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Decomposition of Fallen Trees: Effects of Initial Conditions and Heterotroph Colonization Rates*

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Abstract

Decomposition of an experimental cohort of conifer boles in a temperate rainforest was studied during the first two years after cutting. The decomposing bole was viewed as a successional ecosystem with measurable inputs, outputs, internal cycling processes, and controlling factors. Inputs included nitrogen fixation, interception of canopy throughfall, and immigration of xylophages (insects) and decomposers (fungi and bacteria), all small relative to nutrient pools in boles. Different xylophage functional groups colonized different tree species and inoculated galleries with different decomposer assemblages. Outputs included fragmentation via gallery excavation by insects (< 1 per cent/yr), respiration (1 per cent/yr) and leaching (0.02 per cent/yr). Bole chemistry, temperature, and moisture influenced colonization and biodegradation by xylophages and decomposers. These results from the initial stage of bole decomposition provide new information on processes contributing to decomposition of fallen trees. Our study challenges the assumptions of chronosequence studies (the traditional approach to studying long-term successional processes) that initial conditions and heterotroph colonization patterns (especially lag times) do not influence decomposition rates.

INTRODUCTION

Decomposition of woody litter is a major process contributing to biogeochemical cycling in forest ecosystems, but has been studied primarily in temperate regions. Woody tissues comprise as much as 75 per cent of forest biomass, and represent a substantial pool of energy and resources (Fahey 1983; Kira 1978; Swift 1977). Large woody litter (tree boles and major branches) can amount to 22 per cent of aboveground biomass and 81 per cent of aboveground detrital input (Harmon *et al.* 1986; Kira 1978).

* Paper included in this volume because of its methodological relevance to tropical ecosystems.

Large woody material decays relatively slowly. In temperate ecosystems decay rates vary among tree species with angiosperms typically showing decay rate constants > 0.05/yr, and gymnosperms < 0.05/yr (Harmon *et al.* 1986). *Quercus* (oak) boles decay at rates of 0.03/yr (half-time = 25 yr) while *Pseudotsuga* (Douglas-fir) boles decay at rates of 0.005/yr (half-time 150 yr) with fragments remaining for up to 400 yrs. (Harmon *et al.* 1986). Decay rates in tropical forests may be 0.2-0.4/yr (Bultman and Southwell 1976; Kira 1978; Lang & Knight 1979).

The persistence of these large litter structures is important to the structural and functional integrity of forest ecosystems. Fallen tree boles stabilize soils (especially in montane regions), provide substrate for seedling germination of key plant taxa, provide habitat for invertebrates and vertebrates (including vectors of mycorrhizal fungi), and provide an important pool of water and nutrients for uptake by tree roots and mycorrhizae (Ausmus 1977; Christy & Mack 1984; Franklin *et al.* 1987; Harvey *et al.* 1979; Swift 1977). Therefore, factors governing the decomposition of tree boles are important to the productivity and stability of forest ecosystems. However, relatively few studies have addressed these factors (Ausmus 1977; Harmon *et al.* 1986; Swift 1977).

Typically, studies of long-term processes, such as wood decomposition, have involved comparison of characteristics among structures of different estimated ages (chronosequence). This approach assumes that the structures were initially similar and that decomposition begins immediately upon tree death. These assumptions ignore the potential effects of differences in initial conditions (resulting from physiological state of the tree at time of death) or of heterotroph colonization patterns (e.g., Schowalter 1985). Chronosequences yield results of decomposition but do not provide information on the processes producing those results.

We have chosen to study decomposition of tree boles using an alternative approach. In addition to examining conditions in fallen boles of different ages, we are studying various processes associated with decomposition of a cohort of freshly-cut conifer boles. This paper represents a synopsis of our results for the first two years of decomposition. These results indicate that initial conditions and heterotroph colonization patterns may play a major role in establishing long-term decomposition rates.

MATERIALS AND METHODS

Site Description

The H.J. Andrews Experimental Forest is located 80 km east of Eugene, Oregon, U.S.A., on the west slope of the Cascade Range. The Andrews Forest has been a IBP site, is currently a Long Term Ecological Research (LTER) site and is targeted to be a Geosphere-Biosphere Observatory for studying global change (Dyer *et al.* 1988). This forest is administered jointly by the U.S. Forest Service and Oregon State University.

The climate of the Andrews Forest is maritime with wet, relatively mild winters and dry, warm summers. Mean annual temperature is 8.5°C, and mean annual precipitation is 2300 mm with >75 per cent falling as rain between October and March. Soils are deep, well-drained typic distrochrepts; slope gradients range from 20 to 60 per cent. Elevation ranges from 500 to 1500 m.

The temperate rainforest vegetation of the Andrews Forest is largely undisturbed coniferous forest. These forests are dominated by 400-yr old *Pseudotsuga menziesii* (Mirb.) Franco, commonly exceeding 80 m in height and 125 cm diameter at 2 m height. *Tsuga heterophylla* (Raf.) Sarg.

(western hemlock) and *Thuja plicata* Donn (western red cedar) are abundant at elevations below 1100 m; *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) is abundant above 1000 m.

Experimental Boles

We are comparing decomposition of boles (logs) of *Pseudotsuga, Tsuga, Abies* and *Thuja.* These species were selected on the basis of their dominance of the temperate rainforests of northwestern North America and the range of decay rates represented : 0.03/yr for *Abies* vs. < 0.005/yr for *Thuja* (Harmon *et al.* 1986; Scheffer & Cowling 1966). Boles were cut from freshly-felled, live, undiseased trees from on or near the Andrews Forest in September 1985. All boles were 45-60 cm in diameter, 5.5 m long, and had at least 90 per cent bark cover. Mass was ca. 5000 kg/bole. These initial conditions were selected to control the potential effects of bole size, bark integrity, and prior fungal infection on colonizing heterotrophs and decomposition processes (Harmon *et al.* 1986; Witcosky *et al.* 1987). Fall of live, undiseased trees during autumn storms accounts for 40 per cent of the input of boles to the forest floor in the Cascades (Harmon *et al.* 1986).

Sixteen boles of each tree species were randomly placed at 3×3 m spacing on either side of a circular access road (2 ha area) at each of six undisturbed sites between 500 and 1100 m elevation. This number of sites and boles permits replication of boles destructively sampled after 1, 2, 3, 4, 5, 6, 8, 16, 22, 30, 60, 90, 120, 150, 180, and 210 years of decomposition.

Sampling Procedures

We view decomposing tree boles as distinct ecosystems with measurable nutrient inputs, outputs, and internal nutrient cycling patterns. Accordingly, we are measuring nutrient inputs as interception of canopy throughfall, nitrogen-fixation, and immigration of heterotrophs; outputs as fragmentation, respiration, leaching, and emigration of heterotrophs; internal cycling as substrate mineralization and trophic transfers. Factors which influence these processes include temperature, moisture, biochemical conditions, and heterotroph interactions.

Initial conditions of each bole were measured at the time of bole placement on the ground. One 8 cm thick cross section was cut from the end of each bole. Samples were divided into outer bark, inner bark (phloem), sapwood and heartwood components. Initial density (mass/volume measurement) and moisture content (weight loss after drying) were measured for each bole component. Component samples then were ground to pass a 40-mesh screen and analyzed for N, P, and K (argon plasma spectrophotometry, ICAP), lignin and cellulose (acid-detergent digestion). Terpenes (gas chromatography) and phenols (Folin-Ciocalteu reagent) were measured later in a separate sample of spring-cut boles immediately after cutting. One bole of each tree species at each site was destructively sampled at the end of each of the first two years and analyzed as above.

Bole temperature and moisture content were monitored in one bole of each species at each of four sites during the second year. Thermocouples recording air temperature or inserted into outer and inner bark, sapwood, and heartwood were read continuously by a data logger. Moisture content of each component was measured monthly as weight loss of material from a radial core.

Canopy throughfall was intercepted in galvanized steel collectors placed near boles of each species at each site during the second year (Parker 1983). Runoff from a 0.5 m length of one bole of each species per site was funnelled into a separate collector. Volume was measured every 3-4 weeks and samples analyzed for N, P, K, and dissolved organic carbon (DOC), as above. Nitrogen-fixation was measured in bole components in the lab in spring of the second year. Samples from the set of

spring-cut boles were measured immediately after cutting, for comparison. Samples were incubated at 15°C under anaerobic and microaerophilic (1 per cent O_2) conditions (Silvester *et al.* 1982). Fixed nitrogen was measured as acetylene reduced over a 24-hr period.

Heterotroph immigration was measured during the first two years. At the end of the first (September 1986) and second (September 1987) years, bark was peeled from two 0.0625 m^2 samples on each harvested bole (1/tree species/site/yr). The densities of adult ambrosia beetle (Coleoptera:Scolytidae) galleries in the sapwood, adult bark beetle (Coleoptera:Scolytidae) galleries in the phloem, and larval wood-borer (Coleoptera:Cerambycidae) galleries also, at this stage, in the phloem were recorded (Schowalter *et al.* 1981). Fungi carried by insects prior to their entry into boles were assessed by culturing water rinses, exoskeletons (after rinsing) and guts of insects collected by sterile techniques. Fungi also were cultured from wood samples at the time of bole harvest. Invertebrates (protozoans, nematodes, and microarthropods) were collected from beetle galleries and from 1 cm^3 wood blocks containing gallery sections by Baerman extractors and modified high-gradient extraction (Ingham *et al.* 1986; Merchant & Crossley 1970).

Fragmentation was measured as mined material removed from boles via excavation by xylophagous insects. Cross sections (10 cm thick) of harvested boles were cut into 90° radial wedges. Bark and heartwood were removed. The volume, surface area at the sapwood-phloem interface, and number and diameter (1-1.5 mm) of ambrosia beetle entrances were recorded. Sapwood of *Pseudotsuga* and *Tsuga*, but not *Abies* or *Thuja* had been mined by ambrosia beetles. *Pseudotsuga* and *Tsuga* samples were sliced radially into 1 cm thick sections. Galleries were traced from their entrances with fine steel wire and total length recorded. The volume of individual galleries multiplied by gallery density was expressed as a proportion of total sapwood volume.

Phloem mined by adult bark beetles and, during this initial period, by larval wood-borers was measured in two 0.5 m^2 bark samples from each harvested bole. Galleries of these insects did not have regular cross-sectional areas as did ambrosia beetle galleries. Therefore, gallery volume could not be measured precisely. Mining was recorded as a proportion of total phloem surface area. Because scolytid bark beetles and ambrosia beetles are largely restricted to recently-killed trees, the samples from year 2 served as replicates for these insects.

Respiration rate was measured in the field and lab during the second year. Field measurements involved the alkalai trap method (Page *et al.* 1982). Two chambers covering 500 cm^2 surface area were mounted on one bole of each species at each site. Measurements were taken monthly as the amount of CO_2 absorbed by NaOH over a 24 hr period. Respiration of bole components from a separate set of freshly-cut (spring) trees and from 1.5 yr-old boles was measured in the lab using gas chromatography.

Leaching was measured during the second year. Leachate from a 0.5 m length of one bole per species per site was funnelled into a galvanized steel collector. Volume was measured at 3-4 week intervals and analyzed for N, P, K, and DOC. Leaching was measured as the difference in nutrient content between leachate and canopy throughfall.

We have not been able to study internal substrate mineralization and cycling patterns. We plan to employ both laboratory bioassays and selective introductions in the field to assess the contributions of various decomposer functional groups to decomposition processes.

RESULTS

Initial composition of wood components in boles of the four conifer species is shown in Table 1. Boles were about 50 per cent carbon. Concentrations of N (1000-3000 mg/kg), P (10-600 mg/kg),

and K (100-3000 mg/kg) were highest in the phloem of all species, followed by outer bark, sapwood and heartwood (Table 2). Phenol concentrations were highest in the outer bark and lowest in the sapwood (Table 2). Concentrations and ratios of these nutrients and inhibitory compounds differed among tree species and bole components. After one year of decomposition, concentrations of K and phenols generally had declined in the outer bark and phloem; P had declined 50 per cent in the phloem of Douglas-fir.

TABLE 1. Initial percent composition (by volume) of boles of four conifer species at the H.J. Andrews Experimental Forest in western Oregon

Species	Outer Bark (%)	Inner Bark (%)	Sapwood (%)	Heartwood (%)
Pseudotsuga	38	6	26	30
Tsuga	4	6	62	30
Abies	4	4	62	30
Thuja	38	6	11	46

TABLE 2. Initial chemical composition (all values mg/kg ± 1 SD) of *Pseudotsuga* and *Thuja* boles at the H.J. Andrews Experimental Forest in western Oregon

Species	Component	N	P	K	Phenols[1]
Pseudotsuga	Outer bark	1700 (100)	110 (20)	510 (130)	140,000 (33,000)
	Phloem	2000 (200)	450 (100)	2300 (540)	38,000 (6,400)
	Sapwood	800 (100)	90 (30)	490 (120)	5,900 (4,100)
	Heartwood	900 (100)	10 (6)	40 (20)	26,000 (6,300)
Thuja	Outer bark	1900 (300)	110 (60)	650 (320)	26,000 (3,000)
	Phloem	3100 (500)	400 (60)	3100 (600)	15,000 (4,300)
	Sapwood	1100 (200)	130 (50)	700(250)	3,900 (1,800)
	Heartwood	1000 (100)	30 (6)	230 (70)	30,000 (15,000)

1. Data from a second set of boles cut in spring 1987.

Temperature and moisture fluctuations were similar for all species, generally reflecting the seasonal pattern. Maximum moisture was observed in March, minimum in September. Maximum temperatures occurred during August, minimum during January. The amplitude of fluctuation declined with depth in the bole, with bark closely tracking ambient fluctuations and heartwood remaining relatively stable.

Canopy throughfall amounted to 1600 l/m^2/yr, of which about 55 per cent was intercepted by boles (2.8 m^2 projected surface/bole). Interception accounted for inputs of 25 g DOC/bole (3.0 mg/kg bole), 0.40 g N/bole (0.07 mg/kg), 0.75 g P/bole (0.15 mg/kg) and 1.5 g K/bole (0.29 mg/kg).

Nitrogen fixation was substantial in boles of *Pseudotsuga* and *Abies* in spring of the second year (Table 3). Anaerobic nitrogen-fixation was the primary pathway in *Abies*; anaerobic and microaerophilic pathways were equally important in the other species. Rates in *Pseudotsuga* are lower, by a factor of 20, than rates measured in *Pseudotsuga* at more advanced stages of decomposition (Silvester *et al.* 1982). By comparison, nitrogen-fixation was not detectable in the set of spring-cut boles.

TABLE 3. Nitrogen-fixation rates in conifer boles after 1.5 years of decomposition (spring) at the H. J. Andrews Experimental Forest in western Oregon[1]

Tree Species	Anaerobic (nmol C_2H_2/g/d)	Microaerophilic (1% O_2) (nmol C_2H_2/g/d)
Pseudotsuga	8.5	8.0
Tsuga	0.3	0.4
Abies	5.5	1.0
Thuja	1.0	2.1

1. Component rates adjusted for their percentage contribution to bole volume.

Distinct heterotroph communities developed in the four conifer species. *Pseudotsuga* and *Tsuga*, but not *Abies* or *Thuja*, were colonized by large numbers of ambrosia beetles (>300/m^2 bole surface) during the first spring after tree cutting (Table 4). *Pseudotsuga* and *Abies*, but not *Tsuga* or *Thuja*, were colonized by bark beetles (>7/m^2 bole surface); only *Abies* was colonized by substantial numbers (4/m^2 bole surface) of wood-borers (Table 4). Wood-borers continued to colonize *Abies, Tsuga* and *Thuja*, but not *Pseudotsuga*, during the second year, reaching larval densities of >5/m^2 bole surface in these species. Reproductive termites (Isoptera:Hodotermitidae) began colonizing phloem, especially of *Abies*, during the second year.

TABLE 4. Colonization of conifer boles by xylophage functional groups (sapwood-boring ambrosia beetles (Coleoptera:Scolytidae), and phloem-boring bark beetles (Coleoptera: Scolytidae) and wood-borers (Coleoptera: Cerambycidae) in western Oregon during the first year after tree cutting

	Number (± 1 S.E.) per m^2 bole surface of		
Tree Species	Ambrosia Beetles	Bark Beetles	Wood Borer Beetles
Pseudotsuga	320 (20)	7.1 (1.5)	2.0 (1.0)
Tsuga	310 (15)	0.3 (0.3)	1.5 (0.7)
Abies	60 (10)	8.1 (2.0)	4.6 (1.7)
Thuja	40 (5)	0.7 (0.7)	1.3 (0.4)

Prior to insect penetration of the bark barrier, fungi, bacteria, and invertebrates (protozoans, nematodes, and microarthropods) were restricted to the outer bark. Xylophagous insects inoculated galleries with a rich symbiotic assemblage of these organisms (Carpenter *et al.* 1988). Bark beetles, but apparently not ambrosia beetles, introduced nitrogen-fixing bacteria, as found by Bridges (1981). All beetle functional groups inoculated boles with a variety of yeasts and ascomycete (soft rot) fungi, especially *Penicillium* and stain fungi, *Ophiostoma* (=*Ceratocystis*). Less than 1 per cent of the fungi carried by these insects were basidiomycete (decay) fungi (Table 5). Only termites apparently transported basidiomycetes at appreciable rates.

The stain fungi colonized 93 per cent of *Pseudotsuga* sapwood and 57 per cent of *Tsuga* sapwood, but <10% of *Abies* or *Thuja* sapwood, by the end of year 1. Basidiomycete fruiting structures appeared in the outer bark of all species by the end of the second year, but only *Abies* showed substantial white rot development in the sapwood.

TABLE 5. Frequency of occurrence (per cent) of fungi transported by xylophage functional groups into conifer boles in western Oregon

Fungal Groups	Ambrosia Beetles (N = 30)	Bark Beetles (N = 20)	Wood Borer Beetles (N = 10)	Termites (N = 10)
Ascomycetes				
Botrytis	2	2	5	2
Cladosporium	5	5	<1	<1
Mortierella	1	8	3	<1
Ophiostoma	20	12	9	<1
Penicillium	11	12	9	69
Thysanophora	3	4	2	2
Trichoderma	1	1	1	<1
Yeasts[1]	26	22	54	11
Basidiomycetes				
Heterobasidion	<1	<1	<1	2

1. Primarily *Candida*

Insect galleries supported a rich food web composed of amoebae, ciliates (protozoa), bacterial- and fungal-feeding nematodes, the fungal-feeding and predaceous microarthropods. Most of these organisms have symbiotic associations with xylophagous insects, but others, including predators and parasites, springtails, and fungivorous Diptera larvae, entered beetle galleries independently.

Sapwood excavation amounted to about 0.2 per cent of sapwood volume in *Pseudotsuga* and *Tsuga*, 0 per cent in *Abies* and *Thuja*. Phloem excavation amounted to 7-9 per cent in *Pseudotsuga* and *Abies*, but was negligible in *Tsuga* and *Thuja* (Table 4). Wood borers accounted for additional phloem excavation during the second year, but overall fragmentation, weighted by bole composition (Table 1) amounted to < 1 per cent moss loss in all species during the first two years.

Respiration rates of whole boles measured in the field showed a single sharp peak during September each year, coinciding with the period of maximum temperature and minimum moisture in boles (Carpenter *et al.* 1988). Respiration measured in the laboratory indicated substantial respiration (3-8 μmol C/g/d) in phloem of freshly-cut (spring) boles, compared to rates generally < 1 μmol C/g/d in other bole components (except *Abies* outer bark at 5 μmol C/g/d). Rates in the phloem of 1.5 yr-old experimental logs measured at the same time ranged from 0.5 to 1.6 μmol C/g/d (Carpenter *et al.* 1988). Weighted rates for the bole indicated a reduction of 30-50 per cent when comparing the freshly-cut to 1.5 yr-old boles. Overall, respiration accounted for mass losses of about 1 per cent/yr.

Concentrations of N, P, K, and DOC were 3-9 times higher in leachate than in canopy throughfall. Leaching accounted for mass losses of about 0.02 per cent/yr. This pathway likely affected phloem most during this initial stage, perhaps accounting for net losses of K and (for some species) inhibitory phenols from this bole component.

DISCUSSION

Our work to date covers only the earliest colonization stage of a long-term and relatively poorly-known process. Nevertheless, our results indicate potentially important effects of initial conditions

and initial colonization patterns on subsequent decomposition of fallen trees. These factors appear to determine the lag time to initiate decomposition and may control long-term rates.

Wood chemistry, especially different balances of nutrients and inhibitory extractives among tree species, is a major factor determining initial xylophage colonization patterns (Bultman & Southwell 1976; Wood 1982). Injured or diseased trees release volatile compounds which attract xylophagous insects searching for suitable resources (Chapman 1963; Schowalter 1985; Witcosky *et al.* 1987; Wood 1982). Chemical composition also changes seasonally.

Different xylophage functional groups respond to different cues. Many bark beetles and other wood borers are attracted or repelled by specific volatile terpenes (Chapman 1963; Wood 1982). We found verbenone to be a major constituent of *Thuja* bark, and also present in *Abies* bark. This monoterpene attracts some bark beetles (*Dendroctonus* spp.) when present at low concentration but often repels these insects at higher concentration (Rudinsky 1973; Wood 1982). Ambrosia beetles and some bark beetles are attracted to sources of ethanol, produced by anaerobic respiration of phloem in combination with moisture saturation (Klimetzek *et al.* 1986; Moeck 1970; Witcosky *et al.* 1987). We verified this by adding ethanol to bark extracts (of the four conifer species) placed on cardboard cylinders at two sites removed from our boles. Ethanol increased the attraction of ambrosia beetles and some wood-borers and predators.

Pheromones produced by the initial colonists synergize this host attraction, resulting in rapid accumulation of xylophage populations and perhaps confounding initial preferences among tree species (Schowalter *et al.* 1981; Wood 1982). Wood infected with pathogenic fungi also attracts xylophagous insects (Witcosky *et al.* 1987).

Penetration of the bark barrier by xylophagous insects is critical for colonization by decomposer fungi (Ausmus 1977, Dowding 1984; Swift 1977). Therefore, chemically-determined patterns of xylophage colonization also may determine decomposer colonization. Because of the dependence of many fungi, bacteria, and invertebrates on bark penetration by insects, life history synchronization and mutualistic interaction characterize many associations (Barras & Hodges 1969; Batra 1966; Blanchette & Shaw 1978; Dowding 1984; French & Roeper 1972; Haanstad & Norris 1985). Different xylophage functional groups apparently transport different decomposer assemblages, e.g., bark beetles carried nitrogen-fixing bacteria, termites carried basidiomycetes. The lag time to colonization by particular xylophages could determine the lag time to colonization by associated decomposers (Käärik 1974).

Microbial establishment and biodegradation activity also are determined by bole environment. Terpenes, phenols, and other inhibitory extractives limit fungal and bacterial growth and substrate biodegradation (Barz & Weltring 1985; Bultman & Southwell 1976; Scheffer & Cowling 1966; Swain 1979). Only a few fungi, yeasts, and bacteria are capable of metabolizing these compounds (Barz & Weltring 1985), including some of the major initial colonists in our study, e.g., *Candida* (yeasts) and *Penicillium* (fungi). Biodegradation of these compounds in boles with high concentrations likely facilitates colonization by other decomposer groups (Rayner & Todd 1979). Some of these associated bacteria and fungi may provide fixed nitrogen, vitamins, or other growth stimulators while exploiting cell wall components released by decomposer fungi (Barz & Weltring 1985). Blanchette & Shaw (1978) reported that basidiomycete growth in wood chips with bacteria and yeasts present was 200 per cent greater than fungal growth in wood without bacteria or yeasts. Because bacteria and ascomycetes tend to prevail at high moisture content and basidiomycetes at low moisture (Cooke & Rayner 1984; Käärik 1974; Rayner & Todd 1979), pulses of biodegradation by

basidiomycetes likely alternate with pulses of biodegradation, nitrogen-fixation, and mineralization by ascomycetes and bacteria in seasonally wet environments. This pattern is evident in the spring (cool, wet) pulse in leaching of K and DOC (perhaps including inhibitory compounds) and the autumn (warm, dry) pulse in respiration in our experimental boles. Mineralization of nitrogen and other nutrients could be enhanced by invertebrate grazers (Crossley 1977; Dyer 1986; Ingham *et al*. 1986; Schowalter 1985; Swift 1977), also largely influenced by patterns of xylophage colonization.

Differences is bole decomposition rate among the four experimental conifers (Harmon *et al*. 1986, Scheffer & Cowling 1966) could be explained by our early results. *Abies* decomposes most rapidly, followed by *Tsuga*, *Pseudotsuga* and *Thuja*. *Abies* was colonized by phloem-borers, but not sapwood-borers, and showed earliest sapwood degradation by white rot (basidiomycete) fungi. *Quercus* (oak) decomposes at a similar rate (0.03/yr, Harmon *et al*. 1986). We are comparing decomposition of *Quercus* boles at four sites (including western Oregon, Cedar Creek LTER, Minnesota, Konza Prairie LTER, Kansas, and Coweeta LTER, North Carolina) across a NW-SE continental gradient. Interestingly, *Quercus* boles at all four sites also were colonized by phloem-borers (but not sapwood-borers) during the first year and showed extensive basidiomycete penetration of the sapwood.

By contrast, *Pseudotsuga* and *Tsuga* were colonized by ambrosia beetles and ascomycete fungi at densities which could have inhibited sapwood penetration by basidiomycete fungi except during the brief period of bole drying (Käärik 1974). Although basidiomycetes are the most efficient lignin-cellulose degraders, many of the ascomycetes and, perhaps, bacteria colonizing our boles are capable of utilizing some structural compounds (Käärik 1974; Ruel & Barnoud 1985). *Thuja*, the most decay-resistant species remains largely uncolonized and unchanged after two years. Nitrogen-fixation was highest in *Pseudotsuga* and *Abies*, the two species colonized by bark beetles.

The decomposition of fallen trees remains a poorly-understood process. We have found that, contrary to the assumptions of traditional chronosequence studies, initial condition of the fallen tree (especially chemical composition at the time of death) and rates of heterotroph colonization determine decomposition pathways and rates during the first two years. We do not know the extent to which these initial differences between boles persist or boles become more homogenous through time as a result of modification by heterotrophs. Käärik (1974) summarized studies showing that wood initially colonised by stain fungi decayed less rapidly during subsequent establishment of decay fungi than did previously-uncolonized wood. Manipulative experiments with different decomposer successions will be necessary to evaluate the effects of initial colonization patterns.

Processes associated with decomposition of fallen trees also require further attention. Boles have not been appreciated as a potential source of nitrogen in forest ecosystems. Aerobic nitrogen fixation rates >5 nmol C_2H_2 reduced/g/hr, have been reported for *Pseudotsuga* boles in advanced stages of decomposition (Silvester *et al*. 1982). Rates were much lower in 2 yr-old boles of *Pseudotsuga* and *Abies*, but suggest that prior colonization and decay are necessary to provide the energy sources for elevated fixation rates. Boles of fallen trees could contribute substantially to the nitrogen budget of forest ecosystems, especially at advanced stages of decomposition. Our study provides new information on processes associated with log decomposition, but process-oriented studies on boles at advanced stages of decomposition will be necessary to refine decomposition models. The relatively rapid rate of bole decomposition in tropical forests (Kira 1978; Lang & Knight 1979) offers the possibility of shorter-term comparative studies.

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REFERENCES

Ausmus, B.S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. *Ecological Bulletin* (Stockholm) **25**: 180-192.

Barras, S.J. & J.D. Hodges. 1969. Carbohydrates of inner bark of *Pinus taeda* as affected by *Dendroctonus frontalis* and associated microorganisms. *Canadian Entomologist* **101**: 489-493.

Barz, W. & K. Weltring. 1985. Biodegradation of aromatic extractives of wood. pp. 607-666. *In*: T. Higuchi (ed.) *Biosynthesis and Biodegradation of Wood Components*. Academic Press, N.Y.

Batra, L.R. 1966. Ambrosia fungi: Extent of specificity to ambrosia beetles. *Science* **153**: 193-195.

Blanchette, R.A. & C.G. Shaw. 1978. Associations among bacteria, yeasts, and basidiomycetes during wood decay. *Phytopathology* **68**: 631-637.

Bridges, J.R. 1981. Nitrogen-fixing bacteria associated with bark beetles. *Microbial Ecology* **7**: 131-137.

Bultman, J.D. & C.R. Southwell. 1976. Natural resistance of tropical American woods to terrestrial wood-destroying organisms. *Biotropica* **8**: 71-95.

Carpenter, S.E., M.E. Harmon, E.R. Ingham, R.G. Kelsey, J.D. Lattin & T.D. Schowalter. 1988. Early patterns of heterotroph activity in conifer logs. pp. 33-43. *In*: R. Watling, A. Lyon & L. Boddy (eds.) *Fungi and Ecological Disturbance*. Proc. Royal Society of Edinburgh 94B.

Chapman, J.A. 1963. Field selection of different log odors by scolytid beetles. *Canadian Entomologist* **95**: 673-676.

Christy, E.J. & R.N. Mack. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. *Journal of Ecology* **72**: 75-91.

Cooke, R.C. & A.D.M. Rayner. 1984. *Ecology of Saprotrophic Fungi*. Longman Inc., New York.

Crossley, D.A., Jr. 1977. The role of terrestrial saprophagous arthropods in forest soils: current status of concepts. pp. 49-56. *In*: W.J. Mattson (ed.) *The Role of Arthropods in Forest Ecosystems*. Springer-Verlag, N.Y.

Dowding, P. 1984. The evolution of insect-fungus relationships in the primary invasion of forest timber. pp. 135-153. *In*: J.M. Anderson, A.D.M. Rayner & D.W.H. Walton (eds.) *Invertebrate Microbial Interactions*. British Mycological Society Symposium 6. Cambridge University Press.

Dyer, M.I. 1986. The role of herbivores in forest ecosystems: the case for biosphere reserves. pp. 97-102. *In*: H. Yang, Z. Wang, J.N.R. Jeffers & P.A. Ward (eds.) *The Temperate Forest Ecosystem*. Institute of Terrestrial Ecology, Cumbria, Great Britain.

Dyer, M.I., F. diCastri & A.J. Hansen. 1988. Geosphere-Biosphere Observatories: Their Definition and Design for Studying Global Change. International Union of Biological Sciences, Paris.

Fahey, T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* spp. *latifolia*) ecosystems, southeastern Wyoming. *Ecological Monographs* **53**: 51-72.

Franklin, J.F., H.H. Shugart & M.E. Harmon. 1987. Tree death as an ecological process. *Bioscience* **37**: 550-556.

French, J.R.J. & R.A. Roeper. 1972. Interactions of the ambrosia beetle, *Xyleborus dispar*, with its symbiotic fungus *Ambrosiella hartigii* (Fungi Imperfecti). *Canadian Entomologist* **104**: 1635-1641.

Haanstad, J.D. & D.M. Norris. 1985. Microbial symbiotes of the ambrosia beetle *Xyloterinus politus*. *Microbial Ecology* **11**: 267-276.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, J.D. Lattin, N.H. Anderson, S.V. Gregory, S.P. Cline, S.G. Aumen, J.R. Sedell, K. Cromack, Jr., & K.W. Cummins. 1986. Role of coarse woody debris in temperature ecosystems. *Recent Advances in Ecological Research* **15**: 133-302.

Harvey, A.E., M.J. Larsen & M.F. Jurgensen. 1979. Comparative distribution of ectomycorrhizae in soils of three western Montana forest habitat types. *Forest Science* 25: 350-358.

Ingham, E.R., C. Cambardella & D.C. Coleman. 1986. Manipulation of bacteria, fungi, and protozoa by biocides in lodgepole pine forest soil microcosms: Effects of organism interactions and nitrogen mineralization. *Canadian Journal of Soil Science* 66: 261-272.

Käärik, A.A. 1974. Decomposition of wood. pp. 129-174. *In*: C.H. Dickinson & G.J.F. Pugh (eds.) *Biology of Plant Litter Decomposition*. Academic Press, London.

Kira, T. 1978. Community architecture and organic matter dynamics in the lowland rain forests of southeast Asia with special reference to Pasoh Forest, West Malaysia. pp. 561-590. *In*: P.B. Tomlinson & M.H. Zimmerman (eds.) *Tropical Trees As Living Systems*. Cambridge University Press.

Klimetzek, D., I. Köhler, J.P. Vité & U. Kohnle. 1986. Dosage response to ethanol mediates host selection by "secondary" bark beetles. *Naturwissenschaften* 73: 270-271.

Lang, G.E. & D.H. Knight. 1979. Decay rates for boles of tropical trees in Panama. *Biotropica* 11: 316-317.

Merchant, V.A. & D.A. Crossley, Jr. 1970. An inexpensive high efficiency tullgren extractor for soil microarthropods. *Journal of the Georgia Entomological Society* 5: 83-87.

Moeck, H.A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum* (Coleoptera: Scolytidae). *Canadian Entomologist* 102: 985-995.

Page, A.L., R.H. Miller & D.R. Keeney. 1982. *Methods of Soil Analysis*. Part 2: *Chemical and Microbiological Properties* (Second ed.). Soil Science Society of America, Madison, Wisconsin.

Parker, G.G. 1983. Throughfall and stemflow in the forest nutrient cycle. *Recent Advances in Ecological Research* 13: 58-133.

Rayner, A.D.M. & N.K. Todd. 1979. Population and community structure and dynamics of fungi in decaying wood. *Advances in Botanical Research* 7: 333-420.

Rudinsky, J.A. 1973. Multiple functions of the southern pine beetle pheromone verbenone. *Environmental Entomology* 2: 511-514.

Ruel, K. & F. Barnoud. 1985. Degradation of wood by microorganisms. pp. 441-467. *In*: T. Higuchi (ed.) *Biosynthesis and Biodegradation of Wood Components*. Academic Press, N.Y.

Scheffer, T.C. & E.B. Cowling. 1966. Natural resistance of wood to microbial deterioration. *Annual Review of Phytopathology* 4: 147-170.

Schowalter, T.D. 1985. Adaptations of insects to disturbance. pp. 235-252. *In*: S.T.A. Pickett & P.S. White (eds.) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, N.Y.

Schowalter, T.D., D.N. Pope, R.N. Coulson & W.S. Fargo. 1981. Patterns of southern pine beetle (*Dendroctonus frontalis* Zimm.) infestation enlargement. *Forest Science* 27: 837-849.

Silvester, W.B., P. Sollins, T. Verhoeven & S.P. Cline. 1982. Nitrogen fixation and acetylene reduction in decaying conifer boles: effects of incubation time, aeration, and moisture content. *Canadian Journal of Forest Research* 12: 646-652.

Swain, T. 1979. Tannins and lignins. pp. 657-682. *In*: G.A. Rosenthal & D.H. Janzen (eds.) *Secondary Plant Metabolites*. Academic Press, N.Y.

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

Witcosky, J.J., T.D. Schowalter, & E.M. Hansen. 1987. Host-derived attractants for the beetles, *Hylastes nigrinus* (Coleoptera:Scolytidae) and *Steremnius carinatus* (Coleoptera:Curculionidae). *Environmental Entomology* 16: 1310-1313.

Wood, D.L. 1982. The role of pheromones, kaironomes, and allomones in the host selection and colonization behaviour of bark beetles. *Annual Review of Entomology* 27: 411-466.

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