

Heterogeneity of decomposition and nutrient dynamics of oak (*Quercus*) logs during the first 2 years of decomposition¹

T.D. SCHOWALTER

Entomology Department, Oregon State University, Corvallis, OR 97331, U.S.A.

Received January 2, 1991

Accepted August 8, 1991

SCHOWALTER, T.D. 1992. Heterogeneity of decomposition and nutrient dynamics of oak (*Quercus*) logs during the first 2 years of decomposition. *Can. J. For. Res.* **22**: 161-166.

Decomposition of oak (*Quercus* spp.) logs (25-35 cm diameter, 3 m long) was compared among log substrates in Oregon, Minnesota, Kansas, and North Carolina during the first 2 years on the ground. Decomposition rates (*k*) for integrated logs averaged $0.28 \pm 0.04 \text{ year}^{-1}$ (mean $\pm 1 \text{ SD}$) during this initial period. Decomposition reflected qualitative differences among log substrates (outer and inner bark, sapwood and heartwood). Inner bark had the highest nutritional quality and was the focus of insect and microbial activity during this early stage of decomposition; only 20% of initial mass remained after 2 years ($k = 0.59 \pm 0.15 \text{ year}^{-1}$). Sapwood decayed more slowly than heartwood, with an overall decay rate of $0.20 \pm 0.15 \text{ year}^{-1}$. Heartwood lost 50% of its mass during the 1st year, but showed no further loss during the 2nd year, for an overall decay rate of $0.31 \pm 0.05 \text{ year}^{-1}$. Nutrient content generally declined during decomposition, but P accumulated in heartwood and Na accumulated in sapwood and heartwood during the 2nd year. Results indicate that decomposition of whole logs integrates different decomposition rates and lag times (i.e., time prior to initiation of decomposition) among log substrates varying in qualitative factors. Multiple-exponential models may be necessary to predict rates and sources of carbon and nutrient release to the atmosphere and soil.

SCHOWALTER, T.D. 1992. Heterogeneity of decomposition and nutrient dynamics of oak (*Quercus*) logs during the first 2 years of decomposition. *Can. J. For. Res.* **22** : 161-166.

La décomposition de billes de chêne (*Quercus* spp.) de 25-35 cm de diamètre et de 3 m de long a été comparée en fonction des différentes parties qui les composent dans l'Orégon, le Minnesota, le Kansas et la Caroline du Nord pendant les 2 premières années au sol. Le taux global de décomposition des billes (*k*) était en moyenne de $0,28 \pm 0,04 \text{ an}^{-1}$ (moyenne ± 1 écart type) pendant cette période initiale. La décomposition reflétait des différences qualitatives dans la composition des billes (écorce interne et externe, bois d'aubier et bois de coeur). L'écorce interne avait la meilleure qualité nutritive et était le lieu principal de l'activité microbienne et des insectes pendant le stade initial de décomposition; seulement 20% du poids initial était encore présent après 2 ans ($k = 0,59 \pm 0,15 \text{ an}^{-1}$). Le bois d'aubier se décomposait plus lentement que le bois de coeur, avec un taux global de décomposition de $0,20 (\pm 0,15 \text{ an}^{-1})$. Le bois de coeur a subi une perte de poids de 50% la 1^{re} année mais n'a subi aucune perte de poids supplémentaire la 2^e année, pour un taux global de décomposition de $0,31 \pm 0,05 \text{ an}^{-1}$. Le contenu en nutriments diminuait généralement pendant la décomposition mais il y avait une accumulation de P dans le bois de coeur et de Na dans le bois de coeur et le bois d'aubier la 2^e année. Les résultats montrent que la décomposition de billes entières intègre différents taux de décomposition et des périodes de délai, c'est-à-dire le temps avant que la décomposition débute, selon les substrats qui varient qualitativement dans les billes. Des modèles représentés par des fonctions exponentielles multiples pourraient être nécessaires pour prédire les taux et les sources de carbone ainsi que la libération d'éléments nutritifs vers l'atmosphère et le sol. [Traduit par la rédaction]

Introduction

Decomposing logs are conspicuous features of forest ecosystems. Their mass can reach 40 Mg·ha⁻¹ in deciduous forests and 500 Mg·ha⁻¹ in coniferous forests, with annual inputs of up to 3 and 7 Mg·ha⁻¹, respectively (Harmon *et al.* 1986). This material decomposes slowly, with a range of decay constants (*k*) of 0.004-0.5 year⁻¹ (Harmon *et al.* 1986; Mattson *et al.* 1987). Consequently, considerable amounts of carbon and other elements are processed through incorporation into, and decomposition of, logs.

Ecologists and forest managers have recognized the potential long-term contributions of decomposing logs to carbon dynamics, nutrient cycling, soil development, ecosystem productivity, and community diversity (Boddy 1983; Harmon *et al.* 1986; Swift 1977). The importance of logs as long-term carbon pools has gained added significance with the prospects of global climate change (Harmon *et al.* 1990). Nevertheless, patterns and processes of log decomposition remain poorly known, largely because of the difficulties and assumptions of long-term study (Harmon *et al.* 1986; Schowalter *et al.* 1991).

Most studies of decomposing logs have involved comparison of logs of different estimated ages in situ and have been based on the assumption that decomposition begins immediately at tree death and is homogeneous within logs (Harmon *et al.* 1986; Schowalter *et al.* 1991). Substrate-level (i.e., outer bark, inner bark, sapwood, and heartwood) variation in decomposition rate and lag time (i.e., time prior to initiation of decomposition) have not been addressed. However, tree species and log substrates are known to differ in structure, chemical quality, and accessibility to saprophages (Scheffer *et al.* 1949; Seastedt *et al.* 1989; Sollins *et al.* 1987; Swift 1977; Zhong and Schowalter 1989).

The objective of this study was to use an experimental approach to compare decomposition rates and lag times and nutrient dynamics among substrates in a cohort of decomposing oak (*Quercus* spp.) logs. This approach addresses potential effects of initial conditions and time lags on decomposition processes. To represent variation in decomposition due to site factors, this study was replicated at four forested sites, having oaks as major components, across a North American gradient. In this paper, I report substrate-level decomposition processes occurring during the first 2 years of study.

¹Paper 9663 of the Oregon agricultural experiment Station.

Materials and methods

This study was replicated (blocked) at four sites across a continental gradient. Sites were selected on the basis of oak representation and site commitment for long-term protection. The range of oak species and climatic conditions across sites increased our representation of factors influencing decomposition processes within logs. For example, red oaks typically decompose more rapidly than do white oaks (Mattson *et al.* 1987; Scheffer *et al.* 1949).

Oregon white oak, *Quercus garryana* Dougl., was represented at MacDonald Forest (44°37'N, 123°19'W) near Corvallis, Oregon. Mean annual temperature at this site is 11°C; mean annual precipitation is 110 cm, with 75% occurring as rain between November and March. During this study, temperatures averaged 12–13°C, and precipitation declined from 111 cm in 1986 to 96 cm in 1987 and to 95 cm in 1988. Logs were placed under a mixed oak – Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, canopy on a gentle, east-facing slope.

Northern red oak, *Quercus rubra* L., was represented at Cedar Creek Natural History Area Long Term Ecological Reserve (LTER) (45°24'N, 93°12'W) near Bethel, Minnesota. Mean annual temperature is 6°C; mean annual precipitation is 66 cm, with June and August being the wettest months. During this study, temperatures averaged 7–9°C, and precipitation was 86 cm in 1986 and 58–59 cm in 1987–1988. Logs were placed under a mixed hardwood canopy on level ground.

Burr oak, *Quercus macrocarpa* Michx. (a white oak), was represented at Konza Prairie LTER (39°05'N, 96°35'W) near Manhattan, Kansas. Mean annual temperature is 13°C; mean annual precipitation is 84 cm, decreasing from winter to summer. During this study, temperatures averaged 13°C, but precipitation was 107 cm in 1986, 82 cm in 1987, and 48 cm in 1988. Logs were placed under a mixed hardwood riparian canopy on level ground.

Chestnut oak, *Quercus prinus* L. (a white oak), was represented at Coweeta Hydrologic Laboratory LTER (35°N, 83°30'W) near Franklin, North Carolina. Mean annual temperature is 13°C; mean annual precipitation is 180 cm and is well distributed throughout the year. However, during this study, temperatures averaged 12–13°C, but precipitation was only 124 cm in 1986, 148 cm in 1987, and 127 cm in 1988. Logs were placed under a mixed hardwood canopy on a gentle, east-facing slope.

At each site, six logs (25–35 cm diameter, 3 m long) were cut from lower boles of live undiseased trees, growing at or near each site, in early June 1986. Use of live undiseased trees simulated windthrow mortality and minimized the influence of initial differences (such as prior colonization by decay organisms) on subsequent decomposition (Schowalter *et al.* 1991). Logs were placed immediately in continuous contact with the forest floor at 1–3 m spacing beneath mature forest canopies. Logs were numbered and randomly allocated to destructive sampling after 1, 2, 5, 10, 20, and 30 years.

Sampling followed methods reported by Schowalter *et al.* (1991) for studying conifer decomposition. At the time of log placement, one 8-cm slice was removed from each end of each log. Diameters of outer bark, inner bark, sapwood and heartwood were measured along two perpendicular axes and averaged for calculation of cross-sectional areas. Two radial wedges were cut from each slice and dissected into the four substrates. Volume of each substrate was calculated from its dimensions, except for outer bark, which was measured by water displacement because of the irregularity of the bark surface. Samples were weighed, dried at 50°C (to avoid volatilization of organic compounds), and reweighed. Water content was recorded. Dry mass was divided by fresh volume to obtain sample density (Foster and Lang 1982). These samples were ground to pass a 40-mesh screen and analyzed for lignin, cellulose, and hemicellulose using standard acid-detergent digestion (Van Soest 1963), for total Kjeldahl N using autoanalyzer techniques, and for P, S, K, Ca, and Na using inductively coupled argon plasma spectroscopy (Jones 1977).

At the end of 1 and 2 years (June each year), the designated log at each site was destructively sampled by removing one 8-cm slice from the middle and one 8-cm slice at 0.5 m from each end of the log.

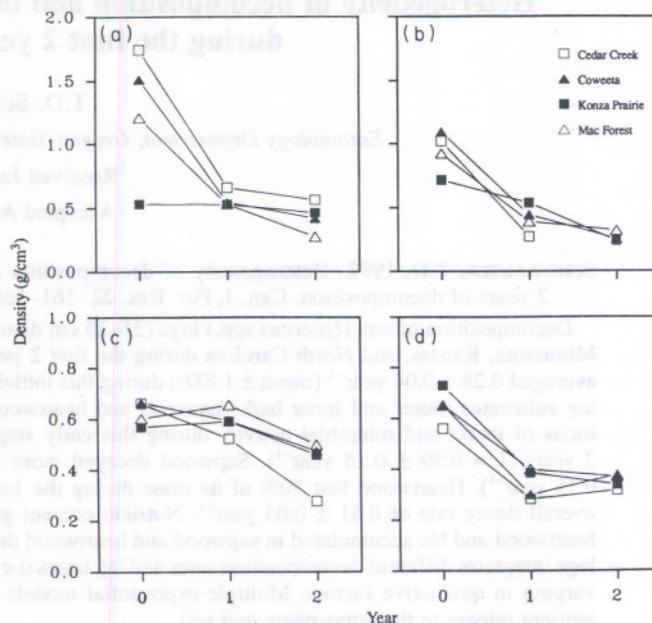


FIG. 1. Changes in substrate densities of oak logs at four sites: Cedar Creek, Minnesota; Coweeta, North Carolina; Konza Prairie, Kansas; and MacDonald (Mac) Forest, Oregon. (a) Outer bark. (b) Inner bark. (c) Sapwood. (d) Heartwood.

Sampled logs were removed from the pool of logs for subsequent sampling. Samples were treated as above, and substrates were examined for excavation by insects. Volume of each substrate excavated by insects was measured (Zhong and Schowalter 1989).

Decomposition rate of each substrate was calculated from change in substrate density. Density of whole logs was calculated as the sum of substrate volume-weighted mass (substrate density \times cross-sectional area \times length) divided by log volume. Decomposition rates (k) were calculated using the formula

$$Y_t = Y_0 e^{-kt} \text{ or } k = \ln Y_0 - \ln Y_t$$

where Y_0 is initial density and Y_t is density at time t .

All variables were pooled by site ($N = 4$) and year ($N = 3$) for each substrate. Means of pooled data were transformed, as necessary, using natural logarithms for analysis of variance. A split-plot design was used, with sites representing experimental blocks and years representing a repeated measure. Degrees of freedom were adjusted as necessary to account for autocorrelation arising from repeated measures (Milliken and Johnson 1984). Treatment means for significant ($P < 0.05$) variables were compared using Fisher's protected LSD test at an 0.05 experiment-wise error rate. All analyses were performed using SAS software (SAS Institute Inc. 1982).

Results

Water content was consistent during the 2 years. Mean percent water (SD is in parentheses) was 19% (6) in outer bark, 42% (16) in inner bark, and 59% (16) in both sapwood and heartwood at year 0. After 2 years, mean percent water was 22% (10), 44% (34), 48% (17), and 59% (11), respectively.

Density differed significantly among substrates and years; substrate \times year interaction was significant, reflecting differences in lag time prior to decomposition among substrates; e.g., 50% loss of bark and heartwood density during year 1 and delay of sapwood decomposition until year 2 (Tables 1 and 2). Examination of density change in individual logs supported these results (Fig. 1).

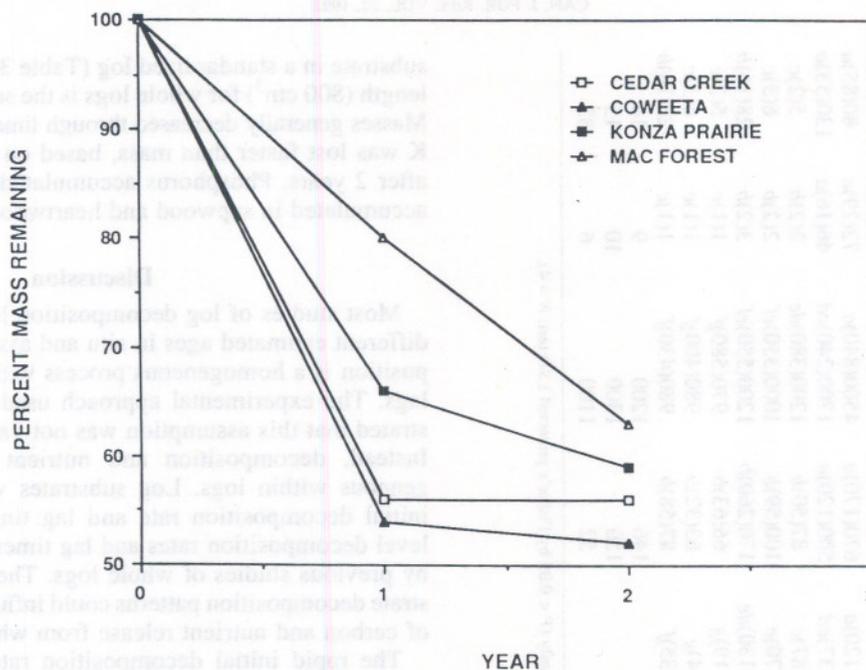


FIG. 2. Decomposition, as percent original mass remaining, of oak logs during the first 2 years on the ground at Cedar Creek, Minnesota; Coweeta, North Carolina; Konza Prairie, Kansas; and MacDonald (Mac) Forest, Oregon.

TABLE 1. Analysis of variance table for density and concentrations of structural compounds and nutrients in decomposing oak logs at four sites (replicate blocks) across a North American gradient

Source of variation	df	Mean squares									
		Density*	Hemi-cellulose	Lignin*	Cellulose	N*	P*	S*	K*	Ca*	Na*
Site	3	0.1	362	0.78	17	0.03	3.6	5.8	1.2	10	15
Substrate	3	1.5	809	6.71	6260	0.35	59.3	47.2	12.4	165	37
Error a	9	0.4	136	0.07	82	—†	1.0	0.7	0.6	—†	3
Year	2	11.0	332	0.37	83	0.14	1.4	0.7	1.6	1	22
Year × substrate	6	4.9	105	0.11	25	0.11	3.1	0.3	0.8	1	2
Error b	23	0.2	14	0.03	26	0.04	0.5	0.3	0.1	1	1

NOTE: *Analysis of variance of natural logarithms

†Owing to the relationship of error a and error b, substrate mean squares were tested against error

Decomposition rates for the 2-year period differed significantly among substrates. Sapwood ($0.20 \pm 0.15 \text{ year}^{-1}$ (mean $\pm 1 \text{ SD}$)) showed a significantly lower rate than inner bark ($0.59 \pm 0.15 \text{ year}^{-1}$), with heartwood ($0.31 \pm 0.05 \text{ year}^{-1}$) and outer bark ($0.45 \pm 0.25 \text{ year}^{-1}$) being intermediate.

Figure 2 shows percent change in mass of whole logs at the four sites. Decomposition rate for whole logs was $0.46 \pm 0.18 \text{ year}^{-1}$ for the 1st year, $0.10 \pm 0.10 \text{ year}^{-1}$ for the 2nd year, and $0.28 \pm 0.04 \text{ year}^{-1}$ for the 2-year period.

Although highly variable among sites, excavation by insects proceeded rapidly in the inner bark (Table 2). Sapwood was excavated to a minor extent. Insect tunnels reached the heartwood by the end of the 2nd year. Fungal growth was conspicuous in the inner bark at the end of the 1st year and in the inner bark, sapwood, and outer heartwood by the end of the 2nd year.

Lignin, cellulose, and hemicellulose concentration differed significantly among substrates, with hemicellulose and lignin concentration highest in inner and outer bark and cellulose

highest in sapwood and heartwood (Tables 1 and 2). Hemicellulose concentration decreased to varying degrees in all substrates, except heartwood, through time. Lignin concentration increased in inner bark. Cellulose concentration did not change through time during the first 2 years. Note that because density is given in grams of wood per cubic centimetre, chemical content (g/cm^3) is the product of density and concentration (g/g wood).

All elements varied significantly among substrates, with initial concentrations being highest in inner and outer bark (Tables 1 and 2). Year was significant for N, K, and Na, and year \times substrate interaction was significant for N, P, K, and Na. Nitrogen concentration decreased in outer and inner bark during the 1st year but increased to initial levels during the 2nd year. Sodium concentration increased consistently in all log substrates.

Substrate concentrations were multiplied by substrate density and mean initial substrate volume (per centimetre log length) to calculate masses of structural compounds and nutrients by

TABLE 2. Insect channelization, density, and concentrations of structural compounds and nutrients by substrate in oak (*Quercus* spp.) logs at four sites across North America

Substrate*	Year	Insect boring (% vol.)	Density (g/cm ³)	Lignin (g/g)	Cellulose (g/g)	Hemi-cellulose (g/g)	N (mg/g)	P (µg/g)	S (µg/g)	K (µg/g)	Ca (mg/g)	Na (µg/g)
OB	0	0	1.10(0.5)a	0.34(0.06)a	0.20(0.05)c	0.44(0.09)b	440(110)a	220(150)c	440(250)a	1700(710)c	38(29)a	52(65)b
OB	1	0.1(0.2)	0.56(0.1)bc	0.38(0.06)a	0.19(0.03)c	0.42(0.08)bcd	170(150)b	230(81)bc	590(240)a	2500(600)b	60(35)a	73(77)a
OB	2	0	0.42(0.1)cd	0.37(0.07)a	0.21(0.03)c	0.41(0.06)bcd	480(90)a	150(38)cde	430(160)a	1300(220)cde	33(20)a	66(43)a
IB	0	0	0.85(0.1)a	0.18(0.04)c	0.30(0.05)b	0.52(0.06)a	380(110)ab	380(110)ab	470(190)a	3200(590)b	44(22)a	47(56)b
IB	1	3.8(4.8)	0.40(0.1)de	0.26(0.08)b	0.31(0.01)b	0.43(0.07)bc	290(260)b	450(120)a	670(170)a	4500(840)a	72(29)a	80(85)a
IB	2	23(43)	0.27(0.1)e	0.26(0.05)b	0.30(0.03)b	0.43(0.05)bcd	490(50)a	150(37)cd	500(120)a	1700(240)cd	46(16)a	130(53)a
SW	0	0	0.63(0)b	0.14(0.02)d	0.47(0.02)a	0.38(0.02)de	150(50)b	190(87)c	87(50)b	1200(380)de	2(2)b	5(2)c
SW	1	0.4(0.6)	0.59(0.1)bc	0.16(0.02)cd	0.45(0.07)a	0.39(0.06)de	230(280)b	92(70)e	100(59)b	1000(350)ef	2(2)b	6(3)c
SW	2	0.6(1.0)	0.43(0.1)cd	0.17(0.03)cd	0.52(0.05)a	0.31(0.06)f	270(40)b	150(130)de	170(260)b	1200(550)ef	3(2)b	28(16)b
HW	0	0	0.64(0.1)b	0.14(0.02)d	0.45(0.02)a	0.40(0.02)cde	80(30)b	18(19)g	66(63)b	970(580)j	1(1)c	5(2)c
HW	1	0	0.34(0.1)de	0.14(0.02)d	0.46(0.02)a	0.40(0.02)cde	240(230)b	14(4)g	63(32)b	980(400)j	1(1)c	6(3)c
HW	2	0.1(0.2)	0.35(0)de	0.14(0.02)d	0.47(0.02)a	0.39(0.03)de	200(20)b	60(35)f	87(58)b	980(430)j	1(1)c	23(10)b
Log†	0	0	0.67	0.17	0.41	0.41	170	110	146	1200	9	14
Log†	1	0.1	0.43	0.18	0.43	0.40	230	81	150	1300	10	15
Log†	2	1.3	0.39	0.17	0.46	0.37	250	95	52	1100	6	32

NOTE: All logs were cut from living trees in spring 1986. Means (with 1 SD in parentheses) in columns followed by the same letter do not differ significantly ($P < 0.05$ by Fisher's protected LSD test; $N = 4$).

*OB, outer bark; IB, inner bark (phloem); SW, sapwood; HW, heartwood.

†Calculated as substrate volume-weighted means.

substrate in a standardized log (Table 3). Mass per centimetre length (800 cm³) for whole logs is the sum of substrate values. Masses generally decreased through time, as expected, but only K was lost faster than mass, based on percentage remaining after 2 years. Phosphorus accumulated in heartwood and Na accumulated in sapwood and heartwood during the 2nd year.

Discussion

Most studies of log decomposition have compared logs of different estimated ages in situ and assumed that log decomposition is a homogeneous process within logs, with no time lags. The experimental approach used in this study demonstrated that this assumption was not valid for these oak logs. Instead, decomposition and nutrient fluxes were heterogeneous within logs. Log substrates varied significantly in initial decomposition rate and lag time. Clearly, substrate-level decomposition rates and lag times have been integrated by previous studies of whole logs. These differences in substrate decomposition patterns could influence rates and sources of carbon and nutrient release from whole logs.

The rapid initial decomposition rate reflected rapid loss from particular substrates. Inner bark showed the highest nutrient and lowest cellulose content and was the focus of initial insect and microbial activity, resulting in rapid decomposition. By contrast, the nutritionally poor, cellulose-rich sapwood decomposed slowly, perhaps because of the absence of sapwood-boring ambrosia beetles that cultivate cellulytic fungi (French and Roeper 1972; Zhong and Schowalter 1989). The rapid, and unexpected, loss of heartwood density during the 1st year may be due to hydrolytic oxidation of phenolic polymers and (or) leaching of water-soluble organic compounds. Heartwood was expected to decompose more slowly than other substrates, but previous studies have not examined initial decomposition of heartwood. Mattson *et al.* (1987) observed a rapid rate of wood (sapwood + heartwood) decay during the 1st year of decomposition, followed by a slower rate (as observed here) for a number of hardwood species.

Although this study was designed to test effects of initial substrate conditions across a range of site conditions, rather than effects of site conditions, the consistency of substrate patterns among sites with distinct oak species and climatic regimes indicates that effects of substrate quality could override other factors influencing decomposition, at least initially. However, site conditions, especially tree species and drought, likely affected decomposition at all four sites to an unknown degree. Whereas MacDonald Forest, Cedar Creek, and Konza Prairie experienced at least average precipitation during 1986 (MacDonald Forest and Cedar Creek with somewhat elevated temperatures), Coweeta received only 69% of average precipitation. By 1988, all four sites were receiving 57–89% of average precipitation. Moisture content of 2-year-old logs was 61% at Cedar Creek, 53% at Coweeta, 50% at Konza Prairie, and 41% at MacDonald Forest. Decomposition rates among sites (Fig. 2) generally increased in the order of increasing moisture content and summer precipitation.

Considerable carbon was lost from these logs during the first 2 years. Assuming that carbon accounted for half of log mass (Harmon *et al.* 1986), a standardized log at 32 cm diameter × 300 cm long and weighing 0.67 g/cm³ initially contained 81 kg carbon. After 2 years, each log had lost 42% mass, or 34 kg carbon. The amounts lost as carbon dioxide or transformed into other compounds were not measured.

TABLE 3. Amounts per centimetre log length (800 cm³) of structural compounds and selected nutrients in oak logs, weighted by substrate cross-sectional area and density, and based on mean initial substrate dimensions

Substrate*	Year	Mass (g)	Hemi-cellulose (g)	Lignin (g)	Cellulose (g)	N (g)	P (g)	S (g)	K (g)	Ca (g)	Na (g)
OB	0	76	33	26	15	0.33	0.016	0.03	0.13	2.9	0.004
OB	1	39	16	15	7	0.07	0.009	0.02	0.10	2.3	0.003
OB	2	29	12	12	6	0.14	0.004	0.01	0.04	1.0	0.002
IB	0	34	18	6	10	0.18	0.013	0.02	0.11	1.5	0.002
IB	1	16	7	4	5	0.05	0.007	0.01	0.07	1.1	0.001
IB	2	10	4	3	3	0.05	0.002	0.00	0.02	0.5	0.001
SW	0	120	46	17	57	0.18	0.023	0.01	0.15	0.28	0.001
SW	1	110	44	18	51	0.26	0.010	0.01	0.11	0.26	0.001
SW	2	83	26	14	43	0.23	0.013	0.01	0.10	0.23	0.002
HW	0	310	126	44	140	0.25	0.006	0.02	0.30	0.41	0.002
HW	1	170	67	23	77	0.40	0.002	0.01	0.16	0.22	0.001
HW	2	170	67	24	80	0.34	0.010	0.01	0.17	0.22	0.004
Log†	0	540	223	93	222	0.94	0.058	0.08	0.69	5.09	0.009
Log†	1	335	134	60	140	0.78	0.028	0.05	0.44	3.88	0.006
Log†	2	292	109	53	132	0.76	0.029	0.03	0.33	1.95	0.009

*OB, outer bark; IB, inner bark (phloem); SW, sapwood; HW, heartwood.

†Sums of substrate values.

Increased lignin concentration in the inner bark indicated that lignin was retained, while more labile components were lost rapidly through leaching or cellulolytic activity. Constant lignin concentration in other substrates indicated a loss rate comparable to loss of mass.

Decomposing logs contributed substantially to soil fertility under logs during the first 2 years. In this study, P, K, and Ca inputs ((g/cm log at year 0 - g/cm log at year 2) × 300 cm log length ÷ 2 years) to soil under logs covering 0.96 m² (32 cm diameter × 300 cm long) averaged 4.5, 56, and 490 g·m⁻²·year⁻¹, respectively (Table 3), an order of magnitude higher than annual inputs as hardwood leaf litter of 0.4, 2, and 5 g·m⁻²·year⁻¹, respectively, in oak forests (Lang and Forman 1978; Seastedt and Crossley 1980). Loss of N mass from logs during the first 2 years (calculated as above) amounted to 28 g·m⁻²·year⁻¹. This rate does not include potential contributions of exogenous N fixed in the inner and outer bark and leached from decomposing logs (Schowalter *et al.* 1991; Silvester *et al.* 1982) nor loss of N through denitrification. Although logs influence a relatively small proportion of forest floor, they may constitute "hot spots" of fertility.

The accumulation of Na in sapwood and heartwood in all oak logs during the first 2 years of decomposition is intriguing. Sodium is a relatively minor constituent in undecayed wood, and its dynamics have been examined infrequently. Sodium immobilization has been reported for decomposing conifer logs (Foster and Lang 1982; Grier 1978; Lambert *et al.* 1980) but not for hardwood logs. Sollins *et al.* (1987) attributed Na accumulation to incorporation in arthropod tissues. Arthropod activity in this study was not adequate to explain the 2 to 4-fold increases in Na concentration in all substrates at all sites. Although Na is not an essential nutrient for fungi and bacteria, basidiomycete (decay) fungi are known to accumulate Na in conifer and hardwood leaf litter (Cromack *et al.* 1975). Regardless of the mechanism, Na accumulation in decomposing wood may attract many Na-limited invertebrates.

In conclusion, differences in decomposition rate and lag time prior to decomposition dictated the rate and source of carbon and nutrient release from a cohort of oak logs. Decom-

position of whole logs was surprisingly rapid during the 1st year but slowed during the 2nd year to yield an overall decay rate at the high end of values reported for long-term decomposition. The contributions of particular substrates to log decomposition and nutrient fluxes have been overlooked in the past owing to an assumption that log decomposition is a homogeneous process. Increased understanding of factors influencing log decomposition will improve our ability to predict rates and sources of carbon and nutrient release from decomposing logs.

Acknowledgments

R. Inouye and D. Bosanko (Cedar Creek), T. R. Seastedt (Konza Prairie), W. T. Swank and J. Buchanan (Coweeta), and M. Rowley (MacDonald Forest) assisted in the field; J. Wernz and T. Righetti performed elemental analyses; S. Philipp performed Van Soest analyses; T.E. Sabin provided statistical and computer assistance; J. Briggs (Kansas State University), G. Calabria (University of Georgia), A. El Haddi (University of Minnesota), and G.H. Taylor (Oregon State University) provided climate data. K. Mattson, T.R. Seastedt, W. T. Swank, and two journal reviewers provided helpful comments on the manuscript. This study was supported by National Science Foundation grants BSR-8516590 and BSR-8717434 and by the Oregon Agricultural Experiment Station.

- Boddy, L. 1983. Carbon dioxide release from decomposing wood: effect of water content and temperature. *Soil Biol. Biochem.* **15**: 501-510.
- Cromack, K., Jr., Todd, R. L., and Monk, C. D. 1975. Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. *Soil Biol. Biochem.* **7**: 265-268.
- Foster, F. R., and Lang, G. E. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. *Can. J. For. Res.* **12**: 617-626.
- French, J. R. J., and Roepel, R. A. 1972. Interactions of the ambrosia beetle, *Xyleborus dispar*, with its symbiotic fungus *Ambrosiella hartigii* (Fungi Imperfecti). *Can. Entomol.* **104**: 1635-1641.

Grier, C. C. 1978. A *Tsuga heterophylla*-*Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. *Can. J. For. Res.* **8**: 198-206.

Harmon, M. E., Franklin, J. F., Swanson, F. J., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **15**: 133-302.

Harmon, M. E., Ferrell, W. K., and Franklin, J. F.. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* (Washington, D.C.) **247**: 699-702.

Jones, J. B., Jr. 1977. Elemental analysis of soil extracts and plant tissue ash by plasma emission spectroscopy. *Commun. Soil Sci. Plant Anal.* **8**: 349-365.

Lambert, R. L., Lang, G. E., and Reiners, W. A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology*, **61**: 1460-1473.

Lang, G. E., and Forman, R. T. T. 1978. Detrital dynamics in a mature oak forest: Hutcheson Memorial Forest, New Jersey. *Ecology*, **59**: 580-595.

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**: 712-721.

Milliken, G. A., and Johnson, D. E. 1984. Analysis of messy data. Vol. 1. Designed experiments. Lifetime Learning Publications, Belmont, CA.

SAS Institute Inc. 1982. SAS user's guide: statistics. SAS Institute Inc., Cary, NC.

Scheffer, T. C., Englerth, G. H., and Duncan, C. G. 1949. Decay resistance of seven native oaks. *J. Agric. Res.* **78**: 129-152.

Schowalter, T. D., Caldwell, B. A., Carpenter, S. E., et al. 1991. Decomposition of fallen trees: effects of initial conditions and heterotroph colonization rates. In, *Tropical ecosystems: ecology and management*. Edited by K.P. Singh. Wiley Eastern, Ltd., Bombay. pp. 371-381.

Seastedt, T. R., and Crossley, D. A., Jr. 1980. Effects of microarthropods on the seasonal dynamics of nutrients in forest litter. *Soil Biol. Biochem.* **12**: 337-342.

Seastedt, T. R., Reddy, M. V. and Cline, S. P. 1989. Microarthropods in decaying wood from temperate coniferous and deciduous forests. *Pedobiologia* **33**: 69-77.

Silvester, W. B., Sollins, P., Verhoeven, T., and Cline, S. P. 1982. Nitrogen fixation and acetylene reduction in decaying conifer boles: effects of incubation time, aeration, and moisture content. *Can. J. For. Res.* **12**: 646-652.

Sollins, P., Cline, S. P., Verhoeven, R., et al. 1987. Patterns of log decay in old-growth Douglas-fir forests. *Can. J. For. Res.* **17**: 1585-1595.

Swift, M. J. 1977. The ecology of wood decomposition. *Sci. Prog.* (Oxford) **64**: 175-199.

Van Soest, P. J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. *J. Assoc. Off. Agric. Chem.* **46**: 829-835.

Zhong, H., and Schowalter, T. D. 1989. Conifer bole utilization by wood-boring beetles in western Oregon. *Can. J. For. Res.* **19**: 943-947.

Acknowledgments

R. Inouye and B. Swanson (Cedar Creek), J. R. Swanson (Knox Forest), W. T. Swank and I. Buchanan (Cowardin), and M. Gowley (MaDonald Forest) assisted in the field. J. Wertz and T. R. Seastedt performed elemental analyses. J. Phillips performed Van Soest analyses. T. E. Sabin provided statistical and computer assistance. A. Briggs (Kansas State University), G. Calhoun (University of Georgia), A. G. Heath (University of Minnesota), and G. H. Taylor (Oregon State University) provided climate data. K. Mansueti, T. K. Seastedt, W. T. Swank, and two journal reviewers provided helpful comments on the manuscript. This study was supported by National Science Foundation grants BSR 8212390 and BSR 8217234 and by the Oregon Agricultural Experiment Station.

Boyd, J. 1983. Carbon dioxide release from decomposing wood: effect of water content and temperature. *Soil Biol. Biochem.* **15**: 501-510.

Coward, K. L., Todd, R. L., and Monk, C. D. 1977. Factors of pathogenic micro-organisms in conifer and deciduous forest litter. *Soil Biol. Biochem.* **7**: 285-294.

Frank, R. K., and Lang, G. E. 1983. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. *Can. J. For. Res.* **13**: 811-824.

Frank, R. K., and Kozner, R. A. 1971. Interaction of the soilborne fungus *Kretzschmaria* with its substrate fungus *Amphibia*. *Mycol. Transl. J. Ecol.* **194**: 1873-1881.

Decomposing log conditions substantially to soil fertility under logs during the first 2 years in this study. P, K, and Ca forms (light log at year 0 - gram log at year 2) x 100 cm log length + 2 years) to soil under logs containing 0.96 m² (21 cm diameter x 100 cm length) averaged 2.3, 3.6, and 490 g m⁻² year⁻¹, respectively (Table 2), an order of magnitude higher than annual inputs as hardwood forest litter of 0.4, 1.1, and 2 g m⁻² year⁻¹, respectively, in oak forests (Lang and Forman 1978; Swanson and Crossley 1980). Loss of N mass from logs during the first 2 years (calculated above) amounted to 28 g m⁻² year⁻¹. This rate does not include potential contributions of nitrogen N fixed in the litter and other but and leached from decomposing logs (Schowalter et al. 1991; Swanson et al. 1983) nor loss of N through denitrification. Although logs influence a relatively small proportion of forest floor they may constitute "hot spots" of fertility.

The accumulation of P in xylem and heartwood in all oak logs during the first 2 years of decomposition is interesting. Xylem is a relatively minor constituent in unpeeled wood, and its dynamics have been examined infrequently. Sodium accumulation has been reported for decomposing conifer logs (Frank and Lang 1982; Grier 1978; Lambert et al. 1980) but not for hardwood logs. Sollins et al. (1987) studied N accumulation in unpeeled litter and explained the accumulation in this study was not adequate to explain the 2- to 4-fold increase in N concentration in all substrates at all sites. Although N is not an essential nutrient for fungi and bacteria, peatbrowns (Kozner) fungi are known to accumulate N in conifer and hardwood forest litter (Kozner et al. 1975). Regardless of the mechanism, N accumulation in decomposing wood may attract many N-fixing invertebrates. In conclusion, differences in decomposition rate and source of carbon and nutrient release from a forest of oak logs, duration