United States
Department of
Agriculture

Forest Service

United States
Department
of the Interior

Bureau of
Land Management

General Technical
Report PNW-164

March 1984

The Seen and Unseen World of the Fallen Tree

Authors

CHRIS MASER
U.S. Department of the Interior
Bureau of Land Management
Forestry Sciences Laboratory
Corvallis, Oregon 97331

JAMES M. TRAPPE
U.S. Department of Agriculture, Forest Service
Pacific Northwest Forest and Range
  Experiment Station
Forestry Sciences Laboratory
Corvallis, Oregon 97331

STEVEN P. CLINE
Oregon State University
School of Forestry, Department of
  Forest Science
Corvallis, Oregon 97331

KERMIT CROMACK, JR.
Oregon State University
School of Forestry, Department of
  Forest Science
Corvallis, Oregon 97331

HELMUT BLASCHKE
Lehrstuhl für Forstbotanik
Universität München
Amalienstrasse 52
D-8000 München 40
West Germany

JAMES R. SEDELL
U.S. Department of Agriculture, Forest Service
Pacific Northwest Forest and Range
  Experiment Station
Forestry Sciences Laboratory
Corvallis, Oregon 97331

FREDERICK J. SWANSON
U.S. Department of Agriculture, Forest Service
Pacific Northwest Forest and Range
  Experiment Station
Forestry Sciences Laboratory
Corvallis, Oregon 97331

Cover: Ant's view of the seedling, moss, lichen, and mushroom cover on the surface of a fallen class III Douglas-fir tree.

The Seen and Unseen World of the Fallen Tree

Chris Maser
James M. Trappe
Technical Editors

This page was intentionally left blank

Abstract

Large, fallen trees in various stages of decay contribute much-needed diversity to terrestrial and aquatic habitats in western forests. When most biological activity in soil is limited by low moisture availability in summer, the fallen tree-soil interface offers a relatively cool, moist habitat for animals and a substrate for microbial and root activity. Intensified utilization and management can deprive future forests of large, fallen trees. The impact of this loss on habitat diversity and on long-term forest productivity must be determined because managers need sound information on which to base resource management decisions.

Keywords: Fallen trees, decay (wood), decomposition, old-growth stands, Douglas-fir, *Pseudotsuga menziesii,* mycorrhizae, soil moisture.

Contents

Prolog

. . . dying and dead wood provides one of the two or three greatest resources for animal species in a natural forest . . . if fallen timber and slightly decayed trees are removed the whole system is gravely impoverished of perhaps more than a fifth of its fauna.

(Elton 1966, p. 279)

Introduction

Large, fallen trees are unique, critical, dynamic components of old-growth forests (Franklin and Hemstrom 1980, Franklin and others 1981, Maser and others 1979). Each is a microcosm. Harvey and others (1979b) stated:

Evidence that soil organic reserves, particularly wood, play important roles in maintaining forest site quality emphasizes the need to properly manage woody materials. Thus, the viewpoint that woody residue represents only waste or a fire hazard must be reassessed. Forest users and managers must recognize the benefits, equivalent to long-term fertilization, that woody and other organic reserves contribute to forest ecosystems.

Even a casual observer of present western forests would note the abundance of fallen trees in various stages of decay, whether in a virgin old-growth stand or a recent clearcut (fig. 1). Up to a century ago western stream systems also characteristically contained abundant pieces and aggregations of large, woody debris, but that debris has been systematically removed to improve navigation, flood control, and drainage. We now have the technological capability to remove more and more woody debris from the forest floor. Conversion of forests from virgin to managed status reduces rotation ages from centuries to decades with a consequent reduction in average size of trees and change in wood quality. Forests of the future will have far less woody material contributed to the forest floor than forests of the past, and that material will differ in size and quality from the woody debris that has been historically prominent in forest habitats.

Woody debris is generally removed from streams or forests in the name of economic progress, but what are the short-term and long-term biological consequences? How is habitat diversity affected, and what is the impact on long-term site productivity? Our purpose is to encourage awareness and to facilitate thought on these issues by synthesizing available data on fallen trees in unmanaged old-growth forests. In so doing, we can also identify some research needs. The geographic scope is primarily the Douglas-fir region, but the principles and concepts should apply elsewhere.

Figure 1.—A Douglas-fir recently recruited to the forest floor.

The Seen World of the Fallen Tree

Life on earth, as humans view it, carries but a single certainty, what lives shall die. Life and death are interdependent. In forests, this is readily apparent in the large, fallen trees that area major component of the forest floor. Although dead, they are an integral part of the living old-growth forest.

Recruitment of Fallen Trees

Fallen trees are recruited to the forest floor by natural catastrophic events, such as windstorms that uproot and blow over whole trees or break their tops (Childs and Clark 1953, Cline and others 1980, Dahms 1949, Falinski 1978, Roth 1970, Ruth and Yoder 1953) (fig. 2). Heavy snow also breaks out treetops; and avalanches, mass soil movements, and floods knock down whole trees (Rothacher and Glazebrook 1968). Snags-dead, standing trees-on the other hand, usually deteriorate and simply collapse (Boyce 1923, Boyce and Wagg 1953, Cline and others 1980, Graham 1982, Keen 1929) (table 1, figs. 3 and 4).

Figure 2.—Fallen trees are natural components of the forest floor in unmanaged forests.


Figure 3.—Snags are also natural components of the unmanaged forest.

Table 1—Stage and condition of snag by decay class of fallen tree[1]

Snag stage and condition	Decay class
1-3, hard snag	I
4-5, hard snag	II
5-6, soft snag	III
7, soft snag, 70 + percent soft sapwood	IV

[1] Adapted from Maser and others (1979).

Figure 4.—When they fall, trees and snags immediately enter one of the first four decay classes (modified from Maser and others 1979).
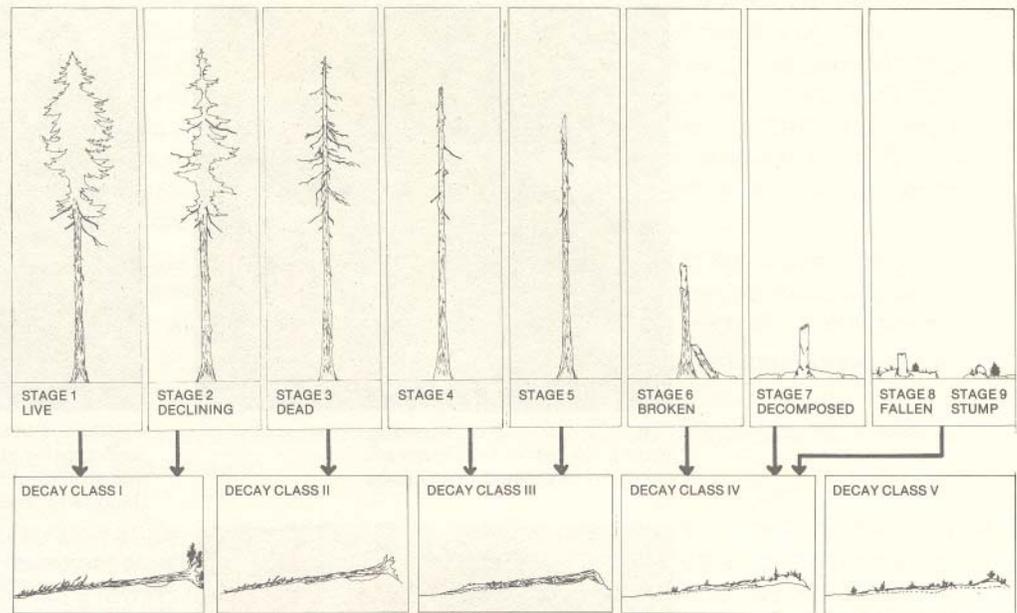
Mass of Fallen Trees Trees recruited to the forest floor accumulate through time (table 2, fig. 5); accumulation and rate of decomposition vary with the type of forest, slope, and aspect (Franklin and others 1981, Grier 1978, Graham and Cromack 1982, Maser and others 1979). In one midelevation stand of unmanaged 470-year-old Douglas-fir in western Oregon, the recruitment rate was estimated to be 0.49 fallen tree per acre (1.2 trees/ha) per year (Grier and Logan 1978). The decaying Douglas-fir trees represented from 53.4 to 265.4 short tons per acre (120 to 595 metric tons(t)/ha) (MacMillan and others 1977). Franklin and Waring (1980) showed values ranging from 31.2 to 69.4 short tons per acre (70 to 156 t/ha) in stands of widely different ages; their work included both young stands with large, carryover pieces of rotting wood and old-growth forests. Grier and Logan (1978) found that as much as 60 percent of the annual litter fall in a 450-year-old Douglas-fir stand may be woody debris. Sollins (1982) found that coarse woody debris contributed about 50 percent of the litter on a long-term basis. Further, decomposing trees in western Douglas-fir forests represent more volume above ground than is represented by the aboveground woody debris of typical deciduous forests in the Eastern United States (Day and Monk 1974, McFee and Stone 1966, Sollins and others 1980) (fig. 6).

Table 2—Fallen trees in an old-growth Douglas-fir stand, by decay class[1]

Decay class	Fallen trees per hectare	Fallen trees per acre
	Number	
I	27	11
II	15	6
III	31	13
IV	39	16
V	185	75
Total	297	121

[1] Adapted from MacMillan and others (1977).

Figure 5.—Douglas-fir tree, decay class I, fell before the Douglas-fir snag, which entered decay class III.

Figure 6.—Substantial volumes of decomposing fallen trees are typical of old-growth forests in the Douglas-fir region.
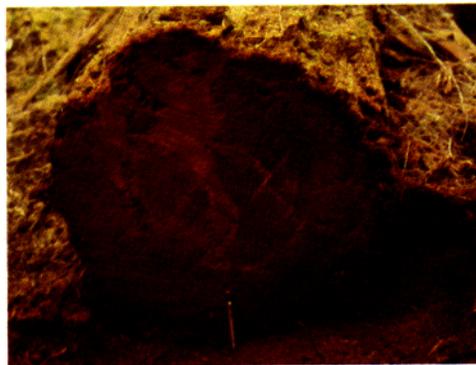

Figure 7.—A fallen tree oriented along the contour of a slope. The upslope side is filled with humus and inorganic material that allows invertebrates and small vertebrates to tunnel alongside. The downslope side provides protective cover for larger vertebrates.

Placement of Fallen Trees Fallen trees that are oriented along the contours of a slope seem to be used more by vertebrates than are trees oriented across contours, especially on steep slopes. Large, stable trees lying along contours help reduce erosion by forming a barrier to creeping and raveling soils (fig. 7). Soil and nutrients deposited along the upslope side of fallen trees reduce loss of nutrients from the site. Such spots are excellent for the establishment and growth of vegetation, including tree seedlings.

Vegetation becomes established on and helps stabilize this "new soil" (Maser and others 1979), and as invertebrates and small vertebrates begin to burrow into the new soil, they not only nutritionally enrich it with their feces and urine but also constantly mix it by their burrowing activities.

The interactions of fallen trees with soil are directly affected by steepness of slope and ruggedness of terrain; a fallen tree on flat ground, for example, is much more likely to contact the soil over its entire length than is one oriented either across or along contours on steep or rough terrain. The proportion of a tree in contact with the soil affects the water-holding capacity of the wood (Graham 1925). In our studies of fallen trees in old-growth Douglas-fir forests, the moisture retention through the summer drought was best in the side of trees in contact with the soil. The moisture-holding capacity of the wood affects in turn its internal processes and therefore the succession of plants and animals. In addition, the orientation of a fallen tree to aspect and compass direction and the amount and duration of sunlight it receives, drastically affect its internal processes and biotic community (Graham 1924, 1925; Graham and Knight 1965).

Decay Classes of Fallen Douglas-Fir Trees

Dead, fallen trees decay continuously, passing through recognizable stages or classes of decomposition. Fogel and others (1973) described broad classes of decay, based on the physical condition of the bark, wood, and twigs; the presence and pattern of vegetation on a fallen tree and its degree of root development; and the genera of fungi (identified from fruiting bodies or sporocarps) associated with the fallen tree. The five decay classes (Maser and others 1979; table 3), refined by subsequent study (Sollins 1982, Triska and Cromack 1980) are indispensable to research on wood decomposition for three reasons:

1. These stages of decay are inevitable; despite variation in the original material and surrounding environment, a classification of decay based on general processes can be used. (A publication by Minore (1966) can be used to key fallen trees to species.)

2. Decay class can be used without having to determine when the tree fell, a difficult problem that requires destructive techniques.

3. The original decay classes form ecological units that function as distinctive habitats for plants and animals.

The major limiting factor of this decay classification is that it is based on the external characteristics of a fallen tree and does not adequately convey the internal diversity of niches. We have found, however, that internal development of niches relates reasonably well to decay class.

A 450-year-old Douglas-fir stand on the H. J. Andrews Experimental Forest in the Willamette National Forest in western Oregon had a distribution of fallen trees in decay classes II to V that covered an average of 24 percent of the ground surface, ranging from 11 to 35 percent on different subplots. Although class V trees produced the most coverage, many were evident only as mossy or humus-covered mounds on the forest floor. Class I fallen trees, on the other hand, accounted for the least coverage for two reasons: (1) mortality rates are low in old-growth stands (Cline and others 1980) and (2) a rapid rate of decomposition in class I trees quickly converts them to class II. Subsequent change to higher decay classes progresses more and more slowly as the most readily decomposed fractions of the wood are utilized by decomposers (Hulme and Shields 1970).

Variation within and among fallen trees.--One must be aware of two sources of variation when using the decay classification: (1) within a particular fallen tree and (2) among fallen trees of the same decay class.

Variation within a fallen tree.-An old-growth Douglas-fir tapers along the length of its trunk, from its root collar to the tip of its crown (fig. 8). Much of the variation within a fallen tree relates to this taper. The smaller diameter parts of a fallen tree decay faster than the larger ones because the volume of the wood decreases toward the crown, the ratio of sapwood to heartwood increases (Dadswell and Hillis 1962), and fragmentation and contact with the forest floor increase. As decay proceeds, variation within the tree gradually changes; by the time the tree enters decay class V, the entire tree becomes a relatively amorphous, homogeneous mass.

Table 3—A 5-class system of decay based on fallen Douglas-fir trees[1]

Characteristics of fallen trees	Decay class				
	I	II	III	IV	V
Bark	Intact	Intact	Trace	Absent	Absent
Twigs, 1.18 inches (3 cm)	Present	Absent	Absent	Absent	Absent
Texture	Intact	Intact to partly soft	Hard, large pieces	Small, soft blocky pieces	Soft and powdery
Shape	Round	Round	Round	Round to oval	Oval
Color of wood	Original color	Original color	Original color to faded	Light brown to reddish brown	Red brown to dark brown
Portion of tree on ground	Tree elevated on support points	Tree elevated on support points but sagging slightly	Tree is sagging near ground	All of tree on ground	All of tree on ground
Invading roots	None	None	In sapwood	In heartwood	In heartwood

[1] Adapted from Maser and others (1979).

Figure 8.—Diameter-height relationships in seven individual old-growth Douglas-fir trees.
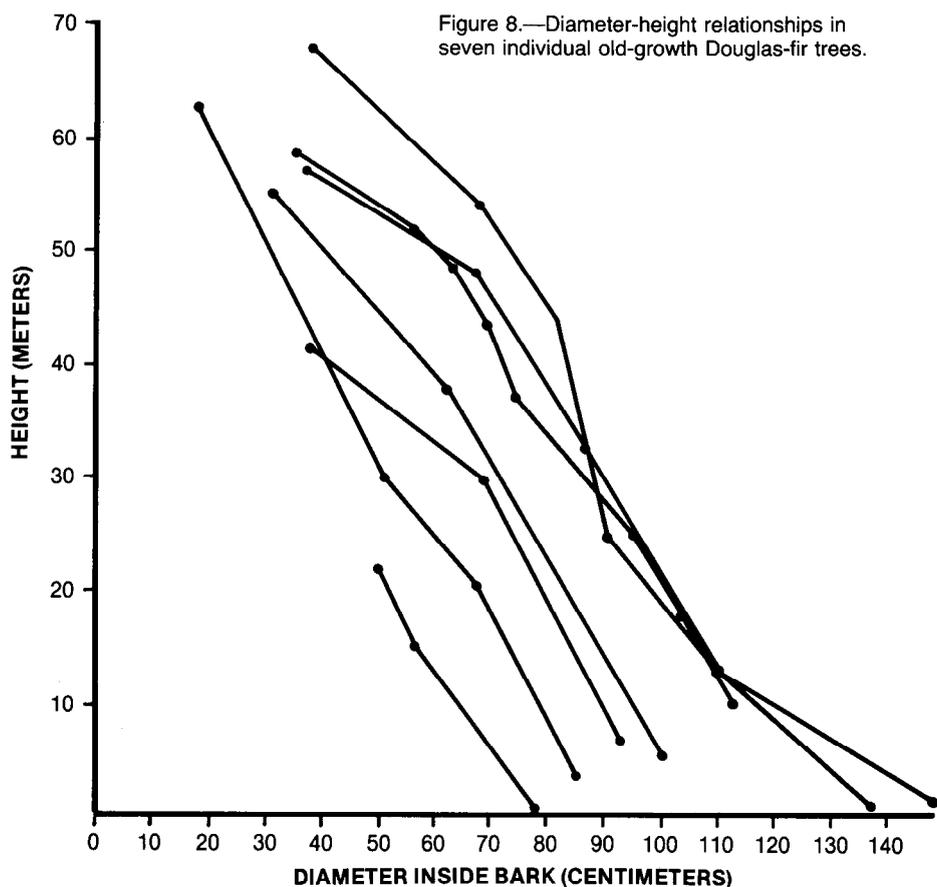
Variation among fallen trees.—The second source of variation—among fallen trees of the same decay class—is partly a consequence of classification itself. A single decay class necessarily contains a variety of fallen trees because they are assigned to a discrete class from a decay continuum. Additional variation, however, is caused by differences among trees at the time they fall. For example, trees vary in size, original diameter, age, old growth versus young growth, decay condition, live tree versus standing dead tree, and presence of heart rot.

A Fallen Tree's Relationship With Time

The age of a fallen tree—the number of years it lies on the forest floor—is positively correlated with decay class, but the relationship is logarithmic rather than linear. The time lapse between classes IV and V is exponentially greater than between decay classes III and IV, and so on. Decay classes I and II evolve rapidly, whereas the later classes develop slowly; variation in residence time within a decay class increases in the later classes. Estimating the residence time or age of a fallen tree becomes increasingly difficult as decay proceeds. Further, decay classes can evolve at different rates, depending on the physical setting of a forest stand, such as a north-facing slope versus a south-facing slope, or low elevation versus high elevation.

Determining the Age of a Fallen Tree

The time a fallen tree has rested on the forest floor can be determined by two standard methods: (1) aging the scars left on adjacent, living trees that were hit by the tree when it fell, and (2) aging the oldest tree growing on the fallen tree (fig. 9).

Scars.—Although aging scars left on the living, woody vegetation by the tree as it fell is the most reliable way to age what is now the fallen tree, such scars are often difficult to locate because they heal over or are inaccessible. Moreover, the healing pattern of wounds varies greatly, so increment cores taken around scars often produce inaccurate estimates of residence time.

A more reliable, but destructive, method of aging is to saw either a wedge or a complete cross section from the scar area; however, sawing injures or kills trees, an intolerable effect on long-term research sites.

Figure 9.—Western hemlock tree and seedlings (background) growing on a fallen tree that has decomposed into a mound on the forest floor.

Seedlings.-The second method of aging a fallen tree is to age the seedlings growing on it. Aging seedlings is a less reliable method than is aging scars because the lapse of time between the fall of a tree and the establishment of the oldest seedling is not known. But this lag can be calculated for a fallen tree by determining ages for both the scar and the oldest seedling and then subtracting the latter from the former. Several pairs of these age counts will reveal the mean lag for the stand. Mean lag can vary markedly from one stand to another.

Age for fallen trees that did not produce scars but do support rooted seedlings can be calculated by adding the mean lag to the age of the oldest seedling. This method of aging fallen trees, however, also requires the sacrifice of living trees that may be important in the development of a stand or in future studies.

Size and Shape of Fallen Douglas-Fir

There are three major sources of coarse woody debris in an old-growth Douglas-fir forest: (1) uprooting of live trees, with or without complete crowns; (2) breakage of crown and stem of live trees; and (3) breakup and fall of snags (Graham 1982). Because size of trees and the manner in which woody material comes to be on the ground vary widely, the resulting pieces of woody debris are heterogeneous in size and shape. Regardless of its original size, wood passes through the various stages of decay; the smaller it is, the faster it breaks down and disappears.

Surveys of large, coarse woody debris in old-growth forests show that broken, fallen trees are typically more abundant than whole fallen trees are (fig. 2).[1] To illustrate the changes in the size and shape of fallen Douglas-fir trees during the decomposition process, however, we will use a generalized whole, uprooted tree with a complete crown as an example.

Volume.-The first noticeable decrease in the volume of a fallen tree is in decay class III (Graham 1982). Bark alone can account for about 20 percent of the volume of a fallen Douglas-fir (Snell and Max 1981). As the sapwood is consumed and fragmented by both plants and animals and sloughs off, about 50 percent of the volume is lost, most of it during the transition from decay class III to decay class IV. This transition is called the basic fragmentation stage because of the cubical chunks of throughly brown-rotted heartwood. Fragmentation continues in decay class V, but the wood is held together by the prolific rooting of plants (fig. 10). Consequently, only 20 percent of the volume of a decay class V tree is lost; but with the loss of that 20 percent, only a tenth of the fallen tree's original volume remains (Graham 1982).

The bark and wood that slough off a rotting fallen tree accumulate alongside the tree. This material forms a mulch that extends over the ground area influenced by the tree.

Diameter.-The diameter of a fallen Douglas-fir decreases as the outer bark, sapwood, and heartwood slough off. So most of the overall volume loss is in diameter rather than in length; in our studies, the transition from decay class III to IV, when the maximum volume is lost, corresponded to the largest reduction (44 percent) in diameter. By decay class V, 68 percent of the original diameter has been removed through decomposition (see footnote 1). Some of the "lost" material is still present as crumbly fragments of wood and bark on the soil adjacent to the fallen tree, and some is incorporated into the soil by animal activity. Some has been physically removed by weather or animals, and some has been used as food by decomposer organisms.

Figure 10.—Prolific rooting of western hemlock saplings on a decay class V fallen tree holds the rotten wood together; ground cover is Oregon oxalis.
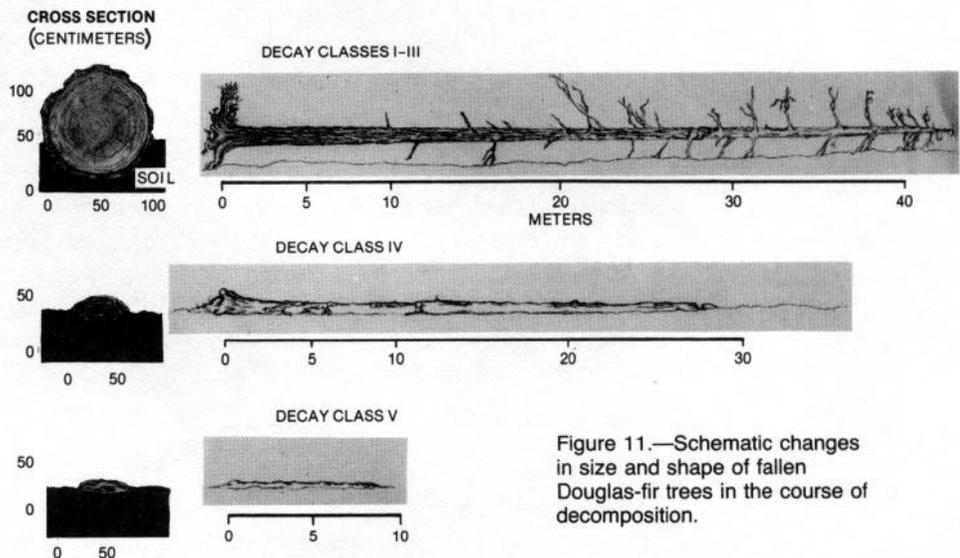

Figure 11.—Schematic changes in size and shape of fallen Douglas-fir trees in the course of decomposition.

A diameter of about 12 inches (30 cm) seems to be a critical boundary between slow or rapid decay and disintegration of fallen trees. Pieces smaller than that have a higher proportion of sapwood to heartwood and disappear more rapidly than pieces of larger diameter. This relationship between diameter of fallen trees and speed of decomposition has important ramifications in managed forests in which total tree size will be controlled.

Length.—The length of a fallen Douglas-fir tree decreases over time from the top toward the roots because the top has the smallest diameter and decomposes fastest (fig. 11). Little change in length takes place in decay classes I through III. By the time a tree reaches decay class IV, its length has been reduced about 15 percent because the top has begun to be incorporated into the soil. The largest reduction in length (about 40 percent) occurs during the transition from decay class IV to V, because the diameter decreases through fragmentation. Therefore, only a fraction of the original length of a fallen tree remains by the time it reaches class V (see footnote 1).

Shape.—Viewed from above, an intact, fallen tree changes in shape from a frustum (a truncated cone, tapered at the top) in decay classes I through III (fig. 5) to nearly cylindrical (both ends with a similar diameter) in decay classes IV and V. This change in shape can be demonstrated by comparing the ratio of basal diameter to top diameter: decay classes I and II = 5:1; decay class III = 4.4:1, decay class IV = 2.1:1; and decay class V = 1.6:1 (see footnote 1).

In a cross-sectional view, a fallen tree is circular in decay classes I through III. By settling and sloughing, it becomes elliptical in decay class IV. The elliptical shape becomes exaggerated, approaching a lens shape, in decay class V and later stages.

Substrates as Niches

Every living conifer is composed of tissues that perform specific functions. When a tree dies, the various tissues provide distinguishable substrates that provide different niches.

The four major tissues of a Douglas-fir tree are outer bark; inner bark or phloem; sapwood, the living portion of the xylem; and heartwood, the dead portion of the xylem (fig. 12). A class I fallen Douglas-fir is mostly xylem, heartwood (60 to 80 percent) and sapwood (5 to 20 percent). The thick, outer bark of an old-growth Douglas-fir may be 5 to 20 percent of the cross-sectional area, whereas the inner bark is usually less than 5 percent.

The outer bark and heartwood of a Douglas-fir tree are physiologically inactive. Outer bark forms a physical and chemical barrier between the inner tree and the atmosphere, insects, and diseases. Heartwood supports the tree and stores metabolic wastes (Brown and others 1949, Hillis 1962). The inner bark and sapwood are physiologically active. Inner bark is the growing portion of a tree and is the site of both formation of new cells and transportation of food, whereas sapwood transports and stores water and dissolved mineral salts (Brown and others 1949).

Decay rate	IB	>	SW	>	HW	>	OB
Soluble carbohydrates	IB	>	SW	>	HW	>	OB
Taxifolin content	IB	<	SW	<	HW	<	OB
Nitrogen content	IB	>	OB	>	SW	>	HW
Mineral content	IB	>	OB	>	SW	>	HW
Water content	SW	>	IB	>	OB	>	HW
Lignin content	OB	>	IB	>	SW	≥	HW
Total extractives	OB	>	IB	>	HW	>	SW
Cellulose content	HW	>	SW	>	IB	>	OB
C:N ratios	HW	≥	SW	>	IB	>	OB
Density	OB	≥	IB	>	HW	>	SW

Figure 12.—Relative decay rates and composition of different substrates of fallen trees: OB = outer bark; IB = inner bark; SW = sapwood; HW = heartwood (adapted from Clermont and Schwartz 1948; Gardner and Barton 1960; Graham and Kurth 1949; Hergert and Kurth 1952; Kurth 1948, 1949; Kurth and Chan 1953; Scheffer and Cowling 1966; and this study).

These parts of the fallen tree provide substrates of differing quality for use by other organisms. Quality of the substrate depends on physical and chemical properties; the higher the quality, the faster it disappears through respiration and fragmentation Lambert and others 1980). Respiration is the enzymatic transformation by decomposer organisms of organic compounds to carbon dioxide, water, and other simple products. Fragmentation occurs when the substrate is eaten, sloughed, and leached.

The main chemical differences among substrates are: (1) nitrogen content; (2) the mineral or ash content-phosphorus, potassium, calcium, magnesium; (3) the carbon matrix-cellulose, lignin, pentosans (Lewis 1950); and (4) the content of other organic compounds-waxes, pigments, carbohydrates, fats, resins, phenolic compounds (Graham and Kurth 1949, Hergert and Kurth 1952, Kurth 1948).

Many chemical substances are associated with the carbon matrix but are not chemically bonded to it. Bark contains more such extractable materials than wood does (Kurth 1948, 1949) (fig. 12); for example, taxifolin, a natural component of Douglas-fir, has fungicidal properties (Kennedy 1956).

Tissues that were physiologically active in the live Douglas-fir decay most rapidly after the tree falls because they are higher in quality than inactive tissues are (fig. 12). Inner bark and sapwood of freshly fallen trees attract the initial decomposers-beetles that feed on these tissues. By penetrating the protective outer bark, the beetles open the inner bark and sapwood to invasion by other decomposers. These tissues contain more soluble carbohydrates, more moisture, and less taxifolin than do the lower quality outer bark and heartwood (fig. 12). The substrate of poorest quality is the decay-resisting outer bark, which is low in moisture, carbohydrates, cellulose, and carbon to nitrogen (C:N) ratio but high in lignin, taxifolin, total extractives, and density (fig. 12).

Regardless of substrate, changes develop during decay of fallen trees: (1) density decreases; (2) water content increases until decay classes III and IV are reached, at which time the water content stabilizes; (3) mineral and nitrogen contents increase; (4) the cellulose content decreases; (5) the relative lignin content increases; and (6) the C:N ratio decreases (Fogel and Cromack 1977, Foster and Lang 1982, Graham and Cromack 1982, Grier 1978, Lambert and others 1980, Sollins 1982).

Inner bark disappears fastest because it has the highest substrate quality and the smallest volume. Both sapwood and outer bark disappear by decay class IV, but for different reasons. Sapwood elicits high biological activity and disappears because of insect consumption and microbial breakdown (fig. 13). Outer bark disappears almost solely by fragmentation and sloughing from the top and sides of a fallen tree. Large trees are mostly heartwood when they fall and by decay class IV only heartwood remains; without the initial association with higher quality substrates, such as sapwood and inner bark, heartwood would undoubtedly decay more slowly (see footnote 1). When decay reaches the advanced class V stage, the fallen tree appears as a mound on the forest floor, usually covered with humus and litter or moss and often supporting several to many hemlocks. Much of the crumbly, brown-rotted heartwood remains in place. That which has disappeared, however, is not all lost through metabolism of decomposers. Much of it merges into the humus or becomes incorporated into the soil profile (Denny and Goodlett 1956; Harvey and others 1978, 1979b; McFee and Stone 1966).
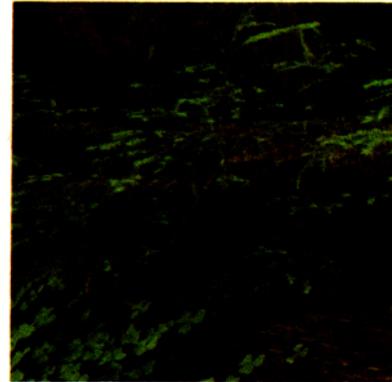
Figure 14.—A fallen Douglas-fir tree in decay class IV, with wood separated into the characteristic angular blocks known as brown cubical rot; this decay stage provides superb rooting substrate for hemlock seedlings.

Figure 13.—The inner bark and part of the sapwood of this decay class II fallen tree have decomposed; the outer bark and heartwood are still intact.

Internal Surface Area

The importance of internal surface areas is that, through such surfaces, a fallen tree interacts with its environment. A newly fallen tree, for example, interacts only passively with the surrounding forest because its interior is not accessible to plants and most animals. But once fungi and bacteria, which are smaller than the wood fibers, gain entrance, they slowly dissolve and enter the wood cells. And wood-boring beetles and termites chew their way through the wood fibers. Meanwhile, many other organisms, such as plant roots, mites, collembolans, amphibians, and small mammals, must await the creation of the internal spaces before they can enter. The flow of plant and animal populations, air, water, and nutrients between a fallen tree and its surroundings increases as the aging process continues.

Surface area within a fallen tree develops through physical and biological processes. A tree cracks and splits when it falls and subsequently dries. Microbial decomposition breaks down the material in the cell wall and further weakens the wood. Wood-boring beetle larvae and termites tunnel through the bark and wood; this activity not only inoculates the substrates with microbes but also opens the tree to colonization by still other microbes and small invertebrates. Wood-rotting fungi produce zones of weakness, especially between annual rings, by causing spring wood to decay faster than summer wood; and plant roots that penetrate the decayed wood split it as the roots elongate and thicken in diameter. Because of all this internal activity, the longer a fallen tree rests on the forest floor, the greater the development of its internal surface area. Most internal surface area results from biological activity, the cumulative effects of which not only increase through time but also act synergistically—insect activity promotes decomposition through microbial activity that encourages the establishment and rooting of plants.

Most splitting of the sound wood found in decay classes I-III in fallen trees is radial as the wood dries. Later, the weakening of annual rings by the more rapid decomposition of spring wood than summer wood leads to circumferential cracking as well. The blocky structure in class IV and V fallen trees results from brown cubical rot (fig. 14).

Temperature

Gross environmental features regulate temperature regimes. Latitude, elevation, aspect, and vegetation not only set the maximum and minimum temperature of a site but also control the seasonal range in temperature. For fallen trees, the question is twofold: (1) What is the relationship between the temperatures of air, tree, and soil? and (2) How is this relationship modified through the year by characteristics of the tree itself?

Summer data (see footnote 1, p. 8) indicate the following temperature relationships at all elevations sampled: air > fallen tree > soil. The absolute differences were greater at low elevations than at midelevations or high elevations; mean winter temperatures of the air, a fallen tree, and the soil were nearly identical at each elevation.

Substrate temperatures within fallen trees of a particular decay class differ little at a given time and site, but each decay class responds differently to the temperatures of the surrounding air and soil in summer. Measurements (see footnote 1, p. 8) in August showed the following relationship: air = I = II>III>IV = V>soil. These relationships develop because, as decay proceeds, a fallen tree more closely hugs the soil, which buffers it against fluctuations in air temperature. Thus, trees in decay classes I and II are cylindrical and contact the soil relatively little. Trees in class III have sloughed and slumped somewhat, and those in classes IV and V are partially to mostly embedded in the soil.

Moisture

Whole fallen tree.—Three trends are visible in the water-holding capacity of a fallen tree; the same is true for individual substrates—outer bark (OB), inner bark (IB), sapwood (SW), and heartwood (HW):

1. Water content increases with residence time on the forest floor and with stage of decay (fig. 15, sapwood) because of the microbial breakdown of woody substrates that produces water and carbon dioxide; also, microbial activity increases as decay advances. Simultaneously, the water-holding capacity of woody substrates increases as cell walls break down.
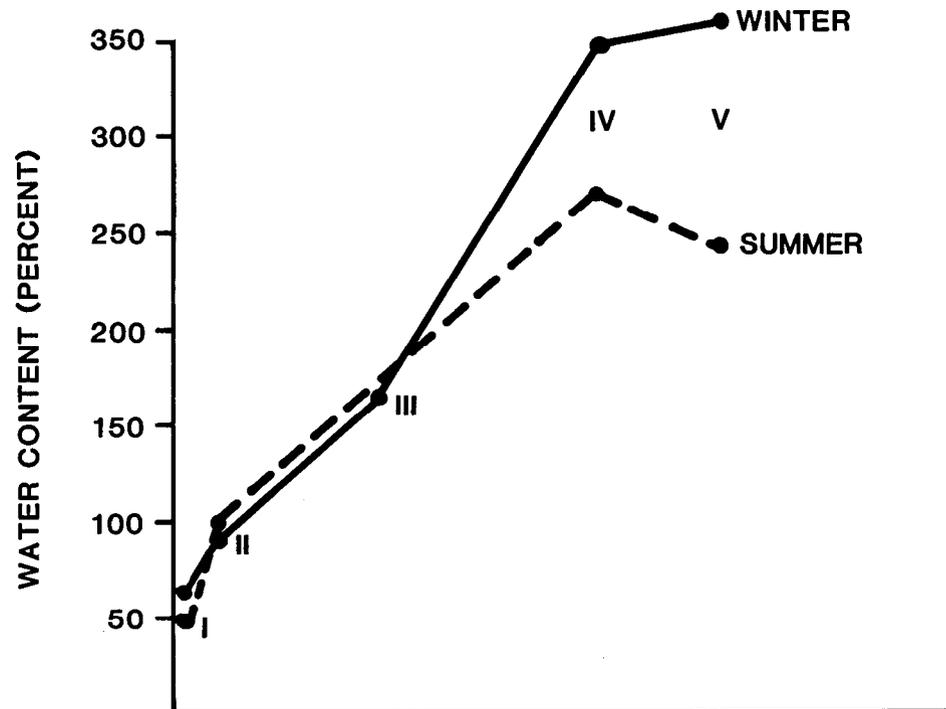

Figure 15.—Water content of fallen Douglas-fir trees in winter and summer; each point represents a decay class from I (newly fallen trees) to V (fallen trees decomposed to a mound of brown cubical rotted wood).

2. In decay classes I through III, the mean water content of fallen trees is nearly equal in summer and winter; but in decay classes IV and V, trees hold more water in winter than in summer. There are two reasons: (1) Winter usually provides abundant water, so the complete storage capacity of the woody substrates is used; and (2) evaportranspiration potential is normally low because days are short, temperatures are cool, and humidity is high.

3. As the overall water-holding capacity of woody substrates increases with stage of decay, so does the seasonal fluctuation of the water content (fig. 15).

Substrates. -Four trends are visible in the water-holding capacity of the substrates within a fallen tree:

1. When a tree falls (decay class I), the water content of the substrates is: IB>SW>OB>HW. Initially, the inner bark and sapwood (both physiologically active (alive) at the time the tree fell) contain more water than do the outer bark and heartwood (both physiologically inactive (dead) at the time the tree fell). Nearly all of the living cells are located in the inner bark and sapwood of a live tree.

2. The water content of all woody substrates increases during the residence time of a tree and its stage of decay. Again, as with the whole tree, breakdown of woody substrates by microbial activity produces water and carbon dioxide, and microbial activity increases as decay proceeds.

3. The water content of substrates increases at different rates within and among seasons. In winter, for example, water content increases (percent per year): IB>SW>HW>OB. The water retention capacity depends on a given substrate's stage of decay; the more advanced the decay, the more porous the wood and the more water it retains. In summer, however, water-holding capacity shifts in response to exposure of the substrate to evapotranspiration. A fallen tree dries because of the dramatic increase in evapotranspiration brought about by the simultaneous increase in day length and air temperature and decrease in rainfall and relative humidity. The inner bark, for example, is protected from excessive drying because inner bark is sandwiched between the thick outer bark and the relatively moist sapwood And, being the most nutrient-rich substrate, it supports the highest microbial activity, through which additional water is produced. Heartwood retains water because of its large volume; thus, although the exposed outer surface of a tree may dry, the center retains moisture. Microbial activity continues in the moister areas and produces more water. Outer bark, on the other hand, is prone to drying not only because it is exposed to direct sunlight and wind but also because microbial activity is low, so little water is produced. As the outer bark sloughs off, the sapwood is no longer protected from sun and wind, so it begins to dry out. The drying of sapwood is speeded up because sapwood is more porous than outer bark; therefore, the ability of sapwood to retain water against the forces of evapotranspiration decreases as porosity increases.

4. Seasonal fluctuations of water content increase as the water-holding capacity of the woody substrate increases (fig. 15).

Plant Rooting	Woody plants do not root in fallen trees in decay class I. A tree in decay class II may have plants rooting in its inner bark, which decays fastest of all the substrates; these roots would have reached the inner bark through fissures in the outer bark. By the time a tree reaches decay class III, its inner bark is completely decomposed, and the outer bark and sapwood are often penetrated by roots (in 50 percent of our samples). Only about a third of the heattwood samples in decay class III trees were colonized by roots. When a tree reaches decay class IV, however, only heartwood remains, and nearly all our samples (87 percent) contained roots, Finally, trees in decay class V are not only completely colonized by roots but are actually held together by them (see footnote 1, p. 8).

Within a decay class, plant rooting differs among substrates for two reasons: (1) Substrates decay at different rates, and (2) substrates are not equally accessible to plant roots. In general, as decay proceeds, plant rooting increases in all substrates because they become excellent rooting medium-density and hardness decrease, and water content increases.

Insect Galleries and Frass (Excrement)	Wood-boring insects, such as beetles, carpenter ants, and termites, tunnel within fallen Douglas-fir trees and consume the woody tissues. Their activities are evidenced by their galleries and tunnels often packed with borings and feces. The collective activity of such wood-boring insects appears to be the most important factor in initiating early decomposition of fallen trees-decay classes I-III-for three major reasons.

First, wood is broken down by consumption and digestion by insects and by enzymatic attack by microbes. Insects, however, can penetrate the wood matrix faster than microbes can. Second, consumption and digestion of wood also fragment it. As a fallen tree is fragmented by insect tunnels and galleries, its internal volume is opened to decomposer plants and animals. The wood matrix is reduced to particles (borings and feces), and more surface area is availalbe for microbial attack (Crossley 1976). Third, wood-boring insects serve as vectors for decomposer micro-organisms, such as intestinal inhabitants that are expelled in the feces (Breznak 1982). They are also introduced as external associates; fungal spores, for instance, are transported in special pits and cavities in adult beetles (Francke-Grosmann 1967). Fungal spores and hyphae are also picked up and carried by insect larvae. In addition, each species of insect that tunnels in Douglas-fir bark or wood has its attendant predators, parasites, and scavengers (Deyrup 1981).

Frequency of galleries by decay class of tree.-Studies in the H. J. Andrews Experimental Forest in western Oregon showed that the percentage of wood samples with galleries increased as decomposition of the fallen trees proceeded (see footnote 1, p. 8). When the substrates within a decay class were compared for galleries, they ranked as follows: IB>SW>HW. Outer bark was not included in this comparison because the nature of the galleries differed. Insects simply chew through, not within, the outer bark to gain access to the nutritious inner bark and sapwood Inner bark disappeared before the frequency of galleries reached 100 percent. But all the sapwood samples had galleries by the time they reached decay class III and the heartwood, by decay class V.

Effects of galleries on wood properties.-Samples of a substrate with insect galleries in a fallen tree were softer and wetter and had a lower density, more plant roots, higher microbial activity, higher nitrogen fixation activity, higher microarthropod populations, and higher exchangeable and mineralizable nitrogen than did samples from the same substrate without insect galleries (see footnote 1, p. 8).

The Unseen World of the Fallen Tree

Decaying trees comprise considerable accumulations of mass and nutrients in unmanaged, old-growth forest ecosystems (Triska and Cromack 1980). Some of the largest accumulations occur in the unmanaged forest stands of the Pacific Northwest. Coarse woody debris can range from 130 to 276 tons per acre (118 to 251 t/ha) in stands from 100 to more than 1,000 years old (Franklin and Waring 1980). Although here we are concerned with Douglas-fir, neither decaying wood nor research data are unique to forests of the Pacific Northwest. McFee and Stone (1966) observed that decaying wood persisted for more than 100 years in New York, and Falinski (1978) noted substantial accumulations of coarse woody debris in an old-growth forest in Poland. Appreciable accumulations of fallen trees also occur in the temperate forests of the Andes of central Chile, in the course of long-term forest succession (Veblen 1979). These observations evidence the long-term continuity of decaying trees as structural components in forest ecosystems.

The decomposing wood of a fallen tree serves as a savings account of nutrients and organic material in the forest soil. Nitrogen, for example, accumulates in decaying trees and branch wood in forests of the Pacific Northwest and other regions (Graham and Cromack 1982, Lambert and others 1980, Lang and Forman 1978, MacMillan 1981, Sollins 1982, Swift 1977b). In old-growth Douglas-fir forests, about as much nitrogen accumulates in decaying, fallen trees as in the forest floor. Other nutrients, such as calcium and magnesium, also accumulate in decomposing woody substrates (Cromack and others 1979, Grier 1978, Rennerfelt and Tamm 1962, Sollins and McCorison 1981, Sollins and others 1980).

Nitrogen fixation by free-living bacteria is another mechanism of nitrogen accrual (Cornaby and Waide 1973, Larsen and others 1978, Sharp 1975, Sharp and Millbank 1973, Silvester and others 1982, Triska and others 1982). Although nitrogen fixation in wood is modest compared with that occurring in other substrates in forests, the persistence of decaying wood allows small increments of nitrogen to accrue over many decades.

Further, decomposing wood undergoes changes in other chemical constituents and pH, as well as in physical structure (Aho 1976, Aho and others 1979, Johannson and Theander 1974, Shortle and Cowling 1978, Tatter and others 1971). Very old, decayed wood can even become somewhat humified and leave a long-lasting substrate resistant to further decay.

Fallen trees harbor a myriad of organisms, from bacteria and actinomycetes to higher fungi. Of these, only some of the fungi might be noticed by the casual observer as mushrooms or bracket fungi (fig. 16). These structures, however, are merely the fruiting bodies produced by mold colonies within the log. Many fungi fruit within the fallen tree, so they are seen only when the tree is torn apart (fig. 17). Even when a fallen tree is torn apart, only a fraction of the fungi present are noticed because the fruiting bodies of most appear only for a small portion of the year. The smaller organisms, not visible to the unaided eye, are still important components of the system.

Figure 16.—Mushrooms of
Inocybe lanuginosa (Bull.: Fr.)
Kumm, a mycorrhizal fungus that
fruits only with roots growing in
rotten wood.

Figure 17.—*Ceratiomyxa
fruticulosa* (Mill.) Macbr., a tiny
fungus that typically fruits in
cracks within brown cubical rotted
wood.

|⎦ 0.5 mm ⎣|

**Microhabitats and
Inhabitants**

Fallen trees offer multitudes of both external and internal habitats that change and yet
persist through the decades. One needs an understanding of the synergistic effects of
constant small changes within a persistent large structure to appreciate the dynamics
of a fallen tree and its function in the forest ecosystem.

Within fallen trees.—The most obvious changes in fallen trees over time are described
in the classification system shown in table 3. The class I tree, mostly intact and
undecayed, offers habitat and substrate to only a few primary invaders: bark or
wood-boring insects, a few fungi, and bacteria. The entry of these organisms opens the
tree to profound changes that render it amenable to many additional tenants. The
decayed sapwood enclosed by intact bark in the class II tree provides a soft, fragmented,
moist environment much of the year. Many organisms inhabiting the class II tree lose
out as decay progresses to class III, when the bark and decayed sapwood slough off.
Meanwhile, the heartwood becomes increasingly decayed, but the process is much
slower than in the sapwood so the class IV stage lasts a long time.

It is in the class IV stage that the fallen tree presents the most diversified habitat and
hence supports the greatest array of inhabitants. The decayed heartwood is relatively
stable, so plants that become established on it have time to grow substantial root
systems. Decayed heartwood splits into chunks; roots grow down the resulting cracks
as well as along insect channels. Invertebrates—from minute mites to centipedes,
millipedes, slugs, and snails—find shelter in these openings and passage along them
(fig. 18). Vertebrates, such as salamanders, shrews, shrew-moles, and voles, find cover
under debris of sloughed bark and rotten wood alongside the class IV tree; they also
find the rotten wood on the underside of the tree crumbly enough for digging tunnels
or burrows (fig. 19). Fungi and other micro-organisms abound on the wood itself as well
as on the new substrates offered by the feces of animals.

Gradually, the class IV tree breaks down into increasingly smaller crumbles of rotten
wood to become class V. The intricate labyrinth of cracks, tunnels, and chambers
collapses into a mulchlike mound that is excellent rooting material (fig. 20). It is, however,
too homogeneous and unstructured to provide good animal habitat. Because it is now
composed primarily of residual materials highly resistant to decay, it does not support
as diverse a community of micro-organisms as it did in the class IV stage.

17

Figure 18.—A millipede (*Har-paphe haydeniana*) in a molting chamber made of organic debris under the loose bark of a class III fallen Douglas-fir tree.

Figure 19.—Clouded salamander, an inhabitant of class III fallen Douglas-fir trees in forest openings (photo courtesy of Greg Courtney).

Figure 20.—Two decay class V fallen Douglas-firs in the foreground are decomposed into mounds covered with highlighted Oregon oxalis; the background fallen tree is in decay class IV.

Ultimately, the entire tree is incorporated into the soil. It has gone full circle, having been formed as a product of soil and of photosynthetically captured carbon, it now returns to the soil through release of carbon by decomposition.

Checklists of plants and animals.—There are few checklists of either plants or animals that inhabit fallen Douglas-fir in the Pacific Northwest. No checklist of the micro-organisms in fallen trees of western old-growth forests is available; the subject has hardly been studied. (Higher fungi have been cataloged for many kinds of rotten wood in Europe: Kreisel (1961), Pirk and Tüxen (1957), Ricek (1967, 1968), Runge (1975).) Lawton (1971) listed the mosses that occur on rotten wood or stumps in the Pacific Northwest. Deyrup (1975, 1976) has done a thorough job with the insects and has identified about 300 species associated with fallen Douglas-fir. The only published checklist for vertebrates that use fallen trees is for northeastern Oregon (Maser and others 1979).

Nutrient Cycling

As carryover structural components of old-growth forests, large snags and large fallen trees contribute to the internal cycling of nutrients. Such snags and fallen trees also interact with hydrological cycles and serve as habitat for numerous micro-organisms and higher plants and animals. For example, in one portion of an old-growth Sitka spruce forest in the Olympic National Park, fallen trees covered about 12 percent of the forest floor. A similar proportion of surface area interactions occurs in many old-growth Douglas-fir forests, which resemble some stands in the Olympic National Park (Christensen 1977, Elton 1966, Franklin and Waring 1980, Franklin and others 1981, Grier 1978, Triska and Cromack 1980). Fallen trees in various stages of decay covered 21 percent of the floor of an old-growth Douglas-fir stand in the Cascade Range in western Oregon (Fogel and others 1973).

Fallen trees interact with nutrient cycling processes in a forest through such mechanisms as litter fall (freshly fallen or slightly decomposed plant material from the canopy), throughfall (rain or dew that picks up nutrients as it falls through the canopy), nitrogen fixation, and nutrient uptake by plants associated with the fallen trees. Litter fall and throughfall are major pathways for the flow of nutrients and energy within forests (Carlisle and others 1966, Rodin and Bazilevich 1967, Sollins and others 1980); they contribute nutrients and water to rotten wood. The larger a fallen tree, the more litter it accumulates on its surface and the more nutrient-rich moisture it intercepts from the canopy. The moisture gathers nutrients as it passes through the accumulated litter and soaks into the fallen tree. In addition, a snag may accumulate moisture-carried nutrients and have a higher nutrient capital when it falls than does a live tree.

Ground contact by fallen trees creates opportunities for various interactions with the bioticcomponentsof soil and litter. Fungi, for instance, translocate nutrients within the soil-litter system, as both decomposers and root symbionts. Fungi also immobilize translocated nutrients and thereby enrich the decomposing wood substrates they inhabit. In addition, the colonization of decomposing fallen trees by nitrogen-fixing bacteria permits additional nitrogen accretion within the decaying wood (Cornaby and Waide 1973; Dowding 1976, 1981; Larsen and others 1978; Melin and Nilsson 1950, 1952; Silvester and others 1982; Sollins and others 1981; Swift 1977a 1977b).

Colonization of decomposing wood by animals helps microbes to enter interior surfaces of the wood and creates additional openings for entry of water and nutrients; and penetration of the wood by roots of trees, such as western hemlock, facilitates entry by mycorrhizal fungi (fig. 21). Western hemlocks colonize rotten wood over many decades (figs. 9,10, and 14) to insure long-term interactions by root zone processes. Decaying wood thus serves as a savings account of soil organic materials and nutrients in forest ecosystems (Christy and others 1982, Graham and Cromack 1982, Kuhnelt 1961, Lambert and others 1980, Swift and others 1979).

Interactions-Nutrients, Plants, and Animals

The continuum of a fallen tree is composed of, and driven by, an increasingly complex network of simultaneously developing minisystems-all interdependent. These minisystems are: (1) animal-plant-nutrient, (2) plant-nutrient, (3) plant-plant, (4) animal-plant, (5) animal-animal, and (6) nutrient-plant-animal-nutrient. The cumulative effect of these systems is far greater than the sum of their parts. Ausmus (1977) stated the impact simply: ". . . wood decomposition represents a long-term stabilizing force within the forest ecosystem."
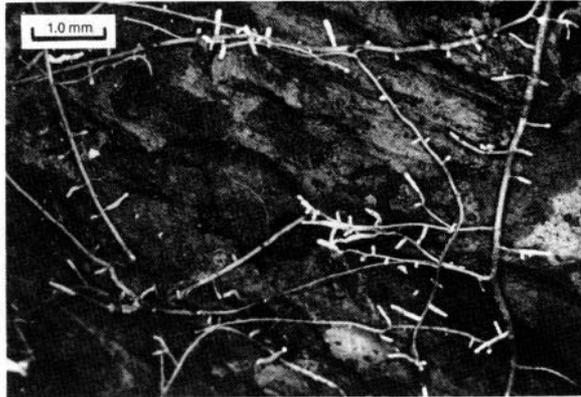
Figure 21.—Small roots and mycorrhizal feeder root tips of western hemlock in rotten wood.

The following simplified scenarios illustrate known facets of each minisystem, and each internal minisystem builds on the preceding one. They are continually being added to, subtracted from, and variously interwoven (Kimmey and Furniss 1943). Some grossly simplified activity levels might be:

1. Animals that eat the fallen tree, which opens it to the outside and initiates nutrient cycling: wood-boring beetles, carpenter ants, termites, and wood-tunneling mites.

2. Micro-organisms that live on the fallen tree: bacteria, yeasts, and ambrosia fungi.

3. Animals that eat live micro-organisms that grow on the fallen tree: collembolans, mites, and ambrosia beetles.

4. Live plants, such as western hemlock or huckleberry, that form a specific symbiotic (mycorrhizal) association with other live plants (particular fungi), both of which are partially or completely rooted in the fallen tree.

5. Animals that depend on the fungal portion of the mycorrhizal association for their food supply: mites, beetles, and the California red-backed vole.

6. Animals that eat live animals: mites, spiders, pseudoscorpions, centipedes, and salamanders.

7. Animals that eat detritus (dead plant and animal material and animal feces): earthworms, mites, millipedes, isopods, and earwigs.

Trees fall on the forest floor in various stages of decomposition, from sound windthrown trees to snags to stubs of old snags toppled because they are so badly decayed that they can no longer support themselves. Each is unique when it begins its new "life" as a fallen tree. Some of the decay organisms living in standing trees in an old-growth forest may continue their activity after a tree falls. Others, especially those that were in the tops of the standing trees, soon die out after the tree falls and are replaced by ground inhabitants. In the following discussions, we describe the events and organisms in live trees that were windthrown. Fallen snags or stubs are recruited at more advanced stages of decay.
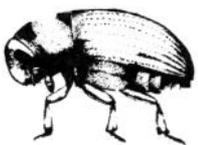
Animal-plant-nutrient.—Tree bark is such an effective protective barrier that the first minisystem to develop in a new, class I fallen tree is the animal-plant-nutrient minisystem. For example, a bark beetle (Scolytidae) (an animal) chews through the bark and thus connects the outside world with the inside of the tree. As the beetle enters and begins to use the tree, it not only introduces fungal spores but also initiates the nutrient cycle with its first deposit of bodily waste.

Bark beetle

The character of the available food is decidedly varied in the different parts of a newly fallen tree. Proteins are concentrated in the living tissues (phloem—the inner bark and cambium); carbohydrates, on the other hand, are concentrated in the dead woody tissue (xylem). In addition, the living inner bark and cambium are more easily digested than is the sapwood; but the moist sapwood is more digestible than the drier heartwood. So each portion of a fallen tree supports a characteristic group of insects adapted to a specific set of circumstances. Further, the numbers of a given species are regulated by the availability (quantity and quality) of their food supply. Since the inner bark and cambium furnish the most nutritious food, this microhabitat is promptly occupied. The area of next importance is the sapwood, then the heartwood, and finally the bark (Anderson 1960, Graham 1925).

The insects occupying the live inner bark and cambium must be able to chew or bore their way through the dead outer bark and are called borers. There are two groups: (1) those that spend all their developmental or immature stages in this substrate and (2) those that spend only part of their developmental stages in this substrate (Anderson 1960, Graham 1925).
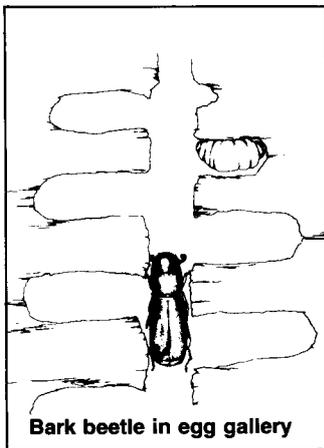
Bark beetle in egg gallery

The first group is typified by a bark beetle. For example, the Douglas-fir beetle breeds in both live trees and class I fallen trees that result from windthrow. Because these beetles depend on the fresh, green tissues of the inner bark and cambium, they must develop rapidly before their perishable habitat and food supply dry out or become chemically and physically altered by other organisms.

A female Douglas-fir beetle attacks class I wood in early spring by chewing through the outer bark. When she reaches the inner bark and cambium, she chews an egg gallery that is usually 2 feet (60 cm) or more in length along the axis of the tree. The egg gallery is about one-quarter of an inch (6 mm) wide and has small "grooves" on alternate sides; 10 to 36 eggs are laid together in the grooves. When the eggs hatch, the larvae chew lateral feeding galleries through their food supply—the phloem. As the larvae grow, the feeding galleries increase in size. Larvae pack their feeding galleries with borings (refuse) and frass as they eat. The larvae dine throughout the spring, summer, and autumn. In autumn, a larva creates a pupal cell at the end of its feeding gallery where it overwinters as a mature larva. Adults overwinter also and begin to emerge in April. The cycle, from egg to sexually mature adult, requires about 1 year, and one generation is produced annually (Anderson 1960, Chamberlin 1949, Furniss and Carolin 1977, Furniss and Orr 1970, Graham and Knight 1965).
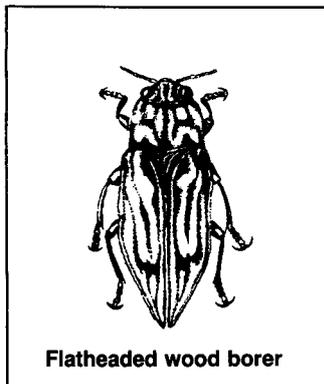
Flatheaded wood borer

The second group is typified by some members of such wood-boring beetle families as Buprestidae (flatheaded or metallic wood borers) and Cerambycidae (roundheaded wood borers). Some flatheaded wood borers, for example, develop in the inner bark and cambium, but others feed there only for a time and then enter the sapwood. Still others go directly into sapwood and heartwood.

Figure 22.—The golden buprestid prefers the sapwood and heartwood of class I fallen Douglas-fir trees.

A good example of the family Buprestidae is the golden buprestid (fig. 22). The golden buprestid feeds briefly in the cambium but prefers the sapwood and heartwood of class I wood. It will, however, inhabit partially to completely seasoned wood.

A female deposits her eggs in flat masses wedged in crevices in the bark or in cracks in exposed wood. The young hatch and immediately start boring into the wood. Their oval tunnels increase in size as the larvae grow. The tunnels range in length from 3 to 15 feet (0.91 to 4.6 m) from where the eggs hatch to where the larvae mature. As they feed and grow, the larvae pack their tunnels with borings and frass. The larvae mature in 2 or more years, construct pupal cells near the surface of the fallen tree, overwinter, and emerge in spring as adults. Before laying eggs, the newly emerged adults feed on needles of Douglas-fir, then find a class I fallen tree and start the cycle again.

Although the normal life cycle of the golden buprestid from egg to mature adult is usually 2 to 4 years, the length of the cycle is influenced by the quality of a larva's habitat. In poor quality habitat, the life cycle may take a decade or two (Anderson 1960, Chamberlin 1949, Furniss and Carolin 1977).

Within the family Scolytidae is a group of bark beetles called ambrosia beetles that live primarily in the sapwood of class I trees. They are unique among the wood-boring insects in that they do not eat the wood, so the borings are cast out of the tunnels where they collect on the surface of the bark or wood as light-colored powder. Adult beetles, depending on the species, construct a variety of tunnels as follows: (1) an open cavity; (2) a long, winding, branched or unbranched cylindrical gallery in which larvae move about freely; and (3) a compound tunnel, in which "larval cradles" or small pockets are chewed, at right angles, along the main channel (Barras and Perry 1975, Francke-Grosmann 1967, Furniss and Carolin 1977). Ambrosia beetles, especially the females, store certain fungi in specialized structures called mycangia. The fungi, called ambrosia fungi, are introduced into the beetles' galleries during the beetles' burrowing. Particular species of fungi are host specific to certain species of beetles. As the fungi grow, they are eaten by both the adults and the larvae. The beetles' requirements, however, are very exacting; if moisture conditions in the galleries are unsuitable, the crop of fungi either fails and the beetles starve or the crop explodes and the beetles smother in their own food. Hence, the stage of decomposition of a fallen tree is critical (Furniss and Carolin 1977).
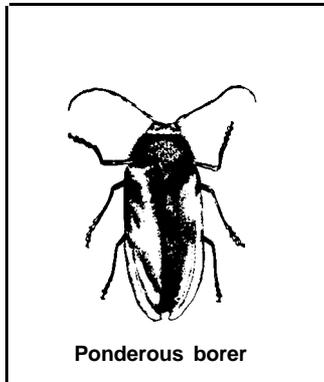
Ponderous borer

The ponderous borer (family Cerambycidae), the largest western cerambycid, directly penetrates the sapwood and heartwood. Adults emerge during the summer. After they mate, a female deposits her eggs in crevices in the bark or in cracks in exposed wood of class I fallen trees. The eggs hatch and the larvae chew their way into the sapwood and then deep into the heartwood of the tree. They grow to nearly 3 inches (7.5 cm) in length by the time they are mature; one generation requires 3 to 7 years to mature. The oval, meandering galleries of mature larvae are large (1 to 2 inches (2.5-5.0 cm) in cross section) and are filled with frass and refuse. When they are mature, larvae construct pupal chambers at the ends of their feeding tunnels and pupate. They emerge as adult beetles in summer, mate, lay their eggs, and die (Anderson 1960, Chamberlin 1949, Furniss and Carolin 1977).

Another penetrator of fallen trees is the carpenter ant. The abundance of dead wood in an old-growth forest provides numerous sites for queen carpenter ants to establish new colonies, but as these sites deteriorate, the queens die, and the weaker colonies subsequently become decadent and also die. Although fallen trees, stumps, and the bases of snags serve as initial nesting sites, they are not permanent. "Permanent" nesting sites are provided by living trees. The reproductive success of carpenter ant colonies is related to the age of the colonies, and large (old-growth) trees provide permanent nesting sites. When a nesting site finally deteriorates, a strong ant colony can move to another site and withstand catastrophes that would eliminate a weak colony (Sanders 1970).

In brief, the carpenter ant's life history is as follows: the young males and females leave the nest in early spring and, being winged at that time, disperse in all directions. The air is sometimes filled with these flying ants that emerge simultaneously from many nests in their mating flight (Graham and Knight 1965).

The males die shortly after mating, but the young, mated females may go into old, established colonies to replace decrepit queens or each may establish a new colony. In the latter case, a young queen seeks a small cavity (for example, in a fallen tree) and constructs her brood cell by completely enclosing the cavity, leaving neither exit nor entrance. In this sense, members of the genus *Camponotus* differ from ants of other genera in that a queen works alone in founding a colony (Graham and Knight 1965).

Once the brood cell is complete, the young queen breaks off her wings; they are no longer of use. And after sealing herself in, she does not feed again until her first brood of young is mature. She lays a few eggs that hatch in about 10 days. The newly hatched larvae are fed a secretion from the queen's salivary glands. The larvae complete their development, spin their cocoons, pupate, and emerge as adults about 30 days after hatching. The only food the first brood has during their development is the material from the queen's salivary glands. Although this first brood of workers is small, they take over the work of the nest as soon as they mature (Furniss and Carolin 1977, Graham and Knight 1965).

The workers cut approximately parallel, concentric galleries that run longitudinally through the wood, primarily where it is soft from decay. These galleries are continually increased to accommodate the enlarging colony. The wood is not eaten, as it is by beetles, but is cast out through openings cut to the outside, sometimes called windows. Excavation of the galleries causes piles of wood fiber or sawdust to accumulate below the access holes. Food secured by the workers is also brought into the colony though these openings (Furniss and Carolin 1977, Graham and Knight 1965).

The workers feed the queen, care for the eggs she lays and for the larvae that hatch from the eggs, and feed the larvae secretions from their mouths. The "nurses" continually move both larvae and pupae to the most favorable places within a colony. When young adults are fully developed, the nurses assist them from their cocoons and treat them with the "greatest consideration" (Graham and Knight 1965).

At home in shady, wet places, carpenter ants are catholic in diet. Their menu includes animal food, such as caterpillars of certain butterflies, and sweets, such as honeydew secreted by aphids. Carpenter ants have even been known to shelter aphid eggs in their nests during winter and to carry them out in the spring and place them on plants to develop (Furniss and Carolin 1977). With this exchange of materials, the ants establish a purposeful, physical link between the inside and the outside of a fallen tree.
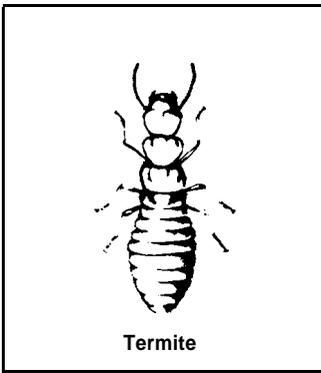

Termite

By the time a fallen tree reaches late class II, it has a relatively high moisture content, but the wood is still sound. At this stage of decomposition, it is suitable for habitation by the Pacificdampwood termite, which sooner or later colonizes most large fallen trees in the coastal forest (Furniss and Carolin 1977).

Colonies of Pacific dampwood termites contain reproductively active individuals (primary reproductives), soldiers (that are sterile), and nymphs; but they do not have workers. The winged, reproductively active individuals, the most familiar form, sally forth on warm evenings in August, September, and October to mate and form new colonies. Tevis (1953) aptly described the termites' appearance: ". . . on a particular quiet, sultry afternoon . . . shortly before sundown the forest became alive with the wing-rattling of termites streaming from slit-like holes in damp logs and taking to flight."

Typically, colonies are formed by swarms of primary reproductives. Such individuals appear in established colonies and accumulate for a short period before departing on their nuptial, colonizing flights. During the predeparture period, the primary reproductives are sexually immature. Their sexual maturity culminates as they take wing, in about equal numbers of males and females. Termites are weak fliers and seldom travel far without the assistance of a breeze. They are also vulnerable to predators, such as bats. The survivors, on completing their flights, cast their wings. When a survivor encounters an individual of the opposite sex that has also cast its wings, the pair walks in tandem-the male following the female-as they seek a fallen tree in which to excavate a small nuptial chamber and copulate (Imms 1960, Whitaker and others 1977).

Individuals produced during the early stages of colony development are sterile; winged, reproductive individuals develop when a colony is about 4 years old and contains 400 to 500 individuals. Individual termites are long lived (several years), an important factor in permitting a close relationship between successive generations and an important element in the termite's social organization (Imms 1960).

Pacific dampwood termites feed on the rotting wood in which they live. They even appear to be attracted to a specific fallen tree when it is ready for their habitation; its readiness depends on the presence of certain acids and aldehydes produced by particular tree-inhabiting fungi. These substances initially attract termites to a fallen tree and then attract them within the tree to the wood that is appropriate for consumption (Becker 1971).

A termite can digest the wood it eats because of a mutually beneficial, three-way relationship between the individual termite, cellulose-digesting Protozoa, and nitrogen-fixing bacteria that live in its gut. The Protozoadigest the cellulose in the wood and convert it to a form that the termite can use as food. In turn, the termite's body provides an anaerobic chamber that is replete with food for the Protozoa. Wood particles eaten by the termite pass into the chamber and are engulfed by the Protozoa that ferment the cellulose. Major products of fermentation are carbon dioxide, hydrogen, and acetic acid. The acetic acid is absorbed through the wall of the termite's hindgut and is oxidized as energy (Breznak 1975).

Nitrogen is important in the termite's diet, especially because it is required by the cellulose-digesting Protozoa. Wood, the primary ingredient of the diet, is low in nitrogen, although termites consume mostly wood colonized by fungi that probably supply vitamins and some nitrogen (Esenther and Kirk 1974). Whenever the nitrogen intake by a termite is deficient, the nitrogen-fixing bacteria in a termite's gut make up the difference. The nitrogen-fixing activity varies inversely with the amount of nitrogen contained in a termite's diet. The nitrogen-fixing response of the bacteria to changes in dietary nitrogen is rapid. The nitrogen-fixing system is efficient and is potentially capable of quickly supplying a termite with usable nitrogen should its dietary level suddenly drop (Breznak 1975).

The Pacific dampwood termite lives in a series of galleries, eaten in the wood, without any external sign of a colony. Even so, by the time a colony has run its course, it has greatly altered the interior microhabitats of a fallen tree. The abandoned galleries form a major network of passages used by other animals and through which plant roots find easy access and ready nutrition.

Some mites also eat the well-decomposed class IV wood (Hartenstein 1962, Luxton 1972). A particular group of organisms in fallen trees, immature wood-tunneling mites, preferentially feeds on the fecal material of such organisms as wood borers. These immature mites probably consume wood that has already been chewed and partially digested until they develop an adult's capability of chewing and digesting wood first-hand and can excavate their own tunnels (Wallwork 1967, 1976).

Plant-nutrient.-The succession of plants on fallen trees is mediated by changes in nutrient availability and physical properties over time. Three broad phases can be defined: initial, optimal, and final (Kreisel 1961; Ricek 1967, 1968). Early invaders prepare the tree for later colonization by altering its physical and chemical properties during the initial phase. The altered tree provides the best substrate for a wide array of organisms during the optimal phase. Ultimately, the depletion of nutrients and physical deterioration of the wood during the optimal phase diminish its value for many organisms, so fewer species inhabit the final phase.

The initial phase encompasses class I and early class II fallen trees, those with bark intact and heartwood still sound. The earliest use of a newly recruited tree is likely to be by heart rot or butt rot fungi and associated micro-organisms that inhabited it before it fell. Other organisms quickly enter where its interior is exposed at breaks or splits in the bark. When beetles chew through the bark, they create additional ports of entry. The beetles also carry spores of decomposition fungi that thrive in the beetle galleries, which are excellent incubators filled with nourishment for the fungus and protected by the bark from drying and from temperature extremes. These earliest invaders are opportunistic scavengers-fungi and bacteria that join the insects in exploiting the readily available carbohydrates of cambium, phloem, and sapwood of a recently fallen trunk. As the most easily extracted nutrients are depleted, these early invaders sporulate. The spores are then carried off by the emerging new generation of insects reared from eggs laid after the tree fell.

Meanwhile, free-living, nitrogen-fixing bacteria may be active at low levels in the wood to add to the nitrogen pool available for growth of the wood decay fungi (Aho and others 1974, Larsen and others 1978, Silvester and others 1982). Other nitrogen is added by rain falling through the old-growth canopy, which is rich in lichens that fix nitrogen (Sollins and others 1980); and much of the nitrogen extracted by initial decomposers is still present in their dead cells or in frass, ready to be recycled.

Later in this initial successional phase, the early scavengers are succeeded by fungi more competent in decomposing cellulose and lignin in the sapwood This process moves relatively fast, as long as the bark hangs together on the fallen tree to preserve the incubator environment within. Furrows in the bark on the upper side fill with leaf litter and provide sites for several years for seeds to germinate. Where the bark is intact, seedlings generally die during summer drought. If a seedling's roots find a crack or hole in the bark and grow into the decomposed layer between bark and wood, however, it may find enough moisture to survive the summer. Western hemlock, huckleberry, and salal commonly become established this way on fallen trees, as do spruces (Christy and others 1982, Eichrodt 1969, Gobl 1968, Minore 1972, Mork 1927). Seedling top growth is generally poor at this successional phase because nutrients are limiting and the roots may not have contacted the mycorrhizal fungi needed for nutrient acquisition (see "Plant-plant"). Root growth, however, may be extensive but it is trapped in the zone of decomposition between bark and heartwood.

A transition from the initial stage to the optimal stage of plant succession on a fallen tree occurs in late class II and class III stages; sloughing of bark is a major event in this transition. When the bark sloughs off, it may take with it some of the plants that have grown through it to form roots in the decaying sapwood Plants that remain will have much of their root systems exposed to air and sun. As sapwood deteriorates and sloughs off, additional plants are removed with it.

As the tree enters class IV (most bark and sapwood removed), it also enters the optimal stage of plant succession. The heartwood is much decayed, usually as brown cubical rot. Wood thus rotted becomes spongy and tends to separate into angular chunks, and the intervening cracks provide interior surfaces for the fruiting of fungi and for the growth of roots. Insect tunnels provide additional passages for root growth. Mineral content of the fallen tree at this stage may exceed the original content because minerals have been added by litter fall from the canopy and by throughfall of rain, have been brought

in by animals, or have been translocated from underlying soil by fungi or roots. Nitrogen may be added by similar means and by biological fixation (Larsen and others 1978, 1982; Silvester and others 1982). These circumstances provide an excellent rooting medium for plants. A great variety of fungi, both decomposers and symbionts, thrive in the complex of niches within the fallen tree. Lichens, mosses, and liverworts become established on the surface and stabilize it after the sapwood sloughs off. Hemlocks and other plants become established on the upper surface of class IV trees, but their roots grow through it into underlying soil as well as along its length. Nutrients may be acquired from the tree itself or from the soil.

The optimal stage may last for many decades, but in time the fallen tree enters the final, more depauperate stage of class V. It loses structure and shape and becomes increasingly low and covered with forest floor material that buries the lichens, mosses, and liverworts. Roots of overstory trees and of trees that became established in earlier stages now permeate it and bind it together. New plants seldom become established because of the humus cover and the intense competition of roots already there. Relatively few decomposers remain because only the lignins, the most resistant to decay, are left. Mycorrhizal fungi seem to predominate and are the primary fruiters. The moisture content of such material remains high compared with that of soil during summer drought, and roots and fungi can grow actively in it long after most roots in nearby, dry soil have become dormant or desiccated (Harvey and others 1978, 1979a, 1979b; Place 1950).

Plant-plant.- The earliest interactions between plants in the newly recruited, class I fallen tree are between micro-organisms, the initially invading scavengers. Competition for the readily available carbon, nitrogen, and minerals is simple: The first to arrive gets the most. More subtle interactions may also develop between specific organisms; for example, some fungi produce antibiotics that suppress certain bacteria, or volatiles, such as ethylene, that may inhibit some organisms and stimulate others (Graham and Linderman 1980, Marx 1973). Free-living, nitrogen-fixing bacteria may provide some of the nitrogen required by wood-rotting fungi (Aho and others 1974).

As fallen trees progress from decay class I to class II, the scavengers are replaced by competitors with the enzyme systems needed to decompose the more complex compounds in wood. The fungi involved in this activity are often mutually antagonistic, so that a given part of the tree may be occupied by only one fungus that excludes others by physical or chemical means (Li 1981, Nelson 1967).

The penetration of plant roots through openings in the bark of an advanced class II tree introduces new possibilities for fungal or microbial colonization because the roots offer carbon and nitrogen compounds quite different from those of the wood. Some of these compounds may be secreted from the roots to selectively promote growth of certain micro-organisms (Slankis and others 1964, Smith 1969). Some fungi are capable of penetrating feeder roots to tap the nutrients within. Fungi that damage or kill roots in the process are pathogens. Certain fungi, however, grow on and in plant feeder roots as symbionts that not only acquire photosynthetic products from the host root but also provide nutrients, vitamins, and growth regulators to the host. These symbiotic, fungus-root structures (mycorrhizae) are extremely important in colonization of rotten wood by higher plants (fig. 21).

Most plants that grow on rotten wood in old-growth Douglas-fir forests require mycorrhizae to survive; without the mycorrhizal fungi, the host plant cannot acquire adequate nutrients. Western hemlock, spruces, and the Ericaceae are all dependent on mycorrhizae. Hemlock seedlings may survive a year or more without mycorrhizae, but growth is minimal until the mycorrhizal fungi colonize the roots (Christy and others 1982). The fungi must first be introduced into the fallen tree as spores or resting cells; they are transported there by insects, small mammals (Maser and others 1981), wind, rain, or a combination thereof. In a class II tree, the spores need to get through the same openings in the bark used by the plants. They are most likely to be moved through the openings by water or as "hitchhikers" on insects or other arthropods.

Some plants on rotten wood form mycorrhizae when the fungi are available but can also grow without them. Many ferns appear to be in this category (Boullard 1979). A few other plant families, such as the sedge and rush families, rarely form mycorrhizae. None of these are as abundant as the mycorrhizal plants on rotten wood in Douglas-fir forests, perhaps because they are less competitive for the nutrients in rotten wood: Many of the nutrients are in organically bound forms that can be cracked only through action of enzymes not produced by green plants. Mycorrhizal fungi, in contrast, are able to decompose some of these compounds and to translocate the released nutrients to the host (Todd 1979).

As a fallen tree progresses through decay class III, the diversity of plants and associated mycorrhizal fungi may increase, especially if roots grow down through the rotted sapwood into the underlying soil. Sloughing of bark, however, suddenly exposes roots in decayed sapwood to freezing in winter and drying in summer, and many of the fine roots die. As the decayed sapwood sloughs off, plants rooted in it may slough off with it. Even if their roots penetrate partially rotted heartwood underneath, they fall over and often die.

The optimal stage of plant development is attained in the class IV tree; plant roots and mycorrhizae grow through cracks and channels of the brown cubical rotted heartwood. Numbers of species of mycorrhizal and decomposer fungi increase, as does the potential variety of interactions among the fungi and between the fungi and higher plants. The variety of mycorrhizal fungi further increases as lichens and mosses become established on the upper surface of the fallen tree (Gobl 1968). Moss communities capture and accumulate many nutrients from rain, and these nutrients can be cycled into higher plants by the mycorrhizal fungi (Binkley and Graham 1981, Nadkarni 1981). At the same time, fungi and roots that bridge rotten wood to underlying soil may transfer soil nutrients to the fallen tree. Asfungal cells or fine roots within the wood die, the minerals acquired from the soil add to the nutrient capital of the tree. These tissues can then be decomposed and their nutrients recycled into further growth of wood-inhabiting organisms.

The class IV tree gradually becomes well permeated with roots as it decays into class V. The well-rotted heartwood provides a moist substrate in which mycorrhizal fungi and roots can continue to interact into the summer, well beyond the time that fungi and fine roots have become dormant or dead from drought in the upper layers of mineral soil (Harvey and others 1978, 1979a; Place 1950).

Relatively few species of mycorrhizal fungi seem able to grow in rotten wood compared with the number that grow in soil (Gobl 1968, Kropp and Trappe 1982) perhaps because most mycorrhizal fungi do not produce the enzymes needed to decompose the tannins and other phenolic compounds in wood (Giltrap 1982). Some of the mycorrhizal fungi that inhabit both mineral soil and rotten wood develop much more strongly in the wood than in the soil (Trappe 1962, 1965) and some appear to be restricted to rotten wood (Kropp and Trappe 1982). Most mycorrhizal fungi in rotten wood produce mushrooms or truffles as their spore-bearing, reproductive bodies, but they can do this only if they are in symbiotic association with host roots. This particular result of a fungus-plant interaction occurs mostly in class IV to V trees and is an important feature of the animal-plant interactions discussed in the following sections.

Animal-plant.- The introduction of fungal spores into a recently windthrown, class I tree by bark beetles and wood borers initiates a sequence of complex animal-plant interactions that continues until the tree disappears altogether. Once established and growing under the bark, the fungal colonies are grazed by a variety of invertebrates (McMillen 1976, Petersen 1971, Russell 1979). Many decomposer fungi sporulate within fallen trees and depend on insects for dispersal of spores. Thus, the young bark beetles, emerging from under the bark where they began life as eggs, take with them spores of the associated fungi. Similar relationships between insects and fungi probably occur through all decay stages of fallen trees. Insects eat the fungi and disperse the spores. Many of the fungal grazers are food for predators, so the animal-plant interactions are a prelude to animal-animal interactions.

As the fallen tree progresses through decay classes II and III, the zone of decomposition beneath the bark provides shelter to additional invertebrates and substrate for roots and mycorrhizae. The mycorrhizal fungi are thus introduced to the system as an additional food source to grazers, such as nematodes (Riffle 1971) aphids (Zak 1965) and collembolans (Warnock and others 1982). Slippage of the bark, and eventually of decayed sapwood removes that favorable environment and the organisms within it from the top and sides of the tree; that material, however, does not disappear. Most of it accumulates loosely alongside the log to provide a new habitat favorable to many of the same organisms as before, plus larger animals, such as slugs, snails, salamanders, and small mammals.

Various mites, insects, slugs, and snails feed on the higher plants that become established on rotten wood. These plants also provide cover for the animals, as do the lichens, mosses, and liverworts that colonize fallen trees in decay class IV. Wood-boring beetles, termites, and carpenter ants produce channels in the heartwood that provide passageways for roots. The fruiting bodies of the mycorrhizal fungi, produced from energy supplied by the host plant, can also be a major source of food for insects (Fogel and Peck 1975); other arthropods (Buller 1922); and small mammals, such as the California red-backed vole (Fogel and Trappe 1978; Maser and others 1978a 1978b; Ure and Maser 1982).
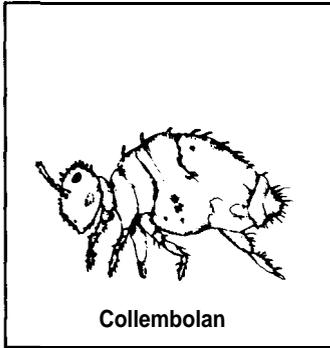
Collembolan

Specific groups of animals exemplify these generalities. Collembolans are tiny, wingless insects, most of which jump by means of a springlike appendage on the abdomen-hence, the common name "springtail." Collembolans living in the soil can be divided into two groups: (1) those that live in the surface layer and feed on fungi, algae, lichens, and decaying vegetation; and (2) those that live deeper in the soil and graze on micro-organisms (Edwards and others 1970, Furniss and Carolin 1977, Zachariae 1962). Both groups probably also exist in fallen trees. Those that feed on fungi, algae, lichens, and detritis could inhabit the protected areas in the exterior bark of a class I tree as their food supply begins to accumulate. As the tree's interior is made available, first by inner bark feeders and then by wood borers, collembolans gain a new dimension in habitats and niches. By the time a decomposing tree reaches decay class III, insect tunnels have penetrated all levels and the entire tree is "open" so collembolans can live deep within it and graze on such micro-organisms as bacteria.

Because collembolans occupy essentially any atmospheric habitat, they are extremely versatile. The greatest number and variety of species are found in the soil or in contact with it, especially where organic materials abound. Most species are susceptible to desiccation; but in damp environments, species that normally would be restricted to the soil or to litter may occur on the surface of the ground or even in standing trees (Christiansen and Bellinger 1980).

Development of collembolans is not necessarily continuous; growth is interrupted in cold seasons. Development of eggs and immature stages may also be interrupted by dry conditions. Dry periods are survived by a form of diapause, a suspension of growth or development. In a few genera, diapause is even associated with a regressive modification of the mouthparts and digestive tract, and sometimes also with striking external modifications (Christiansen and Bellinger 1980).

Collembolans molt throughout life, from 2 times to over 50 times. Growth apparently continues throughout an individual's life, but at a decreasing rate after sexual maturity. Sexual activity of adults appears to be restricted to alternate instars (Christiansen and Bellinger 1980).

As with collembolans, the mite fauna diversifies within a fallen tree over time. In fact, the mite fauna in rotten wood may be surprisingly complex. As stated by Krantz (1978, p. 57), "The remarkable diversity in morphology . . . is more than equalled by the variety of behavioral characteristics . . .Specializations in habitat often are paralleled by specializations in structure."
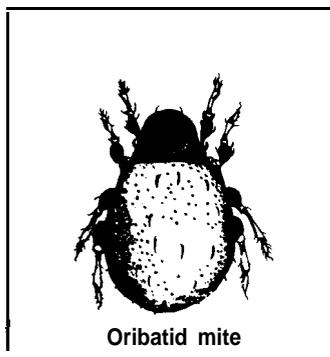

Oribatid mite

Mites can be divided initially into two groups-free living and parasitic. The free-living forms exhibit a variety of food habits.

Small-plant eaters include mites that feed on bacteria, algae, fungi, and lichens. Such mites occur in the soil and the litter of the forest floor, and they can inhabit the outer bark of a class I fallen tree as it becomes suitable. As dead plant and animal materials accumulate on a fallen tree, mites (which relish putrid material) become part of the community. The strategy of feeding on dead organisms has been even further refined by the mites; some feed on the decaying material of higher plants (large-plant eaters), whereas others are considered to be general plant eaters, consuming fungi, bacteria, and algae, as well as decaying material from higher plants. The general plant eaters often depend on fungi to soften, decay, and prepare the plant tissues. As organic materials increase, an array of fungi becomes established, and mites that prefer fungi for food appear on the scene (Krantz 1978, Luxton 1972).

Mites immigrate into a fallen tree as other organisms, such as wood-boring beetles, penetrate it and modify its habitability. As a fallen tree is colonized by bacteria, fungi, and yeasts, mites that dine on these organisms also take up residence. As these organisms live and die, mites that feed on dead tissues join the community and add to its diversity. Our observations suggest that the mite fauna really begins to flourish as a fallen tree approaches class IV. Finally, as the fauna increases and diversifies, the fecal output generates still another level in the partitioning of food resources available to the mite community.

Even in death, mites and other invertebrates interact with plants. Their empty exoskeletons serve as incubators for the spores formed by certain mycorrhizal fungi (Rabitin and Rhodes 1982).
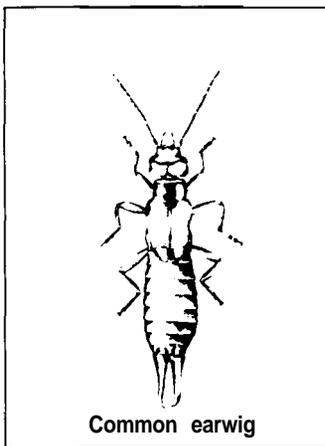
Common earwig

A larger inhabitant of fallen trees is the common earwig. The earwig is mainly nocturnal and spends the day in cracks and crevices and under the bark of large fallen trees, as well as in other places. Although reputed to feed on tender foliage and dead or decaying vegetable matter, it also devours both living and dead insects (Borror and Delong 1964, Imms 1960, Langston and Powell 1975).

Unlike most insects, the common earwig cares for its eggs and young. After depositing a group of eggs in the soil in winter or early spring, the female rests over them much as a hen does her chicks. The newly hatched earwigs remain under and around their parent until they are able to fend for themselves. Common earwigs become adults in summer, and having wings and being capable of flight, they can disperse. There appears to be one generation per year (Imms 1960, Langston and Powell 1975).

Although some common earwigs may be primary tenants of large fallen trees, others may be secondary or part-time tenants. Nevertheless, they are an important part of the food chain, as will be seen in the next section.

The California red-backed vole is the quintessential example of interactions within fallen trees (fig. 23). The vole heavily uses them for cover; we have found that most class II through class V old-growth Douglas-fir trees have vole tunnels underneath. The vole eats mostly fungi and includes lichens but prefers truffles (Ure and Maser 1982). Some truffles, such as *Rhizopogon vinicolor* fruit mostly in rotten wood, where their mycelium forms the tuberculate mycorrhizae of conifers (Trappe 1965, Zak 1971) (figs. 24 and 25). The truffle spores are dispersed by animals that eat the truffle (Trappe and Maser 1976). Thus, there is a tight cycle of interdependence: the vole needs the truffle for food; the truffle depends on the vole for dispersal of spores and on a mycorrhizal tree host for energy; the tree requires mycorrhizal fungi for uptake of nutrients and provides the rotten wood needed by the vole for cover. Moreover, since both voles and *Rhizopogon* vivicolor specialize in rotten wood as habitat, the vole disperses the *Rhizopogon* spores to the kind of substrate in which the fungus thrives.

Figure 23.—The California red-backed vole depends on decayed fallen trees as habitat (photo, courtesy of D. Ure).

Figure 24.—Fruiting bodies of *Rhizopogon vinicolor* A. H. Smith: left and right, surface views; center, cross sections. This fungus typically forms mycorrhizae with Douglas-fir roots in rotten wood.

Figure 25.—Mycorrhizae of Douglas-fir formed with the fungus *Rhizopogon vinicolor.*
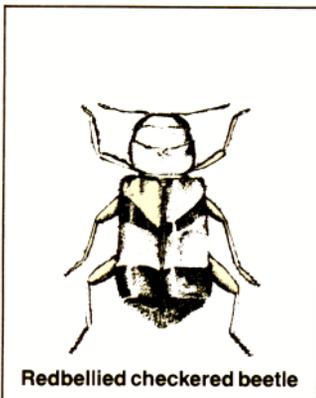
Redbellied checkered beetle

Animal-animal.—As a class I fallen tree is penetrated by the wood-boring beetles and they begin to thrive within it, Nature's system of checks and balances is also activated. At first this system is composed primarily of predaceous beetles in the families Cleridae (checkered beetles) and Trogositidae (no common name). The redbellied checkered beetle, for example, is an important predator of the bark beetle in Douglas-fir trees (Cowan and Nagel 1965). Adult redbellied checkered beetles prey on adult bark beetles, and their larvae prey on the larvae of bark beetles. There is one generation of redbellied checkered beetles annually in Oregon (Furniss and Carolin 1977).

As the diversity of fauna within a fallen tree increases, so do the number and variety of predators. Among the smallest predators are the predaceous mites. Predaceous mites are common near the surface of the soil and in mosses, humus, rotten wood, and animal waste products. They prey on small arthropods, such as collembolans, on arthropod eggs, on small roundworms, and occasionally on each other. Predaceous mites are commonly long legged and fast, and they have strong mouthparts for capturing and chewing their prey (Krantz 1978, Luxton 1972).

The next level of predation may be pseudoscorpions. These little creatures are related to spiders. They look like miniature scorpions with pinchers but without tails and stingers.
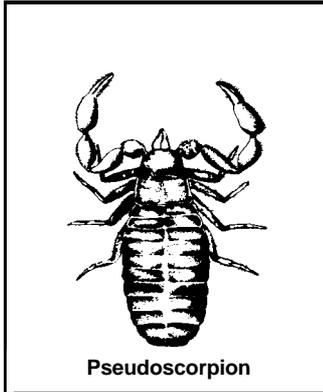
Pseudoscorpion

Pseudoscorpions move in a slow walk, but they can climb and can walk upside down on the ceilings of small caverns within rotten wood; they move backward much faster than forward. They construct silken nests in which they rest. A pseudoscorpion not occupied in spinning silk often sits in its nest with its pinchers (technically called pedipalps) and the anterior of its body protruding through the opening. From this position, it can grab a passing collembolan or mite to eat. Some species of pseudoscorpions seem to prefer small flies, small beetles and their larvae, ants, and even small earthworms (Comstock 1948, Weygoldt 1969). The pseudoscorpion keeps its nest clean, discarding prey remains as far away from its nest as possible without actually leaving the nest. An individual may leave its nest in search of food or a mate; when it cannot find its way back, it makes a new nest or occupies an empty one (Weygoldt 1969).

A female pseudoscorpion carries its eggs and developing embryos in a brood sac attached at its genital opening. The eggs are small, with little yolk, so the embryos are nourished by a nutritive fluid produced by the female. Most species reproduce in spring or summer and may have several broods per season (Weygoldt 1969).
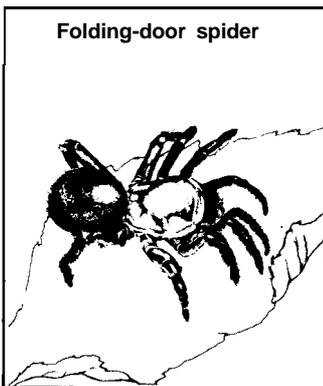
Folding-door spider

The next order of predaceous magnitude is probably spiders, of which the Pacific folding-door spider is the largest spider inhabiting fallen trees. In general, spiders undergo little metamorphosis or change during development; when hatched, they look like miniature adults. Legs lost during development are usually regenerated. Although spider eggs hatch soon after they are laid, spiderlings that hatch in the autumn remain in the brood sac until the next spring. All spiders are predaceous; they eat mainly insects. A spider normally kills its prey by injecting poison into the captured prey with its "fangs" (Borror and DeLong 1964, Comstock 1948).

The folding-door spider's abode is a tube constructed in an existing crack within the outer layer of a class III or IV fallen tree with many cracks and crevices. The horizontal tube is completely lined with silk. To close its tube, a spider grasps the rim on opposite sides and pulls it in toward the middle. Except when capturing prey, a female seldom leaves her tube, but a male wanders in search of a mate (Levi and others 1968).

From our observations, Pacific folding-door spiders prey on whatever they can catch and subdue. Although we have occasionally found evidence of food refuse around the entrance of a spider's tube, it was usually scattered as we dissected a fallen tree and was not identifiable.

Another group of predators is the centipedes, of which *Scolopocryptops sexspinosa* (Say) (no common name) is the largest found in fallen Douglas-firs. Centipedes have one pair of legs per segment. Centipedes overwinter as adults in a protected place, such as within rotten wood. They lay their eggs in the spring and early summer. Some species have sticky eggs that a female hides with debris, but a female *S. sexspinosa* usually coils around her eggs to protect them and may periodically lick them to keep them clean (Borror, and DeLong 1964, Levi and others 1968).

Centipedes are predaceous. They feed on spiders, insects, and other small animals. All centipedes have poison jaws with which they paralyze their prey. Some species, such as *S. sexspinosa,* have such stong poison jaws that they are effective even against such predators as birds and large insects (Borror and DeLong 1964, Levi and others 1968, Maser and Hooven 1974). Centipedes figure prominently as predators in trees in decay classes III, IV, and V.

As the bark becomes loose on a late class II fallen tree, lungless salamanders (family Plethodontidae) join the internal community. Three species of salamanders are associated, as predators, with rotten wood in western Oregon: Oregon slender salamander, Oregon salamander, and clouded salamander.

Oregon slender salamanders are endemic to the northern half of the Cascade Range in western Oregon (Stebbins 1966). They are most often associated with trees in decay classes III to V, either under intact bark or in termite channels deep within (Stebbins 1954). Females lay about 8 to 11 eggs in June. Large, moist, cool fallen trees are important to the Oregon slender salamander in the heat of summer because they, and other species of slender salamanders, seem to be particularly prone to fatality from heat stress (Maiorana 1977). They may actually need a suitable fallen tree for only a few weeks in summer, but without it during that time they could die.

Although we know of no specific data on the food habits of the Oregon slender salamander, a similar species that occurs in extreme southwestern Oregon and in northwestern California, the California slender salamander, will serve as an example. Both species are about the same size and inhabit forested areas. The major items in the diet of California slender salamanders are collembolans and mites, followed by such groups as flies, spiders, and small snails (Bury and Martin 1973). Evidence suggests that the California slender salamander even selects collembolans (specifically family Sminthuridae) and mites (specifically family Oribatidae) over other types of prey (Maiorana 1978). These small, slender salamanders are well suited to a role of predator within the narrow confines of wood-boring beetle and termite galleries in classes III through V fallen trees.

Another salamander, the Oregon salamander, although thought to primarily inhabit rodent burrows in forested areas (Stebbins 1954), is frequently found under pieces of bark that sloughed off large, fallen Douglas-firs. It is also found within classes III through V trees, particularly during cold or dry weather (Stebbins 1966). Individuals are usually solitary except when they are breeding or are associated with young. Egg clutches, averaging 11 or 12 eggs, are often deposited under the bark or within fallen, rotting Douglas-firs. One female with a clutch of 12 eggs was found on June 30, **1982,** in a very wet class IV Douglas-fir in an old-growth Douglas-fir stand on Mary's Peak, Benton County, Oregon.

The two most important foods of the Oregon salamander are collembolans and spiders, followed by isopods (sowbugs), millipedes, and adult beetles (Bury and Martin 1973).

The third salamander is the clouded salamander (fig. 19). It frequents rotten wood, particularly Douglas-fir in late classes II through IV (Stebbins 1966). These salamanders are often found under the loose bark of large fallen trees in spaces excavated by wood-eating insects (Fitch 1936). In fact, young clouded salamanders show a striking affinity for bark (McKenzie and Storm 1970). According to Stebbins (1954) they are especially abundant in well-illuminated openings in a forest. In addition, the clouded salamander is the most arboreal member of the genus and has been found 20 feet (6.1 m) up in standing trees (Stebbins 1954).

Eggs laid in late spring or early summer under bark and in cavities in rotten wood are guarded by the female. The eggs may be attached separately by their stalks but close together, or they may have their stalks twisted around one another and be attached to a common point on the ceiling or wall of the nesting chamber (Stebbins 1954).
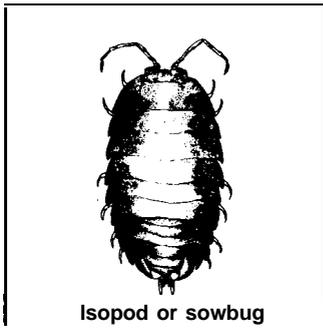
Isopod or sowbug
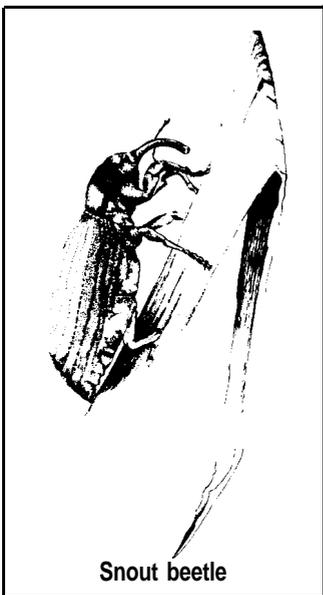
Snout beetle

Bury and Martin (1973) and Storm and Aller (1947) listed ants as the most important food of clouded salamanders. We also found ants to be an important food item, but only in summer.[2] The major food of the adult clouded salamanders in winter, spring, and fall were isopods and beetles, particularly snout beetles. Isopods, ants, beetles, and common earwigs were important in summer, when foods were eaten in greater diversity. Important foods for small juvenile salamanders (as large as three-fourths inch (19 mm) in snout-vent length) were mites, collembolans, flies, and very small beetles. Largerjuveniles (more than three-fourths inch (20 mm) in snout-vent length) consumed, in order of importance, flies, isopods, beetles, mites, and centipedes in winter; beetles, ants, and isopods in spring; ants and beetles in summer; and isopods, beetles, and ants in fall (see footnote 2). Storm and Aller (1947) also found termites, probably the Pacific dampwood termite, in the stomachs of some individuals, which indicated that the salamanders had been feeding within a class III to class IV fallen tree.

The final level of predation within large, rotten, fallen Douglas-firs in classes III through V is probably that of small mammals, such as shrews and shrew-moles.

Shrews are small, with short legs, tiny eyes, and long, pointed noses. Although they cannot see well, their senses of touch, smell, and hearing are acute. Thecommon shrew in western Oregon Douglas-fir forests is the Trowbridge shrew. This small, "nervous" mammal is abundant around fallen trees, particularly classes III and IV, that are well settled on the forest floor and have been in place long enough to act as the shrew's grocery. The Trowbridge shrew has the most catholic diet of all western Oregon shrews. It eats at least 47 types of food, the most important of which are centipedes, spiders, internal organs of invertebrates (probably mostly beetles), slugs, and snails. In addition, it shows a definite affinity for fallen trees, as do some of its prey (Maser and others 1981, Terry 1981, Whitaker and Maser 1976).

The American shrew-mole is a tiny mole. As are other moles' ears, the shrew-mole's ears are merely holes near the shoulders and are not visible because of the dense fur. It has minute eyes nearly concealed by fur, and broad front feet with stout claws adapted for digging (Maser and others 1981).

These small moles spend much time burrowing in the surface soil-litter layer and along and under classes II and III fallen trees. When trees reach classes IV and V, shrew-moles also burrow within them. Their close tie with fallen trees in old-growth forests is probably reflected in their diet (Maser and others 1981, Terry 1981); for example, in a study by Whitaker and others (1979), the three foods eaten with the highest frequency were earthworms (81.8 percent), centipedes (54.5 percent), and flies (36.4 percent).

The shrew-mole is ideally equipped to forage in and around fallen trees because its nose is extremely sensitive to touch; it is much like a blindman's cane. In almost constant motion, it quickly identifies any object it contacts. Further, this mole's small size, adaptions for digging, and herculean strength make it an efficient, burrowing predator within and beneath rotten wood (Maser and others 1981).

---

[2] J. O. Whitaker, Jr., and C. Maser. Unpublished data on file at Indiana State University, Department of Life Sciences, Terre Haute, Indiana 47809.

Nutrient-plant-animal-nutrient.- A tree begins life with nutrients from the soil and ends life with nutrients that diffuse into the forest floor and become parts of other trees. It is appropriate, therefore, to select an element (nitrogen) that is necessary for the growth and reproduction of all organisms within a forest and to use it to represent full cycle the minisystems within a fallen tree.

As a tree grows, nitrogen is incorporated into the wood-cell structure. After it dies, processes of decomposition begin to break down the structure of the wood and ultimately to recycle the nitrogen.

During decomposition, micro-organisms (such as fungi and bacteria) incorporate nitrogen from the wood into their own cellular structures as they digest the carbon from the wood substrates. As the microbes decompose wood, the carbon-to-nitrogen ratio gradually shifts until nitrogen becomes relatively more available for plant uptake. As microbial colonization and decay increase, animals varying in size from small mites and collembolans to large beetle larvae feed on microbial tissues enriched in nitrogen from digestion of wood; and vertebrates, from California red-backed voles to black-tailed deer, may obtain some of their protein nitrogen from decaying trees by feeding on fungal fruiting bodies, such as truffles and mushrooms (Fogel and Trappe 1978, Maser and others 1978a, Trappe and Maser 1978).

As decomposition proceeds in a fallen tree, other sources of nitrogen are added in the form of leaf litter and other litter components that fall on the surface of the tree. As these decay, their nitrogen becomes available to enrich the wood; and as rainwater-rich in nutrients from passing through the tree canopy and surface litter-accumulates on the fallen tree's upper surface, some nitrogen is leached into the wood.

Microbes that colonize a fallen tree from the ground surface provide additional nitrogen, as do animals that take up residence in the tree or eliminate their metabolic waste products on its upper surface. As decay proceeds, plant roots penetrate the fallen tree's surface and tap the rotting wood as a source of available nitrogen, other nutrients, and water.

A fallen tree disappears gradually through the decades, and its nitrogen capital is returned to the forest. Weathering processes, such as freezing and thawing, and animal activities contribute to the disintegration and disappearance of the tree. Some residue may remain for centuries in the forest as it slowly becomes incorporated into the organic portion of the soil (fig. 20).

Biotic Succession Within and Around Fallen Trees

As a fallen tree decomposes, it creates a gradually changing myriad of internal and external habitats (Maser and others 1979). Plant and animal communities within a fallen tree are very different from those outside, but both progress through a series of orderly changes. As a fallen tree decomposes, its internal structure becomes simpler, whereas the structure of the plant community surrounding the fallen tree becomes more complex (figs. 26 and 27).

Figure 26.—Plant and animal communities are very different inside this class III Douglas-fir than they are outside.

EXTERNAL SUCCESSION

GRASS-FORB/ SHRUB-SEEDLING	POLE-SAPLING	YOUNG FOREST	MATURE FOREST	OLD GROWTH

INTERNAL SUCCESSION

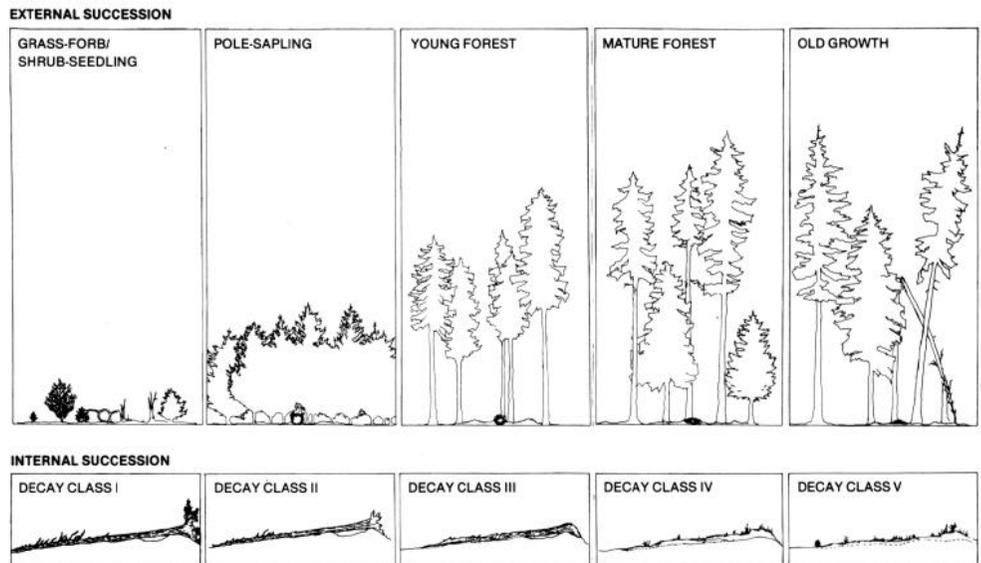| DECAY CLASS I	DECAY CLASS II	DECAY CLASS III	DECAY CLASS IV	DECAY CLASS V

Figure 27.—Fallen trees progress through two simultaneous successional processes—internal and external (modified from Maser and others 1979).

Internal succession in a fallen tree is related to the following factors: (1) the tree species and its inherent decay-resistant chemical properties; (2) its size—the larger it is, the longer it lasts; (3) what killed the tree; (4) whether it originated as a tree or a snag; (5) the microclimate around it; (6) its placement on the ground; and (7) the biotic community peculiar to it.

Internal succession is also influenced by temperature, moisture, and stage of decay. A class I fallen tree, for example, has many readily available nutrients that support opportunistic colonizers. As decay proceeds, its moisture-holding capacity increases, but nutrients become less available because either they have been used or they remain locked in the more decay-resistant compounds of the wood. Ultimately, the rapidly growing opportunists are succeeded by organisms with more sophisticated enzyme systems, and decay continues.

External succession is related to the changes that take place in the plant community surrounding a fallen tree. A fallen tree is a connector between the successional stages of a community; it provides continuity of habitat from the previous forest through subsequent successional stages. A large fallen tree therefore provides a physical link-a nutrient savings account-through time and across successional stages. Because of its persistence, a fallen tree provides a long-term, stable structure on which some animal (both invertebrate and vertebrate) populations appear to depend for survival.

External succession is influenced by the same factors as internal succession, with the additional influence of light. Consider, for instance, a class IV or V tree that supports a lush community of mosses, liverworts, hemlocks, and other flowering plants. As the canopy closes over the opening created by the original falling of the tree, light becomes limiting to the growth of green plants. If, at this point, a nearby tree falls, the environment can change immediately and strikingly. Greater solar radiation increases the amount of light but may also raise the daytime temperature of the fallen tree. In turn, nighttime temperature may be lower because of the increased heat that reradiates to the atmosphere. In addition, more rain and snow reach the ground.

Stream Characteristics and Fallen Trees

Fallen trees and other large pieces of wood significantly shape the energy flow, nutrient dynamics, and structure of biota in streams of the Douglas-fir region (fig. 28). Streams in old-growth forests contain large quantities of organic debris: 220 to 770 tons per acre (200 to 700 t/ha). Large, organic debris shapes a stream channel by damming it, which creates ponds that trap sediments, or by obstructing it, which redirects waterflow that creates meanders and pools (Anderson and others 1978, Franklin and others 1981, Naiman and Sedell 1979, Sedell and others 1982b, Swanson and others 1976, Triska and Cromack 1980, Triska and others 1982).

Large pieces of wood in streams provide a diversity of spawning and rearing habitats for salmonids. In the smallest (first order) streams, for example, over 50 percent of the habitat is related to presence of large wood (fig. 29) and about 25 percent is created and maintained by wood in larger (third order) streams (Anderson and Sedell 1979, Franklin and others 1981, Swanson and Lienkaemper 1978, Triska and others 1982).

Most large wood is randomly spaced in small streams (first and second order) because flow volume is insufficient to transport large trees downstream. Intermediate streams (third to fifth order) have less wood. Big chunkstypically accumulate where the channel is obstructed by immobile dead trees or channel constrictions; such obstructions provide sites for collection of small to intermediate size debris that moves downstream at high flows. Most debris comes to rest on the flood plains or on the outsides of bends of larger streams or rivers (sixth to eighth order). But even in big rivers, historical records show that large pieces of wood contribute significantly to in-channel structures that trap sediment, pond water, and create side channels and sloughs (Franklin and others 1981, Naiman and Sedell 1979, Sedell and Luchessa 1982, Swanson and others 1978, Swanson and Lienkaemper 1978).

The food base or energy supply of a stream in an old-growth Douglas-fir forest is primarily litter from the adjacent forest combined with algae produced in reaches of streams exposed to light. Pristine streams retain much of the forest litter. Fallen trees in a stream form "stairsteps" that allow over 70 percent of the litter to be retained long enough to be biologically processed by stream organisms. Similar relationships exist for pristine streams in the Canadian boreal forest (Naiman 1982, Sedell and others 1975, Triska and others 1982).

Figure 28.—Note how the fallen tree (foreground) channels the water against the rootwad (left) that, in turn, buffers the stream-bank from the current.

Figure 29.—The stable, fallen tree forms an obstruction that dissi-pates some of the stream's energy and creates a pool used by salmonids.

The influence of the forest as a source of energy and as a channel structure diminishes as a stream gets larger. Edges of an unmanaged stream, however, are dominated by forest vegetation, and fallen trees create and maintain side channels and small backwater areas that are prime sites for deposition of organic materials and rearing of coho salmon (Sedell and others 1982a). Further, old-growth forests typically have a mix of herbaceous and shrubby plants and areas of various sizes exposed to sunlight; this combination provides a stream with a mix of coniferous and deciduous leaf litter as well as patches of algae. Such diversity of habitat and energy provides an interactive aquatic system with a stable, rich mix of both invertebrate and vertebrate species.

A Historical Sketch of Woody Debris in Northwest Waterways

Most early descriptions of Northwest streams and rivers are recorded in British and United States army journals. They tell, for example, of valleys so wet that early travel was along the edges of the hills and not along the valley bottoms (Dicken and Dicken 1979). The Tualatin Valley was described in British army journals as "mostly water connected by swamps" (Ogden 1961, p. 122). Much of this flooding was a result of beaver activity and accumulated sediment, fallen trees, and living vegetation in the channels. Because the valley bottoms had accumulated fine silt and organic material of alluvial origin, the land was fertile, and the task of draining it for farming began early in Oregon and Washington.

Oregon State Agricultural College soils scientist, I. A. Williams (1914, p. 13), wrote of the condition of Willamette Valley streams in 1910:

> Many of the smaller streams. . . through these flat sections of the valley flow sluggishly and frequently overflow their banks during periods of heavy winter rainfall. . . . Most of these have sufficient grade to carry even more water than ordinarily comes to them; seldom less than 3, and usually more, feet of fall per mile. The annual overflow is caused from the obstructing of the channel by the growth of trees and the extension of their roots, the dams thrown across the channels by beavers and the consequent accumulation of sediment and other debris, etc. . . . It is a common condition, however, and usually all that is necessary is a clearing out and opening up of the clogged channel of the stream to afford entire relief . . . to the farmer . . . .

Descriptions of streams in the Puget Sound lowland and the Willamette Valley were similar. Most consisted of a network of sloughs, islands, beaver ponds, and driftwood dams with no main channel. The Skagit River lowlands encompass about 198 square miles (512 km^2), of which over 50 square miles (128 km^2) were marsh, sloughs, and wet grass meadows. U.S. Army Corps of Engineer maps for 1875-91 for the lower Nooksack and Snohomish Rivers in Washington show large areas of sloughs, swamps, and grass marshes (Reports of the Secretary of War 1875-99). All the coastal Oregon valleys contained marshy areas and numerous sloughs. The interaction of the streams and their flood plains in the lowlands of both States was great before they were cleared and channeled by pioneer farmers (U.S. Congress, House 1848).

The channels of fast, turbulent rivers and low-gradient rivers, regardless of alluvial or bedrock control, were influenced by large amounts of wood. The lower Siuslaw River and lower North Fork Siuslaw River were so filled with fallen trees that trappers were unable to explore much of these river systems in 1826 (Ogden 1961). The Willamette River flowed in five separate channels between Corvallis and Eugene in 1870.

Reports of the Secretary of War (1875-99) state that the "obstacles were . . . great above Corvallis" and the riverbanks were heavily timbered for half a mile (0.8 km) on either side. Over 5,500 drifted, dead trees were pulled from a 50-mile (80-km) stretch of river in a 10-year period. The trees ranged from 5 to 9 feet (1.5 to 2.8 m) in diameter and from 90 to 120 feet (27.7 to 37 m) in length. The river was also confined to one channel by engineering activities. In both Oregon and Washington, other rivers were completely blocked by driftwood in the lower, main channels. The Skagit River, for example, had a driftwood jam that was three-fourths of a mile (1.2 km) long and one-fourth of a mile (0.4 km) wide. The Stillaguamish River was closed by six driftwood jams from the head of tidewater to river mile 17 (km 27.2). Drifted, dead trees were so numerous, large, and deeply imbedded in the bottom that a steam "snag boat" had to operate for 6 months to open a channel 100 feet (30 m) wide.

Driftwood jams in high-gradient river systems were often located where the channel gradient abruptly decreased. Morse (1883, p. 9) described the South Fork Nooksack River:

> . . . we came to a place where the river, during freshets had ground sluiced all the earth away from the roots of the trees, and down some 6 feet to the gravel. This covered a region of country a mile in width by five in length. Overgrown yellow fir timber had once covered most of that section. If the river below there was only clear of jams that place would be a paradise of hand loggers. On the gravel lay many million feet of sound fir timber, which only needed to be junked up during the summer and the winter freshets would float the logs down to the sea. Immediately below this place, the jams first extend clear across the river, and for the next 20 miles there is a jam across the river nearly every mile.

From the above scenario, it is obvious that large, woody debris was an important factor in the early river systems of the Pacific Northwest (figs. 30 and 31). Human objectives, other than watershed management, however, dictated clearing the rivers; so present practices downplay the ecological role of large, woody debris in modern river systems.

Figure 30.—Logs in a small stream awaiting enough water to be floated to the mill (photo from USDA Forest Service historical files).

Figure 31.—A splash dam at Austin Place, Hamilton Creek, Oregon, August 16, 1907. Such dams were used to regulate the flow of water to float logs down a stream to the mill. (Historical photo, courtesy of the Horner Museum, Oregon State University.)

Figure 32.—Note the large pieces of wood on the flood plain, especially in the lower right corner where the stable wood has formed a protected site that has allowed the alder to grow.

Vegetation of Streamsides and Gravel Bars

Large, fallen trees have both positive and negative effects on live vegetation that borders watercourses. Trees carried by floodwaters can severely batter live plants on a flood plain, but this is normally restricted to a narrow belt along the immediate channel. Stabilized, large pieces of wood, on the other hand, provide protected sites where alder and other species of plants can become established (fig. 32).

Once established, live vegetation begins to stabilize a stream channel. Such features as a gravel bar also become stabilized and enriched with fine sediments and organic materials as plant root systems develop and the stems resist the flow of water and reduce its velocity.

Fallen trees protect thickets of vegetation on exposed channel bars. Alders growing in bordering areas not protected by down trees sustain heavy, repeated pruning by floating woody debris and moving bedloads (Swanson and Lienkaemper 1982). The down trees that protect the outer edge of a thicket and those in the thicket itself create local environments of quiet water where fine sediments and organic debris are deposited during high flows. This process, coupled with the production of leaf and woody litter by the stand, results in soil development and growth of the stand. The large, down trees thus help a stand to reach the stage of structural development that allows it to better withstand floods.

Fallen trees on gravel bars also provide sites where some stream-transported species of hardwoods and shrubs can reroot and grow.

Restabilization of streams after major floods, debris torrents, or massive landslides is accelerated by the presence of large, woody debris along and within a channel. Swanson and Lienkaemper (1978) found that after a fire an aquatic habitat was maintained by the large, woody debris (supplied to the stream by the prefire forest) while the postfire forest was developing. In many instances, however, salvage logging of streamsides destabilizes the structure of the channel and thereby the quality of the habitat.

Decomposition and Nutrients in Streams

Small streams that drain heavily forested watersheds depend on organic materials from the adjacent forest as a source of carbon and nutrients for biological processes. Energy flow and nutrient cycling are measured by calculating the budgets of carbon and nitrogen in a stream. By examining the internal transfer of organic materials and nutrients, we can gain significant insights on the ability of a small stream to process incoming sources of energy. Sedell and others (1974) and Triska and others (1982) studied a small stream in the western Cascade Range of Oregon. They found that 85 percent of the organic material in the stream was large, fallen trees or branches from large trees. Of the tree leaves and needles that fell into the stream during the year, only 10 to 20 percent were transported downstream. The remainder were either stored in the channel or used as food by microbes. Microbial respiration accounted for about 55 percent of the carbon produced. There also was a large amount of fine detritus that was partly formed as a byproduct of the decomposition of large pieces of wood.

Large wood was the primary structural feature of small streams, and it dominated the carbon budget. The structural characteristics of large wood allowed leaves and needles to be retained in a stream long enough to be used as food by microbes and invertebrates. Without the wood, such material would be rapidly transported downstream, and the stream system would not be as efficient in processing organic material. The ability of a small stream to process organic material is also important because the stream provides preconditioned food to biotic communities in larger streams and rivers.

Retention of organic material is important to a stream ecosystem in that large quantities of stored organic material buffer the annual fluctuations in energy flow. During periods of drought, for example, enough moisture and waterlogged material remain available in a stream to provide habitat and food for aquatic organisms; during major floods when large amounts of organic material are transported downstream or washed up on the banks, enough remains to continue to provide habitat and food for aquatic organisms.

It is important to understand that carbon, nitrogen, and all the other materials that leave a watershed either pass through or accumulate in the stream environment, which encompasses less than 1 percent of the watershed area. Such a concentration of nutrients, the capacity of a stream to store organic material, and the efficiency to process it depend on the number and quality of fallen trees in the stream.

Figure 33.—Some of these fallen trees will become waterlogged; others will be submerged only during high water. Both circumstances affect the rate of decomposition.

Decomposition and nutrient cycling.—Trees that fall into streams decompose at different rates and in different patterns than those that fall on the ground. Decomposition in water is slower than on land because waterlogging prevents deep diffusion of oxygen into the wood; the fungi and invertebrates that cause the most rapid decomposition of fallen trees on land are strongly aerobic (Triska and Cromack 1980). Waterlogged parts of fallen trees tend to decompose in thin surface layers, about one-fourth inch (0.5 cm) thick. As the decomposed surface is grazed or abraded, oxygen can penetrate farther into the underlying wood, which in turn becomes substrate for the decomposers. If only part of a fallen tree is in constant contact with water, that part decomposes slowly but the exposed part may decompose quite rapidly because neither a low level of oxygen nor extremely high or low moisture content limits decomposer activity. Trees that fall in very small streams may contact water only during the rainy season when the stream is flowing at its highest, and lack of moisture the rest of the year may slow their decomposition (fig. 33).

As decomposition of large pieces of wood advances, the concentration of essential nutrients, such as nitrogen and phosphorous, increases. Nitrogen increases primarily through biotic use of the carbon and through fixation of nitrogen. Nitrogen-fixing micro-organisms use both the wood and the bark of a fallen tree. Although bark decays more slowly than wood, the tannins in Douglas-fir bark are not effective in reducing nitrogen fixation (Baker and others 1983). Nitrogen fixation on fallen trees in streams accounts for 5 to 10 percent of the annual nitrogen supply to the stream (Triska and others 1982).
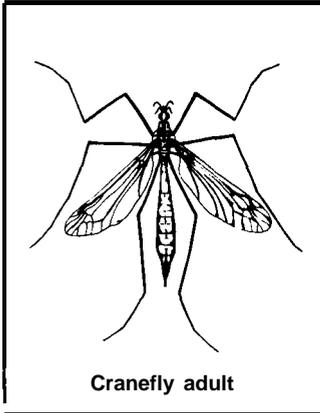
Aquatic Invertebrates

Midge adult
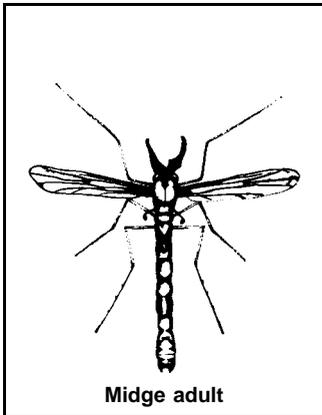
The continuum of animal associations on woody debris in aquatic systems varies from being restricted to the wood to using it opportunistically. The sequence of colonists parallels the stage of wood decay. New wood entering a stream is used primarily as habitat, although some species of midges (Chironomidae) tunnel in the cambium and phloem. The wood is then colonized by a community of algae and microbes that provides food for a group of insects, functionally called grazers or collectors. Although this type of feeding does not significantly affect the structure of the wood, the colonization of the superficial layer of the wood by fungi softens it enough that it may be abraded and ingested by invertebrates that scrape their food off surfaces. Most important, however, the wood becomes suitable for obligate wood grazers and the more generalized wood shredders, such as caddisflies (Trichoptera) and stoneflies (Plecopteia), that ingest the wood infested by fungi. These activities result in a more sculptured surface texture that in turn provides habitat for many organisms. Decades of fungal colonization and growth soften the wood and allow oxygen to penetrate. Invertebrates that bore into the internal matrix of a fallen tree speed the decomposition process by consuming the wood and by transporting microbes into the tree. In the final phase of decay, detritivores-such as annelid worms (earthworms)-penetrate the material; continued decomposition then resembles that in soil and damp, terrestrial habitats (Anderson and others 1978, Dudley and Anderson 1982).

In contrast to sound wood that enters a small stream as described above, some wood is already conditioned by fungi and other terrestrial organisms before it enters the water. Such preconditioning shortens the aquatic decomposition process by allowing more rapid internal colonization by aquatic microbes and invertebrates. Decomposition is also faster in larger streams during periods of high water because the physical abrasion removes softened tissue as the wood is transported downstream or deposited on a flood plain or the outside of a bend in the stream. Only in small headwater streams or in backwaters of larger streams can rotting wood retain enough structural integrity to provide a substrate for aquatic invertebrates during the final stages of decomposition.

Dragonfly adult
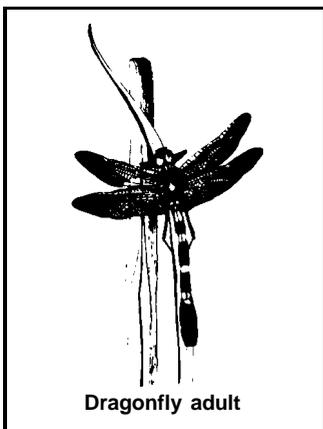
Invertebrate use of wood substrates. -Quality and texture of wood are important in determining the kinds of organisms that will colonize it. The species of wood, degree to which it is waterlogged, and decay class all affect the quality. The extent of colonization by terrestrial fungi and wood-boring insects also influences the attractiveness of the wood once it enters the water because such activity is closely associated with decay class. Dudley and Anderson (1982) found that about two-thirds of the obligate wood-using organisms were generally in soft wood; one-third in grooved, textured wood; and less than 10 percent in solid, smooth wood. In contrast, the facultative organisms occurred as follows: 20 percent on solid, smooth wood; 60 percent on grooved wood; and 20 percent on or in soft wood.

Aquatic invertebrates are also functionally classified by how they use wood substrates: (1) boring or tunneling; (2) ingesting of wood by grazing, scraping, or rasping; (3) scraping algal communities growing on wood; (4) attaching to the wood or hiding in its grooves; and (5) preying. Classification based on function are interrelated with the texture of the wood, which partly explains why a higher incidence of facultative organisms are associated with smooth, firm wood and obligate organisms with soft wood. Smooth wood surfaces are suitable for attachment and for grazing the microbial film, whereas soft wood is more easily penetrated by borers and contains fungal mycelia as a source of nutrients (Anderson and others 1978).

Cranefly adult

Many of the surface-associated invertebrates are more opportunistic in their selections of feeding sites and habitat than are the internal associates. Invertebrates that use the surface probably do so for protection from the stream current, suspended sediments, and predation but not for obtaining food. The many grooves, crevices, and loose pieces of bark on a well-conditioned fallen tree held the majority of invertebrates collected by Dudley and Anderson (1982).

Borers include some families of semiterrestrial or semiaquatic beetles (Coleoptera) and some caddisflies that hollow out twigs for cases in which they live and others that tunnel into soft wood to pupate. Fly (Diptera) larvae, however, are among the dominant borers, both in abundance and species richness. The depth to which a species (insect or microbe) can penetrate the wood is probably restricted by oxygen gradients that account for the fact that galleries are located just under the surface of the wood.

Boring activity exposes new surfaces of sound wood to microbial inoculum and colonization. When such activity is associated with some of the obligate species of fly larvae, a visible zone of stained wood often radiates outward from the larval galleries; the staining is caused by fungi that may be symbionts carried by the fly larvae. Existing galleries of terrestrial beetles increase fungal activity after the wood is submerged in water, and they are also prime habitat for cranefly (Tipulidae) larvae.

In essence, feeding activities of borers, grazers, scrapers, and raspers result in continual utilization and decomposition of wood. The amount of wood ingested depends not only on the method of feeding and the rate of consumption but also on the firmness of the wood and the amount of fungal penetration into its superficial layer. Firm but grooved or textured wood generally has a soft, stained layer one-eighth to three-sixteenths inch (2 to 5 mm) deep that has been colonized by fungal mycelia. Grazers and shredders (beetles, caddisflies, and some stoneflies) exploit this area enriched by fungi, which contains about five times as much nitrogen as occurs in nonenriched wood.[3] Scrapers (mayflies, Ephemeroptera) and raspers (snails, Mollusca) also ingest the soft layer and the periphyton-an assemblage of minute organisms attached to surfaces submerged in water.
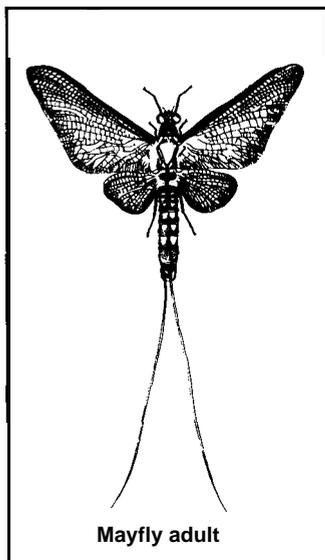
Many species associated with thoroughly decomposed wood are detritus feeders that just happen to be in the wood instead of in some other soft, organic material, such as leaves. The feeding and burrowing activities of the detritivores reduce the size of particles and cause mineralization of the woody material.

Net-spinning caddisflies frequently use textured, wood surfaces to attach their nets and to conceal themselves. Fallen trees also direct streamflow in a manner that provides net-spinning caddisfly larvae with ideal sites, both of surface structure and water velocity, for attaching their nets and filtering food from the water. In one study, for example, Dudley and Anderson (1982) found densities of 120 caddisfly *(Hydropsyche* sp.-no common name) larval nets per 12 square inches (100 cm^2) of wood.

---

[3] K. Cromack, Jr. Unpublished data on file at Oregon State University, Department of Forest Science, Corvallis, Oregon 97331.

Mayfly adult

Stonefly adult
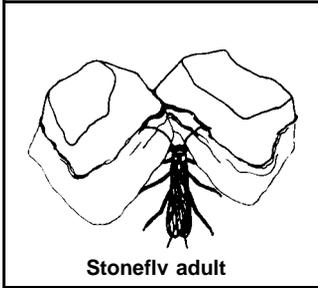
Another use of wood in streams is for pupation. Many caddisfly larvae pupate on or in wood; and several families of flies, especially crane flies, bore into soft, saturated wood to pupate. In addition, many species of insects use partially submerged wood to crawl out of the water so they can emerge as terrestrial adults. Stoneflies and some species of mayflies and dragonflies exemplify taxa that seem to prefer wood to mineral substrates for emergence as terrestrial adults.

Fish Habitat

The important role of large, woody debris in creating and maintaining spawning and rearing habitat for fish has been recognized and documented within the last 10 years (Swanson and Lienkaemper 1978, Swanson and others 1976). But we are only now beginning to really appreciate the seasonal differences in function provided to salmonids by woody debris.

Summer.-Several streams were examined in western Washington so that the population biomass of salmonids in streams flowing through old-growth forests could be compared with that in recentlyclearcut areas (Bisson and Sedell, in press). Although the total salmonid biomass increased in a clearcut, the species richness declined to a population of steelhead trout, the majority less than 1 year old. Coho salmon and cutthroat trout, between 1 and 3 years old, were proportionately less abundant in the clearcuts. Bisson and Sedell (in press) related the shifts in composition of species and age groups to changes in the habitat caused by the cutting of old-growth trees and by the removal of large, stable, woody debris from the stream channel. The amount of stable debris declined and the amount of unstable debris increased after passage of the 1976 Washington Forest Practices Act that mandated immediate removal of debris after logging. Pool size appeared to decrease and riffle size to increase as a result of clearcutting and channel clearing. The frequency (number per kilometer or mile) of both pools and riffles appeared to decline in clearcuts, which suggested that the normal stairstep stream profiles had been altered to a more even gradient.

Pools and backwaters are used by coho salmon and large cutthroat trout; in fact, pool volume is directly related to coho biomass in coastal streams in Oregon. In addition, large, stable, woody debris is preferred as protective cover by young coho salmon, yearling steelhead, and older cutthroat trout, particularly in high-gradient river systems (Bustard and Narver 1975a, 1975b; Everest and Meehan 1981; June 1981; Lister and Genoe 1979; Nickelson and others 1979; Osborn 1981; Sedell and others 1982a, 1982b) (fig. 34).

Winter. -Most species of salmonids exhibit shifts in preference between summer and winter habitat. Large, stable, woody debris is important to the selection of winter habitat by coho salmon, steelhead trout, and cutthroat trout. The presence of large, woody debris enhances the use of different habitats within pools. Pools are preferred by all species at base streamflows during the winter. The level of preference, however, is determined by the quality of the pool and the abundance of woody debris; the more woody debris, the greater the use of the pool. Further, large, stable debris tends to attract fish more to pools along the edge of a stream than to pools in the middle of a channel.

Figure 34.—Large, stable, woody debris increases the habitat value of a pool for salmonids.

Figure 35.—Salmonids use the stable wood on the flood plain as protective cover during winter floods.

When winter storms cause streams to flood, the pool-riffle sequences or stairstep stream profile is transformed into a continuous, high-velocity torrent, and there is little protection for salmonids from moving bedload sediment or swift, turbulent waters. During these unpredictable but brief periods, slack water refuges are associated almost exclusively with such large, woody debris as fallen trees and with standing vegetation in riparian flood plains (fig. 35). All three species of salmonids enter these debris-enhanced refuges until streamflows subside. Large, woody debris may also expand the feeding space by creating or enhancing the amount of slow-moving or standing water in organic-rich flood plains, even along the smallest streams (Bustard and Narver 1975a, 1975b).

Management Impacts on Fallen Trees

The Douglas-fir forests of the Pacific Northwest evolved with a continuing deposition of fallen trees to the forest floor and to streams. Fallen trees may periodically have been partially destroyed by fire but were ultimately replaced during development of successive stands (Harris and others 1982, Swanson and Lienkaemper 1978).

What will happen to the Douglas-fir ecosystem when fallen trees are no longer added, as will be the case under intensive forest management with increased utilization of wood fiber? And what will happen under short rotation management, when large trees are no longer produced?

These questions—and others that we do not yet know to ask—can be answered only through careful research. Until such research has been done, we only speculate. Our speculation in turn can be based only on what we know about the functions of fallen trees. These functions relate to the size, shape, placement, porosity, and cohesiveness of a fallen tree; its suite of functions is altered when any one of these factors is changed (Fellin 1980). We can thus begin to consider how stand management will affect each function.

On Land

Trees in an unmanaged forest generally fall randomly, although a storm or catastrophic event, such as the explosion of Mount St. Helens, sometimes causes all the trees to fall in one direction over a substantial area. Diversity results from the common random placement; some fallen trees lie along a slope, others across it. Trees that fell two centuries ago are mixed with those that fell two decades ago, 2 years ago, and 2 days ago. Some fell on the ground, some across others; some are whole, some broken. The resultant diversity provides a myriad of habitats in both time and space.

Machine entry in a stand reduces diversity because heavy equipment fragments and scatters class IV and V rotten wood. Class I and II trees may be salvaged or cut for firewood; class III trees that hang together and are not removed as salvage or firewood tend to become bunched or aligned along the direction of skidding. Habitat diversity declines to a fraction of what had been available (Eckholm 1975); probably fewer kinds of organisms can thrive. Further, because woody substrates serve as long-term soil organic material and nutrient reservoirs, increasingly intensive timber management, coupled with shorter rotations, could significantly alter the role of decaying wood in the nutrient cycling processes.

A forest manager can take steps to maintain the present diversity of fallen trees on a site. Machine trails can be designed to minimize the scattering of class IV and V trees. Wood utilization standards can be adjusted to leave a good representation of younger classes. Some trees-both defective and sound trees for built-in diversity-an be left to become fallen trees of the future. Where necessary, burning of slash can be designed and timed to minimize destruction of woody residue. These are all feasible practices, but they will cost money. Hence, the forest manager needs to know how a stand will benefit from the fallen trees over the long run.

In Streams   When fallen trees and other large pieces of wood are removed from stream channels and riparian zones by massive debris torrents or excessive postlogging channel cleanup, carrying capacity for salmonids in winter is reduced (Bisson and Sedell, in press; Swanson and Lienkaemper 1978; Toews and Moore 1982). In turn, the smolt yield of anadromous salmonids is reduced the next spring. Sedell and others (1982b) examined the long-term history of debris management. They concluded that the systematic removal of fallen trees and debris jams for navigation and transportation of logs in the late 19th and early 20th centuries destroyed a major structural component of fish habitat in intermediate to large rivers.

Enhancement or mitigation efforts designed to improve fish passage by removing debris jams and logging slash have resulted in declines in wintering populations of salmonids in small streams[4] (Bryant 1982, Lestelle 1978). The decline in the summer rearing capacity of a stream for coho salmon is a direct result of less large wood that provides cover and forms pools in streams (Bisson and Sedell, in press).

---

[4] Elliott, S. T. Ecology of rearing fish. Annual performance report, study OIB. Alaska Department of Fish and Game; 1979; 19: 39-52.

Hall, James D.; Baker, Calvin O. Biological impacts of organic debris in Pacific Northwest streams: Proceedings of workshop 1; 1975 September; Corvallis, OR. Oregon State University; 13 p.

Research Needs

Recent and current research in old-growth forest is revealing much about the roles and qualities of fallen trees. Understanding this information may allow use of fallen trees as sensitive barometers of the "habitat health" of a stand (Harris and others 1982). To learn how the functions of fallen trees differ in an old-growth stand, a clearcut, and a young stand, we need to compare the characteristics and inhabitants of fallen trees in such areas. The physical qualities of a fallen tree-moisture, temperature, nutrient content, pH--are likely to change markedly with stand removal, regeneration, and regrowth. We need to learn how the plants and animals change with such alterations within and around a fallen tree. We especially need to know much more about the fallen tree-soil interface, probably the single most important habitat niche for the survival of organisms in drastically altered stands. To fully interpret the long-term significance of fallen trees and the old-growth forests from which they come, we need to learn more about their contribution to the forest ecosystem as a whole and to the quality of the soil in particular.

Research on fallen trees in streams needs to address the quality and quantity of the woody debris that is required in riparian zones to maintain or enhance the aquatic ecosystem. Because saturated wood decomposes slowly, it accumulates on the bottom of a stream to become a site of nitrogen fixation and nitrogen, to form habitat, and to help capture and hold leaf litter that in turn is a source of energy for the stream ecosystem. How many live trees are needed (and of what diameter) to provide a future source of fallen trees in a stream for structure, nutrient cycling, and fish habitat? Although most fisheries biologists have focused their attention on wood in streams, of equal importance is the large wood (quality and quantity) along channel margins and in overflow areas because this is the winter habitat of the salmonids.

In summation, we must not sacrifice the options of future generations on the altar of cost-effectiveness through decisions based on insufficient data. It is the professional charge of researchers to obtain the needed data and of managers to apply it.

Epilog

When thinking of and dealing with diversity in a forest, conventional vision focuses on structure and habitat. Diversity, however, has another dimension-one that is only now being perceived: function. The basic components of structural and functional diversity are inseparably interwoven in a forest. A broadened philosophical view of management-a forest versus a commodity-is necessary if certain structurally related functions, such as retention of water and cycling of nutrients in large, fallen trees, are to be options in managed forests of the future.

(Maser and Trappe 1984)

Common and Scientific Names

Plants:

Alder	*Alnus* spp.
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
Huckleberry	*Vaccinium* spp.
Oregon oxalis	*Oxalis oregana* Nutt. ex T. and G.
Salal	*Gaultheria shallon* Pursh
Sitka spruce	*Picea sitchensis* (Bong.) Carr.
Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.

Invertebrates:

Carpenter ant	*Camponotus* spp.
Common earwig	*Forficula auricularia* L.
Douglas-fir beetle	*Dendroctonus pseudotsugae* Hopkins
Golden buprestid	*Buprestis aurulenta* L.
Pacific dampwood termite	*Zootermopsis angusticollis* (Hagen)
Pacific folding-door spider	*Antrodiaetus pacificus* (Simon)
Ponderous borer	*frgates spiculaus* (Le Conte)
Redbellied checkered beetle	*Enoclerus sphegeus* F.

Vertebrates:

Beaver	*Castor canadensis* Kuhl
Black-tailed deer	*Odocoileus hemionus* Rafinesque
California red-backed vole	*Clethrionomys californicus* (Merriam)
California slender salamander	*Batrachoseps attenuatus* (Eschscholtz)
Clouded salamander	*Aneides ferreus* Cope
Coho salmon	*Oncorhynchus kisutch* (Walbaum)
Cutthroat trout	*Salmo clarki* Richardson
Oregon salamander	*Ensatina eschscholtzi* Gray
Oregon slender salamander	*Batrachoseps wrighti* (Bishop)
Shrew-mole	*Neurotrichus gibbsi* (Baird)
Steelhead trout	*Salmo gairdneri* Richardson
Trowbridge shrew	*Sorex trowbridgei* Baird

Acknowledgments

The interdisciplinary nature of the work reported in this paper evokes the fond memory of our friend, colleague, and teacher, Gerry S. Strickler. Gerry's life of research was dedicated to understanding how different organisms in wildlands interact with each other and their environment. And he left us with a greater appreciation of the importance of cause-and-effect relationships between humans and forests.

Literature Cited

Aho, Paul E.; Cromack, Kermit, Jr.; LI, Ching Yan; Hutchins, Anita. Occurrence of calcium oxalate and oxalate-utilizing bacteria in *Echinodontium tinctorium* decay zones in *Abies concolor. Res.* Note PNW-326. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1979.** 8 p.

Aho, Paul E.; Seidler, Ramon J.; Evans, Harold J.; Raju, P. N. Distribution, enumeration, and identification of nitrogen-fixing bacteria associated with decay in living white fir trees. Phytopathology. 64: 1413-1420: **1974.**

Aho, Paul Eugene. Fungal and bacterial associations in heart rots of *Abies concolor* (Gord. and Glend.) Lindl. and techniques for estimating damage in southwestern Oregon. Corvallis, OR: Oregon State University; 1976. 202 p. Ph.D. thesis.

Anderson, Norman H.; Sedell, James R. Detritus processing by macroinvertebrates in stream ecosystems. Annu. Rev. Entomol. 24: 351-377; **1979.**

Anderson, Norman H.; Sedell, James R.; Roberts, Lynn M.; Triska, Frank J. Role of aquatic invertebrates in processing wood debris in coniferous forest streams. Am. Midl. Nat. 100: 64-82; **1978.**

Anderson, R. F. Forest and shade tree entomology. New York: John Wiley & Sons, Inc.; **1960.** 428 p.

Ausmus, B.S. Regulation of wood decomposition rates by arthropod and annelid populations. Soil organisms as components of ecosystems. Ecol. Bull. 25: 180-l92; **1977.**

Baker, J. H., Morita, R. Y .; Anderson, N. H. Bacterial activity associated with the decomposition of woody substrates in a stream sediment. Appl. and Environ. Microbiol. 45: 516-521; **1983.**

Barras, S. J.; Perry, T. J. Interrelationships among microorganisms, bark and ambrosia beetles, and woody host tissue: an annotated bibliography, 1965-l974. Gen. Tech. Reo. SO-10. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station; **1975.** 34 p.

Becker, Gunther. Physiological influences on wood-destroying insects of wood compounds and substances produced by microorganisms. Wood Sci. Technol. 5: 236-246; **1971.**

Binkley, Dan; Graham, Robin Lambert. Biomass, production, and nutrient cycling of mosses in an old-growth Douglas-fir forest. Ecology. 62: 1387-1389; **1981.**

Bisson, Peter A.; Sedell, James R. Salmonid populations in logged and unlogged stream sections of western Washington. in: Proceedings of a symposium on fish and wildlife relationships in old-growth forests; 1982 April 12-13; Juneau, AK. Juneau, AK: Alaska District, American Institute of Fishery Research Biologists; [in press].

Borror, Donald J.; Belong, Dwight M. An introduction to the study of insects. Rev. ed. New York: Holt, Rinehart and Winston, Inc.; 1964. 819 p.

Boullard, Bernard. Considerations sur la symboisefongiquechez les Pteridophytes. Syllogeus Natl. Mus. Nat. Sci. Can. 19: l-59; **1979.**

Boyce, J. S. A study of decay in Douglas-fir in the Pacific Northwest. Agric. Bull. 1163. Washington, DC: U.S. Department of Agriculture; **1923.** 19 p.

Boyce, John S.; Wagg, J. W. Bruce. Conk rot of old-growth Douglas-fir in western Oregon. Bull. 4. Corvallis, OR: Oregon State College, Forest Research Laboratory; **1953.** 96 p.

Breznak, J. A. Symbiotic relationships between termites and their intestinal microbiota. In : Jennings, D. H.; Lee, D. L., eds. Symbiosis symposium; Society of Forest Experimental Biology. Ser. 29. Cambridge, MA: Cambridge University; **1975:** 559-580.

Breznak, John A. Intestinal microbiota of termites and other xylophagous insects. Annu. Rev. Microbiol. 36: 323-343; **1982.**

Brown, H. P.; Panshin, A. J.; Forsaith, C. C. Textbook of wood technology. Vol. I: Structure, identification, defects,and uses of the commercial wood of the United States. New York: McGraw-Hill; 1949. 652 p.

Bryant, Mason D. Organic debris in **salmonid** habitat in southeast Alaska: measurement and effects. In: Armantrout, Neil B., ed. Acquisition and utilization of aquatic habitat inventory information: Proceedings of a symposium; 1981 October 28-30; Portland, OR. Bethesda, MD: American Fisheries Society, Western Division; **1982:** 259-265.

Buller, A. H. Reginald. Researches on fungi; vol. II. London: Longmans, Green and Co.; **1922.** 492 p.

Bury, R. Bruce; Martin, Michael. Comparative studies on the distribution and foods of plethodontid salamanders in the redwood region of northern California. J. Herpetol. 7: 331-335; **1973.**

Bustard, David R.; Narver, David W. Aspects of the winter ecology of juvenile coho salmon *(Oncorhynchus kisutch)* and steelhead trout *(Salmo gairdneri).* J. Fish. Res. Board Can. 32: 667-680; **1975a.**

Bustard, David R.; Narver, David W. Preferences of juvenile coho salmon *(Oncorhynthus kisutch)* and cutthroat trout *(Salmo clarki)* relative to simulated alteration of winter habitat. J. Fish. Res. Board Can. 32: 681-687; **1975b.**

Carlisle, A.; Brown, A. H. F.; White, E. J. Litter-fall, leaf production and the effects of defoliation by *Tortix viridana* in a senile oak *(Quercus petraea)* woodland. J. Ecol. 54: 65-85; **1966.**

Chamberlin, W. J. insects affecting forest products and other materials. Corvallis, OR: Oregon State College Cooperative Association; **1949.** 159 p.

Childs, T. W.; Clark, J. W. Decay of windthrown timber in western Washington and northwestern Oregon. Spec. Release 40. Beltsville, MD: U.S. Department of Agriculture, Agricultural Research Administration, Bureau of Plant Industry, Soils, and Agricultural Engineering, Division of Forest Pathology; **1953.** 20 p.

Christensen, O. Estimation of standing crop and turnover of dead wood in a Danish oak forest. Oikos. 26: 177-186; **1977.**

Christiansen, Kenneth; Bellinger, Peter. The collembola of North America north of the Rio Grande, a taxonomic analysis. Part 1: Introduction, general, families Poduridae and Hypogoastruridae. Grinnell, IA: Grinnell College; **1980.** 1,322 p.

Christy, E. Jennifer; Sollins, Phillip; Trappe, James M. First-year survival of Tsuga *heterophylla* without mycorrhizae and subsequent ectomycorrhizal development on decaying logs and mineral soil. Can. J. Bot. 60: 1601-1605; **1982.**

Clermont, L. P.; Schwartz, H. Studies on the chemical composition of bark and its utilization for structural boards. Pulp and Pap. Mag. Can. 49: 90-94; 1948.

Cline, Steven P.; Berg, Alan B.; Wight, Howard M. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44: 773-786; **1980.**

Cornstock, John Henry. The spider book. Ithaca, NY: Cornell University Press, Comstock Publishers Association; **1948.** 729 p.

Cornaby, B. W.; Waide, J. B. Nitrogen fixation in decaying chestnut logs. Plant and Soil. 39: 445-448: **1973.**

Cowan, B. D.; Nagel, W. P. Predators of the Douglas-fir beetle. Tech. Bull. 86. Corvallis, OR: Oregon State University, Agricultural Experiment Station; **1965.** 32 p.

Cromack, K., Jr.; Swanson, F. J.; Grier, C. C. A comparison of harvesting methods and their impact on soils and environment in the Pacific Northwest. In: Youngberg, C. T., ed. Forest soils and land use. Fort Collins, CO: Colorado State University; **1979:** 449-476.

Crossley, D. A., Jr. The roles of terrestrial saprophagous arthropods in forest soils: current status of concepts. In: Mattson, W. J., ed. The role of arthropods in forest ecosystems. New York: Springer Verlag; **1976:** 49-56.

Dadswell, H. E.; Hillis, W. E. Wood. In: Hillis, W. E., ed. Wood extractives and their significance to the pulp and paper industry. New York: Academic Press; 1962. 513 p.

Dahms, Walter G. How long do ponderosa pine snags stand? Res. Note 57. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1949. 7 p.

Day, Frank P., Jr.; Monk, Carl D. Vegetation patterns on a southern Appalachian watershed. Ecology. 55: 1064-1074; 1974.

Denny, C. S.; Goodlett, J. C. Microrelief resulting from fallen trees. In: Surficial geology and geomorphology of Potter County, Pennsylvania. U.S. Geol. Surv. Prof. Pap. 288: 59-68; 1956.

Deyrup, Mark. Deadwood decomposers Nat. Hist. 90: 64-91; **1981.**

Deyrup, Mark Amidon. The insect community of dead and dying Douglas-fir. 1: The Hymenoptera. Ecosyst. Anal. Stud. Bull. 6. Seattle, WA: University of Washington, Coniferous Forest Biome; **1975.** 104 p.

Deyrup, Mark Amidon. The insect community of dead and dying Douglas-fir: Diptera, Coleoptera, and Neuroptera. Seattle, WA: University of Washington; **1976.** 540 p. Ph.D. dissertation.

Dicken, S. N.; Dicken, E. F. The making of Oregon: a study in historical geography. Portland, OR: Oregon Historical Society; **1979.** Vol. 1. 207 p.

Dowding, J. P. Nutrient uptake and allocation during substrate exploitation by fungi. In: Wicklow, G. C.; Carroll, J. E., eds. The fungal community. New York: Marcel Dekker, Inc.; **1981:** 621-635.

Dowding, P. Allocation of resources; nutrient uptake and utilization by decomposer organisms. In: Anderson, J. M.; Macfadyen, A., eds. The role of terrestrial and aquatic organisms in decomposition processes. Oxford: Blackwell Scientific Publications; **1976:** 169-193.

Dudley, Tom; Anderson, Norman H. A survey of invertebrates associated with wood debris in aquatic habitats. Melanderia. 39: 1-22; **1982.**

Eckholm, Erik. The other energy crisis: firewood. Worldwatch Pap. 1. [Place of publication unknown]: Worldwatch Institute; **1975.** 22 p.

Edwards, C. A.; Reichle, D. E.; Crossley, D. A., Jr. The role of soil invertebrates in turnover of organic matter and nutrients. In: Reichle, D. E., ed. Ecological studies. Analysis and synthesis. Berlin: Springer Verlag; **1970;** vol. 1: 147-172.

Eichrodt, R. Ueber die Bedeutung von Moderholz fiir die naturliche Verjungen in subalpinen Fichtenwald. Zurich: Eidg. Tech. Hochsch.; **1969.** 123 p. Diss. No. 4261.

Elton, Charles S. Dying and dead wood. In: The pattern of animal communities. New York: John Wiley & Sons, Inc.; **1966:** 279-305.

Esenther, G. R.; Kirk, T. K. Catabolism of aspen sapwood in *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). Ann. Entomol. Soc. Am. 67: 989-991; 1974.

Everest, Fred H.; Meehan, William R. Forest management and anadromous fish habitat productivity. Trans. North Am. Wildl. and Nat. Resour. Conf. 46: 521-530; **1981.**

Falinski, Janusz Bogdan. Uprooted trees, their distribution and influence in the primeval forest biotope. Vegetatio. 38: 175-183: 1978.

Fellin, David G. Effect of silvicultural practices, residue utilization, and prescribed fire on some forest floor arthropods. In: Environmental consequences of timber harvesting in Rocky Mountain coniferous forests. Gen. Tech. Rep. INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; **1960:** 287-316.

Fitch, Henry S. Amphibians and reptiles of the Rogue River basin, Oregon. Am. Midl. Nat. 17: 634-652; **1936.**

Fogel, Robert; Cromack, Kermit, Jr. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Can. J. Bot. 55: 1632-1640; 1977.

Fogel, Robert; Ogawa, M.; Trappe, James M. Terrestrial decomposition: a synopsis. United States-International Biological Program. U.S. Int. Biol. Program-Coniferous For. Biome Intern. Rep. 135. Seattle, WA: University of Washington; **1973.** 12 p.

Fogel, Robert; Peck, Stewart B. Ecological studies of hypogeous fungi. In: Coleoptera associated with sporocarps. Mycologia. 67: 741-747; **1975.**

Fogel, Robert; Trappe, James M. Fungus consumption (mycophagy) by small animals. Northwest Sci. 52: 1-31; **1978.**

Foster, Jeffrey R.; Lang, Gerald E. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Can. J. For. Res. 12: 617-626; **1982.**

Francke-Grosmann, H. Ectosymbiosis in wood inhabiting insects. In: Henry, S. M., ed. Symbiosis. New York: Academic Press; **1967;** vol. 2: 142-205.

Franklin, Jerry F.; Cromack, Kermit, Jr.; Denison, William; McKee, Arthur; Maser, Chris; Sedell, James; Swanson, Fred; Juday, Glen. Ecological characteristics of old-growth Douglas-fir forests. Gen. Tech. Rep. PNW-118. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1981.** 48 p.

Franklin, Jerry F.; Hemstrom, Miles A. Aspects of succession in the coniferous forests of the Pacific Northwest. In: West, D. C.; Shugart, H. H.; Botkin, D. B., eds. Forest succession: concept and application. New York: Springer Verlag; **1980:** 212-229.

Franklin, Jerry F.; Waring, Richard H. Distinctive features of the northwestern coniferous forest: development, structure, and function. In: Forests: fresh perspective from ecosystem analysis. Corvallis, OR: Oregon State University; **1980:** 59-85.

Furniss, M. M.; Orr, P. W. Douglas-fir beetle. For. Pest Leafl. 5. Washington, DC: U.S. Department of Agriculture, Forest Service; 1970. 4 p.

Furniss, R. L.; Carolln, V. M. Western forest insects. Misc. Publ. 1339. Washington, DC: U.S. Department of Agriculture, Forest Service; **1977.** 654 p.

Gardner, J. **A. F.; Barton,** G. M. The distribution of dihydroquercetin in Douglas-fir and western hemlock. For. Prod. J. 10: 171-173: **1960.**

Giltrap, N. J. Production of polyphenol oxidases by ectomycorrhizal fungi with special reference to *Lactarius* spp. Trans. Brit. Mycol. Soc 78: 75-81; **1982.**

Gobl, F. Mykorrhiza-Untersuchungen an Jungfichten im Urwald von Brigels. Schweiz. Z. Forstwes. 119: 148-150; **1968.**

Graham, H. M.; Kurth, E. F. Constituents of extractives from Douglas-fir. Ind. Eng. Chem. 41: 409-414; 1949.

Graham, J. H.; Linderman, R. G. Ethylene production by ectomycorrhizal fungi, *Fusarium oxysporum* f. sp. *pini,* and by aseptically synthesized ectomycorrhizae and Fusarium-infected Douglas-fir roots. Can. J. Microbial. 26: 1340-1347; **1980.**

Graham, Robin Lambert. Biomassdynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range. Corvallis, OR: Oregon State University; **1982.** 152 p. Ph. D. thesis.

Graham, Robin Lambert; Cromack, Kermit, Jr. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Can. J. For. Res. 12: 511-521; **1982.**

Graham, S. **A.** Temperature as a limiting factor in the life of subcortical insects. J. Econ. Entomol. 17: 377-383; **1924.**

Graham, S. **A.** The felled tree trunk as an ecological unit. Ecology. 6: 397-411; **1925.**

Graham, S. A.; Knight, F. B. Principles of forest entomology. 4th ed. New York: McGraw-Hill Book Co.; **1965.** 417 p.

Grier, C. C.; Logan, R. S. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecol. Monogr. 47: 373-400; **1978.**

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

Harris, Larry D.; Maser, Chris; McKee, Arthur. Patternsof old-growth harvest and implications for Cascades wildlife. Trans. North Am. Wildl. and Nat. Resour. Conf. 47: 374-392; **1982.**

Hartenstein, R. Soil Oribatei. I: Feeding specificity among forest soil Oribatei (Acarina). Ann. Entomol. Soc. Am. 55: **202-206; 1962.**

Harvey, A. E.; Jurgensen, M. F.; Larsen, M. J. Seasonal distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. For. Sci. 24: 203-208; **1978.**

Harvey, A. E.; Larsen, M. J.; Jurgensen, M. F. Comparative distribution of ectomycorrhizae in soils of three western Montana forest habitattypes. For. Sci. 25: 350-358; **1979a.**

Harvey, A. E.; Larsen, M. J.; Jurgensen, M. F. Fire-decay: interactive roles regulating wood accumulation and soil development in the northern Rocky Mountains. Res. Note INT-263. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; **1979b.** 4 p.

Hergert, Herbert L.; Kurth, E. F. The chemical nature of cork from Douglas-fir bark. Tappi. 35: 59-66; **1952.**

Hillis, W. E. The distribution and formation of polyphenols within the tree. In: Hillis, W. E., ed. Wood extractives and their significance to the pulp and paper industry. New York: Academic Press; 1962. 513 p.

Hulme, M. A.; Shields, J. K. Biological control of decay fungi in wood by competition for non-structural carbohydrates. Nature (London). 227: 300-301; **1970.**

Imms, A. D. A general textbookof entomology. New York: E. P. Dutton & Co., Inc.; **1960.** 886 p.

Johannson, M.; Theander, O. Changes in sapwood of roots of Norway spruce, attacked by *Fomes annosus.* Part I. Physiol. Plant. 30: 218-225; **1974.**

June, Jeffrey A. Life history and habitat utilization of cutthroat trout *(Salmo clarki)* in a headwater stream on the Olympic Peninsula, Washington. Seattle, WA: University of Washington; **1981.** 116 p. M.S. thesis.

Keen, F. P. How soon do yellow pine snags fall? J. For. 27: 735-737; **1929.**

Kennedy, R. W. Fungicidal toxicity of certain extraneous components of Douglas-fir heartwood. For. Prod. J. 6: 80-84; **1956.**

Kimmey, J. W.; Furniss, R. L. Deterioration of fire-killed Douglas-fir. Tech. Bull. 851. Washington, DC: U.S. Department of Agriculture; **1943.** 61 p.

Krants, Gerald W. A manual of acarology. 2d ed. Corvallis, OR: Oregon State University Book Stores, Inc.; **1978.** 509 p.

Kreisel, Hanns. Die Entwicklung der Mykozbnose an Fagus-Stubben auf norddeutschen Kahlschlagen. Feddes Repert. Beih. 19: 227-232; 1961.

Kropp, Bradley R.; Trappe, James M. Ectomycorrhizal fungi of *Tsuga heterophylla. Mycologia.* 74: 479-488; 1982.

Kuhnelt, Wilhelm. Soil biology with special reference to the animal kingdom. London: Faber and Faber; **1961.** 397 p.

Kurth, E. F. The chemical analysis of western woods. Part I. Pap. Trade J. 126: 56-58; **1948.**

Kurth, E. F. The chemical analysis of western woods. Part II: Douglas-fir bark analysis. Tappi. 32: 175-176; **1949.**

Kurth, E. F.; Chan, F. L. Extraction of tannin and dihydroquercetin from Douglas-fir bark. J. Am. Leather Chem. Assoc. 48: **20-32; 1953.**

Lambert, Robin L.; Lang, Gerald E.; Reiners, William A. Loss of mass and chemical change in decaying boles of a subalpine fir forest. Ecology. 61: 1460-1473; **1980.**

Lang, G. E.; Forman, R. T. Detrital dynamics in a mature forest: Hutcheson Memorial Forest. Ecology. 59: 580-595; **1978.**

Langston, Robert L.; Powell, J. A. The earwigs of California (order Dermaptera). Bull. Calif. Insect Surv. 20: 1-5; **1975.**

Larsen, M. J.; Jurgensen, M. F.; Harvey, A. E. N_2 fixation associated with wood decayed by some common fungi in western Montana. Can. J. For. Res. 8: 341-345; **1978.**

Larsen, M. J.; Jurgensen, M. F.; Harvey, A. E. N_2 fixation in brown-rotted soil woods in an intermountain cedar-hemlock ecosystem. For. Sci. 28: 292-296; **1982.**

Lawton, E. Moss flora of the Pacific Northwest. Nichinan, Japan: Hattori Botanical Laboratory; **1971.** 362 p.

Lestelle, C. Larry. The effects of forest debris removal on a population of resident cutthroat trout in a small headwater stream. Seattle, WA: University of Washington; **1978.** 85 p. M.S. thesis.

Levi, Herbert W.; Levi, Lorna R.; Zim, Herbart S. Spiders and their kin. New York: Golden Press; **1968.** 160 p.

Lewis, H. F. The significant chemical components of western hemlock, Douglas-fir, western red cedar, loblolly pine and black spruce. Tappi. 33: 299-301; **1950.**

Lewis, J. O. E. The biology of centipedes. New York: Cambridge University Press; **1981.** 476 p.

Li, C. Y. Phenoloxidase and peroxidase activities in zone lines of *Phellinus weirii.* Mycologia. 73: 811-821; **1981.**

Listor, D. B.; Genoe, H. S. Stream habitat utilization by cohabiting underyearlings of chinook *(Oncorhynchus tshawytscha* and who salmon *(0. kisutch* in the Big Qualicum River, British Columbia. J. Fish. Res. Board Can. 27: 1215-1224; **1979.**

Luxton, M. Studies on the oribatid mites of a Danish beech wood soil. Pedobiology. 12: 434-463; **1972.**

McFee, W. W.; Stone, E. L. The persistence of decaying wood in the humus layers of northern forests. Soil. Sci. Soc. Am. Proc. 30: 513-516; **1966.**

McKenzie, Donald S.; Storm, Robert M. Patterns of habitat selection in the clouded salamander, *Aneides ferreus* (Cope.). Herpetologica. 26: 450-454; **1970.**

MacMillan, Paul C. Log decomposition in Donaldson's Woods, Spring Mill State Park, Indiana. Am. Midl. Nat. 106: 335-344; **1981.**

MacMillan Paul C.; Means, Joseph; Hawk, Glenn M.; Cromack, Kermit, Jr.; Fogel, R. Log decomposition in an old-growth Douglas-fir forest. In: Northwest Scientific Association abstract of papers presented at the 50th annual meeting. Pullman, WA: Washington State University Press; **1977:** 13.

Mcmillen J. H. Laboratory observations on the food preference of *Onychiurus armatus* (Tullb.) Gisin (Collembola, family Onychiuridae). Rev. Ecol. Biol. Soil. 13: 353-364; **1976.**

Malomna, Virginia C. Observations of salamanders (Amphibia, Urodela, Plethodontidae) dying in the field. J. Herpetol. 11: 1-5; **1977.**

Malomna, Virginia C. Behavior of an unobservable species: diet selection by a salamander. Copeia. 1978: 664-672; **1978.**

Marx, D. M. Mycorrhizae and feeder root diseases. In: Marks, G. C.; Kozlowski, T. T., eds. Ectomycorrhizae-their ecology and physiology. New York: Academic Press; **1973:** 351-382.

Maser, Chris; Anderson, Ralph G.; Cromack, Kermit, Jr.; Williams, Jerry T.; Martin, Robert E. 6. Dead and down woody material. In: Thomas, Jack Ward, tech. ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: U.S. Department of Agriculture; **1979:** 76-95. In cooperation with: Wildlife Management Institute and the U.S. Department of the Interior, Bureau of Land Mangement.

Maser, Chris; Hooven, Edward F. Notes on the behavior and food habits of captive Pacific shrews, *Sorex pacificus pacificus.* Northwest Sci. 48: 81-95; **1974.**

Maser, Chris; Mate, Bruce R.; Franklin, Jerry F.; Dyrness C. T. Natural history of Oregon coast mammals. Gen. Tech. Rep. PNW-133. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1981.** 496 p. In cooperation with: U.S. Department of the Interior, Bureau of Land Management.

Maser, Chris; Trappe, James M. The fallen tree--a source of diversity. In: Newforests for a changing world. Proceedings, Society of American Foresters National Convention; 1983 October 16-20; Portland, OR. Bethesda, MD; 1984.

Maser, Chris; Trappe, James M.; Nussbaum, Ronald A. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology. 59: **799-809; 1978a.**

Maser, Chris; Trappe, James M.; Ure, Douglas C. Implications of small mammal mycophagy to the management of western coniferous forests. Trans. North Am. Wildl. and Nat. Resour. Conf. 43: 76-88; **1978b.**

Melin, Elias; Nilsson, Harold. Transfer of radioactive phosphorus to pine seedlings by means of mycorrhizal hyphae. Physiol. Plant. 3: 88-92; **1950.**

Melin, Elias; Nilsson, Harold. Transfer of labelled nitrogen from an ammonium source to pine seedlings through cycorrhizal mycelium. Sven. Bot. Tidskr. 46: 281-265; **1952.**

Minore, Don. Identification of rotten logs in the coastal forests of Oregon and Washington. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1988.** 16 p.

Minore, Don. Germination and early growth of coastal tree species on organic seed beds. Res. Pap. PNW-135. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1972.** 18 p.

Mork, Ellas. Granskogensforyngelsesforhold i namdalstraktene. Meded. Nor. Skogforsoksves. 8: 40-70; **1927.**

Morse, E. Morse's monthly: a Puget Sound magazine for the people of the Northwest. Snohomish City, Washington Territory. 1: 1-14; **1883.** Available from: Washington State Archives, Olympia, WA.

Nadkarnl, Nalini M. Canopy roots: convergent evolution in rainforest nutrient cycles. Science. 214: 1023-1024; **1981.**

Nalman, Robert J. Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. Can. J. Fish. and Agric. Sci. 39: 1699-1718; **1982.**

Nalman, Robert J.; Sedell, James R. Characterization of particulate organic matter transported by some Cascade mountain streams. J. Fish. Res. Board Can. 36:17-31; **1979.**

Nelson, Earl E. Factors affecting survival of *Poria weirii* in small buried cubes of Douglas-fir heartwood. For. Sci. 13: 78-84; **1967.**

Nickelson, T. E.; Beidler W. M.; Willis, M. J. Streamflow requirements of salmonids. Fed. Aid Prog. Rep. AFS-62. Portland, OR: Oregon Department of Fish and Wildlife, Research and Development Section; **1979.** 30 p.

Ogden, P. S. Peter Skene Ogden's Snake Country journal 1826-27. Davies, K. G., ed. London: Hudson's Bay Record Society; **1961;** 23: 1-225.

Osborn, Jeffrey Gard. The effects of logging on cutthroat trout *(Salmo clarki)* in small headwater streams. FRI-UW-8113. Seattle, WA: University of Washington, Fisheries Research Institute; **1981.** 89 p.

Petersen, Henning. Collembolemes emaeringsbiologi cg dennes okologiske betydning. Entomol. Medd. 39: 97-118; **1971.**

Pirk, Walter; Tuxen, Reinhold. Das *Trametetum gibbosae,* eine Pilzgesellschaft modernder Buchenstumpfe. Mitt. Florist.-Soziol. Arb. 6/7: 120-126: **1957.**

Place, I. C. M. Comparative moisture regimes of humus and rotten wood. Silvic. Leafl. 37. Ottawa, ON: Canada Department of Research and Development, Forest Research Division; **1950.** 2 p.

Rabitin S. C.; Rhodes, L. H. Acaulospora *bireticulata* inside oribatid mites. Mycologia. 74: 859-861; **1982.**

Fiennerfelt, E.; Tamm, O. The content of major plant nutrients in spruce and pine attacked by *Fomes annosus* (Fr.) ckc. Phytopathol. Z. 43(4): 371-382; **1962.**

Reports of the Secretary of War. Reports of the Chief of Engineers. In: House executive documents, sessions of Congress. Washington, DC: U.S. Government Printing Office; **1875-99.** (Annual reports.)

Ricek, E. W. Untersuchungen uber die Vegetation auf Baumstumpfen. Teil I. Obertoesterr. Musealver. Jahrb. 112: 185-252; **1967.**

Ricek, E. W. Untersuchungen uber die Vegetation auf Baumstumpfen. Teil II. Oberoesterr. Musealver. Jahrb. 113: **229-256; 1968.**

Riffle, Jerry W. Effect of nematodes on root-inhabiting fungi. In: Hacskaylo, E., ed. Mycorrhizae. Misc. Publ. 1189. Washington, DC: U.S. Department of Agriculture, Forest Service; **1971: 97-113.**

Rodin, L. E.; Baxilevich, N. I. Production and mineral cycling in terrestrial vegetation. London: Oliver and Boyd; **1967.** 288 p.

Roth, L. F. Disease in young-growth stands of Douglas-fir and western hemlock. In: Berg, A. B., ed. Management of young-growth Douglas-fir and western hemlock. Pap. 666. Corvallis, OR: Oregon State University, School of Forestry; **1970:** 38-43.

Rothacher, J. S.; Glazebrook, T. B. Flood damage in the National Forests of Region 6. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1968.** 20 p.

Runge, A. Pilzsukzession auf Laubholzstumphen. Z. Pilzkd. 41: 31-38; **1975.**

Russell, Loren K. Beetles associated with slime molds (Mycetozoa) in Oregon and California (Coleoptera: Leiodidae, Sphindidae, Lathridiidae). Pan-Pac. Entomol. 55: 1-9; **1979.**

Ruth, Robert H.; Yoder, Ray A. Reducing wind damage in the forests of the Oregon Coast Range. Res. Pap. 7. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1953.** 30 p.

Sanders, C. J. The distribution of carpenter ant colonies in the spruce-fir forests of northwestern Ontario. Ecology. 51: 865-873; **1970.**

Savely, Harvey Epperson, Jr. Ecological relations of certain animals in dead pine and oak logs. Ecol. Monogr. 9: 322-385; **1939.**

Scheffer, Theodore C.; Cowling, Ellis B. Natural resistance of wood to microbial deterioration. Annu. Rev. Phytopathol. 4: 147-170; **1966.**

Sedell, J. R.; Triska, F. J.; Buckley, B. M. The processing of coniferous and hardwood leaves in two coniferous forest streams. 1: Weight loss and associated invertebrates. Verh. Int. Ver. Limnol. 19: 617-627; **1975.**

Sedell, James R.; Bisson, Peter A.; June, Jeffrey A.; Speaker, Robert W. Ecology and habitat requirements of fish populations in South Fork Hoh River, Olympic National Park. In: Starkey, E. E.; Franklin, J. F.; Matthews, J. W., tech. coords. Ecological research in National Parks of the Pacific Northwest: Proceedings, 2d conference on scientific research in the National Parks; 1979 November; San Francisco, CA. Corvallis, OR: Oregon State University, Forest Research Laboratory; **1982a:** 35-42.

Sedell, James R.; Everest, Fred H.; Swanson, Frederick J. Fish habitat and streamside management: past and present. In: Proceedings of the Society of American Foresters, annual meeting. 1981 September 27-30 Orlando, FL. Bethesda, MD: Society of American Foresters; **1982b:** 244-255.

Sedell, James R.; Luchessa, Karen J. Using the historical record as an aid to salmonid habitat enhancement. In: Armantrout, Neil B., ed. Acquisition and utilization of aquatic habitat inventory information: Proceedings of a symposium; 1981 October 28-30; Portland, OR. Bethesda, MD: American Fisheries Society, Western Division; **1982:** 210-223.

Sedell, James R.; Triska, Frank J.; Hall, James D.; Anderson, Norman H.; Lyford, John H. Sources and fates of organic inputs in coniferous forest streams. In: Waring, R. H.; Edmonds, R. L., eds. Integrated research in the coniferous forest biome. Coniferous For. Biome Bull. 5. Seattle, WA: University of Washington; **1974:** 57-69.

Sharp, R. F. Nitrogen fixation in deteriorating wood: the incorporation of $^{15}N_2$ and the effect of environmental conditions on acetylene reduction. Soil Biol. Biochem. 7: 9-14; **1975.**

Sharp, R. F.; Yillbank, J. W. Nitrogen fixation in deteriorating wood. Experientia. 29: **895-896; 1973.**

Shortle, W. C.; Cowling, E. B. Development of discoloration, decay, and microorganisms following wounding of sweet gum and yellow-poplar trees. Phytopathology. 68: 609-616; **1978.**

Sllvester, W. B.; Sollins, P.; Verhoeven, T.; Cllne, S. P. Nitrogen fixation and acetylene reduction in decaying conifer boles: effects of incubation time, aeration, and moisture content. Can. J. For. Res. 12: 646-652; **1982.**

Slankis, V.; Runeckles, V. C.; Krotkov, G. Metabolites liberated by roots of white pine *(Pinus strobus* L.) seedlings. Physiol. Plant. 17: 301-313; **1964.**

Smith, William H. Release of organic materials from the roots of tree seedlings. For. Sci. 15: 138-143; **1969.**

Snell, J. A. Kendall; Max, Timothy A. Bark-to-wood ratios for logging residue in Oregon, Washington, and Idaho. Res. Pap. PNW-295. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1981.** 10 p.

Sollins, P.; Grier, C. C.; McCorison, F. M.; Cromack, K., Jr.; Fogel, R.; Fredriksen, R. L. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecol. Monogr. 50: 261-285; **1980.**

Sollins, P.; McCorison, F. M. The nitrogen and carbon solution chemistry of an old-growth coniferous forest watershed before and after cutting. Water Resour. Res. 17: 1409-1418; **1981.**

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

Sollins, Phillip; Cromack, Kermlt, Jr.; Fogel, Robert; Li, Chlng Yan. Role of low-molecular-weight organic acids in the inorganic nutrition of fungi and higher plants. In: Wicklow, Donald T.; Carroll, Georae C., eds. The fungal community: its organization and role in the ecosystem. New York: Marcel Dekker, Inc.; **1981:** 607-619.

Stebbins, Robert C. Amphibians and reptiles of western North America. New York: McGraw-Hill Book Co., Inc.; **1954.** 536 p.

Stebbins, Robert C. Afield guide to western reptiles and amphibians. Boston: Houghton Mifflin Co.; **1966.** 279 p.

Storm, Robert M.; Aller, Alvin R. Food habits of *Aneides ferreus.* Herpetologia. 4: 59-62; **1947.**

Swanson, Frederick J.; Lienkaemper, George W. Physical consequences of large organic debris in Pacific Northwest streams. Gen. Tech. Rep. PNW-69. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1976.** 12 p.

Swanson, Frederick J.; Lienkaemper, George W. Interactions among fluvial processes, forest vegetation, and aquatic ecosystems, South Fork Hoh River,. Olvmoic National Park. In: Starkev, E. E.; Franklin, J. F.; Matthews, J. W., tech. coords. Ecological research in National Parks of the Pacific Northwest: Proceedings, 2d conference on scientific research in the National Parks; 1979 November; San Francisco, CA. Corvallis, OR: Oregon State University, Forest Research Laboratory; **1982:** 30-34.

Swanson, Frederick J.; Lienkaemper, George W.; Sedell, James R. History, physical effects, and management implications of large organic debris in western Oreaon streams. Gen. Tech. Rep. PNW-56. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1976.** 15 p.

Swift, M. **J.** The ecology of wood decomposition. Sci. Prog. Oxford. 64: 179-203; **1977a.**

Swift, M. **J.** The role of fungi and animals in the immobilization and release of nutrient elements from decomposing branch-wood. In: Lohm, U.; Persson, T., eds. Soil organisms as components of ecosystems. Ecol. Bull. 25. Stockholm: Swedish Natural Science Research Council; **1977b:** 193-202.

Swift, M. J.; Heal, O. W.; Anderson, J. M. Decomposition in terrestrial ecosystems. Berkeley, CA: University of California Press; **1979.** 84 p.

Tatter, T. A.; Shortle, W. C.; Rich, A. E. Sequence of microorganisms and changes in constituents associated with discoloration and decay of sugar maples infected with *Fomes connatus.* Phytopathology. 61: 556-558; **1971.**

Terry, Carol J. Habitat differentiation among three species of Sorex and *Neurotrichus* gibbsiin Washington. Am. Midl. Nat. 106: 119-125; **1981.**

Tevis, Lloyd, Jr. Stomach contents of chipmunks and mantled squirrels in northeastern California. J. Mammal. 34: 316-324; **1953.**

Todd, Allen W. Decomposition of selected soil organic matter components by Douglas-fir ectomycorrhizal associations. In: Abstracts of the 4th North American Conference on Mycorrhizae. Fort Collins, CO: Colorado State University; **1979.**

Toews, D. A. A.; Moore, M. K. The effects of streamside logging on large organic debris in Carnation Creek. Land Mange. Rep. 11. Victoria, BC: Province of British Columbia, Ministry of Forests; **1982.** 29 p. ISSN 0702-9861.

Trappe, James M. Fungus associates of ectotrophic mycorrhizae. Bot. Rev. 28: 538-606; **1962.**

Trappe, James M. Tuberculate mycorrhizae of Douglas-fir. For. Sci. 11: 27-32; **1965.**

Trappe, James M.; Maser, Chris. Germination of spores of *Glomus macrocarpus* (Endogonaceae) after passage through a rodent digestive tract. Mycologia. 68: 433-436; **1976.**

Trappe, James M.; Maser, Chris. Ectomycorrhizal fungi: interactions of mushrooms and truffles with beasts and trees. In: Walters, Tony, ed. Mushrooms and man, an interdisciplinary approach to mycology. Albany, OR: Linn-Benton Community College: **1978:** 163-179.

Triska, Frank J.; Cromack, Kermit, Jr. The role of wood debris in forests and streams. In: Forests: fresh perspectives from ecosystem analysis. Proceedings of the 40th Annual Biology Colloquium. Corvallis, OR: Oregon State University Press; **1980:** 171-190.

Triska, Frank J.; Sedell, James R.; Gregory, Stanley V. Coniferous forest streams. In: Edmonds, R. L., ed. Analysis of coniferous forest ecosystems in the Western United States. US/IBP Synth. Ser. 14. Stroudsburg, PA: Hutchinson Ross Publishing Company; **1982:** 292-332.

U.S. Congress, House. Report of Lt. Neil M. Howison, United States Navy, to the Commanderof the Pacific Squadron; being the result of an examination in the year 1846 of the coast, harbors, rivers, soil, productions, climate, and population of the Territory of Oregon, by Neil M. Howison. 39th Congress, 1st session, House Misc. Doc. 29; **1848.**

Ure, Douglas C.; Maser, Chris. Mycophagy of red-backed voles in Oregon and Washington. Can J. Zool. 60: 3307-3315; **1982.**

Veblen, Thomas T. Structured dynamics of *Nothofaqus* forests near timberline in south-central Chile. Ecology. 60: 937-945; **1979.**

Wallwork, J. A. Acari. In: Burges, A.; Raw, F., eds. Soil biology. New York: Academic Press: **1967:** 363-395.

Wallwork, J. **A.** The distribution and diversity of soil fauna. New York: Academic Press; **1976.** 355 p.

Wornock, A. J.; Fitter, A. H.; Usher, M. B. The influence of a springtail *Folsomia candida* (Insecta, Collembola) on the mycorrhizal association of leek *Allium porrum* and the vesicular-arbuscular mycorrhizal endophyte *Glomus fasciculatus* New Phytol. 90: 285-292; **1982.**

Weygoldt, Peter. The biology of **pseudoscorp**ions. Cambridge, MA: Harvard University Press; **1969.** 145 p.

Whitaker, John O., Jr.; Maser, Chris. Food habits of five western Oregon shrews. Northwest Sci. 50: 102-107; **1976.**

Whitaker, John O., Jr.; Maser, Chris; Keller, Laurel E. Food habits of bats of western Oregon. Northwest Sci. 51: 46-55; **1977.**

Whitaker, John O., Jr.; Maser, Chris; Pederson, Richard J. Food and ectoparasitic mites of Oregon moles. Northwest Sci. 53: 268-273; **1979.**

Williams, I. A. Drainage of farm lands in the Willamette and tributary valleys of Oregon. The mineral resources of Oregon. Salem, OR: Oregon Bureau of Mines and Geology; **1914;** 1: 3-81.

Zachariae, G. Zur Methodik **bei** gelandeuntersuchungen in der Bodenzoologie. Z. Pflanzenernaehr. Dung. Bodenkd. 97: 224-233; **1962.**

Zak, B. Characterization and classification of mycorrhizae of Douglas-fir. II: *Pseudotsuga menziesii + Rhizopogon vinicolor.* Can. J. Bot. 49: 1079-1084; **1971.**

Zak, Bratislav. Aphids feeding on mycorrhizae of Douglas-fir. For. Sci. 11: 410-411; **1965.**

Large, fallen trees in various stages of decay contribute much-needed diversity to terrestrial and aquatic habitats in western forests. When most biological activity in soil is limited by low moisture availability in summer, the fallen tree-soil interface offers a relatively cool, moist habitat for animals and a substrate for microbial and root activity. Intensified utilization and management can deprive future forests of large, fallen trees. The impact of this loss on habitat diversity and on long-term forest productivity must be determined because managers need sound information on which to base resource management decisions.