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The Seen and Unseen World of the Fallen Tree

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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

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Abstract

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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.

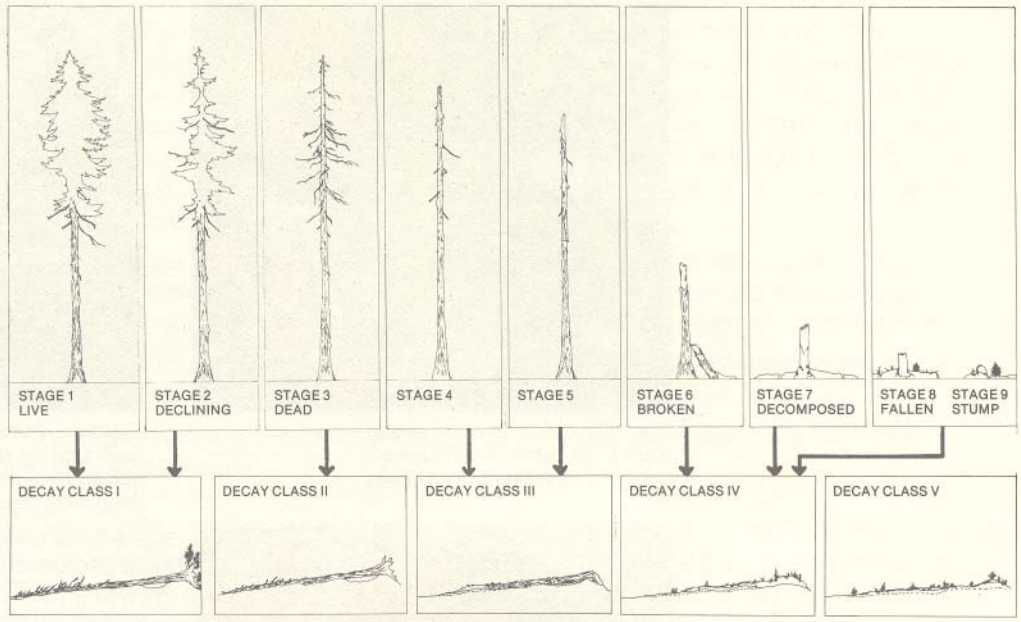
Figure 3.—Snags are also natural components of the unmanaged forest.

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).

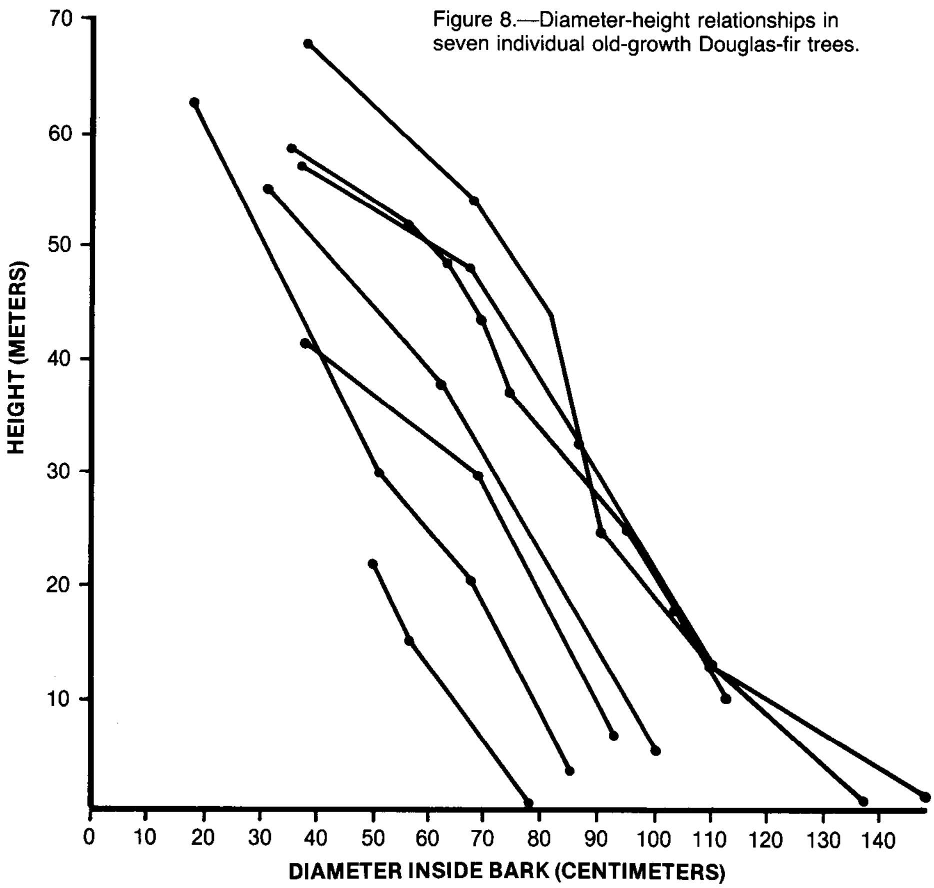


Figure 8.—Diameter-height relationships in seven individual old-growth Douglas-fir trees.

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.

[1] P. Sollins and S. P. Cline. Unpublished data on file at Oregon State University, School of Forestry, Department of Forest Science, Corvallis, Oregon 97331.

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.

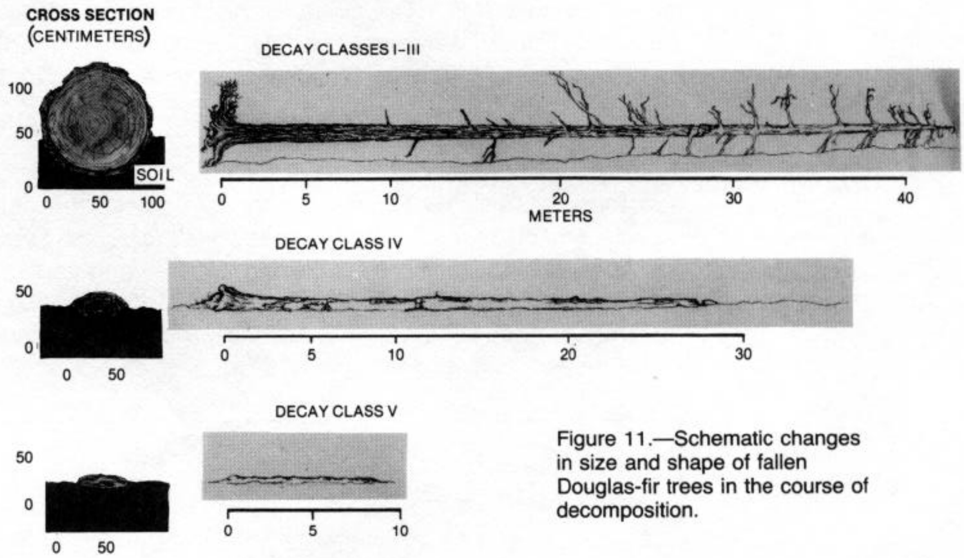


Figure 11.—Schematic changes in size and shape of fallen Douglas-fir trees in the course of decomposition.

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 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.

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.

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.

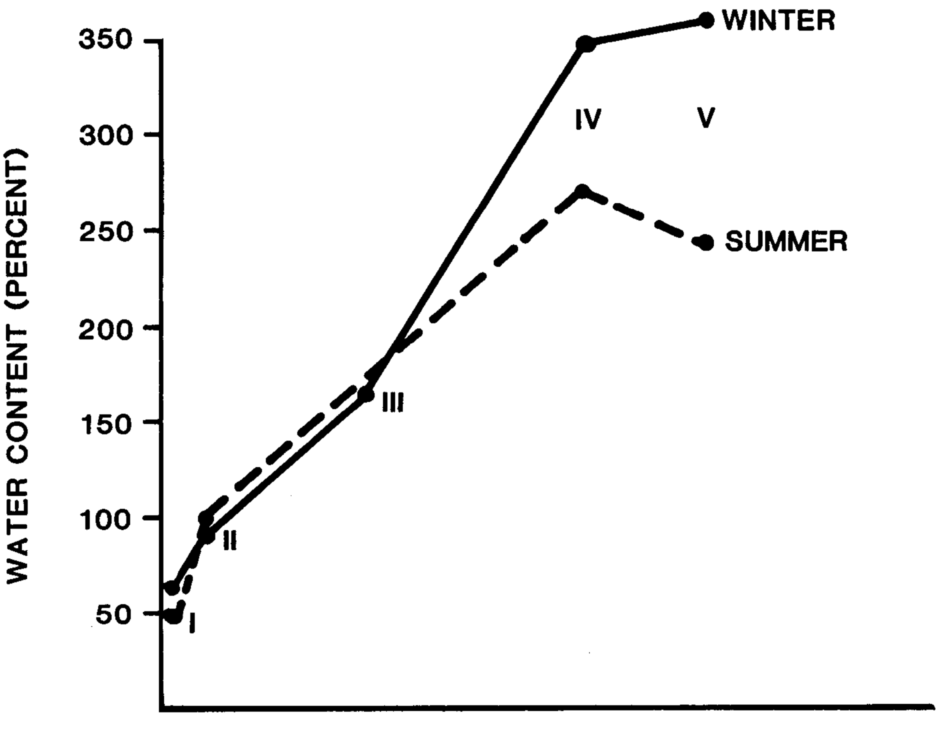


Figure 15.—Water content of fallen Douglas-fir trees in winter and summer; each point represents a decay class from I (newly fallen trees) to V (fallen trees decomposed to a mound of brown cubical rotted wood).

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).