Conifer bole utilization by wood-boring beetles in western Oregon

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We studied wood excavation by scolytid and cerambycid beetles in decomposing boles of four conifer species during the first two years on the ground in western Oregon. Colonization density and gallery volumes were measured in experimental boles (0.5 m diameter × 5 m length) of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), and western red cedar (*Thuja plicata* Donn). Ambrosia beetles (Coleoptera: Scolytidae) colonized boles only during the 1st year and were essentially restricted to Douglas-fir and western hemlock (removing 0.2% of the sapwood volume). Bark beetles (Coleoptera: Scolytidae) colonized boles only in the 1st year, primarily in Douglas-fir and Pacific silver fir (removing 7–8% of the phloem surface area). Wood borers (Coleoptera: Cerambycidae) excavated an additional 2.3% of the phloem surface area of Pacific silver fir in the 1st year and continued to excavate all species except Douglas-fir during the 2nd year. Consequences for the decomposition process are discussed.

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L'excavation du bois par les coléoptères dans les troncs en décomposition de quatre espèces de conifères a été étudiée durant les 2 premières années de leur position au sol dans l'ouest de l'Orégon. La densité de la colonisation ainsi que le volume des galeries ont été mesurés sur des troncs d'essai (0,5 m de diamètre et 5 m de longueur) de Sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco), de Pruche occidentale (*Tsuga heterophylla* (Raf.) Sarg.), de Sapin gracieux (*Abies amabilis* (Dougl.) Forbes) et de Thuya occidental (*Thuja plicata* Donn). Les Coléoptères du bois (Coleoptera : Scolytidae) ont colonisé les troncs seulement durant la 1re année et étaient restreints essentiellement au Sapin de Douglas et à la pruche (prélevant 0,2% du volume de l'aubier). Les Coléoptères de l'écorce (Coleoptera : Scolytidae) ont colonisé les troncs seulement durant la 1re année, et surtout ceux de Sapin de Douglas et de Sapin gracieux (prélevant 7 à 8% de la surface du phloème). Les Perceurs du bois (Coleoptera : Cerambycidae) ont excavé 2,3% de plus de la surface du phloème du Sapin gracieux durant la 1re année et ont continué à excaver toutes les espèces à l'exception du Sapin de Douglas durant la 2e année. Les auteurs discutent des effets du processus de décomposition.

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Introduction

Forest managers are becoming increasingly aware of the value of decomposing boles (logs) of fallen trees for stabilizing soils, providing reservoirs of water and nutrients, and providing habitat for mammalian dispersers of mycorrhizal fungi. Hence, factors affecting decomposition rates, especially wood-boring insects and decay organisms, have become a focus of attention.

The decomposition of large boles of fallen trees is a long-term ecological process spanning many decades to centuries and involving a complex community of invertebrates and microorganisms in the progressive fragmentation, catabolism of organic molecules, and nutrient turnover. Critical to the initiation of this process are the beetles that colonize recently fallen boles, because they penetrate the bark and provide access to the rich carbohydrate reserves within. In addition to providing points of entry for innumerable invertebrates and microorganisms, these beetles directly inoculate their mines with a diverse and characteristic community of soft-rot and decay fungi, nitrogen-fixing and carbohydrate-reducing bacteria, and associated invertebrates. Factors that influence colonization and excavation of fallen boles by beetles may largely determine subsequent decomposition patterns (Ausmus 1977; Dowding 1984; Savely 1939; Swift 1977).

Host selection and the rate of wood channelization by the boring beetles are influenced by many factors (e.g., chemical composition, temperature, and moisture) associated with tree species (Harmon et al. 1986; Schowalter 1985). Different beetle species typically colonize different tree species, although some may colonize several tree species (Chapman 1963; Wood 1982).

Little information is available on rates of wood utilization by these beetles in different tree species. Shore et al. (1987) examined wood removal from Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) logs by an ambrosia beetle (*Trypodendron lineatum* (Olivier)). Wood excavation by other early colonizing beetles has not been investigated.

This study of wood utilization by bark- and wood-boring beetles represents only one component of a long-term, multidisciplinary study of the decomposition of large conifer logs. We compared wood excavation by beetles among logs of four conifer species during the first 2 years of their decomposition on the ground at the H. J. Andrews Experimental Forest in western Oregon.

Materials and methods

Site description

The H. J. Andrews Experimental Forest is located 80 km east of Eugene, Lane County, Oregon, on the west slope of the Cascade Range. The climate of the Andrews Forest is maritime with wet, relatively mild winters and dry, warm summers. Mean temperature is 7.9°C. Mean annual precipitation is 2300 mm, with 75% falling as rain (little snow) between October and March. Soils are deep, well-drained typic distrochrepts. Slope gradients range from 20 to 60%.

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Our study of decomposing boles was replicated at six sites within the western hemlock zone (500–1100 m elevation). All sites were dominated by old-growth (400-year-old) Douglas-fir commonly exceeding 80 m in height and 125 cm dbh. Western hemlock and western red cedar (*Thuja plicata* Donn) were abundant at all sites; Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) was common above 1000 m.

Experimental boles

We selected Douglas-fir, western hemlock, western red cedar, and Pacific silver fir for comparison of decomposition rates on the basis of their dominance of northwestern conifer forests and the range of decay resistance represented: western red cedar > Douglas-fir > western hemlock > Pacific silver fir (Harmon et al. 1986). Over 500 experimental logs were cut from live trees as part of harvest operations on or adjacent to the Andrews Forest. Although we made no attempt to ensure that all experimental logs came from different trees, the diameter requirement and our random distribution of these logs among six sites and 16 sample times (periodically from years 1 to 200) ensured that any two logs from the same tree would provide statistically independent samples. Boles were selected on the basis of diameter (45–60 cm), length (5.5 m), damage to bark cover (<10%), and absence of decay (as indicated by lack of visible discoloration, fungal hyphae, or soft or crumbling heart wood) so that the initial condition of the boles and its effect on colonizing heterotrophs was controlled. Our use of undecayed logs was intended to simulate natural tree fall, 40% of which occurs as windthrow of live, undiseased trees in autumn and winter (Harmon et al. 1986).

Sixteen experimental logs of each tree species were placed side by side in random order at 3-m spacing at each of the six sites during September 1985. The large number of boles permitted destructive sampling, on a periodic basis, to measure decomposition over an extended time period.

Beetle density

In September 1986, after 1 year on the ground, one bole of each tree species per site (six boles per species) was sampled for colonization by sapwood-boring ambrosia beetles (Scolytidae), phloem-boring bark beetles (Scolytidae), and long-horned wood borers (Cerambycidae). These three functional groups were distinguished on the basis of excavation by adult beetles, which directly introduce mutualistic microflora (scolytids) and excavation of sapwood (ambrosia beetles) vs. phloem (bark beetles and, initially, cerambycids). On each bole, we collected two samples, at 1 and 3 m along the bole, from top, side, and bottom portions of the bole, i.e., six samples per log. Because different beetle species prefer different positions on fallen logs, these six samples per log represented the maximum within-log variation.

Densities of colonizing bark beetles were measured by counting the number of adult entrances in 0.5-m^2 bark samples after the bark was peeled from the bole. Some species of bark beetles could be identified by specimens (if present) and by characteristic gallery patterns (Dowding 1984). Adult cerambycids do not excavate galleries, but lay eggs in bark crevices. Therefore, densities of colonizing adults of this functional group could not be measured.

Because of the high density of colonizing ambrosia beetles, a 625-cm^2 sample of the exposed sapwood surface was examined for ambrosia beetle entrances (six samples per log, as above). Ambrosia beetle species can be identified by adult specimens or by diameter of the entry holes (Johnson 1958).

In September 1987, after 2 years on the ground, a second bole of each tree species at each site was sampled using the same technique to replicate and account for new colonists. Because bark beetles and ambrosia beetles are largely restricted to freshly felled trees, the samples from the 2nd year served as replicates for these insects.

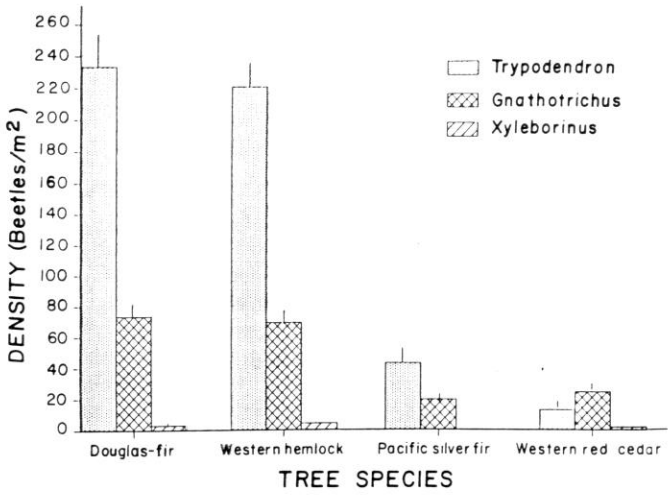

FIG. 1. Mean density of ambrosia beetles, averaged for the first 2 years of decomposition, in sapwood of four conifer species in western Oregon. Vertical lines represent 1 SE. $N = 6$.

Excavation by beetles

Bark beetles and, initially, cerambycid beetles excavate galleries in the phloem. In September 1986, bark samples were sealed in zip-lock plastic bags and returned to the laboratory for estimation of wood utilization. Bark beetle and cerambycid galleries were distinguished by size and configuration. Because galleries did not have regular cross-sectional areas, precise measurement of gallery volume was not possible. Rather, the phloem surface area excavated by bark beetles and cerambycid beetles was calculated and related to phloem surface area.

Ambrosia beetles excavate galleries in sapwood. Successful galleries were found only in Douglas-fir and western hemlock; galleries in Pacific silver fir and western red cedar were sparse and ended at the sapwood, indicating nonestablishment in these species. Because sapwood dissection for gallery measurement was labor intensive, only Douglas-fir and western hemlock boles from three sites were dissected (three replicate logs per species). One 8 cm thick cross section from each bole was cut radially into quarters, which were dissected into 1 cm thick radial wedges. Dimensions of each quarter disk and the number of entry holes on the surface were recorded before dissection. We dissected a total of 36 galleries in Douglas-fir and 20 galleries in western hemlock. Beetle galleries were traced from the entry holes by using a length of steel wire. To locate brood chambers, the 1-cm wedges frequently were dissected. The length and diameter of adult galleries and brood chambers were recorded, and volume was calculated assuming a cylindrical shape. The total volume excavated by each species of ambrosia beetle in each tree species could be estimated from mean gallery volume and mean density.

Because taper was <5% along 5.5-m logs, the total sapwood volume of each bole (V_t) was calculated by the formula

$$V_t = (\pi r_o^2 L) - (\pi r_i^2 L)$$

where r_o is the outer radius of the sapwood, r_i is the inner radius of the sapwood, and L is the length of bole. The percent sapwood volume excavated by ambrosia beetles was then calculated.

Data analysis

Within-log variation was addressed by sampling six positions on each log, as mentioned earlier. These data were pooled by tree species, site, and year (six replicates per tree species per year). Means for each log were transformed as necessary to the natural logarithm. The effects of tree species and site on beetle density and gallery volume were analyzed using randomized complete block analysis of variance (ANOVA), using sites as blocks. We used SAS statistical software (SAS Institute Inc. 1985) for all analyses.

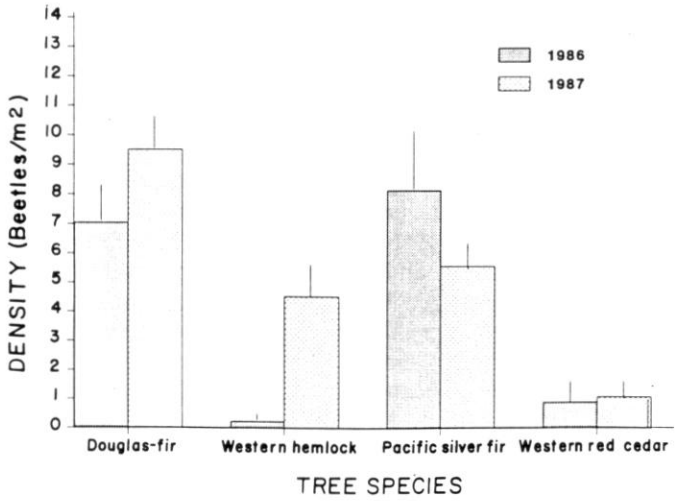

FIG. 2. Cumulative mean density of bark beetles in phloem during the first 2 years of decomposition of four conifer species in western Oregon. Vertical lines represent 1 SE. $N = 6$.

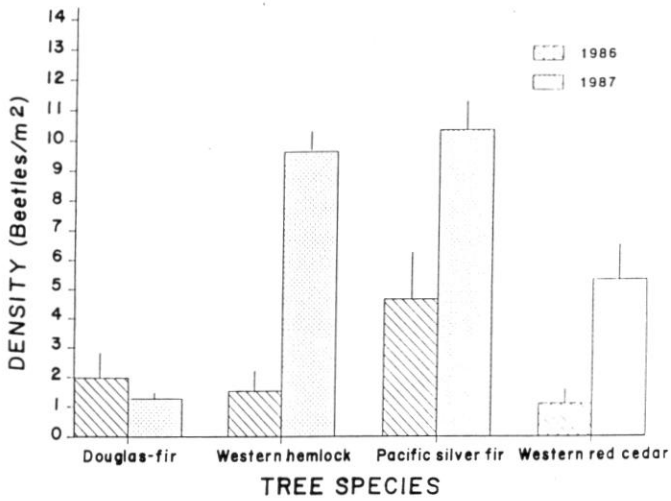

FIG. 3. Cumulative mean density of long-horned wood borers in phloem during the first 2 years of decomposition of four conifer species in western Oregon. Vertical lines represent 1 SE. $N = 6$.

TABLE 1. Percent phloem excavated by bark beetles and cerambycid beetles in logs of four conifer species during the 1st year of decomposition on the ground in western Oregon

Tree species	% phloem excavated (±1 SD)	
	Bark beetles	Cerambycid beetles
Douglas-fir	7.6 ± 10	0.05 ± 0.06
Western hemlock	0.13 ± 0.13	0.18 ± 0.27
Pacific silver fir	6.8 ± 8.5	2.3 ± 2.2
Western red cedar	0.42 ± 0.80	0.16 ± 0.26

Results

Beetle density

The effect of block (site) was significant ($P < 0.05$) only for ambrosia beetles in 1986 samples and bark beetles in 1987 samples. Significant effects ($P < 0.05$) of tree species were observed for densities of all beetle functional groups.

The major ambrosia beetle species in this study were *T. lineatum*, *Gnathotrichus retusus* (LeConte), and *G. sulcatus* (LeConte). Galleries of the latter two species could not be distinguished and are hereafter combined as *Gnathotrichus* spp. Ambrosia beetles were significantly more abundant in Douglas-fir and western hemlock than in Pacific silver fir or western red cedar (Fig. 1) based on 95% confidence limits. About 90% of *T. lineatum* and 75% of *Gnathotrichus* spp. (Fig. 1) attacked these two tree species in roughly equal proportions. A third ambrosia beetle, *Xyleborinus saxeseni* (Ratzeburg), attacked all four tree species at low densities (Fig. 1).

Ambrosia beetle colonization was limited to the 1st year. *Trypodendron lineatum* did not attack boles during the 2nd year. A very few *Gnathotrichus* spp. and *X. saxeseni* were observed attacking some boles in the 2nd year, but cumulative ambrosia beetle density did not differ significantly ($P > 0.05$) between the 2 years.

Bark beetles showed a different pattern of host utilization (Fig. 2). Major species were *Dendroctonus pseudotsugae* Hopkins and *Dryocoetes autographus* Ratzeburg in Douglas-fir, *D. autographus* in western hemlock, *Pseudohylesinus sericeus* (Mannerheim) in Pacific silver fir, and *Phloeosinus* spp. in western red cedar. Based on 95% confidence limits, Douglas-fir and Pacific silver fir had significantly higher bark beetle densities than did western hemlock and western red cedar during the 1st year (Fig. 2). This beetle functional group typically does not colonize 2-year-old phloem, but *D. autographus* was observed colonizing western hemlock in substantial numbers during 1987 (Fig. 2).

The number of cerambycid wood-borer galleries was significantly ($P < 0.05$) higher in Pacific silver fir than in the other tree species during the 1st year (Fig. 3). Cerambycid colonization continued during the 2nd year and increased significantly in western hemlock, Pacific silver fir, and western red cedar, but not in Douglas-fir (Fig. 3). Based on 95% confidence limits, the densities of cerambycid galleries in 1987 were significantly higher in western hemlock and Pacific silver fir than in western red cedar, which had higher densities than did Douglas-fir. Because cerambycids were represented by larvae that are difficult to identify to species, different tree species likely were colonized by different cerambycid species.

Beetle excavation

Ambrosia beetle galleries in Douglas-fir and western hemlock boles did not extend to the heart wood. Mean sapwood thickness was 4.2 cm in Douglas-fir and 8.8 cm in western hemlock. The maximum depth of penetration by *T. lineatum* was 3.1 cm in Douglas-fir and 3.8 cm in western hemlock; *Gnathotrichus* penetrated to 3.4 cm in Douglas-fir and 7.7 cm in western hemlock.

The mean (±1 SD) length of *T. lineatum* galleries was 9.4 ± 6.5 cm in Douglas-fir (36 galleries in three logs) and 13.6 ± 8.3 cm in western hemlock (20 galleries in three logs), which are similar to results reported by Shore et al. (1987). Each *T. lineatum* removed about 0.33 ± 0.33 cm^3 of sapwood from Douglas-fir and about 0.35 ± 0.03 cm^3 of sapwood from western hemlock. Average gallery lengths for *Gnathotrichus* spp. were 17.8 ± 5.0 in Douglas-fir and 51.3 ± 15 in western hemlock; average gallery volumes were 0.24 ± 0.07 cm^3 in Douglas-fir and 0.68 ± 0.21 cm^3 in western hemlock.

Gallery volumes multiplied by estimated number of galleries per bole provided estimates of the total sapwood

volume excavated by ambrosia beetles. About 0.17% of Douglas-fir sapwood and 0.24% of western hemlock sapwood was excavated by ambrosia beetles during the 1st year of decomposition and none thereafter.

Bark beetles excavated about 7.6% of the inner surface area of Douglas-fir phloem and 6.8% of the inner surface area of Pacific silver fir phloem during the 1st year (Table 1). In addition, cerambycid wood borers excavated about 2.3% of the inner surface area of Pacific silver fir phloem during the 1st year (Table 1). By the end of the 2nd year, the wood borers had excavated 4–5% of the phloem surface area of western hemlock and Pacific silver fir and about 2.5% of the phloem surface area of western red cedar.

Discussion

Our study indicated that tree species determined initial patterns of wood utilization by boring beetles. Ambrosia beetle channelization in Douglas-fir and western hemlock during the 1st year of decomposition resulted in removal of 0.2% of the sapwood volume in these species. Bark beetle and cerambycid beetle channelization in Douglas-fir and Pacific silver fir affected 7–9% of the phloem surface area.

The effect of tree species on beetle colonization patterns probably reflected the influences of physical and chemical factors in boles. Injured trees release volatile compounds, especially terpenes, which attract or repel dispersing adult beetles, especially bark beetles (Chapman 1963; Witcosky et al. 1987; Wood 1982). Ethanol produced by respiring tissues in logs is a primary attractant for ambrosia beetles and some bark beetles (Klimetzek et al. 1986; Moeck 1970; Witcosky et al. 1987).

Our data show that mass losses resulting from beetle channelization are quantitatively small (<0.6% of log volume) during this initial stage of bole decomposition. However, the order of mass losses, Pacific silver fir > Douglas-fir > western hemlock > western red cedar, after 2 years in our study is also the order of overall decomposition rates (Harmon et al. 1986). This suggests that early colonization by wood-boring beetles and their associated microflora could influence, or reflect, long-term patterns of decomposition.

Furthermore, gallery patterns increased the surface area of phloem and (or) sapwood of colonized boles exposed to leaching of soluble compounds and to microbial colonization. Ambrosia beetles in our study were found (Carpenter et al. 1988) to inoculate colonized logs with a diverse microfloral assemblage. The mutualistic *Ambrosiella* fungus was quickly replaced following ambrosia beetle emergence. By the time of our late summer sampling, beetle galleries and surrounding wood were colonized by ascomycete (soft-rot) fungi, especially *Penicillium* and stain fungi, *Ophiostoma* (= *Ceratocystis*) spp., but by few basidiomycete (decay) fungi (Carpenter et al. 1988). Bark beetles inoculated these logs with a somewhat different fungal assemblage (Carpenter et al. 1988) and are known to transport nitrogen-fixing bacteria (Bridges 1981). We have found significant anaerobic nitrogen fixation only in Douglas-fir and Pacific silver fir logs (T.D. Schowalter et al., unpublished data).

Many insect–fungus associations are mutualistic, with beetles providing access to carbohydrate resources and fungi providing nutritional enhancement; these relationships require synchronized life histories (Barras and Hodges 1969; Batra 1966; Dowding 1984; French and Roeper 1972; Haanstad and Norris 1985). Thus, each beetle species or functional group could be expected to inoculate colonized boles with a distinct microflora. Subsequent decomposition rate can be influenced by previous colonization by competing or insect-tended species, e.g., ascomycetes vs. basidiomycetes (Batra 1966; Dowding 1984; French and Roeper 1972; Haanstad and Norris 1985). For example, Käärik (1974) summarized findings that decomposition by decay fungi was more rapid in previously uncolonized wood than wood previously colonized by soft-rot fungi.

Our study indicates that wood excavation by beetles is small during the initial stage of bole decomposition. Nevertheless, the patterns of wood utilization by the various beetle functional groups may be instrumental in initiating decomposition and, perhaps, in determining long-term rates of decomposition in boles of different tree species.

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