Nitrogen content, decay rates, and decompositional dynamics of hollow versus solid hardwood logs in hardwood forests of Minnesota, U.S.A.

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Abstract: Decay rates and nutrient dynamics of hardwood logs have been quantified in only a few studies over the last two decades. This study quantified and compared the nitrogen dynamics, residence times, and decay rates of hollow and solid maple and oak logs in decay classes 1 through 4. Decay parameters were not correlated with log age but did correlate with decay class. Hollow logs generally had lower percent original density and higher %N than did solid logs in each decay class. The point of maximum net immobilization of N and initial net N mineralization occurred late in decay class 1 or early in decay class 2. Residence time of logs in each decay class was low in decay class 1 (2 years), high in decay class 2 (17 years), and low in decay classes 3 and 4 (3 and 4 years, respectively). Decay rates varied by decay class, being low in decay classes 1 and 2 and high in decay classes 3 and 4.

Résumé : Le taux de décomposition et la dynamique des nutriments de billes feuillues ont été quantifiés dans seulement quelques études au cours des deux dernières décades. Cette étude a permis de quantifier et de comparer la dynamique de l'azote, le temps de résidence et le taux de décomposition de billes d'érable et de chêne, creuses et solides, dans les classes de décomposition 1 à 4. Les paramètres de la décomposition n'étaient pas corrélés avec l'âge de la bille mais l'étaient avec la classe de décomposition. Généralement, les billes creuses avaient un pourcentage de la densité originale plus faible et un pourcentage d'azote plus élevé que les billes solides dans chaque classe de décomposition. Le point d'immobilisation nette maximum de N et de minéralisation nette initiale de N survient tard dans la classe de décomposition 1 ou tôt dans la classe de décomposition 2. Le temps de résidence des billes dans chaque classe de décomposition était court dans la classe de décomposition 1 (2 ans), élevé dans la classe de décomposition 2 (17 ans) et court dans les classes de décomposition 3 et 4 (respectivement 3 et 4 ans). Le taux de décomposition variait selon la classe de décomposition; il était faible dans les classes de décomposition 1 et 2 et élevé dans les classes de décomposition 3 et 4.

[Traduit par la Rédaction]

Introduction

Coarse woody debris (CWD) in forested ecosystems has been studied extensively in the past two decades, and decay rates and nutrient content of hardwood logs have been quantified for a variety of species in different systems (Harmon et al. 1986; Tyrell and Crow 1992; Schowalter et al. 1992). Many of these studies used the log decay-class system first outlined by Triska and Cromack (1979) to place the logs on a decay continuum. This system assigns down logs to one of five decay classes based on visual indicators. Decay class 1 refers to a freshly fallen log with both outer and inner bark intact. Decay class 2 logs are still firm, with some inner and possibly outer bark remaining and may show partial invertebrate and (or) fungal colonization into the sapwood. Decay class 3 generally is associated with extensive invertebrate and (or) fungal colonization and color change in sapwood and heartwood. Additionally, some fragmentation and bryophyte colonization of the log have generally occurred, but the shape of the log has not yet begun to change. Decay class 4 logs are often completely colonized by invertebrates, fungi, bryophytes, and (or) other vegetation. They are highly fragmented and have collapsed into a ellipsoidal shape. Decay class 5 logs are highly fragmented, highly collapsed, and generally sunken into the humus layer. Consequently, they are often difficult to detect.

The starting point for quantification and examination of litter decomposition and decay rates is the negative exponential decay function (Olsen 1963; Minderman 1968), which assumes that the decay rate (k) is constant. Therefore, logs would move through the decay-class continuum of Triska and Cromack (1979) at relatively constant rates. Although some proponents of the decay-class system acknowledge that rates of decay may change drastically with decay class (Harmon et al. 1986; Maser and Trappe 1984), no one has yet proposed an experimental method for quantifying residence times and rates of decay along this continuum.

The decay-class system also does not consider the effects

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Table 1. Study sites.

	Townsend Woods	Taylors Woods	Melcher Ridge	Sheldon Woods
Cover type	Maple	Maple	Oak	Oak
Latitude (N)	44°14′30″	45°11′40″	44°07′50″	43°41′15″
Longitude (W)	93°31′15″	93°29′00″	92°00′	91°32′50″
Soil	Deep silty loam, well drained	Deep silty loam, well drained	Sandy loam, rocky, well drained	Sandy loam, rocky, well drained
Landform	Prior Lake moraine	Faribault moraine	La Cresent Uplands	La Cresent Uplands
Elevation (ft)	920	1090	950	1000
Slope and aspect	16°, NW	0°, level	26°, NE	22°, E

Note: The mean growing season for all study sites is 158 days. The mean annual precipitation and temperature are the same for all sites at 29 in. and 44°F, respectively (1 ft = 0.3048 m; 1 in. = 2.54 cm; 1°F = 0.56°C).

of heart rot prior to tree death on the dynamics of decaying logs. Heart rot of live trees has not been reported in the published literature as a significant feature in old-growth Pacific Northwest conifer forests, where much of the CWD dynamics work has been completed. However, several studies have demonstrated that heart rot is very common in deciduous forests of the Midwest, particularly in old-growth forests (Hale et al.;[2] Berry 1969; Berry and Beaton 1972; Shigo 1986). Forest inventories of state forest lands in Minnesota often report an incidence of heart rot of 50% or greater in older hardwood stands (Minnesota Department of Natural Resources 1991). The level of rot prior to tree death may potentially alter the subsequent decay rates and patterns of nutrient flow in hollow logs as compared with solid.

The objectives of this study were to quantify and compare the nitrogen dynamics of hollow versus solid logs and to determine residence times and decay rates of hollow and solid logs for decay classes 1 through 4 in maple and oak hardwood forests of Minnesota.

Materials and methods

Field and laboratory methods

Study sites

Two old-growth oak forests in southeastern Minnesota and two old-growth maple forests in south-central Minnesota were sampled (Table 1). These four stands had been surveyed in a previous study (Hale et al.[2]) and were selected for this study, because they contained the volume and decay-class distribution of down logs necessary for collection of the desired numbers, sizes, and decay classes of both solid and hollow logs. The oak stands were both on steep southeast-facing slopes with well drained, rocky, sandy-loam soils. The maple stands were level to slightly rolling with well drained, silty-loam soils.

Cross sections

Cross sections of down logs were collected in each of the four stands (Table 2). Red oak (*Quercus rubra* L.) logs were collected in the two oak forests and sugar maple (*Acer saccharum* Marsh.) logs were collected in the two maple forests. Both hollow and solid log cross sections were collected from decay classes 1 through 3. In decay class 4, no hollow versus solid designations were made, since it was generally impossible to visually determine whether or not the log had been hollow. Decay class 5 (Triska and Cromack 1979) was not included in this study because of the fact that well decayed hardwood logs in these forests fragment extensively and are readily incorporated into the forest floor, making them extremely difficult to detect. A total of 83 log cross sections were collected (Table 2). Logs were selected such that the visual indicators for each decay class were as similar as possible to minimize expected variation. In general, the logs selected for sampling were solitary, indicating that they were single-tree gap makers and did not have the appearance of having stood as snags for a long period of time before falling. The cross sections collected ranged in diameter from 20 to 40 cm, with an average diameter of approximately 30 cm.

Table 2. Sampling distribution of log cross sections collected.

Decay class	1	2	3	4	Total
Maple logs					
Hollow	5	5	7	—	17
Solid	9	7	5	3	24
Oak logs					
Hollow	7	6	7	—	20
Solid	6	6	6	4	22
Total	27	24	25	7	83

Cross sections, 4–7 cm wide, were cut from each log with a chainsaw. Since the decay state of a given log can vary dramatically from one end to the other, the place on each log from which the cross section was collected varied such that the visual indicators for each decay class were as similar as possible to minimize expected variation. After the first cut, mylar transparencies were made outlining the shape, outer bark, inner bark, sapwood, heartwood, hollow areas and noting changes in wood color and texture. The second cut was then made, and the cross section was bagged and labeled.

Wood density

Wood density (g/100 cm^3) was determined for the combined sapwood–heartwood portion of each cross section. Because of the lack of inner and outer bark in advanced decay-state logs and losses during the cutting process, these portions were excluded from calculations of wood density.

Log cross sections were oven-dried at 60°C until they no longer lost weight, approximately 2 days, and then the final dry weights were recorded. Volumes were estimated to the nearest 5 cm^3 using water displacement by laying a large, thin piece of plastic (0.01 mil; 1 mil = 25.4 μm) loosely across the top of a large water-filled container. As the cross section was slowly pushed into the water the loose plastic was forced around the irregular surface of the wood. The amount of water displaced flowed out of a drain at the

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[2] Hale, C.M., Pastor, J., and Rusterholz, K. Comparison of structural and compositional characteristics in old-growth versus mature hardwood forests of Minnesota, USA. Unpublished data.

Table 3. Regression functions for determining the maximum %N, maximum % original density and fractional decay class at the point of maximum immobilization and initial mineralization in decaying oak and maple logs (Aber and Melillo 1982).

Regression	Equation
Percent original density (Y_d) as a function of %N (X_n)	$Y_d = b_1 + a_1X_n$
Maximum %N at initial mineralization	$X_{nmax} = b_1/-2a_1$
Percent original density at X_{nmax}	$Y_{dmax} = b_1/2$
Decay class (Y_s) as a function of %N (X_n)	$Y_s = b_2 + a_2X_n$
Fractional decay class at X_{nmax}	$Y_{smax} = b_2 + a_2X_{nmax}$
Decay class (Y_s) as a function of percent original density (X_d)	$Y_s = b_3 + a_3X_d$
Fractional decay class at Y_{dmax}	$Y_{smax} = b_3 + a_3Y_{dmax}$

top of the container and was collected and measured in a graduated cylinder.

Chemical analysis

The inner and outer bark of each cross section was removed. The remaining portion of the cross sections, sapwood and heartwood, were chipped to approximately 0.5 × 2 cm size pieces using a spiked roller and (or) a hammermill (Forest Products Laboratory, Michigan Technological University, Houghton). Approximately one third of the chips were ground to 2-mm particles using a Wiley Mill. A 2–3 cm^3 subsample of the 2-mm particles was then taken for the final grinding stage using a Cyclone mill, producing dust-like particles needed for complete combustion. Three 20–30 mg samples of this final product were used to determine %N. Nitrogen concentration for each of the final samples was determined using the LECO CHN-800 elemental analyzer.

Log ages

The age of each log was estimated by dating the most recent detectable release from suppression in three nearby saplings. Saplings were selected that appeared to have had the highest probability of responding to any canopy gap formed when the log fell to the forest floor (McCune and Henckel 1993). So that we could have confidence that the suppression-release event in the saplings corresponded to the death of the log being sampled, the logs selected were generally solitary indicating that they had been single-tree gap makers.

Two increment cores were collected from each of three saplings nearest the log. If appropriate saplings did not exist, then seedlings that may have been suppressed or germinated in the gap were harvested and their cross sections collected. Increment cores were mounted on grooved boards. Both the cores and cross sections were sanded with 80-, 120-, and 600-grain sandpaper, which provided excellent readability.

Suppression-release events were noted preliminarily by visual inspection of the growth-ring patterns of each sapling core or cross section. Apparent releases were evaluated by comparing the width of rings before and after the apparent release event (L. Frelich, Department of Forestry, College of Natural Resources, University of Minnesota, St. Paul, personal communication). If the rings following the apparent release event exhibited sufficient increase in width as compared with the rings preceding the apparent release event, then it was considered a true release. Four different criteria were used to determine a sufficient increase in ring width to demarcate a true release event. The most rigorous criterion required a doubling of the mean width of the 10 rings following the apparent release compared with the mean width of the 10 rings preceding the apparent release. The three additional criteria used to evaluate each apparent release included 10 rings – 50% width increase, 5 rings – 100% increase, and 5 rings – 50% increase. An apparent release was considered to be a true release if it met at least one of the above criteria. Measurements were made with a 10-power dissecting microscope and digital micrometer to the nearest 0.01 mm.

Log age was assumed to be equal to the number of years since release. In cases where there was some discrepancy of release dates between the increment cores for a given log, the core(s) that met the most rigorous suppression release criterion were used to estimate the age of the log. If all of the sapling cores or cross sections met the same selection criterion, then the oldest date was used. If the releases shown by the saplings were gradual, then an average release date was taken to be the age of the log.

Statistical and mathematical methods

Immobilization or mineralization

Aber and Melillo (1982) provide methods for describing N immobilization and mineralization patterns in hardwood leaf litter from regressions of %N against percentage of original biomass remaining. These methods are equally useful in describing similar patterns in woody litter. In this study, percent original density in each decay class was substituted for Aber and Melillo's percentage of original biomass remaining. In each of the four groups of logs being analyzed (maple hollow, maple solid, oak hollow, and oak solid), the original density was taken to be the highest density of undecayed logs measured in each respective group.

Regressions of percent original density as a function of %N (Table 3) were calculated for each group (SYSTAT, Inc. 1990). From the parameters of these regressions, the %N (X_{nmax}) and percent original density (Y_{dmax}) at the point of maximum N immobilization and initial N mineralization were determined (Aber and Melillo 1982). Regressions of decay class as a function of %N and percent original density provide two equations with which to calculate the fractional decay class (Y_{smax}) at which maximum N immobilization and initial N mineralization occur (Table 3).

Residence time

The residence time in this study refers to the median amount of time a log stays in a particular decay class. The median residence time (years/stage) for a given decay class is defined as the median age of that decay class minus the median age of the previous decay class. Median ages were used, as opposed to mean ages, because of the non-normal distribution of log age data. While the departures from normality were not significant enough to seriously violate assumptions of statistical tests, when mean age is used to calculated residence time, decay class 4 oak logs have a negative residence time, which is clearly impossible.

Where residence time is used to calculate decay rates (below) the log age data from both hollow and solid, oak and maple logs were pooled to prevent the problem of a negative residence time in decay class 4. This was necessary because of the small sample size in decay class 4 (Table 2) and high variability of log age data in both decay classes 3 and 4 (Table 6).

Table 4. Ranges and means of density, %N, and total N for hollow and solid, oak and maple logs in each decay class.

		Decay class			
		1	2	3	4
Maple logs					
Density (g/100 cm^3)					
Hollow	Range	29–47	32–41	18–48	—
	Mean	39.9	36	32.8	—
Solid	Range	27–68	33–60	15–46	12-23
	Mean	47.4	45.2	32.4	18.2
%N					
Hollow	Range	0.45–0.55	0.48–0.60	0.50–0.74	—
	Mean	0.51	0.53*	0.57	—
Solid	Range	0.38–0.56	0.45–0.53	0.47–0.71	0.53-0.82
	Mean	0.47	0.48*	0.57	0.65
Total N (g/100 cm^3)					
Hollow	Range	0.15–0.26	0.16–0.35	0.13–0.24	—
	Mean	0.20	0.23	0.18	—
Solid	Range	0.13–0.29	0.18–0.27	0.11–0.22	0.08-0.15
	Mean	0.21	0.21	0.18	0.12
Oak logs					
Density (g/100 cm^3)					
Hollow	Range	37–61	42–57	24–54	—
	Mean	46.3*	46.8†	38.9	—
Solid	Range	53–66	46–54	25–45	12-27
	Mean	61.7*	53.7†	40.5	23.4
%N					
Hollow	Range	0.42–0.55	0.39–0.54	0.45–0.62	—
	Mean	0.49*	0.47	0.55*	—
Solid	Range	0.33–0.52	0.42–0.50	0.45–0.57	0.52-0.64
	Mean	0.42*	0.45	0.48*	0.55
Total N (g/100 cm^3)					
Hollow	Range	0.16–0.31	0.21–0.26	0.16–0.25	—
	Mean	0.23	0.22	0.21	—
Solid	Range	0.21–0.35	0.20–0.26	0.14–0.26	0.08-0.18
	Mean	0.25	0.24	0.19	0.16

*Hollow versus solid significant at 0.05 level.
†Hollow versus solid significant at 0.10 level.

Results

Wood density

Maple log densities (g/100 cm^3) ranged from 68 to 15 in solid logs and from 48 to 18 in hollow logs (Table 4). Oak log densities ranged from 66 to 25 in solid logs and from 61 to 24 in hollow logs (Table 4). There were no statistically significant correlations between log age and density or ln(density) in any of the four sample groups or overall (Fig. 1). However, mean densities decreased in relation to decay class for both maple and oak logs, with the exception of oak hollow logs, where density remained the same from decay class 1 to decay class 2 (Fig. 1). Mean densities generally decreased moderately from decay class 1 to decay class 2 and then more dramatically from decay class 2 through decay classes 3 and 4.

For both maple and oak logs, the mean density of hollow logs was lower than solid logs in decay class 1. In maple logs, this difference was maintained through decay class 2. However, by decay class 3 the densities of hollow and solid maple logs had converged. For oak logs, the mean densities converged in decay class 2 (Table 4, Fig. 1).

Percent nitrogen

Maple %N values ranged from 0.38 to 0.71 in solid logs and from 0.45 to 0.74 in hollow logs (Table 4). Oak %N values ranged from 0.33 to 0.57 in solid logs and from 0.39 to 0.62 in hollow logs (Table 4). Percent N was not strongly correlated to increasing log age for either maple or oak logs (Fig. 2). In relation to decay class, mean %N stayed nearly the same through decay classes 1 and 2 and then increased in decay classes 3 and 4 (Table 4, Fig. 2).

Mean %N values were higher for hollow logs as compared with solid logs in maple decay classes 1 and 2 but converged in decay class 3. For oak logs, %N values were higher for hollow logs as compared with solid logs in decay classes 1 and 3 but were the same in decay class 2 (Table 4, Fig. 2).

Fig. 1. Wood density and ln (wood density) against log age and mean wood density by decay class for hollow and solid, oak and maple logs. N = 17 and 24 for hollow and solid maple logs, respectively; N = 20 and 22 for hollow and solid oak logs, respectively. For both species decay class 4 logs were included in the solid log data set. *, difference of hollow versus solid ($p < 0.05$).

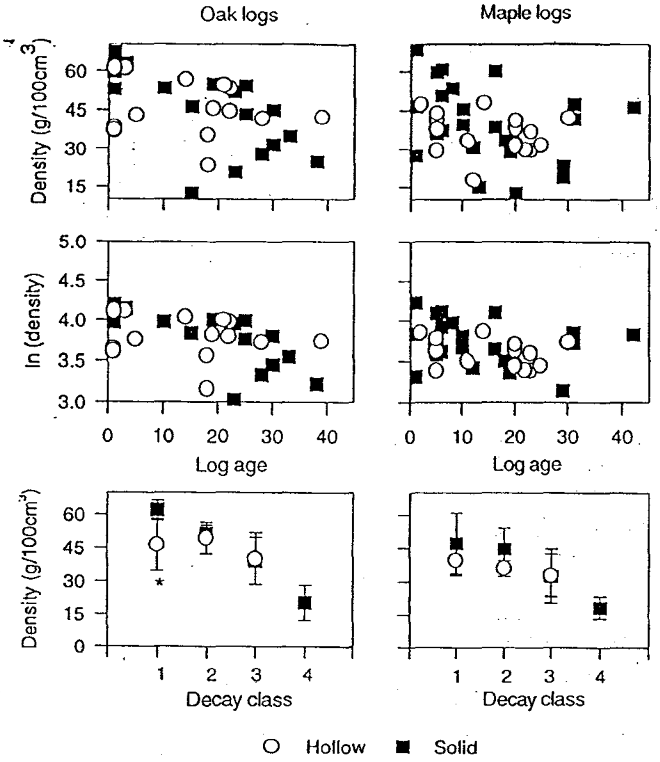
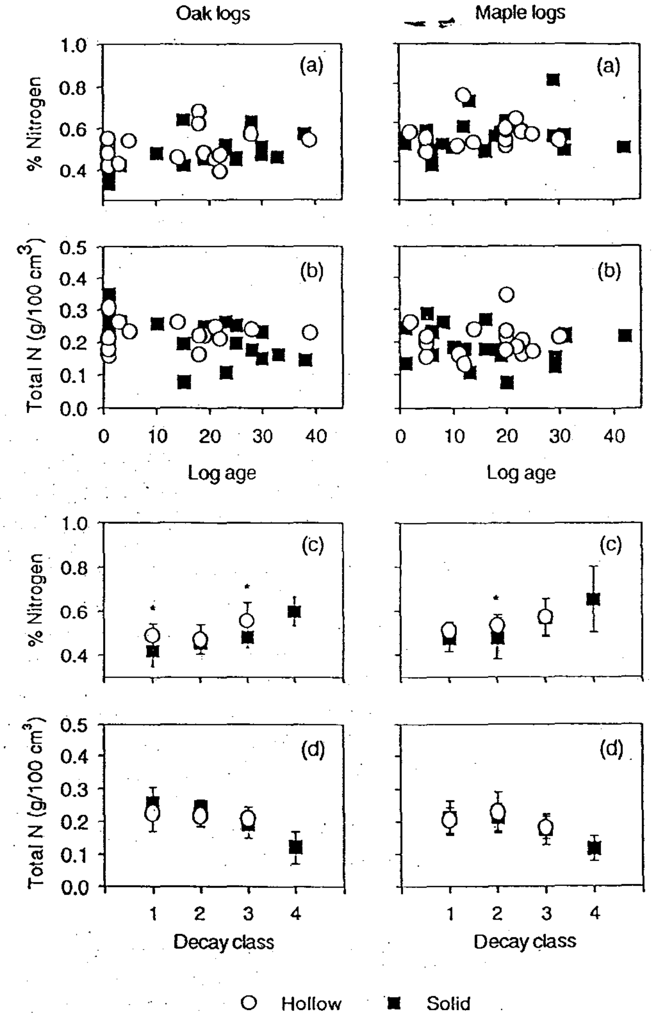


Fig. 2. Percent N (a) and total N (b) plotted against log age and mean %N (c) and mean total N (d) plotted against decay class for hollow and solid, oak and maple logs. N = 17 and 24 for hollow and solid maple logs, respectively; N = 20 and 22 for hollow and solid oak logs, respectively. For both species, decay class 4 logs were included in the solid log data set. *, difference of hollow versus solid ($p < 0.05$).



Total nitrogen

Total N (g/100 cm^3) was not significantly correlated with age for either maple or oak logs (Fig. 2). However, total N exhibited a distinctive pattern in relation to decay class for both species (Table 4, Fig. 2). Total N increased slightly from decay class 1 to decay class 2 for maple logs and stayed the same from decay class 1 to 2 for oak logs. Through decay classes 3 and 4 total N decreased for both species of logs. This pattern suggests that net N immobilization is occurring primarily in decay class 1 and net N mineralization begins early in decay class 2 and continues through decay class 4.

Immobilization and mineralization

The results of the regressions and parameter calculations outlined in Table 3 are listed in Table 5. All four regressions of percent original density as a function of %N were significant ($p \leq 0.004$). However, for the regressions of decay class as a function of %N and percent original density only the regressions of the solid logs were significant at the 0.01 level or greater (Fig. 3). This was due in large part to the higher variability seen in the hollow log data sets overall and the lack of hollow logs and small sample size in decay class 4.

For both maple and oak, hollow and solid logs had significantly different regression equations describing the relationship between %N and percent original density (Table 5). The slopes of hollow versus solid regressions for maple logs were not statistically different, indicating that the rate of change in %N in relation to percent original density is the same for both hollow and solid logs. However, the Y intercepts were higher for hollow logs than for solid logs ($p \leq 0.01$) (Table 5). This result indicates that hollow maple logs have a higher mean %N value at any given percent original density than do solid maple logs (Fig. 3). Both the slopes and the Y intercepts were higher for oak solid logs than for oak hollow logs ($p \leq 0.005$) (Table 5). This result indicates that oak solid logs not only start at a higher %N than oak hollow logs but also increase the %N levels more rapidly as percent original density decreases and the logs move through the decay-class continuum (Fig. 3). Nitrogen accumulation in relation to percent original density is clearly different in hollow logs as compared with solid logs. More detailed

Fig. 3. Data points and regression lines for plots of percent original density remaining as a function of %N and fractional decay class as a function of %N or percent original density (Table 3) for hollow and solid, oak and maple logs. $N = 17$ and 24 for hollow and solid maple logs, respectively; $N = 20$ and 22 for hollow and solid oak logs, respectively. For both species, decay class 4 logs were included in the solid log data set. *, p value for the regression of solid logs, **, p value for the regression of hollow logs. If no p value is shown then there was no significant regression for that data set.

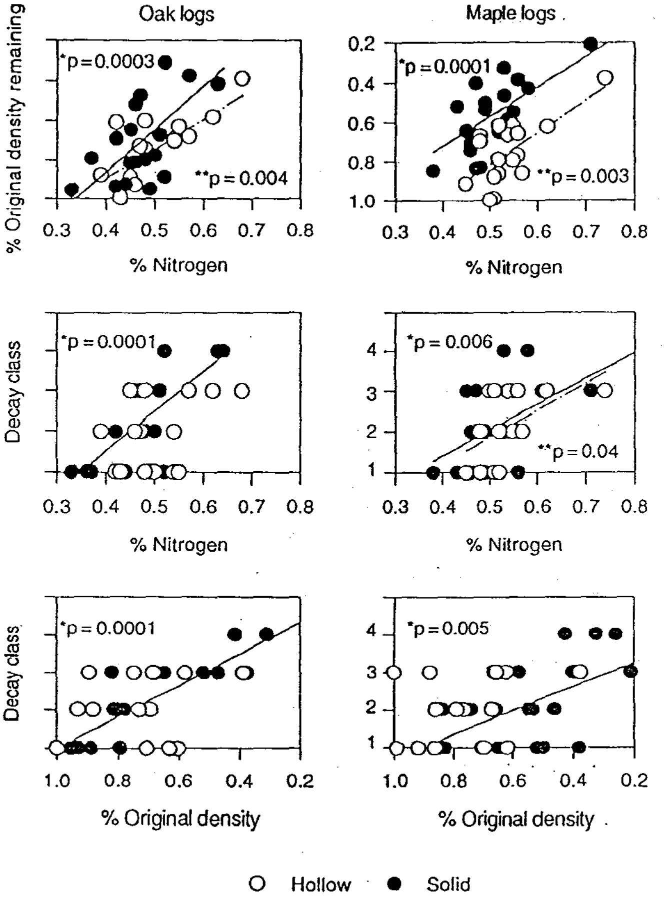
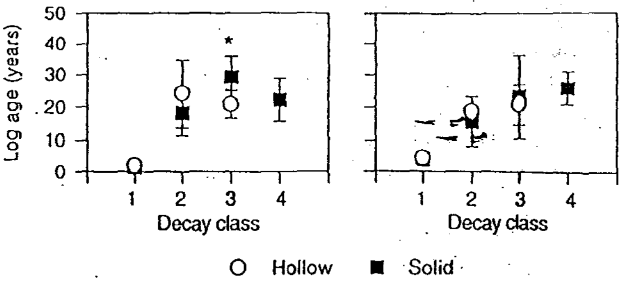


Fig. 4. Mean log age by decay class for hollow and solid, oak and maple logs. *, significant difference of hollow versus solid ($p < 0.05$).



work is needed to better describe this relationship for each species and how it relates to decay class and log age.

For both maple and oak, hollow logs reached a higher %N level at the point of maximum immobilization and initial mineralization (X_{nmax}) than did solid logs (Table 5). This result indicates that hollow logs immobilize proportionally more N than do solid logs. Additionally, maple hollow logs reach X_{nmax} at a higher percent original density (Y_{dmax} = 82%) than do maple solid logs (Y_{dmax} = 66%). In contrast, oak hollow logs reach X_{nmax} at a lower percent original density (Y_{dmax} = 75%) than do oak solid logs (Y_{dmax} = 87%).

There was considerable variability in calculating the fractional decay class at which maximum net immobilization of N and initial net N mineralization occurs (Table 5, Fig. 3). This variability was more dramatic in hollow logs as compared with solid logs and contributed in large part to the lack of significant regression results for hollow logs (Table 5). However, both methods for calculating the fractional decay class at which X_{nmax} and Y_{dmax} occur (Table 3) indicate that the point of maximum net N immobilization and initial net N mineralization (X_{nmax} and Y_{dmax}) occurs late in decay class 1 for all logs (Table 5).

Log ages and residence times in decay classes

Overall, log age ranged from 2 to 42 years in maple logs and from 1 to 38 years in oak logs (Table 6). Mean age of hollow logs was significantly different from that of solid logs only in decay class 3, oak logs (Table 6, Fig. 4). For both maple and oak logs, mean age of hollow and solid logs increased greatly from decay class 1 to decay class 2. The mean age of both hollow and solid maple logs continued to increase slightly from decay class 2 through decay class 4. The mean age of hollow oak logs decreased slightly from decay class 2 to decay class 3 and then increased slightly in decay class 4 while the mean age of solid oak logs increased slightly from decay class 2 to decay class 3 and then decreased in decay class 4. Thus, log ages do not increase by constant amounts as they move through the decay-class continuum of Triska and Cromack (1979), implying that logs reside in different decay classes for different lengths of time.

The overall pattern of residence time in each decay class was similar for both maple and oak logs (Table 7, Fig. 5). Residence times were short in decay class 1 for both hollow and solid logs (1 and 5 years, oak and maple, respectively); then increased in decay class 2 (21 and 18 years for oak logs and 15 and 11 years for maple logs, hollow and solid, respectively) and decreased in decay class 3 (–3 and 11 years for oak logs and 2 and 3 years for maple logs, hollow and solid, respectively). No hollow or solid designations were made for decay class 4 logs, which had residence times of 8 years for maple logs and –2 years for oak logs. When all samples are pooled (hollow and solid, oak and maple), residence times are 2, 17, 3, and 4 years in decay classes 1, 2, 3, and 4, respectively.

Decay rates in relation to decay class

Decay rates for each decay class (k) were estimated for both maple and oak logs. First, equations describing density (D) as a function of decay class (S) were determined by multiple regression (SYSTAT, Inc. 1990) for maple and oak logs (eqs. 1 and 2, $R^2 = 0.473$, $p = 0.001$ and $R^2 = 0.829$, $p = 0.0001$, respectively). Separate functions for hollow and solid logs were not definable, largely because of the high variability in the hollow log data set (Table 4). Therefore, hollow and solid log data were pooled, and one equation of

Table 5. (A) Results of the regressions (SYSTAT, Inc. 1990) and (B) calculations for determining the maximum %N, maximum percent original density, and fractional decay class at the point of maximum immobilization and initial mineralization in decaying oak and maple logs (Table 4; Aber and Melillo 1982).

(A) Regression results

Regression	Equation	R_2	p
Percent original density (Y_d) versus %N (X_n)			
Maple, hollow	$Y_d = 1.65 - 1.66(X_n)$	0.45	0.003
Maple, solid	$Y_d = 1.32 - 1.50(X_n)$	0.54	0.0001
Difference of slope			NS
Difference of intercept			0.001
Oak, hollow	$Y_d = 1.51 - 1.52(X_n)$	0.48	0.004
Oak, solid	$Y_d = 1.74 - 2.20(X_n)$	0.53	0.0003
Difference of slope			0.001
Difference of intercept			0.001
Decay class (Y_s) versus %N (X_n)			
Maple, hollow	$Y_s = -1.53 + 6.75(X_n)$	0.27	0.04
Maple, solid	$Y_s = -1.15 + 6.37(X_n)$	0.34	0.006
Difference of slope			NS
Difference of intercept			0.02
Oak, hollow	No significant regression		
Oak, solid	$Y_s = -2.42 + 2.36(X_n)$	0.49	0.0001
Decay class (Y_s) versus percent original density (X_d)			
Maple, hollow	No significant regression		
Maple, solid	$Y_s = 3.88 - 3.16(X_d)$	0.36	0.005
Oak, hollow	No significant regression		
Oak, solid	$Y_s = 5.16 - 4.17(X_d)$	0.81	0.0001

(B) Calculations

Parameter	Hollow	Solid
Maximum %N at initial mineralization (X_{nmax})		
Maple	0.50	0.44
Oak	0.50	0.40
Percent original density at X_{nmax} (Y_{dmax})		
Maple	82	66
Oak	75	87
Fractional decay class at X_{nmax} (Y_{smax})		
Maple	1.8	1.7
Oak	—	1.5
Fractional decay class at X_{dmax} (Y_{smax})		
Maple	—	1.8
Oak	—	1.5

density as a function of decay class (S) was determined for each species.

$$[1] \qquad \text{Maple:} \quad D = 44.6 + 6.29(S) - 3.28S^2$$

$$[2] \qquad \text{Oak:} \quad D = 66.5 + 2.73(S) - 2.19S^2$$

Equations 1 and 2 were then used to calculate beginning (D_b) and ending densities (D_e) respectively, in each decay class (Table 8). The overall pooled residence time (hollow and solid, oak and maple logs combined) for each decay class (Table 7) provided the time elapsed between D_b and D_e in each case. The slope of the regression of percent original density at the beginning, middle, and end of each decay class (D_b, D_m, D_e) as a function of time (calculated from median residence time) yielded the estimated decay rates (Table 8, Fig. 6).

The decay rates (k) of oak logs were low in decay classes 1 and 2 (–0.055 and –0.012, respectively) and then increased dramatically in decay classes 3 and 4 (–0.138 and –0.168, respectively) (Table 8, Fig. 7). The decay rate of decay class 1, maple logs was moderately low (–0.097) and then decreased to a very low level in decay class 2 (–0.008). Maple log decay rates then increased to high levels in decay classes 3 and 4 (–0.134 and –0.188, respectively) (Table 8, Fig. 7).

Discussion and conclusions

It has been well demonstrated by previous studies that the decomposition of wood, and logs in particular, is mediated

Table 6. Ranges, mean, and median log age (years) of hollow and solid oak and maple logs in each decay class.

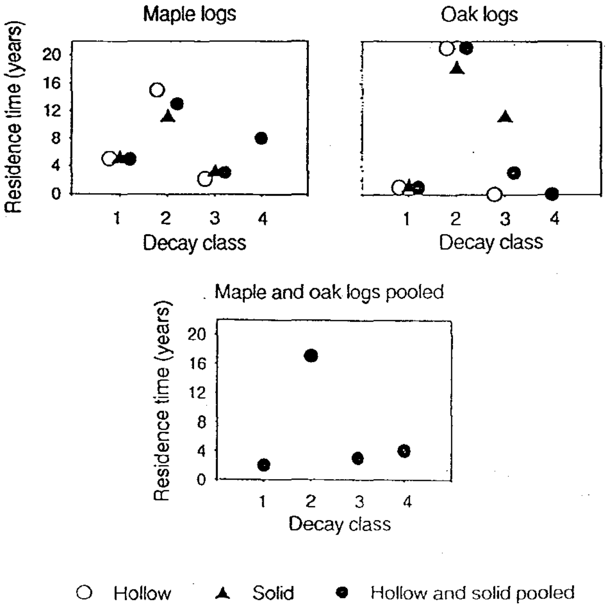
		Decay class			
		1	2	3	4
Maple logs					
Hollow	Range	2–5	11–23	12–30	—
	Mean	4	19	21	—
	Median	5	20	22	—
Solid	Range	1–6	8–31	12–42	—
	Mean	4	16	23	—
	Median	5	16	19	—
Hollow and solid pooled	Range	1–6	8–31	12–42	20–29
	Mean	4	17	22	26
	Median	5	18	21	29
Oak logs					
Hollow	Range	1–5	14–39	18–28	—
	Mean	2	24	21*	—
	Median	1	22	19	—
Solid	Range	1–3	10–25	19–38	—
	Mean	1	18	29*	—
	Median	1	19	30	—
Hollow and solid pooled	Range	1–5	10–39	18–38	15–28
	Mean	2	21	25	22
	Median	1	22	25	23
Maple and oak pooled					
Hollow and solid pooled	Mean	3	19	24	24
	Median	2	19	22	26

*Difference between hollow versus solid significant at 0.05 level.

Table 7. Residence time in each decay class for hollow and solid, oak and maple logs calculated as the difference of median log age (Table 3) between decay class (*i*) and the previous decay class (*i* – 1).

	Decay class			
	1	2	3	4
Maple logs				
Hollow	5	15	2	—
Solid	5	11	3	—
Hollow and solid pooled	5	13	3	8
Oak logs				
Hollow	1	21	-3	—
Solid	1	18	11	—
Hollow and solid pooled	1	21	3	-2
Maple and oak pooled				
Hollow and solid pooled	2	17	3	4

Fig. 5. Median residence time of hollow and solid oak logs, maple logs, and oak and maple logs pooled for decay classes 1 through 4. Residence time for each age-class is calculated as the median age of that decay class minus the median age of the previous decay class.



by many factors including the initial chemical composition, size, moisture content, temperature, and position of the log (Harmon et al. 1986; Erickson et al. 1985; Mellillo et al. 1984; Mattson et al. 1987; Rayner and Boddy 1988). These factors were controlled for, to the degree possible, in this study by selecting logs of only two species and of similar size, position, and visual indicators for each decay class. The effects of temperature and moisture through time were controlled as well by collecting logs of a given species at only two very similar sites (Table 1). With these important factors controlled, this study demonstrated that the changes occurring in a decomposing log are not well correlated with chronological age. Instead, the decay rate and decay parameters of a given log vary depending on its species, the degree

Table 8. Beginning density (D_b), ending density (D_e) and mean density (D_m) for each decay class.

	D_b (g/100 cm^3)	D_m (g/100 cm^3)	D_e (g/100 cm^3)	D_e/D_b	K	SE of k
Maple logs						
DC 1	58.0	47.4	46.7	80	–0.097	0.049
DC 2	46.7	45.2	39.8	85	–0.008	0.002
DC 3	39.8	32.4	26.4	66	–0.134	0.008
DC 4	26.4	18.2	6.5	25	–0.188	0.019
Oak logs						
DC 1	64.6	61.7	57.5	89	–0.055	0.006
DC 2	57.5	53.2	46.0	80	–0.012	0.002
DC 3	46.0	40.5	30.1	65	–0.138	0.024
DC 4	30.1	23.4	9.9	33	–0.168	0.032

Note: The percent original density remaining from the beginning of each decay class (D_e/D_b) and decay rates (k) for oak and maple logs in each decay class (hollow and solid logs are pooled in each species). Beginning and ending densities are calculated from species specific density by decay class (S) functions. oak: $D = 66.5 + 2.73S - 2.19S^2$; maple: $D = 44.6 + 6.29S - 3.28S^2$. Mean density is the measured mean density for each decay class (Table 6). Decay rates are calculated as the slope of the regression of D_b, D_e, and D_m against residence time (Table 5) in each decay class.

Fig. 6. Plot of regressions of percentage of original density remaining at the beginning, middle, and end of each decay class versus median residence time in each decay class for oak and maple logs. The slope of each regression yields the decay rate for each decay class (Table 8).

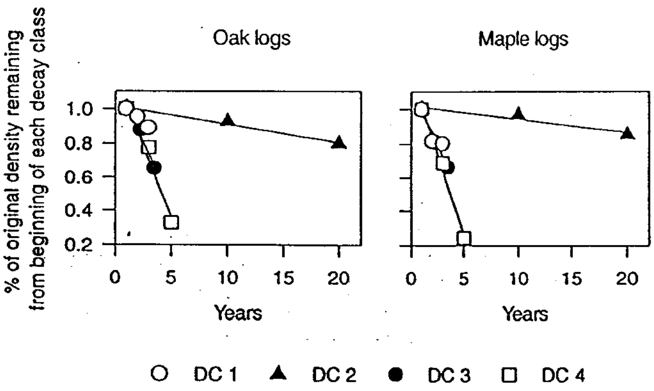
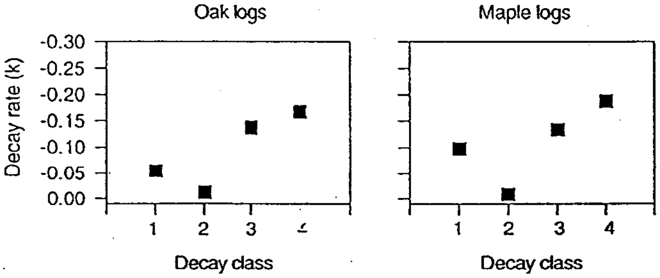


Fig. 7. Decay rates (k) for decay classes 1 through 4 for oak and maple logs.



of heart rot, and the decay-class designation based on visual indicators.

The ages of logs do not fall regularly along the decay-class continuum. In this study, residence times in the different decay classes vary quadratically, with short residence times in decay classes 1, 3, and 4 and a long residence time in decay class 2. The result is that a given log will experience the decay rates and decay parameters specific to each decay class for significantly different amounts of time, making the overall decompositional pathway quite complex.

Heart rot and the decay of hollow and solid logs

In this study, hollow logs had lower densities and higher %N than did solid logs in the same decay class, with the exception of maple logs in decay class 3 (Table 4). The fact that maple hollow logs reached a higher level of %N at a higher percent original density than did maple solid logs (Table 5) suggests that maple hollow logs not only accumulate N more rapidly than do solid logs but begin to mineralize this pool of N earlier in the decay process as well. For oak logs, the results suggest that hollow logs may accumulate more nitrogen than do solid logs but may begin to mineralize N later in the decay process. The underlying assumption for this interpretation is that the decrease in percent original density in relation to time and (or) decay class is the same for both hollow and solid logs. The lack of significant regression results for decay class as a function of %N or percent original density for hollow logs precludes making any conclusions on this point.

The inability to distinguish a decay class 4 hollow log from a decay class 4 solid log by visual indicators prevents any comparison of their potentially different decay parameters. Additionally, the lack of these data points partly contributed to the nonsignificant regression results in Table 5 (Fig. 3), which prevented comparison of the generalized decay pathways for hollow versus solid logs in relation to decay class. For example, if the decay class 4 data points were included in the regression of decay class versus %N for maple hollow logs (Fig. 3), then the slope of the regression would be much higher than that for solid logs. That would indicate that hollow logs increase their %N much more rapidly than do solid logs as they move through the decay-class continuum. We must look to the long-term log decomposition studies (Harmon 1992) for more detailed study of the changed occurring in decay classes 3 and 4 to better understand the decomposition process in the later stages. More precise determinations of log age, changes in decay rate with age, and the sequence of visual indicators for later decay classes are required. The highest variability of decay parameters occurred in decay class 3. Log ages of decay class 3 ranged from 19 to 30 years (Table 6) indicating the need for long-term log decomposition experiments to last at least 20–30 years (Harmon 1992). Further, to detail the changes occurring in decay class 3 we would suggest frequent sampling of experimental logs during this period of the study to adequately describe the changes at this point along the decay continuum.

Hollow logs introduce a great deal of variability into the decay parameter measurements as compared with solid logs. At the very least, significant levels of heart rot will introduce a great deal of variability in decay parameters of the coarse woody debris pool overall. A long-term log decomposition study including hollow versus solid logs is needed to both elaborate on results seen in this study and to answer questions that this study was unable to address about the effects of heart rot and previous colonization by rot fungi of live trees on the decompositional process and nitrogen dynamics in the eastern deciduous hardwood forest types.

References

Aber, J.D., and Melillo, J.M. 1982. Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. Can. J. Bot. 60: 2263–2269.

Berry, F.H. 1969. Decay in the upland oak stands in Kentucky. USDA For. Serv. Northeast. For. Range Exp. Stn. Res. Pap. No. NE-126.

Berry, F.H., and Beaton, J.A. 1972. Decay of oak in the Central Hardwood Region. USDA For. Serv. Northeast. For. Range Exp. Stn. Res. Pap. No. NE-242.

Erickson, H.E., Edmonds, R.L., and Peterson, C.E. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. Can. J. For. Res. 15: 914–921.

Harmon, M.E. 1992. Long-term experiments on log decomposition at the H.J. Andrews Experimental Forest. USDA For. Serv. Gen. Tech. Rep. No. PNW-GTR-280.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. No. 15. pp. 133–302.

Maser, C., and Trappe, J.M. 1984. The seen and unseen world of the fallen tree. USDA For. Serv. Gen. Tech. Rep. No. PNW-164.

Mattson, K.G., Swank, W.T., and Waide, J.B. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. Can. J. For. Res. 17: 712–720.

McCune, B., and Henckel, C.L. 1993.Tree mortality rates in two contrasting forests in Mammoth Cave National Park. Nat. Areas J. 13: 115–123.

Melillo, J.M., Naiman, R.J., Aber. J.D., and Linkins, A.E. 1984. Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. Bull. Mar. Sci. 35: 341–356.

Minderman, G. 1968: Addition, decomposition and accumulation of organic matter in forests. J. Ecol. 56: 355–362.

Minnesota Department of Natural Resources. 1991. Forest inventory data. Unpublished manuscript. Minnesota Department of Natural Resources, 550 Lafayette Road, St. Paul, Minn.

Olsen, J.S. 1963. Energy storage and balance of producers and decomposers in ecological systems. Ecology, 44: 322–331.

Rayner, A.D.M., and Boddy, L.1988. Fungal decomposition of wood: its biology and ecology. John Wiley & Sons, Bath, Avon, U.K.

Schowalter, T.D., Caldwell, B.A., Carpenter, S.E., Griffiths, R.P., Harmon, M.E., Ingham, E.R., Kelsey, R.G., Lattin J.D., and Moldenke, A.R. 1992. Decomposition of fallen trees: effects of initial conditions and heterotroph colonization rates. *In* Tropical ecosystems: ecology and management. *Edited by* K.P. Singh and J.S. Singh. Wiley Eastern Ltd., New Delhi. pp. 373–383.

Shigo, A.L. 1986: The pattern of decays and discolorations in northern hardwoods. Phytopathology, 55: 648–652.

SYSTAT, Inc. 1990. Intelligent software, version 7.0. SYSTAT, Inc., Evanston, Ill.

Triska, F.J., and Cromack, K. 1979. The role of wood debris in forests and streams. *In* Forests: Fresh Perspectives from Ecosystem Analysis. Proceedings, 40th Biology Colloquium. Oregon State University, Corvallis. pp. 171–190.

Tyrell, L.E., and Crow, T.R. 1992. Analysis of structural characteristics of old-growth hemlock–hardwood forests along a temporal gradient. *In* John T. Curtis: fifty years of Wisconsin plant ecology. *Edited by* J.S. Fralish, R.P. McIntosh, and O.L. Loucks. Wisconsin Academy of Sciences, Arts and Letters, Madison. pp. 237–246.