Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition[1]

MARK E. HARMON,[2] JAY SEXTON, BRUCE A. CALDWELL, AND STEVE E. CARPENTER
Department of Forest Science, Oregon State University, Corvallis, OR 97331-5705, U.S.A.

Received November 4, 1993
Accepted April 12, 1994

HARMON, M.E., SEXTON, J., CALDWELL, B.A., and CARPENTER, S.E. 1994. Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. Can. J. For. Res. **24**: 1883–1893.

The export of mass and nutrients associated with the formation of fungal sporocarps during the first 7 years of decomposition of logs of four conifer species (*Abies amabilis* Dougl. ex Forbes, *Pseudotsuga menziesii* (Mirb.) Franco, *Thuja plicata* D. Don, and *Tsuga heterophylla* (Raf.) Sarg.) was investigated in western Oregon. Abundance of the most common fungal species, *Naematoloma capnoides* (Fr.:Fr.) P. Kumm, differed significantly with log species; the fungus was most abundant on *Abies* and least abundant on *Thuja*. Fungi increased concentrations of N, K, and P over those found in associated logs by as much as 38, 115, and 136 times, respectively. Thus, a fair proportion of the initial N (0.9–2.9%), K (1.8–4.5%), and P (1.9–6.6%) was transported out of logs via sporocarps at a time when immobilization would have been predicted from critical element ratios (e.g., C/N).

HARMON, M.E., SEXTON, J., CALDWELL, B.A., et CARPENTER, S.E. 1994. Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. Can. J. For. Res. **24** : 1883–1893.

L'exportation de matière et l'éléments nutritifs associée à la formation du carpophore des champignons pendant les 7 premières années de décomposition des billes de quatre espèces de conifère, *Abies amabilis* Dougl. ex Forbes, *Pseudotsuga menziesii* (Mirb.) Franco, *Thuja plicata* D. Don et *Tsuga heterophylla* (Raf.) Sarg. a été étudiée dans l'ouest de l'Orégon. L'abondance de l'espèce de champignon la plus commune, *Naematoloma capnoides* (Fr.:Fr.) P. Kumm, variait significativement selon l'espèce des billes; le champignon était le plus abondant sur *Abies* et le moins abondant sur *Thuja*. Les champignons provoquaient une augmentation des concentrations de N, K et P respectivement 38, 115 et 136 fois plus élevées que celles observées dans des billes correspondantes. Par conséquent, une proportion appréciable de N (0,9–2,9%), K (1,8–4,5%) et P (1,9–6,6%) initialement présents était exportée hors des billes via les carpophores au moment où une immobilisation aurait pu être soupçonnée à partir des ratios des éléments critiques tel le ratio C/N.

[Traduit par la rédaction]

Introduction

During decomposition, logs and other forms of coarse woody debris (CWD) reduce erosion (Swanson and Lienkaemper 1978), affect soil development (McFee and Stone 1966), store nutrients (Sollins et al. 1987) and water (M.E. Harmon and J. Sexton, in preparation), are a potentially large source of energy and nutrients, serve as a seed bed for plants (Harmon and Franklin 1989), and form an important habitat for fungi (Frankland et al. 1982; Rayner and Boddy 1988) and arthropods (Deyrup 1976; Ausmus 1977). Despite growing recognition that dead trees play major roles in ecosystem function (Triska and Cromack 1980; Franklin et al. 1981, 1987; Harmon et al. 1986), many aspects of the specific processes involved are poorly understood.

Consider, for example, the importance of CWD in forest nutrient cycles. Aside from nitrogen fixation, few studies have directly examined the processes responsible for the net changes in nutrient content of decaying wood (Sollins et al. 1987). The actual proportion of tree nutrition that is derived from CWD is not known. On one hand, the low nutrient content and small mass of tree mortality relative to fine litterfall, as well as the slow decomposition rate of wood suggest that CWD plays a minor role in forest nutrient cycles during periods of normal stand development (Arthur and Fahey 1990; Harmon and Chen 1991). On the other hand, following catastrophic blowdown or fire, large amounts of nutrients can become available to the regrowing forest when nutrients stored in the large mass of newly created CWD are released. Although nutrients stored in CWD are released at slower rates than they are from fine litter, the timing of their release may closely match the requirements of the recovering forest (Harmon and Chen 1991). The importance of CWD in older, more stable forests may also have been underestimated by focusing on the short-term dynamics of wood decay. In many conifer forests, large accumulations of extremely old, well-decayed wood are found in the forest floor (McFee and Stone 1966; Little and Ohmann 1988; Keenan et al. 1993) or in the mineral soil (Harvey et al. 1981).

Understanding of nutrient immobilization and mineralization in CWD is rudimentary. Most of our current knowledge on these processes has been derived from chronosequences of log decomposition. Changes in nutrient content of log chronosequences indicate a net influx of N and Ca, but a net efflux of P and K (Grier 1978; Lambert et al. 1980; Foster and Lang 1982; Sollins et al. 1987; Chen 1989). Unfortunately few of the specific processes responsible for these changes in nutrient content have been examined. Those processes that have been examined indicate that chronosequence patterns of nutrient content may give a misleading view of the timing of nutrient immobilization and release. For example, fragmentation, which may transfer significant quantities of nutrients from logs to the forest floor, is not considered in the nutrient content of the remaining log sampled

[1]Paper 2953, Forest Research Laboratory, Oregon State University, Corvallis.
[2]Author to whom all correspondence should be addressed.

in a chronosequence. As fragmentation tends to remove the most decayed and nutrient-rich portions of logs, CWD may release nutrients faster and in greater abundance than is generally believed.

In this study we examine a previously unmeasured pathway of mass and nutrient loss from logs; the pathway involves the formation of fungal fruiting bodies or sporocarps. In many wood-decaying basidiomycete species, sporocarps (mushrooms) that contain high levels of nutrients compared with fresh or decomposing plant tissues are formed annually (Hinneri 1975; Vogt and Edmonds 1980). Because many of these sporocarps are consumed or sloughed off before nutrients can be translocated back into the log, sporocarps may represent a net efflux from the log to the surrounding environment. Log nutrients may also be exported from logs by basidiomycetes with perennial sporocarps, in the form of spores (Frankland et al. 1982), or when they eventually die and fall to the forest floor. Our objective was to quantify the mass and nutrient loss associated with the formation of sporocarps on logs.

We have been investigating the early stages of decomposition and nutrient cycling in a time series of logs at the H.J. Andrews Experimental Forest (Harmon 1992). To date these logs have been examined to determine initial tannin, phenolic, and pentane extractive chemistry (Kelsey and Harmon 1989), fungal colonization and food web structure (Carpenter et al. 1988; Schowalter et al. 1992), insect colonization and fragmentation (Zhong and Schowalter 1989), and successional patterns of nitrogen fixation (Griffiths et al. 1993). In addition, considerable unpublished data on decay colonization patterns, seasonal respiration rates, mass loss, nutrient concentrations, and leaching rates have been gathered. This ongoing research provides an ideal context for examining long-term patterns of sporocarp mass and nutrient export.

Study area

The H.J. Andrews Experimental Forest is located 80 km east of Eugene, Oreg., on the west slope of the Cascade Range (44°10′N, 122°25′W). The climate is maritime, with wet, relatively mild winters and dry, cool summers. Mean annual temperature is 8.5°C, and mean annual precipitation is 230 cm, with more than 75% falling between October and March (McKee and Bierlmaier 1987). Annual actual evapotranspiration is 530 mm. Soils are deep, well-drained typic dystrochrepts (Brown and Parsons 1973). The forests are classified into two major zones, the *Tsuga heterophylla* (Raf.) Sarg. zone (300–1050 m elevation) and the *Abies amabilis* Dougl. ex Forbes zone (1050–1550 m elevation) (Dyrness et al. 1976). Coarse woody debris is a major form of aboveground detritus in these forests, which contain a mass of 140–220 Mg/ha (Harmon et al. 1986; Sollins et al. 1987; Spies et al. 1988).

Our study was conducted within six old-growth forest stands that have been the focus of a number of ongoing studies on the early stages of log decomposition (Carpenter et al. 1988; Kelsey and Harmon 1989; Zhong and Schowalter 1989; Harmon 1992; Schowalter et al. 1992; Griffiths et al. 1993). Elevations at the sites range from 533 to 1133 m (Table 1). Topographic position of the sites ranges from valley bottom to side slopes, the slopes of all sites are less than 20%, and the aspects are south facing. Only a subset of climatic conditions that occur at the H.J. Andrews Experimental Forest are represented at the sites. Mean annual temperature during 1986–1988 ranged from 8.0 to 9.9°C. Mean annual precipitation at the nearest gauging stations ranged from 207 to 232 cm during the 1979–1986 period. All sites were in either the *Tsuga* or the *Tsuga–Abies* transition forest zones.

Methods

Logs

The methods used to determine initial log characteristics used in analyses are described in detail by Harmon (1992). In September 1985, live, healthy trees of four conifer species (*Abies amabilis*, *Pseudotsuga menziesii* (Mirb.) Franco, *Thuja plicata* D. Don, and *Tsuga heterophylla*; hereafter referred to by genus only) were felled, cut in logs, and placed on the forest floor at six study sites. The logs were selected, not by position along the bole, but to fit a range of 45–65 cm in diameter. Logs used in the study averaged 5.5 m in length, and 52 cm in diameter, were almost completely covered with bark, and had a mean volume of approximately 1.2 m^3. To characterize initial density, nutrient concentration, and volume of each tissue (i.e., outer bark, inner bark, sapwood, and heartwood) in a log (Table 2), a cross section from 8 to 10 cm thick was removed from each end. Photographs of the cross sections were digitized to estimate the volume of outer bark, inner bark, sapwood, and heartwood. Wood density was estimated by measuring the external dimensions of blocks cut on a table saw, and determining dry weight. Similarly, measurements of the dimensions of bark peeled from the cross sections were used to estimate inner bark density. Outer bark densities were determined by water displacement volumes. All densities were calculated as oven-dry weight (7 days at 55°C) divided by green volume. Initial nutrient concentration of each tissue was sampled from a subset of 10 logs of each species. Nutrient concentration of outer bark was determined from samples that had not been soaked during the water displacement measurements. All tissues were first coarse ground, and then fine ground with a Wiley mill to pass a 40-mesh screen. Nitrogen concentration (N) was measured with micro-Kjeldahl digestion of 1.0 g of sample. Concentrations of Ca, Fe, K, Mg, Mn, P, and Zn were measured on 1.0 g samples by inductively coupled argon spectroscopy (Thermo Jarrell Ash ICP 9000). The mass of each tissue in each log was estimated by multiplying the volume of each tissue by its undecayed density. Total nutrient stores in the undecayed logs were estimated by multiplying the nutrient concentration of each tissue type by the mass of each tissue in each log.

Fungi

The mass and nutrient losses from logs via the formation of fungal sporocarps were calculated from the number, mean mass, and mean nutrient concentration of sporocarps. For 7 years, starting in 1985, the total number of sporocarps was counted on two or three logs each of *Abies*, *Pseudotsuga*, *Thuja*, and *Tsuga* at each of the six sites. Counts were made during late November through early December, the midseason of fungal sporocarp formation, when old decaying sporocarps as well as those beginning to form are present. Individuals were counted for mushroom-forming species. For resupinate polypores, the area covered was estimated to the nearest 100 cm^2. Individual masses of the jelly fungus *Dacrymyces palmatus* (Schw.) Bres. were counted, although these often contained numerous small lobes. Conk-forming polypores were noted as alive or dead, and the longest and shortest dimensions of each individual were recorded.

Subsamples from fresh, undecayed sporocarps of the dominant fungal species were taken in order to determine the mean mass per individual or area and to measure nutrient concentrations. For mushroom-forming species, 20–50 individuals were harvested to determine the mean mass per individual. For resupinate species, a section approximately 100 cm^2 in area was removed; the number of major lobes in the section was counted and the mass per unit area determined. In the case of *Fomitopsis pinicola* (Swartz ex Fr.) Karst, a number of individuals were harvested to establish a regression between the product of the long and short axis and dry mass:

[1] $Y = 0.633X_1X_2, \quad r^2 = 0.98, N = 22$

where Y is the dry mass (grams), X_1 is the long axis (centimetres),

TABLE 1. Description of experimental sites at H.J. Andrews Experimental Forest, Oregon

Site number	Elevation (m)	Temperature[a] (°C)	Precipitation[b] (cm/year)	Habitat type[c]
1	1065	8.9	229	TSHE/ABAM/RHMA/BENE
2	935	9.6	207	TSHE/RHMA/BENE
3	535	9.4	209	TSHE/RHMA/BENE
4	865	9.9	219	TSHE/RHMA/BENE
5	1135	9.0	232	TSHE/ABAM/LIBO
6	935	8.0	222	TSHE/ABAM/RHMA/BENE

[a]Based on 1986–1988 period.
[b]Based on 1979–1986 period.
[c]Based on map of habitat types of the H.J. Andrews Experimental Forest: TSHE/ABAM/RHMA/BENE, *Tsuga heterophylla/Abies amabilis/Rhododendron macrophyllum* G. Don/*Berberis nervosa* Pursh; TSHE/RHMA/BENE, *Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa*; TSHE/ABAM/LIBO, *Tsuga heterophylla/Abies amabilis/Linnea borealis* L.

TABLE 2. Characteristics of logs used in the decomposition experiments at H.J. Andrews Experimental Forest, Oregon

Parameter	Genus of log			
	Abies	*Pseudotsuga*	*Thuja*	*Tsuga*
Diameter (cm)	51.7 (0.6)	51.8 (0.4)	53.1 (0.5)	51.4 (0.4)
Length (m)	5.52 (0.01)	5.51 (0.01)	5.52 (0.01)	5.52 (0.01)
Volume (m^3)	1.164 (0.025)	1.178 (0.019)	1.246 (0.026)	1.170 (0.019)
Surface area (m^2)	8.904 (0.099)	8.963 (0.069)	9.207 (0.095)	8.924 (0.074)
Bark cover (%)	99.0 (0.2)	98.4 (0.1)	99.3 (0.1)	97.5 (0.2)
Mass (kg/log)	445 (10)	531 (9)	419 (9)	480 (8)
Ca (g/log)	924 (31)	356 (10)	718 (18)	709 (2)
Fe (g/log)	9.31 (0.47)	10.22 (0.40)	14.4 (0.5)	4.38 (0.30)
K (g/log)	362 (9)	156 (3)	180 (5)	430 (12)
Mg (g/log)	73.9 (2.5)	28.8 (0.6)	48.3 (1.5)	55.0 (0.1)
Mn (g/log)	17.8 (0.5)	11.4 (0.1)	2.0 (0.1)	22.6 (0.6)
N (g/log)	492 (13)	524 (9)	471 (10)	392 (9)
P (g/log)	48.0 (0.1)	32.1 (0.1)	26.1 (0.1)	85.7 (0.4)
Zn (g/log)	3.60 (0.22)	2.14 (0.06)	2.32 (0.22)	1.22 (0.06)
Sample size	107	120	108	120

NOTE: Values are means with standard errors given in parentheses.

and X_2 is the short axis (centimetres). All dry weights were determined after drying at 55°C for 4 days, or until the mass was stable for the larger sporocarps.

After drying, fungal sporocarps were fine ground with a Wiley mill to pass a 40-mesh screen. Nitrogen concentrations of 0.5g samples were measured with a LECO Nitrogen determinator (Model FP-42P). Concentrations of Ca, Fe, K, Mg, Mn, P, and Zn (1.0 g samples) were measured by inductively coupled argon spectroscopy after digestion in aqua regia (Jones 1977).

Sporocarp exports for mushroom-forming species were calculated from annual biomass and nutrient concentrations. Sporocarp exports for perennial sporocarps were calculated from the annual changes in biomass, mortality losses, and nutrient concentrations. Estimating the exact year of export by perennial sporocarps is difficult because few die or fall off logs during the year of formation. However, as these nutrients are no longer available for internal processes, we have assumed that perennial exports occur during the year of sporocarp production.

Statistical analysis

Analysis of variance (ANOVA) for a one-way randomized factor design was used to test whether or not time and species of fungi influenced the mass and nutrient concentration of sporocarps. In the case of the species test, only data from years 4 and 7 were used for *Naematoloma capnoides* (Fr.:Fr.) P. Kumm to make the sample size for this species similar to that of the other fungal species. In addition, only *N. capnoides* data were used for the test of temporal variation, because this species was most common and had been sampled each year that sporocarps were present. Regression analysis was used to test whether significant differences among sampling times were systematic (a significant regression) or random (nonsignificant regression).

Differences in mass and nutrients exported from the four log species were also tested by ANOVA with a randomized block experimental design. Log species was the main plot treatment and site was the block. This statistical design was also used to test whether or not the density (number per square metre of surface) of *N. capnoides* sporocarps differed among log species. Procedure GLM was used for all statistical tests (SAS Institute Inc. 1985), which were considered significant when $p < 0.05$ and highly significant when $p < 0.01$.

Results

Fungal sporocarps began to appear on logs during the second autumn following log placement. Although sporocarps were quite numerous on logs, the total number of species observed was quite low. The most common species, *N. capnoides*, was one of the first to appear and grew on all four log species. *Trametes versicolor* (L.:Fr.) Pilát also appeared in the second year on *Tsuga* logs. In the fourth fall, the number of sporocarp-forming species increased.

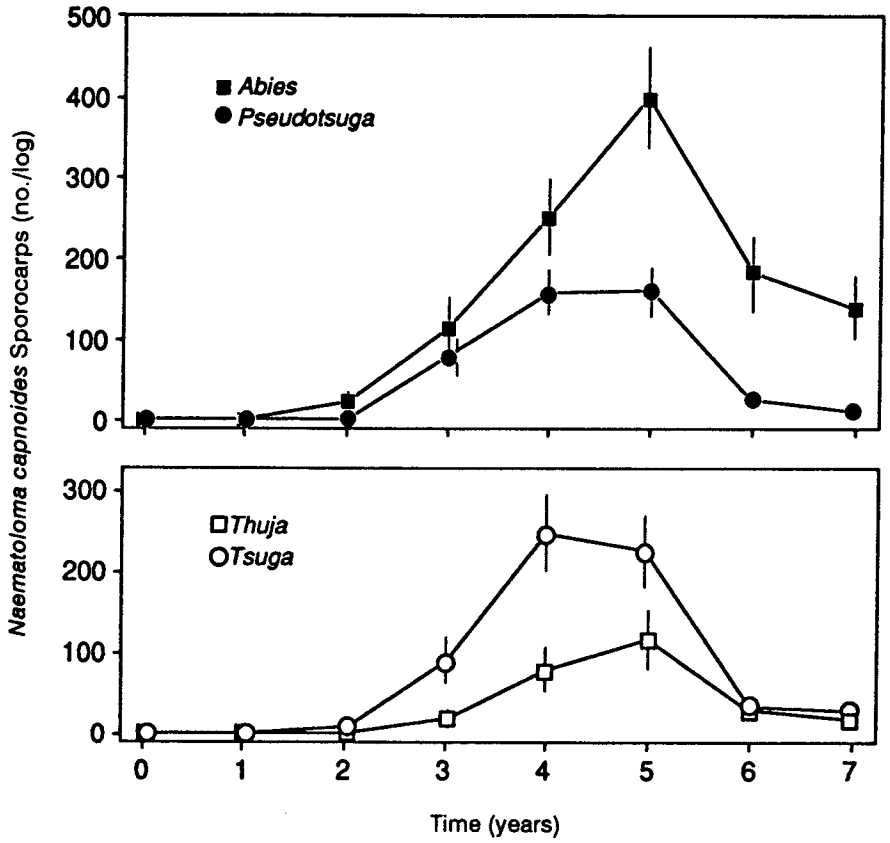

FIG. 1. Mean number (±1SE) of *Naematoloma capnoides* sporocarps on logs of four conifer species during the first 7 years of decomposition.

TABLE 3. Mass of sporocarps emerging from four species of conifer logs

Fungus	Year	Sporocarp mass (g/individual) Mean	SE	Sample size
Dacrymyces palmatus	All	0.106	0.013	5
Hericium abietis	All	46.450	5.543	3
Mycena occidentalis	All	0.031	0.008	5
Naematoloma capnoides	1987	0.072	0.156	7
	1988	0.211	0.303	9
	1989	0.403	0.625	5
	1990	0.468	0.449	3
	1991	0.387	0.053	4
	1992	0.528	0.037	4
Oxyporus cuneatus	All	0.115	0.018	8
Trametes versicolor	All	0.589	0.063	2

The jelly fungus *Dacrymyces palmatus* and the perennial sporocarp-forming *Fomitopsis pinicola* appeared on *Abies*, *Pseudotsuga*, and *Tsuga* logs. Sporocarps of the polypore *Oxyporus cuneatus* (Murr.) Aoshima and the mushroom *Mycena occidentalis* Murr. also began to form on *Thuja* logs at this time, as did the perennial sporocarps of *Ganoderma applanatum* (Pers. ex Wallr.) Pat on *Abies* logs. Uncommon fungal species observed growing on *Abies* logs after 5 years included *Boletus mirabilis* Murr., *Hericium abietis* (Weir ex Hubert) K.A. Harrison, *Phlebia tremellosus* (Schrad.:Fr.) Nakasone & Burdsall, and *Mycena epiterygia* (Fr.) S.F. Gray. The only other occasional species observed at this time were *Nidula canida* Pk. and *Pholiota lenta* (Fr.) Singer, which occurred on *Thuja* logs.

Sporocarp abundance

Abundance of the most common fungal species, *N. capnoides*, differed with both log species and time (Fig. 1). Analysis of variance indicated highly significant differences associated with time, log species, and the interaction of these two terms. *Naematoloma capnoides* was generally most abundant on *Abies* logs, and decreased in relative abundance on *Tsuga*, *Pseudotsuga*, and *Thuja* logs, respectively. This pattern changed with time, however. For example, abundance of *N. capnoides* decreased on *Tsuga* logs and increased on *Thuja* logs in years 5 and 6. This pattern was probably responsible for the highly significant log species × time interaction. The slower increase of *N. capnoides* on *Thuja* logs may have been the result of low numbers of insect galleries in that log species (Zhong and Schowalter 1989). The cause of the rapid decrease on *Tsuga* logs is not clear, especially because *Tsuga* logs had as many *N. capnoides* sporocarps in year 5 as did *Abies* logs.

The mean mass of *N. capnoides* sporocarps increased sevenfold during the period of observation (Table 3). Differences in size among years for this species were highly significant. Moreover, except for year 6 when an extensive autumn drought occurred, mean biomass increased steadily from 0.072 to 0.528 g/sporocarp. This trend resulted in a highly significant polynomial regression:

$$[2]\quad M_T = -0.358 + 0.255T - 0.019\,27\,T^2, \qquad r^2 = 0.90$$

where M_T is mass (grams) at time T (years). The pattern of the increase suggests that the size of the sporocarps increased as the wood became colonized.

Sporocarp nutrients

Temporal variations in nutrient concentrations appeared to be relatively minor (i.e., ± 25%) compared with the order of magnitude differences among species of fungi (Table 4). Concentrations of most nutrients in *N. capnoides* did not change greatly during the 6 years in which analyses were performed. Results of ANOVA indicated that only N, Mg, and Zn concentrations differed significantly over this period, whereas concentrations of Ca, Fe, K, Mn, and P were not significantly different. Zinc, which showed a significant linear decrease with time ($r^2 = 0.35$), was the only element to exhibit a systematic change in concentration.

In contrast to temporal variation, differences in nutrient concentrations among species of fungi were large (Table 4). The largest differences were for Ca (37-fold) and K (26-fold), whereas N, Fe, Mg, Mn, and Zn showed 6- to 10-fold differences among species. Although results of ANOVA indicated that differences among fungal species were highly significant, the species with the highest and lowest concentrations varied element by element. *Fomitopsis pinicola* had the lowest concentrations of N, Ca, Fe, K, and P, which might be expected from its "woody" nature. This species, however, also had the highest Mg concentration and the second highest Zn concentration. The concentrations of N, K, and P were highest in *M. occidentalis* and *N. capnoides*, both of which form fleshy mushrooms with a minimum of structural material. The highest concentrations of Ca, Fe, and Mn were found in resupinate forms such as *O. cuneatus* and *Trametes versicolor*, which have semi-woody sporocarps. Although the higher concentrations of N, K, and P occurred in species with a minimum of structural strength, it is not clear why higher Ca, Fe, or Mg concentrations were associated with more woody sporocarps.

Bioconcentration

The degree to which fungi concentrated nutrients from log tissues (hereafter referred to as "bioconcentration") depended upon both the element and the log species. *Naematoloma capnoides* concentrated K and P the most; these elements were 42–115 and 36–106 times greater than the initial concentrations in logs, respectively (Fig. 2). Other elements that exhibited higher concentrations in *N. capnoides* sporocarps than in logs included Mg (5–16 times greater), N (27–37 times greater), and Zn (6–20 times greater). In contrast, Ca concentrations for *N. capnoides* were 16–51% of the initial log concentration. The degree to which log species influenced the concentrations is best illustrated with the element Mn. For *Abies* and *Tsuga*, log species with relatively high concentrations of Mn, *N. capnoides* concentrations of Mn were similar to those of logs. However, for *Pseudotsuga* and *Thuja*, log species with low concentrations of Mn, *N. capnoides* concentrations were 2 and 11 times those found in logs, respectively.

The degree of bioconcentration was also a function of the fungal species growing on logs (Figs. 3*a* and 3*b*). The overall pattern of element concentrations was quite similar to that for *N. capnoides*, except that woody and perennial sporocarps (i.e., *Trametes versicolor* and *F. pinicola*) generally exhibited a lower increase in N, K, and P concentrations than did fleshy species. *Mycena occidentalis* was also notable in that it had relatively high Mn concentrations, despite the fact it grew exclusively on *Thuja* logs which were lowest in Mn concentrations. The only fungal species that had Ca

TABLE 4. Nutrient concentration of sporocarps emerging from four species of conifer logs

Fungus	Year	Nutrient content (μg/g)								Sample size
		Ca	Fe	K	Mg	Mn	N	P	Zn	
Fomitopsis pinicola	All	137 (35)	29 (7)	1 548 (178)	2686 (255)	45 (6)	5 120 (490)	545 (54)	70 (8)	6
Hericium abietis	All	222 (42)	68 (10)	20 012 (429)	341 (41)	13 (1)	12 300 (1080)	1697 (247)	18 (1)	9
Mycena occidentalis	All	691 (49)	74 (14)	40 121 (959)	1426 (77)	78 (2)	42 830 (4570)	8459 (367)	103 (4)	6
Naematoloma capnoides	1987	369	69	40 217	995	28	40 700	7098	64	1
	1988	331 (52)	196 (93)	33 301 (1259)	891 (28)	46 (5)	31 900 (900)	6751 (327)	62 (2)	7
	1989	368 (113)	88 (15)	32 456 (1754)	901 (31)	53 (13)	26 900 (1900)	6011 (314)	50 (3)	8
	1990	184 (32)	83 (19)	34 520 (1763)	826 (14)	30 (5)	26 900 (440)	6555 (324)	43 (1)	5
	1991	366 (40)	152 (41)	33 485 (1211)	771 (29)	92 (21)	27 770 (770)	6271 (456)	45 (1)	6
	1992	401 (25)	52 (3)	34 562 (840)	982 (7)	46 (13)	35 030 (770)	6557 (140)	50 (1)	8
	All	341 (30)	111 (22)	33 799 (614)	887 (16)	53 (6)	30 300 (820)	6437 (137)	51 (1)	35
Oxyporus cuneatus	All	5149 (194)	149 (18)	4 203 (257)	579 (23)	136 (21)	27 010 (450)	2486 (96)	51 (3)	8
Phelbia tremellosus	All	1240 (13)	52 (1)	9 533 (110)	731 (7)	81 (1)	20 150 (50)	4954 (53)	44 (1)	2
Trametes versicolor	All	2818 (382)	205 (9)	2 837 (502)	588 (31)	141 (5)	12 360 (1640)	1465 (194)	40 (6)	7

NOTE: Values are means with standard errors given in parentheses.

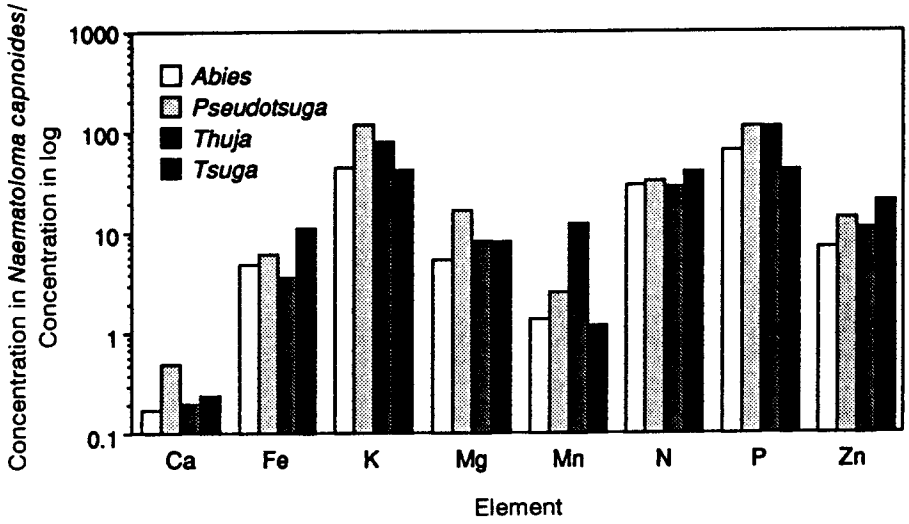

FIG. 2. Ratio of nutrient concentrations in *Naematoloma capnoides* sporocarps to those found in undecayed logs of four conifer species.

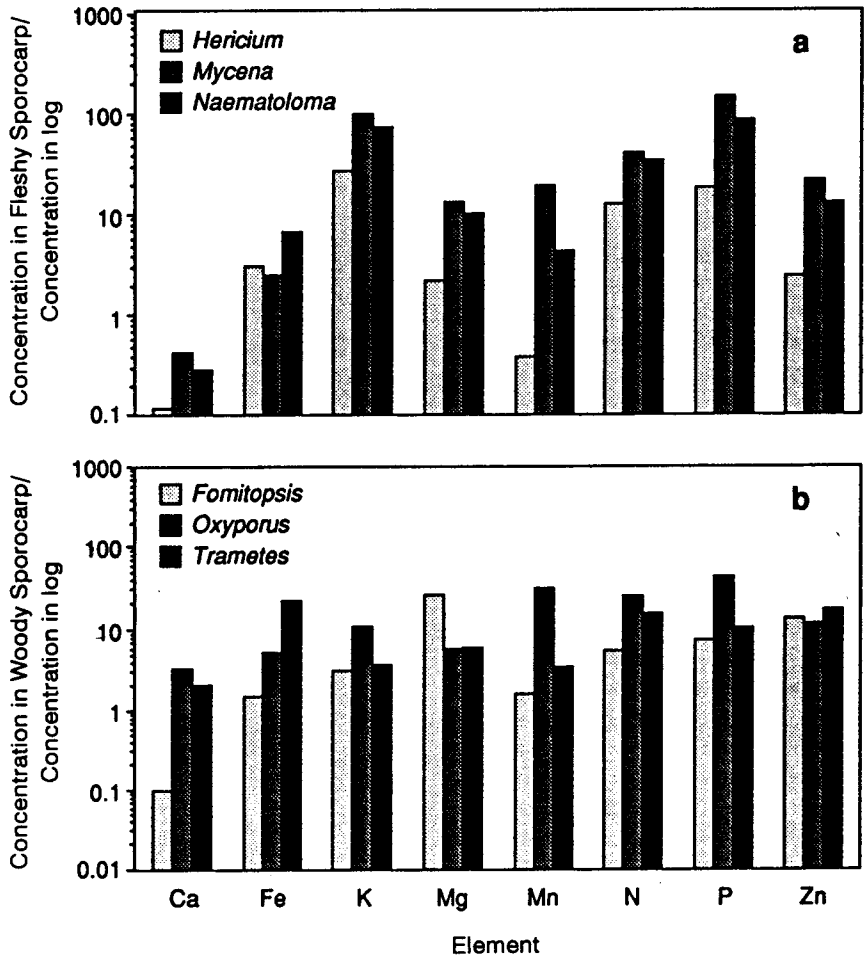

FIG. 3. Ratio of nutrient concentrations in selected (*a*) fleshy and (*b*) woody sporocarps to those found in undecayed logs of four conifer species. Nutrient concentrations in logs were for the log species most typical of the fungus in question, excepting *Naematoloma capnoides*, for which the average ratio was for all four species of conifer logs.

concentrations above those found in wood were *Trametes versicolor* (two times) and *O. cuneatus* (three times).

Nutrient export

Biomass and nutrients were exported from logs primarily in the form of annual sporocarps (Tables 5 and 6). Results of ANOVA indicated that differences in the amount of biomass and nutrients exported were highly significant among log species. *Abies* logs had the greatest cumulative production of annual and perennial sporocarps with 533 and 136 g/log, respectively. *Abies* logs exported the greatest amounts of all elements, except Ca and Zn; export from *Tsuga*,

TABLE 5. Cumulative mass and nutrients lost from logs (g/log) via annual sporocarps during the first 7 years of decomposition of four species of conifer logs

	Genus of log			
	Abies	*Pseudotsuga*	*Thuja*	*Tsuga*
Ca	0.206 (0.036)	0.059 (0.009)	0.367 (0.126)	0.242 (0.048)
Fe	0.051 (0.007)	0.018 (0.002)	0.018 (0.003)	0.045 (0.007)
K	16.250 (2.540)	5.653 (0.796)	3.250 (0.851)	8.333 (1.417)
Mg	0.432 (0.063)	0.148 (0.020)	0.115 (0.022)	0.261 (0.035)
Mn	0.027 (0.004)	0.008 (0.001)	0.013 (0.003)	0.026 (0.004)
N	14.080 (2.120)	4.709 (0.643)	4.257 (0.791)	7.536 (1.129)
P	3.122 (0.471)	1.074 (0.149)	0.729 (0.156)	1.638 (0.263)
Zn	0.024 (0.003)	0.008 (0.001)	0.008 (0.001)	0.140 (0.002)
Mass	543.1 (78.8)	177.3 (23.1)	154.3 (29.0)	342.4 (43.6)
Sample size	17	17	16	14

NOTE: Values are means with standard errors given in parentheses.

Pseudotsuga, and *Thuja* followed, in that order. Calcium differed in that *Thuja* exported the largest amount followed by *Tsuga*, *Abies*, and *Pseudotsuga*. The pattern for Ca is the result of *O. cuneatus*, which is one of the only species that concentrates Ca, and only grows on *Thuja*. The explanation for high Zn exports by *Tsuga* is less clear, because the fungi that grow on *Tsuga* logs do not appear to greatly concentrate this element.

The temporal pattern of nutrient export paralleled that of sporocarp numbers and biomass production (Figs. 4 and 5). As indicated by ANOVA for the annual sporocarps, effects associated with log species, time, and the interaction of these two terms for mass and for all elements except Ca were highly significant. Time differences for Ca were highly significant, and the time × log species interaction was significant. In addition, ANOVA for the perennial sporocarps indicated that effects associated with log species, time, and the interaction of these two terms for mass and for all elements were highly significant. The highly significant time × log species interaction for annual sporocarps was probably the result of the large decrease in sporocarp production on *Pseudotsuga* logs in years 6 and 7 compared with the other species. For perennial sporocarps the highly significant interaction was caused by both the rapid increase in abundance on *Abies* and the absence of perennial forms on *Thuja*.

The elements with the largest absolute mass exported (Tables 5 and 6) and proportional export (i.e., export divided by the initial element store in logs) were K, N, and P (Fig. 6). An exception in terms of proportional loss was Zn; 11.6% of the initial Zn store was exported from *Tsuga* logs. For the other three log species, however, <1% of the initial Zn was exported by sporocarps. Although sporocarps represented a very small mass loss (0.037–0.152% of the initial mass), they represented an important loss of nutrients. In *Abies* logs, for example, 2.95% of the N and 6.58% of the P initially stored in logs were exported within 7 years by sporocarps. Although this may appear to be a small proportion, it is occurring at a time when logs are generally considered to be immobilizing nutrients. Moreover, the initial stores used in these calculations include some log tissues, such as outer bark and heartwood, which are not presently being decomposed. During the first 7 years, *Abies* exported 5.4 and 8.5% of the N and P in decaying tissues, respectively. For *Thuja*, which had the lowest proportion of tissues decaying, 3.2% of the N and 4.7% of the P in decaying tissues were exported.

TABLE 6. Cumulative mass and nutrients lost from logs (g/log) via perennial sporocarps during the first 7 years of decomposition of four species of conifer logs

	Genus of log[a]		
	Abies	*Pseudotsuga*	*Tsuga*
Ca	0.011 (0.003)	0.003 (0.001)	0.002 (0.001)
Fe	0.002 (0.001)	0.001 (0.0002)	0.0004 (0.0001)
K	0.127 (0.037)	0.035 (0.012)	0.023 (0.009)
Mg	0.220 (0.064)	0.061 (0.010)	0.041 (0.016)
Mn	0.004 (0.001)	0.001 (0.0003)	0.0007 (0.0003)
N	0.420 (0.123)	0.116 (0.039)	0.077 (0.031)
P	0.045 (0.013)	0.012 (0.004)	0.008 (0.003)
Zn	0.005 (0.002)	0.001 (0.0005)	0.001 (0.0004)
Mass	135.8 (43.9)	24.7 (7.81)	19.1 (6.81)
Sample size	17	17	14

NOTE: Values are means with standard errors given in parentheses.
[a] *Thuja* did not have perennial sporocarps and was excluded.

Discussion

Traditionally logs have been viewed as long-term nutrient sinks, primarily because decomposers immobilize those log nutrients present in low concentrations until the later stages of decomposition (Harmon et al. 1986). This view is supported by chronosequence data for many elements, such as N, but is not necessarily indicated by the direct measurements of decomposition and nutrient cycling processes in logs. In one of the few time series studies of log decomposition, Edmonds and Eglitis (1989) found a net release of N, P, K, Ca, and Mn from *Pseudotsuga* logs that had decomposed for 10 years. For some elements, such as N, these losses exceeded 20% of the original store. Viewed from the perspective of critical element ratios (i.e., C/N), the net release of N, for example, at a C/N ratio of 1000 is indeed puzzling (Edmonds and Eglitis 1989). There are, however, numerous pathways that do not necessarily involve critical element ratios by which nutrients may leave logs. These pathways include leaching (Yavitt and Fahey 1985), absorption from mycorrhizae and roots, fragmentation (Sollins 1982; Harmon and Chen 1991), insects (Edmonds and Eglitis 1989), and fungal sporocarps.

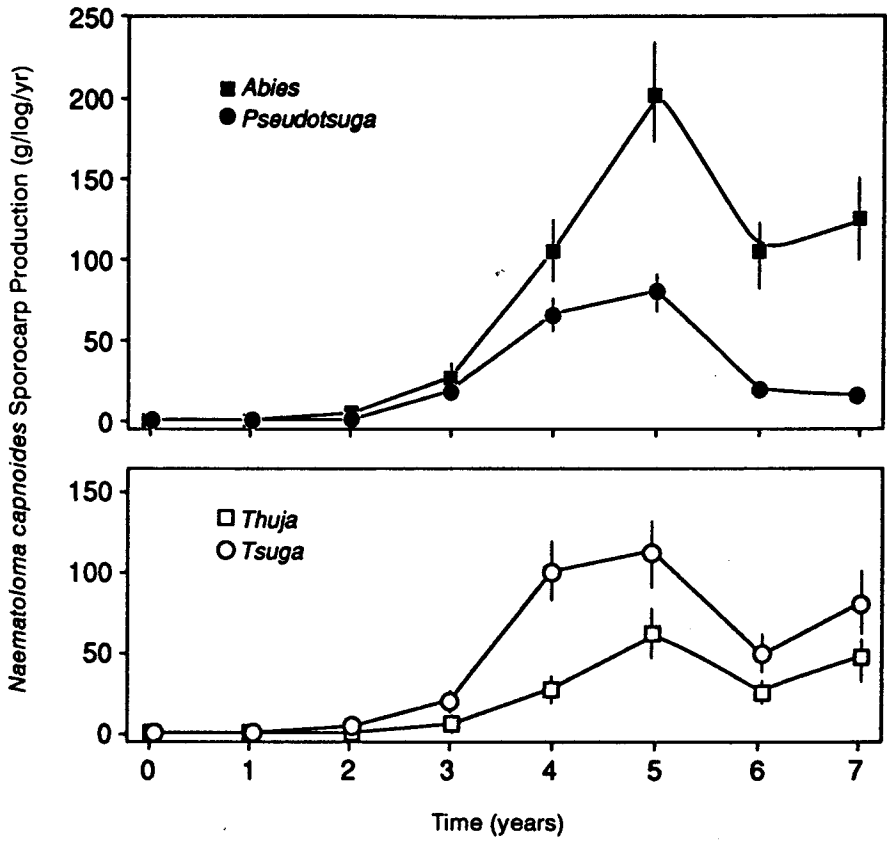

FIG. 4. Sporocarp production (±1SE) during the first 7 years of decomposition for four species of conifer log.

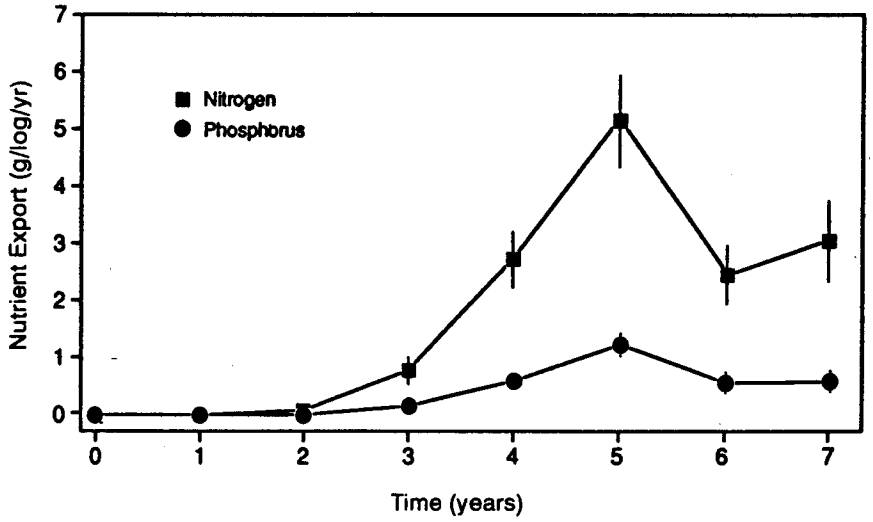

FIG. 5. Nitrogen and phosphorus losses (±1SE) during first 7 years of decomposition for *Abies* logs.

The discrepancy between earlier chronosequence studies and time series studies (Edmonds and Eglitis 1989; this study) of the timing of nutrient immobilization versus mineralization may stem, in part, from the fact that chronosequences measure the result of many processes, rather than the processes themselves. Moreover, the interpretation of chronosequences is strongly influenced by consideration of certain processes, such as fragmentation. For example, if nutrient concentrations increase during fragmentation, measurements would indicate a net mineralization of nutrients from logs. Fragmentation losses are ignored in most chronosequence studies, and this leads to the mistaken conclusion that nutrients are being immobilized. Finally, compared with such materials as leaves, the nutrient concentrations of wood and bark are low and spatially variable. Thus, considerable variation can be associated with sample collection (i.e., degree and type of pooling) and the precision of the analysis method. This variation can obscure actual changes in nutrient concentrations. Moreover, very small fluxes may be measured directly and with greater precision than is possible by inference from changes in chronosequence concentration.

The observed patterns of nutrient concentrations are quite similar to those observed in other studies of basidiomycete sporocarps (Hinneri 1975; Vogt and Edmonds 1980) and mycelia (Lodge 1987). Fungi are known to have increased concentrations of N, K, and P relative to plant tissues or

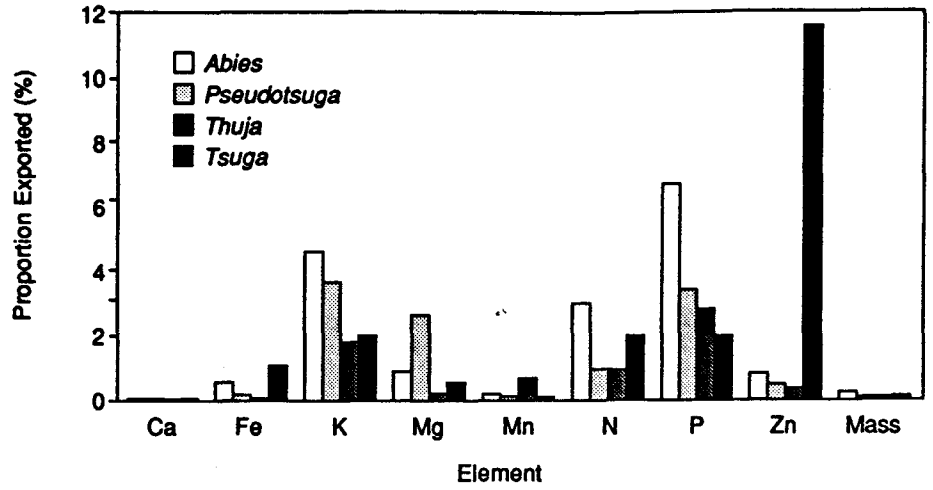

FIG. 6. Proportion of the initial mass and nutrient stores exported by fungal sporocarps in the first 7 years of decomposition of four species of conifer log.

decomposing litter. In contrast, fungal sporocarps are typically lower in Ca than are either plant tissues or decomposing litter. The primary difference with past studies is that sporocarps formed on wood increase nutrient concentrations to a far greater degree than do those growing on forest floors or soil. For example, Vogt and Edmonds (1980) found that N, P, and K concentrations in sporocarps averaged 2.7, 4.6, and 15 times greater than those found in forest floors, respectively. Results of this study indicate that sporocarps growing on logs had concentrated these same elements to a much greater extent (i.e., an order of magnitude). This means that, in terms of a nutrient flux, an order of magnitude less biomass loss is required to remove a similar proportion of these elements from decomposing wood.

In the log species examined in this study, sporocarp formation appears to be the major pathway of N and P loss from logs in the early stages of decomposition. Edmonds and Eglitis (1989) found that 0.04 and 0.02% of the N and P, respectively, were removed from *Pseudotsuga* logs by the formation of bark beetle (*Dendroctonus pseudotsugae* Hopkins) galleries. Zhong and Schowalter (1989) found that ambrosia beetles (*Trypodendron lineatum* Oliver and *Gnathotrichus sulcatus* LeConte) removed up to 0.20% of the wood and bark volume during the first 2 years of decomposition. Given the observed concentrations of N and P in wood and the bark of these logs, this amount of removal would account for 0.1 and 0.2% of the N and P, respectively. Leaching losses are also small compared with that removed by fungal sporocarps. We have been measuring the flow of water, C, and N associated with leaching from a subset of 24 logs at these same six sites (M.E. Harmon and J. Sexton, in review). These measurements take into account the inputs to logs via throughfall, the nutrients washed from the surface via runoff, and the leachates draining from the bottom. Preliminary data indicate that logs were net sources of N in each of the first 7 years; according to preliminary estimates, a total of 3.9–5.5 g of N and 570–675 g of organic matter were lost via water from logs during this time. This amounts to 0.7–1.5% and 0.2–0.3% of the initial N and organic matter, respectively. In contrast, sporocarps removed 0.9–3.0% and 0.04–0.15% of the initial N and organic matter, respectively. These exports are occurring in logs with C/N ratios of 400–600 (Harmon 1992).

Sporocarp formation on logs differs from that in soil or on litter on the forest floor. Logs are separate structures lying above the forest floor. When a sporocarp decomposes on the forest floor, it basically returns to the forest floor (although in some cases at a different location). In the forest floor context, the case has been made that sporocarps immobilize highly mobile nutrients such as K (Vogt and Edmonds 1980). In contrast, when a sporocarp falls from a log, it is transferred to the forest floor. Thus, this transfer should be viewed as a mobilizing process. The nutrient efflux from logs occurs when fungi are concentrating and immobilizing nutrients within the log. Therefore, fungi appear to be simultaneously transferring nutrients outside the log "ecosystem" and immobilizing nutrients within the log.

The factors that control the spatial and temporal extent of sporocarp-mediated fluxes from decaying wood in most forest ecosystems are unknown. Results of this study suggest that the size of the sporocarp-mediated nutrient flux from logs depends upon the log species, the fungi decomposing the log, and the stage of log decay. *Abies*, which had the fastest rate of decay, supported a greater production of sporocarps and nutrient export than did *Thuja*, which had the slowest rate of decay. Thus, as the decay resistance of the log species increases, the flux apparently decreases. In terms of fungal species, logs being decomposed by species with woody perennial sporocarps export more Mg and less of the other nutrients than do logs being decomposed by fungi that form fleshy sporocarps. In addition, time influences sporocarp-mediated fluxes in a more complicated way than do either fungal or log species. During the early stages of decay, increases in the flux over time are probably associated with increased colonization by decomposers. Carpenter et al. (1988) found little colonization by basidiomycetes in the first year; however, by the 2nd year basidomycetes had started to colonize logs and form sporocarps (Griffiths et al. 1993). The complete colonization of sapwood by wood-decomposing fungi can take many years in the Pacific Northwest (Buchanan and Englerth 1940). Ongoing studies indicate that the spread of decay in sapwood has not been completed in the first 7 years of decay for any of the species examined except *Abies* (M.E. Harmon, unpublished data). Eventually the sporocarp-mediated flux from logs should decrease when extensive sapwood and inner bark decay

occurs. This process may have already started, and would explain the decrease in sporocarp fluxes in years 6 and 7 for most logs. The temporal pattern in sporocarp-mediated flux also parallels temporal change in respiration rates (M.E. Harmon, unpublished data), and indicates that the vigor of the fungal community decreases once the initial colonization phase nears completion.

Acknowledgments

This study has been supported by grants from the National Science Foundation (DEB 80-12162, BSR-8514325, BSR-8516590, BSR-8717434, BSR-8918643, and BSR-9011663) and research work units 4151 and 4356 of the USDA Forest Service, Pacific Northwest Research Station, Portland, Oreg.

Arthur, M.A., and Fahey, T.J. 1990. Mass and nutrient content of decaying boles in an Engelmann spruce – subalpine fir forest, Rocky Mountain National Park, Colorado. Can. J. For. Res. **20**: 730–737.

Ausmus, B.S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. Ecol. Bull. **25**: 180–192.

Brown, R.P., and Parsons, R.B. 1973. Soil of the reference stands—Oregon IBP. University of Washington, Seattle. US/IBP Coniferous For. Biome Internal Rep. 128.

Buchanan, T.S., and Englerth, G.H. 1940. Decay and other volume losses in windthrown timber on the Olympic Peninsula, Washington. U.S. Dep. Agric. Tech. Bull. 733.

Carpenter, S.E., Harmon, M.E., Ingham, E.R., Kelsey, R.G., Lattin, J.D., and Schowalter, T.D. 1988. Early patterns of heterotroph activity in conifer logs. Proc. R. Soc. Edinburgh, **94B**: 33–43.

Chen, H. 1989. Studies on tree mortality and log decomposition of main species in conifer–deciduous mixed forest on Changbai Mountain Reserve. M.S. thesis, Academia Sinica, Shenyang, People's Republic of China.

Deyrup, M.A. 1976. The insect community of dead and dying Douglas-fir: Diptera, Coleoptera and Neuroptera. Ph.D. thesis, University of Washington, Seattle.

Dyrness, C.T., Franklin, J.F., and Moir, W.H. 1976. A preliminary classification of forest communities in the central portion of the west Cascades in Oregon. University of Washington, Seattle. US/IBP Coniferous For. Biome Bull. 4.

Edmonds, R.L., and Eglitis, A. 1989. The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. Can. J. For. Res. **19**: 853–859.

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.

Frankland, J.C., Hedger, J.N., and Swift , M.J. (*Editors*). 1982. Decomposer basidiomycetes: their biology and ecology. Cambridge University Press, Cambridge, UK.

Franklin, J.F., Cromack , K., Jr., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F., and Juday, G. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-118.

Franklin, J.F., Shugart, H.H., and Harmon, M.E. 1987. Tree death as an ecological process. BioScience, **37**: 550–556.

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

Griffiths, R.P., Harmon, M.E., Caldwell, B.A., and Carpenter, S.E. 1993. Acetylene reduction in conifer logs during early stages of decomposition. Plant Soil, **148**: 53–61.

Harmon, M.E. 1992. Long-term experiments on log decomposition at the H.J. Andrews Experimental Forest. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-280.

Harmon, M.E., and Chen, H. 1991. Coarse woody debris dynamics in two old-growth ecosystems: comparing a deciduous forest in China and a conifer forest in Oregon. BioScien **41**: 604–610.

Harmon, M.E., and Franklin, J.F. 1989. Logs as sites of tree reg eration in *Picea–Tsuga* forests of coastal Washington a Oregon. Ecology, **70**: 48–59.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Grego S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., a Cummins, K.W. 1986. Role of coarse woody debris in te perate ecosystems. Adv. Ecol. Res. **15**:133–302.

Harvey, A.E., Larsen, M.J., and Jurgensen, M.F. 1981. Rate woody residue incorporation into northern Rocky Mounta forest soils. USDA For. Serv. Res. Pap. INT-282.

Hinneri, S. 1975. Mineral elements of macrofungi in oak-ri forests on Lenholm Island, inner archipelego of SW Finlan Ann. Bot. Fenn. **12**: 135–140.

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

Keenan, R.J., Prescott, C.E., and Kimmins, J.P. 1993. Mass an nutrient content of woody debris and forest floor in western r cedar and western hemlock forests on northern Vancouv Island. Can. J. For. Res. **23**: 1052–1059.

Kelsey, R.G., and Harmon, M.E. 1989. Distribution and variati of extractable total phenols and tannins in the logs of fo conifers after 1 year on the ground. Can. J. For. Res. 1 1030–1036.

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

Little, S.N., and Ohmann, J.L. 1988. Estimating nitrogen lo from forest floor during prescribed fires in Douglas-fi western hemlock clearcuts. For. Sci. **34**: 152–164.

Lodge, D.J. 1987. Nutrient concentrations, percentage moistu and density of field collected fungal mycelia. Soil Biol. Bi chem. **19**: 727–733.

McFee, W.W., and Stone, E.L. 1966. The persistence of deca ing wood in humus layers of northern forests. Soil Sci. So Am. Proc. **30**: 513–516.

McKee, A., and Bierlmaier, F. 1987. H.J. Andrews Experiment Forest, Oregon. *In* The climate of long-term ecological resear sites. *Edited by* D. Greenland. Institute of Arctic and Alpi Research, University of Colorado, Boulder. Occas. Pap. 4 pp. 11–17.

Rayner, A.D.M., and Boddy, L. 1988. Fungal decomposition wood, its biology and ecology. John Wiley & Sons, New Yor

SAS Institute Inc. 1985. SAS/Stat guide for personal comput ers, version 6 edition. SAS Institute Inc., Cary, N.C.

Schowalter, T.D., Caldwell, B.A., Carpenter, S.E., Griffiths, R.P., Harmon, M.E., Ingham, E.R., Kelsey, R.G., and Lattin, J.D. 1992. 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.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Can. J. For. Res **12**: 18–28.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D., and Spycher, G. 1987. Patterns of log decay in old-growth Douglas-fir forests. Can. J. For. Res. **17**: 1585–1595.

Spies, T.A., Franklin, J.F., and Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology, **69**: 1689–1702.

Swanson, F.J., and Lienkaemper, G.W. 1978. Physical consequences of large organic debris in Pacific Northwest streams. USDA For. Serv. Gen. Tech. Rep. PNW-69.

Triska, F.J., and Cromack, K., Jr. 1980. The role of wood debris in forests and streams. *In* Forests: Fresh Perspectives from Ecosystem Analysis. Proceedings, 40th Annual Biology

Colloquium, 27–28 Apr. 1979, Corvallis, Oreg. *Edited by* R.H. Waring. Oregon State University Press, Corvallis. pp. 171–190.

Vogt, K.A., and Edmonds, R.L. 1980. Patterns of nutrient concentration in basidiocarps in western Washington. Can. J. Bot. **58**: 694–698.

Yavitt, J.B., and Fahey, T.J. 1985. Chemical composition of interstitial water in decaying lodgepole pine bole wood. Can. J. For. Res. **15**: 1149–1153.

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