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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 percent/yr), respiration (1 percent/yr) and leaching (0.02 percent/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 percent 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 percent of aboveground biomass and 81 percent 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 dultrochrepts; 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.
DECOMPOSITION OF FALLEN TREES

(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 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 O₂) 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 m² 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 cm³ 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. Samples 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 m² 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 cm² surface area were mounted on one bole of each species at each site. Measurements were taken monthly as the amount of CO₂ 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

<table>
<thead>
<tr>
<th>Species</th>
<th>Outer Bark (%)</th>
<th>Inner Bark (%)</th>
<th>Sapwood (%)</th>
<th>Heartwood (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pseudotsuga</em></td>
<td>38</td>
<td>6</td>
<td>26</td>
<td>30</td>
</tr>
<tr>
<td><em>Tsuga</em></td>
<td>4</td>
<td>6</td>
<td>62</td>
<td>30</td>
</tr>
<tr>
<td><em>Abies</em></td>
<td>4</td>
<td>4</td>
<td>62</td>
<td>30</td>
</tr>
<tr>
<td><em>Thuja</em></td>
<td>38</td>
<td>6</td>
<td>11</td>
<td>46</td>
</tr>
</tbody>
</table>

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

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

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.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Anaerobic (nmol C₂H₂/g/d)</th>
<th>Microaerophilic (1% O₂) (nmol C₂H₂/g/d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudotsuga</td>
<td>8.5</td>
<td>8.0</td>
</tr>
<tr>
<td>Tsuga</td>
<td>0.3</td>
<td>0.4</td>
</tr>
<tr>
<td>Abies</td>
<td>5.5</td>
<td>1.0</td>
</tr>
<tr>
<td>Thuja</td>
<td>1.0</td>
<td>2.1</td>
</tr>
</tbody>
</table>

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/m² 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/m² bole surface); only Abies was colonized by substantial numbers (4/m² 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/m² 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.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Ambrosia Beetles (± 1 S.E.)</th>
<th>Bark Beetles</th>
<th>Wood Borer Beetles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudotsuga</td>
<td>320 (20)</td>
<td>7.1 (1.5)</td>
<td>2.0 (1.0)</td>
</tr>
<tr>
<td>Tsuga</td>
<td>310 (15)</td>
<td>0.3 (0.3)</td>
<td>1.5 (0.7)</td>
</tr>
<tr>
<td>Abies</td>
<td>60 (10)</td>
<td>8.1 (2.0)</td>
<td>4.6 (1.7)</td>
</tr>
<tr>
<td>Thuja</td>
<td>40 (5)</td>
<td>0.7 (0.7)</td>
<td>1.3 (0.4)</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Fungal Groups</th>
<th>Ambrosia Beetles (N = 30)</th>
<th>Bark Beetles (N = 20)</th>
<th>Wood Borer Beetles (N = 10)</th>
<th>Termites (N = 10)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ascomycetes</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Borytis</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Cladosporium</td>
<td>5</td>
<td>5</td>
<td>&lt;1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Mortierella</td>
<td>1</td>
<td>8</td>
<td>3</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Ophiostoma</td>
<td>20</td>
<td>12</td>
<td>9</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Penicilliun</td>
<td>11</td>
<td>12</td>
<td>9</td>
<td>69</td>
</tr>
<tr>
<td>Thysanophora</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Trichoderma</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Yeasts¹</td>
<td>26</td>
<td>22</td>
<td>54</td>
<td>11</td>
</tr>
<tr>
<td>Basidiomycetes</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heterobasidion</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>2</td>
</tr>
</tbody>
</table>

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 in 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_H_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


DECOMPOSITION OF FALLEN TREES


