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ECOGRAPHY 21: 3–10. Copenhagen 1998

Decomposition and nutrient dynamics of oak *Quercus* spp. logs after five years of decomposition

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Schowalter, T. D., Zhang, Y. L. and Sabin, T. E. 1998. Decomposition and nutrient dynamics of oak *Quercus* spp. logs after five years of decomposition. – Ecography 21: 3–10.

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 five years on the ground. Decomposition of whole logs (weighted by substrate) averaged 0.069 yr^{-1} ($\pm$0.16 SD), but followed a 2-exponential model ($k = 0.12$ yr^{-1} year 1 and $k = 0.06$ yr^{-1} years 2–5), reflecting qualitative differences among log substrates (outer and inner bark, sapwood and heartwood). Rapid loss from bark substrates contributed to the initial rapid decay rate. Sapwood decay rate averaged 0.15 yr^{-1} and dominated the second log decay rate. Heartwood lost only 6% mass during the first five years, for an overall decay rate of 0.012 yr^{-1} that likely will represent a longer-term third exponential decay rate.

Carbon loss amounted to ca 5 kg yr^{-1} per 170 kg log. Nutrient concentrations generally declined during the first five years, but nitrogen, sulfur, and sodium accumulated in sapwood and heartwood during this period. Sulfur content increased in all substrates and doubled in whole logs during this 5-yr period. Complex patterns of nutrient content suggest patterns of microbial colonization and nutrient utilization. Polynomial models were developed to describe rates of carbon and nutrient flux in log substrates.

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Coarse woody debris (CWD) is a conspicuous feature of forest ecosystems. This material decomposes slowly (Harmon et al. 1986) and influences a variety of ecosystem processes over long time periods. This material provides important habitat for a diversity of forest species and is a source of considerable amounts of carbon and other elements released into the soil or atmosphere as woody substrates decompose.

Ecologists and forest managers have recognized the potential long-term contributions of decomposing logs to carbon dynamics, nutrient cycling, soil development, ecosystem productivity, and biotic diversity (Swift 1977, Boddy 1983, Harmon et al. 1986). The importance of logs as long-term carbon pools has gained added significance with the prospects of global climate change (Harmon et al. 1990). Hence, management of CWD and factors influencing its turnover in forest ecosystems has become an important component of forest management (Harmon et al. 1986, Schowalter et al. 1992).

Schowalter (1992) previously reported patterns of decomposition among substrates (inner and outer bark, sapwood and heartwood) of decomposing oak logs *Quercus* spp. across a North American gradient during the first two years on the ground. This study was replicated at four sites having oaks as major components in order to represent variation in decomposition due to site factors. The objective of this paper is to compare decomposition rates and nutrient content among substrates in this cohort of decomposing oak logs after five years of decomposition in order to compare initial and longer term decomposition processes.

Accepted 20 May 1997

ISSN 0906-7590

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 (Scheffer et al. 1949). We included different oak species across a continental gradient in order to represent the range of conditions that affect decomposition of a common genus at a continental scale and thereby maximize our scope of inference for evaluating differences in decomposition patterns between bark and wood substrates through time at a continental scale. Replication was insufficient to evaluate the effects of oak species or site conditions on decomposition.

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 remained depressed through 1992. Logs were placed under a mixed oak-Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, canopy on a gentle, east-facing slope.

Northern red oak, *Q. rubra* L., was represented at Cedar Creek Natural History Area Long Term Ecological Research (LTER) site (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 the wettest months. During this study, temperatures averaged 5–9°C, and precipitation declined from 86 cm in 1986 to 58–61 cm in 1987–1989, then increased to 106–116 in 1990–1991. Logs were placed under a mixed hardwood canopy on level ground.

Burr oak, *Q. macrocarpa* Michx. (a white oak), was represented at Konza Prairie LTER (39°05′N, 96°35′W) near Manhatten, Kansas. Mean annual temperature is 13°C; mean annual precipitation is 84 cm, with most rain occurring in late spring. During this study, temperatures averaged 13–14°C, but precipitation fluctuated widely with 107 cm in 1986, 82 cm in 1987, 51 cm in 1988, 82 cm in 1989, 90 cm in 1990, 67 cm in 1991 and 103 cm in 1992. Logs were placed under a mixed hardwood riparian canopy on level ground.

Chestnut oak, *Q. 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 12–14°C, but precipitation fluctuated widely with 124–148 cm in 1986–1988, 220–250 cm in 1989–1990, 164 cm in 1991 and 204 cm in 1992. 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. 1992). 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 yr.

Sampling followed methods reported by Schowalter (1992). 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 dried at 50°C (to avoid volatilization of organic compounds) and weighed. 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 other organic compounds using standard acid-detergent digestion (Van Soest 1963), for total Kjeldahl N using autoanalyzer techniques, and for P, S, K, Ca, Na and Mg using inductively coupled argon plasma (ICAP) spectroscopy (Jones 1977).

At the end of 1, 2 and 5 yr (June each year), the designated log at each site was destructively sampled by removing one 8-cm slice from the middle and one slice at 0.5 m from each end of the log. 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 × cross-sectional area × length) divided by log volume. Decomposition rates (k) were calculated using the formula:

$$Y_t = Y_0 e^{-kt}$$

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 = 4) for each substrate. The three logs/site harvested in yr 1, 2 and 5 were removed from the yr 0 samples. Inner bark was not included in the current analyses

Table 1. Analysis of variance 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	Lignin	Cellulose	Other organic	N	P	S	K	Ca	Na	Mg	$F_{0.5}$
Log	3	0.01	137	17	148	0.7	1.5	1.5	0.5	2.9	1.4	2.3	4.8
Substrate[1]	2	0.61	2509	4198	251	2.6	23.8	17.1	1.5	53.0	11.0	53.3	5.1
Error a	6	0.19	53	17	68		0.3	0.4	0.2	1.1	1.2		
Year	3	0.58	45	46	161	3.0	0.4	6.1	0.1	2.5	4.7	2.0	3.9
Error b	9				9			0.2	0.1	0.3	0.4	0.8	
Subst. × year	6	0.23	3	32	34	0.8	0.8	0.3	0.2	0.8	1.0	2.6	2.7
Error c	18	0.03	5	11	6	0.7	0.2	0.1	0.0	0.2	0.2	0.8	

[1] Substrates are outer bark, sapwood and heartwood.

because this substrate had disappeared by yr 5, creating an unbalanced design, and initial rapid decomposition was reported previously by Schowalter (1992). Analysis of variance (ANOVA) was performed on the density and concentrations of structural compounds and nutrients in outer bark, sapwood and heartwood as a split-plot in time (Steel and Torrie 1980). All observations were independent because different logs were measured at each time period. In cases where the data did not meet the assumptions of equal variance and normally distributed errors, data were transformed to their natural logarithms to meet these assumptions. For some variables the whole plot error was smaller than the subplot error. This can only happen by random chance, so the error terms were combined when this occurred to obtain a better estimate of the variance (Steel and Torrie 1980). Treatment means were modeled with time using orthogonal polynomials (Mize and Schultz 1985). Results of all analyses were considered significant if $p < 0.05$. All analyses were performed using SAS (SAS 1989).

Results

Density differed significantly among substrates and years; substrate × year interaction was significant, reflecting both differences in lag time prior to decomposition, e.g., 50% loss of bark density during yr 1 and delay of heartwood decomposition until after yr 2, and differences in decay rates among substrates (Tables 1, 2, Fig. 1). Inner bark lost 70% of initial mass within the first two years and was insufficient for sampling in 5-yr-old logs but data are included here for comparison. Heartwood lost only 6% mass during this period. Slight difference in values between this study and Schowalter (1992) reflect different statistical approaches to dealing with sample independence. Discrepancies in heartwood values between this study and Schowalter (1992) reflect errors in the dataset that were detected and corrected during this study.

Decomposition rates for the 5-yr period differed significantly among substrates. Heartwood (0.012 $yr^{-1} \pm$ 0.045 SD) decayed more slowly than did sapwood (0.15 $yr^{-1} \pm 0.14$) and outer bark (0.16 $yr^{-1} \pm 0.37$). From year 2 through 5, inner bark disappeared and outer bark showed little further change. During year 2–5, sapwood and heartwood decomposition rate was 0.13 yr^{-1} (± 0.40) and 0.041 yr^{-1} (± 0.09) respectively.

Lignin, cellulose and other organic compound concentrations (g/g) differed significantly among substrates, with lignin and other organic compound concentrations highest in inner and outer bark and cellulose highest in sapwood and heartwood (Tables 1, 2). These organic components also showed significant temporal trends, and substrate × year interaction was significant for cellulose and other organic compounds. The other organic compounds concentration decreased through time to varying degrees in all substrates except outer bark. Cellulose concentration increased through time in all substrates except outer bark. Lignin concentration increased through time in all substrates.

Concentrations of all elements varied significantly among substrates, with initial concentrations highest in inner and outer bark (Tables 1, 2). Year was a significant factor for N, S, Ca and Na, and year × substrate interaction was significant for P, K, Ca, Mg and Na. Nitrogen concentration decreased in outer and inner bark during the first year but increased to initial levels during yr 2–5. Sulfur concentration increased consistently in all log substrates. Fungal fruiting bodies in yr 5 had N and P concentrations at least twice those in log substrates. Concentrations of other elements generally reflect bark levels.

Lignin and S concentrations showed significant linear trends through time in all substrates (Table 3, Figs 1–3). For most wood components and substrates, polynomial equations (suggested to represent net leaching (X), immobilization (X^2), and mineralization (X^3) phases) were used to explain patterns of loss and recovery through time (Table 3). Note that substrate equations for lignin, N and S represent parallel lines.

Substrate concentrations multiplied by substrate density and mean initial substrate volume (per cm log length) provided estimates of masses (content) of structural compounds and nutrients by substrate in a stan-

Table 2. Concentrations of structural compounds and nutrients by substrate in oak *Quercus* spp. logs at four sites across North America and fungal fruiting bodies at two sites.[1] OB = outer bark, IB = inner bark, SW = sapwood, HW = heartwood.

Subst.	Yr	Density ($g\ cm^{-3}$)	Lignin ($g\ g^{-1}$)	Cellu. ($g\ g^{-1}$)	Other Org. ($g\ g^{-1}$)	N ($mg\ g^{-1}$)	P ($\mu g\ g^{-1}$)	S ($\mu g\ g^{-1}$)	K ($\mu g\ g^{-1}$)	Ca ($mg\ g^{-1}$)	Na ($\mu g\ g^{-1}$)	Mg ($\mu g\ g^{-1}$)
OB	0	1.18 (0.64)	0.34 (0.06)	0.20 (0.04)	0.43 (0.08)	4.7 (1.5)	220 (130)	450 (240)	1900 (850)	39 (29)	53 (73)	700 (430)
	1	0.57 (0.07)	0.38 (0.06)	0.19 (0.03)	0.42 (0.08)	1.7 (1.6)	230 (59)	590 (260)	2500 (620)	60 (39)	73 (85)	710 (360)
	2	0.49 (0.25)	0.38 (0.09)	0.21 (0.03)	0.41 (0.07)	4.8 (0.7)	150 (33)	420 (180)	1300 (230)	32 (22)	63 (46)	410 (80)
	5	0.52 (0.10)	0.39 (0.09)	0.18 (0.03)	0.42 (0.11)	5.0 (2.5)	230 (98)	1800 (870)	1600 (450)	57 (40)	36 (30)	400 (86)
IB	0	0.96 (0.33)	0.18 (0.04)	0.30 (0.05)	0.52 (0.06)	5.3 (0.8)	380 (110)	470 (190)	3200 (5900)	44 (22)	47 (56)	690 (220)
	1	0.41 (0.11)	0.26 (0.08)	0.31 (0.07)	0.43 (0.03)	2.9 (2.4)	450 (83)	680 (190)	4500 (800)	72 (310)	80 (93)	900 (310)
	2	0.27 (0.04)	0.26 (0.04)	0.31 (0.02)	0.43 (0.05)	4.9 (0.3)	150 (30)	500 (140)	1700 (22)	46 (18)	130 (60)	480 (80)
SW	0	0.62 (0.06)	0.14 (0.01)	0.47 (0.02)	0.38 (0.01)	1.5 (0.1)	200 (95)	74 (15)	1200 (260)	2 (1)	5 (2)	160 (58)
	1	0.59 (0.05)	0.16 (0.01)	0.45 (0.02)	0.39 (0.02)	2.3 (2.5)	92 (64)	100 (63)	1000 (340)	2 (2)	6 (3)	84 (66)
	2	0.43 (0.10)	0.17 (0.02)	0.52 (0.05)	0.31 (0.06)	2.7 (0.3)	150 (89)	170 (150)	1200 (280)	3 (1)	28 (12)	250 (54)
	5	0.29 (0.03)	0.19 (0.07)	0.56 (0.08)	0.24 (0.02)	3.3 (0.4)	160 (32)	620 (290)	1300 (430)	11 (8)	21 (6)	260 (57)
HW	0	0.67 (0.10)	0.14 (0.02)	0.46 (0.01)	0.40 (0.01)	0.8 (0.3)	20 (15)	62 (51)	870 (350)	1 (1)	5 (2)	33 (42)
	1	0.68 (0.12)	0.14 (0.02)	0.46 (0.01)	0.40 (0.02)	2.4 (2.3)	14 (4)	63 (34)	980 (410)	1 (1)	6 (3)	16 (10)
	2	0.71 (0.06)	0.14 (0.02)	0.46 (0.01)	0.39 (0.03)	2.0 (0.2)	60 (41)	87 (38)	980 (250)	1 (1.5)	23 (5)	88 (71)
	5	0.63 (0.08)	0.17 (0.03)	0.50 (0.02)	0.33 (0.03)	1.7 (0.2)	17 (7)	230 (200)	1200 (510)	2 (2)	11 (12)	25 (50)
Fungi	5					11.0 (3.2)	850 (350)	1550 (490)	3050 (3040)	29 (16)	30 (3.5)	950 (920)

[1] Mean (±SD).

dardized log (Table 4). Mass per cm length for whole logs (800 cm^3) was calculated as the sum of substrate values. Decomposition rate for the resulting whole log averaged 0.069 yr^{-1} (±0.16), but followed a 2-exponential model with $k = 0.12\ yr^{-1}$ yr 1 and $k = 0.06\ yr^{-1}$ yr 2–5. Masses of all components generally decreased through time in inner and outer bark, as expected, but N and S accumulated and Na remained relatively constant in sapwood and heartwood. Data integrated for the entire log indicate that most components were lost at about the same rate as mass loss. Lignin and cellulose were lost more slowly than mass, as expected, and S accumulated.

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 between death and decay. The experimental approach used in this study demonstrated that this assumption is not valid for these oak logs. Instead, decomposition rate and nutrient fluxes varied significantly among log substrates, following a 2-exponential decay model during this period with the two exponents reflecting decay of different substrates during different time periods. These differences in substrate decomposition patterns influenced rates and sources of carbon and nutrient release from whole logs.

The initial decomposition rate (first exponent, $k = 0.12\ yr^{-1}$) during yr 1 reflected decay dominated by rapid loss of inner bark; the subsequent decomposition rate (second exponent, $k = 0.06\ yr^{-1}$) yr 2–5 reflected decay dominated by the moderate loss of sapwood. The slow rate of heartwood decay ($k = 0.012\ yr^{-1}$) likely will dominate a third exponent describing long-term decomposition following disappearance of the other substrates. Inner bark showed the highest nutrient and lowest cellulose content and was the focus of initial invertebrate and microbial activity, resulting in rapid decomposition. The nutritionally-poor, cellulose-rich sapwood decomposed more slowly with little influence of insects. Overall, heartwood typically decomposes more slowly than other substrates.

The decay rate reported here is within reported values for oak logs (Harmon et al. 1986). Logs lost 29% of initial mass during the 5-yr period, reflecting losses of 12% of initial lignin, 18% of initial cellulose and 43% of initial other organic compounds. The slow loss of lignin may provide a means of standardizing future changes in other components as continued fragmentation and compaction during decomposition limit the use of mass and volume for calculation of density.

This study was not designed to test effects of oak species or site conditions. Rather, representation of different oak species across a continental gradient

increased our scope of inference for evaluating effects of substrate conditions over time. The consistent pattern of substrate-level decomposition among sites with distinct oak species and climatic regimes indicates that substrate quality has had a greater effect on decomposition than have other factors influencing decomposition, at least during this period. Nevertheless, the different tree species and the differential drought conditions experienced by all four sites during the first 2 yr likely affected decomposition to an unknown degree.

Considerable carbon was lost from these logs during this 5-yr period. Assuming that carbon accounted for half of log mass (Harmon et al. 1986), the 50 kg lost from entire logs [from Table 4; (g cm^{-1} log year 0–g cm^{-1} log year 5) × 300 cm log length] represents a 25 kg loss of C (ca 5 kg yr^{-1}).

Decomposing logs also contributed substantially to soil fertility under logs during the first five years. In this study, P, K, and Ca inputs to soil under logs covering 1 m^2 (33 cm diameter × 300 cm long) averaged 2.4, 13, and 120 g m^{-2} yr^{-1}, respectively, an order of magnitude higher than annual inputs from hardwood leaf litter of 0.4, 2, and 5 g m^{-2} yr^{-1}, respectively, in oak forests (Lang and Forman 1978, Seastedt and Crossley 1980). Most of this loss from logs occurred during the first two years as the nutrient-rich inner bark decomposed. Loss of N mass from logs during the first five years (calculated as above) amounted to 7 g m^{-2} yr^{-1}. This rate does not account for potential contributions of exogenous nitrogen fixed in, and leached from, decomposing logs (Silvester et al. 1982, Schowalter et al. 1992) nor loss of N through denitrification. Although logs influence a relatively small proportion of forest floor, they may constitute "hot spots" of fertility.

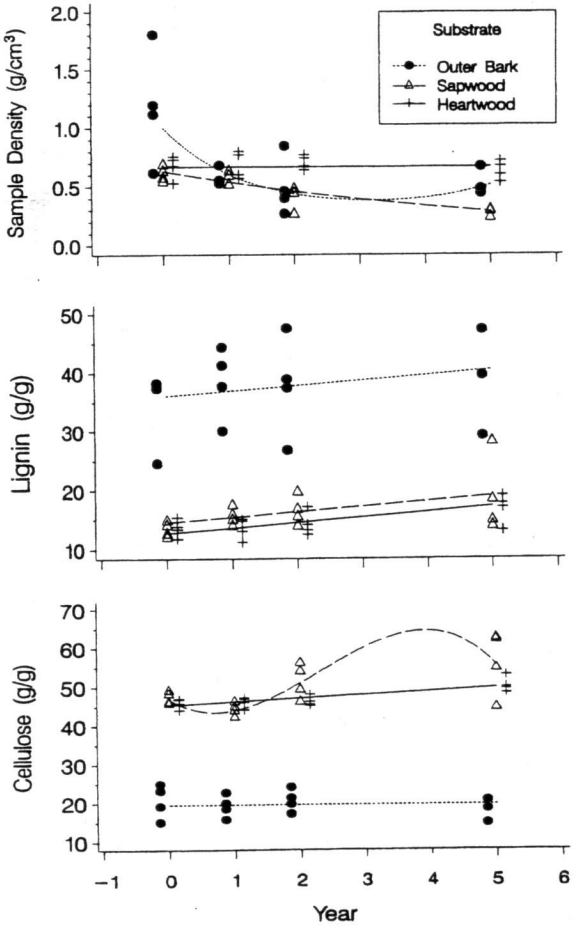

Fig. 1. Changes in density and concentrations of lignin and cellulose in outer bark, sapwood, and heartwood of oak logs at four sites across North America. See Table 3 for regression coefficients.

The increased concentration of N, S and Na in sapwood and heartwood in all oak logs during the first five years of decomposition is intriguing. These increases could represent physico-chemical immobilization (such as increased absorption, chelation or chemical reaction) or biological immobilization as logs decompose. Increased N could represent fixed N (Silvester 1982, Schowalter et al. 1992) or N moved into logs by microorganisms (Waite and King 1979). Sodium was a minor constituent in undecayed wood and is highly mobile. Its accumulation cannot be attributed in this study to incorporation in arthropod tissues as suggested by Sollins et al. (1987).

Accumulation by basidiomycete (decay) fungi (Cromack et al. 1975) is a more likely explanation, especially since mushrooms contained relatively high concentrations (Table 2). Sodium is not an essential nutrient for fungi or bacteria, and its accumulation in decomposing wood may represent an adaptation to attract Na-limited animals important to fungal dispersal.

The substantial accumulation of S in logs, especially during yr 2–5 also suggests accumulation in fungi, especially given high concentrations in mushrooms (Table 2). Fungi and bacteria are known to incorporate S in biomass and to catalyze organic sulfur-humus polymerization (Strickland and Fitzgerald 1986, Autry and Fitzgerald 1993). High C content (as in decomposing logs) apparently promotes organo-sulfate formation (Stanko-Golden et al. 1994).

Although our sampling of fungi in these logs was limited, our data indicate that mushrooms are a major avenue for nutrient export from logs. Mushrooms represent a nutritious and accessible resource for animals (which transport these nutrients) and also may contribute nutrients to leachate. Concentrations of N and P in mushrooms were 2–3 times higher than in log substrates. Concentrations of other nutrients in mushrooms were equivalent to concentrations in bark. Fungal mycelium could not be separated from wood and likely influenced nutrient concentration in log substrates.

In conclusion, differences among substrates in decomposition rate and lag time prior to decomposition

Table 3. Coefficient values for polynomial models of change in density, carbohydrate and nutrient concentrations in substrates of decomposing oak logs. All regressions were significant at $p < 0.05$. See Table 2 for substrate types.

Components	Substrate	X^3	X^2	X	C
Density	OB	–	0.094	−0.60	0.001
	SW	–	–	−0.16	−0.46
	HW	–	–	–	0.67
Lignin	OB	–	–	0.89	36
	SW	–	–	0.89	15
	HW	–	–	0.89	13
Cellulose	OB	–	–	–	20
	SW	−1.3	8.8	−10	47
	HW	–	–	0.88	45
Ln N	OB	−0.21	1.39	−1.67	−1.36
	SW	−0.21	1.39	−1.67	−1.81
	HW	−0.21	1.39	−1.67	2.17
Ln P	OB	–	–	–	193
	SW	−0.19	1.29	−2.04	5.21
	HW	−0.21	1.27	−1.23	2.78
Ln S	OB	–	–	0.32	5.76
	SW	–	–	0.32	4.35
	HW	–	–	0.32	3.75
Ln Ca	OB	0.16	−1.05	1.38	10.3
	SW	–	–	0.41	7.04
	HW	–	–	0.16	6.73
Ln Na	OB	–	−0.12	0.60	3.30
	SW	−0.19	1.10	−0.46	1.23
	HW	−0.23	1.38	−1.01	1.47
Ln K	OB	0.13	−0.89	1.09	7.45
	SW	–	–	–	1104
	HW	–	–	0.06	6.74

Table 4. Amounts per centimeter log length of structural compounds and selected nutrients in oak logs, weighted by substrate cross-sectional area and density. Values are per 65 cm^3 for OB, per 38 cm^3 for IB, per 201 cm^3 for SW, 496 cm^3 for HW, and per 800 cm^3 for whole logs.[1] See Table 2 for substrate types.

Subst.	Yr	Mass (g)	Lignin (g)	Cellu. (g)	Other (g)	N (g)	P (g)	S (g)	K (g)	Ca (g)	Na (g)	Mg (g)
OB	0	77	26	15	33	0.34	0.017	0.035	0.15	3.0	0.004	0.05
	1	37	14	7	16	0.06	0.009	0.022	0.09	2.2	0.003	0.03
	2	32	12	7	13	0.15	0.005	0.013	0.04	1.0	0.002	0.01
	5	34	13	6	14	0.17	0.008	0.061	0.05	2.0	0.001	0.01
IB	0	36	7	11	19	0.19	0.014	0.017	0.12	1.6	0.002	0.03
	1	16	4	5	7	0.05	0.007	0.011	0.07	1.1	0.001	0.01
	2	10	3	3	4	0.05	0.002	0.005	0.02	0.5	0.001	0.01
SW	0	125	17	59	47	0.19	0.025	0.009	0.15	0.2	0.001	0.02
	1	119	19	53	46	0.27	0.011	0.012	0.12	0.2	0.001	0.01
	2	86	15	45	27	0.23	0.013	0.015	0.10	0.3	0.002	0.02
	5	58	11	33	14	0.19	0.009	0.036	0.08	0.6	0.001	0.02
HW	0	332	47	153	133	0.27	0.006	0.021	0.29	0.3	0.002	0.01
	1	337	47	155	135	0.81	0.005	0.021	0.33	0.4	0.002	0.01
	2	352	49	162	137	0.70	0.021	0.031	0.35	0.4	0.008	0.03
	5	312	53	156	103	0.53	0.005	0.072	0.37	0.6	0.003	0.01
Log[2]	0	570	97	238	232	0.99	0.062	0.082	0.71	5.1	0.009	0.11
	1	509	84	220	204	1.19	0.032	0.066	0.61	3.9	0.007	0.06
	2	480	76	217	181	1.13	0.041	0.061	0.51	2.2	0.013	0.07
	5	404	77	195	131	0.89	0.022	0.170	0.50	3.2	0.005	0.04

[1] Values for logs are the sum of substrate values.

dictated the rate and source of carbon and nutrient release from a cohort of oak logs. Decomposition of whole logs was relatively rapid during the first year, due to rapid loss of nutritious inner bark, but slowed during the remainder of this period to reflect primarily sapwood decay. Overall decay rate was within values reported for long-term decomposition of oak logs. We expect our future sampling to demonstrate that the slow decay rate for heartwood defines a third decay constant for a multiple-exponential model of long term decomposition. Our data suggest that logs increasingly function as nutrient "hot spots", perhaps due to microbial immobilization of N, P, S, and Na. Increased understanding of factors influencing log decomposition

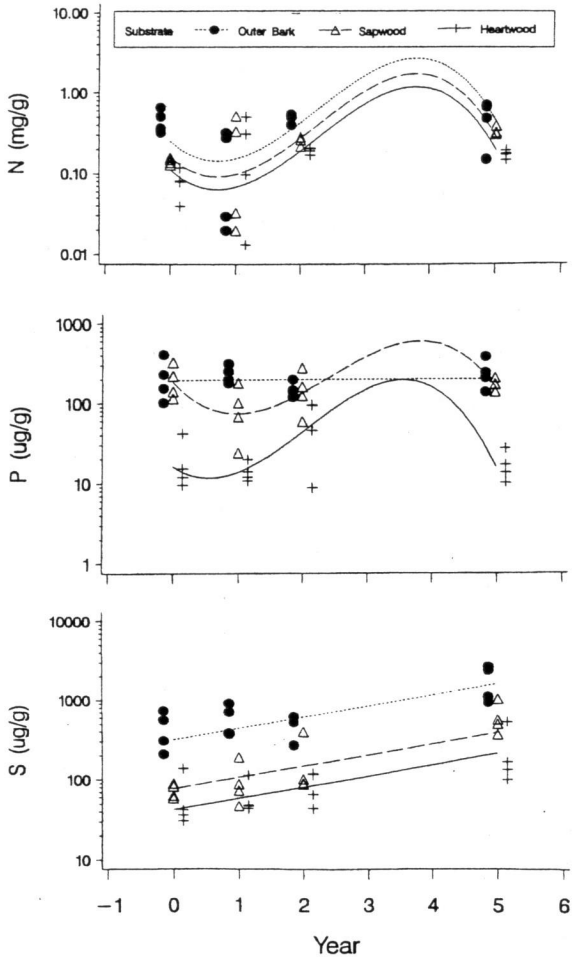

Fig. 2. Changes in concentrations of N, P, and S in outer bark, sapwood and heartwood of oak logs at four sites across North America. See Table 3 for regression coefficients.

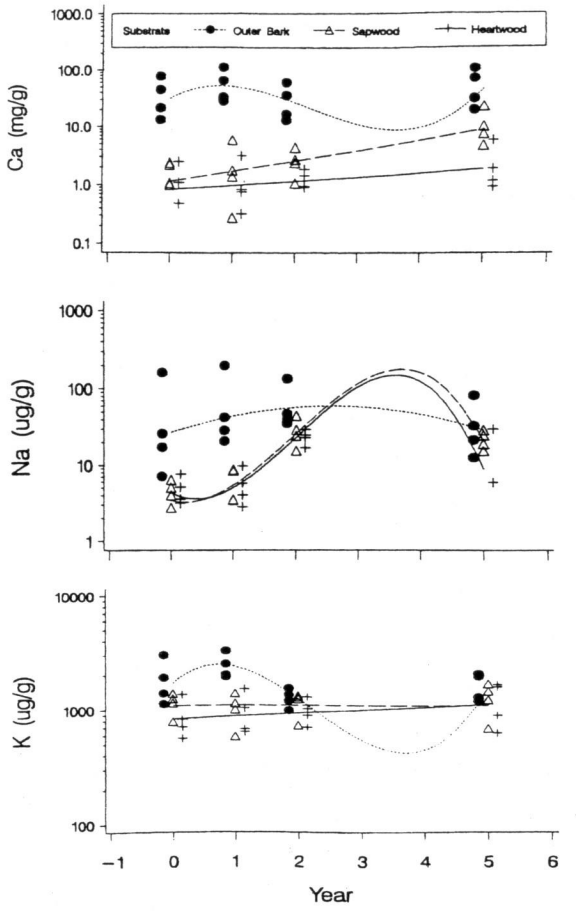

Fig. 3. Changes in concentrations of Ca, Na and K in outer bark, sapwood and heartwood of oak logs at four sites across North America. See Table 3 for regression coefficients.

will improve our ability to predict rates and sources of carbon and nutrient release from decomposing logs and to appreciate the roles of these substrates in biogeochemical and ecological processes of forest ecosystems.

Acknowledgments – R. Inouye, D. Bosanko, J. Briggs, T. R. Seastedt, W. T. Swank and J. Buchanan provided samples; elemental analyses were done at the OSU Plant Analysis Lab.; S. Philipp performed Van Soest analyses; J. Briggs, G. Calabria, A. El Haddi and G. H. Taylor provided climate data. K. Cromack, Jr., D. A. Crossley, Jr., B. Dail and T. R. Seastedt provided constructive reviews. This study was supported by NSF grants BSR-8516590, BSR-8717434 and DEB-9408169 and by the Oregon Agricultural Experiment Station (paper no. 9663).

References

Autry, A. R. and Fitzgerald, J. W. 1993. Relationship between microbial activity, biomass and organo sulfur formation in forest soil. – Soil Biol. Biochem. 25: 33–39.

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.

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. 15: 133–302.

– , Ferrell, W. K. and Franklin, J. F. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. – Science 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.

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.

Mize, C. W. and Shultz, R. C. 1985. Comparing treatment means correctly and appropriately. – Can. J. For. Res. 15: 1142–1148.

SAS 1989. SAS/STAT User's Guide, Ver. 6, Fourth Ed., Vol. 2. – SAS Inst., 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. 1992. Heterogeneity of decomposition and nutrient dynamics of oak (*Quercus*) logs during the first two years of decomposition. – Can. J. For. Res. 22: 161–166.
– , 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: Singh, K. P. and Singh, V. S. (eds), Tropical ecosystems: ecology and management. Wiley, 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.
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., Sachs, D. and Spycher, G. 1987. Patterns of log decay in old-growth Douglas-fir forests. – Can. J. For. Res. 17: 1585–1595.
Stanko-Golden, K. M., Swank, W. T. and Fitzgerald, J. W. 1994. Factors affecting sulfate absorption, organic sulfur formation, and mobilization in forest land, grassland spadosols. – Biol. Fert. Soils 17: 289–296.
Steel, R. G. D. and Torrie, J. H. 1980. Principles and procedures of statistics: a biometrical approach, 2nd ed. – McGraw-Hill.
Strickland, T. C. and Fitzgerald, J. W. 1986. Organosulfur recalcitrance in soil and litter from a hardwood forest. – Soil Biol. Biochem. 18: 661–662.
Swift, M. J. 1977. The ecology of wood decomposition. – Sci. Prog. 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. Ass. Off. Agric. Chem. 46: 829–835.
Waite, J. and King, B. 1979. Total nitriogen balances of wood in soil. – Mat. Org. 14: 27–41.
Zhong, H. and Schowalter, T. D. 1989. Conifer bole utilization by wood-boring beetles in western Oregon. – Can. J. For. Res. 19: 943–947.