Early patterns of heterotroph activity in conifer logs

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Synopsis

Findings from the first two years of a long-term study of conifer log decomposition are presented. Log decomposition is regulated by the physical and chemical states, and development of decomposer foodwebs. The functional group with the greatest initial effect on the log is the channelisers, represented in our study by ambrosia and bark beetles. They not only create multitudes of channels into the logs but vector the initial decomposer community. Ambrosia beetles exclude certain elements of the decomposer community from channels until they vacate the log, at the end of their reproductive phase. The foodweb during the early stages of decomposition includes nitrogen-fixing and other bacteria, fungi, protozoa, nematodes, and arthropods. Seasonal fluctuations of temperature and moisture are hypothesised to work in tandem to modulate the activities of the decomposer community.

Introduction

Our study focuses upon the fallen tree as a unit of disturbance. Although the plant succession and tree population aspects of this disturbance have been examined in detail (Watt 1947; Pickett & White 1985; Harcombe 1987), fewer studies have examined the succession of decomposers initiated by this event.

Dead trees represent a large mass of persistent and widespread decomposer habitat in the Pacific Northwest. Dead trees persist for centuries (McFee & Stone 1966; Triska & Cromack 1980), and therefore may influence an ecosystem for as long a time as living trees. Western Oregon and Washington contain c. 60 million km² of coniferous forest, of which 25% is over 250 years old and considered old-growth (Haynes 1986). Coarse woody debris (CWD) comprises 22% of the aboveground mass and 81% of the aboveground detritus inputs in old-growth forest (Sollins *et al.* 1980). Logs comprise *c*. 60% of CWD, with an average volume and mass of 500 m³ ha⁻¹ and 110 Mg ha⁻¹, respectively (Harmon *et al.* 1986).

The large dead tree mass in the Pacific Northwest results from a combination of high input rates and low decomposition rates (Harmon *et al.* 1986). Tree mortality is a major detrital pathway in old-growth conifer forests, accounting for 55% of the above-ground detritus (Sollins 1982). Cause of mortality varies throughout the region, but 40% of the trees are felled by wind in the Cascade Mountains (Harmon *et al.* 1986). Thus, a large portion of log inputs are from living trees and not solely from dead trees. Decomposition rates in the Pacific Northwest are slower than most other temperate forests (Harmon *et al.* 1986). The half-time of decay for large *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) logs is fifty years (Graham 1982), although fragments may persist up to 400 years (Triska & Cromack 1980).

The majority of biological activity in the first year occurs near galleries excavated by scolytid beetles. Scolytid beetles excavate galleries in the inner bark and sapwood of newly-fallen logs, innoculating them with phoretic fungi, nematodes, bacteria and other organisms that form a decomposer foodweb. Free-living nitrogen fixing bacteria carried by bark beetles (Bridges 1981) may be an important foodweb component, as wood has a high C:N ratio (Ausmus 1977; Cowling & Merrill 1966). Galleries also increase gaseous exchange in logs and create entry sites for nonphoretic decomposers. Despite the fact that Scolytids initiate decomposition within the inner bark and sapwood, parasitic, wood-decomposing basidiomycetes such as *Armillaria mellea* (Vahl:Fr.) Kummer, *Heterobasidion amnosum*, Bref., *Fomitopsis pinicola* (Fr.) Karst., *Phaeolus schweinitzii* (Fr.) Pat., and *Phellinus pini* (Fr.) Ames are often present within the heartwood of newly fallen trees (Boyce 1932; Englerberth 1942).

We are studying log decomposition using a time-series. To date our observations include two years of decomposition, but the study is planned to continue into the twenty-first century. We have designed the study for the following reasons:

- (1) Chronosequence studies give only approximate decay rates.
- (2) The community ecology of conifer log decomposers has been neglected (Käärik 1974; Frankland *et al.* 1982). Most studies have focused on either the ambrosia beetle symbiosis (Francke-Grosmann 1963; Batra 1966, 1985) or the vectoring of blue-stain organisms in commercial timber (Davidson 1953; Dowding 1984).
- (3) Most existing decomposition studies of conifer logs emphasise fungi, ignoring the effects of other species (Blanchette & Shaw 1978; Ausmus 1977).
- (4) Detailed log decomposition studies in old-growth conifer forests are lacking. Past studies of heterotroph decomposition of logs have focused on angiosperms, rather than gymnosperms (Swift & Boddy 1984; Chapela *et al.* 1988).

Methods

Our study is being conducted within intact old-growth *Pseudotsuga-Tsuga* forests at the H. J. Andrews Experimental Forest, on the west slope of the Cascade mountain

range in Oregon. Mean annual temperature is 8.5°C, and mean annual precipitation is 230 cm with 75% falling as rain between October and March. Four conifer species are being studied: *Abies anabilis* Dougl. ex Forbs (silver fir), *Pseudotsuga menziesii* (Douglas fir), *Thuja plicata* D. Don (western red cedar), and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock).

In late summer 1985, living trees were harvested from nearby forests, cut into 500 logs and placed on the forest floor at six old growth forest sites. The time of year was selected to simulate natural log-throw, the majority of which takes place in autumn and winter (Gratkowski 1956). Logs were 5.5 m long and 45–60 cm in diameter. Only logs without heartrot and with bark cover >90% were used. Cross-sections were removed from the ends of each log for analysis of initial density, moisture content and chemistry. We destructively sampled forty-eight logs during the first two years of the study.

Fungi were isolated from wood samples and from live arthropods before they entered the logs. Fungi carried by live insects were isolated from water rinses and dissections of the exoskeleton and gut. Fungi were isolated from surface scrapings of scolytid galleries and small chips from outer and inner bark, sapwood and heartwood of all log species.

Insects were caught in traps placed on or near logs at each site. Nematodes were isolated from material scraped from along 1 cm lengths of galleries or from 1 cm³ blocks of wood containing a known gallery length using Baermann extractors. Microarthropods were extracted from thin sections of wood using a modified Merchant-Crossley extractor (Merchant & Crossley 1970).

Numbers of protozoa, fungi, and bacteria inside sapwood galleries were determined from scrapings of gallery surfaces. Our work centred on galleries, because most taxa except fungi were probably not present within the wood itself. This procedure does underestimate the total abundance of fungi within a log. Scrapings were placed in phosphate buffer at pH 7.6 and serially diluted. Fungal length was determined following the methods of Ingham & Klein (1984) and bacterial numbers were calculated following staining of an aliquot with fluorescein isothiocyanite (Babiuk & Paul 1970), filtering and destaining for counting (Tate & Klein 1983). Total protozoan numbers were calculated using a Most Probable Number (MPN) technique (Darbyshire *et al.* 1974; Frey *et al.* 1985).

Respiration rates were measured in the field using the alkali trap method (Page *et al.* 1982). Two respiration chambers were mounted on twenty-four logs and measurements were taken at monthly intervals.

Results and discussion

Chemical composition

The initial chemical composition of logs determines, in part, which species initially colonise and become established. When a tree is felled, it is not biologically dead: respiration continues (Table 1). During winter, inner bark becomes saturated with moisture. This condition combined with spring warming leads to ethanol fermentation within the phloem and cambium (Moeck 1970). Ethanol production in turn attracts nonaggressive bark beetles and ambrosia beetles (Klimetzek *et al.* 1986). This attraction is increased by the presence of volatile terpenes (Bauer & Vite 1975;

	Outer Bark		Inner Bark		Sapwood		Heartwood	
Douglas fir	0.740	$(0.253)^1$	3.810	(0.702)	0.191	(0.027)	0.0045	(0.0040)
Silver fir	5.040	(0.739)	4.550	(0.749)	0.300	(0.132)	0.2700	(0.0080)
Western hemlock	0.909	(0.351)	3.050	(1.084)	0.080	(0.005)	0.0000	(-()-)
Western red cedar	0.335	(0.280)	8.720	(0.922)	0.724	(0.089)	0.0081	(0.0021)

Table 1. Respiration rates in newly-cut logs; mole $CO_2/g/da$.

¹Mean standard deviation, N = 3

Borden *et al.* 1982). Ethanol may signal host acceptability, indicating an environment suitable for fungal cultivation and successful brood establishment. This phenomenon may differ for each tree species, as Chapman (1963) reported western red cedar vapours were less attractive to scolytid beetles than those of Douglas fir and western hemlock.

The initial chemical composition also influences the rate at which tissues decompose once a decomposer community has established in logs. Dihydroquercetin in Douglas fir bark and heartwood is believed to be partially responsible for its durability (Kennedy 1956; Rudman 1962, 1963); and thujaplicins and lignans both contribute to the decay resistance of western red cedar heartwood (Rennerfelt 1948; Roff & Atkinson 1954; Rudman 1962, 1963; Barton & McDonald 1971; MacRae & Towers 1984). Phenolics, particularly tannins, bind and precipitate protein, deactivating hydrolytic enzymes produced by the microorganisms for the digestion of plant cell walls (Swain 1979).

Introduction of decomposers by scolytids

There appeared to be three important first-year decomposition events in these conifer logs: (1) introduction of phoretic community by beetles; (2) domination of sapwood community by the ambrosial symbiosis (3–4 weeks); (3) colonisation of scolytid galleries by a microaerophilic community.

The decomposer community introduced to logs by beetles consists of fungi, nitrogen-fixing bacteria and other bacteria (Bridges 1981; Haanstad & Norris 1985), nematodes (Massey 1966) and acarids (Krantz 1965; Lindquist 1967, 1970). Although our discussion centres around ambrosia beetles, other arthropods also enter galleries and innoculate logs with additional species of bacteria, fungi, protozoa, and nematodes (Ausmus 1977; Massey 1974; Dowding 1974, 1984). Most fungi do not become established in ambrosia beetle galleries until *after* the beetles have completed their reproductive phase: we do not yet know how these scolytids exclude other fungi (Batra 1966), although phoretics are found on overwintering ambrosia beetles, on emigrating young adults and in vacated galleries. Fungi can colonise vacated galleries within twenty-four hours (Batra 1966).

Ambrosia beetles are abundant and have a large potential to vector fungi and other organisms to logs. The average Douglas fir log in our experiment had 295 ambrosia beetle galleries per square metre of surface area. Given this attack density, a single dead tree with a surface area of 40 m² (dbh = 50 cm) would have c. 12,000 galleries and 24,000 beetles. The total potential reproductive output would be c. 188,000 offspring (15.7 offspring per gallery, Shore *et al.* 1987). Table 2 demonstrates the ability of this population to inoculate fungi into logs.

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Reproduction of phoretic species is tied to the scolytid life-cycle. We identify two reproductive types: obligate and facultative. Obligate phoretics are like ambrosial fungi: their life-cycles are in strict phase with those of the scolytids. This group includes nematode parasites and phoretic mites of scolytids. Facultative phoretics may be generally adapted to a group of morphologically related vectors such as scolytids (the auxiliary fungi of Batra [1985]) or may lack specific adaptations to vectors but are carried by chance occurrences. In the present study the latter were represented by the litter fungi, none of which survived in the insect galleries (Table 2).

An example of these strategies is provided by the fungal community carried by the ambrosia beetle *Trypodendron lineatum* (Olive), the most common vector in our study. *Ambrosiella ferruginea* (Mathieson–Käärik) Batra, an obligate symbiont of ambrosia beetles, dominates the community first in sapwood galleries. Other fungi are actively excluded by *T. lineatum* for 3–4 weeks until larvae pupate (Bright 1976). Other decomposers flourish where parent beetles leave the galleries and while larvae mature to adulthood. At this time, obligate phoretics begin their reproductive cycle so that propagules will be transported to a new log, by emerging adults. Organisms such as *Ophiostoma* with extended life-cycles may be opportunistically carried on ambrosia beetles, but they are also vectored by animals visiting brood chambers after the scolytids have left. Other facultative organisms such as litter fungi are not vectored from galleries, but are acquired by adult beetles, during their overwintering stage in litter and bark crevices (Kinghorn & Chapman 1959). Even though many propagules of litter fungi are moved by beetles, few survive and reproduce there. The

Table 2.	Estimated propagule inputs and outputs in Douglas fir logs mediated by	ſ
	Trypodendron lineatum ¹ .	

			%Freq			
Taxon	Propagules per beetle	Propagule input/tree	propagules in gallery	Propagule output/tree		
Basidiomycetes	1.30	31125	10.9	26576		
Mucorales	0.50	12375	0	-		
Yeasts	17.00	405375	3.6	114316		
Acremonium	0.10	2625	0	-		
Botrytis	1.70	41625	0	-		
Cladosporium	2.20	51750	0	-		
Drechslera	0.50	12375	0			
Epicoccum	0.01	375	0	-		
Hormonema	0.06	1500	0	-		
Mortierella	0.40	9375	0			
Nectria	0.05	1125	1.4	123		
Oidiodendron	0.08	1875	0			
Ophiostoma	7.72	185250	68.8	998374		
Penicillium	7.81	187500	8.0	117500		
Thysanophora	0.95	22875	0	_		
Trichoderma	0.36	8625	0.7	473		

¹Estimates based on colonisation of 24,000 beetles/tree with emigrating brood of 188,000; propagule numbers determined from washings of ten individual beetles from each of six sites and isolations from galleries in twenty-four logs from the same sites; propagule input calculated as (propagules/ beetle) × (24,000 beetles/log); propagule output calculated as (propagules/ beetle) × (% freq. in galleries) × (188,000 brood/log); estimates do not include fungi isolated from insect guts.

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overall effect of gallery construction in newly fallen trees is a massive inoculation of decomposer fungi, most notably, *Ophiostoma* and *Penicillium*.

Foodweb structure

Analysis of the foodweb structure of vacant ambrosia beetle galleries of logs eighteen months after felling revealed that bacteria and fungi (including yeast states) form the base of the decomposer foodweb in insect galleries (Table 3). Bacteria are grazed by amoebae, ciliates and nematodes, including *Parasitorhabditis*, *Panagrolaimus* and *Acrostichus*. Fungi are grazed by fungal-feeding amoebae if present, and by insects. The insect portion of the foodweb was not thoroughly examined, but its structure is probably complex. Savely (1939), for example, found that one-year-old pine logs contained thirteen fungal feeding insect genera, ten genera of phloem feeding insects, and ten predaceous genera.

Total hyphal lengths in Douglas fir sapwood were c. four times longer than that of red cedar. More fungal biomass occurs within the wood, but this was not sampled. There were 10^6 yeast cells per cm of gallery, but this must be used cautiously as samples were incubated for seven to ten days before quantification.

Protozoan numbers were fairly consistent: flagellates were not found in any eighteen-month-old gallery examined; amoebae and ciliates generally averaged 10^3 to 10^4 per cm of gallery. The estimate of amoebal numbers was typical of soil levels (1,000 to 10,000 per gram), but that of ciliates was 100 to 1000 times greater than numbers commonly found in local forest soils.

Nematode numbers varied more than bacteria, protozoa or fungi. Many galleries were found without any nematodes present, while others were found to contain 400 to 600 per cm. The structure of nematode communities was limited in the first year of colonisation: only nematodes, such as *Parasitorhabditis*, *Aphelenchoides*, *Panagrolaimus* and *Acrostichus*, which have been shown to be beetle associates, were found.

Organism	Douglas fir	Red cedar	
Bacteria	1×10^{10}	$1 \times 10^{4} - 10^{5}$	
Fungi	250 metres	60 metres	
Protozoa			
Flagellates	-0-	-0-	
Amoebae ^a	5×10^{4}	-0-	
Ciliates ^b	3×10^{4}	-0-	
Nematodes			
Bacterial feeders ^e	80	2	
Fungal feeders ^d	23	3	
Nematode predators	-0-	-0-	

 Table 3.
 Food web components and densities in insect galleries in eighteen-monthold logs of Douglas fir and western red cedar (# per cm length of gallery).

^aNaeglaria and some Myxoamoebae.

^bColpoda exclusively.

^eParasitorhabditis thornei, undescribed Digastroidea, Panagrolaimus sp.

^dAphelenchoides, Tylenchorhynchus, Tylenchus.

Seasonal moisture changes

Little information exists on moisture fluctuations in logs (Harmon *et al.* 1986), despite its importance in determining decomposer activity. Unlike branchwood, which undergoes large, short-term fluctuations (Boddy 1983), logs are more buffered from dry/wet cycles. Large seasonal variation occurred in the outer and inner bark, with maximum moisture content in March and minimum moisture content in September (Fig. 1). During the summer, the outer bark often drops below the fibre saturation point, limiting decomposer activity. On the other hand, inner bark during winter is excessively wet which restricts gaseous exchange and consequently aerobic biological activity is also probably restricted. There was much less variation in the moisture content of heartwood and sapwood than for bark.

Ecosystem processes

In addition to defining the decomposer community, it is important to know how it controls decomposition and nutrient cycling processes. Measurements of leaching,



Figure 1. Seasonal changes in moisture content of western hemlock logs; the vertical lines indicate standard error of the mean (N=6);

- (A) Inner (\bullet) and outer bark (\blacktriangle);
- (B) Heartwood (▲) and Sapwood (●).

fragmentation, and respiration rates integrate decomposer community activity and indicate the constraints it operates under. Respiration data illustrate how the interaction of decomposers and environment influence ecosystem processes.

No single factor controls log respiration rates (Fig. 2). The most obvious explanation for the difference in respiration rates between the two years is that the foodweb of logs in the second year is much more efficient in degrading the log than the foodweb in the first year. Respiration rate also changes seasonally, with the highest rates in late summer and the lowest in winter and spring. This is caused by an interaction of temperature and moisture content: when moisture is high or temperature low, respiration is low (Boddy 1986). The dramatic increase in respiration in August–September 1987, for example, is correlated with the drying of the inner bark and not temperature increase.

The species of log also influences respiration rate in the early stages of decomposition, but in unexpected ways. Douglas fir logs respired faster than western hemlock logs during the first two years of decomposition; at first sight this may seem inconsistent with the greater decay resistance of the former species (U.S. Forest Products Laboratory 1967). However, these decay resistance ratings are based on



Figure 2. Respiration of (A) Douglas fir and (B) western hemlock during second year of decomposition; the mean is indicated by lines with circles, while the standard error of the means is indicated by the vertical lines (N = 6).

 Table 4. Hypothetical interactive community oscillations in logs.

	Spring	Autumn	
Active community	Ascomycetes & anamorphs	Basidiomycetes	
Moisture content	High	Low	
Oxygen content	Low	High	
Nitrogen fixation	High	Low	
Log respiration	Low	High	

heartwood, and this layer does not initially decay. Losses from western hemlock will probably exceed those of Douglas fir, when heartwood of the latter begins to decompose.

We hypothesise that seasonal changes in log moisture content leads to seasonal shifts in decomposer activity during the early phases of log decomposition (Table 4). For example, acetylene-reduction activity in the inner and outer bark was high in late winter and low in summer, indicating an inverse relationship with moisture content. In the early stages of decomposition ascomycetes and basidiomycetes are both present in logs. During autumn and winter, the high moisture content of bark may be more favourable for anamorphic ascomycetes and bacteria than for basidiomycetes (Levy 1982; Boddy 1986). The dryer conditions of autumn in our ecosystem may be more favourable to basidiomycetes.

Acknowledgments

Sincere appreciation is extended to our technical assistants: Jay Sexton, Joyce Eberhart, Anthony Floyd, John Chamard, and Karen Andersen. We are indebted to Bruce Caldwell and Robert Griffiths, who freely shared their observations on nitrogen fixation and respiration in logs. We are grateful for facilities provided by the USDA Forest Service, Forestry Sciences Laboratory (without which, this work could never have been done) and for funding provided by National Science Foundation grants BSR-8508356, BSR-8516590, and BSR-8500434.

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