

A comparison of techniques for measuring density and concentrations of carbon and nitrogen in coarse woody debris at different stages of decay

I.F. Creed, K.L. Webster, and D.L. Morrison

Abstract: This research considered the relationship between the stage of decay and the concentration of nitrogen (N, %) and the ratio of carbon to N (C/N) in coarse woody debris. Density (g/cm^3) was used as an indicator of the stage of decay. In samples collected from the red spruce – Fraser fir (*Picea rubens* Sarg. – *Abies fraseri* (Pursh) Poir.) forest of the southern Appalachians, density explained up to 60% of the variation in N and C/N in coarse woody debris. The technique used to estimate density was important. Laboratory-based methods (including displacement and mensuration density) explained the greatest degree of the variation, with coefficients of determination (r^2) ranging from 0.39 to 0.59 ($p < 0.001$) for N and from 0.39 to 0.58 for C/N ($p < 0.001$). Field-based methods (including penetrometer and resistograph readings) explained a smaller but still significant degree of the variation, with r^2 ranging from 0.17 to 0.25 ($p < 0.01$) for N and from 0.14 to 0.26 for C/N ($p < 0.05$). Consideration of within-bole heterogeneity in density improved the explanation of variation in N and C/N for a single bole. Density provides a continuous indicator of stage of decay that is not bound by the artificiality of discrete decay classification systems. Furthermore, statistical models relating density to N and C/N provide a means of hind casting and (or) forecasting changes in N and C/N in coarse woody debris at different stages of decay.

Résumé : Cette étude porte sur la relation entre le stade de décomposition et la concentration d'azote (N) (%) ainsi que le rapport C/N dans les débris ligneux grossiers. Le poids spécifique (g/cm^3) a été utilisé comme indicateur pour le stade de décomposition. Le poids spécifique explique jusqu'à 60 % de la variation pour N et C/N dans les échantillons de débris ligneux grossiers prélevés dans la forêt d'épinette rouge et de sapin de Fraser (*Picea rubens* Sarg. – *Abies fraseri* (Pursh) Poir.) des Appalaches méridionales. La méthode utilisée pour mesurer le poids spécifique est importante. Les méthodes de laboratoire, incluant celles qui sont basées sur les dimensions ou le déplacement, expliquent une plus grande proportion de la variation avec des coefficients de détermination (r^2) allant de 0,39 à 0,59 ($p < 0,001$) pour N et de 0,39 à 0,58 pour C/N ($p < 0,001$). Les méthodes utilisées sur le terrain, incluant celles qui sont basées sur les valeurs obtenues avec le pénétromètre ou le résistographe, expliquent une plus faible proportion, quoique toujours significative, de la variation avec des r^2 allant de 0,17 à 0,25 ($p < 0,01$) pour N et de 0,14 à 0,26 pour C/N ($p < 0,05$). Le fait de tenir compte de l'hétérogénéité du poids spécifique dans les billes améliore l'explication de la variation dans la concentration de N et le rapport C/N pour chaque bille. Le poids spécifique constitue un indicateur continu du stade de décomposition qui n'est pas limité par le caractère artificiel des systèmes discontinus de classification de la décomposition. De plus, des modèles statistiques reliant le poids spécifique à la concentration de N et au rapport C/N procurent un moyen de prédire ou de reconstituer les variations dans la concentration de N et le rapport C/N dans les débris ligneux grossiers à différents stades de décomposition.

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Introduction

Coarse woody debris (CWD) is a significant component of forest ecosystems, often accounting for 10% to 20% of

the aboveground biomass in mature forests (Harmon et al. 1993; Brown 2002). Consideration of the role of decaying CWD in biogeochemical cycles is made difficult by the timescale over which these changes occur (i.e., years to decades). While recent studies have started to monitor these changes (e.g., Harmon 1992), the scientific community will have to wait decades to benefit from these results. An alternative is to predict the changing role of CWD as a function of the relationship between the stage of decay and the biogeochemical character of CWD. In this study, we develop models for red spruce (*Picea rubens* Sarg.) and Fraser fir (*Abies fraseri* (Pursh) Poir.) that relate stage of decay to

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the concentration of nitrogen (N, %) and the ratio of carbon to N (C/N) in CWD.

Decay classes have been established for estimating the stage of decay in CWD, including the three (established by Schenstrom (1929), as described in Stone et al. (1998)) and five (Fogel et al. 1973) class decay classification system. However, there are major disadvantages to using decay classes for estimating the stage of decay. First, decay class is a subjective measure, dependent on the interpretative skills of a specific researcher. Second, decay class is based on discrete rather than continuous measurements. Third, decay class is based on external (surface) rather than internal (sub-surface) characteristics. Fourth, decay class provides a mean rather than a range of values measured along a cross section of a bole of CWD.

Density provides an alternative means of predicting the state of decay. Techniques for estimating density range from "difficult" (involving laboratory-based methods) to "easier" (involving field-based methods). Displacement density (g/cm^3), while accurate, is perhaps the most difficult technique, as it requires collection and transport of intact samples to the laboratory, drying and weighing the samples to obtain dry mass, and then submersing carefully covered samples in water to obtain displacement volumes. Other methods for estimating density include mensuration density (g/cm^3), another laboratory-based method that measures the dry mass of samples in geometrically derived volumes; penetrometer reading (kg/cm^2), a field-based method that may provide a surrogate for density by measuring the resistance of the bole to outside pressure; and resistograph reading (cm^2/cm of diameter), a field-based method that may provide a surrogate for density by measuring resistance along a drilling axis. Density within CWD may be highly heterogeneous depending on the pattern of decomposition. For example, if decay proceeds from the exterior to the interior of a bole of CWD, the outer, more decayed region is less dense than the inner, less decayed region. Conversely, trees with "heart rot" will have a less dense interior and a denser exterior. A more accurate assessment of the stage of decay may be achieved if we consider not only the mean density of a bole but also the heterogeneity of density within the bole.

Changes in density may be related to changes in N and C concentration and C/N ratio in CWD. As CWD decays, density decreases as C is converted to carbon dioxide through decomposition processes. Some of the more recalcitrant portions remain and thus retain the structural integrity of the wood, resulting in a reduction in mass per unit volume (Harmon et al. 1986). The concentration of N may change if the rate of N loss differs from the rate of C loss. Previous studies have shown that decay class is related to changes in N concentration and C/N ratio in CWD (e.g., Graham and Cromack 1982; Means et al. 1992; Harmon and Sexton 1996; Krankina et al. 1999; Rose 2000; Creed et al. 2004). However, density may be better than decay class in predicting changes in N concentration and C/N ratio because it is an objective measure, it is measured on a continuous scale, and it is based on the entire bole and not just the surface characteristics of the bole.

The objectives of this study were (1) to compare four techniques for measuring density, including displacement, mensuration, penetrometer, and resistograph; and (2) to

compare the ability of each of these four techniques in measuring density to predict changes in N and C concentration and C/N ratio in CWD. The establishment of statistical models relating density with N and C concentration and C/N ratio will facilitate hind casting and (or) forecasting of changes in N and C concentration and C/N ratio in CWD at different stages of decay.

Materials and methods

Study area

The study was conducted in the Noland Divide watershed (NDW) ($35^{\circ}34'\text{N}$, $83^{\circ}29'\text{W}$), a small (17.4 ha) first-order drainage basin, in the red spruce – Fraser fir forest of the Great Smoky Mountains National Park in the southern Appalachians. The NDW has a climate that is classified as a cool, temperate rain forest (Shanks 1954). Based on the 25-year record of the nearest meteorological recording station (Newfound Gap), located about 100 m below the watershed outlet, the mean annual air temperature is 8.5°C , ranging from an average of -2°C in January to 18°C in July, with a frost-free period from May through September. Mean annual precipitation at this station is around 2300 mm, ranging from 1500 to 3000 mm in any given water year (April to March), with snow accounting for about 10% of the mean annual precipitation. The climatic conditions at high altitudes result in forests that experience a relatively short growing season (100–150 days), that are exposed to frequent cloud immersion, and that experience high-velocity winds (Johnson et al. 1992). Rounded summits and ridges characterize the topography, which ranges from 1680 m at the watershed outlet to 1920 m where it meets the Appalachian Trail. The soils are Inceptisols with spodic characteristics classified as Dystrochrepts or Haplumbrepts (McCracken et al. 1962; Van Miegroet et al. 1993) underlain by the Thunderhead Sandstone formation of the Great Smoky Group (Johnson et al. 1991). The forest that covers the NDW is dominated by red spruce and Fraser fir, with minor amounts of yellow birch (*Betula alleghaniensis* Britt.) (Smith and Nicholas 1998). The forests of the Great Smoky Mountains have been affected by acidic atmospheric pollution, exotic insect infestation by the balsam wooly adelgid (*Adelges piceae* Ratz.), and extreme weather, including hurricanes and ice storms. These disturbances have resulted in extensive Fraser fir mortality, with 70% of the standing Fraser fir dead (Rose 2000), creating a forest community structure with large variations in stand age, structure (gaps), and density of standing and fallen dead trees (Pauley and Clebsh 1990; Pauley et al. 1996).

CWD sampling strategy

CWD bole samples of red spruce and Fraser fir, representing the range of five decay classes (Fogel et al. 1973), were collected at NDW during the summers of 1998 and 1999 (Table 1). The criteria for collection of the CWD boles were (1) that the diameter of each bole be $\geq 10\text{ cm}$; (2) that there be a minimum of 15 boles in each of the five decay classes; and (3) that the boles be located over the range of elevations within which each species occurred (Creed et al. 2004). Each criterion was not always met, as the abundance and distribution of CWD within the watershed was not uniform.

Table 1. Number of samples collected for bole analyses of density, nitrogen, carbon, and the ratio of carbon to nitrogen.

Decay class	Measurement technique			
	Displacement	Mensuration	Penetrometer	Resistograph
Red spruce				
1	17	17	17 (0)	5 (5)
2	17	17	17 (0)	10 (10)
3	22	22	22 (13)	11 (11)
4	15	15	13 (15)	8 (5)
5	11	11	11 (10)	6 (2)
Total	82	82	82 (38)	40 (33)
Fraser fir				
1	5	5	5 (0)	3 (2)
2	15	15	15 (1)	12 (11)
3	15	15	15 (6)	14 (12)
4	15	15	15 (14)	12 (4)
5	15	15	15 (15)	12 (2)
Total	65	65	65 (36)	53 (31)

Note: The number in parentheses indicates the reduced number of samples used in regression analyses once samples at or below the detection limit of the instruments were removed.

Bole analyses

For each CWD bole, displacement density (g/cm^3), mensuration density (g/cm^3), penetrometer readings (kg/cm^2), and resistograph readings (cm^2/cm of diameter) were measured with discs (or cross sections) removed from the bole:

- (1) For displacement density discs ranging in length from 5 to 15 cm were removed from boles using a bow saw. Prior to sawing, the bole was covered in plastic wrap, and duct tape was placed around the circumference to be cut to minimize fragmentation of the bole during sawing. Immediately after sawing, the sections of CWD were enclosed in plastic wrap and duct tape, placed in plastic bags, and transported to the laboratory. In the laboratory, the CWD sections were oven-dried at 60°C to constant mass. The bark from the CWD sections was removed, and the CWD sections were then rewrapped, weighed, and submerged in a known volume of water to determine the displacement volume. Displacement density was then calculated as the ratio of the dry mass of the CWD section (g) to the displacement volume of the CWD sample (cm^3).
- (2) Mensuration density was calculated as the ratio of the dry mass of the CWD section (g) to the calculated volume of the CWD section (cm^3) using the following equation:

$$[1] \quad V = \pi \left[\left(\frac{d_{\max} + d_{\min}}{4} \right)^2 \times \left(\frac{l_{\max} + l_{\min}}{2} \right) \right]$$

where V (cm^3) is the calculated volume, $d_{\max}$ and $d_{\min}$ (cm) are the maximum and minimum diameters, respectively, and $l_{\max}$ and $l_{\min}$ (cm) are the maximum and the minimum lengths, respectively.

- (3) Penetrometer readings (kg/cm^2) were taken using a penetrometer (Model CL700, Soil Test, Inc., Evanston, Ill.). The penetrometer was pressed into the bole directed at its centre at the same point where the section was subsequently removed for laboratory analyses, and the pen-

etrometer reading was recorded when the top of the disc attachment was level with the surface of the bole.

- (4) Resistograph readings (cm^2/cm) were taken using the Resistograph F300 (Instrument Mechanic Labor, Inc., Kennesaw, Ga.). The Resistograph F300 is a microdrill that measures resistance along a drilling axis and records this resistance on a chart. The charts were scanned, converted into pixels, and used to calculate the area under the resistance line (cm^2), normalized for a specific bole by dividing the total area by the geometric diameter (cm) of the bole.

For determination of N and C in the CWD, cross sections were chipped using a wood chipper (Vermeer Manufacturing Co., Pella, Iowa), ground on a Thomas–Wiley Mill (Thomas Scientific, Swedesboro, N.J.) using a 40-mesh (with an opening size of 0.381 mm), and analyzed using an EA 1108 CHNS AutoAnalyzer (Carlo Erba, Milan, Italy). The concentrations ($\text{g}/100 \text{ g}$ or %) of N and C were determined by averaging the concentrations of two 5-mg subsamples.

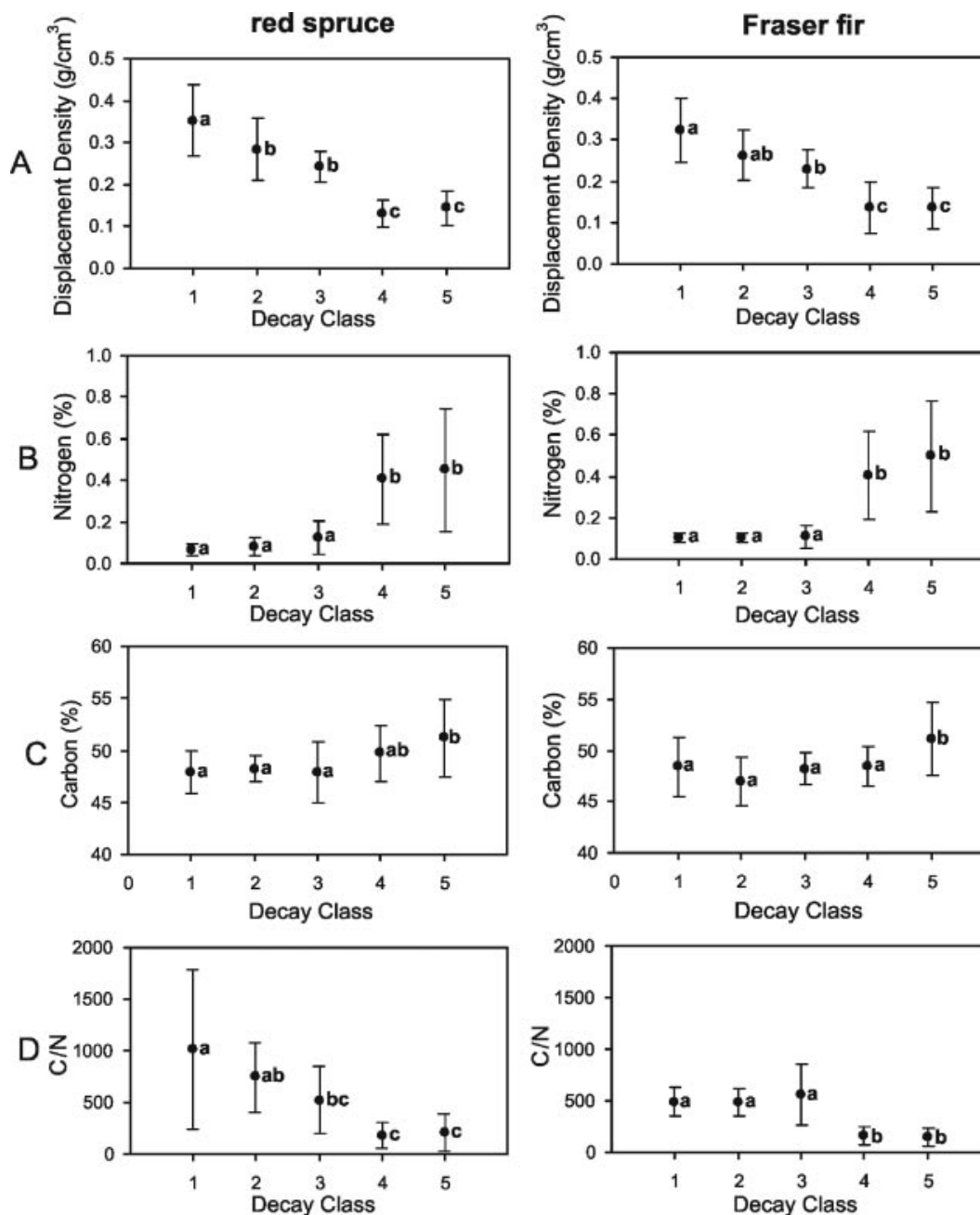
Within-bole analyses

Two boles, one red spruce and one Fraser fir, in intermediate stages of decay (i.e., decay class 3, based on the five-decay-class system), were divided into subsections based on constant readings on the resistograph charts and analyzed for physical properties (displacement density and resistograph readings) and for chemical properties (N, C, and C/N) using the methods previously described.

Data analysis

An analysis of variance with the Tukey method for multiple comparisons using Minitab version 11.2 (Minitab, Inc. 1996) was conducted to determine the significance ($p < 0.05$) of the differences in density, N and C concentration, and C/N ratio among decay classes, separately for each tree species. Prior to conducting the analysis of variance, the concentration data had to be transformed ($\arcsin(y^{0.5})$) to pass the test for normality. Linear regression analyses using

Fig. 1. The mean ($\pm$ standard deviation) for (A) displacement density (g/cm^3), (B) nitrogen (%), (C) carbon (%), and (D) the ratio of carbon to nitrogen for each decay class of coarse woody debris for red spruce and Fraser fir. Among decay classes, means with different letters are significantly different ($p < 0.05$) as determined by ANOVA using the Tukey method for pairwise mean comparisons.



Sigma Stat version 2 (SPSS Inc. 1997) were conducted to compare the performance of the different techniques for estimating density and to examine the ability of these techniques to predict N and C concentration and C/N ratio. Prior to conducting the linear regression analyses, the N and C concentration and C/N ratio data had to be transformed ($\log(y)$) to pass the test for normality.

Results and discussion

Decay class as a predictor of density, C, and N

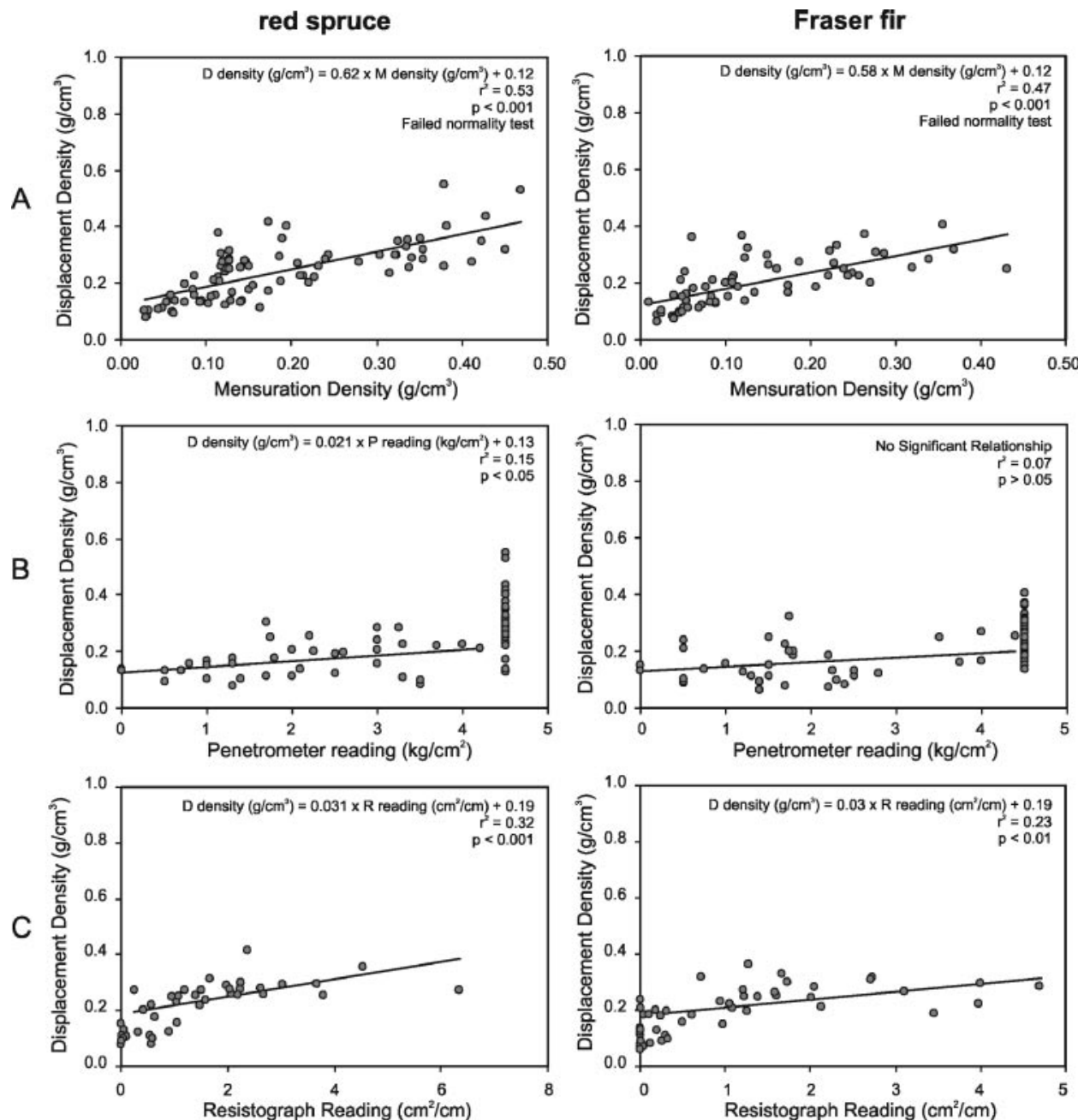
Decay class was a reasonable predictor of displacement density, N and C concentration, and C/N ratio of red spruce

and Fraser fir boles of CWD (Fig. 1). For example, for displacement density, there was a significant decrease from 0.353 to 0.144 g/cm^3 between decay class 1 and 5 for red spruce and from 0.324 to 0.135 g/cm^3 between decay class 1 and 5 for Fraser fir (Fig. 1A). However, the large degree of variability in displacement density highlights the limitations of decay class as a predictor of the stage of decay. Similar observations were made for N and C concentration and C/N ratio (Figs. 1B–1D).

Comparing techniques for estimating density

Mensuration density and the penetrometer and resistograph readings correlated significantly with displacement

Fig. 2. Relationship of (A) mensuration density (g/cm^3), (B) penetrometer reading (kg/cm^2), and (C) resistograph reading (cm^2/cm of diameter) to displacement density (g/cm^3) for red spruce and Fraser fir coarse woody debris.



density (Fig. 2). Mensuration density explained the largest degree of variation in displacement density, but consistently underestimated displacement density (i.e., where a slope of 1.00 would have been an accurate estimate, the slopes were 0.62 for red spruce and 0.58 for Fraser fir). However, for both red spruce and Fraser fir, the data were not normally distributed (Fig. 2A). Penetrometer readings explained the smallest degree of variation in displacement density (Fig. 2B), and resistograph readings explained an intermediate degree of variation in displacement density (Fig. 2C).

Despite the significant relationships between the alternative techniques and displacement density, none of the techniques could explain more than 53% of the variation in displacement density. Possible reasons include the precision,

accuracy, and the detection limits of the methods. The penetrometer and resistograph show problems related to detection limits when estimating density of CWD. The penetrometer has an upper detection limit of $4.50 \text{ kg}/\text{cm}^2$ and thus is unable to provide an accurate reading in CWD that has relatively high density. In contrast, the resistograph has a lower detection limit of about $0.20 \text{ cm}^2/\text{cm}$ of diameter for CWD in advanced stages of decay with some remaining structural integrity, and thus the resistograph is unable to provide a reading in CWD that has relatively low density. If we use the regression model that relates penetrometer readings to displacement density (Table 2), the penetrometer's upper detection limit is approximately $0.290 \text{ g}/\text{cm}^3$ for red spruce and $0.249 \text{ g}/\text{cm}^3$ for Fraser fir. Similarly, if we use

Table 2. Summary of linear regression analyses between different estimates of density and nitrogen and the ratio of carbon to nitrogen in red spruce and Fraser fir coarse woody debris.

	Red spruce				Fraser fir			
	Slope	Intercept	r^2	p	Slope	Intercept	r^2	p
Among bole								
Displacement density vs.								
N	-3.11	-0.16	0.59	<0.01	-3.26	-0.074	0.59	<0.01
C/N	3.06	1.86	0.57	<0.01	3.19	1.78	0.58	<0.01
Mensuration density vs.								
N	-2.16	-0.50	0.39	<0.01 ^a	-2.43	-0.40	0.47	<0.01
C/N	2.15	2.19	0.39	<0.01 ^a	2.39	2.09	0.46	<0.01
Penetrometer reading vs.								
N	-0.12	-0.36	0.17	<0.05	-0.14	-0.27	0.23	<0.05
C/N	0.11	2.07	0.14	<0.05	0.13	1.97	0.20	<0.01
Resistograph reading vs.								
Displacement density	0.031	0.19	0.32	<0.01	0.03	0.19	0.23	<0.01
N	-0.13	-0.69	0.25	<0.01	-0.12	-0.68	0.24	<0.01 ^b
C/N	0.12	2.35	0.25	<0.01	0.12	2.35	0.26	<0.01 ^b
Within bole								
Displacement density vs.								
N	-1.80 (-0.68)	-0.49 (-0.72)	0.87 (0.16)	<0.01 (ns)	-0.131	-0.32	0.80	<0.01
C/N	1.79 (0.70)	2.18 (2.40)	0.86 (0.17)	<0.01 (ns)	1.33	2.01	0.81	<0.01
Resistograph reading vs.								
Displacement density	0.08 (0.07)	0.11 (0.16)	0.51 (0.22)	<0.05 (ns)	0.12	0.14	0.68	<0.05
N	-0.13	-0.70	0.30	ns	-0.18	-0.47	0.69	<0.05
C/N	0.13	2.40	0.30	ns	0.18	2.17	0.68	<0.05

Note: Data for N concentration and C/N ratio were log transformed. For the within-bole analysis, for displacement density versus N, displacement density versus C/N, and resistograph reading versus displacement density, regression statistics are based on analysis of data with a single outlier removed, with analysis of all data in parentheses.

^aFailed test for constant variance.

^bFailed test for normality.

the regression model that relates resistograph readings to displacement density (Table 2), the resistograph's lower limit of detection is 0.168 g/cm³ for both red spruce and Fraser fir. Only data that were within the respective detection limits of the penetrometer and resistograph were included in the regression analyses (Table 2). A greater degree of the variation in displacement density may have been explained if the complete range in displacement density could have been estimated.

Density as a predictor of C and N

Displacement density was a reasonable predictor of N concentration and C/N ratio, but not of C concentration (Fig. 3). Compared with decay class, displacement density is better for predicting N concentration and C/N ratio, because (1) it explains a significant degree of the variation in N concentration and C/N ratio; and (2) it provides an objective measure on a continuous scale that integrates both the external and internal properties of each bole of CWD.

The alternative, less labor-intensive methods for estimating density were also related to N concentration and C/N ratio (Table 2). Mensuration density explained the largest degree of variation in N concentration and C/N ratio. Red spruce data failed to meet the assumption of regression analysis of constant variance. Closer examination of the red spruce data showed a threshold at about 0.25 g/cm³ mensuration density, below which there was a larger variation in N

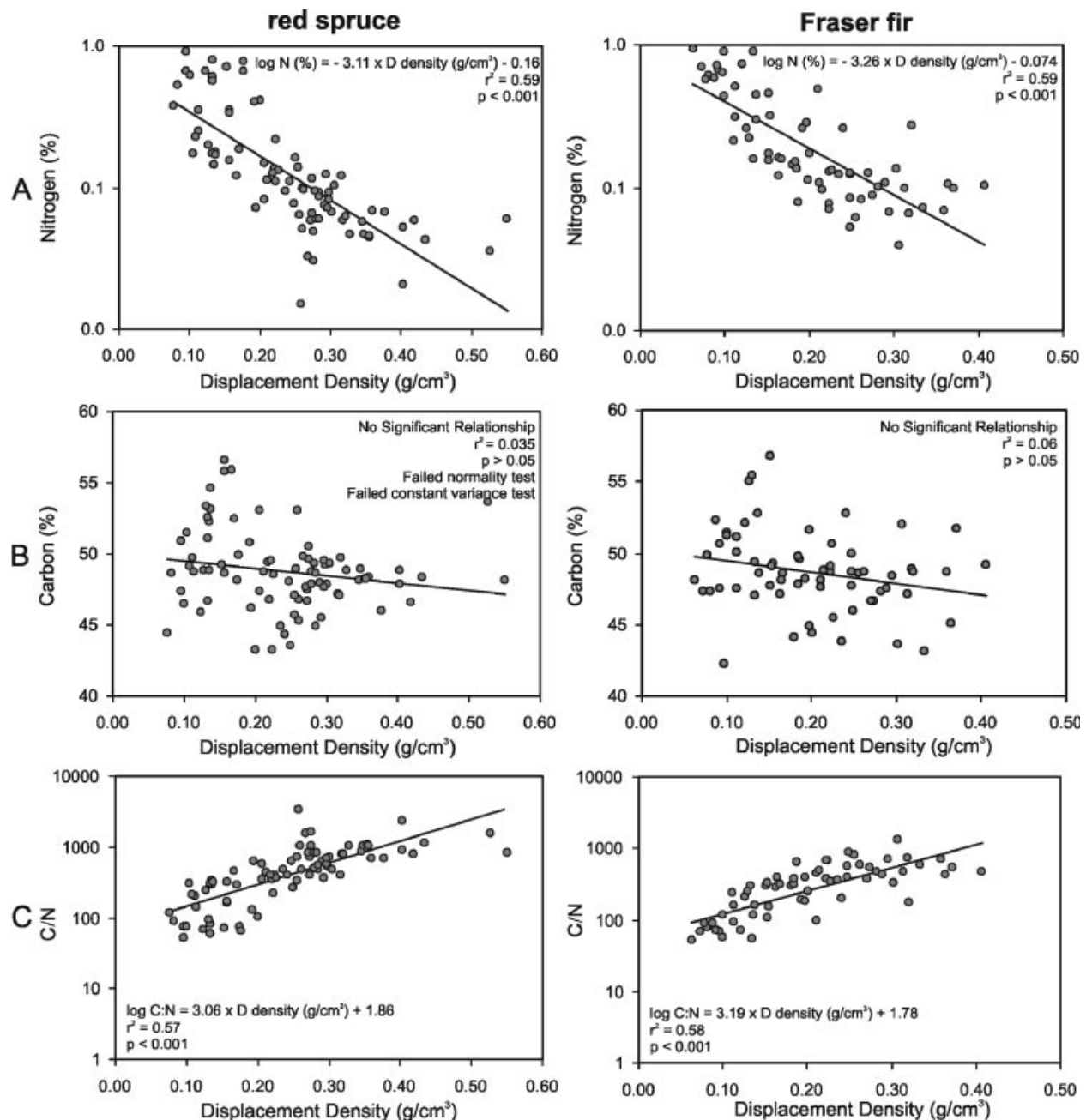
concentration and C/N ratio. This threshold probably marks the density at which red spruce boles lose structural integrity. Overall, 39% of the variation in N concentration and C/N ratio can be explained by mensuration density, but 44% of the variation in N concentration and 45% of the variation in C/N ratio are explained if the data below the threshold are removed. Fraser fir data met the assumption of constant variance, suggesting that this species has better structural integrity in the more advanced stages of decay (Table 2). No significant relationships between mensuration density and C concentration were observed (data not shown).

The two field-based techniques did not perform as well as the laboratory-based techniques. The penetrometer explained the smallest degree of variation in N concentration and C/N ratio. The resistograph explained a larger degree of the variation in N concentration and C/N ratio. While both of these field-based techniques explained a significant degree of the variation in N concentration and C/N ratio, neither performed as well as the laboratory-based techniques (Table 2). It is likely that the detection limits of these instruments, particularly the penetrometer, limit their use for estimating density, N and C concentration, and C/N ratio in CWD.

Comparing bole versus within-bole density

Bole density explained up to 60% of the variation in N concentration and C/N ratio within CWD. A possible source of the unexplained variation in N concentration and C/N ra-

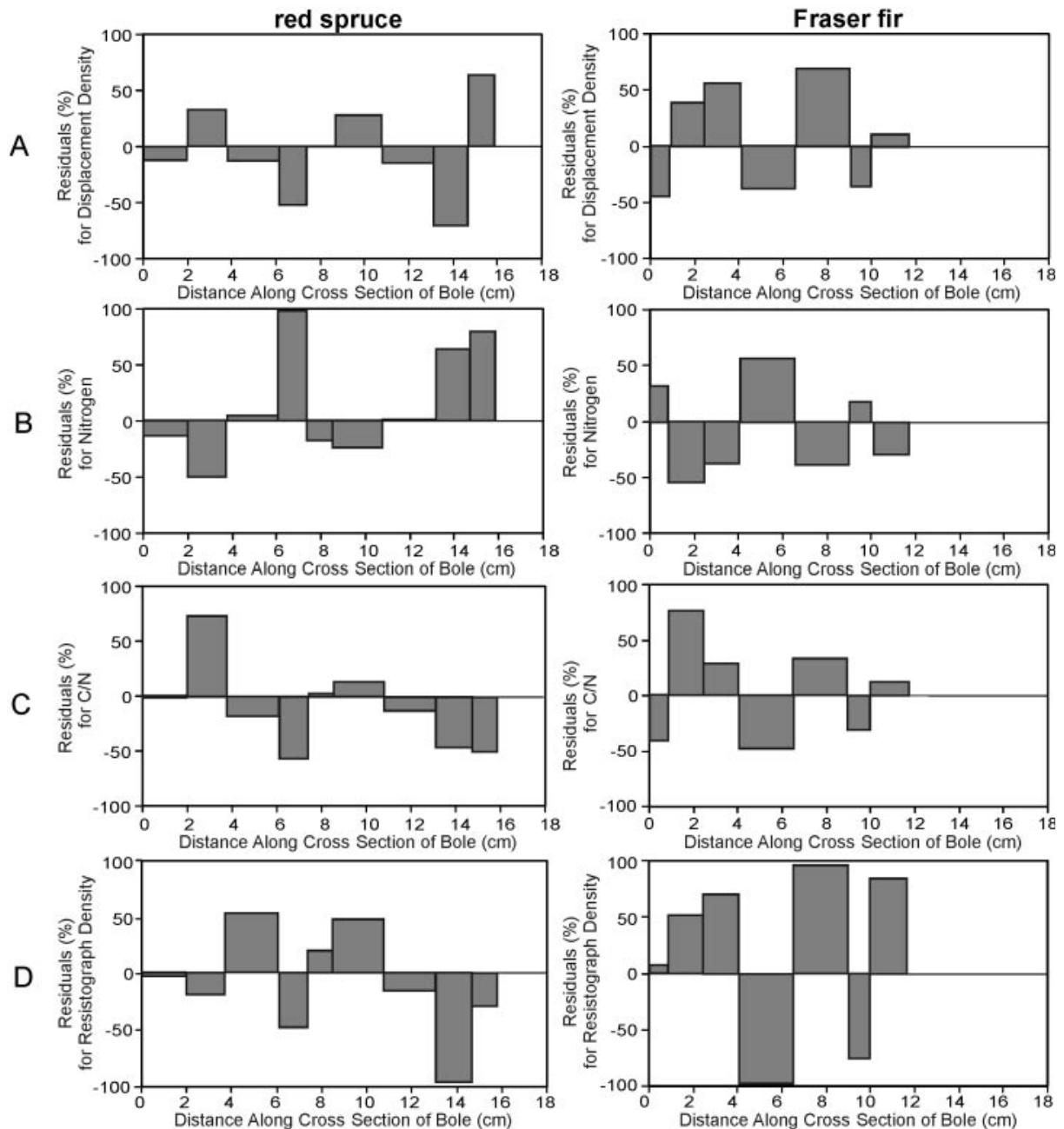
Fig. 3. Relationship of displacement density (g/cm^3) to (A) nitrogen (%), (B) carbon (%), and (C) the ratio of carbon to nitrogen for red spruce and Fraser fir coarse woody debris.



tion was the heterogeneity in density within the boles. There was substantial heterogeneity in physical and chemical properties within the boles (Fig. 4). For example, within a single red spruce bole, displacement density of subsections ranged from 0.079 to 0.453 g/cm^3 , compared with the weighted mean of 0.277 g/cm^3 . Similarly, for a single Fraser fir bole, displacement density of subsections ranged from 0.161 to 0.488 g/cm^3 , compared with the weighted mean of 0.291 g/cm^3 (Fig. 4A). A similar degree of heterogeneity was observed in N concentration and C/N ratio (Figs. 4B and 4C). There were no systematic patterns in the displacement density, N concentration, or C/N ratio from the exterior to the interior of the cross section of the bole.

Consideration of within-bole displacement density improved the prediction of N concentration and the C/N ratio (Table 2). For red spruce and Fraser fir, the proportion of variation explained in the relationships between displacement density and both N concentration and C/N ratio was greater in the within-bole analysis than in the among-bole analysis. Similarly, the proportion of variation explained in the relationships between resistograph density and both N concentration and C/N ratio was greater in the within-bole analysis than in the among-bole analysis. It is possible that if a better technique was used to define the within-bole homogeneous subsections, then a greater degree of variation in N concentration and C/N ratio would have been explained (i.e.,

Fig. 4. Deviations (%) between subsections and the weighted mean of the subsections of a single red spruce and Fraser fir bole of coarse woody debris (both boles were in decay class 3) for (A) displacement density (g/cm^3), (B) nitrogen (%), (C) the ratio of carbon to nitrogen, and (D) resistograph reading (cm^2/cm of diameter).



the relationship between resistograph readings and displacement density within the boles was not particularly strong; Fig. 4A versus 4D and Table 2).

Implications

There has been growing interest in the role of CWD in biogeochemical dynamics, including contributions to greenhouse gases (e.g., Wang et al. 2002; Bond-Lamberty et al. 2003) and surface water quality (e.g., Creed et al. 2004). To accurately assess the contribution of CWD in biogeochemical dynamics, we need to move away from the use of decay class and towards the use of density to estimate bio-

mass and N and (or) C contents. Brown (2002) recommended the development of a nondestructive portable tool for measuring the density of CWD. We found that while nondestructive techniques, such as penetrometer and resistograph, provided a rapid assessment of density in CWD, these techniques were not as accurate as destructive techniques, such as displacement or mensuration. Nondestructive portable tools for measuring density of CWD require the development and application of new technology (Brown 2002). Furthermore, we need to establish density versus N and C relationships in different forests and in different regions. Currie and Nadelhoffer (2002) found that N and C in CWD

may be affected by stand history (e.g., forest plantation on abandoned agricultural land), and Creed et al. (2004) found that N and C in CWD may be affected by stand pollution (e.g., N-limited versus N-saturated forests). In future research, we will integrate relationships between density and N and C contents into process models of biogeochemical dynamics, and we will use the model to characterize past and future contributions of CWD to the N budget of the Noland Divide watershed and other N-saturated watersheds.

Conclusions

Density is superior to decay class in predicting N concentration and C/N ratio, as it provides a more objective measure, based on both external and internal characteristics, and continuous measurements. Displacement density explained the largest degree of variation in N concentration and C/N ratio in boles, with values of 59% and 57% for red spruce and 59% and 58% for Fraser fir, respectively. The predictive ability improved when the heterogeneity in density and N and C concentration within the bole was considered. Other estimates of density did not perform as well as displacement density. The penetrometer offered an inexpensive, simple field-based method, which explained a small but significant degree of the variation in N concentration and C/N ratio in CWD: in red spruce, 17% of the variation in N concentration and 14% of the variation in C/N ratio were explained, and in Fraser fir, 23% of the variation in N concentration and 20% of the variation in C/N ratio were explained. The resistograph offered a more expensive, simple field-based method that explained a slightly larger degree of the variation in N concentration and C/N ratio in CWD: in red spruce, 25% of the variation in both N concentration and C/N ratio was explained, and in Fraser fir, 24% of the variation in N concentration and 26% of the variation C/N ratio were explained. Ultimately, the method that is selected for estimating density will be determined by a combination of factors, including budget, time, and the required precision and accuracy of the data.

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