and bit was used to sample decay class I and II snags. An earlier evaluation of the data indicates that the brace and bit method and the cross-section method are not significantly different for sound boles (Jimmy Shen - personal communication). All samples (excluding bark) were immediately wrapped in foil for transportation to the laboratory.

Foil wrapped samples collected for density measurements were frozen after arriving in the laboratory. Each sample was weighed and submerged in a known volume of water to determine displacement volume of the fresh samples. 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 volume. Using the fresh weight and dry weight of each sample, moisture content was determined.

Volume loss and decay rates. The twenty NAPAP plots originally measured in 1984 for CWD are the basis for the volume loss and decay rate estimates for this study.

The plots were revisited in 1996 to relocate and re-measure CWD, and note changes (if any) in decay class. The field methods used on these plots are nearly identical to the methods described above, the main difference being that NAPAP plot boles were not measured at their mid-point, only on the ends.

Data analysis. Moisture content was calculated on a dry weight basis as the difference between the wet and dry weight divided by the dry weight, expressed as a percentage (Equation 1):

$$Moisture\ Content = (Wet\ Weight - Dry\ Weight)/Dry\ Weight * 100 \quad (1)$$

The volume for logs at both study sites was calculated using the formula for a frustum of a cone (Equation 2):

$$V = (L/3)*(A_l + sqrt(A_l*A_s) + A_s) \quad (2)$$

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 (Equation 3):

$$V = \tfrac{1}{2}*A_b*Ht \quad (3)$$

where A_b is the area of the base taken at breast height (1.37 m), and Ht is the height of the tree. (For a discussion of volume calculations see Appendix 5).

Biomass of dead boles per hectare within the NDW was calculated based on the bole volumes and mean densities by species and decay class. The magnitude of carbon and nitrogen pools contained in standing and down wood in each decay class by species was determined by multiplying the biomass of the wood by its mean nutrient concentration. Decay class II boles were not sampled for nutrient analysis. Therefore,

nitrogen and carbon concentrations for decay class II boles were calculated by species using Equation 4:

$$N = B_0 e^{xp} \tag{4}$$

where N is percent nutrient (either carbon or nitrogen), B_0 and x are the parameter estimates calculated using the nonlinear procedure in SAS (SAS Institute Inc. 1990), and p is the percent penetrability. For this calculation, it was necessary to transform decay class into a continuous variable (penetrability). This was done by assigning each decay class a measure of penetrability expressed as a percentage of average bole diameter. Decay class I boles were estimated to have a penetrability of 3%, decay class II and III boles were estimated to have a penetrability of 25% and 75%, respectively.

Volume loss was calculated on an individual bole basis by subtracting a bole's final volume from the initial volume and dividing by the initial volume, expressed as a percentage. Mass loss was likewise calculated by subtracting a bole's final mass from the initial mass and dividing by the initial mass, expressed as a percentage. This calculation was done by bole, species, decay class, plot, and on a per-hectare basis. A paired t-test was used to determine if final volumes were significantly different from initial volumes.

The single exponential model (Equation 5) for decay was used to calculate the annual decomposition constant (Olson 1963):

$$V_t = V_0 e^{-kt} \tag{5}$$

where V_0 is the initial volume of material, V_t is the volume at time t, and k is the annual decomposition constant. The annual decomposition constant (k) is the proportion of a

bole lost per year. It is also known as the annual decay constant. Similarly, mass loss (Equation 6) was calculated as:

$$M_t = M_0 e^{-kt} \tag{6}$$

where M_0 is the initial mass of material, M_t is the mass at time t, and k is the annual decomposition constant. This equation takes into account a bole's average density in a particular decay class, and may be a better estimate of decay rate than volume, because boles lose volume and become less dense as they decay. Separate rate constants were calculated based on all CWD by species and decay class. The approximate time required to decompose by 50% (Equation 7) and 95% (Equation 8) was calculated as:

$$t_{0.50} = 0.693/k \tag{7}$$

$$t_{0.95} = 3/k \tag{8}$$

where t = time and k = annual decomposition constant (For a description of how these equations were calculated see Appendix 6).

Main effects of species, decay class, length, diameter, plot, elevation, aspect, and interactions on k-values, density, percent nitrogen, percent carbon, and C : N ratios were examined statistically using separate analysis of variance (ANOVA) tests in SAS (SAS Institute Inc. 1990). ANOVAs for unbalanced data sets and regression analyses were performed using the general linear models procedure. For all tests of main effects, independent variables were treated as categorical. Length and diameter were transformed into categorical variables by grouping into three approximately equal classes. Length classes were defined as 0 - 3.0 m, 3.1 - 6.0 m, and 6.01+ m; and diameter classes were defined as 0 - 14 cm, 15 - 29 cm, and 30+ cm. Because plot,

elevation, aspect, and the interaction of these were not significant, data were pooled to include all sites. Tukey's multiple range test was used to determine if differences existed among species and decay classes for moisture content, density, *k*-values, percent nitrogen, percent carbon, and C : N ratios. Annual decay constants using individual logs were computed by species and decay class using the nonlinear models procedures in SAS. Departures from normality in the distributions of *k*-values, density, percent nitrogen, percent carbon, and C : N ratios within any classification were examined via a Shapiro-Wilks test of the UNIVARIATE procedure of SAS. Most classifications of *k*-values, density, percent nitrogen, and C : N ratios were judged to be nonnormal (at the 0.01 level), and a square root transformation was used for multiple comparisons between classifications and to test for significant independent variables. Unless otherwise noted, differences for all tests were considered to be significant at the 0.05 level.

3. RESULTS AND DISCUSSION

Moisture Content and Density

An analysis of variance indicated a significant increase in moisture content in decaying wood during the decay process (Figure 2, Table 1). There were no clear differences among the three species. Both Fraser fir and red spruce tended to show a slight, although not significant, decrease in moisture content in standing boles as compared to live wood. A sharp increase of over 200% occurred in decay class II and III down logs for all three species. An increase in moisture content with decay has been noted by others (Lambert et al. 1980, Hope 1987, Sollins et al. 1987). A moisture content over 200% may be high enough to inhibit obligate aerobes such as white-rot fungi (Hedges et al. 1988).

Density decreased during decomposition, but did not differ significantly until decay class II in down boles (Figure 3, Table 2). Density decreased by about 50% from decay class I boles to decay class III boles. It has generally been observed that density decreases over the decay process (Alban and Pastor 1993, Arthur and Fahey 1990, Busse 1994, Erickson et al. 1985). The density values obtained in this study are comparable to those obtained in studies on similar species. Foster and Lang (1982) obtained density values for red spruce of 0.43 g/cm^3 in decay class I boles to 0.13 g/cm^3 in boles of advanced decay. Likewise, they calculated a density of 0.33 g/cm^3 in decay class I balsam fir (*Abies balsamea* (L.) Mill.) boles to 0.19 g/cm^3 in boles of advanced decay.

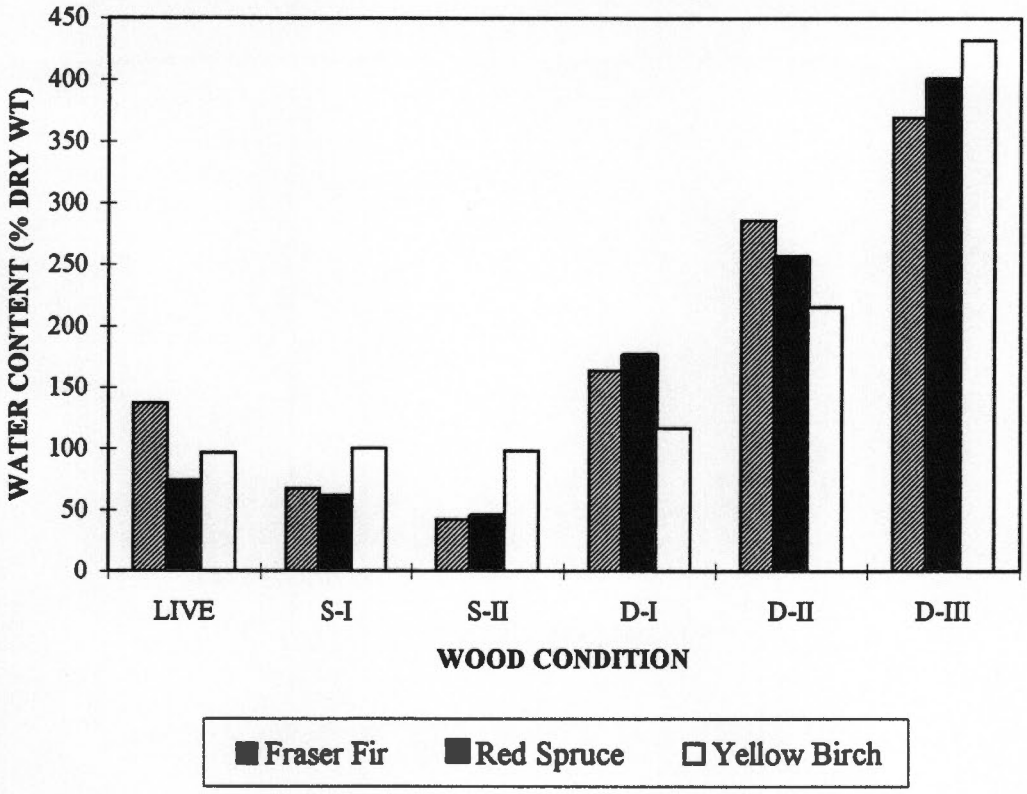

Figure 2. Percent water content (expressed on a dry weight basis) for Fraser fir, red spruce and yellow birch wood by decay class in the spruce-fir forest of GRSM. S-I - standing dead decay class I; S-II - standing dead decay class II; D-I - down dead decay class I; D-II - down dead decay class II; D-III - down dead decay class III.

Table 1. Means of percent water content (dry weight basis) for live, standing dead, and down dead Fraser fir, red spruce, and yellow birch wood in each decay class in the spruce-fir forest of GRSM.

Species	Condition	Decay Class			
		Live	I	II	III
Fraser Fir	Live	136.6*a* (19.6)* n=18	-	-	-
	Standing Dead		67.1*b* (11.4) n = 30	42.1*b* (7.3) n = 13	-
	Down Dead		163.4*a* (12.4) n = 33	286.6*c* (18.5) n = 20	370.0*d* (26.8) n = 19
Red Spruce	Live	72.8*a* (8.9) n=27	-	-	-
	Standing Dead		60.6*a* (10.8) n = 19	45.3*a,b* (16.1) n = 3	-
	Down Dead		176.1*b,c* (38.4) n = 9	256.4*c* (31.3) n = 10	400.5*d* (30.3) n = 13
Yellow Birch	Live	96.3*a* (5.9) n=22	-	-	-
	Standing Dead		100.2*a,b* (17.9) n = 13	98.1*a,b* (4.7) n = 6	-
	Down Dead		117.1*a,b* (13.6) n = 23	215.3*b* (33.3) n = 10	432.2*c* (122.7) n = 6

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

* Values in parentheses represent the standard error.

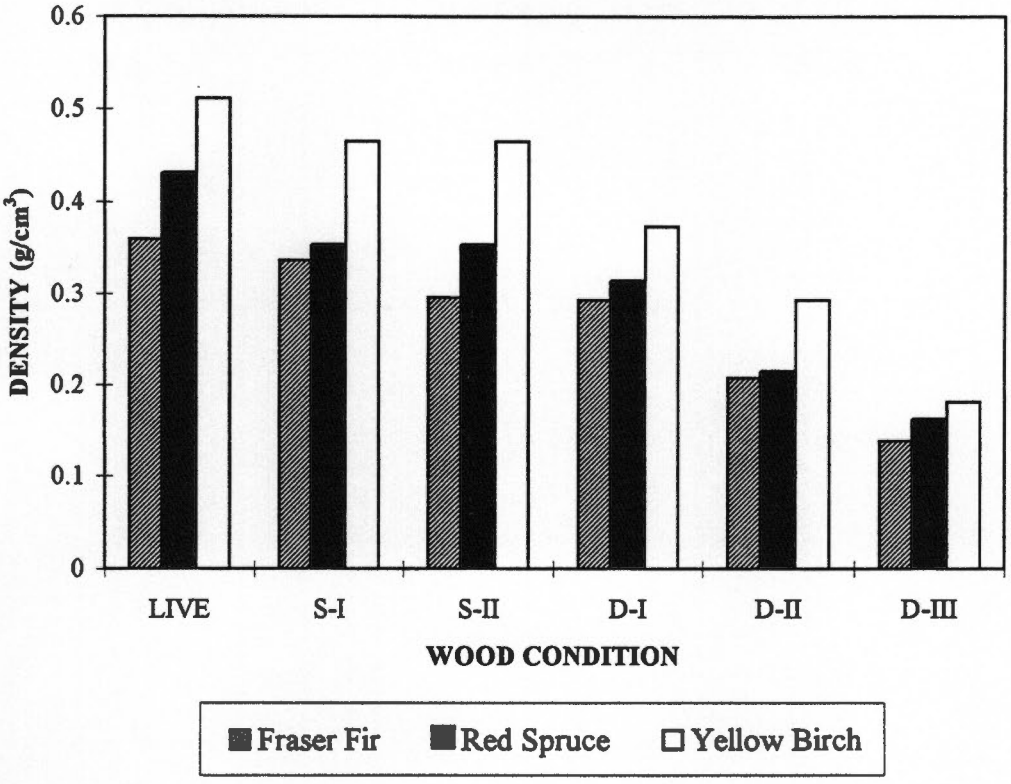

Figure 3. Density (g/cm^3) for Fraser fir, red spruce, and yellow birch wood by decay class in the spruce-fir forest of GRSM. S-I - standing dead decay class I; S-II standing dead decay class II; D-I - down dead decay class I; D-II - down dead decay class II; D-III - down dead decay class III.

Table 2. Range and means of density (g/cm^3) for live, standing dead, and down dead Fraser fir, red spruce, and yellow birch wood in each decay class in the spruce-fir forest of GRSM.

Species	Condition		Decay Class			
			Live	I	II	III
Fraser Fir	Live		0.36[a]			
	Standing Dead	Range		0.135 - 0.540	0.085 - 0.414	-
		Mean		0.337*a* (0.02)*	0.296*a* (0.02)	-
				n = 27	n = 25	
	Down Dead	Range		0.193 - 0.406	0.094 - 0.420	0.079 - 0.224
		Mean		0.293*a* (0.02)	0.208*b* (0.01)	0.130*c* (0.01)
				n = 14	n = 28	n = 15
Red Spruce	Live		0.43[a]			
	Standing Dead	Range		0.106 - 0.497	0.288 - 0.438	-
		Mean		0.336*a* (0.04)	0.383*a* (0.02)	-
				n = 12	n = 7	
	Down Dead	Range		0.227 - 0.468	0.124 - 0.295	0.106 - 0.154
		Mean		0.314*a,b* (0.05)	0.193*b,c* (0.01)	0.126*c* (0.01)
				n = 5	n = 13	n = 7

Table 2 (continued).

Species	Condition		Decay Class			
			Live	I	II	III
Yellow Birch	Live	Range	0.408 - 0.539			
		Mean	0.511*a* (0.02)			
			n = 7			
	Standing Dead	Range		0.211 - 0.577	0.246 - 0.576	-
		Mean		0.452*a* (0.05)	0.481*a* (0.04)	-
				n = 10	n = 7	
	Down Dead	Range		0.110 - 0.617	0.152 - 0.529	0.073 - 0.376
		Mean		0.373*a,b* (0.03)	0.293*b,c* (0.03)	0.181*c* (0.06)
				n = 18	n = 13	n = 5

NOTE: Values within the same species followed by the same letter are not significantly (p = 0.05) different based on Tukey's studentized range test for contrasts among means using square root transformed values to correct for non-normality.

* Values in parentheses represent the standard error.

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

Among the factors assessed in this study, species and decay class accounted for most of the variation in wood density differences in standing and down boles. An analysis of variance on square root transformed density values indicated a highly significant species and decay class effect (Tables 3 and 4). Length class and diameter class showed no significant effect on wood density, with the exception of a slight effect of diameter class for red spruce (Table 4).

Volume Changes

Significant changes in volume over a 12 year period were observed for boles of all species in the NAPAP plots. Forty nine percent of all Fraser fir boles that were originally dead and down were gone, as were 45% of all red spruce boles, and 77% of all yellow birch boles. After 12 years, most of the down CWD < 3.0 m in length disappeared, as well as down logs of all sizes with an original decay class of III (Table 5). A paired t-test found initial volumes to be significantly different from volumes at 12 years for all species. Fraser fir down boles (all decay classes considered together) lost an average of 67% of volume over 12 years; red spruce down boles lost an average of 61%, and yellow birch down boles lost an average of 84%. Average percent volume loss for snags that were still standing after 12 years was 27%, 28%, and 53% for Fraser fir, red spruce, and yellow birch, respectively. To create values for comparison with other studies, the annual decomposition constant (k) on an individual bole basis for change in volume was calculated using Equation 5 (Olson 1963). To represent boles that were not re-located in 1996 in the calculation of k, a final volume of one-half the smallest volume recorded was calculated. Annual decay rate constants for down boles, considering all

Table 3. Analysis of variance of standing and down coarse woody debris samples for the main effects of SPP - species (Fraser fir, red spruce, yellow birch); DC - decay class for (*k*) and density - (standing dead - I, II; down dead - I, II, III), for percent nitrogen and percent carbon - (live, standing dead - I, down dead - I, III); LCLS - length class (0 - 3.0 m, 3.1 - 6.0 m, 6.01+ m); and DCLS - diameter class (0 - 14 cm, 15 - 29 cm, 30+ cm) in the spruce-fir forest of GRSM.

	Decay Constant (*k*)*			Density (g/cm^3)*			Nitrogen (%)*			Carbon (%)		
Source	df	*F* value	Pr > *F*	df	*F* value	Pr > *F*	df	*F* value	Pr > *F*	df	*F* value	Pr > *F*
SPP	2	6.40	0.0018	2	8.33	0.0004	2	8.46	0.0005	2	4.51	0.0120
DC	4	26.42	0.0001	4	19.76	0.0001	3	46.96	0.0001	3	8.10	0.0001
SPP*DC	6	0.46	0.8357	8	1.28	0.2586	6	3.55	0.0023	6	1.97	0.0720
LCLS	2	9.31	0.0001	2	0.60	0.5513	2	7.96	0.0005	2	1.08	0.3430
DCLS	2	0.18	0.8341	2	1.87	0.1569	2	0.60	0.5477	2	0.53	0.5908

*Square-root transformed

Table 4. Results of separate analysis of variance for each species of standing and down coarse woody debris samples for the main effects of DC - decay class for (*k*) and density - (standing dead - I, II; down dead - I, II, III), for percent nitrogen and percent carbon - (live, standing dead - I, down dead - I, III); LCLS - length class (0 - 3.0 m, 3.1 - 6.0 m, 6.01+ m); and DCLS - diameter class (0 - 14 cm, 15 - 29 cm, 30+ cm) in the spruce-fir forest of GRSM.

	Decay Constant (*k*)*			Density (g/cm^3)*			Nitrogen (%)*			Carbon (%)		
Source	df	*F* value	Pr > *F*	df	*F* value	Pr > *F*	df	*F* value	Pr > *F*	df	*F* value	Pr > *F*
Fraser Fir												
DC	4	65.13	0.0001	4	17.44	0.0001	3	7.86	0.0001	3	2.99	0.0360
LCLS	2	10.86	0.0001	2	0.86	0.4283	2	4.60	0.0130	2	0.45	0.6396
DCLS	2	0.28	0.7579	2	1.97	0.1451	2	2.02	0.1397	2	1.38	0.2566
Red Spruce												
DC	4	3.62	0.0098	4	11.73	0.0001	3	19.22	0.0001	3	3.50	0.0197
LCLS	2	1.54	0.2213	2	0.61	0.5494	2	4.02	0.0221	2	0.47	0.6293
DCLS	2	0.39	0.6797	2	3.74	0.0352	2	1.75	0.1817	2	0.14	0.8684
Yellow Birch												
DC	2	3.16	0.0665	4	2.48	0.0635	3	19.69	0.0001	3	3.96	0.0128
LCLS	2	1.21	0.3223	2	0.17	0.8457	2	0.71	0.4960	2	1.73	0.1866
DCLS	1	0.07	0.7930	2	0.27	0.7632	2	0.06	0.9410	2	1.15	0.3252

*Square-root transformed

Table 5. Decay class changes for Fraser fir, red spruce and yellow birch over 12 years by length of CWD in the spruce-fir forest of GRSM. The transition values are the proportion of the number of CWD pieces of an initial decay class that were present in a decay class 12 years later.

		I to:				II to:				III to:		
Species	Length (m)	I	II	III	Unknown	I[a]	II	III	Unknown	II	III	Unknown
Fraser Fir	0 - 3.0	0.14	0.29	0.00	0.57	0.00	0.22	0.15	0.63	0.00	0.05	0.95
n=205	3.01 - 6.0	0.30	0.35	0.05	0.30	0.07	0.37	0.26	0.30	0.11	0.22	0.67
	6.01 +	0.29	0.58	0.04	0.08	0.06	0.50	0.38	0.06	0.00	0.67	0.33
Red Spruce	0 - 3.0	0.50	0.17	0.00	0.33	0.00	0.33	0.17	0.50	0.00	0.00	1.00
n=73	3.01 - 6.0	0.44	0.11	0.00	0.44	0.00	0.62	0.15	0.23	0.00	0.33	0.67
	6.01 +	0.38	0.38	0.00	0.25	0.00	0.75	0.25	0.00	0.00	0.00	0.00
Yellow Birch	0 - 3.0	0.00	0.00	0.17	0.83	0.12	0.12	0.25	0.50	0.00	0.00	0.00
n=22	3.01 - 6.0	0.00	0.20	0.00	0.80	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	6.01 +	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00

[a]A decrease in decay class can occur, as the criteria are based on the remaining wood rather than the entire original log.

decay classes together, were 0.030, 0.068, and 0.053 for Fraser fir, red spruce, and yellow birch, respectively (Table 6). Decay rate constants for standing boles were 0.022, 0.008, and 0.073 for Fraser fir, red spruce, and yellow birch, respectively (Table 7). The majority of standing dead trees fell during the 12 year period; 72% of Fraser fir, 84% of red spruce, and 86% of yellow birch were no longer standing in 1996. Since snags that fell between measurement periods were not re-measured in 1996, k on an individual basis was calculated only for those snags that were still standing after 12 years. The low k-value for standing dead red spruce may be attributed to the fact that only 77 stems were originally measured in 1984, and of those, 65 had fallen by 1996, therefore only 12 trees were used in the calculation of k, and the same possibility exists for yellow birch. For a southern temperate deciduous forest in Tennessee, Onega and Eickmeier (1991) also found that 74% of trees that died in a 12 year period had subsequently fallen over.

Studies often calculate k-values for snags by examining snag decay on a population and not on an individual basis (Lambert et al. 1980, Harmon 1982, Harmon et al. 1986). For comparison, k was calculated for snags on a population basis (plot by plot). Annual decay rate constants were 0.055, 0.034, and 0.104 for Fraser fir, red spruce, and yellow birch, respectively. These values are comparable to k-values, obtained by Harmon (1982) for 10 species of trees in east Tennessee, which ranged from a low of 0.04 for *Pinus virginiana* (Mill.) to a high of 0.20 for *Nyssa sylvatica* (Marsh.). The higher values in this study for the population calculated k-values may be attributed to an inclusion of the snags that fell ($V_t = 0$). Since a high percentage of snags fell, the final volume of snags was significantly lower than the initial volume, possibly causing this

Table 6. Annual decay rate constants (k) for Fraser fir, red spruce, and yellow birch down boles in the spruce-fir forest of GRSM by initial decay class on a volume basis (V_t) and mass basis (M_t) with associated R^2 values.

Species	n	Decay Class	$V_t = V_0e^{-kt}$*			$M_t = M_0e^{-kt}$**		
			k	SE***	R^2	k	SE***	R^2
Fraser Fir	n=199	all	0.030	0.002	0.90	0.051	0.003	0.84
	n=59	I	0.019*a*	0.003	0.91	0.029*a*	0.004	0.88
	n=110	II	0.032*b*	0.002	0.92	0.067*a*	0.003	0.91
	n=30	III	0.255*c*	0.035	0.17	0.237*b*	0.037	0.15
Red Spruce	n=69	all	0.068	0.008	0.59	0.062	0.008	0.61
	n=19	I	0.020*a*	0.006	0.92	0.036*a*	0.010	0.79
	n=37	II	0.090*a*	0.014	0.50	0.097*a*	0.015	0.46
	n=13	III	0.276*b*	0.045	0.22	0.270*b*	0.042	0.25
Yellow Birch	n=21	all	0.053	0.018	0.52	0.097	0.018	0.51
	n=12	I	0.191*a*	0.012	0.81	0.217*a*	0.014	0.77
	n=9	II	0.045*a*	0.026	0.56	0.084*a*	0.026	0.57
	n=0	III	-	-	-	-	-	-

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

*V_t = volume at time t; V_0 = initial volume; t = 12 years; k = decay rate constant.

**M_t = mass at time t; M_0 = initial mass; t = 12 years; k = decay rate constant.

***SE = Asymptotic standard error.

Table 7. Annual decay rate constants (k) for Fraser fir, red spruce, and yellow birch standing dead boles in the spruce-fir forest of GRSM by initial decay class on a volume basis (V_t) and on a mass basis (M_t) with associated R^2 values.

Species	n	Decay Class	$V_t = V_0 e^{-kt}$*			$M_t = M_0 e^{-kt}$**		
			k	SE***	R^2	k	SE***	R^2
Fraser Fir	n=170	all	0.022	0.002	0.92	0.022	0.002	0.92
	n=151	I	0.022	0.002	0.92	0.022	0.002	0.92
	n=19	II	0.023	0.004	0.96	0.023	0.004	0.96
Red Spruce	n=12	all	0.008	0.004	0.97	0.008	0.004	0.97
	n=9	I	0.006	0.003	0.99	0.006	0.003	0.99
	n=3	II	0.125	0.042	0.66	0.125	0.042	0.66
Yellow Birch	n=3	all	0.073	0.011	0.97	0.073	0.011	0.97
	n=3	I	0.073	0.011	0.97	0.073	0.011	0.97
	n=0	II	-	-	-	-	-	-

NOTE: Values within and between species and decay classes are not significantly (p = 0.05) different based on Tukey's studentized range test for contrasts among means.

*V_t = volume at time t; V_0 = initial volume; t = 12 years; k = decay rate constant.

**M_t = mass at time t; M_0 = initial mass; t = 12 years; k = decay rate constant.

***SE = Asymptotic standard error.

type of calculation to over-estimate the decay rate. This calculation assumes that snags that fell decayed completely, whereas they are now likely a part of the down bole cohort. More frequent remeasurements of standing and down CWD would help to alleviate the problems associated with calculating *k* incurred in this study. Dead trees that remain standing may lose moisture, as was found in this study for Fraser fir and red spruce. This seasoning may cause snags to have slower rates of decay than down boles. Krankina and Harmon (1995) found that snags rarely stand longer than 10 years, and very little decomposition (decrease in density) occurs during this period. Therefore, the *k*-values for snags reported in this study are probably a result of fragmentation, i.e., loss of volume.

Loss of Mass

To better model decay, mass was calculated for individual logs by multiplying a log's volume by the average density for the decay class. In 12 years, Fraser fir boles (all decay classes considered together) had lost an average of 74% of their mass, red spruce had lost 70%, and yellow birch had lost 91%. However, mass loss was much lower for logs that could be relocated that were originally decay class I. Fraser fir decay class I down boles lost an average of 49% ± 3.4 (mean ± SE) of their mass, and red spruce boles lost an average of 36% ± 6.4 of their mass. This agrees well with the 40% and 38% loss of biomass for subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), respectively, over a 14 year period as reported by Laiho and Prescott (1999). The high variability of mass loss within a species and decay class may indicate a wide range of time since death for a given decay class.

The *k*-values generated from mass loss are a better representation of decay rates than those generated from only volume loss, as it accounts for both a loss of volume and a decrease in density. Annual decay rate constants calculated from mass loss, considering all decay classes together, were 0.051, 0.062, and 0.097 for Fraser fir, red spruce, and yellow birch, respectively. The predicted time required for decomposition of one-half of the biomass for all decay classes considered together, where $t_{0.50} = 0.693/k$, is 14 years for Fraser fir, 11 years for red spruce, and seven years for yellow birch. Likewise, the predicted time required for decomposition of 95% of the biomass, where $t_{0.95} = 3/k$, is 59 years, 48 years, and 31 years for Fraser fir, red spruce, and yellow birch, respectively. Fraser fir boles of decay class I may require up to 24 years for decomposition of one-half the biomass, and up to 103 years for 95% decomposition. Decay class I red spruce boles may require up to 19 years for decomposition of one-half the biomass, and up to 83 years for 95% of the biomass. The *k*-values calculated via volume and mass loss by species and by species and decay class can be found in Tables 6 and 7. Annual decay rate constants calculated for down boles using mass loss were slightly higher than those calculated using only volume loss. Since decay class showed no significant effect on density for snags, density values were combined within a particular species. As a result, decay rate constants for snags calculated via volume loss are the same as those calculated via mass loss.

Initial decay class accounted for most of the variation in mass loss in down boles. An ANOVA on square root transformed *k*'s indicated a highly significant effect of species, initial decay class, and initial length class (Table 3). Diameter class and the

interaction of species and decay class, however, showed no significant effect. Similarly, most previous studies fail to show a significant diameter effect on decay rates (Foster and Lang 1982, Mattson et al. 1987, Alban and Pastor 1993). The few studies that have reported a significant diameter effect (Erickson et al. 1985, Edmonds and Marra 1999, Naesset 1999) found that large diameter boles decayed faster than small diameter boles. While a simple linear regression on individual boles found initial mass to have a significant effect on k-values (F value = 9.79, Pr > F = 0.0019), initial length seemed to play a more significant role in decay rates (F value = 27.01, Pr > F = 0.0001). The range of k-values within a species varied by more than 10-fold, and k was therefore calculated by decay class for each species (Table 6). Decay class I and II k-values were not significantly different from each other within a species, but were different from decay class III. Fraser fir and red spruce were not significantly different from each other in any decay class in either standing or down boles. Only in decay class I down boles did species show a significant effect, yellow birch being different from Fraser fir and red spruce. No species or decay class effects were detected in standing boles. An analysis of variance showed no effect of plot, aspect, elevation, or slope on k-values for standing or down boles.

The k-values calculated in this study, particularly those using mass loss, are slightly higher than some of those calculated for similar species in other studies. Foster and Lang (1982) calculated k-values of 0.033 and 0.029 for red spruce and balsam fir, while Erickson et al. (1985) calculated a k-value of 0.009 for Pacific silver fir (*Abies amabilis* (Dougl.) Forbes). The k-values in this study agree well with those of Harmon

et al. (1987) for *Abies concolor* (Gord. & Glend.) (0.05) and those of Mattson et al. (1987) who calculated a range of *k*-values for 17 different species of 0.015 to 0.261 in the southern Appalachians. Differences in *k*-values may be due to several factors. Most studies often begin with fresh wood, either by selecting for fresh wood, or by actually harvesting select trees (Foster and Lang 1982, Alban and Pastor 1993). In these instances, comparing the *k*-values calculated for decay class I boles in this study to *k*-values of other studies, proves to be a better comparison. The *k*-values of 0.029 for Fraser fir and 0.036 for red spruce decay class I boles compare well with those of Foster and Lang (1982) and Lambert et al. (1980), as mentioned above. Also, different studies use different methods for calculation of *k*. Often studies involving decay rates use only change in density to calculate *k*-values (Graham and Cromack 1982, Sollins et al. 1987). In a study by Lambert et al. (1980), decay rate for balsam fir increased more than twofold from 0.011 to 0.03 $year^{-1}$ when fragmentation losses were included. This study indicates that volume loss is a significant source of mass loss. According to Lambert et al. (1980) the loss of biomass due to fragmentation at any given time may be as high as 63%.

Decomposition is also highly variable within a given species, between different species, and between different locations. A *k*-value range of 0.049 - 0.215 was calculated for several Australian species (Brown et al. 1996). Tropical boles were found to have *k*-values as high as 0.461 (Lang and Knight 1979). Microclimatic factors may also play a significant role in decay rates. Hornsby et al. (1995) found that within the first two years after a tree dies, 95 - 99% percent of the variation in decomposition could

be explained by temperature and moisture differences. Although not addressed in this study, lag time between death and onset of decomposition may be considerable for certain species. This may account for the high variability of *k*-values for individual boles within species in this study, and for the high variability within percent mass loss as mentioned earlier. Lag time for studies reviewed by Harmon et al. (1986) may be as short as one year for certain hardwood species and snags, or as long as 80 years for *Pseudotsuga menziesii* ((Mirb.) Franco).

Carbon and Nitrogen

The carbon concentration averaged 47% for all three species and changed only slightly during decomposition (Table 8, Figure 4). An analysis of variance showed a significant decay class effect, a slight species effect, but no significant length class effect (Table 3). Decay class II boles were estimated as having an average of 47% carbon.

Significant increases in nitrogen concentration over decay classes were recorded for all species (Table 9, Figure 5). An analysis of variance showed a significant effect of species, decay class, and interaction of species and decay class (Table 3). Bole length class proved to be slightly significant for Fraser fir (Table 4). All three species were significantly different from each other for live tissue. In decay class II and III wood, Fraser fir and red spruce did not differ significantly, but both were different from yellow birch. Nitrogen concentration was highest in yellow birch, followed by Fraser fir and red spruce.

To determine changes of nitrogen content in wood, the average nitrogen concentration of a given species and decay class was multiplied by the average density

Table 8. Range and means of percent carbon for live, standing dead, and down dead Fraser fir, red spruce, and yellow birch wood in each decay class in the spruce-fir forest of GRSM.

Species	Condition		Decay Class			
			Live	I	II	II
Fraser Fir	Live	Range	43.3 - 49.9	-	-	-
		Mean	47.0*a* (0.36)*			
			n=17			
	Standing Dead	Range		46.3 - 51.9	-	
		Mean		48.2*a* (0.33)	47.9**	-
				n = 27		
	Down Dead	Range		44.5 - 50.9	-	46.2 - 55.3
		Mean		47.6*a* (0.25)	47.9**	48.5*a* (0.66)
				n = 34		n = 14
Red Spruce	Live	Range	45.6 - 47.8			
		Mean	46.6*a* (0.11)	-	-	-
			n=29			
	Standing Dead	Range		44.7 - 55.6	-	
		Mean		47.5*a* (0.42)	47.7**	-
				n = 30		
	Down Dead	Range		45.7 - 50.7	-	45.0 - 55.4
		Mean		47.4*a,b* (0.34)	47.7**	49.0*b* (1.01)
				n = 15		n = 10

Table 8 (continued).

Species	Condition		Decay Class			
			Live	I	II	III
Yellow Birch	Live	Range	43.4 - 48.1			
		Mean	45.9*a* (0.21)*	-	-	-
			n=27			
	Standing Dead	Range		42.7 - 52.2	-	
		Mean		46.3*a* (0.46)	47.2**	-
				n = 18		
	Down Dead	Range		44.3 - 49.3	-	45.9 - 51.8
		Mean		46.6*a* (0.32)	47.2**	49.3*b* (0.80)
				n = 20		n = 6

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

* Values in parentheses represent the standard error.

** Values were calculated using the nonlinear procedure in SAS.

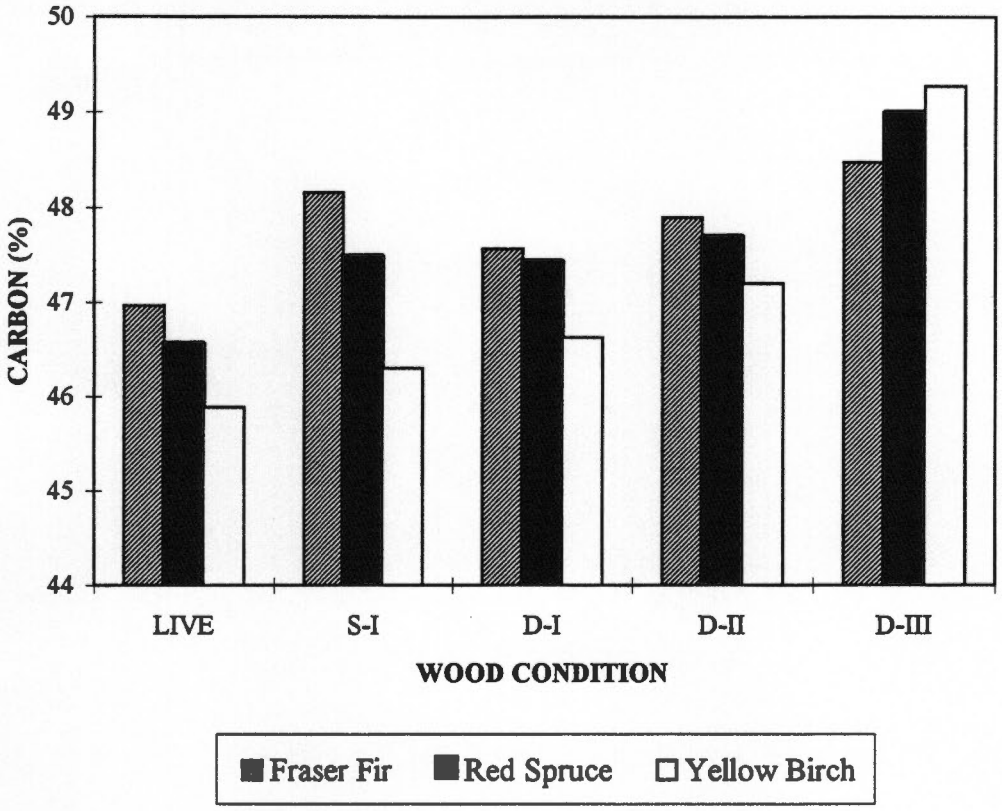

Figure 4. Percent carbon for Fraser fir, red spruce, and yellow birch wood by decay class in the spruce-fir forest of GRSM. S-I - standing dead decay class I; D-I - down dead decay class I; D-II - down dead decay class II (calculated values); D-III - down dead decay class III.

Table 9. Range and means of percent nitrogen for live, standing dead, and down dead Fraser fir, red spruce, and yellow birch in each decay class in the spruce-fir forest of GRSM.

			Decay Class			
Species	Condition		Live	I	II	III
Fraser Fir	Live	Range	0.051 - 0.101	-	-	-
		Mean	0.075*a* (0.004)*			
			n=17			
	Standing Dead	Range		0.052 - 0.280	-	
		Mean		0.116*a* (0.01)	0.141**	-
				n = 27		
	Down Dead	Range		0.033 - 0.257	-	0.030 - 0.680
		Mean		0.106*a* (0.01)	0.141**	0.283*b* (0.06)
				n = 34		n = 14
Red Spruce	Live	Range	0.024 - 0.057			
		Mean	0.044*a* (0.001)	-	-	-
			n=29			
	Standing Dead	Range		0.026 - 0.194	-	
		Mean		0.087*b* (0.01)	0.108**	-
				n = 30		
	Down Dead	Range		0.044 - 0.215	-	0.084 - 0.533
		Mean		0.094*b* (0.01)	0.108**	0.262*c* (0.04)
				n = 15		n = 10

Table 9 (continued).

Species	Condition		Decay Class			
			Live	I	II	III
Yellow Birch	Live	Range	0.081 - 0.153			
		Mean	0.107*a* (0.004)*	-	-	-
			n=27			
	Standing Dead	Range		0.069 - 0.316	-	
		Mean		0.136*a* (0.02)	0.211**	-
				n = 18		
	Down Dead	Range		0.083 - 0.398	-	0.272 - 0.952
		Mean		0.159*a* (0.02)	0.211**	0.583*b* (0.10)
				n = 20		n = 6

NOTE: Values within the same species followed by the same letter are not significantly (p = 0.05) different based on Tukey's studentized range test for contrasts among means using square-root transformed data.

* Values in parentheses represent the standard error.

** Values were calculated using the nonlinear procedure in SAS.

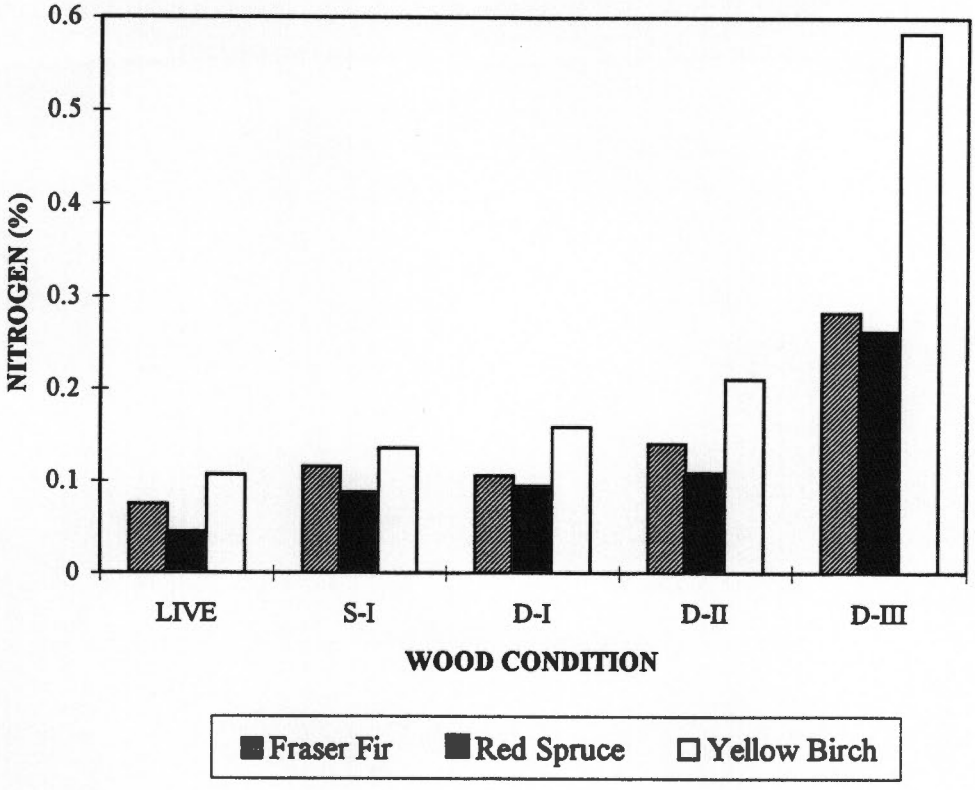

Figure 5. Percent nitrogen for Fraser fir, red spruce, and yellow birch wood by decay class in the spruce-fir forest of GRSM. S-I - standing dead decay class I; D-I - down dead decay class I; D-II - down dead decay class II (calculated values); D-III - down dead decay class III.

or that species and decay class to give the absolute amounts of nitrogen on a unit volume basis. Trend analysis indicated that there was an (but not statistically significant) increase in nitrogen content in decaying boles. Nitrogen content in live wood to down decay class III wood increased from 270 g/m^3 to 368 g/m^3 for Fraser fir, from 189 g/m^3 to 330 g/m^3 for red spruce, and from 547 g/m^3 to 1055 g/m^3 for yellow birch (Figure 6). This phenomenon has been documented by others (Foster and Lang 1982, Busse 1994, Sollins et al. 1987, Alban and Pastor 1993, Brown et al. 1996).

In contrast, Hale and Pastor (1998) found decreasing nitrogen contents on a unit volume basis over decay classes for maple and oak logs. Krankina et al. (1999), as well, found that although nitrogen concentration increased between decay classes, stores of nitrogen generally decreased due to the loss of biomass. Given that logs in this study lost a high percentage of biomass over the 12 year period (74% for Fraser fir, 70% for red spruce, and 91% for yellow birch), the increase in nitrogen content may not be enough to offset this loss. However, the logs in this study were serving as sites for nitrogen immobilization at any given point, even if they lost a substantial portion of biomass. Therefore, early in the decay process, logs may act primarily as a sink for nitrogen; as they begin to fragment and lose structural integrity they may act both as a sink and a source of nitrogen to the environment. Volume loss, however, does not necessarily indicate nutrient release. As pointed out by Krankina et al. (1999), a snag or bole may become fragmented, but the pieces may or may not be completely decayed and incorporated into the forest floor. As was the case in this study, snags often fragmented, but the sampling methodology in this study did not include searching for the fragmented

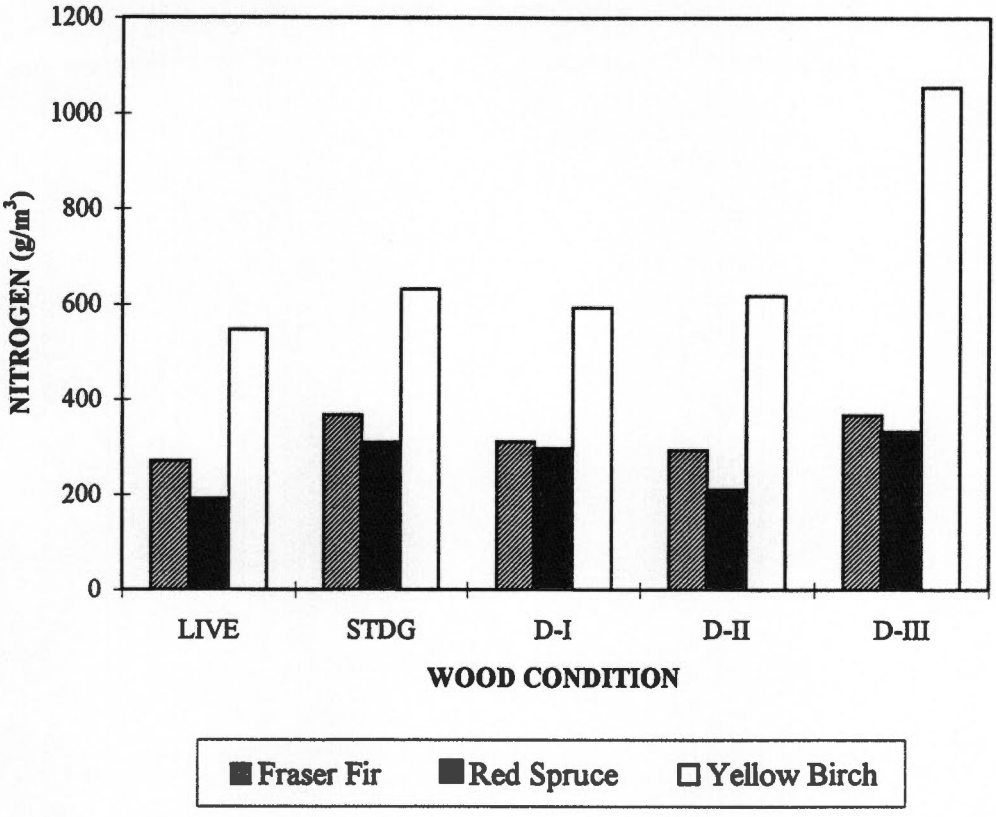

Figure 6. Nitrogen content (g/m^3) for Fraser fir, red spruce, and yellow birch wood by decay class in the spruce-fir forest of GRSM. STDG - standing dead, D-I - down dead decay class I, D- II down dead decay class II (calculated values), D-III - down dead decay class III.

pieces. This may have resulted in an over-estimation of volume loss. Also, boles that were not easily located were noted as "missing" while, in actuality, all or portions of a bole may have become buried or barely indistinguishable from the surrounding forest floor. To avoid these types of problems in the future, it was determined that extreme care should be taken when searching for dead wood to avoid an overestimation of loss. Also, tagging of boles and less time between samplings would help to alleviate this problem.

The C : N ratio showed a steady decline over decay class. Average initial C : N ratios for live wood were highest in red spruce (1113), followed by Fraser fir (654), and yellow birch (443). By the time debris reached decay class III, ratios had dropped to 246 for red spruce, 350 for Fraser fir, and 101 for yellow birch. The lowest C : N ratio value obtained was 51 for a decay class III birch bole. Values for nitrogen concentration and content, as well as C : N ratios, were highly variable within decay classes, indicating that there may not be a good correlation between decay class and time since death. Daniels et al. (1997) found that decay class showed little relationship to time since tree death for *Thuja plicata* (Donn ex D. Don *in* Lamb.), indicating that using time since death rather than decay class may better predict nutrient cycling within decaying wood. The C : N ratios in this study for highly decayed wood are much higher than would be expected for mineral soil (ca. 20 - 30) and may be indicative of net nitrogen immobilization (McNulty and Aber 1993). Hart (1999), however, found highly decayed boles with C : N ratios of around 117 to be sites of nitrogen mineralization. He suggested that this may be due to either the organically bound nitrogen in boles being

more readily mineralized, or the carbon in boles being less readily metabolized by microbial heterotrophs than in mineral soil.

An analysis of variance on square root transformed C : N ratios for live, standing dead, and down dead boles together, showed significant effects of species (F value = 27.31 Pr > F = 0.0001), decay class (F value = 25.28, Pr > F = 0.0001), the interaction of species and decay class (F value = 5.54, Pr > F = 0.0001), and length class (F value = 9.51, Pr >F = 0.0001).

Stand Level Coarse Woody Debris Quantification

The density (stems/ha), biomass (Mg/ha), and total nitrogen (Kg/ha) for the 50 Noland Divide plots is summarized by species in Tables 10 and 11. The majority of Fraser fir (70% of standing boles), 15% of standing red spruce, and 12% of standing yellow birch were dead. Overall, 44% of all standing stems were dead. This is well above the range of 5 - 36% of standing dead trees in the Northeast, as reported by Tritton and Siccama (1990). Distributions of live, standing dead, and down dead volume were highly variable between plots. Plots with a high number of standing dead stems tended to have a low number of down dead stems or the reverse situation. Live volume ranged from 146 m^3/ha to 839 m^3/ha. Standing dead volume ranged from 4.5 m^3/ha to 306.8 m^3/ha, and down dead volume ranged from 21.2 m^3/ha to 402.7 m^3/ha. The average down CWD volume of 156 m^3/ha falls well within the range measured by Nicholas and White (1985) of 71 - 251 m^3/ha in the GRSM spruce-fir forest. Down CWD was also higher, sometimes as much as three times higher, than the average down

Table 10. Density (stems/ha) of live, standing dead, and down dead stems for Fraser fir, red spruce, and yellow birch in the Noland Divide Watershed in GRSM. Data for live and standing dead are from Pauley et al. (1996), and are for stems ≥ 5.0 cm diameter at 1.37 m in height. Data for down dead are for boles ≥ 10 cm at the largest end.

Species	Density (stems/ha)		
	Live	Standing Dead	Down Dead
Fraser Fir	199 (49.9)*	469 (51.2)	422 (25.9)
Red Spruce	363 (22.1)	64 (7.7)	181 (18.2)
Yellow Birch	135 (20.7)	18 (3.7)	53 (10.3)

* Values in parentheses represent the standard error.

Table 11. Biomass (Mg/ha) and nitrogen (Kg/ha) pools for Fraser fir, red spruce, and yellow birch in the Noland Divide Watershed in GRSM.

Species	Live Boles	Standing Dead		Down Dead			Total
		I	II	I	II	III	
Fraser Fir							
Biomass (Mg/ha)	1.25	7.92	9.14	4.11	10.79	1.07	34.28
Nitrogen (Kg/ha)	0.94	9.19	12.90	4.36	15.20	3.03	45.62
Red Spruce							
Biomass (Mg/ha)	165.70	10.79	8.27	3.60	15.17	1.20	204.73
Nitrogen (Kg/ha)	72.9	9.39	8.93	3.38	16.39	3.14	114.13
Yellow Birch							
Biomass (Mg/ha)	34.50	1.59	0.48	2.24	0.806	0.048	39.66
Nitrogen (Kg/ha)	36.90	2.17	1.01	3.56	1.70	0.28	45.62
Total Biomass (Mg/ha)	201.45	20.3	17.89	9.95	26.77	2.32	278.67
Total Nitrogen (Kg/ha)	110.74	20.75	22.84	11.3	33.29	6.45	205.37

wood volume for eight other forests types measured in the GRSM (30 - 109 m^3/ha) (Nicholas 1984).

The majority (70%) of down dead red spruce and Fraser fir boles were in decay class II, and this may be due to several reasons. Boles may spend a significant amount of time in decay class II as compared to the other two decay classes, especially given the much higher rate of decay for decay class III boles (Table 6). Also, Fraser fir boles that were killed by the original BWA infestation in the late 1970's may have had sufficient time to decay to the second decay class. Eagar (1978) documented a large infestation with severe fir mortality in the Noland Divide Watershed in 1977. This corresponds well with the findings of Lambert et al. (1980), who found that in fir waves of New Hampshire, it took 15 - 20 years for the down bole cohort to move into the moderate decay stage, and it took approximately 40 years for fir boles to reach an advanced state of decay. Elevation, in the NDW study, had a significant effect on volume of standing CWD (F value = 9.96, Pr > F = 0.0028) and down (F value = 6.98, Pr > F = 0.0111) CWD for Fraser fir, indicating that there was significantly more dead Fraser fir at the higher elevations. Elevation was not significant for any other species. Aspect and slope were not significant for any species.

Diameter distributions tended to vary between decay classes. Average diameter for decay class I Fraser fir boles (15.1 cm ± 0.001) (average ± SE) was two times the average live diameter (7.4 cm ± 0.14); average diameters for decay class II and III were successively bigger, 19.0 cm ± 0.01, 23.3 cm ± 0.03, respectively. The largest live Fraser fir tree had a diameter of 34.5 cm, while the largest standing dead tree had a

diameter of 53.6 cm. The largest down dead bole had a diameter of 79 cm. One explanation of the uneven diameter distribution could be the more rapid disappearance of smaller boles, however this study did not find diameter to be a significant factor in decay rates. The more likely explanation is that the BWA infestation has killed the majority of mature Fraser fir trees. Prior to the BWA, Fraser fir trees typically attained diameters of at least 50 cm (Eagar 1978). The BWA continues to infest young trees once they develop bark fissures, which usually happens when they reach 4 cm in diameter at breast height (Eagar 1984). The same trend in diameter distribution held true for red spruce, although not quite as substantial. Average diameter for decay class I red spruce boles was 23.0 cm ± 0.02, while the average diameter for live trees was 24.8 cm ± 0.79. Average diameter for decay class II boles was 27.5 cm ± 0.01, and 34.1 cm ± 0.03 for decay class III boles. The majority of down boles were in the 0 - 15 and 15 - 30 cm diameter size class (Figure 7). Because volume increases geometrically with size, the majority of down volume was in the 15 - 30 and 30 - 45 cm diameter size class (Figure 8).

Total down dead wood biomass for all species was estimated to be 39 Mg/ha. Standing dead contributed an additional 38 Mg/ha to the pool for a total of 77 Mg/ha. This equates to approximately 28% of the total aboveground biomass (278 Mg/ha) which includes standing stems of 5 cm in diameter at breast height or greater and down boles of 10 cm or greater in diameter at the large end. A more accurate measure of aboveground biomass would include seedlings, saplings, and fine woody debris. The range of dead bole biomass among the different forest types reviewed by Harmon et al.

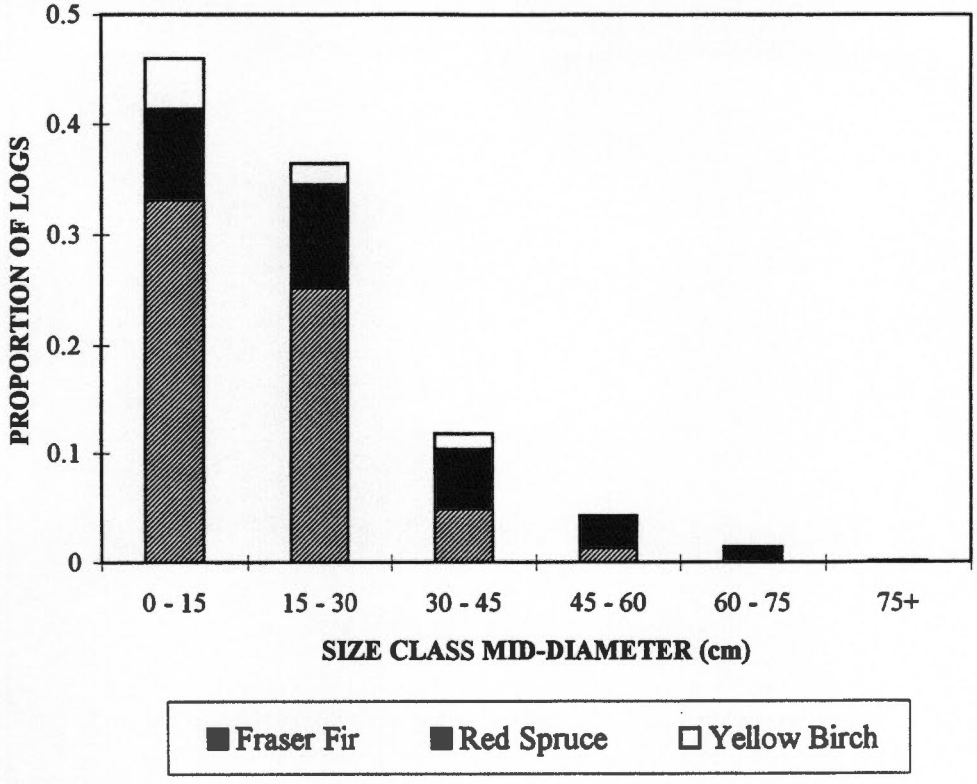

Figure 7. Diameter (cm) distributions for down coarse woody debris by species in the Noland Divide Watershed of GRSM.

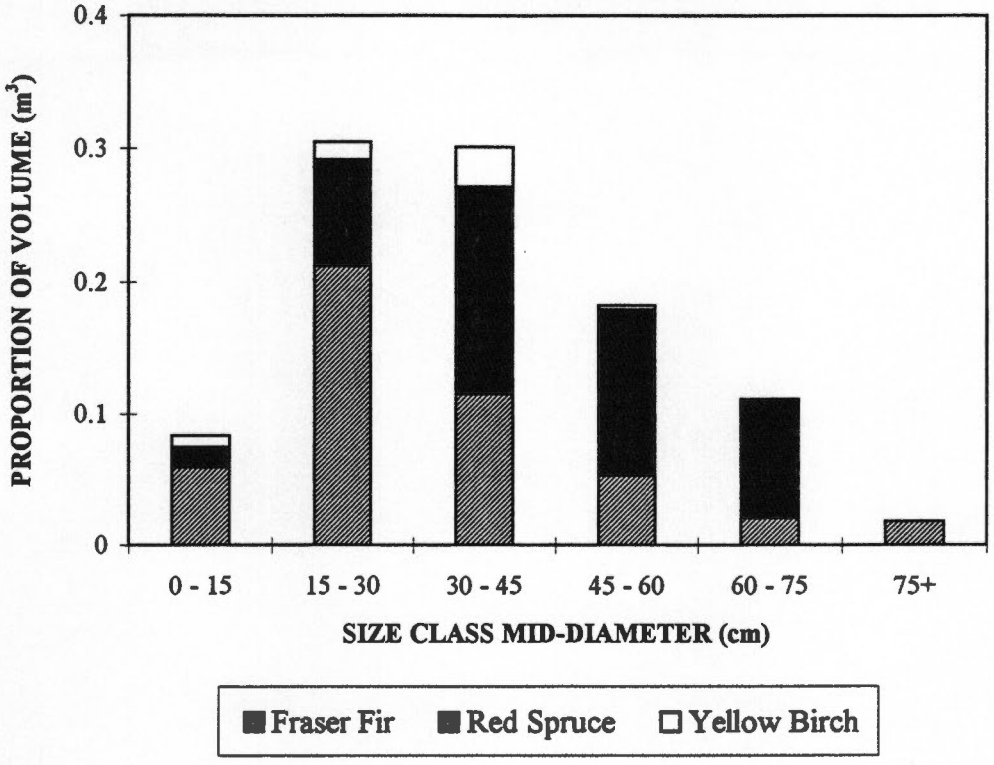

Figure 8. Volume (m^3) distributions for down coarse woody debris by species in the Noland Divide Watershed of GRSM.

(1986) was 10 - 511 Mg/ha. Ratios of dead wood biomass to total aboveground biomass range from 1.3 to 45.1 % (Harmon et al. 1986). Total biomass of dead red spruce and Fraser fir were similar (Table 11), despite the fact that there were much fewer spruce boles (Table 10). To include estimates for biomass and nitrogen content of foliage and live branches, values were taken from Pauley et al. (1996). Although the CWD in this ecosystem accounted for a small percentage of the total above-ground biomass, it accounted for 46% of the total nitrogen in the above-ground biomass (Table 11). If, however, foliage (159 Kg/ha) and branch wood (54 Kg/ha) total nitrogen is included, the percentage goes down to 23% of the total (419 Kg/ha) (Figure 9). For NDW, most of the nitrogen in CWD was held in decay class II standing and down boles (Figure10).

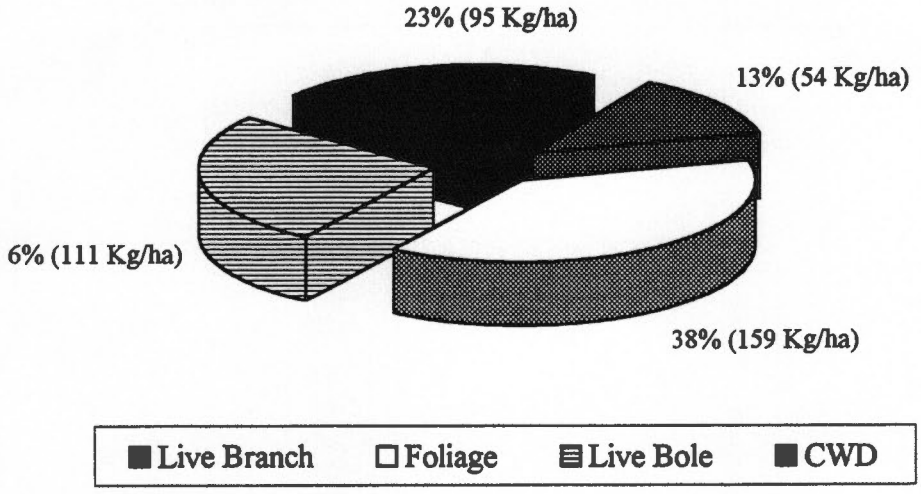

Figure 9. Total nitrogen (Kg/ha) pools in the Noland Divide Watershed of GRSM; all species considered together.

NOTE: Values for live branch and foliage are taken from Pauley et al. (1996).

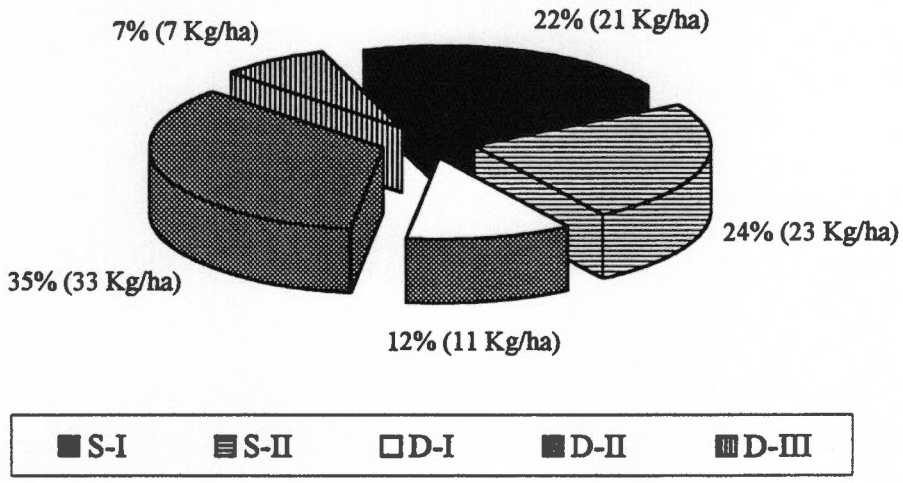

Figure 10. Coarse woody debris nitrogen (Kg/ha) pools in the Noland Divide Watershed of GRSM by decay class; all species considered together. S-I - standing dead decay class I; S-II - standing dead decay class II; D-I - down dead decay class I; D-II - down dead decay class II; D-III - down dead decay class III.

4. CONCLUSIONS

Coarse woody debris production varies spatially and temporally (Harmon et al. 1986). Often windthrow is a major source of coarse woody debris, especially in spruce-fir forests, due to shallow rooting and ridge top exposure. Gaps created by windthrow are often very unevenly distributed or clustered, but CWD created from competition or suppression can be fairly randomly distributed (Harmon et al. 1986). Episodic events or stand replacement disturbances, such as insect infestation, can create large amounts of dead wood and have a substantial impact on the nutrient cycling in the affected area. The BWA has killed the majority of mature Fraser fir in the Noland Divide Watershed, thereby creating large amounts of CWD and large canopy gaps.

Moisture content and percent nitrogen both increased significantly from live wood to highly decayed wood (decay class III). Density decreased significantly over decay classes. While net immobilization likely occurred in dead wood, this study can only claim a relative constancy of nitrogen content over decay class on a unit volume basis for Fraser fir, and a slight increase for red spruce boles. Yellow birch boles were more obviously acting as sinks for nitrogen, which may be of greater significance in ecosystems with a higher proportion of this species. On a unit area basis, however, the increase in nitrogen content, in all three species, may not be enough to offset the high volume losses observed in this study. The determination of nitrogen content accumulation depends on the temporal scale. Decay rates for Fraser fir and red spruce indicated that up to 100 years may be necessary for the complete disappearance of bole wood. Yellow birch took less time to decay, although only significantly for slightly

decayed boles (decay class I), and had a higher nitrogen content on a unit volume (g/cm^3) basis. Since microclimatic factors, i. e., temperature and moisture, play such a significant role in decay, the recent large openings in the canopy may increase forest floor temperatures, thereby increasing rates of decay (Hornsby et al. 1995).

An increase in nitrogen content in bole wood may affect the progression of nitrogen saturation that is thought to be occurring in mature southern Appalachians spruce-fir forests. Many studies conducted show negative effects on tree growth and nutritional status attributed to nitrogen saturation, subsequent soil acidification, and cation leaching (Agren and Bosatta 1988, Garten and Van Miegroet 1994). A knowledge of nitrogen accumulation processes within decaying wood is necessary to determine the extent to which these logs are offsetting nitrogen saturation. It may simply be that these boles are retaining their original nitrogen content, or that nitrogen from the bark is absorbed into the wood by fungal translocation. This would indicate that CWD would not significantly affect the nitrogen inputs and outputs in this watershed. If however, fungi and nitrogen fixers within the wood are absorbing nitrogen from the soil, or from throughfall, these boles could make a significant impact on how much and when nitrogen reaches soil or stream water. A substantial amount of evidence exists for the fixation of nitrogen in wood by bacteria (Larsen et al. 1978, Jurgensen et al. 1984, Hendrickson 1991), supporting the idea of external sources of nitrogen.

It has been suggested that higher rates of nitrogen inputs may increase rates of decomposition (Adams and Attiwill 1984). However, Prescott (1995) examined the influence of exogenous and endogenous nitrogen availability on rates of litter

decomposition and found little effect. She concluded that increased nitrogen availability, through fertilization or deposition, in the absence of changes in vegetation composition, will not alter rates of litter decomposition factors. Fog (1988) found that the addition of nitrogen to organic matter with a high C : N ratio had no long-term positive effect on decay rates, and often had negative effects. This might not be so surprising if it is the lignin:nitrogen ratio that controls rate of decomposition, as suggested by Means et al. (1992). Berg et al. (1998) found enhanced atmospheric nitrogen inputs to result in strong reductions in long-term decomposition. While he noted that enhanced nitrogen inputs may hasten decay early in the process, in the long-term, an aggravated carbon-limitation for microbial degradation may occur. Therefore, high nitrogen inputs in forests such as the southern Appalachian spruce-fir, may actually slow decomposition rates.

Reversal of nitrogen saturation in the southern Appalachian spruce-fir may be possible if there is a decrease in nitrogen deposition, which would help to decelerate the progression of nitrogen saturation (Aber et al. 1991). The disturbance in this ecosystem from the BWA has also created 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 could also become a sink for nitrogen, because plant nitrogen uptake depends on the vigor and successional stage of the forest. Rapidly growing younger trees have less nitrogen storage reserves, depend more on the soil for nitrogen, and are more effective at retaining nitrogen in plant biomass than older trees (Fenn et al. 1998).

In addition to its importance in the nutrient cycle, CWD plays other substantial roles in the ecosystem. It can provide substrate for seedling establishment, and can be a refuge for invertebrates, small mammals, and a variety of other organisms (Christy and Mack 1984, Harmon et al. 1986, McKenny and Kirkpatrick 1999). Harmon and Franklin (1989) found logs to be major seedbeds for trees in coastal *Picea sitchensis - Tsuga heterophylla* forests. CWD in the form of snags is essential to a number of cavity nesting birds. Twenty to 40% of the birds in a forest community can be dependent on cavities (Hagan and Grove 1999). Given the high number of nurse logs observed in the Noland Divide Watershed, it is highly likely that the CWD in this area is serving other such purposes.

This ecosystem is in a state of flux, and will be continually monitored for further change. This study is part of a larger project aimed at improving the understanding of nitrogen cycling within nitrogen saturated mature forests at the watershed scale. The inclusion of CWD in the research currently under way at Noland Divide makes it possible for future studies to predict the fate of the southern Appalachian spruce-fir ecosystem. When combined with the other components of the NDW study, such as deposition, tree uptake rates, nitrogen mineralization, and stand dynamics, a projection of long-term watershed response to high levels of nitrogen input can be constructed.

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APPENDICES

APPENDIX 1

The Nitrogen Cycle

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The Nitrogen Cycle

Nitrogen may be deposited to a watershed as nitrate (NO_3^-), ammonium (NH_4^+), or organic nitrogen in wet and dry deposition. Lovett (1992) found that dry deposition was dominated by nitrate. Additionally, plants may absorb gaseous nitrogen from the atmosphere (Stoddard 1994). The amount of nitrogen deposited may vary widely between ecosystems, and depends on its concentration in precipitation, the volume of water falling as precipitation, and the amount of nitrogen in dry deposition (Lindberg et al. 1986). Nitrogen deposition rates can range from less than 0.17 kg/ha/year in Alaska to more than 11.2 kg/ha/year in the northeastern U. S. (Stoddard 1994). High elevation systems, such as the spruce-fir forest, can have even higher deposition rates because of cloud/fog deposition. For example, the Integrated Forest Study (IFS) found nitrogen deposition rates of approximately 27 kg/ha/year in the southern Appalachian spruce-fir. This deposition was dominated by dry and cloud-water deposition (Lovett 1992).

The transformations deposited nitrogen goes through (e.g., by microbial action in soils and in plants) determine what forms and amounts of nitrogen eventually reach surface waters. Nitrogen assimilation, mineralization, nitrification, denitrification, and nitrogen fixation are important processes that affect the fate of nitrogen from atmospheric deposition (Stoddard 1994).

Nitrogen assimilation is the uptake and metabolic use of nitrogen by plants and soil microbes. The form of nitrogen used strongly affects the acidifying potential of nitrogen deposition. Ammonium uptake is an acidifying process:

$$NH_4^+ + R\text{-}OH \rightarrow R\text{-}NH_2 + H_2O + H^+$$

In contrast, the biological uptake of nitrate is an alkalinizing process:

$$R\text{-}OH + NO_3^- + H^+ \rightarrow R\text{-}NH_2 + 2O_2$$

Nitrate assimilation shows a greater seasonality than does ammonium assimilation. Even in systems with moderate nitrogen deposition, a pulse of nitrate in surface waters is often observed during the winter and early spring. Concentrations of ammonium in surface waters are rarely elevated at any season. Soil cation exchange; low mobility; and competition among vegetation, mycorrhizal roots, and nitrifiers all contribute to watershed ammonium retention (Stoddard 1994).

Nitrogen mineralization and immobilization. Nitrogen mineralization is the biological process by which assimilated nitrogen again becomes available to plants and microorganisms. This process begins with the release of NH_4^+ by heterotrophic microbes (Tate 1995, Schlesinger 1991). Once the ammonium is released from decomposing material (e.g., plant biomass, microbes) a variety of processes affect the concentration of NH_4^+. The ammonium can be assimilated by plants, or can be immobilized by microbes. Nitrogen immobilization is the assimilation of nitrogen by the microbes in the soil (Tate 1995, Schlesinger 1991). The ammonium can be nitrified to nitrate, which is in turn subject to assimilation, immobilization, leaching, and denitrification (Schlesinger 1991). Rates of nitrogen mineralization in the spruce-fir have been found to be very high (80 to 100 kg of N/ha/year) (Sasser and Binkley 1989).

Nitrification is the oxidation of ammonium to nitrate by bacteria and fungi. Like ammonium assimilation, nitrification is an acidifying process (Stoddard 1994).

$$NH_4^+ + 2O_2 \rightarrow NO_3^- + 2H^+ + H_2O$$

These oxidative reactions are catalyzed by two mutually exclusive groups of organisms, ammonium and nitrate oxidizers (Tate 1995).

Denitrification is the biological reduction of nitrogen oxides to nitrous oxide (N_2O) and/or dinitrogen (N_2) (Tate 1995). This process returns N_2 to the atmosphere. Mean values for loss of nitrogen by denitrification are typically less than 2 kg/ha/year in upland forests and grasslands. Denitrification usually proceeds most rapidly when organic carbon and nitrate are readily available. This process also requires anaerobic conditions, although anaerobic microsites in otherwise aerobic conditions can mediate the occurrence of this process (Schlesinger 1991). Denitrification is an alkalinizing process that consumes 1 mole of hydrogen for every mole of nitrogen denitrified (Stoddard 1994).

In *nitrogen fixation*, the nitrogen atom is reduced from its most oxidized state (N_2) to its most reduced form (NH_4^+). This process is catalyzed by bacteria living among the general soil microbial population or in symbiotic associations. In nutrient poor conditions, this process can play an important role. However, in mature forests with significant accumulations of organic matter such as the spruce-fir, this process can be secondary to the internal cycling of organic and inorganic nitrogen (Tate 1995).

APPENDIX 2

Nitrogen Saturation

APPENDIX 2

Nitrogen Saturation

Nitrogen saturation is reached when nitrogen inputs to a system are in excess of biotic demands (Aber et al. 1989). Nitrogen saturation is described as occurring in stages. Stage 0 represents a system which is nitrogen deficient, with little or no loss of NO_3^- regardless of inputs. Stage 1 systems show peaks of NO_3^- in stream waters in winter when demand is low. Stage 2 is marked by declining nitrogen retention and elevated NO_3^- concentrations in the stream throughout the year. Subtle negative effects begin to occur in this stage, but Stage 3 can result in major environmental impacts. In Stage 2, the annual nitrogen cycle is dominated by nitrogen loss through leaching and denitrification. Also, nitrification may be stimulated because of the buildup of ammonium in soils (Stoddard 1994). Stage 3 systems are a net source of nitrogen as NO_3^- to the aquatic system as outputs exceed inputs. The key characteristic of this stage is nitrogen losses in excess of deposition alone and the lack of any seasonal pattern in nitrate concentrations (Stoddard 1994).

Data from the Noland Divide Watershed (NDW) show levels of nitrate in soil and stream waters consistent with Stage 2 estimates (Nodvin et al. 1995). Additionally, the IFS found high-elevation spruce sites to be nitrogen saturated as indicated by consistently high soil solution nitrate levels. These sites are characterized by a combination of moderate to high atmospheric nitrogen deposition, large pools of soil nitrogen with low C : N ratios, high internal nitrogen mineralization rates, and moderate

to low tree uptake values. Uptake rates are generally lower in coniferous forests than in deciduous forests (Van Miegroet et al. 1992a).

Spruce-fir forests uptake rates rarely exceed 20 kg/ha/year, compared to 50 kg/ha/year in some hardwood forests (Van Miegroet et al. 1992a). Since nitrification is generally limited in systems that are nitrogen deficient, the production and leaching of nitrate suggest nitrogen availability in excess of biological retention capacity. Thus, nitrate leaching is a practical indicator of nitrogen saturation. For example, the IFS and a related study (Nodvin et al. 1995) in the southern Appalachian spruce-fir ecosystem found soil leaching fluxes and watershed export of NO_3-N to be approximately 15 kg/ha/year (Van Miegroet et al. 1992b). These high levels of nitrate may have serious forest health consequences. Increased leaching of NO_3-N may cause soil and water acidification. Losses of base cations (Ca^{2+} and Mg^{2+}) from soils and the immobilization of soil aluminum may contribute to nutritional imbalances and ultimately to forest decline as well as to water quality degradation (Agren and Bosatta 1988; Garten and Van Miegroet 1994). Due to the low levels of nutrients present in wood, the extra nitrogen in the NDW system may accelerate the decomposition of the CWD present (McNulty and Aber 1993; Harmon et al. 1982).

Consequences of nitrogen saturation on terrestrial systems. Given that soil nitrogen exists primarily as an anion, and calcium, magnesium, and potassium exist as cations in solution, the most immediate impact of high nitrate leaching rates is the accelerated leaching of these and other cations displaced from the exchange complex (Van Miegroet et al. 1992a). Calcium deficiencies may negatively affect root growth and

cambial growth. A decrease in photosynthesis:respiration ratios has been observed with decreasing growth and decreasing foliar calcium and magnesium amounts (Joslin et al. 1992). Calcium is a major component of permanent plant tissues, such as pectates in cell walls. It continues to accumulate in foliage up to the time of senescence. Calcium can be directly leached from foliage or from soil via acidic deposition (Van Miegroet et al. 1992a).

Another consequence of nitrogen saturation is soil acidification. This acidification can in turn mobilize inorganic aluminum. Joslin and Wolfe (1992) found that aluminum concentration was tightly related to nitrate concentration in soil solutions. They found aluminum concentrations at several points in their study to be high enough to cause root toxicity. Mobile aluminum may also interfere with cation uptake. This interference can occur even when aluminum concentrations are not at directly toxic levels (Joslin and Wolfe 1994). It should be noted that some studies of experimental nitrogen additions (Emmett et al. 1995, Gilliam et al. 1995) found little effect on tree health.

Consequences of nitrogen saturation on aquatic systems. Surface-water acidification and eutrophication may result from nitrogen loss from watersheds. Surface waters are termed acidic if their acid-neutralizing capacity (ANC) is less than zero (Stoddard 1994). A study conducted by Flum and Nodvin (1995) in the Great Smoky Mountains National Park found decreasing pH and ANC values with increasing elevation. ANC values were often less than zero. The decreasing values were attributed to the nitrogen saturation and acidic deposition occurring in the spruce-fir ecosystem

(Flum and Nodvin 1995). Eutrophication of bodies of water is the progression toward a state of eutrophy. Eutrophy is a condition of increased algal biomass and productivity, the presence of nuisance algal populations, and a decrease in oxygen availability for heterotrophic organisms. This process can occur naturally over a long period of time, but can be significantly accelerated by anthropogenic nutrient inputs (Stoddard 1994).

APPENDIX 3

The Southern Appalachian Spruce-Fir Ecosystem

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Location. Spruce-fir forests in the southern Appalachians occur in several disjunct mountain top locations at elevations greater than 1400 m including: Mount Rogers, VA; Grandfather Mountain, NC; Roan Mountain, TN; the Black Mountains, NC; the Balsam Mountains, NC; the Plott Balsam Mountains, NC; Long Hope Mountain, NC; and the Great Smoky Mountains, TN and NC. The spruce-fir forests of the Southeast occupy about 26,577 ha, with 74% located in the Great Smoky Mountains (Dull et al. 1988). These forests are considered a relict of montane spruce-fir forests that existed in an unbroken chain throughout the Appalachians during the Pleistocene glaciation (Oosting and Billing 1951). Apart from the Smokies, very few of the present-day spruce-fir areas include undisturbed old-growth stands (Pyle and Schafale 1988; Saunders 1979).

Floristics. This ecosystem, though rich in endemism and rare plants and animals, has an overstory dominated by three species (red spruce , (*Picea rubens* Sarg.) Fraser fir (*Abies fraseri* (Pursh) Poir.), and yellow birch (*Betula alleghaniensis* Britt.)). Overstory species distribution tends to follow an elevational gradient: spruce forest from 1370 to 1675 m, spruce-fir from 1675 to 1890 m, and fir forest above 1890 m (Whittaker 1956). Besides spruce and fir, yellow birch may be codominant at lower elevations and in moist, sheltered sites. Other overstory species may include: mountain-ash (*Sorbus americana* Marsh.), mountain maple (*Acer spicatum* Lam.), and pin cherry (*Prunus pensylvanica* L.f.). These trees can occupy suppressed or intermediate canopy positions. Major

understory species can include thornless blackberry (*Rubus canadensis* L.), witch hobble (*Viburnum alnifolium* Marsh.), Vaccinium sp., various ferns, other herbaceous species, a wide variety of bryophytes, and a substantial amount of spruce-fir regeneration (Crandall 1958). Species nomenclature follows Wofford (1989).

Stresses to the spruce-fir ecosystem. In the early 1900's spruce-fir in the southern Appalachians was reduced to a fraction of its former range by logging and associated fires (Korstain 1937, Saunders 1979). Areas such as the Balsam Mountains, the Plott Balsam Mountains, Roan Mountain, Mt. Rogers and Whitetop Mountain have little remaining old-growth spruce-fir. Currently, there are no active logging operations in the spruce-fir in the southern Appalachian region.

A second stressor to this region is the balsam woolly adelgid (BWA) (*Adelges piceae* Ratz.), introduced in the northern United States in the early 1900's. The BWA is a small wingless insect that is native to Caucasia and central Europe. It spread through Europe in the 1800's and was brought to Maine on nursery stock in 1908 (Kotinsky 1916). In the 1940's it was introduced from the northeastern U.S. on nursery stock during a replanting effort in the southern Appalachian region (Eagar 1984). The adelgid is known to survive cold temperature extremes of -25° to -35° C if the approach to these temperatures is gradual, making it a good candidate for survival in the South (White and Cogbill 1992). The adelgid feeds primarily in bark fissures of trees over 4 cm diameter at breast height (Eagar 1984). The insect inserts its feeding tube through the bark of the tree into cortical parenchyma cells and reduces sapwood conductance and produces water stress in infested fir. Death of a tree usually occurs in two to seven years

(Ammans and Speers 1965; Eagar 1984). Smaller, smooth barked trees are more resistant to attack but may suffer from crown infestation which is usually lethal only under a heavily infested overstory (Eagar 1984). This insect infestation has devastated populations of Fraser fir in the southern Appalachians. The recent plot-level sampling conducted at NDW reveals that most (78%) standing fir are dead (Pauley et al. 1996). A study by Nicholas et al. (1992a) found 48% of standing fir were dead at high elevations in the Smokies. Fortunately, a dense stand of healthy regeneration exists in the understory (Witter 1988; Nicholas et al. 1992b).

A third major stressor to this region is atmospheric deposition. Deposition occurs via three main pathways: (1) precipitation or wet deposition, where material is dissolved in rain or snow; (2) dry deposition, involving direct deposition of gases and particles (aerosols) onto surfaces; and (3) cloud-water deposition, involving material dissolved in cloud droplets, which is deposited when cloud or fog droplets are intercepted by vegetation (Mohnen 1992). The fluxes of atmospheric sulfur and nitrogen deposition to these systems are some of the highest measured in North America (Lindberg 1992, Lovett 1992, Shubzda et al. 1995). This high rate of deposition in the high elevations, the old growth status of these ecosystems (which translates to less nitrogen utilization), and the presence of a large pool of soil nitrogen may result in nitrogen availability in excess of biotic demand, or 'nitrogen saturation' (Nodvin et al., 1995).

Changing disturbance regimes. These various stresses, especially the invasion of the BWA, have resulted in changing disturbance regimes in the southern Appalachian

spruce-fir. White and Pickett (1985) define a disturbance as any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment. Disturbances can further be defined as either destructive events, or environmental fluctuations. The invasion of the BWA can be viewed as a destructive disturbance with catastrophic consequences, while acidic deposition, which is driving nitrogen saturation, might be seen as a forced environmental fluctuation. Disturbances in this ecosystem were historically dominated by wind-throw, debris slides and ice/snow damage (Nicholas et al. 1992b).

Despite wide differences in vegetation and types of disturbance, the average rate of forest disturbance (~1% per year) shows fairly little variation (Runkle 1985). Overstory trees in temperate systems can show an annual mortality rate of up to 5 to 7% (Harcombe 1987). Red spruce in the Great Smoky Mountains has an average mortality rate of 1% per year (Nicholas 1992). However, Fraser fir trees in the southern Appalachians currently have a mortality rate of 7% per year (Nicholas 1992). Mortality rates for balsam fir (*Abies balsamea* (L.) Mill.), which is found in northern Appalachian spruce-fir forests, over the age of 55 in a closed canopy are estimated to be around 4% per year, which may serve as a good average of Fraser fir mortality rates pre-BWA infestation (Sprugel 1984).

The BWA has created both large disturbance patches (in areas of pure fir stands) and small disturbed patches where fir is co-dominant with spruce. A result of this changing disturbance regime is the loss of fir as a canopy dominant, and a subsequent change in species composition. In fact, vegetation changes have been reported to

include a large increase in *Rubus canadensis* L. densities, which may impact woody species seedling survival (Pauley and Clebsch 1990, Nicholas et al. 1992a). If the current dense stand of regenerating fir reaches reproductive maturity (20 - 30 years of age) before BWA mortality, the Fraser fir may survive in this ecosystem, although in a more limited capacity (Nicholas et al. 1992a, Eagar 1984).

APPENDIX 4

Decomposition

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Decomposition

An important part of any nutrient cycle is the return of nutrients to the system via decomposition. Coarse woody debris goes through a number of physical as well as biological and chemical changes as it decays. Loss of mass can be caused by leaching, fragmentation, and the respiration of carbon by microbes (Harmon et al. 1986). This respiration causes density (g/cm^3) to decrease exponentially over time (Lambert et al. 1980, Foster and Lang 1982, Arthur and Fahey 1990). Boles begin to collapse and settle to the ground as they become unable to support their own weight, and some may be transported out of a system by down slope movement or by water in a stream (Harmon et al. 1986). In general, moisture content (based on dry weight) may increase from approximately 100% in living tissue to approximately 300% in highly decayed wood (Jurgensen et al. 1984, Hope 1987).

Over time, CWD becomes host to a wide variety of organisms which metabolize the wood. Decomposer organisms can be divided into two groups, microbes and invertebrates. Microbes can further be divided into those that live on cell contents (i.e., molds and staining fungi) and those that degrade cell wall components (i.e., bacteria, soft rots, brown rots, and white rots). Cellulose and lignin are both degraded by white-rot fungi, but soft-rot and brown-rot fungi can only degrade cellulose. The presence of chitin in CWD indicates that basidiomycetes are participating in the decay process. Insects primarily make up the invertebrate category, and they can attack the wood directly, such as carpenter ants reducing CWD to dust. They can also create cavities and

modify wood particles making the CWD more inviting to other microorganisms (Harmon et al. 1986).

The concentration of nutrient elements in CWD can also influence decay, and is generally an order of magnitude less than that of leaves. Angiosperms tend to have higher elemental concentrations than gymnosperms. As decay proceeds, the loss of carbon by respiration and processes such as nitrogen fixation, leaching, and fragmentation can all lead to higher nitrogen concentrations (Harmon et al. 1986). C : N ratios typically decrease from a high of 1000 in live material to approximately 100 in decayed material (MacMillan 1988, Foster and Lang 1982). Conversely, potassium tends to decrease throughout decay (Alban and Pastor 1993). Like nitrogen, phosphorous tends to increase, resulting in an N : P ratio of approximately 20 in the most advanced decay stage (Foster and Lang 1982, Arthur and Fahey 1990, Brown et al. 1996). Elemental concentration tends to be higher in bark than in wood (Harmon et al. 1986, Arthur and Fahey 1990).

Temperature, moisture, oxygen, carbon dioxide, substrate quality, and size can affect the rates and methods of decomposition. Hornsby et al. (1995) found that during the first two years of decomposition, temperature, and moisture together accounted for 95 - 99% of the variation in decomposition rates. Most wood-decaying fungi have a temperature optimum of 25-30°C. Extremely low and high moisture content can limit the activity of organisms. A range of 30-160% moisture content appears to support growth of basidiomycetes, but other types of fungi may be able to tolerate a moisture content up to 240% (Harmon et al. 1986). White-rot fungi are obligate aerobes and can

not effectively degrade waterlogged wood with a moisture content above 200% (Hedges et al 1988). Oxygen decreases and carbon dioxide increases as temperature and moisture increase, both of which are caused by increased respiration (Harmon et al. 1986).

Although analysis of sapwood and heartwood were combined in this study, CWD is a structurally and chemically heterogeneous substrate. The ratio of bark to sapwood to heartwood can vary greatly with species and size. Living versus dead tissue and vessel size influences the rate of fungal colonization. Gymnosperms have less living tissue and smaller water conducting vessels than angiosperms. Cell walls are composed largely of cellulose, the hemicelluloses, and lignin. A higher lignin content in conifer boles may be another reason for slower conifer decay, as lignin is the hardest for organisms to process. Wood extractives, such as terpenoids, flavonoids, tropolones, and stilbenes, appear to be a principal source of decay resistance in heartwood. These decay-inhibiting compounds can be inactivated by several mechanisms: deactivation by enzymes in the heartwood, self-oxidation, microbial degradation, and loss via leaching (Harmon et al. 1986).

A negative correlation is assumed to exist between size and decay rate (Harmon et al. 1986). This effect, however, is not always demonstrated in decomposition studies. Alban and Pastor (1993), for example, found no diameter effect on decomposition rates. Edmonds and Marra (1999) found that large diameter logs had a faster decomposition than small diameter logs. This discrepancy is often attributed to small sample size. The negative correlation, although not fully understood, is often attributed to the ratio of surface area to volume. For example, decomposers colonize leaves and small

branchwood within a period of days to months from the time they fall to the forest floor, but in tree boles, this decomposition process can take years.

APPENDIX 5

Volume Calculations

APPENDIX 5

Volume Calculations

The volume for downed boles at both study sites was calculated using the formula for a frustum of a cone:

$$V = (L/3)*(A_l + sqrt(A_l)(A_s) + A_s)$$

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. A more accurate measure of volume may be Newton's formula for the volume of a paraboloid:

$$V = L*((A_l + 4A_m + A_s)/6)$$

where A_m is the cross-sectional area of the log at middle (Bell et al. 1984). On an individual log basis Newton's formula has the smallest average deviation from the 'true' volume (± 13%), and the formula for a frustum of a cone has the greatest average deviation from the true volume (± 22%) (Harmon and Sexton 1996). Mid-diameters were only measured in the NDW plots, and for sake of consistency, the formula for a frustum of a cone was used on all logs in the study. Another alternative method for measuring the volume of a log is the Smalian's formula for a frustum of a paraboloid:

$$V = L*(A_l + A_s)/2$$

The volume of standing dead trees was calculated as the volume of a paraboloid:

$$V = ½*A_b*Ht$$

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. This formula may introduce error, because the cross sectional area of the paraboloid is actually the cross sectional area at breast height,

and not the cross sectional area at the base, as is assumed in this equation. Another possibility for snags is calculating the volume as the sum of a cylinder and a cone. It is assumed that the portion below diameter at breast height (DBH) is a cylinder and the portion above DBH is a cone:

$$V = {}^{1}/_{3} * A_b * (HT - 1.37) + A_b * 1.37$$

This formula, however, assumes a snag to be intact, and would underestimate the volume of a snag with a broken top.

APPENDIX 6

Decomposition Formulas

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Decomposition Formulas

Using the single exponential model (Equation 5) found in the Methods section, time to 50% or 95% decomposition can be calculated:

$$V_t = V_0 e^{-kt} \tag{5}$$

where V_t = volume at time t, V_0 = initial volume of material, k = the annual decay constant, t = time.

For a 50% decomposition (Equation7), $V_t = V_0(0.50) = V_0/2$:

$$V_0/2 = V_0 e^{-kt_{0.50}}$$

$$\ln(V_0/2) = \ln(V_0 e^{-kt_{0.50}})$$

$$\ln(V_0/2) = \ln V_0 + \ln e^{-kt_{0.50}}$$

$$\ln(V_0/2) = \ln V_0 - kt_{0.50}$$

$$kt_{0.50} = \ln V_0 - \ln(V_0/2)$$

$$kt_{0.50} = \ln(V_0/(V_0/2))$$

$$kt_{0.50} = \ln 2$$

$$t_{0.50} = (\ln 2)/k$$

$$t_{0.50} = 0.693/k \tag{7}$$

For a 95% decomposition (Equation 8), $V_t = V_0(0.05) = V_0/20$:

$$V_0/20 = V_0 e^{-kt_{0.95}}$$

$$\ln(V_0/20) = \ln(V_0 e^{-kt_{0.95}})$$

$$\ln(V_0/20) = \ln V_0 + \ln e^{-kt_{0.95}}$$

$$\ln(V_0/20) = \ln V_0 - kt_{0.95}$$

$$kt_{0.95} = \ln V_0 - \ln(V_0/20)$$

$$kt_{0.95} = \ln(V_0/(V_0/20))$$

$$kt_{0.95} = \ln 20$$

$$t_{0.95} = (\ln 20)/k$$

$$t_{0.95} = 3/k \qquad (8)$$

VITA

Anita Rose was born in Kingsport, Tennessee on July 12, 1970. She graduated from Sullivan Central High School in May 1988. She entered the University of Tennessee in August of 1988 and graduated with a Bachelor of Science in Biology with an emphasis in Ecology, and a Bachelor of Science in Botany in December 1992. She began working at the National Park Service Cooperative Park Studies Unit at the University of Tennessee in May of 1993, and in January of 1994 began working on a Master of Science degree on a part-time basis. She formally entered the Graduate Program in Ecology in May 1996. Starting in July of 1997 she became a graduate research assistant in what is now the Tennessee Valley Authority's Public Power Institute. She received her Master of Science in Ecology in August, 2000. She is currently living in Knoxville, Tennessee.