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I. INTRODUCTION

Woody debris is an important, but often neglected component of many terrestrial and aquatic ecosystems. Coarse woody debris (CWD), primarily in the form of standing dead trees and downed boles and large

branches, is abundant in many natural forest and stream ecosystems, forming major structural features with many crucial ecological functions—as habitat for organisms, in energy flow and nutrient cycling, and by influencing soil and sediment transport and storage.

CWD includes a wide variety of types and sizes of materials. Types of CWD include snags, logs, chunks of wood (which result from disintegration of larger snags and logs), large branches, and coarse roots. The size used to define CWD has varied widely among studies, making exact comparisons difficult. Typical minimum diameters are 7.5–15 cm in western North American studies and 2.5–7.5 cm elsewhere. Some ecologists (e.g., Christensen, 1977) make no distinction between coarse and fine woody debris. For the purposes of this article, we consider CWD as being any woody material >2.5 cm in diameter, although many of the studies that we review consider only larger material.

A brief review of the roles of CWD highlights its importance. CWD is habitat for many species, including autotrophs and heterotrophs. "Nurse logs" are a widely recognized example of logs acting as habitat for autotrophs (Kirk, 1966). Indeed, in some environments, such as the rain forests of the Pacific Northwest, logs are the major site of tree seedling establishment (McKee *et al.*, 1982). Snags (also called standing dead trees) are used by many animal taxa, particularly birds; snags are of emerging concern in wildlife research and management (e.g., Davis *et al.*, 1983). In contrast, the use of logs by forest vertebrates has not been as widely appreciated (e.g., Maser *et al.*, 1979), nor has the dependence of some vertebrates, such as salamanders, on CWD (Maser and Trappe, 1984). Invertebrate use of and dependence on both snags and logs is well known to entomologists. Finally, many decomposer bacteria and fungi utilize CWD as an energy and nutrient source as well as a habitat (Frankland *et al.*, 1982; Swift, 1977a).

The importance of CWD in energy flow and nutrient cycles of ecosystems has not always been appreciated by ecologists. Low in nutrient concentration and slow to decompose, these materials are ignored in many ecological studies despite the large amounts of organic matter represented. Although CWD may be a nutrient sink in the short run, these materials can be a major long-term source of both energy and nutrients in many ecosystems (Larsen *et al.*, 1978; McFee and Stone, 1966; Triska and Cromack, 1980; Triska *et al.*, 1984). Furthermore, although intrinsically poor in nitrogen (Merrill and Cowling, 1966), nitrogen fixation in CWD is an important source of this limiting element in both terrestrial and aquatic ecosystems (Cornaby and Waide, 1973; Sharp and Milbank, 1973).

In stream and river systems, CWD has a major influence on geomorphic processes (Swanson et al., 1982a,b). Woody structures are critical in regulating sediment transport and storage. Debris accumulations in small and moderate-sized streams dissipate energy and store organic and inorganic sediment. In large streams and rivers, CWD provides a diverse array of habitats that significantly influence biological productivity (e.g., Franklin et al., 1982; Sedell and Frogatt, 1984; Sedell et al., 1982).

CWD is biologically important to the freshwater and estuarine ecosystems in which it occurs. In forested streams, CWD serves as an energy and nutrient source, a site for nitrogen fixation, and habitat for organisms (Triska et al., 1982). CWD influences the physical structure of forest streams, creating a variety of habitats—debris dams, plunge pools, and gravel and sandbars; as much as 50% of the habitat in small forested streams of the Pacific Northwest may be provided or controlled by CWD (Swanson and Lienkaemper, 1978). CWD is instrumental in retaining organic material, particularly forest litter, in small streams until it can be utilized by aquatic organisms (Bilby and Likens, 1980; Cummins, 1979).

Despite the role of CWD as habitat, an influence on geomorphic processes, and an integral component of energy flow and nutrient cycles, this material has often been ignored. Some of this "neglect" may have arisen because of the many problems associated with the study of CWD; it varies widely in space and time, which creates sampling difficulties, and is massive, making manipulative experiments difficult. The rate of CWD production is difficult to measure, requiring long periods of observation over large areas. Decomposition is slow and also requires long periods of time for investigation.

This article partially parallels the structure of a forest-ecosystem compartment model (Fig. 1). We emphasize CWD in temperate forest and stream ecosystems and include only selected references on CWD in tropical and boreal ecosystems for comparative purposes. In Section II, the rate at which CWD is added to ecosystems via tree mortality and breakage of stems and branches, as well as by physical transport from adjacent ecosystems, is considered. As soon as CWD is created, biological and physical processes begin to degrade it. Section III examines the processes involved in decay and decomposition rates of CWD. Of these, respiration and fragmentation have received most study, whereas leaching, burial, and physical transport have received least. In Section IV, we examine how rates of tree death and decomposition as well as disturbances to forests control the amounts of CWD in temperate ecosystems. The functional importance of CWD depends not only on the amount of CWD, but also on its distribution in terms of size, spatial arrangement, degree of
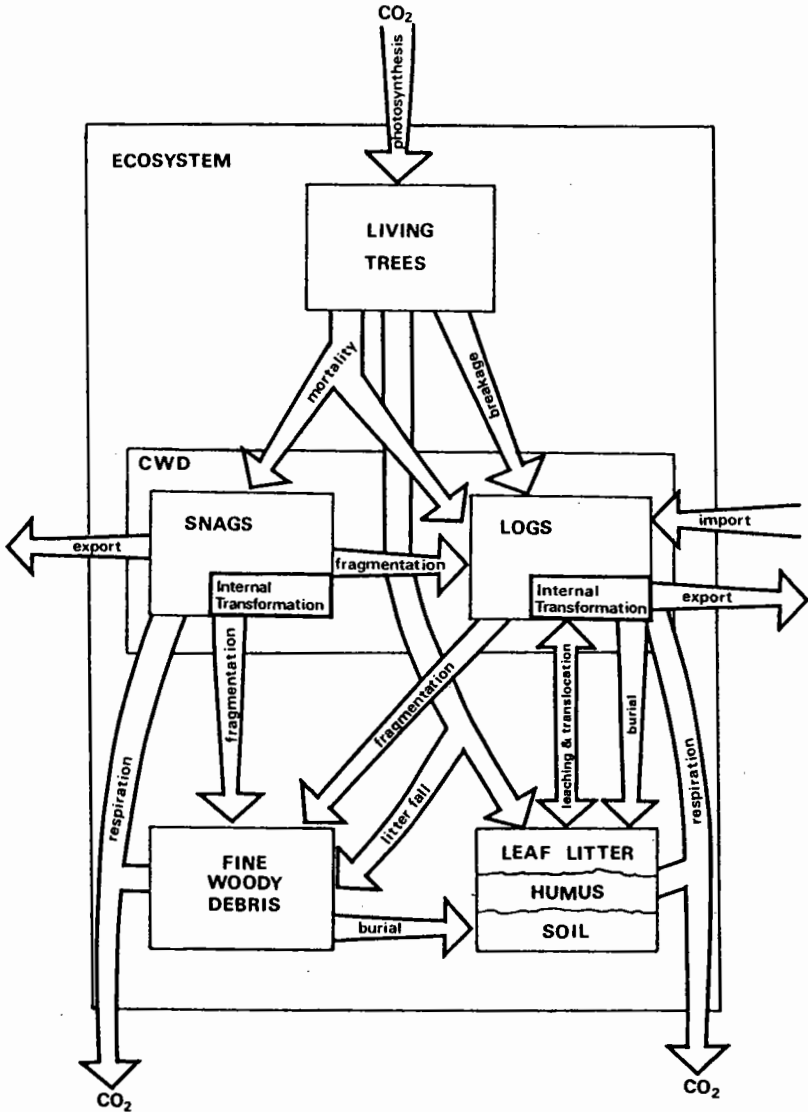
Fig. 1. The flow of CWD into, within, and from an ecosystem. Physical transport (e.g., floods) adds CWD to an ecosystem, while respiration and physical transport are the major pathways of loss from an ecosystem. Within an ecosystem, CWD is added from live trees by mortality and breakage. Fragmentation and, to a far lesser extent, burial and leaching are the most important losses from CWD and result in a transfer of material to the fine woody debris and soil compartments. Fragmentation of snags also changes the form of CWD from the standing position to downed logs and large chunks of wood. Finally, numerous internal decay processes transform woody material within the snag and log compartments.

decay, species, and position (i.e., snags versus logs). In Section V, we focus on the influence that CWD exerts on organisms and processes within ecosystems, as a plant, vertebrate, and invertebrate habitat, as well as its role in nutrient cycles and in controlling geomorphic processes. The ecological behavior and significance of CWD varies markedly between aquatic and terrestrial environments and between managed and "natural" lands. The article concludes with a comparison of these environments.

II. INPUT OF COARSE WOODY DEBRIS

Addition or input of CWD can be considered on three levels of the ecosystem hierarchy shown in Fig. 1. However, whether these processes are considered inputs or transformations depends upon the level of the hierarchy being examined. When only logs are considered, snag fragmentation is an input to logs. On the other hand, if both snags and logs are considered, then snag fragmentation is a transformation from one form of CWD to another. Similarly, tree death and breakage is an input when only CWD is considered, but is a transformation when the entire forest is examined. Finally, CWD can be moved from one part of a watershed to another, and this process may also be viewed as an input. The movement of CWD to streams from the surrounding forests is an example.

In this section, we consider the input of CWD on two levels. In forest studies, the transfer of living to dead wood is considered an input to the CWD components. In studies of streams, the transfer of CWD and living trees from streamside forests to the stream channel has also been considered an input, but obviously on a different level than in forest studies.

A. Methods

The simplest and most direct method to assess the input of CWD from living trees is to determine tree mortality within permanently marked plots or of tagged trees (Franklin *et al.*, 1984; Grier, 1978; Harcombe, 1984; Harcombe and Marks, 1983; Harris *et al.*, 1973; MacMillan, 1981; Sollins, 1982). However, this technique alone underestimates input to CWD because large branches and broken tops of boles are not included.

Input to CWD can be measured on cleared plots. This method has been used most commonly in studying input of fine woody debris such as branches, but it is occasionally used for CWD as well (e.g., Gentry and Whitford, 1982). For large material, it is more practical to mark or map the pieces present at the start of the observation period than to remove them (Gosz *et al.*, 1972; Swanson and Lienkaemper, 1978). Modern forest-management practices that remove all or most CWD may be potential

study areas. Instead of using plots, Tritton (1980) measured the input rate of logs along line transects on which the original CWD had been removed.

These methods are designed primarily to provide estimates of input in intact stands. Stand reconstructions (Henry and Swan, 1974; Oliver and Stephens, 1977) can be used to assess input from catastrophes such as wildfires, windstorms, floods, avalanches, and insect epidemics that kill complete or major portions of stands.

B. Rates of Input

Measured input rates of CWD in forest ecosystems range from 0.12 to 30 Mg ha^{-1} year^{-1} (Table 1). Input rate varies primarily with the productivity and massiveness of the trees in the ecosystem, although disturbances during the observation period can increase overall rates markedly (e.g., Wright and Lauterbach, 1958). Factors influencing measurement of input rate are the size used to define CWD, the length of the study, and the area observed. Generally, precision of measurement improves with increasing the length of the study and the size of the sample area.

Smallest input rates were observed in a scrub *Quercus nigra* stand (Gentry and Whitford, 1982) and the largest in undisturbed, old-growth

Table 1

Aboveground Input of Coarse Woody Debris for Various Temperate Ecosystems

Ecosystem	Location	Sample period (year)	Sample area (ha)	Biomass input (Mg ha^{-1} year^{-1})	References[a]
Coniferous forests					
Abies amabilis (second growth)	Washington	5	0.13	0.3	14
Picea engelmanii–Abies lasiocarpa	Colorado	11	12.8	0.18	2
Picea rubens–Abies balsamea	Maine	20	—[b]	1.45[c]	7
Picea sitchensis–Tsuga heterophylla	Oregon	40	0.4	2.8	12
Picea sitchensis–Tsuga heterophylla	Oregon	43	4.5	3.11	20
Picea sitchensis–Tsuga heterophylla	Washington	6	4	4.1	15
Picea abies–Carpinus betulus	Poland	10	1	~1.6[c]	6
Pinus banksiana	Minnesota	30	—	~2.3[c]	17

Table 1 (continued)

Ecosystem	Location	Sample period (year)	Sample area (ha)	Biomass input (Mg ha⁻¹ year⁻¹)	References[a]
Pinus contorta	Colorado	12	8	0.17[c]	1
Pinus palustris	Georgia	1	0.2	0.79	8
Pinus ponderosa	Arizona	50	15.8	0.25	3
Pinus strobus– *Acer saccharum*	Minnesota	26	0.48	1.1[d]	19
Pinus echinata– *Pinus virginiana*	Tennessee	5	3.52	1.9	16
Pseudotsuga menziesii (old)	Oregon	2	10.2	7.0	13
Pseudotsuga menziesii (old)	Washington	29	41.6	4.54	20
Pseudotsuga menziesii (mature)	Oregon	10	80–265	0.5–30	23
Pseudotsuga menziesii (mature)	Oregon and Washington	16–46	0.2–2.8	1.55–4.25	20
Pseudotsuga–Abies–Picea	Arizona	5	—	~3.8[c]	11
Deciduous forests					
Acer saccharum	Michigan	9	6.3	0.42[c]	5
Acer saccharum	Michigan	12	4	0.35–0.54[c]	5
Acer saccharum	Michigan	6	16	0.56[c]	5
Acer–Betula–Fagus	New Hampshire	2	—	0–14.5	22
Fagus–Acer–Betula	New Hampshire	1	13.2	1.0	10
Liriodendron tulipifera	Tennessee	4	0.15	1.18	16
Liriodendron tulipifera	Tennessee	8	0.04	1.1	21
Populus tremuloides	New Mexico	5	3.4	0.45	9
Quercus–Carya	Tennessee	4	2.56	1.18	16
Quercus nigra	Georgia	1	0.2	0.12	8
Quercus prinus	Tennessee	4	2.88	0.55	16
Quercus robur	Denmark	2	—	0.77	4
Quercus mixed	Indiana	20	3.35	~0.64[f]	18
Quercus–Liquidambar– *Liriodendron*	Georgia	1	0.2	2.87	8

[a](1) Alexander (1954), (2) Alexander (1956), (3) Avery *et al.* (1976), (4) Christensen (1977), (5) Eyre and Longwood (1951), (6) Falinski (1978), (7) Frank and Blum (1978), (8) Gentry and Whitford (1982), (9) Gosz (1980), (10) Gosz *et al.* (1972), (11) Gottfried (1978), (12) Grier (1978), (13) Grier and Logan (1977), (14) Grier *et al.* (1981), (15) Harmon (unpublished), (16) Harris *et al.* (1973), (17) Jensen and Zasada (1977), (18) MacMillan (1981), (19) Peet (1984), (20) Sollins (1982), (21) Sollins *et al.* (1973), (22) Tritton (1980), (23) Wright and Lauterbach (1958).
[b]Not available.
[c]Assumes density of 0.4 Mg m⁻³.
[d]Converted data from Fig. 1 to biomass using equations in Ker (1980) and Tritton and Hornbeck (1982).
[e]Assumes wood density of 0.6 Mg m⁻³.
[f]Based on addition of 2.52 trees ha⁻¹ year⁻¹ with a mean volume of 0.44 m³ and a density of 0.58 Mg m⁻³.

coniferous stands in northwestern North America. Generally, deciduous forests appear to produce less CWD than conifer forests, although some undisturbed conifer forests such as *Pinus contorta* (Alexander, 1954) and *Pinus ponderosa* (Avery *et al.,* 1976) also have low rates of input.

Rates of CWD input to streams have been measured directly in only a few cases, all in western North America and over periods of <9 years. Lienkaemper (unpublished) monitored CWD input for 8 years for five streams ranging in size from first to fifth order in the H. J. Andrews Experimental Forest in Oregon. Input rates averaged 5.2 Mg ha^{-1} year^{-1} and ranged from 2.0 to 8.8 Mg ha^{-1} year^{-1}, which is similar to old-growth forests for this region. However, there are situations where the input rate to streams may be larger or smaller than the transfer of live to dead wood found in old-growth forests. Earthflows and other mass-movement processes may import CWD to stream channels at rates that greatly exceed the normal transfer rate of living trees to CWD found in forests. When stream channels are wider than the canopy height, input to streams may be smaller than the transfer of living to dead wood found in adjacent forests.

All of the data reported on input of CWD, whether for forests or streams, are based on short observation periods. Although a decade is long in terms of the life of most research programs, it represents only a fraction of the turnover time for CWD and, given the episodic nature of much tree mortality, such data must be viewed conservatively.

C. Spatial Patterns

The input of CWD varies spatially on a number of scales. Within a stand, mortality may be aggregated or distributed randomly or regularly (see Pielou, 1977, for discussion of terms). On this scale, it is also of interest to consider the orientation (direction) and interrelationships of the pieces. Moving to a larger scale of a watershed, it is important to consider the relationship between source areas and zones of deposition. This is very important when considering input to streams from forests, because the area of initial input does not always correspond to the final resting site. Finally, variations in input on the regional scale may be considered. This perspective is important because the cause as well as the rate of input is apt to change from region to region.

1. Patterns within Stands

Although comprehensive studies of the spatial pattern of CWD input are lacking, input is probably not distributed randomly over a forest stand or stream reach. Many causes of mortality, such as windthrow, insects,

and diseases, affect patches of trees and exhibit highly contagious spatial patterns (aggregated or clumped). Therefore, CWD generated by these agents can be expected to be aggregated. Wind often uproots several nearby trees, for example. Other examples of patches of mortality include *Phellinus weirii* root rot centers (McCauley and Cook, 1980) and fir waves observed in the northeastern United States (Sprugel, 1976). Inputs of CWD due to suppression mortality are likely to be among the most evenly or regularly distributed.

2. Patterns within Watersheds

Considerable redistribution of CWD can occur on steep slopes or in streams and rivers. Substantial transfers of CWD can also be associated with catastrophic events, such as mass soil movements, floods, snow avalanches, and volcanic eruptions.

No published data exist on the effect of slope position and steepness on input and accumulation of CWD within ecosystems. Stands located on steep slopes should tend to lose material to downslope areas and accumulate CWD from upslope areas. Stands lacking source areas for CWD (upper slope or ridgetop positions or stands with nonforested areas upslope) should tend to have low accumulations because of the net downslope movement of CWD. Conversely, stands on lower slopes retain as well as receive CWD from upslope stands and therefore have high accumulations.

The source area of CWD input to streams extends substantial distances from stream channels in mountainous areas. In third-order streams flowing through old-growth *Pseudotsuga menziesii* forests, CWD pieces came from as far as 45 m from the channel; median distances of movement were ~15 m (M. H. McDade, unpublished). The probability that a falling tree or snag will be added to a stream was found to be inversely related to the distance between the channel and the site of CWD origin. Assuming uniform tree height and a random orientation of falling, those trees or snags closest to streams are most likely to contribute CWD to the channel. Stands with shorter trees would be expected to have a narrower source area of CWD for streams, while those with taller trees would contribute from a greater distance.

3. Regional Patterns

Patterns of tree mortality vary regionally because the relative importance of catastrophic and noncatastrophic agents varies widely with forest type (White, 1979). In northwestern North America, the importance of mortality agents varies along a transect from the Pacific Ocean across the Coast and Cascade Ranges into more continental regions (Franklin *et al.*,
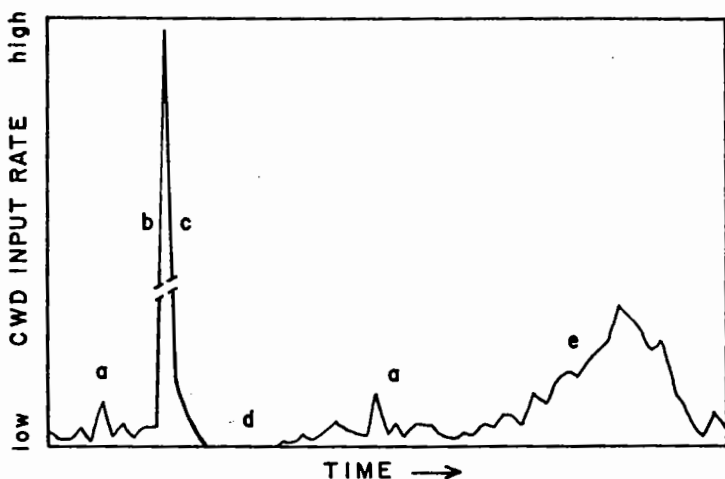
M. E. HARMON *ET AL.*

Fig. 2. The hypothetical types of changes in CWD input rate over time. (a) Represents minor annual fluctuation of the input rate (10^{-1} to 10^1 Mg ha^{-1} year^{-1}) around a long-term mean. (b) A large, rapid, but temporary increase in CWD input rate caused by a sudden, catastrophic disturbance that adds 10^2 to 10^3 Mg ha^{-1} during a few years. (c) Declining input rate as injured trees continue to die for a period after the disturbance. (d) Initial lack of input and then increase in input rate to long-term mean during the course of forest succession. (e) Gradual increase of CWD input rate associated with a gradually increasing disturbance (such as a pathogen).

1984). In coastal *Picea sitchensis–Tsuga heterophylla* forests, wind-related mortality provides 70% of the stem input (Greene, 1984). Forests of *P. menziesii–T. heterophylla* in the Cascade Range have 17–47% of the stems killed by wind-related injuries. Insects and diseases are rated as proximate causes of death for less than 1% of the stems in these two environments. In Rocky Mountain *P. ponderosa* (Avery *et al.*, 1976) and mixed-conifer forests (Gottfried, 1978), wind-related death amounted to only 18 and 17% of the stems added, respectively. Insects and diseases accounted for 40% of the stems killed in the *P. ponderosa* stand (Avery *et al.*, 1976). Most CWD input in Rocky Mountain forests is as snags; most CWD in the coastal and Cascade forests is as logs.

D. Temporal Patterns

Important temporal variations in CWD input are associated with seasonal, annual, and successional time scales (Fig. 2). The variation within each of these scales is probably large. A clearer understanding of variation associated with annual and successional time scales will be required

before comprehensive comparisons of CWD input rates for various eco-system types can be made.

1. Seasonal

The few studies that document seasonal patterns of CWD input show wide variation between seasons. A 16-month study of seasonal input patterns in three forest types in Georgia showed a peak in late summer and fall for *Pinus* and *Liriodendron* stands that was caused by hurricane winds (Gentry and Whitford, 1982); in a *Q. nigra* stand in the same area, however, there was little consistent variation from season to season.

In a tropical forest in Panama, there was a distinctive seasonal cycle of tree falls, with a maximum in August to September and a minimum in December to March (Brokaw, 1982). The maximum rate of treefall corresponded to the middle of the wet season. Other agents of mortality that can cause seasonal variations in input rate include snow and ice, fire, insects, and floods.

2. Annual

Annual variation in input of CWD can be very large, even excluding catastrophic events that destroy the whole stand. Again, data are very limited because few studies of mortality have involved yearly observations. Annual studies are in progress in several localities, however (Franklin et al., 1984; Harcombe and Marks, 1983), and suggest low background levels of input, with occasional spikes of mortality associated with a specific event, such as a windstorm (Harcombe, 1984) or a bark beetle epidemic (Wright and Lauterbach, 1958). In a 180-year-old *P. menziesii* stand in coastal Oregon, input reached 69.8 m^3 ha^{-1} $year^{-1}$ (30 Mg ha^{-1} $year^{-1}$) during a bark beetle epidemic, with an average input of 39.2 m^3 ha^{-1} $year^{-1}$ (17 Mg ha^{-1} $year^{-1}$) over a 10-year period (Wright and Lauterbach, 1958). However, prior to the epidemic, the rate of input averaged ~0.5 Mg ha^{-1} $year^{-1}$.

3. Long Term

The amount and type (i.e., snags versus logs) of CWD input change with succession (see also Section IV,C). Many years may be required for the new stand to become fully stocked with trees and to grow boles large enough to exceed the minimum CWD size limit. These two factors markedly reduce the input rate of CWD for many years following catastrophic disturbance. The input rate and average size of pieces added to CWD generally increase with succession. However, the development of a reverse "J"-shaped size structure in older forests may cause a reduction in the size of pieces and the input rate. The type of CWD added, either as

snags or logs, and the decomposability of this material also change with succession. In young stands, suppression is a major cause of mortality and many pieces are therefore added as snags. In contrast, wind-related mortality is probably more important in older forests, shifting input to fallen boles and broken branches.

Tritton's (1980) study of succession in northern hardwood forests following clear-cutting illustrates these patterns. No CWD was input to the 10-year-old stand during the 2 years of observation. CWD accrued at a rate of 0.4 Mg ha^{-1} year^{-1} in a 20-year-old stand, and this rate increased 10-fold over the next 20 years to 4.1 Mg ha^{-1} year^{-1} in a 40-year-old stand. In stands older than 40 years, the input rate of CWD varied considerably from a minimum of 1.3 Mg ha^{-1} year^{-1} at 60 years to a maximum of 14.5 Mg ha^{-1} year^{-1} in old-growth forests. These variations may have been due, in part, to the relatively small plots and short observation period. However, as Tritton (1980) points out, the peak at 30–40 years is due to the death of large numbers of *Prunus pensylvanica,* an early successional species with a short life span. The form of input also varied with succession. During the period between 30 and 40 years, snags comprised 78–87% of the CWD input, but at other times, snags comprised <61% of the input. The peak in snag production observed by Tritton (1980) reflects the senescence of *P. pensylvanica.*

E. Agents of Mortality

1. Wind

Wind is an agent of mortality throughout temperate forests, generating CWD by uprooting and snapping trees and breaking branches. Trees may also be crushed and broken by pieces generated by wind.

Catastrophic windstorms, common in many temperate and tropical regions (White, 1979), result in very large inputs of CWD at irregular intervals. Effects of hurricanes have been studied in New England (Henry and Swan, 1974; Stephens, 1955) as well as in other locales in eastern North America (e.g., Reiners and Reiners, 1965) and the Carribean (e.g., Wadsworth and Englerth, 1959). Holtam (1971) describes extensive wind damage in forests of Scotland. Typhoons are characteristic of eastern Asia; the Japanese Forestry Agency (1955) describes loss of around 5 × 10^6 m^3 of growing stock in the Ishikari River region of Hokkaido in two typhoons in 1954. A severe windstorm on October 12, 1962 blew down an estimated 2.6 × 10^7 m^3 of timber in northwestern North America (Orr, 1963).

Wind also creates CWD on a much smaller scale by killing single or small clusters of trees. Chronic wind-caused mortality in many temperate

forests has been reported (e.g., Falinski, 1978; Gentry and Whitford, 1982; Grier, 1978; Harcombe and Marks, 1983; Sollins, 1982). The importance of wind as an agent of mortality varies among forest types; for example, in northwestern North America, wind kills 70% of the stems in coastal *P. sitchensis–T. heterophylla* forests (Greene, 1984), but only 15–20% of the stems in interior *P. ponderosa* forests (Avery *et al.*, 1976). However, in other interior forests, such as *P. contorta* forests of Colorado, wind can cause up to 70% of the stem mortality (Alexander, 1954). The importance of wind also varies considerably within deciduous forests. Eyre and Longwood (1951) observed that wind-related mortality produced 87% of the CWD volume added to an *Acer saccharum* forest in Michigan. In a *Fagus–Magnolia* forest in Texas, wind accounted for 10% of tree death over a 5-year period (Harcombe and Marks, 1983). In part, these differences are related to differences in the variables measured: Eyre and Longwood (1951) considered volume, while Harcombe and Marks (1983) considered number of stems. The latter study found larger trees were more prone to windthrow, indicating more than 10% of the volume was input by wind.

The importance of wind also varies with topographic and edaphic conditions (Alexander, 1954; Gratkowski, 1956; Ruth and Yoder, 1953). Trees growing on wet sites are generally more susceptible to windthrow than those on dry sites because of shallow rooting. Rooting can also be shallow on drier ridgetop sites because of shallow, rocky soils, increasing the chances of windthrow, although consistent wind exposure on ridges may produce more windfirm trees (Gratkowski, 1956). Topographic position and valley configuration can also affect the chances of windthrow. For example, trees growing in saddles of main ridges or in areas of valleys that are constricted have a high probability of wind damage (Gratkowski, 1956). Heavy mortality has been observed on lee slopes with moderate slope gradient during strong windstorms (Ruth and Yoder, 1953).

Species also differ in wind firmness, although these patterns tend to be confounded with size, age, habitat, and position within a stand. Species with open-grown crowns appear to be less prone to wind damage than those with dense crowns (Boyce, 1929; Curtis, 1943; Gratkowski, 1956). The strength properties of wood are also related to susceptibility to wind breakage (Putz *et al.*, 1983). Root and heart rot structurally weaken trees and predispose them to wind damage.

2. Fire

Trees are killed directly by fire by stem girdling, scorching of crowns, and burning of root systems. In addition, fire indirectly contributes to other causes of mortality. By causing basal wounds, fire allows decay

organisms to weaken the stem, contributing to windthrow. Survivors of severe fires experience greater exposure to winds than in the original stand and may have an increased risk of wind damage. Removal of part of the crown or phloem by heat weakens trees and makes them susceptible to insect attack. Healthy trees can also be killed by insects that came from adjacent fire-killed trees (Furniss, 1936).

The amount of mortality caused by fire depends on the type of fire (i.e., ground, surface, and crown) and its intensity, as well as the species and size structure of the forest. Species vary in their tolerance to fire (Starker, 1934). However, this tolerance changes with tree size. Increasing fire intensity increases the size of the trees killed by fire (Van Wagner, 1973). The frequency and average intensity of fires varies between regions and forest types. Such differences, recently considered by Mooney *et al.* (1981) and Wright and Bailey (1982), are beyond the scope of this article.

Although fire is typically less frequent as a cause of mortality than wind, insects, and competition, it is important over the long term; the input from a single fire can be equivalent to centuries of "normal" input. For example, normal input of CWD in the Pacific Northwest ranges from 1 to 5 Mg ha^{-1} year^{-1} (Sollins, 1982). In contrast, biomass of living tree stems may range from 447 to 892 Mg ha^{-1} (Grier and Logan, 1977), and if this is the assumed range of fire-caused input, then between 105 and 575 years of "normal" input could be added by a single intense fire.

3. Insects

Snags are input when insects kill trees. Coleoptera (beetles) larvae and adults kill trees by girdling the phloem. In the case of angiosperms, repeated defoliation is required to cause mortality (Churchill *et al.*, 1964). Even in the case of gymnosperms, repeated and rather complete defoliation must occur before mortality is assured (Wickman, 1978). An initial attack by defoliators may weaken a tree and allow a successful attack by a secondary insect, often a bark beetle (McMullen *et al.*, 1981; Wickman, 1978). Insects also cause mortality when they introduce pathogens, as in the case of Dutch elm disease [*Ceratocystis ulmi* (Buisman) C. Moreau] being spread by *Scolytus multistriatus* (Marsham). Although sucking insects usually do not cause mortality, some such as the balsam woolly aphid [*Adelges picea* (Ratz)] may alter the host tree's anatomy to the point of causing death (Balch *et al.*, 1964).

Insects periodically reach epidemic proportions and may add a large amount of CWD over an extensive area. Outbreaks covering areas up to 1.9×10^7 ha have been observed in western North America (Furniss and Carolin, 1977). Various causes of outbreaks have been proposed. In the case of bark beetles, stress induced by drought, flooding, excessive com-

petition, and mechanical damage reduces the ability of host trees to repel attacking insects (Berryman, 1982; Larsson *et al.*, 1983; Mitchell *et al.*, 1983).

4. Diseases

There are an exceedingly large number of biotic diseases that generate CWD within forests and most cannot be discussed here (see Hepting, 1971, for an extensive listing of North American diseases). The majority are caused by fungi, although parasitic vascular plants, e.g., *Arceuthobium* spp., also cause disease. In many ecosystems, diseases generate small amounts of CWD and are a contributing factor to wind and insect-caused mortality. However, diseases—especially those newly introduced to a host—may generate large amounts of CWD over extensive areas. *Endothia parasitica*, which virtually eliminated its host, *Castanea dentata*, from the eastern United States between 1904 and 1935, is a dramatic case in point (Beattie and Diller, 1954). Other examples of newly introduced biotic diseases that are greatly increasing the rate of CWD generation in forests include Dutch elm disease, beech bark disease, white pine blister rust, and *Phytophthora lateralis* Tucker and J. Milb., which is currently decimating *Chamaecyparis lawsoniana*. Abiotic diseases caused by industrial and other forms of pollution may also generate considerable amounts of CWD (Tomlinson, 1983). An example is the recent decline in *Picea rubens* noted in the northeastern United States (Scott *et al.*, 1984; Siccama *et al.*, 1982), which may be related to acid deposition.

5. Suppression and Competition

Suppression mortality is defined as the death of trees because of slow growth caused by competition. Suppressed trees die standing and often exhibit slow radial or height growth and often lack apical dominance. The smaller trees in a stand often die from suppression (Harper, 1977). Low vigor may predispose trees to fatal attack by insects and pathogens; it is difficult to determine, for instance, whether bark beetles attacked a tree after the tree's death or killed a weakened one.

Suppression mortality occurs in stands of all ages, but probably is most important as a source of CWD during succession in mature forests with closed canopies because of the combination of high competitive stress coupled with large tree size. Forest managers have used the $-\frac{3}{2}$ power model (Yoda *et al.*, 1963) and yield tables to estimate suppression mortality. Statistical models also exist relating the probability of survival to relative diameter, crown class, crown ratio, growth rate, or other indices of tree vigor (Monserud, 1976). These models have generally not been applied to natural stands.

6. *Agents Adding Coarse Woody Debris to Streams*

All agents creating CWD discussed above apply to aquatic as well as terrestrial ecosystems. Three additional processes add CWD to streams and rivers: stream and river undercutting of banks, mass movement of soil on hillslopes, and transport by floods. Slow mass-movement processes, such as soil creep, slumping, and earthflows on hillslopes, add CWD to the stream by moving forests toward streams and tipping trees into the channel. Very rapid mass movements, such as landslides, debris flows, and snow avalanches, produce CWD by knocking over and uprooting trees and then depositing them into stream channels. Deposition of soil and physical damage to live trees by these processes can also lead to mortality. Flooding and movement of ice add CWD to streams by tearing trees from the bank. Floods also remove CWD from floodplains, adding it to stream ecosystems. Bank undercutting is a very important process that adds material along most forested reaches; it is particularly significant along meandering rivers with high rates of lateral migration.

Generalizations about the relative importance of mechanisms have been made for particular landscapes and ecosystems by Keller and Swanson (1979) (Fig. 3). At sites of earthflows and tributary streams that have frequent debris-torrent activity, CWD is added to streams at a very high rate. There are no reports quantifying the relative importance of mechanisms by which CWD is delivered to streams and rivers, but several studies suggest major differences exist between landscapes. In Soguel Creek, California, mass movement from heavily forested areas adjacent to hillslopes is the most important source of large trees for streams (Singer and Swanson, 1983). In 7 years of observation along 520 m of third-order streams flowing through old-growth *P. menziesii* in Oregon, undercutting may have contributed 25% of the trees added (Lienkaemper, unpublished). Bank undercutting and CWD entrainment during floods adds much of the CWD in sandbed channels where lateral migration is rapid, such as the Little Missouri River (Everitt, 1968).

III. DECOMPOSITION OF COARSE WOODY DEBRIS

The following section considers the many ways CWD is decomposed in ecosystems, the rates at which these processes have been observed to operate, and, finally, the factors that control these rates.

SNOW AVALANCHE

SLIDING DOWN ADJACENT HILLSLOPES

BLOWDOWN ◄───

BANKCUTTING ───►

TRANSPORT FROM UPSTREAM ───►

DEBRIS TORRENT FROM TRIBUTARY

DEBRIS AVALANCHE, STREAMSIDE SLIDES

EARTHFLOWS INTO CHANNEL

| 0.1 | 0.3 | 1 | 3 | 10 | 30 | 100 | 300 |

DISTANCE FROM HEADWATER (km)

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |

STREAM ORDER
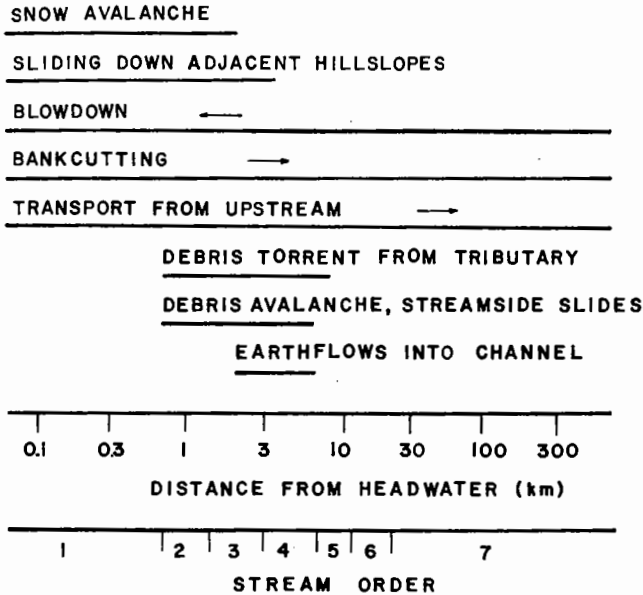
Fig. 3. Stream distribution of input–output processes associated with organic debris in the Lookout Creek–McKenzie River System, Oregon. Arrows indicate direction of increasing importance. From Keller and Swanson (1979). Reprinted by permission of John Wiley & Sons, Ltd.

A. Types of Decay Processes

1. Leaching

Water percolating through CWD dissolves some materials and results in a weight loss. Leaching is a very important process in the loss of mass from decomposing leaf litter in terrestrial (Singh and Gutpka, 1977; Swift *et al.*, 1979) and aquatic ecosystems (Petersen and Cummins, 1974) as well as from living plants (Tukey, 1970). However, little work has been published on leaching losses from CWD (Matson and Swank, 1984). Leaching is probably of minor importance initially, largely because CWD is high in polymeric material and low in soluble substances. As microbes transform these polymers to soluble material, leaching may increase. Another consideration is the low surface-to-volume ratio of CWD, which may reduce leaching losses relative to that found in leaf litter. Fragmentation may increase the importance of leaching as a loss of CWD because it increases the surface-to-volume ratio.

2. Fragmentation

Fragmentation or communition of CWD takes many forms. Physical fragmentation, caused by gravity and flowing water, is accelerated by decay organisms that weaken wood and bark. In terrestrial ecosystems, the fragmentation of snags creates a range of sizes from entire logs to chunks to finer woody debris. The latter two size classes may fall directly from snags or may be created when extremely decayed snags hit the forest floor and shatter into many fine particles. The range in particle size created by log fragmentation is probably smaller. Perhaps the smallest particles are created by the abrasion of the decayed surface layers of logs in streams by flowing water. Separation of individual wood cells (i.e., tracheids) occurs to a minor extent in terrestrial systems where tracheids are washed off the upper portions of sun-exposed logs.

Given the slow rates of microbial decay in streams, one would expect that CWD would remain longer in aquatic than in terrestrial environments. However, erosion of decayed wood surfaces by flowing water accelerates the overall rate of CWD loss in streams (Aumen, 1985). Of the five major decay classes used to classify wood debris in the Pacific Northwest (see Section IV,A), only the three least decayed stages are commonly found in streams (Triska and Cromack, 1980). CWD in the two most decayed stages appears to be fragmented and transported by flowing water and rarely accumulates. The erosive effects of current are probably more pronounced in larger streams than in small headwater tributaries.

Biological fragmentation of CWD is caused by both plants and animals, with invertebrates probably the most important. By chewing, ingesting, and excavating, invertebrates create a dust that decays more rapidly than the original CWD because of increased surface-to-volume ratio. Depending on the species, invertebrates may either transport these particles from the log or snag or leave them inside. The galleries made by invertebrates allow microbes to colonize CWD more rapidly (Ausmus, 1977; Leach *et al.*, 1934, 1937). Invertebrates such as bark and ambrosia beetles may actively bring microbe symbionts into CWD. Invertebrates in CWD are an important food source for vertebrates, such as bears and birds, that fragment the material while foraging. By growing on CWD and then subsequently falling off, trees and shrubs can cause CWD to fragment (see Section V,A). Finally, when trees and snags fall over, they often fragment CWD by knocking over other snags or crushing parts of logs.

Material exported from CWD as fragments has important influences on other ecosystem components. Fragmentation may be a large source of fine-particulate organic matter in stream sediments. Addition of ground bark and heartwood of *Alnus* and *Pseudotsuga* to muddy sediments in a

small stream in Oregon increased rates of respiration and methane production, with *Alnus* wood causing the greatest increase (Baker *et al.*, 1983). Rates of nitrogen fixation associated with the sediments were unaffected by increases of ground bark and wood, except that *Alnus* wood enhanced nitrogen fixation. Sugars with low molecular weight were identified by Baker *et al.* (1983) as a possible factor in the stimulation of nitrogen fixation in *Alnus* wood.

3. Transport

Transport rates of CWD within stream channels appear to be larger than those of terrestrial ecosystems, although there are no published studies that quantify the role of transport in either type of ecosystem. The transport of CWD in stream systems is a function of stream size; the wider the stream relative to a log's length, the more likely the log will be moved (see Section V,D). Trees, large rocks, and other pieces of CWD anchor logs and reduce movement within stream channels. Trees and rock outcrops are also probably important in reducing downslope movement of CWD on steep hillslopes.

4. Collapse and Settling

As decay proceeds and structural strength declines (Hartley, 1958; Toole, 1969), logs are unable to support their own weight and settle to the ground. Sollins (1982) found settling coincided with structural weakening of the heartwood to the point that branch stubs can be pulled from logs by hand. Settling increases the degree of contact between soil and log and changes the suitability of CWD as microbial, vertebrate, and invertebrate habitat (Maser and Trappe, 1984). During settling, the cross-sectional profile of logs changes from circular to elliptical and the contact between soil and log increases.

5. Seasoning

As CWD ages in dry environments, it undergoes a series of changes known as seasoning (Panshin and deZeeuw, 1980). This comprises a decrease in moisture, shrinkage, and formation of checks or cracks that increase access to microbes. Case hardening is a form of seasoning in which the outer rind of wood a few centimeters thick becomes sun bleached and dried, which may initially protect CWD from fragmentation losses and reduce loss of moisture from the interior.

6. Respiration

Respiration, primarily by microbes, removes matter from CWD. In terrestrial ecosystems, basidiomycetes are responsible for the majority of

respirational loss (Käärik, 1974; Swift, 1977a), but in aquatic ecosystems, bacteria, including actinomycetes, are most important (Crawford and Sutherland, 1979).

Field studies indicate that respiration rates (rate of CO_2 evolution) of CWD increase as wood density decreases (Ausmus, 1977; Yoneda, 1975; Yoneda et al., 1977). To calculate a combined respiration and leaching decay rate, the density or specific gravity of CWD can be plotted against the time CWD has been exposed to decay. Assuming volume remains constant, any decreases in density with time will reflect losses in mass (Christensen, 1984). However, a number of problems can arise when using this method.

Measuring volume is difficult. In regularly shaped solids, such as cylinders and cubes, volume can be calculated from external measurements of lengths and diameters. For very decayed wood, it is important to measure these dimensions in the field because samples often compress during transport. The volume of irregularly shaped pieces can be estimated by displacement, usually of water.

The dependence of density on moisture below the fiber saturation point causes errors in estimating decay rate. In undecayed wood, density at 30% moisture content is typically 10% less than that at 0% moisture (U.S. Forest Products Laboratory, 1976). It is therefore important to control moisture content when volumes are measured below the fiber saturation point and to report moisture content so valid comparisons can be made between studies.

Variations in the initial density of wood also cause problems in estimating decay rates. Density in living trees is influenced by species, age, and position along radial and longitudinal axes (Spurr and Hsuing, 1954). In many gymnosperms, density declines with height along the bole, although in some species density remains constant (Heger, 1974; Okkonen et al., 1972). Density also increases in young trees from the pith outward, while in mature to overmature trees, the outermost wood tends to have lower density (Spurr and Hsuing, 1954). Growth rate apparently has little influence on density (Spurr and Hsuing, 1954). There also appears to be little difference between open- versus forest-grown trees in the case of Abies balsamea (Heger, 1974). The wood density of some species has been studied in detail (U.S. Forest Service, 1965a,b; Wahlgren and Fassnacht, 1959; Wahlgren et al., 1968).

7. Biological Transformation

CWD is metabolized by microbes and, to a lesser degree, by invertebrates (Käärik, 1974; Swift, 1977a). The cell walls of basidiomycetes contain chitin, and because chitin is not present in undecayed wood, fungal

biomass can be estimated if a chitin–biomass conversion factor is known. Using this technique, Swift (1973) calculated that when 39% of the original wood mass was lost, an additional 35% had been converted to fungal biomass, demonstrating that much heterotrophic activity is overlooked when only respiration is considered.

Lignin decays more slowly than cellulose and hemicelluloses (Crawford, 1981), leading to an increase in the lignin-to-cellulose ratio as decay proceeds. This pattern has been observed for fine litter (see Swift *et al.*, 1979), but has received much less attention in the case of CWD. In undecayed wood, the lignin-to-cellulose ratio ranges from 0.6 to 1.2 for angiosperms and from 0.5 to 0.9 for gymnosperms (Table 2). Means *et al.* (unpublished) measured lignin and cellulose in a chronosequence of *Pseudotsuga* logs. In undecayed wood, the lignin-to-cellulose ratio was ~0.9, increasing to ~1.3, 1.9, and 2.7 after 50, 100, and 150 years of decay, respectively. The changes in this ratio may be affected by the type of decomposers present. White-rot fungi can degrade both lignin and cellulose and therefore may not increase the ratio. Conversely, soft-rot and brown-rot fungi only degrade cellulose, and the proportion of lignin should increase markedly in wood decayed by these organisms.

Many nutrients occur in fresh wood in very low concentrations. However, as decay proceeds and carbon is lost via respiration, the concentration of nutrients may increase; other mechanisms, such as N fixation, leaching, and fragmentation, also contribute to increased nutrient concentrations (see Section V,C). Nitrogen content of *Pseudotsuga* wood increased ~3.5-fold from the initial to the final stages of decay (Sollins *et al.*, unpublished). Other nutrients also increased in *Pseudotsuga* wood, with P, K, Ca, Mg, Mn, and Na exhibiting 5.3-, 2.2-, 3.0-, 6.8-, 1.6-, and 2.2-fold increases, respectively, as wood proceeded from the least to the most decayed stages. In many cases, the C : N ratio decreases as decay proceeds (Foster and Lang, 1982; Grier, 1978; Harris, 1978; Lambert *et al.*, 1980), although an exception has been found in a tropical forest (Yoneda *et al.*, 1977).

B. Decay Models

Many of the models proposed for leaf decomposition have been used in CWD studies. Wieder and Lang (1982) examined the models commonly used in litterbag experiments and concluded that the single-exponential (Jenny *et al.*, 1949; Olson, 1963) and the double-exponential models were the most useful and realistic biologically, whereas the asymptotic, linear, quadratic, and power models of decay were less useful. Their conclusions might also reasonably apply to CWD.

Table 2

Cellulose, Hemicellulose, and Lignin Content of Wood from Selected Temperate Tree Species[a]

| Species | Percentage of dry weight | | | References[b] |
	Cellulose	Hemicellulose	Lignin	
Angiosperms				
Acer rubrum	44–45	29–32	24	2,5
Acer saccharum	40	35	25	3
Betula lutea	43	31	26	3
Betula papyrifera	41	40	19	6,5
Betula verrucosa	39	39	21	4
Fagus grandifolia	39–42	31–36	22–26	5,3
Populus tremuloides	43–53	27–34	16–23	2,5,1,3
Quercus rubra	44	31	25	7
Robinea pseudoacacia	40	28	32	3
Ulmus americana	51	23	24	6
Mean[c]	43	32	24	
Range	39–53	23–40	16–32	
Gymnosperms				
Abies balsamea	42–49	22–27	29–30	2,5,1,3
Larix larcina	42–44	27–31	27–29	5,3
Picea abies	43	27	30	4
Picea glauca	40–50	20–31	27–30	6,5,1,3
Picea mariana	48–51	22–24	27–28	1,7
Pinus banksiana	42–47	26–29	27–29	5,1
Pinus elliotii	39	31	30	3
Pinus strobus	41–48	26–30	26–29	6,1,3
Pinus sylvestris	45	25	30	4
Pinus taeda	47	24	29	7
Pseudotsuga menziesii	43–48	24–31	26–28	3,7
Sequoia sempervirens	38	28	34	3
Thuja occidentalis	41–45	24–26	31–33	2,5,3
Thuja plicata	47	21	32	7
Tsuga canadensis	40–53	17–26	30–34	6,5,1,3
Tsuga heterophylla	44	26	30	7
Mean[c]	44	26	30	
Range	38–53	17–31	26–34	

[a]Values are based on extractive free wood.
[b](1) Clermont and Schwartz (1951), (2) Côte (1977), (3) Panshin and deZeeuw (1980), (4) Rydholm (1965), (5) Timell (1957), (6) Timell (1967), (7) Wise and Jahn (1952).
[c]The overall mean was based on the mean for each species.

The most commonly used model in CWD studies has been the single-exponential model discussed in detail by Olson (1963). The assumption that decay is proportional to the amount of material remaining leads to the model
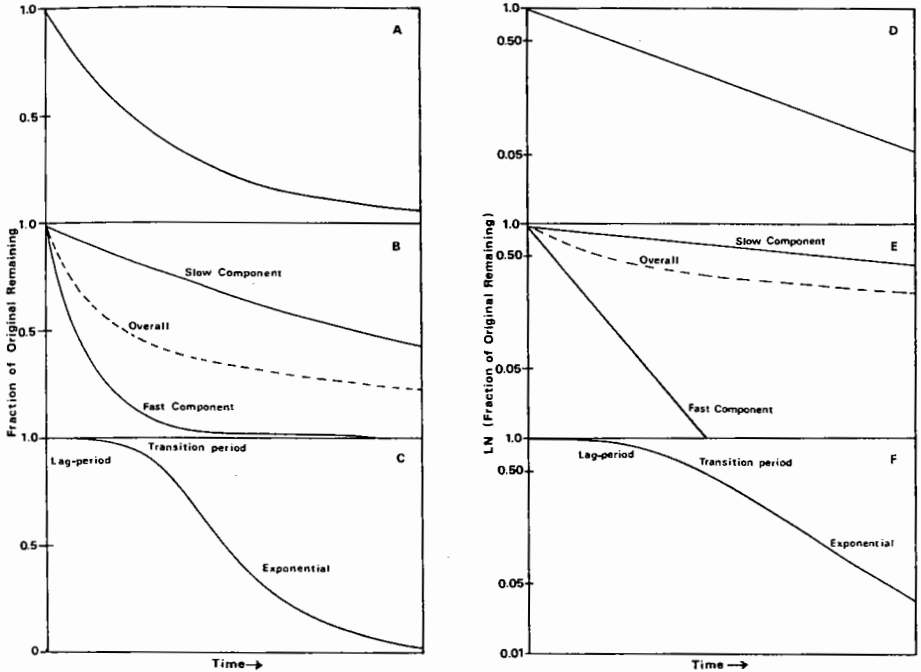
Fig. 4. Examples of three equations used to model losses from CWD. (A–C) Examples of single-exponential, multiple-exponential, and lag-time models, respectively, plotted on arithmetic scale. (D–F) The same models plotted when the fraction remaining has been transformed to natural logarithmic scale. The multiple-exponential model used here has fast and slow components, each composing half of the original mass and having rate constants differing by an order of magnitude.

$$Y_t = Y_0 e^{-kt}$$

where Y_0 is the initial quantity of material, Y_t is the amount left at time t, and k is the decay rate constant. In most CWD studies, wood density is used as the Y variable, although mass, volume, or cover of bark could also be used. The times to decompose one-half ($t_{0.50}$) and 95% ($t_{0.95}$) of the material are often reported, where $t_{0.50} = 0.693/k$ and $t_{0.95} = 3/k$. It is also common practice to report the turnover time, which is equal to the reciprocal of k.

Minderman (1968) objected to the single-exponential model because most substrates are not homogeneous, but contain substances decaying at different rates. If some substances are labile and others are recalcitrant, actual decay curves can depart markedly from the single-exponential model (Fig. 4). This problem has led to the use of double-exponential

models where the substrate is partitioned into two fractions, each of which is characterized by its own decay rate constant.

In the case of CWD, where decomposition is complex, it might be considered useful to expand the double-exponential into a multiple-exponential model. Multiple-exponential models may prove quite useful in understanding how components such as bark, sapwood, and heartwood contribute to the overall decay of CWD and how they might control differences between species and sizes of material. Means et al. (unpublished) adapted this model to examine the decay of Pseudotsuga boles as a function of three components: cellulose, lignin, and an acid detergent-soluble fraction. Although the lignin decayed at one-third the rate of the other fractions, the single-exponential model fit the data as well as the multiple-exponential one. This result was caused, in part, by the low coefficients of variation associated with both models. Other factors that might influence the comparison are the proportions of the components and the differences in decay rates of the components. The predicted difference between the single- and multiple-exponential models will increase as the differences between the decay rate of components increases. The differences between models also increase as the proportion of components becomes equal.

In the single-exponential model, material is assumed to be homogeneous, and the multiple-exponential model was developed to address this problem. However, an assumption of both models is that detritus is not transformed into more or less decomposable forms. This is an important shortcoming given the large amount of biological transformation occurring during decay. Carpenter (1981) developed a more general decay model with three parameters that, under special conditions, simplifies to either of the models presented above. Carpenter's general model incorporates the notion that more or less decomposable substances may be created during decay and deserves further examination.

All of the models described above are primarily concerned with the loss of mass via respiration and leaching. However, CWD is also lost and transformed via fragmentation (Lambert et al., 1980; Sollins, 1982). To address this problem, the decay rate constant can be divided into two parts so that $k = k_m + k_f$, where k is the overall rate constant, k_m is the rate constant for mineralization losses due to respiration and leaching, and k_f is the decay rate constant for losses due to fragmentation (Lambert et al., 1980; Sollins et al., 1979). In this approach, k_m and k_f are constant with time; however, there is a time lag before fragmentation begins. During this period, k_f is near zero. Harmon (1985) adapted the exponential model to incorporate a lag time. This model is $Y_t = 1 - (1 - \exp[-k_f t])^N$, where Y_t is the amount left at time t, k_f is the fragmentation rate constant, and N

is a constant related to the lag time (Fig. 4). This model may also be useful in examining the effect of fungal colonization and the lag time it introduces into mineralization losses.

C. Methods to Determine Decay Rates

1. Chronosequences

Decomposition of CWD is slow, necessitating long time periods to accurately measure the decay rate of individual pieces. An alternative, short-term method is to determine the length of time snags or logs have been dead and examine how volume, density, or other characteristics change with time. This array of aged pieces forms a chronosequence.

Dating the age of logs and snags requires imaginative detective work. More methods exist for dating fallen boles than standing dead trees. Logs can be aged by aging scars left on live trees adjacent to the fallen boles. In moist climates where tree seedlings can grow on logs, the age of the oldest seedlings gives a minimal estimate of log age (Triska and Cromack, 1980), but the time between tree fall and seedling establishment must be estimated to calculate log age more accurately. Bark sloughing occurs as logs decay, and it is therefore important to note if the aged seedlings are growing on bark; if sloughing has occurred, additional years should be added to the log age. Living stumps can be analyzed to determine the ages of trees snapped by wind (Harmon and Cromack, unpublished).

Historical records have also been used to provide ages of CWD. Permanent-plot records of tagged trees were used by Grier (1978) to date logs in *T. heterophylla* forests in Oregon. MacMillan (1981) used maps of a mixed mesophytic forest to age logs. By comparing maps made a decade apart, Falinski (1978) estimated rates of log disappearance in mixed hardwood and *Picea* forests in Poland. Records of logging and thinning operations were used by Foster and Lang (1982) and Savely (1939).

Records of natural disturbances have also been used to age CWD. Dates of fires have been extensively used to age snags (Harmon, 1982; Kimmey, 1955; Kimmey and Furniss, 1943), as have records of insect outbreaks (Keen, 1929, 1955; Wright and Harvey, 1967) and catastrophic windthrow (Buchanan and Englerth, 1940).

Historical reconstructions of stands have also been used to estimate the age of CWD (McFee and Stone, 1966). Lambert *et al.* (1980) aged dead boles by aging tree seedlings in *A. balsamea* stands. Fahey (1983) assumed all *P. contorta* trees established the same year and then aged snags by noting the difference in age between living and dead trees.

Some studies have monitored the decomposition of individuals and

cohorts over short periods of time. Most of these investigations have monitored snags created by fires (Dahms, 1949; Lyon, 1977) or insect attacks (Bull, 1983; Hinds et al., 1965; Keen, 1955), although Buchanan and Englerth (1940) followed the deterioration of windthrown trees. Trees have also been deliberately felled for later sampling (Gosz, 1980; Harris et al., 1972; Miller, 1983).

2. Input/Biomass Ratio

It is possible to estimate decay rates from the ratio of CWD input to biomass, assuming the biomass of CWD is in steady state. Christensen (1977) estimated wood turnover rate in a Danish Quercus robur forest. Sollins (1982) combined input data derived from long-term mortality records and current biomass of CWD to estimate the decay rate constant of an old-growth Pseudotsuga forest and found that this method yielded a decay rate constant of 0.03 year^{-1}, whereas those based on wood-density change ranged from 0.01 to 0.02 year^{-1} (Graham, 1982).

D. Decay Rates

In this section, we review the rates at which some of these processes have been observed to operate. Because of the limited number of observations for some processes, we have chosen to emphasize fragmentation and mineralization rates of snags and logs.

1. Snag Fragmentation Rates

The rates snags fall and/or fragment have been studied for many coniferous species in the western United States. Less information is available for other forested ecosystems. Most snag studies have used chronosequences, although some (e.g., Bull, 1983; Lyon, 1977) have observed a single population through time. In most studies, proportions of snags standing were noted, but in some the volume standing was estimated. Published data were used to calculate fragmentation rate constants, k_f, of snags and the length of the lag time before fragmentation (Table 3).

The lag time between tree death and the onset of fragmentation is influenced by species, size, microclimate, and type of mortality. Lag times required for snags to begin falling appear to be <20 years for all the species examined. Pseudotsuga menziesii snags have the longest lag time, although considerable variation exists within this species. For example, Cline et al. (1980) observed that as size increased, the lag time also increased. However, Graham (1982) indicated both large and small P. menziesii had lag times of <6 years. Most other species appear to have lag times of <3 years. The increase in lag time with increasing size also

Table 3
Decomposition Rates of Snags and Logs in Temperate Forest Ecosystems

Species	DBH (cm)	Study length (year)	Cause of death[a]	Lag time (year)	Decay rate constant	Half-time (year)	References[b]
			Snag-bole fragmentation				
Abies balsamea	—[c]	5	D	3	0.076	12	3[d]
Abies balsamea	>8	80	FW	<5	~0.085	~13	19[e]
Abies lasiocarpa	<7.5	15	F	2	0.317	4	20[d]
Picea engelmannii	7.5–24	25	BB	10	0.015	56	24[f]
Picea engelmannii	25–39	25	BB	10	0.012	67	24[f]
Picea engelmannii	>40	25	BB	10	0.009	87	24[f]
Picea engelmannii	>12	22	BB	4	0.023	34	16[e]
Picea glauca	—	7	D	0	0.012	57	26[d]
Pinus contorta	7.5–30	15	F	2	0.089[g]	10	20[d]
Pinus contorta	<25	8	BB	2	0.318[g]	4	4[d]
Pinus contorta	>25	8	BB	3	0.133[g]	8	4[d]
Pinus contorta	—	17	BB	<4	0.021	~37	16[e]
Pinus ponderosa	<25	8	BB	3	0.283	5	4[d]
Pinus ponderosa	25–49	8	BB	3	0.113	9	4[d]
Pinus ponderosa	>50	8	BB	5	0.161	9	4[d]
Pinus ponderosa	>20	22	F	<9	0.073[g]	~18	6[d]
Pinus ponderosa	>25	29	BB	1	0.197[g]	4.5	18[e]
Pinus ponderosa	>25	29	BB	2	0.112[g]	8	18[e]
Pinus ponderosa	>25	9	BB	1	0.189[g]	4.6	17[e]
Pseudotsuga menziesii	10–18	25	U	4	0.354[g]	6	5[e]
Pseudotsuga menziesii	29–31	60	U	6	0.109[g]	12	5[e]
Pseudotsuga menziesii	32–46	40	U	11	0.033[g]	32	5[e]
Pseudotsuga menziesii	47–71	45	U	17	0.055[g]	29	5[e]
Pseudotsuga menziesii	<40	50	U	<5	0.026	~31	10[e]
Pseudotsuga menziesii	>65	30	U	<6	0.014	~55	10[e]
Pseudotsuga/Tsuga	—	140	F	<20	0.096	~27	22[e]
Tsuga heterophylla	>25	30	U	<2	0.067	~12	10[e]

Table 3 *(continued)*

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Species	DBH (cm)	Study length (year)	Cause of death[a]	Lag time (year)	Decay rate constant	Half-time (year)	References[b]
Log-bole fragmentation							
Abies balsamea	>8	75	FW	<35	0.019	~71	19[e]
Abies concolor	>15	60	W	25	0.060	36	14[e]
Pseudotsuga menziesii	>20	250	W	80	0.008	166	10[e]
Tsuga heterophylla	>15	50	W	>50	0	—	10[e]
Snag-bark fragmentation[h]							
Picea engelmannii	>7.5	25	BB	—	0.012	57	24[f]
Pinus contorta	>1	20	U	<12	0.231	15	7[e]
Pinus contorta	>1	8	BB	—	0.015	46	4[d]
Pinus ponderosa	>1	8	BB	—	0.005	138	4[d]
Pseudotsuga menziesii	<40	50	U	<5	0.110	~11	10[e]
Pseudotsuga menziesii	>65	30	U	<6	0.038	~24	10[e]
Tsuga heterophylla	>25	30	U	<5	0.140	~10	10[e]
Tsuga heterophylla	>25	30	U	<5	0.096	~12	10[e]
Log-bark fragmentation							
Abies concolor	>15	60	W	7	0.125	12	14[e]
Populus tremuloides	>2	5	C	1	0.145	6	25[d]
Pseudotsuga menziesii	<40	200	W	<30	0.039	~47	10[e]
Pseudotsuga menziesii	40–65	200	W	<30	0.018	~68	10[e]
Pseudotsuga menziesii	>65	250	W	<30	0.021	~63	10[e]
Tsuga heterophylla	<25	50	W	<10	0.026	~36	10[e]
Tsuga heterophylla	>25	50	W	<20	0.019	~56	10[e]

			Snag-bole mineralization				
Abies balsamea	—	2	D	~1	0.062	12	2[d]
Acer rubrum	<15	6	F	~1	0.08	10	12[e]
Cornus florida	<15	6	F	~1	0.05	15	13[e]
Carya spp.	<15	6	F	~1	0.08	10	13[e]
Nyssa sylvatica	<15	6	F	~1	0.20	4.4	13[e]
Oxydendrum arboreum	<15	6	F	~1	0.05	15	13[e]
Pinus contorta	>1	20	U	12	0.006	127	7[e]
Pinus rigida	<15	12	F	~1	0.06	13	13[e]
Pinus virginiana	<15	15	F	~1	0.04	18	13[e]
Pseudotsuga menziesii	<40	50	U	—	0.027	25	10[e]
Pseudotsuga menziesii	40–65	30	U	—	0.013	53	10[e]
Pseudotsuga menziesii	>65	30	U	—	0.003	230	10[e]
Quercus coccinea	<15	6	F	~1	0.10	8	13[e]
Quercus prinus	<15	6	F	~1	0.18	5	13[e]
Tsuga canadensis	<15	6	F	~1	0.04	18	13[e]
Tsuga heterophylla	<25	30	U	—	0.017	40	10[e]
Tsuga heterophylla	>25	30	U	—	0.016	43	10[e]
			Log-bole mineralization				
Abies balsamea	>8	80	FW	—	0.011	63	19[e]
Abies balsamea	10–15	29	C	—	0.029	24	8[e]
Abies concolor	>15	60	W	—	0.05	14	14[e]
Carya spp.	>2.5	4	C	1	0.305	3.3	15[d]
Liriodendron tulipifera	>2.5	4	C	1	0.520	2.3	15[d]
Picea rubens	>10	64	C	—	0.033	21	8[e]
Picea sitchensis	>15	100	W	—	0.011	63	11[e]
Pinus contorta	>1	40	C	—	0.012	57	7[e]
Pinus taeda	>2.5	4	C	1	0.274	3.5	15[d]
Populus tremuloides	>2	5	C	0	0.049	14	25[d]
Populus tremuloides	17	5	C	0	0.070	9.8	9[d]

(*continued*)

Table 3 (*continued*)

Species	DBH (cm)	Study length (year)	Cause of death[a]	Lag time (year)	Decay rate constant	Half-time (year)	References[b]
Pseudotsuga menziesii	<40	200	W	—	0.004	172	10[e]
Pseudotsuga menziesii	40–65	200	W	—	0.004	172	10[e]
Pseudotsuga menziesii	>65	250	W	—	0.006	115	10[e]
Pseudotsuga menziesii	>15	320	W	—	0.007	98	23[e]
Quercus prinus	>2.5	4	C	1	0.266	3.6	15[d]
Quercus prinus	3–5	1	C	0	0.098	7	1[d]
Quercus spp.	>5	23	U	—	0.029	24	21[e]
Tsuga heterophylla	<25	50	W	—	0.012	57	10[e]
Tsuga heterophylla	>25	50	W	—	0.024	29	10[e]
Tsuga heterophylla	>25	38	U	2	0.008	88	12[e]
Tsuga heterophylla	>15	50	W	—	0.010	69	11[e]

[a]BB, bark beetles; C, cutting; D, defoliated; F, fire; FW, fir-wave; U, undetermined; W, windthrow.

[b](1) Abbott and Crossley (1982), (2) Barnes and Sinclair (1983), (3) Basham (1951), (4) Bull (1983), (5) Cline *et al.* (1980), (6) Dahms (1949), (7) Fahey (1983), (8) Foster and Lang (1982), (9) Gosz (1980), (10) Graham (1982), (11) Graham and Cromack (1982), (12) Grier (1978), (13) Harmon (1982), (14) Harmon and Cromack (unpublished), (15) Harris (1976), (16) Hinds *et al.* (1965), (17) Keen (1929), (18) Keen (1955), (19) Lambert *et al.* (1980), (20) Lyon (1977), (21) MacMillan (1981), (22) McArdle (1931), (23) Means *et al.* (unpublished), (24) Mielke (1950), (25) Miller (1983), (26) Riley and Skolko (1942).

[c]Not available.

[d]Monitoring population.

[e]Chronosequence.

[f]One-time sample.

[g]Assumes entire snag falls.

[h]Transfer from standing material only and does not include transfer with stem breakage.

appears to occur in the case of *P. contorta* and *P. ponderosa* (Bull, 1983), but these differences were minor (i.e., 1–2 years).

After the initial period without breakage, snag volume declines exponentially and can be described by a rate constant (see Section III,B). The rate of volume decline varies considerably between studies, species, and sizes. The fastest rates of fragmentation, k_f, have been observed for *P. menziesii*, 10–18 cm diameter at breast height (dbh). After standing unbroken for 4 years, one-half of the average snag would remain standing at 6 years ($k_f = 0.354$ year^{-1}; Cline *et al.*, 1980) and similar values of 0.317 year^{-1} were observed for *Abies lasiocarpa* (Lyon, 1977) and 0.318 year^{-1} for *P. contorta* (Bull, 1983). Smallest fragmentation rate constants ($k_f = 0.009–0.012$ year^{-1}) were observed for *Picea engelmannii* in Utah (Mielke, 1950), indicating a half-time of 67–87 years when a 10-year lag time is included. *Picea glauca* ($k_f = 0.012$ year^{-1}; Riley and Skolko, 1942) and large *P. menziesii* ($k_f = 0.014$ year^{-1}; Graham, 1982) also appear to fragment at slow rates. Snags of both species would have, on the average, 50% of their volume standing 50–57 years after the onset of fragmentation. Fragmentation rate constants appear to decline as snag size increases. Data from Bull (1983), Cline *et al.* (1980), Graham (1982), and Mielke (1950) all confirm this general pattern. However, the data from Cline *et al.* (1980) for *P. menziesii* and Bull (1983) for *P. ponderosa* indicate that above a certain size the fragmentation rate constant remains constant. For *Pseudotsuga*, k_f declines from 0.345 to 0.109, 0.033, and 0.055 as dbh increases from 10–18 to 29–31, 32–46, and 47–71 cm, respectively.

Even within a species and size class, k_f can vary considerably. The most frequently studied species is *P. ponderosa*. For snags >25 cm dbh, k_f ranges from 0.073 to 0.197 year^{-1}, which means that 50% of the population would be standing 3.5–9 years after the onset of fragmentation. Keen (1955) observed that snags fell at slower rates on drier pumice soils ($k_f = 0.112$ year^{-1}) than on moister loam soils ($k_f = 0.117$ year^{-1}). The cause of death also appears to influence k_f, with fire-killed trees (Dahms, 1949) falling slower than trees killed by bark beetles (Keen, 1955; $k_f = 0.073$ year^{-1} versus 0.112 year^{-1}).

All the studies mentioned above examined snag fragmentation on a population and not on an individual basis. On an individual basis, fragmentation is highly variable and therefore harder to predict (Graham, 1982). Until the lag time is exceeded, a population of snags is composed of individuals with no breakage (Fig. 5). Once fragmentation begins, the frequency distribution of the snag population has a strong positive skew; that is, only a few individuals are broken and most of the population is intact. As time progresses, more breakage occurs and the frequency dis-
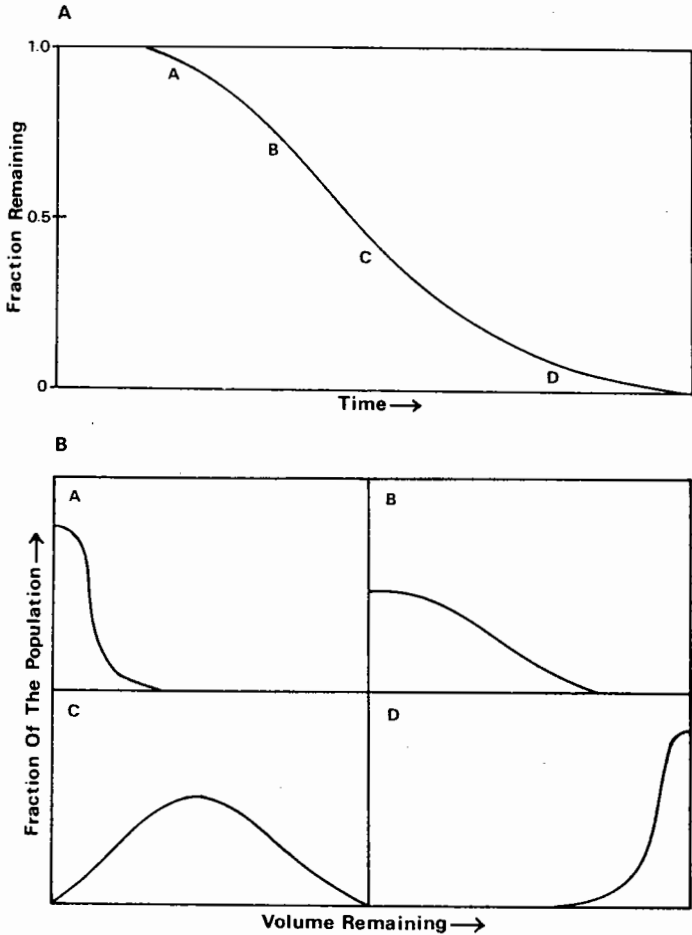
Fig. 5. The loss of volume over time caused by fragmentation from a hypothetical cohort of snags. (A) The mean fraction of volume remaining in the cohort as a function of time. Letters in this part of the figure indicate points along the curve which correspond to the distributions of individuals (B). As time progresses, both the mean, variance, skewness, and kurtosis of the cohort is expected to change.

tribution of the population is more positively skewed. When most of the snags have fallen, a few individuals remain standing, which causes the frequency distribution of the population to be negatively skewed.

Exponential fragmentation curves indicate continuous loss; in fact, many boles may break at the same time, and this causes discrete steps in the fragmentation curve. For example, Lyon (1977) observed trees killed by a fire and found years with breakage followed by years with none.

Loss of bark is an important feature in creating animal habitats and transferring nutrients to the forest floor, but has received little study. Bark moves to the forest floor either on logs broken from snags or by falling off snags (Graham, 1982). The rate constants presented in Table 3 represent changes in bark cover. Lag times for bark to fall from snags is known with less certainty than for bole volume losses. Most species begin to lose bark <6 years after tree death. The longest lag time was <12 years and observed for *P. contorta* (Fahey, 1983). Woodpeckers have a profound effect on bark loss (Bull, 1983) and may begin to remove bark within the first year of tree death.

Rate constants of bark loss are highly variable between species. The smallest ($k_f = 0.005$ year^{-1}) was observed for *P. ponderosa* (Bull, 1983), and because this is much smaller than the bole fragmentation rate constant, most of the bark of this species is probably transferred to the forest floor via bole fragmentation. The largest bark k_f (0.231 year^{-1}) was observed for *P. contorta* in Wyoming (Fahey, 1983), which lost 50% of its bark 3 years after a 12-year period with no loss. Because bole fragmentation was not measured by Fahey (1983), the relative proportion of bark transferred to the forest floor via boles cannot be judged. In contrast to *P. ponderosa,* some species such as *Pseudotsuga* do transfer the majority of bark via direct fragmentation and not via bole fragments. Increasing tree size may cause slower bark fragmentation. Graham (1982) found that *P. menziesii* larger than 65 cm dbh had a k_f of 0.038 year^{-1}, while smaller snags had a k_f of 0.11 year^{-1}. A similar trend was noted by Graham (1982) for *T. heterophylla* snags >25 cm dbh versus those that were smaller, with k_f of 0.096 and 0.140 year^{-1}, respectively.

2. Snag Mineralization Rates

Changes in wood density are caused by a combination of respiration and leaching and are termed mineralization losses here (see Section III,B). Wood density of small snags in the southern Appalachians decreases after 1 year (Harmon, 1982), indicating a short lag time is associated with snag mineralization. In contrast, *P. contorta* snags in Wyoming had no significant change in density for 12 years, and boles in these ecosystems may not be mineralized until they fall to the forest floor (Fahey, 1983).

Mineralization losses will not peak until most of the bole is colonized by microbes. Fungi begin to colonize snags within a year of death (Basham, 1951; Hinds *et al.,* 1965; Kimmey, 1955; Kimmey and Furniss, 1943). However, when the volume of respiring tissue is small compared to the total volume, total mineralization losses may be minimal. There may be an extended transitional period between the time when losses are first

detected and when the snag is losing material at the maximum rate. Kin mey (1955) found that *Abies concolor, Pinus jeffreyi,* and *P. ponderos* snags were completely colonized by fungi within 6 years, while *Pinu lambertiana* and *P. menziesii* snags were not colonized completely eve after 10 years. This indicates that the mineralization lag time probabl differs between species.

Mineralization rate constants, k_m, of snags vary with species and siz The smallest were observed for large *P. menziesii* ($k_m = 0.003$ year⁻ Graham, 1982) and *P. contorta* ($k_m = 0.006$ year⁻¹; Fahey, 1983). Th small k_m of the former species is probably due to a combination of larg size and high decay resistance of heartwood. The largest k_m for snag were observed in *Nyssa sylvatica* (0.20 year⁻¹) and *Quercus prinus* (0.1 year⁻¹) (Harmon, 1980). The large rate constants of the latter specie were probably caused by a combination of small size and a high propor tion of sapwood and/or non-decay-resistant heartwood.

3. Log Fragmentation Rates

In studies of log fragmentation, it has been assumed that all volum changes are associated with fragmentation (Graham, 1982; Harmon an Cromack, unpublished; Lambert *et al.,* 1980). However, volume de creases when boles collapse, and these studies probably overestimat fragmentation rates.

Lag times for log fragmentation, typically 25 years or more, are consid erably longer than those for snags, which are typically less than 10 years The shortest lag time reported for log fragmentation is 25 years for *A. concolor* (Harmon and Cromack, unpublished), while the longest was 8C years observed in *P. menziesii* (Graham, 1982).

Log fragmentation rates, k_f, vary considerably from 0 for *T. heterophyl-la* (Graham, 1982) to 0.06 year⁻¹ for *A. concolor* (Harmon and Cromack, unpublished). The k_f of logs appear to be considerably smaller than those observed for snags for species where data exist for both forms of CWD. This indicates that snags will disappear as recognizable structures much faster than logs.

Although data are rare, there are also some general trends in the loss of bark cover from logs. For the three species that have been studied, *A. concolor, P. menziesii,* and *T. heterophylla,* loss of bark precedes bole fragmentation. The lag time for the onset of bark loss ranges from 1 year in *Populus tremuloides* to 30 years in *T. heterophylla.* Once initiated, bark k_f vary considerably. *Abies concolor* and *P. tremuloides* lost bark fastest, with k_f of 0.125 and 0.145 year⁻¹, respectively. *Pseudotsuga* ($k_f = 0.018$ year⁻¹) and *Tsuga* ($k_f = 0.019$ year⁻¹) have the slowest rates. It is not known why some species lose bark faster than others or why certain

individuals vary. Trees falling during the growing season probably lose bark faster than those falling at other times. Furthermore, suspended logs are apt to lose bark faster than those resting on the ground. Thin bark is more apt to break due to shrinking, but thick bark is heavier and more apt to separate from the underlying wood.

4. Log Mineralization Rates

Most studies of log mineralization have used the single-exponential model without a lag time. However, studies conducted on beetle-killed $P.$ $ponderosa$ (Boyce, 1923) and windthrown trees (Boyce, 1929; Buchanan and Englerth, 1940) indicate lag times exist for many species. Grier (1978) observed a lag of 2 years for $T.$ $heterophylla.$ Harris (1976) reported a lag of 1 year for logs of a range of species in Tennessee. Lag time associated with log mineralization should increase as log size increases.

The k_m of logs vary greatly between species. The smallest k_m, 0.004–0.007 year^{-1}, have been observed for $Pseudotsuga$ (Graham, 1982; Means et al., unpublished). $Pseudotsuga$ logs would have a half-time of 98 to 172 years if only respiration losses were considered. The largest k_m, 0.52 year^{-1}, is for $Liriodendron$ $tulipifera,$ with a half-time of 2.3 years, even with the lag time added (Harris, 1976). Other angiosperm species have k_m an order of magnitude smaller than observed for $Liriodendron.$ The half-time of $P.$ $tremuloides$ logs ranges from 10 years (Gosz, 1980) to 14 years (Miller, 1983). Large mineralization rates are not restricted to angiosperm species. For example, Harmon and Cromack (unpublished) found that $A.$ $concolor$ boles had a half-time of 14 years ($k_m = 0.05$ year^{-1}).

Logs entering streams remain intact for intervals ranging from a few decades to several hundred years (Anderson et al., 1978; Franklin et al., 1981). Decay rates of $Populus$ $balsamifera$ logs in a Canadian beaver pond indicate that ~250 years would be required for 95% of the mass to be lost (Hodkinson, 1975), which is considerably longer than the 43–60 years required on land (Gosz, 1980; Miller, 1983). In streams of the Pacific Northwest, dendrochronological dating indicates that pieces have been in channels for >108 years (Swanson and Lienkaemper, 1978; Swanson et al., 1976). Of the species examined in these two studies, $Thuja$ $plicata$ decayed most slowly, followed in order of increasing decay rate by $P.$ $menziesii,$ $T.$ $heterophylla,$ and $Alnus$ $rubra.$ Using respiration rates, Anderson et al. (1978) calculated that CWD in streams of the Pacific Northwest requires 5–200 years to decay completely. Naiman and Sedell (1980) measured respiration losses from fine wood debris (<10 cm diameter) and estimated that CWD would require 200–300 years for total decomposition. Respiration measurements underestimate the time required for com-

plete decay of CWD by microbial activity because wood surfaces
streams are covered with a film of bacteria, fungi, algae, moss, and proi
zoans, which also add CO_2 to the respiration losses, but do not degra
wood.

E. Factors Controlling Decomposition

Factors that can control decomposition of CWD include temperatur
moisture, oxygen, carbon dioxide, substrate quality, and the organisn
involved. Unfortunately, the effects of most of these factors are know
only qualitatively or from laboratory tests.

1. Temperature

The role temperature plays in the activity of organisms is well studied i
the laboratory. Fungi survive temperatures from below 0° up to 60°(
(Deverall, 1965). However, most wood-decaying fungi are mesophilic
i.e., cannot grow above 40°C, and have a temperature optimum of 25°
30°C (Käärik, 1974). Between 13° and 30°C fungal respiration rate double
to triples for every 10°C increase (Deverall, 1965). Variations in toleranc
to temperature affect the distribution of fungi in CWD; for example, ther
mophilic species are most likely to occur in the outer portions of CWI
exposed to direct sunlight (Käärik, 1974). Savely (1939) found that wood
inhabitating insects had upper temperature limits from 40 to 52°C. More
over, for many species the ability to tolerate elevated temperatures de
creases as relative humidity increases. Relative humidity is apt to be higt
in CWD, and Savely (1939) reported lethal temperatures of 41–44°C foi
insects. Thermophilic insect species inhabit the upper portions of logs,
while those with lower tolerances inhabit the sides and lower portions
(Graham, 1925). The respiration rate and feeding activity of invertebrates
also increases with temperature, although at high temperatures they may
become torpid. For example, fecal production by larvae of the xylopha-
gous aquatic beetle *Lara avara* doubled as temperatures increased from 5
to 15°C (Steedman, 1983). Elevated temperatures shorten the length of the
life cycle of insects (Graham, 1925), which, in turn, may increase the rate
at which CWD is decayed.

Diurnal fluctuations under the bark of *Pinus* and *Quercus* logs were
noted by Graham (1925) and Savely (1939). On nights and cloudy days,
temperatures just below the bark closely followed the sourrounding air,
but under sunny conditions, temperatures on the upper side of logs ex-
ceeded air temperature, often exceeding lethal levels for insects where
logs were exposed to full sunlight (Graham, 1925). However, the under-
side of logs tended to follow the air temperature even during sunny

weather. Temperature fluctuations were increasingly dampened closer to the center of a log (Savely, 1939).

Paim and Becker (1963) monitored changes in oxygen and carbon dioxide in *Fagus grandifolia* logs and found oxygen concentration decreased with temperature increases, while CO_2 concentration increased. Savely (1939) observed similar patterns in CO_2 contents in *Pinus* and *Quercus* logs. Seasonal patterns in CO_2 concentration are probably caused by increasing respiration rates with increasing temperature. However, moisture content is also apt to be unfavorable to microbes during winter months and reduces respiration during this season.

2. Moisture

Both extremely low and high moisture content can limit the activity of organisms. Below 30% moisture content (the fiber saturation point), water is generally not available to microbes (Griffin, 1977; Käärik, 1974). Above 30% moisture content, water becomes available and the activity of organisms increases. However, as the pores fill with water, oxygen diffusion is reduced and aerobic activity is limited.

The moisture content of CWD can be measured a number of ways, but it is not obvious which technique gives the most meaningful measurement in terms of controlling the activity of organisms (Griffin, 1977). Moisture content is often expressed as percentage moisture on a dry weight basis, but it can represent different amounts of water if wood density varies. Water potential may be more appropriate for comparing material of various densities. Griffin (1977) defined three types of pores that store water in wood. The largest pores are cell lumina that contain water when water potential exceeds −0.3 MPa. A second set of smaller pores include pit apertures, pit-membrane pores, and other small voids that drain at water potentials of −0.3 to −14 MPa. At water potentials of < −14 MPa, water is lost from micropores in the cell walls.

The optimal amount of moisture depends, of course, on the organisms involved. A range of 30–160% moisture (dry weight basis) appears to support growth of basidiomycetes (Käärik, 1974). Griffin (1977) found that below −4 MPa basidiomycetes ceased to grow and a decrease in growth occurred below −0.1 MPa. Bacteria, ascomycetes, and fungi imperfecti can tolerate higher amounts of moisture than basidiomycetes. For example, the ascomycetes and fungi imperfecti causing soft rots can tolerate moisture contents up to 240% (Käärik, 1974). Compared to fungi, less work appears to have been done on the tolerance of insects to moisture content. Certain species such as powder post beetles (Anobiidae and Bostrichidae) can live in extremely dry wood.

The radial distribution of microbial activity in CWD differs markedly between terrestrial and aquatic ecosystems. Microbial communities in log-holding ponds are composed primarily of superficial bacterial films (Savory, 1954b). Observations of microbial discolorations and wood firmness indicate microbial decay of logs in streams is also a surface phenomenon (Anderson *et al.,* 1978; Dudley and Anderson, 1982; Triska and Cromack, 1980). Aumen (1985) investigated microbial distributions in *Pseudotsuga* logs in a third-order stream in Oregon. Aerobically incubated samples of the wood surface developed seven times more colonies than anaerobically incubated surface samples, and samples from a depth of 25 cm failed to develop colonies after either aerobic or anaerobic incubation. Cellulose and lignin decomposition was four times faster for surface samples than for samples from the interior of the log. SEM analysis revealed many single-cell bacteria and actinomycete filaments on the surface of the log, but little evidence of microbes from the core of the log. Microbial activity was restricted to the surface of the log, with bacteria and fungi virtually absent from samples taken at a depth of ~5 mm or less (Aumen, 1985).

Most work on the daily and seasonal fluctuations of wood moisture has involved wood products applications with moisture content below 30% (Skaar, 1972). Boddy (1983) observed the moisture regime of branchwood 1.5–2.5 cm in diameter over a year, and presumably some of these observations apply to larger pieces as well. Moisture content was highest during winter, and branchwood remained saturated as long as precipitation remained high and temperatures low. Minimum moisture content was observed during late summer and early autumn, but even then rarely fell below fiber saturation point. Short-term fluctuations in moisture content were highest during summer because storms and droughts caused a series of wetting–drying cycles. The response of branchwood to wetting was very rapid, with most pieces reaching saturation within 24 hours of the onset of rain. Bark cover appeared to have a minor influence on drying rates.

Seasonal variations of moisture in sound CWD have been studied by Hayes (1940) and Brackebusch (1975) in Idaho. Hayes (1940) monitored moisture content for 4 years using electrodes implanted in *Pinus monticola* logs. Drying proceeded from the outer regions toward the inside of the log and in all parts of the log except those in direct contact with the soil. Summer was a period of drying, and fall, winter, and spring were periods of recharge. During wetting cycles, the upper half of the log was the most apt to absorb water, although with longer storms the bottom half of the log was also wetted.

Brackebusch (1975) weighed debarked *T. plicata* logs at biweekly intervals to test the influence diameter, soil contact, and shade had on moisture content. The observation period was 19 years, during which the logs were replaced twice so that sound logs were observed. Unfortunately, the logs were weighed only during the fire season (May to October). However, some facets of log moisture cycles were revealed. As with the other two studies, logs started drying during spring and reached the annual low (15–30%) during August. Moisture content increased during late August and September and presumably remained high during fall, winter, and early spring. Increasing log size, contact with the soil, and shading all significantly increased moisture content.

As decay proceeds, the moisture content of CWD changes. For living trees, gymnosperms generally contain more moisture in the sapwood than angiosperms, 98–249% versus 44–146% (Peck, 1953). The heartwood of both taxa is drier than sapwood and is more similar in moisture content, with gymnosperms ranging between 31 and 121% and angiosperms ranging between 44 and 162%. In the case of undecayed wood, maximum moisture content is negatively correlated with density (Peck, 1953). A similar negative correlation between density and maximum moisture content has also been observed for decayed wood (Boddy, 1983; Yoneda, 1975), indicating that as decay proceeds, maximum moisture content also increases.

Water in CWD does not all come from external sources; for every 1 g of cellulose respired, 0.555 g of water is liberated (Griffin, 1977). However, the contribution of this respirational water to the overall moisture regime is not known.

3. Oxygen and Carbon Dioxide

The quality of the atmosphere within CWD influences the species of organisms present and the rate at which they degrade material. However, few studies have monitored either O_2 or CO_2 concentrations or the factors that control them, or examined their biological consequences.

The composition of air in logs is affected by moisture and temperature. As noted before, O_2 concentration decreases and CO_2 concentration increases as temperature increases (Paim and Becker, 1963) because of increased respiration. As moisture content rises above the fiber saturation point, respiration increases (Griffin, 1977) and causes CO_2 content to rise and O_2 content to fall. However, at very high moisture content, gas diffusion is restricted, and even slow rates of respiration deplete O_2. Gas diffusion even in relatively dry conifer wood is slow (Tarkow and Stamm, 1960) and would probably be even slower in saturated wood.

The response of wood-decaying organisms to elevated CO_2 and reduced O_2 concentrations in wood is known for few species. Oxygen is required for significant rates of microbial decomposition of lignin (Crawford, 1981; Kirk *et al.*, 1978; Zeikus, 1980). Benner *et al.* (1984b) observed fungal degradation of lignin under anaerobic conditions, but at rates far below those observed under aerobic conditions. Paim and Becker (1963) found that the cerambycid beetle *Orthosoma brunneum* inhabited decaying beech logs with O_2 concentrations as low as 2% and CO_2 concentrations as high as 15%. This species was more sensitive to low O_2 rather than high CO_2 concentrations and was not usually found in logs where O_2 concentrations dropped below 2%. The growth response of four wood-decaying fungi to O_2 and CO_2 was examined by Jensen (1967) in liquid-culture experiments where O_2 and CO_2 were varied between 0 and 40% and 0 and 30%, respectively. Fungal growth decreased with increasing CO_2 concentrations and increased with O_2 concentrations up to 20% for all four species. The effects of gaseous environments on fungi were reviewed by Tabak and Cooke (1968). They concluded that O_2 is essential for fungal growth, but the minimum concentrations for survival are very low, and that fungi are more sensitive to elevated CO_2 than low amounts of O_2.

4. Substrate Quality

CWD is a structurally and chemically heterogeneous substrate. This heterogeneity is partially responsible for the variations in CWD decay rates observed between species and within individual pieces of CWD. This section reviews how substrate quality varies from species to species and within individual boles and how these differences in turn influence decay rates.

Most ecological studies of CWD decomposition have considered entire tree boles. While this is a useful starting point, the differences between sizes of material and species will only be understood on a more detailed level. CWD can be divided into four components: outer bark; inner bark, which includes the cambium and the phloem; sapwood; and heartwood (Fig. 6). This classification has proved useful in understanding which tree species are resistant to decay (Scheffer and Cowling, 1966) as well as how CWD varies internally as an invertebrate habitat (Savely, 1939). Each component can, in turn, be considered on an anatomical or chemical level. Although we will emphasize the chemical quality of the wood and bark, it should be noted that anatomical differences are often correlated to chemical differences and that anatomical structure appears to exert a great deal of control over how microbes colonize wood (Wilcox, 1973).

Each component can be divided into cell wall constituents, nutrient elements, and extractives, i.e., substances such as sugars, amino acids,
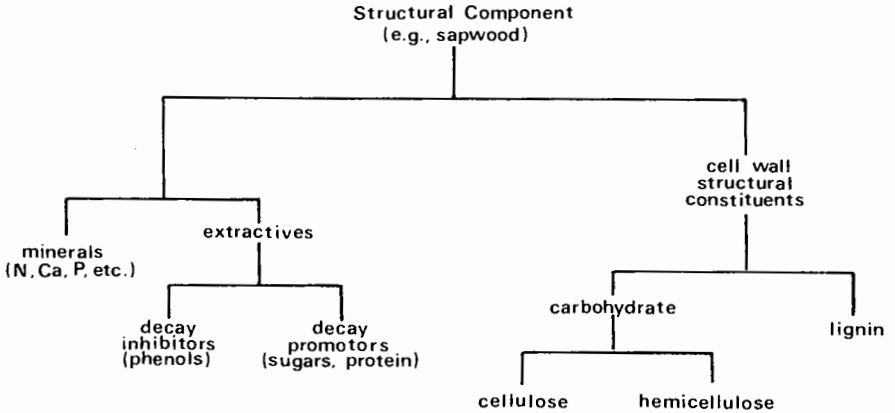
A
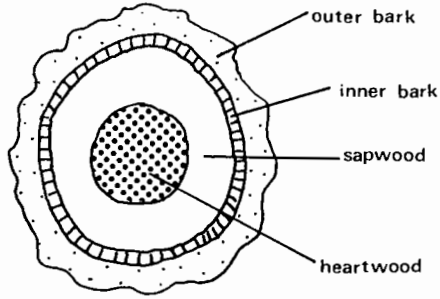
B

Fig. 6. The structural (A) and chemical (B) division of CWD. Structurally, the cross section of a piece of CWD can be divided into outer bark, inner bark, sapwood, and heartwood. Each of these layers can in turn be broken into its chemical constituents, which influence the substrate quality of these structural layers.

fats, and waxes that can be removed using solvents. Cell walls are generally composed of cellulose, hemicelluloses, and lignin, which constitute the majority of CWD biomass. Some elements, such as Ca, may also be a part of cell walls.

  a. Structural Components. The proportion of bark, sapwood, and heartwood in boles varies with species and size. The proportion of heartwood, for example, increases with diameter (Hillis, 1977), and because

heartwood is usually the most resistant component, the overall bole decay rate should decrease with size. Also, decay rate should decline from the base to top of a bole because the proportion of heartwood decreases. The fraction of a bole of a given size in sapwood versus heartwood can often be predicted from diameter (Buchanan and Englerth, 1940). Likewise, bark volume can also be predicted from diameter for log segments (Pneumaticos *et al.*, 1972) or entire trees (Kozak and Yang, 1981).

   b. Anatomical Structure. Gymnosperm wood is less complex and contains less living tissue than that of angiosperms. Gymnosperm sapwood contains 5–10% living tissue by volume (Panshin and deZeeuw, 1980, p. 132), while angiosperm sapwood contains 11–48% living tissues (Panshin and deZeeuw, 1980, p. 181). Increases in living cell volume probably increase decay rates because living tissue has a higher concentration of readily decomposable material such as sugars, starches, and protein. Also, nutrient content is higher in living than dead tissues. For example, Merrill and Cowling (1966) found that N content was positively correlated with parenchyma volume in angiosperm sapwood; increasing N content should speed decay. Most living-wood tissue is composed of rays that have their long axis oriented radially, thus forming pathways of colonization into CWD for microbes (Wilcox, 1973). The longitudinal orientation of water-conducting elements also influences microbial colonization patterns in that longitudinal growth occurs much more rapidly than radial growth. An anatomical feature that may cause angiosperms to decay faster than gymnosperms is the size and continuity of water-conducting elements (Wilcox, 1973). In general, vessels of angiosperms have larger diameters than gymnosperm tracheids and form a more continuous pathway, whereas tracheids are connected by pits. Both factors would tend to favor more rapid fungal colonization in angiosperms. There is considerable variation between angiosperms in the proportion of volume that is composed of vessels, e.g., 6.5% in *Carya ovata*, 50.8% in *Celtis occidentalis* (Panshin and deZeeuw, 1980, p. 181). Tracheids and vessel diameters also vary from spring to summer wood, and it is possible that colonization is faster in the larger diameter elements of the spring wood.

   The size of the conducting elements also influences the depth fungal spores penetrate the exposed ends of CWD. Hintikka (1973), for example, found that spores of *Armillaria mellea* cannot penetrate *Alnus, Betula, Pinus,* or *Picea* wood in the longitudinal direction more than 1–2 cm, whereas few spores are stopped in *Fraxinus* and *Quercus* wood over a distance of 16 cm.

   c. Cell Wall Chemistry. The chemical composition of wood cell walls has been studied extensively (Wenzl, 1970; Wise and Jahn, 1952) and will only be briefly reviewed here. Wood is largely composed of cellulose, the

hemicelluloses, and lignin. The chemical structure of cellulose is well known, although its exact arrangement in fibrils and cell walls is quite complex and still being actively investigated. Cellulose is a linear polymer of D-glucose units joined by β-1,4 linkages and appears to be the major cell wall constituent of both gymnosperms ($\bar{x} = 44\%$) and angiosperms ($\bar{x} = 41\%$). Hemicelluloses are a diverse group of polysaccharides that compose 13–31% of gymnosperm wood ($\bar{x} = 22\%$) and 23–39% of angiosperm wood ($\bar{x} = 33\%$). These compounds are thought to be in an amorphous state surrounding the cellulose fibrils. Unlike cellulose molecules, hemicellulose molecules are branched and are composed of several sugars, including glucose, galactose, mannose, arabinose, xylose, and glucuronic acid. The terminology describing the hemicelluloses is beyond the scope of this article, but is described by Wenzl (1970) and Kirk (1973). Because hemicelluloses are more complex structurally and chemically than cellulose, microbes need a wider variety of enzymes to decompose them. Lignin is more amorphous and highly branched than are the hemicelluloses. This polymer has a highly complex structure (see Adler, 1977; and Gross, 1980, for reviews). It is basically phenylpropane units derived from p-coumaryl, coniferyl, and synapyl alcohols, though the proportion of these varies among taxa. This complexity of lignin makes it difficult for microbes to degrade. Moreover, microbial lignin degradation appears to be more sensitive to variations in O_2, N, and P than that of cellulose (Aumen, 1985). Of the three cell wall constituents, lignin is the most interesting ecologically because of its resistance to decay and the negative correlation between decay rates of leafy litter and increasing lignin content (Cromack and Monk, 1975; Fogel and Cromack, 1977; Melillo et al., 1982). Melillo et al. (1983) found that decay rate constants of wood chips of different tree species were inversely related to lignin : nitrogen ratios in a first-order stream in Quebec; lignin content alone was the best predictor of wood decay in a sixth-order stream. CWD is thought to decay slower than leaf litter because of its higher lignin content (Käärik, 1974; Merrill and Cowling, 1966; Swift, 1977a).

   Development of radioisotope labeling of substrates has permitted more exact measurement of decomposition rates of cellulose and lignin (Crawford and Crawford, 1976, 1978; Crawford et al., 1977a,b, 1980). This approach has been modified and used to examine lignocellulose degradation in a variety of aquatic ecosystems (Aumen, 1985; Aumen et al., 1983; Benner et al., 1984a,b; Federle and Vestal, 1980; Maccubbin and Hodson, 1980). These studies indicate lignin breakdown is much slower than cellulose breakdown in aquatic ecosystems.

   The generally slower decay rates of gymnosperms relative to angiosperms might be attributed, in part, to the higher lignin content of the

latter. Gymnosperms have a higher mean lignin content (30%, range 26–34%) than angiosperms (24%, range 16–32%) (Table 2). The degree that this variation is correlated with decay rates is not clear. In many species, the heartwood is more resistant to decay than the sapwood (Scheffer and Cowling, 1966), and yet the lignin contents of extractive-free heart- and sapwood are quite similar within many species (Hawley and Wise, 1929).

The distribution of cellulose, hemicellulose, and lignin within cell walls is not uniform. Appreciation of these patterns is quite important when considering the ecological niche of microbes (Côte, 1977; Kirk, 1973; Sutherland *et al.*, 1979; Wilcox, 1973). Middle lamellae have higher concentrations of lignin (~75%) than the other cell wall layers and therefore might be expected to decompose slowest (Panshin and deZeeuw, 1980, p. 107). In contrast, cellulose composes only ~5% of the middle lamellae, but 50% of the S2 layer. The S1 layer is intermediate in composition between the middle lamellae and S2 layer, while the S2 and S3 layers are quite similar. The S2 layer dominates the overall cell wall composition because of its thickness.

d. Extractives and Heartwood Decay Resistance. Species vary considerably in the decay resistance of their heartwood. Species ratings are available because decay resistance is important in predicting wood durability in service (Reis, 1972; Scheffer and Duncan, 1947; U.S. Forest Products Laboratory, 1967). Wood extractives appear to be the principal source of decay resistance in heartwoods. In contrast to heartwood, sapwood, with its low level of extractives, has little resistance to decay (Humphrey, 1916). Scheffer and Cowling (1966) present an excellent and detailed review of wood extractives and their importance in promoting decay resistance. The fact that extractives from heartwood inhibit microbial growth was demonstrated over 60 years ago (Hawley *et al.*, 1924). Nevertheless, most ecological studies have failed to take wood extractives into account when comparing species and often seek to explain differences solely on the basis of N content, size, or climate.

Not all wood extractives inhibit microbes, so total extractive content may not predict decay resistance. Of the substances promoting decay in wood, sugars and protein are probably the most important. Smith and Zavarin (1960) measured the mono- and oligosaccharide content of outer bark, inner bark, sapwood, and heartwood in nine California conifers, which contained an average of 0.07, 2.68, 0.32, and 0.05%, respectively, of these substances on a dry weight basis. The protein content of cambium and sapwood was found to be 20–30% in the former, but only 0.83–1.37% in the latter (Allsopp and Misra, 1940). Both studies indicate that inner bark is more nutritious than outer bark or heartwood.

General classes of extractives inhibiting fungal decay include terpe-noids, flavonoids, tropolones, and stilbenes (Scheffer and Cowling, 1966). Most decay-inhibiting compounds are polyphenolic in nature (Hillis, 1962, 1977; Scheffer and Cowling, 1966). Extremely small quantities of extractives give heartwood a large degree of decay resistance. For exam-ple, thujaplicins, which make *T. plicata* very decay resistant, occur in concentrations of less than 1.2% (Scheffer and Cowling, 1966). The ability of one compound to inhibit decay is often enhanced by the presence of other extractives, e.g., *Libocedrus decurrens,* where a mixture of four terpenoids, carvacrol, *p*-methoxycarvacrol, *p*-methoxythymol, and hy-drothymoquinone, imparts greater decay resistance than these com-pounds acting alone (Scheffer and Cowling, 1966).

Extractive concentrations vary both between and within substrates. The distribution of dihydroquercetin in *P. menziesii* provides an excellent example of these patterns (Gardner and Barton, 1960; Hancock, 1957). The highest concentration of dihydroquercetin occurs in bark (7%), while the lowest generally occurs within the sapwood (<0.5%). Although heart-wood contained large quantities of this compound, the concentration is highest near the sapwood–heartwood boundary (1.0–1.5%) and lowest near the pith (<0.6%). In fact, in many trees the heartwood near the pith had less dihydroquercetin than the sapwood. This radial decline in extrac-tive content of heartwood occurs in many species including *Larix occi-dentalis* (Gardner and Barton, 1960), *T. plicata* (MacLean and Gardner, 1956), *Juglans nigra* (Nelson, 1975), and *Quercus rubra* (Nelson, 1975). Field and laboratory tests indicate heartwood decay resistance increases from the pith outward in genera such as *Quercus* (Scheffer *et al.,* 1949), *Robinea* (Scheffer and Hopp, 1949), and *Taxodium* (Campbell and Clark, 1960). Decay resistance also varies with height along the tree stem, with the hightest degree of resistance in the outer heartwood at the base of the bole (Scheffer and Cowling, 1966).

Decay-resistant species appear to have more variability in decay resis-tance than nonresistant species. In soil-block tests, Clark (1957) demon-strated that species losing the least weight on mean basis also had the highest variation in weight loss. For example, in one trial lasting 3 months using *Poria monticola* as the decay fungi on *Pinus palustris,* a mean of 47% of the weight was lost. However, losses ranged from 16 to 52%. In contrast, *Abies* sp. lost a mean of 61% of the original weight, but the range was only 57–65%. Other studies indicate decay resistance varies consid-erably between populations of *Pseudotsuga* (Scheffer and Englerth, 1952), *Quercus* (Scheffer *et al.,* 1949), and *Taxodium* (Campbell and Clark, 1960).

Although extractives initially give the heartwood of many species high decay resistance, this protection gradually decreases with time. The time needed to deactivate extractives introduces a lag time into the decay of species having decay-resistant heartwood. Scheffer and Cowling (1966) listed four mechanisms whereby decay-inhibiting compounds can be inactivated: deactivation by enzymes in the heartwood, self-oxidation of the compounds, microbial degradation, and loss via leaching. Scheffer and Cowling (1966) indicate that microbes responsible for deactivation of extractives are often unable to decay cell walls. Thus, the presence of non-wood-decay fungi, such as molds, may be crucial for the colonization of wood-decay fungi. The role biotic deactivation and leaching play in reducing concentrations of decay-retarding substances is not known. Removal of substances allows factors such as N content to affect decay processes. This is suggested by the work of Eslyn and Highley (1976), who found that under moderate decay conditions, sapwood of American tree species varied in its resistance to decay in spite of the lack of decay-inhibiting extractives. They hypothesized that species low in N decayed slower than those high in N.

e. Nutrient Elements. The nutrient content of CWD influences decomposition rates, nutrient cycling, and the suitability of CWD as a rooting medium. The elements required by microbes, invertebrates, vertebrates, and plants differ. There are 17 elements essential to higher plants: carbon (C), hydrogen (H), oxygen (O), phosphorus (P), potassium (K), nitrogen (N), sulfur (S), calcium (Ca), iron (Fe), magnesium (Mg), boron (B), manganese (Mn), copper (Cu), zinc (Zn), chlorine (Cl), and molybdenum (Mo). Fungi require all of these except Ca and B, but gallium (Ga), scandium (Sc), and vanadium (V) are possibly essential for some fungi (Lilly, 1965). Nitrogen-fixing prokaryotes require cobalt (Co). Animals require iodine (I), sodium (Na), selenium (Se), chromium (Cr), tin (Sn), vanadium (V), fluorine (F), silicon (Si), and nickel (Ni), in addition to the basic set required by plants. Of these elements, C, H, and O comprise all but a few percent of undecayed CWD. The order of the remaining elements from least to most abundant in undecayed wood is approximately Ca = N > K ≫ Mg = Mn > S = P > Na > Fe = Zn > Cu > B > Mo (Table 4).

The concentration of nutrient elements in CWD is generally an order of magnitude less than that of leaves, flowers, or fruits (Likens and Bormann, 1970; Whittaker *et al.*, 1979; Woodwell *et al.*, 1975; Young and Guinn, 1966). The organisms feeding on CWD appear adapted to grow on very low nutrient concentrations (Swift, 1977a). Cowling and Merrill (1966) reviewed adaptations of fungi in terms of N; they may apply to other elements and organisms as well. Physiological adaptations include reduced N content in structural substances so more N is available for

Table 4

Mean Elemental Content of Bark and Wood for Selected
Temperate Species[a]

| | Mean elemental content (ppm) | | | |
| | Gymnosperm | | Angiosperm | |
Element	Bark	Wood	Bark	Wood
Nitrogen	2904	704	5129	1189
Phosphorus	589	54	445	110
Potassium	1711	505	2417	1082
Calcium	7232	741	15747	1248
Magnesium	620	157	709	234
Sulfur	540	117	554	176
Manganese	772	149	636	97
Iron	84	10	60	17
Zinc	57	9	83	16
Copper	7	6	8	5
Sodium	90	25	69	29
Boron	11	1	13	1
Molybdenum	4	<1	7	<1
Aluminum	100	—[b]	22	12

[a]From Alban et al. (1978), Attiwill (1980), Duvigneand and Denaeyer-DeSmet (1970), Fahey (1983), Hart (1968), Lambert et al. (1980), Likens and Bormann (1970), Pastor and Bockheim (1984), Whittaker et al. (1979), Woodwell et al. (1975), Young and Guinn (1966).
[b]Not available.

enzymes; simplified metabolic pathways so the number of enzymes required is minimized; and increased number of times an enzyme is used so the amount of N needed for a metabolic task is minimized. Wood-destroying fungi also conserve nutrients by autolysis and thus reuse elements otherwise locked up in inactive mycelium. Although fungi grow on wood without an outside nutrient source, elements may be taken up from the soil from throughfall and from litter leachates. Conservation of elements from these outside sources would also enable fungi to decay nutrient-poor CWD.

Invertebrates appear to have adapted to the low nutrient concentrations of CWD (see Section V,B,3). Bark beetles attack the relatively nutrient-rich inner bark and generally avoid wood altogether. The cerambycids only attack the wood after feeding extensively on inner bark. Thus, essential elements are gathered from a nutrient-rich region and then moved into a nutrient-poor one. Other insects circumvent low-nutrient concentrations, eating fungi or other insects that have already concentrated essen-

tial elements. Yet another adaptation to growing in CWD is an extended life cycle. While most insects complete one to many life cycles in a year, species feeding on wood, such as *Ergates spiculatus* (LeConte) and *Lara avara* (LeConte), take several years to complete their life cycles.

Initial concentrations of many inorganic elements in wood have been reviewed by Ellis (1965); data on other tissues, however, appear to be scant or only available for a few elements. Data from a number of studies have been summarized in Table 4, and although various analysis methods were used, a general indication of the concentrations to be found is represented.

Elemental concentrations vary with species, structural components, and position within trees. Angiosperm wood generally has higher elemental concentrations than gymnosperm wood (Table 4). When bark is considered, angiosperms have higher concentrations of N, K, and Ca than gymnosperms. Both P and Fe appear to be more concentrated in gymnosperm bark than angiosperm bark. Bark contains higher concentrations of elements than wood in both angiosperms and gymnosperms; sapwood and heartwood have similar concentrations of K, Ca, S, Zn, and Cu (Likens and Bormann, 1970; Woodwell *et al.,* 1975). In contrast, P, Mg, Fe, and Na are more concentrated in the sapwood, while Mn is more concentrated in the heartwood. In the few species in which the inner bark has been separated from the outer bark, it appears that N, P, and K concentrations are higher in the inner bark, but concentrations of other elements vary from species to species (Woodwell *et al.,* 1975).

Merrill and Cowling (1966) found N was most concentrated in cambium and least concentrated in heartwood. Within sapwood, N content steadily declined from the youngest annual ring to the sapwood–heartwood boundary. Concentrations were constant throughout heartwood except in the pith region, where they were very high. Certainly, much remains to be learned about the distribution of elements in both undecayed and decayed CWD.

The exact role nutrient content of CWD plays in controlling terrestrial decomposition rates has yet to be explored. Most work has involved additions of various forms of N, and the results of early experiments were summarized by Cowling and Merrill (1966). N content of natural wood is suboptimal for fungi, and addition of inorganic or organic N increases decay rates. In nature, the exact degree to which nutrient content controls decay rates of CWD is less than clear because of the confounding influences of decay-resistant extractives.

Wood decomposition in streams is strongly influenced by the nutrients available in the surrounding water. Lignin and cellulose degradation were stimulated by addition of either organic or inorganic N (Aumen *et al.,*

1983). The relative increases in rates of breakdown caused by N addition were greater for lignin than for cellulose. Furthermore, lignin degradation was sensitive to the form of inorganic N, whereas cellulose degradation was not. Additions of NO_3^- stimulated lignin decay more than additions of NH_4^+. Repression of nitrate metabolism by NH_4^+ may have caused the lesser stimulation of lignin degradation (Aumen et al., 1983).

Addition of either nitrate or phosphate to the water surrounding wood can increase rates of cellulose breakdown, and addition of both speeds degradation even more dramatically (Aumen, 1985). In contrast, lignin decomposition was enhanced only by addition of nitrate and phosphate in combination. The species of wood modifies the potential influence of exogenous nutrients on wood decay. In a laboratory microcosm study, Melillo et al. (1985) found that addition of inorganic phosphorus stimulated decay rates of Alnus wood shavings, but had no effect on the decay of Picea wood shavings. The authors hypothesized that the higher lignin content of Picea limited the stimulatory effects of phosphorus.

In studies of nitrate stimulation of lignocellulose degradation, Aumen (1985) observed that organic N content of wood samples doubled and that ammonium accumulated in solution. Subsequent experiments with ^{15}N tracers revealed that the rapid depletion of nitrate was related to breakdown of lignin and cellulose. Introduced nitrate was rapidly immobilized as organic N on the wood substrate. Enrichment of the ammonium in solution with ^{15}N lagged behind the incorporation of $^{15}NO_3$ into the organic fraction, suggesting a subsequent release of ammonium from an organic N source. Rates of N fixation and denitrification were insignificant. ^{15}N appeared in the ammonium fraction in solution within 1 hr of introduction of nitrate, possibly as a result of dissimilatory reduction of nitrate to ammonium. Nitrogen transformations associated with microbial decomposition of CWD are potentially complex and tightly coupled, and our understanding of their role in stream ecosystems requires a thorough integration of laboratory and field studies.

Availability of inorganic P in stream water may increase the rate of CWD decay. Decay rates of Alnus, Betula, Populus, Abies, and Picea were greater in a first-order than in a ninth-order stream (Melillo et al., 1983). Concentrations of inorganic P in the first-order stream were more than double the P concentrations in the ninth-order stream (0.005 mg liter^{-1} versus 0.002 mg liter^{-1}).

5. Size Effects

Larger boles decay slower than twigs, branches, and small boles. Studies of small pieces of wood have demonstrated a negative correlation between size and decay rate. Abbott and Crossley (1982) measured decay

of *Q. prinus* branches and found those with diameters of 0–1, 1–3, and 3–5 cm had half-times of 5.5, 6.2, and 7.1 years, respectively. Harris *et al.* (1972) reported that logs averaging 11.4 cm in diameter had half-times of 6.2 years, while those averaging 6.4 cm in diameter had half-times of 2.8 years. Comparisons of studies using different sizes of the same species also strongly suggest a negative correlation between size and decay rate. Fogel and Cromack (1977) found small *P. menziesii* branches in Oregon had half-times of 8 years. In contrast, Graham (1982) reported half-times of 58 years for *P. menziesii* boles in the same region. Boles of *A. balsamea* and *P. rubens* in New Hampshire had half-times of 23 and 22 years, respectively (Foster and Lang, 1982; Lambert *et al.,* 1980), whereas twigs of the same two species 5 mm in diameter had half-times of 6 and 3 years, respectively (Gosz *et al.,* 1973).

Studies of CWD often fail to demonstrate a negative size-to-decay rate correlation. For example, Graham and Cromack (1982) reported *Picea* and *Tsuga* logs over 60 cm in diameter did not decay significantly slower than smaller logs. In the Oregon Cascade Range, smaller *Tsuga* and *Pseudotsuga* snags fragmented faster than large ones, but there was no size effect for logs (Graham, 1982). Decay rate of snags <20 cm in diameter in the southern Appalachians was not significantly affected by size (Harmon, 1982). Harmon and Cromack (unpublished) failed to find a significant effect of size on decay rates in *A. concolor* logs, although they observed that the lower, larger diameter part of the bole remained sound after the upper stem had decomposed. The lack of correlation between size and decay rate in these studies of boles may be in part methodological because the high degree of variation associated with decay curves indicates a very large number of samples is required to detect size differences.

In spite of the relationship sometimes observed between size and decay rate, the cause remains unexplained. Many studies have invoked the changes in the ratio of surface area to volume (SA/V) to explain the pattern (Abbott and Crossley, 1982; Fogel and Cromack, 1977; Harris *et al.,* 1972; Triska and Cromack, 1980). As the size of an object increases, SA/V declines, which reduces the rate of gas and liquid exchange. However, in absolute values, the greatest change in SA/V occurs for small-diameter material. The failure to detect a negative correlation between decay rate and size in boles may be caused by small changes in SA/V for large-diameter pieces.

The negative correlation between size and decay rate may also be caused by changes in substrate quality and/or colonization patterns. The proportion of heartwood increases as diameter increases (Fig. 7) (Hillis, 1977); therefore, decay rate should decline with increased size for decay-
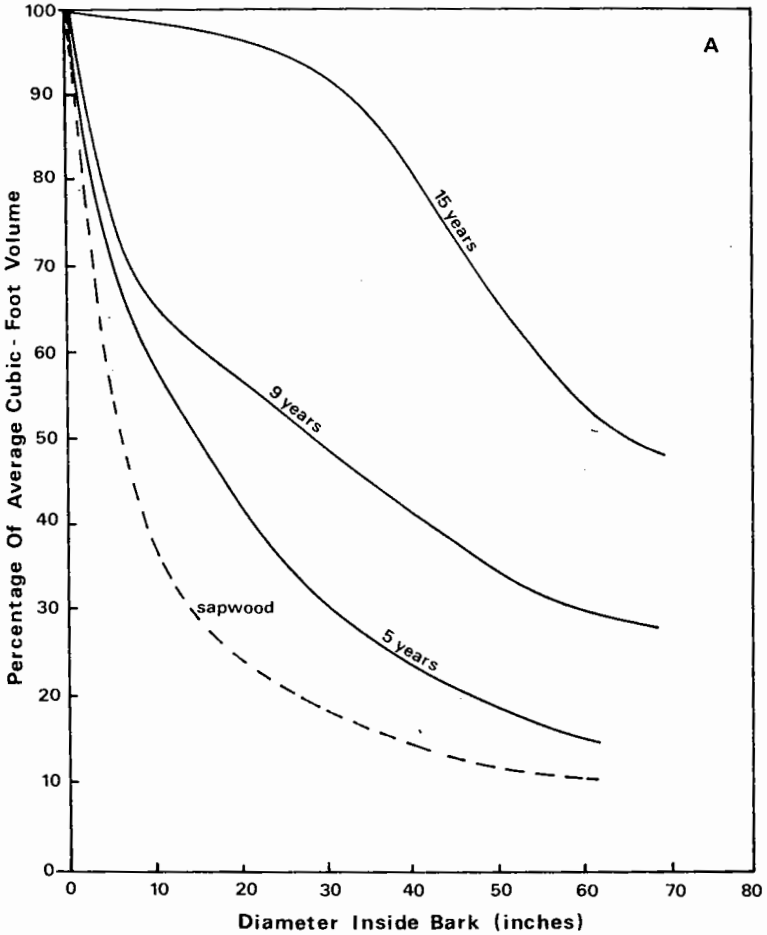
Fig. 7. Fungal colonization of windthrown (A) *Picea sitchensis* and (B) *Pseudotsuga menziesii* boles. The dashed line indicates sapwood volume and the solid line indicates the volume of decayed wood 5, 9, and 15 years after the windstorm. Colonization of *P. sitchensis* is considerably faster than that of *P. menziesii*, but decreases with size for both species.

resistant species. The contribution of the inner bark to total mass also decreases as diameter increases, which reduces the nutrients available for decomposers. Colonization patterns may also cause a negative size-to-decay rate correlation. Decomposers colonize leaves and small branchwood within a period of days to months, but in tree boles, this process takes years. Timber salvage studies after fires and windstorms indicate the rate fungi and insects colonize boles. Decay radially pene-
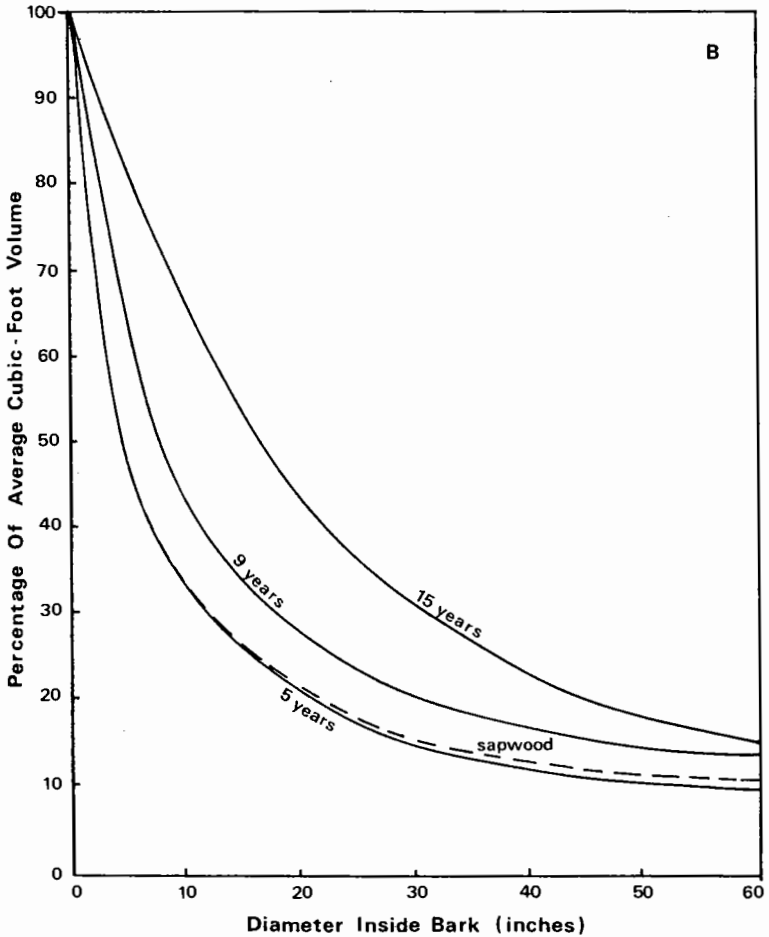
Fig. 7B. See legend on page 183.

trated fire-killed *P. menziesii* boles in Oregon and Washington at rates of
0.8–1.8 cm year^{-1} (Kimmey and Furniss, 1943). In fire-killed trees in
California, the proportion of volume colonized by decomposers increased
with snag age, but decreased with diameter at breast height (Kimmey,
1955). A similar pattern was observed by Buchanan and Englerth (1940) in
windthrown timber in Washington (Fig. 7). Colonization patterns are also
important in aquatic ecosystems, where microbial activity is often re-
stricted to superficial layers. These fungal colonization patterns indicate
larger pieces should decay slower than small pieces.

6. Decomposer Organisms

Perhaps the most important factors determining the rate and type of decay are the organisms involved. Moreover, it is through these organisms that the effects of temperature, moisture, aeration, substrate quality, and size on decay rates are expressed. The following section discusses several taxonomic groups and their importance in terms of CWD decay. It must be borne in mind, however, that most of these taxa act in concert and that they may interact synergistically or antagonistically.

a. Microbes. The microbes that attack CWD can be considered from a taxonomic, synecological, or nutritional and functional perspective. For our purposes, the nutritional and functional perspective is most relevant. However, taxonomic and synecological relationships are also important and have been reviewed by Watling (1982) and Rayner and Todd (1979, 1982), respectively. Functionally, microbes decomposing wood can be divided into those that live on cell contents versus those that degrade cell wall components (Käärik, 1974; Levy, 1982; Swift, 1977a). The former group is frequently divided into molds and staining fungi, while the latter group is divided into bacteria, soft rots, brown rots, and white rots.

The molds are ascomycetes, fungi imperfecti, and phycomycetes that generally feed on cell contents, although some degrade cell walls (Käärik, 1974). Levy (1982) divided molds into primary and secondary types. Primary molds are among the first to colonize CWD and feed on sugars and other simple carbohydrates occurring in parenchyma tissues and sapwood. In contrast, secondary molds are associated with the brown- and white-rot basidiomycetes. The limited amounts of sugars and other simple polysaccharides in wood tissue mean that primary mold fungi do not cause a major loss of biomass from CWD. However, the use of nonstructural carbohydrates by these fungi may inhibit the colonization of wood by basidiomycetes (Hulme and Shields, 1970).

Stain fungi are ascomycetes and fungi imperfecti that have pigmented hyphae and stain-invaded tissues. As with primary molds, stain fungi feed on materials stored in the sapwood and quickly colonize CWD. As in the case of primary molds, the actual loss in weight caused by stain fungi is very small.

Bacteria break down cell walls, but at rates that are much slower than basidiomycetes (Käärik, 1974). These taxa appear to be most important in moist environments. Earlier studies (e.g., Willoughby and Archer, 1973) isolated many fungal species from submerged wood. The biological activity of these species has recently been called into question, however. For example, scanning electron microscopy (SEM) indicates that fungal hyphae are uncommon on the surface of submerged CWD (Aumen *et al.,*

1983). In contrast to fungi, single-celled bacteria and actinomycetes are very common and are probably the major CWD decomposers in aquatic environments (Aumen *et al.,* 1983). Several specific bacteria have been isolated and implicated in soft rot in wood found in aquatic environments—*Bacillus polymixa, Bacillus cereus,* and *Bacillus macerans* (Ellwood and Ecklund, 1959; Knuth and McCoy, 1962). Other bacteria found on submerged wood include *Klebsiella pneumoniae, Enterobacter agglomerans,* and *Enterobacter* spp. (Aho *et al.,* 1974; Buckley and Triska, 1978; Knuth, 1964). As with molds and stain fungi, the parenchyma tissue is decomposed by bacteria. Other important sites of bacterial activity are pit chambers where bacteria are involved in the breakdown of pit membranes (Sutherland *et al.,* 1979). This in turn increases decay rates by allowing gases and water to move more freely within the wood and also by increasing access to those organisms unable to penetrate cell walls (Levy, 1982). Some bacteria and actinomycetes are able to fix atmospheric nitrogen, which may increase the decomposition rates of other decomposers. *Enterobacter* may play an important role in nutrient cycling because of its ability to fix nitrogen in both terrestrial and aquatic environments (Aho *et al.,* 1974; Buckley and Triska, 1978). Bacteria are also undoubtedly important in decomposing dead fungal hyphae.

Soft rots are ascomycetes and fungi imperfecti that break down cell walls, but primarily utilize cellulose and hemicellulose while modifying lignin to a small extent (Levi, 1965). Soft rots are most important in degrading wood in contact with the soil or those pieces with a high or variable moisture content because they tolerate poor aeration better than basidiomycetes (Duncan, 1961). Thus, their action is probably highest in aquatic environments or in riparian zones. Angiosperm wood is more susceptible to attack by soft rots than gymnosperm wood. The manner in which soft rots attack wood is unique on both a macro- and microscale. On the macroscale, these fungi cause a slow degradation, advancing inward from the surface after destroying outer layers (Käärik, 1974). On the microscale, soft rots form distinctive cavities in the S2 layers of tracheids and fibers (Levi, 1965; Savory, 1954a).

Brown rots are caused by basidiomycetes that decompose cellulose and hemicellulose, but not lignin. Their chemical influence on CWD is therefore quite similar to that of soft rots. Brown-rot fungi do not thin cell walls until late in decomposition (Montgomery, 1982). Along with white rots, brown-rot fungi are responsible for the majority of CWD decomposition in terrestrial ecosystems.

White rots are also basidiomycetes, but, unlike brown rots, are able to decompose lignin as well as cell wall polysaccharides. The action of white rots is confined to near the hyphae (unlike the brown rots), and cell wall

material is lost from the cell lumen toward the middle lamella. This sequential loss of material causes furrows to be formed in the cell wall, and in advanced decay, these furrows may join (Montgomery, 1982).

Much is known about how these functional groups modify wood chemically and structurally. Most current knowledge, however, is based on pure cultures, and much remains to be learned about how these organisms interact. Using a scanning electron microscope, Blanchett and Shaw (1978) observed that yeast, bacteria, and basidiomycetes grew in close association in decomposing wood. Furthermore, they demonstrated that mixed cultures decayed wood faster than basidiomycetes alone. In another situation, the presence of mold fungi inhibited the colonization of wood by brown rot (Toole, 1971) and thus inhibited decay.

b. *Invertebrates.* Invertebrates, chiefly insects, play a significant role in the decomposition of CWD by attacking wood directly or by influencing other organisms. The impact invertebrates have on CWD depends upon several factors: the stage of the tree during attack, the part of the tree utilized, and the other associated organisms. Many factors influence the abundance of invertebrates and hence the rate they decompose CWD. Substrate quality and extractives profoundly influence the extent and rate to which CWD is colonized. For example, the wood-boring beetle fauna is very limited in decay-resistant tree taxa such as *Sequoiadendron* and *Taxus* (Smythe and Carter, 1969). Differential feeding trials of *Reticulitermes flavipes* (Kollar) on wood indicate high survival rates on wood of most tree species, but low survival on *J. nigra* and certain death when fed non-oven-dried *Sequoiadendron* and *Taxodium*.

Specific examples of the way invertebrates influence decay include the following. Carpenter ants reduce CWD to dust and deposit this material outside the branch or log without ingestion. Wood-boring bees may do the same. Many insects eat wood, thereby reducing the particle size and modifying the wood during digestion. Insects introduce microbes into the CWD at the time of attack, thus hastening decay (Ausmus, 1977; Swift, 1977b). Invading invertebrates have an associated fauna of parasites and predators that follow and their feces and decomposing body parts contribute nutrients to the CWD ecosystem. The cavities that are created, combined with the variously modified wood particles, create suitable environments for microorganisms. These same microorganisms, besides decomposing CWD, serve as food for invertebrates such as springtails (Collembola), mites, and dipteran larvae. The presence of galleries also allows nonboring invertebrates such as millipedes, centipedes, and wood lice to invade CWD. Invertebrates attract larger vertebrate predators (skunks, bears, and woodpeckers) that fragment CWD while searching for prey.

Despite these general observations on decay caused by invertebrates, few field studies have measured process rates. Hickin (1963) provides a detailed account of the major wood-boring insects of Britain. He includes information on *Xestobium rufovillosum,* the death-watch beetle, including the relationship between the life cycle of the beetle and the reduction of the wood over time. The degree of wood decay at the time of oviposition determined the length of the life cycle of the insect. The life cycle was as long as 55 months when wood (oak sapwood plus white rot) showed 18% weight loss and <12 months when wood showed 73% weight loss. Swift *et al.* (1976) discuss the decomposition of branch wood in a mixed deciduous woodland in Britain and include estimates of decay rates following branch death, branch fall, animal invasion, and termination. Swift (1977b) reports a net loss of nutrients occurred in branches invaded by animals; in this instance, the dominant organism was a crane fly larva.

Laboratory studies of termites indicate wood consumption rates of 10–90 mg (g termites)$^{-1}$ day^{-1} (dry weight of food/fresh weight of termites) (Wood, 1976). Field estimates of consumption rates by populations of known size are virtually nonexistent (Wood, 1976, 1978). Wood and Sands (1978) calculated a mean weight-specific consumption rate of 30 mg g^{-1} live weight per day for all groups of termites except the Macrotermitinae (chiefly fungus feeders). Smythe and Carter (1969) cite consumption figures for *Reticulitermes flavipes* in feeding trials of wooden blocks of different tree species. Their procedure involved placing blocks of wood (oven-dried and non-oven-dried) on sand or sawdust for 8 weeks. Consumption rates ranged from 0.003 mg termite^{-1} day^{-1} (*Sequoia sempervirens,* non-oven-dried, on sawdust) to 0.088 mg termite^{-1} day^{-1} (*Pinus palustris,* oven-dried, on sand). Wood (1976) cautions on extrapolating from feeding trials where only a single food source is provided. Gentry and Whitford (1982) studied several species of subterranean termites in Georgia by placing pinewood blocks (fresh and preinoculated with fungi) on the ground in different habitats and monitoring feeding activity. Blocks placed in the *P. palustris* habitat had lost ~17% of the original weight in 9 months due to termite feeding compared to a 5–7% consumption loss due to termites in *Q. nigra* and *Liriodendron* habitats.

Savely (1939) estimated the amount of wood eaten by the larvae of the cerambycid *Callidium antennatum* ranged from 1.26 to 3.37 g. Expressed as grams of dry wood per gram of dry larvae, the average was 77.9 g. Similar calculations for the buprestid *Chrysobothris* sp. revealed that 0.39–2.06 g of wood was eaten by larvae (Savely, 1939). Expressed as grams of dry wood eaten per gram of dry larvae, the average was 79.0 g, which is remarkably similar to the value for *Callidium.*

IV. AMOUNT AND DISTRIBUTION OF COARSE WOODY DEBRIS

The amount of CWD in an ecosystem represents the balance between additions from tree mortality and breakage, on one hand, and losses caused by respiration, fragmentation, and transport, on the other. However, the quantity of CWD added to ecosystems varies considerably both spatially and temporally (see Section II,C–D), leading to large fluctuations in CWD mass away from the predicted steady-state level of biomass. Moreover, these pulses of CWD input decay slowly (see Section III,D), and a great deal of time must elapse before these departures from the steady-state level are eliminated. This strong historical influence introduces wide fluctuations in CWD amounts, making it difficult to evaluate the influence that temperature, moisture, and substrate quality have on controlling the amount of CWD.

A. Estimating Biomass

1. Volume Estimation

Volume, total surface area, and projected area can be estimated by recording the length, diameter, decay status, orientation, and species of pieces within a quadrat or unit of stream area (Froehlich, 1973; Swanson *et al.*, 1984). Various plot sizes and shapes have been used in this type of sampling; Warren and Olsen (1964) found long rectangles more efficient than circular plots.

The line-intersect method is used extensively to estimate volume of woody fuels and logging residue (Brown, 1974; Pickford and Hazard, 1978; Van Wagner, 1968; Warren and Olsen, 1964) or fine woody debris in streams (Froehlich, 1973; Swanson *et al.*, 1984). In upland areas, a series of lines of known length are established in random directions; lines for sampling streams are oriented at a 90° angle to the channel and located at regular intervals along streams. The diameter, species, and decay status are recorded for all pieces intersecting a horizontal plane defined by the line. Assuming the pieces are cylindrical, horizontal, and randomly oriented, volume can be calculated using the formula

$$V = \pi^2 \Sigma \, d^2/8L$$

where V is the volume, d is the diameter of a piece, and L is the transect length.

2. *Mass Determination*

Conversion of volume to mass requires subsampling of logs and snags for density. The measurement of density is discussed in detail in Section III,A.

In the case of aquatic studies, density has rarely been measured, and a density of 0.5 Mg m^{-3} has often been applied. While this value probably does represent the average for undecayed wood of all species, it overestimates the density of undecayed coniferous wood by as much as 20–40% and underestimates the density of undecayed hardwood by the same amount.

In many fire-fuels studies, wood is separated into sound and rotten classes (Brown and See, 1981; Sacket, 1979), with densities of 0.4 and 0.3 Mg m^{-3}, respectively. However, our studies (Table 5) indicate the mean density of wood for coniferous forests ranges between 0.16 and 0.20 Mg m^{-3}, suggesting that use of the former wood densities may have resulted in overestimates of CWD biomass by a factor of 1.6–2.0.

The density of CWD has been estimated by using a decay-class system. Wood-decay classifications commonly place CWD into three to five decay classes that are then sampled to determine the mean density for each class. Definition of decay classes varies between studies. Using the penetration of a pointed 2.5-cm metal rod into a log as an indicator, Lambert *et al.* (1980) defined three classes: (1) slightly decayed, rod penetrates <0.5 cm; (2) moderately decayed, rod penetrates 0.5 cm to half the diameter; and (3) advanced decay, rod can be pushed completely through the log. Lang and Forman (1978) also used the penetration depth of a pointed rod to define three decay classes, but in the moderate decay class the rod penetrated to 2.5 cm.

External characteristics of CWD have also been used to define decay classes (Fogel *et al.,* 1973; MacMillan, 1981; Sollins, 1982; Triska and Cromack, 1980). These include bark cover; the presence, color, and abundance of attached needles, twigs, and branches; the cover of bryophytes and lichens; species and size of fungal fruiting bodies; the color, crushability, moisture, and structure of the wood; the type of decay present (e.g., brown cubical versus white stringy rot); whether the exposed wood is bleached; whether the log supports itself or has collapsed under its own weight; the cross-sectional profile, ranging from circular to extremely elliptical; the age, size, and density of tree seedlings and saplings growing on the log; the presence and distribution of roots throughout the wood; and the presence of various decay processes such as sapwood sloughing. Although this is a long list, in many cases only the presence or absence of a single characteristic is needed to classify the log or snag. In many studies, the criteria used to define the classes are chosen subjectively by

Table 5

Volume, Biomass, and Projected Area of Logs and Snags for Various Temperate Forested Ecosystems

Ecosystem	Stand age (years)	Lower limit (cm)	Volume (m³ ha⁻¹)		Biomass (Mg ha⁻¹)		Projected area (%)		References[a]
			Logs	Snags	Logs	Snags	Logs	Snags	
Coniferous forests									
Abies amabilis	23	10	—[b]	—	20	60	—	—	7
Abies amabilis	130	10	—	—	75	157	—	—	7
Abies balsamea	12	3	~90	~80	35	27	—	—	14
Abies balsamea	22	3	~107	~52	30	17	—	—	14
Abies balsamea	33	3	~130	~30	32	12	—	—	14
Abies balsamea	46	3	~60	<10	15	0.25	—	—	14
Abies balsamea	52	3	~50	<10	13	0.25	—	—	14
Abies concolor	—	15	216	178	49	52	6.8	2.8	11
Larix occidentalis	—	7.5	—	—	40	—	—	—	1
Picea–Abies	200+	7.5	416	—	97	—	12.1	—	10
Picea–Abies	—	7.5	—	—	53	—	—	—	1
Picea–Tsuga	200+	15	—	—	93	26	6.1	0.1	5
Pinus–Abies	—	15	151	130	33	43	4.5	1.9	11
Pinus jeffreyi	—	15	82	2	28	0.7	2.1	0.04	11
Pinus contorta	—	7.5	—	—	32	—	—	—	1
Pinus contorta	105	—	—	—	6	6	—	—	2
Pinus contorta	70	—	—	—	1	2	—	—	2
Pinus contorta	240	—	—	—	1.5	41	—	—	2
Pinus ponderosa	—	7.5	—	—	23	—	—	—	1
Pinus ponderosa	—	7.5	54	—	18	—	—	—	17
Pinus mixed	50+	7.5	~30	—	7	—	1.5	—	10
Pinus mixed	50+	7.5	—	—	11	—	—	—	9

(continued)

Table 5 (*continued*)

Ecosystem	Stand age (years)	Lower limit (cm)	Volume (m³ ha⁻¹) Logs	Snags	Biomass (Mg ha⁻¹) Logs	Snags	Projected area (%) Logs	Snags	References[a]
Pinus mixed	—	2.5	—	—	17.8	—	—	—	12
Pseudotsuga/Abies– Picea	—	7.5	125	—	42	—	—	—	17
Pseudotsuga–Tsuga	450	—	500	65	190	24.6	—	—	8
Pseudotsuga–Tsuga	450	15	396	270	81	54	—	—	18
Pseudotsuga–Tsuga	100	15	491	153	108	34	13.7	1.6	3
Pseudotsuga–Tsuga	130	15	309	167	65	42	12.3	2.9	3
Pseudotsuga–Tsuga	250	15	488	339	93	80	20.0	4.5	3
Pseudotsuga–Tsuga	450	15	490	349	82	84	16.4	3.9	3
Pseudotsuga–Tsuga	750	15	554	635	97	105	20.1	5.0	3
Pseudotsuga–Tsuga	1000+	15	574	376	115	81	20.2	3.5	3
Pseudotsuga–Tsuga	3	20	673	—	249	—	—	—	13
Pseudotsuga–Tsuga	19	20	981	—	342	—	—	—	13
Pseudotsuga–Tsuga	110	20	389	—	138	—	—	—	13
Pseudotsuga–Tsuga	181	20	376	—	130	—	—	—	13
Pseudotsuga–Tsuga	515	20	1421	—	490	—	—	—	13
Sequoiadendron– Abies	—	15	722	51	247	22	7.0	1.0	11
Thuja–Tsuga	—	7.5	—	—	66	—	—	—	1
Tsuga heterophylla	130	15	—	—	212	—	—	—	6
Tsuga–Picea	200+	15	—	—	167	40	11.3	0.1	5

				Deciduous forests					
Acer–Betula	20	3	—	—	31.6	6.2	—	—	20
Acer–Fagus	30	3	—	—	12.8	7.9	—	—	20
Acer–Betula	40	3	—	—	7.6	8.4	—	—	20
Acer–Fraxinus	57	3	—	—	4.7	5.1	—	—	20
Acer–Fagus	60	3	—	—	10.9	12.2	—	—	20
Acer–Betula	83	3	—	—	16.8	8.2	—	—	20
Acer–Fagus	~200	3	—	—	38.4	10.9	—	—	20
Fagus–Betula	200+	7.5	82	—	29	—	3.0	—	10
Liriodendron	40	7.5	51	—	14	—	4.0	—	10
Liriodendron	—	2.5	—	—	7.5	—	—	—	12
Populus tremuloides	—	—	—	—	14	11	—	—	4
Prunus pensylvanica	10	3	—	—	31.3	4.0	—	—	20
Quercus–Carya	—	2.5	—	—	15	—	—	—	12
Quercus mixed	330+	10	—	—	21	—	—	—	15
Quercus mixed	220+	5	46	—	16	—	1.6	—	16
Quercus mixed	—	—	—	—	—	—	2.0	—	19
Quercus mixed	200+	7.5	94	—	24	—	1.6	—	10
Quercus prinus	200+	7.5	132	—	21	—	1.7	—	10
Quercus prinus	40+	7.5	—	—	11	—	—	—	9
Quercus prinus	—	2.5	—	—	22	—	—	—	12

[a](1) Brown and See (1981), (2) Fahey (unpublished), (3) Franklin et al. (unpublished), (4) Gosz (1980), (5) Graham and Cromack (1982), (6) Grier (1978), (7) Grier et al. (1981), (8) Grier and Logan (1977), (9) Harmon (1980), (10) Harmon (unpublished), (11) Harmon and Cromack (unpublished), (12) Harris et al. (1973), (13) Huff (1984), (14) Lambert et al. (1980), (15) Lang and Forman (1978), (16) MacMillan (1981), (17) Sacket (1979), (18) Sollins (1982), (19) Thompson (1980), (20) Tritton (1980). Unpublished data is on file at Forestry Sciences Laboratory, RWU-1251, Corvallis, Oregon.

[b]Not available.

the investigator (Fogel *et al.,* 1973; MacMillan, 1981; Sollins, 1982; Triska and Cromack, 1980). However, more objective classification methods, such as those traditionally used in plant community analysis, are applicable (see Gauch, 1982; Pielou, 1977). Cline *et al.* (1980), for example, successfully used cluster analysis to define five snag decay states.

3. Statistical Considerations

Statistical distributions of biomass parameters need to be considered along with average values when comparing CWD in ecosystems. These quantities are usually not normally distributed, but tend to be positively skewed (Fig. 8), with the mode lower than the mean or the median. Sample variances associated with CWD biomass are very high, necessitating a large number of samples.

B. Biomass of Coarse Woody Debris

Surface areas, volumes, and biomass of CWD in temperate forest and associated aquatic systems are presented in this section (see Section V,A). Problems arise when interpreting existing data on CWD biomass. Lack of information on the disturbance history, decay rates, input rates, and site characteristics such as slope, aspect, temperature, and soil moisture makes it difficult to explain differences. Data are not entirely comparable because of variations in the lower size limits of included CWD and assumed values for wood density. Another serious problem is differences in scope of the studies—many include downed logs but not snags, a few are concerned only with snags, and some exclude large branches.

1. Area Covered by Coarse Woody Debris

Although less frequently considered than volume or biomass, the area covered by CWD is important ecologically. Area is most commonly reported as projected area for terrestrial sites, but total surface area is sometimes also calculated, particularly for aquatic ecosystems. Projected area is probably most relevant for soil-forming processes and habitat for animals utilizing the interface between soil and CWD, while total surface area is most pertinent for species inhabiting CWD surfaces. Plants usually colonize the upper half of the surface of CWD; therefore, surface areas somewhere between the total and projected are probably most meaningful for plant habitat considerations (see Section V,A). Projected area is not usually measured in stream studies, in part because it does not relate well to the geomorphic functions of wood. For example, CWD may be buried and stacked and yet may control geomorphic processes. It is more common to consider the area of stream influenced by CWD (see Section V,D).
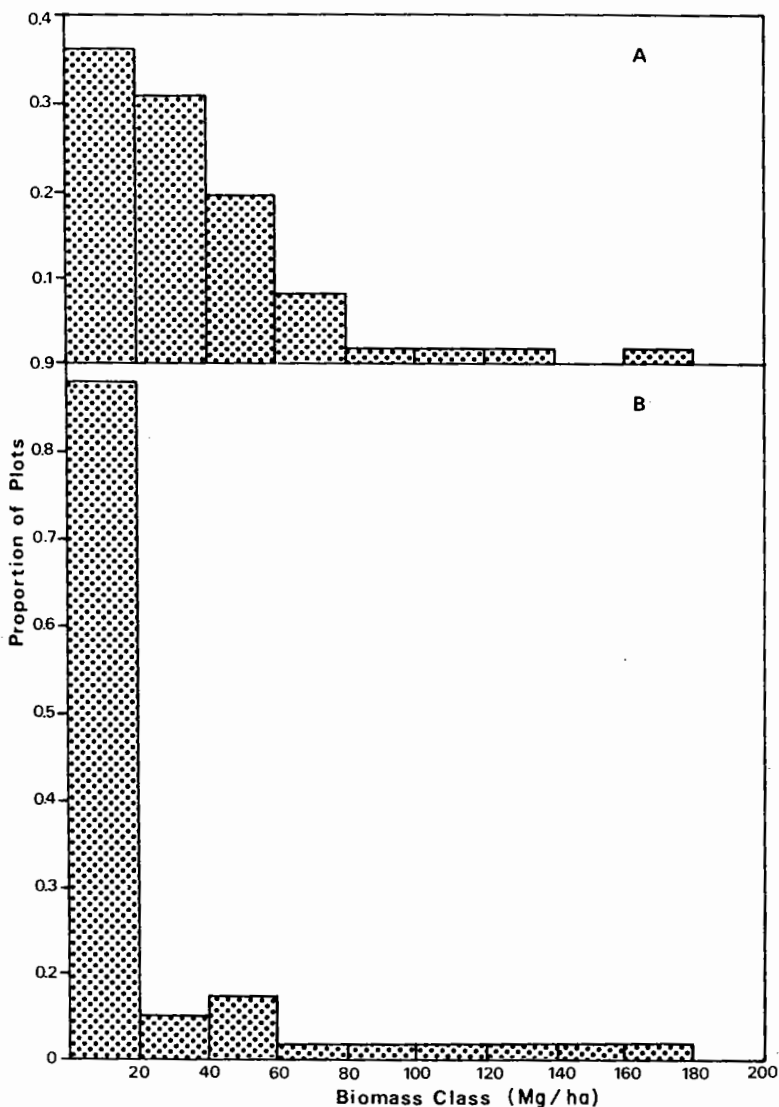
Fig. 8. The distribution of biomass classes (Mg ha^{-1}) for logs (A) and snags (B) from a *Sequoiadendron–Abies* forest in Sequoia–Kings Canyon National Park, United States. Seventy-two 625-m² plots were sampled.

Values for projected cover of CWD range widely in forest systems (Table 5). The highest projected areas—14–25% of the forest floor—are found in the *Pseudotsuga–Tsuga* forests of the Pacific Northwest. The lowest reported cover of CWD is in *Quercus* forests in eastern North

America, with log covers of 1.6–2.0% of the ground surface. Snags were not measured in these studies, but would probably add <0.1% cover to the total CWD cover of *Quercus* forests.

The form of CWD drastically affects the amount of forest floor covered, but has little influence on total surface area. Snags contribute very little to the overall projected area, even though they may comprise a large volume or mass of CWD. In stands with a high proportion of CWD formed by snags, the projected cover will be low.

2. Volume of Coarse Woody Debris

Some representative data on volumes of CWD are provided in Table 5. The total volume of CWD in terrestrial ecosystems ranges from a low of ~60 m^3 ha^{-1} in an *A. balsamea* forest to 1189 m^3 ha^{-1} in a *Pseudotsuga–Tsuga* forest. Unfortunately, snag volumes have not been reported for deciduous hardwood forests. In terms of logs alone, it appears that many coniferous forests have an order of magnitude more volume than deciduous forests. The volume of CWD in aquatic ecosystems also varies considerably, ranging from 2.5 to 4500 m^3 ha^{-1} (Table 6).

3. Biomass of Coarse Woody Debris

A close relationship exists between volume and biomass because of the relatively limited range in wood densities. For example, in *Pseudotsuga–Tsuga* forests, the estimated mean log density ranges from 0.16 to 0.20 Mg m^{-3} for stands between 100 and 1000 years old (Table 5). The mean density of snags in these forests was more variable, ranging from 0.16 to 0.30 Mg m^{-3} over the same age range (Table 5).

Reported values of total CWD mass vary from ~6 to more than 269 Mg ha^{-1} for intact temperate forests. Particularly large values are associated with the coniferous forests of western North America, including old-growth *Pseudotsuga* and *Sequoiadendron* forests. In general, deciduous forests have lower log masses than coniferous forests. The range of values for deciduous forests is 11–38 Mg ha^{-1}, whereas the range of values for coniferous forests is 10–511 Mg ha^{-1} (Table 5). The biomass of snags also varies widely, with masses of 1–157 Mg ha^{-1} reported. Values for biomass of CWD in terrestrial systems are difficult to compare because both logs and snags are often not included within a single study. Relative proportions of logs and snags vary widely (see Section IV,D); therefore, total biomass is difficult to estimate from one component alone.

Biomass of CWD in streams shows a similar large variation in mass (Table 6). Reported amounts for channels undisturbed by management activities range from 1 to 1800 Mg ha^{-1}. In addition to forest type, disturbance history, and successional stage, which also affect CWD amounts in

Table 6

Volume and Biomass of Coarse Woody Debris (>10 cm diameter) in Streams Flowing through Natural (Unmanaged) Temperate Forests[a]

Stream name	Stand age (year)	Drainage area (ha)	Mean channel width (m)	Reach length sampled (m)	Coarse woody debris Volume (m^3 ha^{-1})	Biomass (Mg ha^{-1})	References[b]
Picea sitchensis–Tsuga heterophylla, Prince of Wales Island, Alaska							
Cabbage Creek	300	—[c]	4.1	100	55	22	10
Aha Creek	300	—	4.8	300	230	91	10
Holmgren Creek	300	—	2.1	90	140	57	10
3/10 Mile Creek	300	—	3.0	90	240	94	10
Bonnie Creek	500	—	14.3	200	300	120	10
Picea sitchensis–Tsuga heterophylla, coastal British Columbia, Canada							
Government Creek	200	390	11.0	575	450	180	3
Government Creek	200	680	18.0	696	580	230	3
Government Creek	200	690	16.0	981	580	230	3
Hangover Creek	200	2020	20.0	1852	520	210	3
Reach 5	200	850	—	75	850	340	11
Reach 6	200	850	—	75	550	220	11
Reach 7	200	850	—	75	1700	670	11
Reach 8	200	850	—	75	320	130	11
Reach 4	200	900	—	75	550	220	11
Pseudotsuga menziesii, Klamath Mountains, California							
Horse Flat Tributary	300	7	3.2	74	45	18	5
Rotten Log Creek	300	59	3.8	101	320	130	5
Hidden Creek	300	75	1.6	91	520	210	5
Hidden Creek	300	84	2.6	98	95	38	5

Table 6 (*continued*)

Stream name	Stand age (year)	Drainage area (ha)	Mean channel width (m)	Reach length sampled (m)	Coarse woody debris		References[b]
					Volume (m^3 ha^{-1})	Biomass (Mg ha^{-1})	
Horse Flat Creek	300	110	3.2	90	250	100	5
Lost Glove Creek	300	124	3.6	90	450	180	5
Horse Flat Creek	300	128	2.8	85	1200	460	5
Horse Flat Creek	300	176	3.9	90	75	30	5
Shinbuster Creek	300	600	7.2	185	120	50	5
Shinbuster Creek	300	640	7.2	183	18	7	5
Coon Creek	300	1360	11.8	193	10	4	5
Sequoiadendron gigantia, Sierra Nevada Mountains, California							
Suwanee Creek	1000	160	4.7	210	550	220	7
Crescent Creek	1000	190	5.0	210	1000	420	7
Sequoia sempervirens, California							
Gans West Creek	500	50	4.8	90	1100	450	8
Low Slope Schist Creek	500	70	3.8	90	1000	420	8
Prairie Creek at Hope Creek	500	70	2.3	115	4500	1800	4
Hayes Creek	500	150	4.5	132	3500	1400	4
Little Lost Man Creek	500	350	6.4	253	2800	1100	4
Prairie Creek at Little Creek	500	350	3.9	107	240	96	4
Prairie Creek at Forked Creek	500	660	4.7	200	250	100	4
Prairie Creek at Zig Zag Creek	500	820	6.7	232	420	170	4

Little Lost Man Creek	500	910	9.6	596	980	390	4
Prairie Creek at National Tunnel	500	1120	8.0	269	2200	880	4
Prairie Creek at Brown Creek	500	1670	11.0	335	1700	680	4
Prairie Creek at Campground	500	2720	18.5	395	400	160	4
Picea engelmannii, Idaho							
4th of July Creek	200	900	3.7	90	88	35	6
Roaring Creek	200	1030	2.3	90	50	20	6
Pinus, Idaho							
Squaw Creek	200	6670	7.3	90	120	48	6
West Pass Creek	200	6750	4.7	85	2.5	1	6
East Fork Salmon River	200	19600	14.4	270	2.5	1	6
Bruno Tributary	200	450	1.1	60	42	17	6
Picea–Tsuga, White Mountains, New Hampshire							
Bessililul Creek	100	30	1.9	90	80	32	9
Flume Creek	100	190	6.6	180	30	12	9
Pseudotsuga menziesii, Cascade Mountains, Oregon							
Watershed 10S	300	2	.6	120	1200	470	1
Watershed 10N	300	4	.9	120	1200	490	1
Watershed 9	400	8	3.5	170	500	200	6
Allen Creek Tributary 1	300	8	.9	120	780	310	1
Allen Creek Tributary 2	300	9	.9	120	420	170	1
Watershed 10	300	10	1.8	120	580	230	1
Mortality Creek	85	15	2.0	90	700	280	6
Devils Club Creek	500	20	2.6	85	880	350	6

Table 6 (*continued*)

Stream name	Stand age (year)	Drainage area (ha)	Mean channel width (m)	Reach length sampled (m)	Coarse woody debris Volume (m^3 ha^{-1})	Biomass (Mg ha^{-1})	References[b]
Poodle Creek	190	28	2.3	120	400	160	1
Quartz Creek Tributary 1	300	34	3.4	120	1400	550	1
Quartz Creek Tributary 3	250	36	2.7	120	680	270	1
Christy Creek Tributary	300	39	2.7	120	400	160	1
Quartz Creek Tributary 2	250	49	2.7	120	620	250	1
Clover Creek	135	52	2.8	90	300	120	6
Blue River Tributary	300	57	3.4	120	45	18	1
Cottonwood Creek	90	62	3.0	90	170	69	6
Cold Creek	500	70	7.0	200	850	340	7
Watershed 2	500	80	5.2	150	750	300	6
Hagan Creek	90	85	2.5	90	480	190	6
Winberry Creek North Fork	300	114	8.5	120	700	280	1
Quartz Creek Tributary 4	300	117	5.8	120	320	130	1

Stoney Creek	250	163	4.9	120	780	310	1
Mack Creek	500	536	9.1	120	650	260	1
Mack Creek	500	600	12.0	350	570	228	6
School Creek	160	645	4.6	120	400	160	1
Lookout Creek	500	1200	15.5	550	340	136	6
Lookout Creek	300	3044	16.8	120	150	61	1
Lookout Creek	500	6000	24.0	240	230	92	6
McKenzie River	100	102000	40.0	800	60	24	6
Hardwood, Smoky Mountains, Tennessee							
Minnie Ball Branch	200	44	5.7	90	70	28	2
Pardon Branch	50	52	3.6	90	40	16	2
Ekaneetlee Branch	200	70	5.2	90	160	64	2
Ramsey Prong	200	73	6.5	90	60	24	2
Trillium Creek	200	96	4.6	90	300	120	2
Picea–Abies, Smoky Mountains, Tennessee							
Noland	200	21	6.2	90	140	56	2
Salola	200	70	3.4	90	220	88	2

[a]Specific gravity equals 0.40 for all sites, although many authors used other values.

[b](1) Froehlich (1973), (2) Gregory and Lienkaemper (unpublished), (3) Hogan (1985), (4) Keller *et al.* (1985), (5) Lehre (unpublished), (6) Lienkaemper (unpublished), (7) Luchessa (unpublished), (8) Swanson (unpublished), (9) Swanson and Sedell (unpublished), (10) Swanson *et al.* (1984), (11) Toews and Moore (1982). Unpublished data is on file at Forestry Sciences Laboratory, RWU-1653, Corvallis, Oregon.

[c]Not available.

upland areas, channel size influences CWD amounts in lotic ecosystems. Biomass measurements in streams are also strongly influenced by geomorphic processes (see Section V,D). Erosion and deposition of sediment in channels may also change the biomass estimated in streams. Burial and exposure of CWD change the number of pieces that can be inventoried. Furthermore, changes in channel width alter the area of inventory, which may also change the biomass estimate.

Unfortunately, there are no data available concerning CWD biomass in large rivers. The historical record shows that fast, turbulent rivers as well as low-gradient rivers had large amounts of wood influencing their channels. Great drift jams of logs were reported and described for the Amazon, Congo, Orinoco, Ganges, Mississippi, and McKenzie Rivers as well as for rivers in China (Lyell, 1969). For sixth- to eighth-order streams, log jams were a common feature of pristine streams (Michigan Historical Society, 1883; Sedell and Luchessa, 1982; Triska, 1984).

The lower Siuslaw River and lower North Fork Siuslaw River in Oregon were so filled with fallen trees that trappers in 1826 were unable to explore much of these river systems (Ogden, 1961). The Willamette River between Corvallis and Eugene flowed in five separate channels in 1840 (Secretary of War, 1875). The Captain of the Portland district reported that the "obstacles were so great above Corvallis" and that the river banks were heavily timbered for a distance of 1–3 km on either side. In a 10-year period, over 5500 snags and drift trees were pulled from an 80-km reach of river, as the river was confined to one channel by engineering activities. These trees ranged from 1.5 to 2.7 m in diameter and from 27 to 36 m in length (Secretary of War, 1875). Sedell and Frogatt (1984) and Sedell and Luchessa (1982) list rivers in Oregon and Washington that were completely blocked in their lower main channels by driftwood. The Skagit River, Washington, drift jam was 1–2 km long and 0.5 km wide. The Stillaguamish River had six debris jam closures from the mouth to 28 km upstream. Snags were so numerous, large, and deeply imbedded in the bottom that a stream snag boat was required to operate for 6 months to open a channel 35 m wide on the Stillaguamish (Secretary of War, 1881). Another lower-gradient stream system, the North River, had 11 drift jams along the main river system. Drift jams in high-gradient systems often occurred where the channel gradient decreased abruptly. The Nooksack River is an example (Fig. 9).

C. Factors Controlling Biomass

1. Effects of Forest Type on Biomass

Biomass values illustrate the tendency for greater accumulations of CWD in coniferous than hardwood forests (see Section III). A major
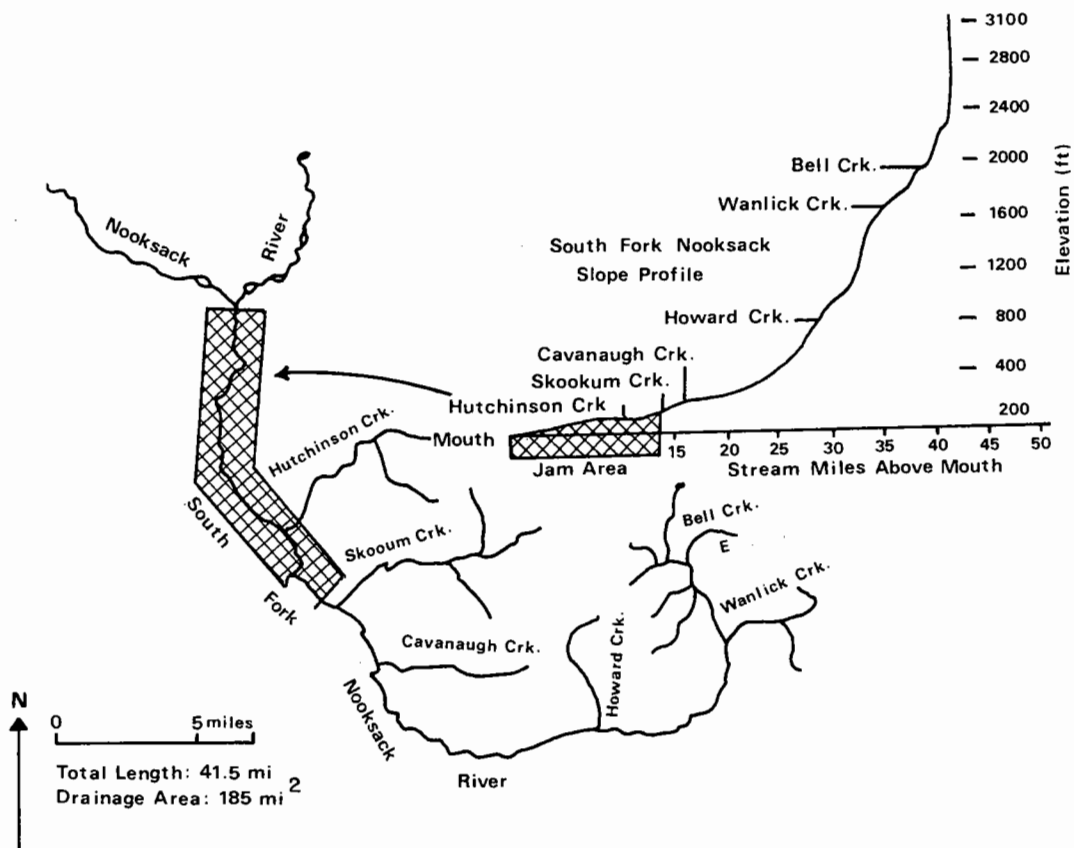
Fig. 9. Map and longitudinal profile of the South Fork of the Nooksack River of western Washington indicating the position of an extensive log jam.

cause of these differences appears to be faster decay in deciduous forests. Smaller sized material, higher substrate quality, and/or a climate more favorable to decay make CWD decay faster in deciduous than in conifer ecosystems. However, input rates are also partially responsible for the difference, as illustrated by a comparison of decay and input rates in *Pseudotsuga–Tsuga* and *Quercus* forests. Assuming the input rate of logs is similar for *Pseudotsuga–Tsuga* and *Quercus* forests, the biomass differences would depend upon decay rates alone. Because the reported decay rate constants are 0.03–0.04, and 0.01–0.03 year^{-1} for *Quercus* (MacMillan, 1981) and *Pseudotsuga* (Graham, 1982; Sollins, 1982), respectively, the latter ecosystem should have ~1–3 times the steady-state log biomass of the former. Biomass values of logs show a 4- to 12-fold difference between the two ecosystems, however, so differences in decay rate account for, at most, only a portion of the difference, and input rates must be considered to fully explain the differences. Direct comparisons of input rates are, unfortunately, not possible, but they can be approximated. MacMillan (1981) presents input as logs ha^{-1} year^{-1} instead of volume or mass. Assuming a mean volume of 0.44 m^3 per log (based on MacMillan's Tables 6 and 8) and a wood density of 0.58 Mg m^{-3}, the input of 2.52 logs ha^{-1} year^{-1} converts to 0.64 Mg ha^{-1} year^{-1}. This value is considerably below the 4.54 Mg ha^{-1} year^{-1} rate reported for old-growth *Pseudotsuga–Tsuga* forests (Table 1). Dividing the input rates for both ecosystems by the reported decay rates gives ideal steady-state biomass of 16–21 Mg ha^{-1} for the *Quercus* forest and >150–450 Mg ha^{-1} for the *Pseudotsuga–Tsuga* forests. These values reflect the differences much more completely than decay rates alone.

The effect of input rates on CWD biomass seems to have been generally overlooked and helps explain why some coniferous ecosystems with slow decay rates have values comparable to those for hardwood stands where decay is rapid. In *P. contorta* forests of Wyoming (T. J. Fahey, personal communication), CWD mass ranges from 0.6 to 20.8 Mg ha^{-1}, but the decay rate constant for this species is 0.01—comparable to *Pseudotsuga*. The *P. ponderosa* forests of Arizona also have a low CWD mass of 18 Mg ha^{-1} (Sacket, 1979), but these also appear to be caused by very low input rates of 0.25 Mg ha^{-1} year^{-1} (Avery *et al.,* 1976).

Coniferous forests can also have low biomass of CWD due to high decay rates. Harmon and Cromack (unpublished) sampled an *A. concolor* forest in the Sierra Nevada, California, with 49 Mg ha^{-1} of logs decaying with a rate constant of 0.06 year^{-1}. A *Sequoiadendron–Abies* forest had 247 Mg ha^{-1} of logs, which illustrates how adding a single species with very slow decay rates can influence biomass. Removing the contribution of *Sequoiadendron* to the CWD in this stand results in log mass values similar to the *A. concolor* ecosystem.

Amounts of CWD in stream ecosystems are also strongly influenced by forest composition (Table 6). Considering stream reaches draining <1000 ha, *S. sempervirens* stands have more than 10 times the CWD amount ($\bar{x}$ = 660 Mg ha^{-1}, N = 9) observed in *P. menziesii* ($\bar{x}$ = 120 Mg ha^{-1}, N = 10) in northwestern California. Streams of drainage area <1000 ha flowing through old-growth *P. menziesii* forests in the Oregon Cascades ($\bar{x}$ = 300 Mg ha^{-1}, N = 18) and *P. sitchensis–T. heterophylla* forests of British Columbia ($\bar{x}$ = 280 Mg ha^{-1}, N = 8) exhibit intermediate debris amounts. Streams in a very limited sampling of hardwood forests in Tennessee, *Tsuga–Abies* forests in New Hampshire, and *Picea–Tsuga* forests of southeastern Alaska exhibit average amounts of 100 Mg ha^{-1}.

2. Effects of Disturbance and Succession on Biomass

Disturbances affect biomass by adding CWD and by initiating a new sere. Some disturbances such as fire, floods, and mass movement of soil also remove CWD. Successional patterns are similar for the various parameters, whether area, volume, or mass is considered. Successional stage affects the size, species, amount, decay class, and distribution (logs versus snags) of CWD.

Effects of disturbance on mass of CWD have been documented for at least four terrestrial ecosystems (Franklin and Waring, 1980; Huff, 1984; Lambert *et al.*, 1980; Tritton, 1980). Changes in CWD following a wave pattern of mortality in *A. balsamea* stands provide one of the clearest examples of disturbance effects (Lambert *et al.*, 1980). Highest overall biomass, ~62 Mg ha^{-1}, occurred 12 years after the onset of mortality, presumably because the entire stand did not die immediately. As the time since disturbance increased, overall biomass and the proportion of snags in the CWD decreased so that after 46 years CWD leveled off at 13–15 Mg ha^{-1}.

Successional trends in CWD mass were also observed by Tritton (1980) in a chronosequence of clear-cut northern hardwood forests. The highest CWD amounts occurred in stands 10 years old and very old stands with 34 and 49 Mg ha^{-1}, respectively. The lowest amount of CWD occurred 40–57 years after clear-cutting, with a total CWD mass of 9.8–16.0 Mg ha^{-1}. The high mass of CWD immediately following clear-cutting was attributable to slash created by logging operations, and 10–20 years after cutting, slash composed 97–98% of the CWD. The decay of slash, coupled with the input of material from the new forest, yield an overall successional curve that is "U"-shaped.

CWD mass appears to be continually high during the later stages of successional development of *P. menziesii–T. heterophylla*-dominated for-

ests in northwestern North America (Franklin and Waring, 1980). The stands examined were 100 to over 1000 years old and developed after catastrophic wildfires. Lowest overall biomass, 107–142 Mg ha^{-1}, occurred at 100–200 years. Older stands had 173–202 Mg ha^{-1} of CWD. CWD biomass would presumably have been much higher earlier in succession, and CWD biomass exceeding 500–1000 Mg ha^{-1} (Grier and Logan, 1977) might occur immediately after a catastrophic fire.

Huff (1984) examined changes in log biomass after catastrophic fires in *Pseudotsuga–Tsuga* forests of the Olympic Peninsula in Washington State. Highest log mass occurred later in succession and lowest values occurred in stands 110–131 years old. This pattern is believed to be the consequence of decay of the fire-killed trees combined with reduced input because as much as 40 years are required for trees to completely colonize the burned sites. Had snags been included, the total CWD biomass would probably have been highest early in succession when the fire-killed stand was contributing significantly to the total.

The recognition that high amounts of CWD can be expected in young, natural stands appears to be relatively recent. High CWD biomass in young stands is a consequence of the fact that most disturbances that kill trees consume relatively small amounts of the wood. Hence, large amounts of CWD as snags and downed logs are the heritage of forests regenerating after wildfire, windstorms, insect epidemics, or other catastrophic disturbances.

CWD in streams and rivers is also strongly affected by disturbances and the successional stage of surrounding forests. The recent occurrence of fire, timber harvest, major floods, and other events drastically affects the rates and size distribution of CWD contributed to the streams and are essential in interpreting the abundance and arrangement of CWD in streams. Swanson and Lienkaemper (1978) examined CWD in small streams flowing through coniferous forests in western Oregon burned by high-intensity wildfires 70–135 years earlier. Material from the prefire stand was found under the smaller diameter pieces of CWD that had fallen in from the postfire stand. In these streams, CWD was continuously present because the residence time of prefire CWD was greater than the time necessary for CWD production by the postfire stand. However, total abundance of CWD in the four streams sampled was about half that observed in streams bordered by old-growth forests.

Disturbance to forests surrounding streams often changes the species of CWD input and this, in turn, may affect CWD biomass. For example, logging and burning of an old-growth *Tsuga*-dominated watershed in Tennessee resulted in a conversion to *Liriodendron*-dominated forests (Silsbee and Larson, 1983). Mean CWD volume in four old-growth streams

was 338 m³ ha⁻¹, whereas in the logged watershed it was 84 m³ ha⁻¹ (Silsbee and Larson, 1983). Although this decline was due in part to the interruption of CWD input caused by disturbance, the conversion to the much faster decaying *Liriodendron* from *Tsuga* also probably caused a decrease in biomass. Presumably CWD biomass will remain low until large *Tsuga* stems are added to the CWD standing crop.

The interactions between succession and stream size also influence CWD mass. Bilby and Likens (1980) studied streams flowing through forests logged ~60 years earlier in the White Mountains of New Hampshire. After estimating CWD production through succession and for first-, second-, and third-order stream channels, they concluded the larger stream would experience a pronounced decline in CWD because ~200 years would elapse before streamside stands produced pieces large enough to remain in the channel for a significant period of time.

Disturbance regimes affect mass of CWD in streams directly by removing or depositing materials, as during floods, and indirectly by influencing the vegetation in and along the channels. CWD production is severely limited where stream and riparian vegetation is removed or pruned frequently by erosion or transported bedload, CWD, and ice. Vegetation may persist along streams, but may never reach a size or substrate quality sufficient to produce large quantities of CWD.

These studies on successional trends in CWD mass suggest a simple general model to explain the different successional patterns (Fig. 10). We assume, for simplicity, that decay rates are constant and that input rates vary only linearly with succession and are not affected by changes in forest type or stochastic events. In this model, CWD is classified as predisturbance, disturbance related, and postdisturbance input. Overall shape of the CWD biomass curve over succession is determined by the amount of original material removed by the disturbance, timing of input, and decay patterns of each category. After disturbance, preexisting CWD declines; the greater the amount of preexisting material removed, the less it contributes to the overall curve. Conversely, the greater the amount of freshly created CWD, the higher the pulse following disturbance. Both the predisturbance and disturbance-created components of CWD will decline with time, and the overall biomass curve will also decline unless counterbalanced by new input.

Development of the new stand after disturbance and creation of "new" CWD strongly influence the shape of the mass curve. Severe disturbances or site conditions retard forest reestablishment, and this factor delays the addition of new CWD which, in turn, allows decay to reduce CWD mass below predicted steady-state values. The longer the time needed to create new CWD relative to the residence time of old CWD, the deeper
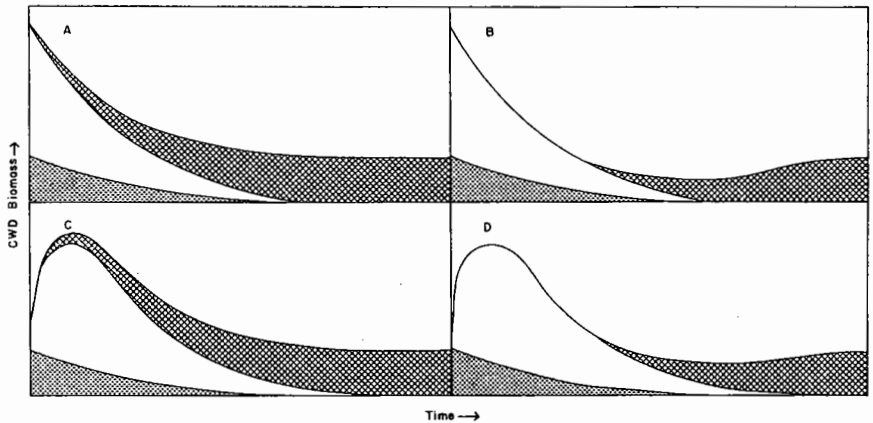
Fig. 10. Four hypothetical patterns of CWD mass following disturbance. CWD is divided into that present before the disturbance (dotted), that created by the disturbance (open), and that added by the stand growing after the disturbance (crosshatched). In each case, we assume the decay rate does not change with time and that postdisturbance input increases linearly to a constant value. (A) In this case, postdisturbance starts immediately after the forest's destruction, which results in an exponential decline to a steady-state value. (B) Same as (A) except that postdisturbance input is delayed. This causes a U-shaped trough to occur during the middle time period, and as postdisturbance inputs offset decay losses, mass increases to a steady-state value. (C) Pattern caused when the initial stand is killed gradually, but the postdisturbance input starts immediately. (D) Same as (C) except that postdisturbance input is delayed.

the depression in the total biomass curve. When regeneration is rapid, the overall pattern will be a peak in CWD mass followed by a decline to a steady-state value. In the case of disturbances, such as debris avalanche or timber harvest that remove CWD, the input curves dominate the successional pattern, leading to the classic linear increases presented by Triska and Cromack (1980). Although this model is conceptually very simple, it does accommodate the wide array of responses that might be encountered after disturbances.

3. Effects of Stream Size on Coarse
Woody Debris

Amounts of CWD are generally highest in the smallest streams and decrease with increasing stream size, given a particular physiographic and forest setting (Table 6). The general downstream decrease in CWD results from several factors. Larger streams have a greater ability to transport CWD downstream and out of channels onto floodplains. Larger channels also have a more limited source of CWD because forests do not grow in the most active channels, while very small streams can flow through

forests without influencing overall stocking amounts. Furthermore, woody vegetation adjacent to rivers may be maintained in an immature stage by frequent disturbance, and the resultant lower biomass of these streamside forests thus limits availability of CWD for channels. However, when large channels migrate laterally and entrain mature forests, a large amount of CWD can be added. Along large floodplain rivers, CWD moves both into and out of the channel during floods, but it is not known whether the floodplain is a net source or sink for CWD.

Comparisons of CWD amounts in and out of a river channel have been made by Wallace and Benke (Wallace and Benke, 1984). They observed less CWD on floodplains than in a fourth-order segment of Black Creek and sixth-order segment of Ogeechee River on the coastal plain of Georgia. They attributed this to transport of CWD into the channel, slower decomposition in the channel, and higher input rates along eroding stream banks. In four small channels in southeast Alaska, Swanson *et al.* (1984) measured no significant differences in CWD amounts between floodplain and channel areas.

D. Distribution of Coarse Woody Debris

The previous section discussed the amount of CWD within various ecosystems, but it is also important to consider how this material is distributed with respect to size, decay state, position (snags versus logs), and spatial arrangement. CWD is not homogeneously spread over the landscape and exhibits patterns that, although not always highly predictable, influence decomposition of CWD and its geomorphic and habitat functions.

1. Position

The proportion of CWD biomass composed of snags and logs is highly variable and exhibits little pattern (Table 5). The lowest percentage of CWD as snags is 2% in a *P. jeffreyi* stand (Harmon and Cromack, unpublished), while the highest was 96% in a *P. contorta* stand (Fahey, 1983). Even within a single watershed there seems to be a wide variation in the fraction of CWD composed of snags. For example, 6–22% of the CWD mass was snags within a watershed dominated by a 450-year-old *Pseudotsuga–Tsuga* forest (Grier and Logan, 1977). This is a considerably lower proportion than the 38–49% reported for forests of similar ages and composition (Franklin and Waring, 1980; Sollins, 1982). Several controlling factors need to be considered before comparisons can be made, including the cause of mortality, the time since disturbance, and the size and decay rate of the material.

Lambert *et al.*'s (1980) study of fir waves details changes in proportion of CWD as snags after disturbance. Snags constituted 58% of the CWD immediately after canopy death. The snag fraction declined with time so that ~41, 33, 24, and 6% of the CWD were snags at 10, 20, 30, and 40 years after stand death, respectively. In this case, the cause of death led to a large input of standing dead trees. Very similar patterns would be expected for disturbances such as fire and beetle outbreaks that also leave standing dead trees. In disturbances such as windthrow, which increase the proportion of logs, the situation would be reversed.

2. Size Class Distributions

Few studies have examined size distributions of CWD. Abundance of pieces declines as diameter increases, which probably is a reflection of the reverse "J"-shaped distribution typical of living tree populations (Harper, 1977). The geometric decline in numbers of logs as diameter increases is exemplified by data from a *Sequoiadendron–Abies* stand (Fig. 11). Of the logs, 50% are in the 15- to 35-cm class, and each subsequent diameter class contains half the number of the preceding class. MacMillan (1981) examined the size distribution of logs in a *Quercus*-dominated forest and also found an inverse relationship between log diameter and numbers. Although the larger size classes have fewer individuals, they often compose the majority of the biomass (Fig. 11) because volume increases geometrically with size. Another factor that may influence this relationship is the faster decay rate of the smaller material (see Section III,E,5).

In addition to the distribution of biomass in CWD size classes, it is also of interest to know the proportion of above-ground woody debris composed by CWD. A complicating factor in making these calculations is the variable lower limit of CWD but, in spite of this problem, it appears that CWD composes the majority of above-ground woody detritus (Table 7). Brown and See (1981) report that 78–89% of the downed woody biomass was >7.5 cm in six forest types examined in Montana and Idaho. Wood >7.5 cm composed 94% of the downed woody biomass in a North Carolina *Quercus–Carya* forest (Triska and Cromack, 1980), while 79% of the dead and downed wood in a mixed *Quercus* forest in New Jersey was >10 cm (Lang and Forman, 1978). Pieces >7.5 cm composed 70–98% of the downed wood biomass in forest types of Tennessee and North Carolina (Harmon, 1980). Although none of these studies examined the fraction of fine (e.g., attached branches) versus coarse standing material, it is likely that the latter would dominate the standing dead biomass. It appears that CWD dominates the terrestrial woody detritus pool and usually composes
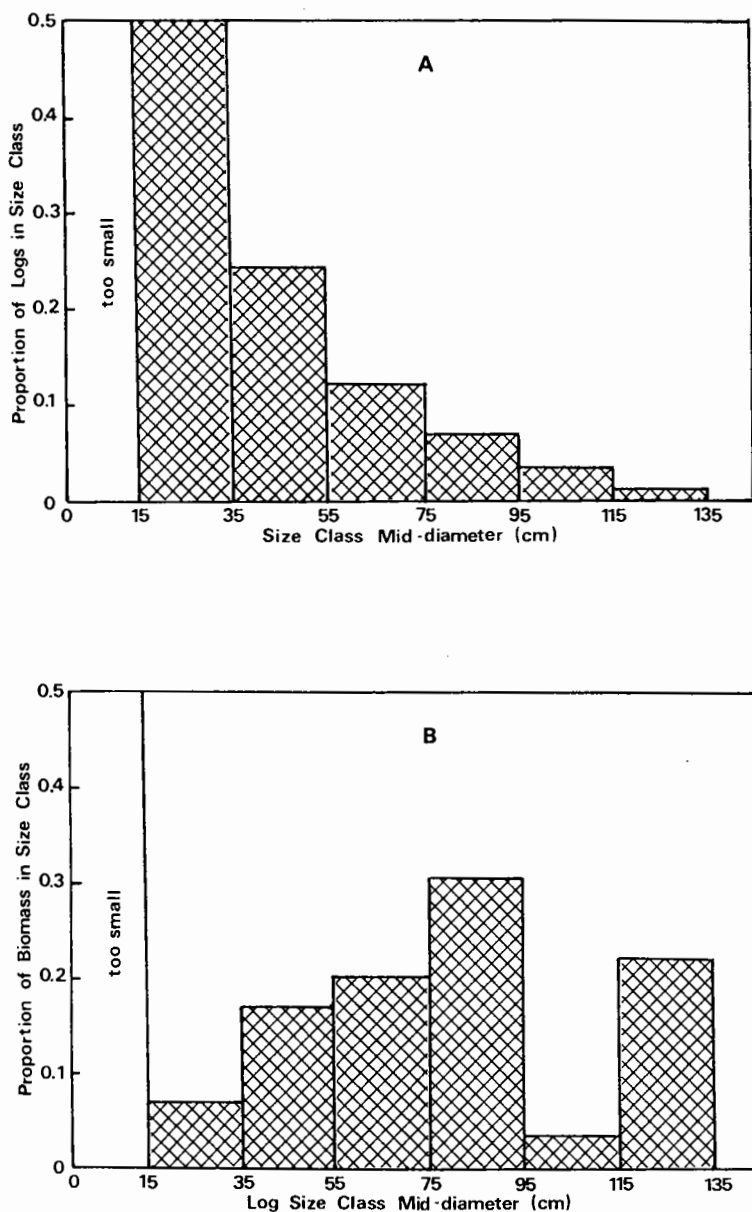
Fig. 11. The distribution of (A) numbers of logs and (B) biomass for 20-cm-diameter size classes in a *Sequoiadendron–Abies* forest.

Table 7

Proportion of Dead and Downed Woody Detritus Composed of Coarse Woody Debris
in Selected Forests and Streams

Ecosystem	Location	Percentage as CWD	Reference[a]
Forests			
Fagus–Betula	Tennessee	91[b]	3,4
Larix occidentalis	Montana/Idaho	83[b]	1
Liriodendron tulipifera	Tennessee	79[b]	3,4
Picea–Abies	Montana/Idaho	89[b]	1
Picea–Abies	Tennessee	98[b]	3
Pinus contorta	Montana/Idaho	82–86[b]	1
Pinus mixed	Tennessee	70–76[b]	3,4
Pinus ponderosa	Montana/Idaho	78–81[b]	1
Pseudotsuga menziesii	Montana/Idaho	80–82[b]	1
Quercus–Carya	North Carolina	94[b]	10
Quercus mixed	New Jersey	79[c]	5
Quercus mixed	Tennessee	85–92[b]	3,4
Quercus prinus	Tennessee	74–83[b]	3,4
Thuja–Tsuga	Montana/Idaho	88[b]	1
Tsuga canadensis	Tennessee	87[b]	4
Streams			
Hardwoods mixed	Tennessee	40–91[c]	2
Picea–Abies	Tennessee	78–79[c]	2
Picea engelmannii	Idaho	37–80[c]	6
Picea sitchensis	Alaska	73–93[c]	8
Picea–Tsuga	New Hampshire	60–72[c]	9
Populus trichocarpa	Idaho	26[c]	6
Pseudotsuga–Tsuga	Oregon	63–94[c]	6
Sequoia sempervirens	California	98[c]	7

[a](1) Brown and See (1981), (2) Gregory and Lienkaemper (unpublished), (3) Harmon (unpublished), (4) Harmon (1980), (5) Lang and Forman (1978), (6) Lienkaemper (unpublished), (7) Swanson (unpublished), (8) Swanson *et al.* (1984), (9) Swanson and Sedell (unpublished), (10) Triska and Cromack (1980). Unpublished data is on file at Forestry Sciences Laboratory, RWU-1251, Corvallis, Oregon.
[b]Lower size limit 7.5 cm.
[c]Lower size limit 10 cm.

>80% of the total biomass. CWD also appears to dominate the biomass in stream systems, although the range in proportions seems larger than in the terrestrial setting. CWD composed only 26% of the woody debris in a *Populus*-dominated stream in Idaho (Lienkaemper, unpublished). Most other stream systems examined have 40–98% of the wood in the coarse fraction. Swanson *et al.* (1984) summarize data showing coarse debris comprising 93% of wood-debris loading in stream reaches in old-growth *Pseudotsuga* forests of Oregon and 91% in old-growth *Picea–Tsuga* forests in southeastern Alaska. In *Picea–Tsuga* and hardwood forests of

Tennessee, coarse debris in small streams constituted 76% of the total wood loading (Gregory and Lienkaemper, unpublished).

3. Decay Class Distribution

In many ecosystems, intermediate decay classes or states tend to compose the largest fraction of CWD biomass, while the most and least decayed comprise the smallest fraction (Franklin *et al.*, unpublished; Graham and Cromack, 1982; Harmon and Cromack, unpublished; Sollins, 1982). Although this may be true, it is helpful to realize that biomass distribution of CWD under steady-state conditions with respect to decay classes (Fig. 12) is dependent on the residence times of the classes. If the residence times of the decay classes are equal, i.e., 1–10 years, 11–20 years, 21–30 years, and so on, then the youngest decay class will contain the most biomass. If, on the other hand, residence time of decay classes increases geometrically, i.e., 0–1 year, 2–3 years, 4–7 years, and so on, then the intermediate-aged decay classes will have the most biomass.

Several factors, most importantly disturbance, cause deviations from the expected steady-state decay class pattern. After the death of an *A. balsamea* forest, there was a rapid increase in the fraction of biomass composed of slightly decayed boles, and as the time since death increased, this cohort of boles progressed from the moderately decayed to the very decayed classes (Lambert *et al.*, 1980). Ten years after stand death, all the boles were in the slightly decayed class. In stands 20 years old, 75% of the boles were slightly decayed and 25% were moderately decayed. In stands 30 years old, the slightly decayed boles composed the lowest fraction of the biomass (8%), while the very decayed class contained 50% of the biomass. The effect of disturbance is also evident in a chronosequence of *Pseudotsuga* stands created by catastrophic fires (Franklin *et al.*, unpublished). In a 100-year-old stand, 75% of the CWD is in an advanced state of decay (class 4), probably representing material from the previous stand. At 130 years, much of this biomass appears to have decayed to the very advanced state (class 5). In stands older than 130 years, the majority of CWD biomass is divided between moderate and advanced states of decay (classes 3 and 4).

Other factors influencing the distribution of biomass in decay classes are the size and decay resistance of the material added. An example from a *Sequoiadendron–Abies* stand illustrates the point. *Sequoiadendron* is very decay resistant; when included, the distribution of biomass in the slightly, moderately, advanced, and very advanced decay classes was 74, 15, 7, and 4%, respectively (Harmon and Cromack, unpublished). However, when *Sequoiadendron* is excluded, the distribution for the same classes was 26, 28, 29, and 17%, respectively.
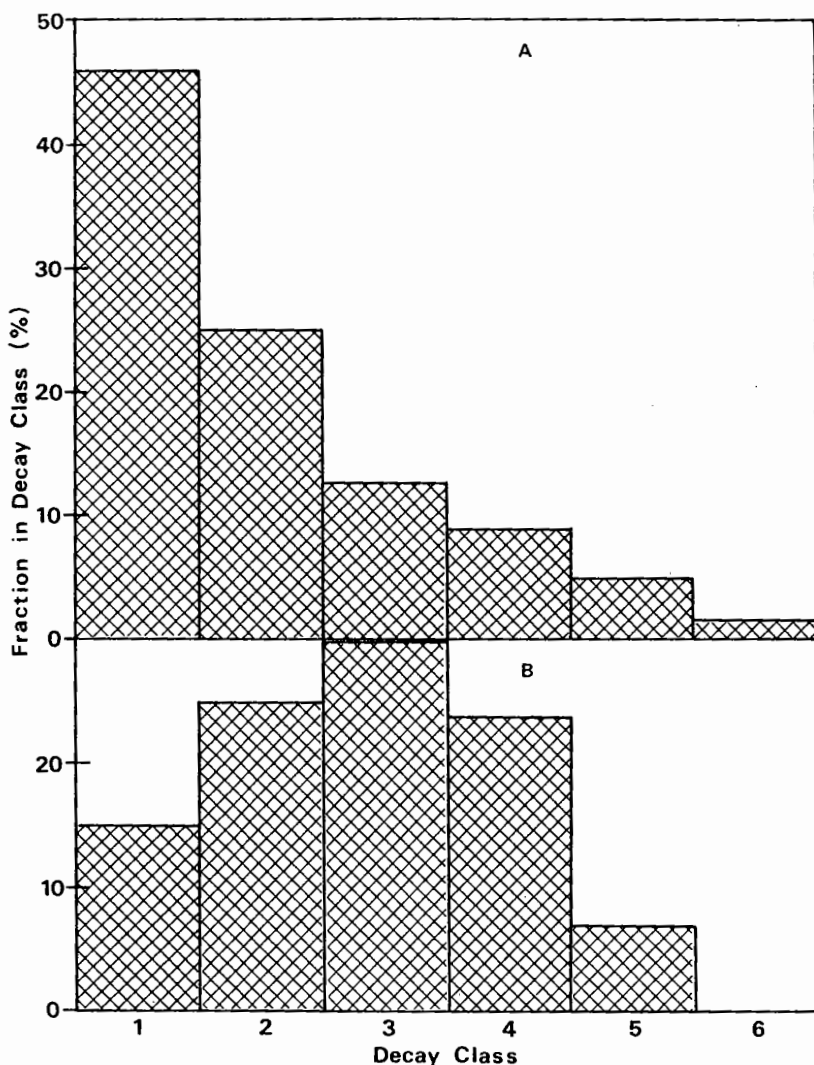
Fig. 12. Hypothetical example of how the distribution of CWD mass over decay class is a function of the residence time of the decay class. In both cases, a steady-state system is assumed, but in (A) the residence time in each class is equal, whereas in (B) the residence time increases geometrically with each class.

4. Spatial Patterns

a. Riparian and Stream Environments. In riparian and stream environments, the arrangement of CWD and architecture of accumulations are influenced by both the mechanisms adding CWD and the geomorphic

processes within streams. Several types of spatial arrangements are common in small (i.e., first- and second-order) channels, but randomly distributed CWD appears to be the most widespread. Small streams cannot move CWD, and the spatial pattern of CWD in these streams reflects the spatial pattern of input.

In small- and intermediate-sized streams, CWD forms large accumulations with a very open structure when windthrow and earthflows are the major agents adding CWD to channels. Addition of CWD to channels by rapid soil mass movements and snow avalanches results in formation of large accumulations with a tight, interlocking fabric. Similarly, rapid mass movements of colluvium, alluvium, and CWD down channels result in tightly meshed accumulations. In these cases, CWD is entrained by and pushed in front of a debris flow moving down a channel. As channel gradient decreases, the debris flow eventually stops, leaving a wedge of sediment up to 10 m thick and several hundred meters long trapped behind a CWD accumulation that has been impregnated with sediment.

CWD has a moderately clumped distribution in intermediate-sized streams where few pieces are large enough to be stable during floods (see Section V,D). Pieces wider than the active channel can remain in place for up to several centuries (Keller and Tally, 1979; Swanson and Lienkaemper, 1978; Swanson *et al.*, 1976) and often trap smaller pieces of CWD as they float downstream. Therefore, stream-transported CWD accumulate above large pieces of CWD as well as above boulders and other stable structures.

In large channels, a high proportion of CWD pieces can be moved during floods. CWD accumulates at sites such as heads of islands, mouths of secondary channels, heads of point bars, and outside of meander bends (Keller and Swanson, 1979; Singer and Swanson, 1983; Swanson and Lienkaemper, 1982; Wallace and Benke, 1984). This leads to a highly clumped distribution of CWD in large channels. The importance of these sites is controlled both by trapping efficiency and proximity to a CWD source.

Published information on the arrangement of CWD in individual stream reaches is limited to Hogan (1985). He measured orientation and clustering of CWD in 11- to 45-m-wide channels in clear-cut and mature *P. sitchensis–T. heterophylla* stands in British Columbia. There was some tendency (not examined statistically) for debris to be oriented diagonally across the channel in unlogged channels and parallel to the main axis of logged channels. CWD pieces formed accumulations with an along-stream spacing of three to four channel widths.

b. Terrestrial Environments. Spatial aggregation occurs in the terrestrial environment, but patterns are not as clear as in streams and are more dependent on patterns of input than on transport mechanisms. Spatial

aggregation can result from aggregated mortality such as blowdown patches, very localized insect attacks, and the spread of pathogens such as *Phellinus weirii* or *Fomes annosus* by root contact (see Section II,C). Yet another cause of CWD aggregations might be spatial discontinuities in the trees that are the source of CWD.

Although there are many potential methods to examine spatial patterns of terrestrial CWD (see Pielou, 1977, p. 113), little quantitative work has been published. By using the techniques employed in analyzing the spatial distribution of live trees, Cline *et al.* (1980) found that snags in unmanaged *Pseudotsuga* forests of western Oregon tended to be random in distribution, although in 25% of the stands the snags were aggregated into patches of 5–10 trees that apparently had died simultaneously. As far as we can tell, no one has examined spatial patterns in logs, although their compass orientation has been explored. Clearly, much remains to be learned about spatial patterns of CWD and the causes of these patterns.

5. Orientation

The arrangement of logs on hillslopes is important because it influences sampling procedures (see Section IV,D), use of CWD as habitat (Maser and Trappe, 1984), and the geomorphic role of CWD. Direction of tree fall should be influenced by prevailing storm winds, slope steepness and aspect, and type of input (e.g., snags versus live trees). Most current work centers on influence of storm winds, but the other factors may be equally important. Topography influences tree form through processes such as soil creep and snow pressure, and biases direction of tree fall. Steep slopes also allow pieces to roll or slide from their original orientation. The combination of slope steepness, topographic configuration, and slope direction can also modify the direction and strength of storm winds (e.g., Gratkowski, 1956).

The role of wind in orientation of logs has been extensively studied. Prevailing storm winds appear to be very important on gentle topography. In their reconstruction of a hardwood forest in New Hampshire, Henry and Swan (1974) found evidence that four storms had blown over 76% of the trees in a southwestern direction. In Poland, Falinski (1978) found that 63% of the *Picea abies* were uprooted in a southeastern direction, reflecting autumn storm winds. Gratkowski (1956) observed that 90% of the windthrows in the Cascade Range of Oregon pointed to the northeast, reflecting the southwestern direction of storm winds. Orientation patterns do vary within a forest type. An example is presented in Fig. 13, which depicts log orientation in two *Tsuga–Picea* stands from coastal Oregon and Washington. Vegetation is similar, but windthrows at Neskowin Crest, Oregon, have a strong northerly orientation, whereas those at
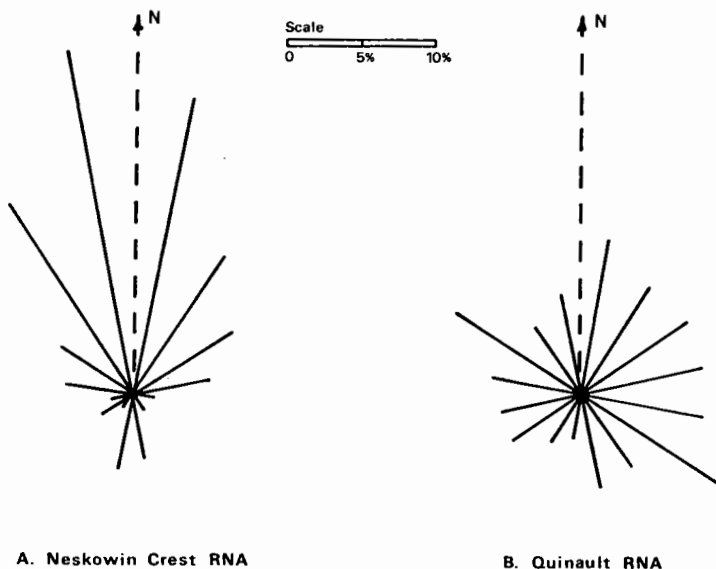
A. Neskowin Crest RNA   **B. Quinault RNA**

Fig. 13. Orientation of logs in two *Picea sitchensis–Tsuga heterophylla* forests from the northwestern United States. The length of the lines indicates the percentage of logs pointing in a given direction. (A) Neskowin Crest Research Natural Area, Oregon. (B) Quinault Research Natural Area, Washington. In spite of similar canopy composition, the logs at Neskowin Crest have a strong northerly orientation, while those at Quinault have a fairly random orientation pattern.

Quinault, Washington, have a weak easterly orientation. At Neskowin, log orientation reflects consistent, strong southwesterly winter winds at a site only 1 km from the Pacific Ocean. In contrast, the Quinault stand is located 60 km inland and is presumably exposed to less consistent wind directions.

V. ROLES OF COARSE WOODY DEBRIS

The previous sections have discussed the creation, decay, and amount of CWD found in various ecosystems. In this section, we explore the numerous functions that CWD performs in these ecosystems. Knowledge of these roles is very important to effectively manage ecosystems because removal of CWD may lead to an "unexpected" alteration of ecosystems unless these roles are appreciated. For many microbes, invertebrates, vertebrates, and plants, CWD and its associated microenvironment represent a habitat and/or food source. Of these taxa, perhaps microbes are the

most closely associated with CWD. We will not treat this group specifi-
cally in this discussion, however, as it has been reviewed by Frankland *et
al.* (1982). CWD is also important as a pool of energy, carbon, and nutri-
ents in ecosystems. The relationship of these CWD pools and nutrient
cycling in most ecosystems has yet to be explored. In both terrestrial and
aquatic environments, CWD is intimately related to certain geomorphic
processes.

A. Coarse Woody Debris as Plant Habitat

The importance of CWD as a substrate for autotrophs has been recog-
nized for some time despite the frequent emphasis on decomposer organ-
isms. The autotrophic taxa associated with CWD are quite varied and
include green algae, diatoms, blue-green algae, lichens, liverworts,
mosses, clubmosses, horsetails, ferns, gymnosperms, and angiosperms.

1. Use of Coarse Woody Debris by Plants

Autotrophs vary in their use of CWD. Many species are superficially
attached to the surface of CWD and, thus, are epiphytes. Vascular plants
may send their roots into rotting wood and bark to extract water and
nutrients. These roots may originate from plants that established them-
selves on CWD or from those initially established on soil (Lemon, 1945).
Other vascular plants root in the mat of decaying fine litter that often
accumulates on the surface of CWD. These three types of exploitation are
not mutually exclusive; an individual may first be epiphytic and then send
roots into the surface organic mat, then into CWD, and, finally, into the
underlying mineral soil.

Rotting wood has lower concentrations of the nutrients required for
plant growth than most mineral and organic soils; therefore, growth can
be slower on CWD than on the rest of the forest floor. Minore (1972), for
example, found tree seedlings grew faster when rooted in needle litter
than in rotten wood. CWD develops greater concentrations of nutrients
and a higher water-holding capacity and therefore becomes a more favor-
able rooting medium as decay proceeds. Despite these changes, rotten
wood remains a nutritionally poor substrate when compared to mineral soil.
The nutrition of plants rooted in CWD appears to be intertwined with
mycorrhiza; this association may make it possible for higher plants to
extract sufficient nutrients from woody debris. Although some species
such as *T. heterophylla* may survive on logs for up to 1 year without
mycorrhizal inoculation, their survival and growth is improved when in-
oculation occurs (Christy *et al.,* 1982). Several species of mycorrhiza-
forming fungi have been isolated from rotten wood (Kropp, 1982).

Plants that are not rooted in or on CWD may also benefit from its presence. This is probably most important on severely disturbed sites where CWD may ameliorate environmental extremes and provide shaded microsites. Woody debris may also protect seedlings from being buried by material moving downslope.

2. Autotrophs and Decomposition

Autotrophs influence CWD decomposition and, conversely, decomposition processes influence the composition and structure of autotrophs using CWD. Superficial growths of plants add organic matter either as their own detrital remains or by trapping fine litter that otherwise would be lost from the surface. These organic matter accumulations serve as a rooting medium for larger, more demanding species (Harmon, 1985; Minore, 1972) and are a potential source of nutrients for organisms decomposing CWD. Plants rooted directly in CWD also influence decay by adding nutrients and more labile carbon by either root turnover or secretions.

Plants growing on CWD influence fragmentation rates of the debris in many ways, both positively and negatively. Root systems may bind the decayed material into a coherent structure (Triska and Cromack, 1980), and cover by bryophytes may reduce the erosive effects of rainfall. On the other hand, plants falling from CWD increase fragmentation rates when their root systems tear off pieces of bark and wood. The expansion of the root systems also contributes to fragmentation of CWD. The occurrence of browse plants on CWD increases fragmentation rates by attracting large mammals that pull plants from the substrate. Sloughing of bark and wood influences the autotrophic community by removing individuals. The larger and more deeply rooted the individual, the less likely it will be disturbed by fragmentation.

3. The Importance of Coarse Woody Debris as Habitat

While CWD is generally known to serve as plant habitat (Falinski, 1978; Lemon, 1945; Thompson, 1980), there is little information on the proportion of plants associated with CWD versus other habitats. Similarly, little information exists on facultative versus obligatory use of CWD.

A few lists of vascular herbs growing on CWD are available (Dennis and Batson, 1974; Lemon, 1945; McCullough, 1948; Sharpe, 1956). However, even a listing of the genera found by these few studies lies beyond the scope of this review. Herbs rarely appear restricted to CWD. Thompson (1980), for example, found that none of the 31 species examined was

confined to logs. Dennis and Batson's (1974) study was an exception; they found 11 flood-sensitive species that were restricted to floating logs and stumps in a North Carolina swamp.

Numerous tree species can apparently grow on wood. In the southeastern United States, *Acer rubrum, Pinus caribaea, P. palustris, Pinus rigida, Pinus rigida* var. *serotina,* and *Q. nigra* grew on rotten wood, although only *P. caribaea* reached maturity on this substrate (Lemon, 1945). *Acer rubrum, Populus heterophylla, Populus deltoides, Quercus lyrata,* and *Taxodium distichum* seedlings grew on floating logs and stumps in a North Carolina swamp (Dennis and Batson, 1974). None of these species appeared to reach maturity on CWD in this setting, however. *Picea rubens* grew on stumps and logs in the southern Appalachian Mountains (Korstian, 1937). Stupka (1964) also reported that *Betula lutea* and *Betula lenta* frequently grew on stumps and logs in this area also. *Abies balsamea, Picea glauca,* and *P. rubens* seedlings grew on logs in New England and New York (Westveld, 1931). In the virgin forests of the Adirondack Mountains of New York, Knechtel (1903) observed *Pinus strobus, Picea rubens,* and *Tsuga canadensis* growing on CWD. *Betula alleghaniensis* rooted on stumps in northern Wisconsin (Kozlowski and Cooley, 1961). Rotten wood was a good seedbed for establishment of *Picea mariana* seedlings (LeBarron, 1950). *Picea engelmannii* and *Abies lasiocarpa* were observed growing on logs in Colorado (McCullough, 1948) and in British Columbia (Griffith, 1931; Smith, 1955; Smith and Clark, 1960). Lowdermilk (1925) reported *P. engelmanii* was often rooted on rotting logs throughout the northern Rocky Mountain region.

In northwestern North America, trees frequently grow on logs and stumps in the *P. sitchensis, T. heterophylla,* and *Abies amabilis* zones (Franklin and Dyrness, 1973). *Picea sitchensis* and *T. heterophylla* are frequently found growing on CWD in the coastal (*P. sitchensis*) zone (Hines, 1971; Kirk, 1966; McKee *et al.,* 1982; Minore, 1972). In addition to these species, *Alnus rubra, P. menziesii,* and *T. plicata* grow on CWD in this zone (Harmon, 1985). In the Cascade Mountains, *T. heterophylla* commonly grows on CWD (Christy and Mack, 1984; Fogel *et al.,* 1973; Franklin *et al.,* 1981; Maser and Trappe, 1984; Thornburgh, 1969; Triska and Cromack, 1980). Taylor (1935) observed *P. sitchensis* and *T. heterophylla* seedlings growing on rotten wood in southeastern Alaska.

Although all of these references are from North America, trees grow on CWD in other areas as well. Baldwin (1927a,b), Jones (1945), and Lachaussée (1947) indicate that *Picea* often establishes on rotten wood in European forests. *Betula pubescens* was noted growing on stumps in a heather moor in England (Dimbley, 1953).

Few studies note the importance of CWD in terms of tree recruitment, and it is therefore difficult to judge if trees rooted on CWD are little more than a curiosity. Because CWD covers a small fraction of the forest floor in most ecosystems, one might assume CWD plays a minor role. While this is often true, there are ecosystems in which CWD is an important seedbed. The *P. sitchensis–T. heterophylla* forests of the north Pacific Coast appear to be an outstanding example. McKee *et al.* (1982) found that 94–98% of the tree seedlings in a forest of this type were growing on CWD, and yet only 6–11% of the forest floor was covered by CWD (Graham and Cromack, 1982).

Logs are important seedbeds for trees in other forests within the Pacific Northwest as well. Christy and Mack (1984) found that 98% of *T. heterophylla* seedlings in an old-growth *Pseudotsuga–Tsuga* forest were rooted on rotten wood that covered 6% of the forest floor.

Subalpine *Picea–Abies* forests in British Columbia provide another example of the importance of dead wood as a seedbed for seedlings. Smith (1955) observed 75% of the tree seedlings grew on rotten wood that covered only 9% of the forest floor. Griffith (1931) found that in another *Abies–Picea* stand, 65% of the *P. engelmanii* and 48% of the *A. lasiocarpa* seedlings grew on rotten wood.

Qualitative observations indicate that CWD can be an important seedbed in eastern North American forests. For example, Knechtel (1903) studied regeneration in virgin forests in the Adirondack Mountains and noted *P. strobus, Picea rubens,* and *T. canadensis* "were reproducing almost entirely on the old decaying tree trunks lying in the forest."

The proportion of seedlings growing on CWD can be misleading in terms of overall reproductive success because CWD is not a stable habitat and fragmentation markedly reduces overall survival rates. Thus, many seedlings may initially establish on CWD, but the chances of survival to maturity may be higher on the forest floor.

4. Factors Controlling the Importance of Coarse Woody Debris as Habitat

The importance of CWD as plant habitat is controlled by moisture, species interactions, decay state of the substrate, and presence of a snowpack. Moisture conditions influence both the type and abundance of plants on CWD. Logs emerging from water may be one of the only sites on which mesophytic species can grow in swamps and bogs (Dennis and Batson, 1974; Hall and Penfound, 1943; Lemon, 1945). Within drier terrestrial environments, the combined effects of moisture and decay

state determine the species using CWD. As moisture decreases, CWD becomes less favorable as a habitat for larger, complex life forms. This tendency is offset by decay, which increases the water-holding capacity of CWD (see Section III,E). The general pattern is illustrated by McCullough's (1948) successional study of logs in Colorado. Herbs, shrubs, and trees colonized logs in a less advanced state of decay in the mesic or bog environment than they did in the xeric environment. In the xeric environment, lichens and bryophytes dominated most of the successional sequence, and shrubs and trees colonized logs only in the most advanced stages of decomposition. There is some indication that rotten wood retains water better than humus. Place (1955) observed that rotten wood remained moist under a forest canopy, while the adjacent humus dried out. Since this would increase seedling survival, rotten wood might become an important seedbed in xeric environments. In northern Rocky Mountain forests, the higher moisture content of rotting wood resulted in a higher level of ectomycorrhizal activity during dry periods than was observed in the surrounding soils (Harvey et al., 1976, 1979).

The state of decay affects growth of root systems and this in turn may influence plant survival. Thornburgh (1969) found that the roots of T. heterophylla growing on very rotten logs tended to ramify throughout the wood and did not penetrate to the mineral soil. In contrast, trees growing on partially decayed logs sent their roots around the solid inner core and into the underlying mineral soil. Tsuga growing under the latter situation had a more stable rooting medium and were less apt to uproot. Root growth patterns are no doubt modified by the size of the CWD. When large, sound pieces of CWD are involved, a tree might not be able to get its roots into the soil before it "outgrows" the support offered by the surface mantle of humus, bark, and rotten sapwood.

Deep snowpacks may increase the importance of CWD. Litter accumulating on the snowpack surface in a subalpine A. amabilis–T. heterophylla forest in the Cascade Range of northwestern North America tended to smother Tsuga seedlings germinating on the forest floor (Thornburgh, 1969). Because the log surfaces were raised above the surface of the forest floor, litter accumulations and seedling burial were reduced. Positioning high on logs could also lengthen the growing season. Christy and Mack (1984) extended the litter-burial hypothesis to lower elevation forests where snowpack is unimportant. They hypothesize that logs in Pseudotsuga–Tsuga forests of the Cascade Range shed much of the litter that falls on them so that litter accumulations on logs are less apt to bury newly germinated seedlings. In the wetter P. sitchensis–T. heterophylla forests of this region, log surfaces that retain litter best also retain seeds best and have the highest rates of seedling recruitment (Harmon, 1985).

Competitive and amensalistic interactions can restrict tree seedlings to logs in areas with heavy bryophyte and herb cover. In the *P. sitchensis–T. heterophylla* forests, competition with bryophytes and herbs dramatically reduced tree-seedling survival on the forest floor and on very old, stable log surfaces (Harmon, 1985). In addition to competitive interactions, deep bryophyte layers may reduce survival by preventing seedling root systems from reaching the mineral soil before drying and nutrient deficiencies occur (Harmon, 1985).

CWD may also provide refuges for plants that are prone to herbivory when growing on the forest floor proper because plants on large logs and stumps are more difficult for animals to reach. Concentrations of logs can also form natural exclosures and allow patches of ungrazed vegetation to develop (Franklin and Dyrness, 1973; Sharpe, 1956).

5. Successional Patterns on Logs

A complex plant succession is initiated as soon as a bole falls to the forest floor. Succession on CWD is complex because a number of processes, including colonization, decomposition, fragmentation, and species interaction, are involved and because boles are added to the forest floor in a continuum of states ranging from sound to very decayed. Moreover, the control these processes exert on community structure varies over the sere.

During the earliest stages of log succession, the community is dominated by the epiphytes that inhabited the living tree. For some of these species the microclimatic changes caused by tree fall may lead to death. For example, the lichen *Letharia vulpina* (L.) Hue usually dies after trees or snags fall in the Sierra Nevada Mountains of California because it cannot tolerate burial under a snowpack (Harmon and Cromack, unpublished). For other species, the change in microclimate may lead to a temporary increase. Thus, the liverwort *Ptilidum californicum,* which spreads rapidly over surfaces of newly fallen logs on the Olympic Peninsula, eventually is replaced by larger mosses such as *Hylocomium splendens* (Sharpe, 1956).

The ability of the log surface to retain both seeds and needle litter increases as the newly created CWD surfaces become colonized with lichens and/or bryophytes (Harmon, 1985). Soon an organic soil accumulates, which allows forest floor species to invade log surfaces. In mesic environments, these processes allow succession to proceed independent of wood decay. For example, Harmon (1985) found that *Picea* and *Tsuga* seedlings could grow on undecayed logs as long as superficial humus deposits were present. However, in xeric environments, wood decay may have to proceed substantially before shrubs and trees can invade.

As colonization proceeds, intra- and interspecific competition increases. There is a tendency for more complex and larger life forms to displace simpler, smaller forms. Sharpe (1956), for example, stated that larger feather mosses such as *Hylocomium splendens* and *Rhytidiadelphus loreus* replaced smaller species such as *Mnium punctatum* and *Dicranum fuscesens* during succession in the Olympic rain forests. However, there are many exceptions to this pattern, and larger plants are often added as succession proceeds, without eliminating previous layers (McCullough, 1948; Sharpe, 1956).

Smaller species may exclude larger species by competing with them during critical life stages. Thus, deep carpets of *Hylocomium* and *Rhytidiadelphus* mosses can prevent log colonization by tree seedlings (Harmon, 1985). In mesic environments, a high density of tree seedlings and shrubs can accumulate on the surface of logs (McKee *et al.*, 1982). This led Sharpe (1956) to conclude that severe competition at this point in succession causes a rapid loss of individuals. Larger individuals may send their roots into underlying soil before smaller individuals do. This greatly increases the amount of nutrients available to the former trees and gives them a strong competitive advantage over the surrounding smaller trees.

Fragmentation tends to offset successional trends and reinitiate the colonization process. Fragmentation may result from sloughing of bark or wood, toppling of individual plants from the log, impacts of falling trees or snags, or animal impacts. Although fragmentation removes plants, it can also accelerate succession. First, it may reduce competition and allow survivors to grow faster. Second, fragmentation may expose uncolonized areas on logs covered with deep bryophyte carpets and allow establishment of tree and shrub seedlings.

B. Coarse Woody Debris as Animal Habitat

1. Terrestrial Vertebrate Habitat

CWD provides habitat for many terrestrial vertebrates, including amphibians, reptiles, birds, and mammals. Elton (1966) recognized this function and noted, "When one walks through the rather dull and tidy woodlands—say in the managed portions of the New Forest in Hampshire [England]—that result from modern forestry practices, it is difficult to believe that dying and dead wood provides one of the two or three greatest resources for animal species in a natural forest, and that if fallen timber and slightly decayed trees are removed the whole system is gravely impoverished of perhaps more than a fifth of its fauna." This situation is by no means restricted to European forests. Thomas (1979)

identified 179 vertebrate species using CWD in the Blue Mountains of Oregon and Washington, which is 57% of the species breeding in that region.

An extensive literature exists that describes the relationship between CWD and animals. For example, a bibliography on cavity-nesting birds alone contained 1713 references (Fischer and McClelland, 1983)! A thorough synthesis of vertebrate–CWD interactions is beyond our scope, and we have selected only a few articles to illustrate important points.

a. Factors Affecting Vertebrate Use of Coarse Woody Debris. Factors influencing the type and extent of animal use include physical orientation (vertical or horizontal), size (diameter and length), decay state, species of CWD, and overall abundance of CWD. Whether CWD is standing or down is a major factor influencing vertebrate use. Birds and bats use snags, for example, whereas mammals other than bats, amphibians, and reptiles typically use logs. Relatively few species use both logs and snags. For example, in the Blue Mountains of Oregon, only 20% of the CWD-using species use both snags and logs (Thomas, 1979).

Initial size of CWD is an important variable and influences the type and duration of use. Cavity-nesting birds (CNB) select trees with larger than average diameters for nesting (Carey, 1983; Mannan *et al.,* 1980; McClelland, 1977; Raphael and White, 1984). Species size dictates the minimum snag diameter for nests. The contrast between two species of woodpecker, *Dryocopus pileatus,* which is ~38 cm long, and *D. villosus,* which is ~19 cm long, illustrates this point. Snags with minimum diameters of ~50 and 25 cm are required by each species, respectively (Thomas, 1979). The influence of log size on wildlife is unknown, but Maser *et al.* (1979) suggested that larger logs are more useful, as they provide more cover than smaller logs. Snag and log size also determine the duration of use because larger CWD generally lasts longer than smaller CWD (Cline *et al.,* 1980; Maser and Trappe, 1984; see also Section III,D–E).

Decay state strongly affects vertebrate use of snags and incipient-to-advanced decay state is needed by most CNB (Connor *et al.,* 1976; Miller and Miller, 1980). Zones of rotten wood are probably selected to reduce the energy required by birds to excavate nests, and heart rots may allow CNB to use freshly created snags (Harris, 1983). Some CWD-using species can only excavate snags in advanced stages of decay (Thomas, 1979).

Log use by vertebrates also differs with decay state. Thomas (1979) describes changes in species and utilization patterns during log decay. Initial use is external (e.g., as perches or cover for runways), reflecting the hard condition of the log. As decay begins, utilization becomes internal. Loose bark, for example, provides spaces for hiding and thermal cover. Very decayed logs are soft enough to be excavated by the burrow-

ing of small mammals, and this activity, in turn, allows amphibians and reptiles access to the log. As logs decay, the types of food, such as invertebrates and fungal fruiting bodies, available to vertebrates change. Feeding by vertebrates probably peaks toward middle to late stages of decay when logs are softer and many prey species are most abundant.

Vertebrate use of CWD is strongly influenced by spatial distribution of CWD as well as by the abundance of CWD. Aggregations of snags in small patches may enhance nesting habitat for some CNB, such as woodpeckers (Bull, 1975; Davis *et al.,* 1983; Jackman, 1974). Similarly, patterns and levels of log use may vary dramatically between isolated logs and those that form a continuous network. Continuity of CWD may allow some species to move through an otherwise hostile environment such as a clearcut or recently burned area.

b. Patterns of Vertebrate Use of Coarse Woody Debris. Terrestrial vertebrates use CWD for many functions. Thomas (1979) recognized cover, feeding, and reproduction as major uses; resting, preening, bedding, lookout, drumming, sunning, bridge, roosting, and hibernating were considered minor uses. A given species may use CWD for all, several, or only one function; therefore, the dependence of species on CWD varies. Some, such as salamanders and CNB, are probably obligatory, as opposed to facultative or opportunistic users of CWD. For many species, however, the level of dependence on CWD is unknown.

The largest and best recognized use of snags for shelter is by cavity-dwelling species. Primary cavity species create cavities in snags, while secondary cavity species use and/or enlarge preexisting cavities. Thomas (1979) recognized 39 bird and 23 mammal species using cavities in snags in the Blue Mountains of Oregon. At least 42 species of CNB are commonly found in temperate forests in North America (Table 8). In addition to cavities, protected sites associated with loose bark are important for bat roosting.

The permanent and winter residents of forest avifauna are generally the species using CWD. Most CNB are nonmigratory (Von Haartman, 1957), while migratory or transient birds generally do not use CWD (Snyder, 1950; Williams, 1936). Across five successional stages of *P. menziesii* forests, CNB accounted for 60% of the species of the winter avifaunas (Mannan, 1977). In an old-growth *Fagus–Acer* forest, 89% of the bird species that were permanent residents and fall and winter visitors used CWD (Williams, 1936).

Logs are used as shelter by many animal species, including a wide range of small mammals (Table 9). Logs provide protective cover immediately after their creation (Thomas, 1979). Loose bark provides thermal protection for salamanders and other temperature-sensitive species in addition to other protective functions (Maser and Trappe, 1984). Burrow-

Table 8
Cavity-Nesting Birds Commonly Censused in Temperate Forest Ecosystems
of North America

Common name	Scientific name[a]	Type of cavity use[b]
Common flicker	*Colaptes auratus*	P(L)[c]
Pileated woodpecker	*Dryocopus pileatus*	P(L)
Red-bellied woodpecker	*Centurus carolinus*	P
Gila woodpecker	*Centurus uropygialis*	P
Red-headed woodpecker	*Melanerpes erythrocephalus*	P
Acorn woodpecker	*Melanerpes formicivorus*	P(L)
Lewis' woodpecker	*Asyndesmus lewis*	P(L)
Yellow-bellied sapsucker	*Sphyrapicus varius*	P
Williamson's sapsucker	*Sphyrapicus throideus*	P
Hairy woodpecker	*Dendrocopos villosus*	P(L)
Downy woodpecker	*Dendrocopos pubescens*	P
Ladder-backed woodpecker	*Dendrocopos scalaris*	P
Nuttall's woodpecker	*Dendrocopos nuttallii*	P
Arizona woodpecker	*Dendrocopos arizonae*	P
White-headed woodpecker	*Dendrocopos albolarvatus*	P(L)
Black-backed three-toed woodpecker	*Picoides arcticus*	P(L)
Northern three-toed woodpecker	*Picoides tridactylus*	P(L)
Wied's crested flycatcher	*Myriarchus tyrannulus*	S
Ash-throated flycatcher	*Myriarchus cinerascens*	S(L)
Olivaceous flycatcher	*Myriarchus tuberculifer*	S
Western flycatcher	*Empidonax difficilis*	S(L)
Violet-green swallow	*Tachycineta thalassina*	S
Tree swallow	*Iridoprocne bicolor*	S
Black-capped chickadee	*Parus atricapillus*	P(L)
Carolina chickadee	*Parus carolinensis*	P
Mountain chickadee	*Parus gambeli*	S(L)
Boreal chickadee	*Parus hudsonicus*	P
Chestnut-backed chickadee	*Parus rufescens*	P
Tufted titmouse	*Parus bicolor*	S
Plain titmouse	*Parus inornatus*	S
Bridled titmouse	*Parus wollweberi*	S
White-breasted nuthatch	*Sitta carolinensis*	S(L)
Red-breasted nuthatch	*Sitta canadensis*	S(L)
Pygmy nuthatch	*Sitta pygmaea*	S(L)
Brown creeper	*Certhia familiaris*	S(L)
House wren	*Troglodytes aedon*	S(L)
Winter wren	*Troglodytes troglodytes*	S(L)
Bewick's wren	*Thryomanes bewickii*	S(L)
Carolina wren	*Thryomanes ludovicianus*	S(L)
Eastern bluebird	*Sialia sialia*	S(L)
Western bluebird	*Sialia mexicana*	S(L)
Mountain bluebird	*Sialia currucoides*	S

[a]After Peterson (1961).
[b]P, Primary excavator; S, secondary nonexcavator; after McClelland (1977), Raphael and White (1984).
[c](L), Also uses logs; after Thomas (1979).

Table 9

Small Mammals Using Coarse Woody Debris in Temperate Forest Ecosystems of North America and Europe[a]

Scientific name[b]	Common name[b]	Type of log use[c]
Order Insectivora		
Family Soricidae		
Blarina brevicauda	Short-tailed shrew	P
Sorex cinereus	Masked shrew	P
Sorex fumeus	Smoky shrew	P
Sorex obscurus	Dusky shrew	P
Sorex trowbridgii	Trowbridge shrew	P
Sorex vagrans	Vagrant shrew	P
Order Rodentia		
Family Sciuridea		
Eutamias amoenus	Yellow-pine chipmunk	P(C)[d]
Glaucomys sabrinus	Northern flying squirrel	S(C)
Spermophilus beecheyi	California ground squirrel	S
Tamias striatus	Eastern chipmunk	S
Tamiasciurus hudsonicus	Red squirrel	S(C)
Family Cricetidae		
Subfamily Cricetinae		
Neotoma cinerea	Bushy-tailed wood rat	S(C)
Peromyscus leucopus	White-footed mouse	P
Peromyscus maniculatus	Deer mouse	P(C)
Subfamily Microtinae		
Clethrionomys gapperi	Southern red-backed vole	P
Clethrionomys glareolus	Common red-backed vole[e]	P[f](C)
Family Muridae		
Subfamily Murinae		
Apodemus flavicollis	Yellow-necked field mouse[e]	P[f](C)
Family Zapodidae		
Zapus hudsonicus	Meadow jumping mouse	S
Zapus princeps	Western jumping mouse	S
Zapus trinotatus	Pacific jumping mouse	S
Order Carnivora		
Family Mustelidae		
Mustela erminea	Ermine	P(C)

[a]Based on references cited in text regarding species richness and abundance of small mammals.
[b]From Golley *et al.* (1975), pp. 361–370.
[c]P, Primary, use logs to fulfill the three major life-history functions: reproduction, feeding, and cover; S, secondary, use logs to fulfill only one or two of the major life-history functions.
[d](C), Also use snag or tree cavities or nest boxes; North American species, Thomas (1979); European, Truszkowski (1974).
[e]European species, Hansson (1971), Grodzinski (1971), Grodzinski *et al.* (1970).
[f]Based on similar ecology, Corbet and Southern (1977).

ing into decayed logs by some species provides opportunities for denning, feeding, and reproduction for other species. The mammals *Peromyscus maniculatus, Tamiasciurus hudsonicus,* and *Pituophus melanoleucus* utilize log burrows as reproduction sites in the Blue Mountains of Oregon (Thomas, 1979). Three species of predatory salamanders, *Batrachoseps wrighti, Ensatina eschscholtzi,* and *Aneides ferreus,* deposit eggs within logs of the coastal coniferous forests of western Oregon (Maser and Trappe, 1984). Hollow logs are used as cover and dens by larger animal species, including bears, and by rodents to store food (Thomas, 1979).

The plants, fungi, and animals inhabitating and decomposing CWD are a major food for many vertebrates. Snags are heavily utilized as feeding sites by insectivorous bird species, such as those of the genera *Centurus, Drycopus, Dendrocopos,* and *Picoides.* The *P. menziesii–T. heterophylla* forests of northwestern North America provide examples of log use for vertebrate food resources (Maser and Trappe, 1984). The vole *Clethrionomys californicus* extensively uses logs for shelter and food. This species eats mostly fungi and prefers truffles (Maser *et al.,* 1978; Ure and Maser, 1982), some species of which fruit mostly in rotten wood, where their mycelium forms a mycorrhizal association with conifers. Vole feeding disperses fungal spores to other suitable habitats. Several salamander species, *B. wrighti, A. ferreus,* and *E. eschscholtzi,* feed in logs, eating most invertebrate species found in logs. Ants, beetles, isopods, and common earwigs are important foods for *A. ferreus,* for example. The shrew *Sorex trowbridgei* and shrew-mole *Neurotrichus gibbsi* are important mammalian predators in rotting logs. The shrew-mole is a particularly efficient burrowing predator, feeding heavily on earthworms, centipedes, and flies (Maser *et al.,* 1981).

CWD provides spatial and temporal continuity of habitat that may be important to the survival and migration of animals. After catastrophic disturbances, logs continue to serve as shelter and fulfill other functions even though other habitat features are drastically altered. Similarly, logs provide a corridor that allows log-related species to migrate.

   c. Importance of Coarse Woody Debris as Habitat. The dependence of CNB on the presence of snags makes them ideal species to illustrate the importance of CWD as vertebrate habitat. The contribution CNB make to the avifauna, however, varies markedly between deciduous and coniferous forests and over the course of succession. CNB account for 9–39% and 8–62% of the total bird species in deciduous and coniferous forests, respectively. Species richness and abundance of CNB appear to be greater in coniferous than in deciduous forests, hence the avifauna of the coniferous ecosystems might be more responsive to changes in the amount and quality of CWD present than those of deciduous ecosystems.

In deciduous forests, the contribution CNB make to the total number of bird species increases from <10% (one species) in early seral stages to 30% (seven species) in old-growth forests (Anderson, 1972; Holmes and Sturges, 1975; Holt, 1974; Johnston and Odum, 1956; Kendeigh, 1948; Martin, 1960; Odum, 1949, 1950; Salt, 1957; Shugart and James, 1973; Shugart *et al.*, 1978; Stewart and Aldrich, 1949; Stiles, 1980). In terms of the total number of individuals, CNB increase from ~1–18% of the total bird population between the same two seral stages. In coniferous forests, CNB species comprise 30% of the species during early seral stages, but this proportion declines to 20% as the new forest develops. As succession proceeds, the proportion of the avifauna comprised of CNB increases again to 30%. The mean contribution CNB make to the total number of individuals increases from 20% (70 individuals 40 ha^{-1}) to 30% (80 individuals 40 ha^{-1}) between early seral stages and old-growth coniferous forest, respectively (Bock and Lynch, 1970; Haapanen, 1965; Hager, 1960; Mannan, 1977; Mannan *et al.*, 1980; Manuwal and Zarnowitz, 1981; Marcot *et al.*, unpublished; Martin, 1960; Raphael, 1980; Raphael *et al.*, 1982; Salt, 1957; Scott *et al.*, 1982; Szaro and Balda, 1979; Wiens and Nussbaum, 1975).

The relative species richness and abundance of secondary CNB (SCNB) and primary CNB (PCNB) have different patterns during deciduous versus coniferous forest succession. The ratio of SCNB species to PCNB species (SCNB : PCNB) does not consistently exceed 1 until late (mature and old-growth) seral stages of deciduous and coniferous forests. The SCNB : PCNB ratio was consistently >1 in middle (sapling/pole timber and small saw timber) to late seral stages of deciduous forests; in contrast, SCNB : PCNB abundance did not consistently exceed 1 until late seral stages of coniferous forests. The relationship between species richness and abundance of SCNB and PCNB is important because SCNB depend partly upon cavity abundance (Brush, 1981; Von Haartman, 1957), and the abandoned cavities of PCNB are one source of nest cavities for SCNB. Another major source of nest sites of SCNB, however, is natural cavities in living and dead trees formed by processes independent of PCNB activity. The major source of nest sites for SCNB is abandoned PCNB cavities in coniferous forests and naturally formed cavities in deciduous forests (Carey, 1983; Raphael, 1980). This difference in the relative importance of natural versus abandoned cavities between forest types may partly explain the tendency for SCNB : PCNB abundance to exceed 1 earlier in deciduous than in coniferous forest succession. SCNB in deciduous forests are apparently able to colonize forests irrespective of PCNB abundance because SCNB depend more upon the abundance of natural cavities than on cavities abandoned by PCNB.

Small mammal communities of forests are, as noted earlier, comprised of many species using CWD. Species using CWD average 70–90% (4–7 species) of the total number of small mammal species richness in both deciduous and coniferous forests over a wide range of seral stages (Ahlgren, 1966; Aldrich, 1943; Gashwiler, 1970; Gunther *et al.*, 1983; Hirth, 1959; Hooven and Black, 1976; Kirkland, 1977; Manville, 1949; Martell and Radvanyi, 1977; Morris, 1955; Odum, 1949; Pearson, 1959; Raphael, 1983; Raphael *et al.*, 1982; Ryszkowski, 1969; Scott *et al.*, 1982; Storer *et al.*, 1944; Wetzel, 1958). Averaged over forest type and successional stage, small mammal species using CWD comprise 75–99% of the total number of individuals. Abundance of mammals using CWD generally follows the abundance of CWD and appears to be highest during the earliest and latest stages of forest succession and lowest during middle successional stages.

The herpetofaunal communities of forests have been studied relatively little qualitatively and even less quantitatively. The available literature shows, however, that CWD-using species may predominate within the herpetofauna. For example, the reptiles and amphibians using CWD comprise 93% (mean of 8 species) and 99% of the individuals (54 individuals ha^{-1}) ranging from the early seral stages to old-growth *Pseudotsuga* (Raphael, 1983; Raphael *et al.*, 1982).

2. Influences on Fish Populations

The perspective of stream ecologists concerning the relationship between CWD and fish populations has changed dramatically during the past two decades. Before 1970, wood generally was considered a hindrance to fish migration and a cause of oxygen depletion in streams. In contrast, recent investigations have emphasized the beneficial role CWD plays in the formation and stabilization of fish habitat.

a. Blockage to Migration. Logging often increases the amounts of CWD in streams above natural levels and causes massive log jams that can potentially block the upstream migration of anadromous salmonids (Elliot, 1978; Meehan *et al.*, 1969; Narver, 1971). After 1936, fishery management agencies in the Pacific Northwest removed log jams from streams to increase fish access to spawning and nursery areas (Hall and Baker, 1982; Sedell and Luchessa, 1982). Early logging practices doubtlessly added debris and increased the potential for blockages, but debris removal operations continued for many years with little evaluation of their need. Narver (1971) felt complete barriers were relatively rare and that migration was only hindered at certain flows.

Although some log jams block fish passage, they rarely remove a major fraction of the potential spawning or rearing habitat in a drainage basin.

For example, log jams prevented fish migration to 12% of the length of potential fish-producing streams in the Coquille River basin in Oregon in the 1940s and early 1950s (Sedell and Luchessa, 1982). Only 5.5% of the length of potential fish-bearing streams in the Siuslaw National Forest in western Oregon were blocked by log jams in the late 1970s (Sedell and Luchessa, 1982).

Removal of log jams was also thought to decrease bank cutting and streambed instability because CWD deflects currents into streambanks (International Pacific Salmon Fisheries Commission, 1966; Pfankuch, 1978). The resulting siltation and shifting sediments caused by bank cutting would then smother and scour salmonid eggs and reduce the abundance of invertebrates (Gammon, 1970). The concept that CWD contributes to channel instability is inconsistent with most recent geomorphic studies (see Section V,D). In fact, removal of log jams may actually increase the adverse effects siltation and sediment instability have on fish and invertebrate populations (Beschta, 1979). Abundance of sea-run *Salvelinus malma* decreased after removal of debris dams in an Alaskan stream, and 2 years after removal, numbers of trout were only 20% of the preremoval population (Elliot, 1978). Log-jam removal in seven stream reaches in Oregon released stored sediments and destroyed fish habitat (Baker, 1979). However, fish populations did not decline in these streams after CWD removal.

b. Water Quality. CWD contains organic compounds that are potentially lethal to aquatic organisms. Leachates of whole *Tsuga* logs, with and without bark, were not toxic to fry of *Salmo gairdneri* and *Oncorhynchus tshawytscha* in 96 hours of exposure (Atkinson, 1971). Leachates of *Pseudotsuga* needles, *Tsuga* needles, and *Alnus* leaves were toxic to *Poecilia reticulata* and *S. gairdneri,* but at concentrations so high that O_2 depletion would become a threat long before toxic effects could be expressed (Ponce, 1974). Foliage terpenes and heartwood tropolenes were more toxic to *Oncorhynchus kisutch* and aquatic insects than bark extractives and heartwood lignins (Peters *et al.,* 1976). Analysis of water from several natural streams and logging-influenced streams revealed that the adverse effects of these leachates would be restricted to freshly logged areas with large amounts of *Thuja* slash or swampy areas with naturally high accumulation of *Thuja* debris (Peters *et al.,* 1976). Extracts of *P. sitchensis* and *T. heterophylla* bark were toxic to *Oncorhynchus gorbuscha* fry (Buchanan *et al.,* 1976). Salmon fry were more sensitive to extracts of *Tsuga* than *Picea* bark extracts; 50% of the fry were killed at a concentration of 56 mg liter^{-1} of *Tsuga* bark extract and 100–120 mg liter^{-1} of *Picea* bark extract (96-hour LC_{50}). As with *Thuja,* these concentrations are sufficiently high that the toxic effects of leachates would be

limited to log-holding facilities or recent clear-cuts with heavy slash deposits.

Although toxic effects are rarely encountered, depletion of dissolved O_2 by microbial respiration and chemical oxidation of wood often affects fish populations adversely. Dissolved O_2 concentrations in stream water and interstitial water in a coastal stream in Oregon decreased to potentially lethal amounts after logging (Hall and Lantz, 1969). Dissolved O_2 concentrations increased after debris removal, but were still significantly lower than prelogging concentrations. Egg-to-fry mortality of *Oncorhynchus nerka* increased significantly when bark debris composed >4% of the volume of spawning gravel (Servizi *et al.*, 1970). Fry emergence was retarded when bark exceeded 1% of the volume. Oxygen in water can be consumed by either microbial respiration or by abiotic oxidation of the substrate. Abiotic oxdation rates (chemical oxygen demand) may exceed biological respiration rates (biological oxygen demand). Ponce (1974), for example, found that the chemical oxygen demand of *Pseudotsuga* wood exceeded biological oxygen demand by an order of magnitude. Thus, addition of CWD to streams may significantly reduce dissolved O_2 even when biological activity is low. Mortality or exclusion of fish by O_2 depletion caused by wood debris is not a major concern under natural conditions and is only likely to occur where unusually large accumulations of fresh CWD occur. Moreover, aeration in moderate- to high-gradient streams will probably offset reductions in oxygen concentrations caused by the presence of CWD.

c. Habitat. CWD plays a major role in stream channel geomorphology (see Section V,D); therefore, fish habitat is intricately linked to CWD dynamics. CWD potentially provides cover, creates important hydrologic features such as pools and backwaters, and stores inorganic sediments. The importance of CWD to fish populations has been recognized in a number of recent review articles (Franklin *et al.*, 1981; Maser and Trappe, 1984; Meehan *et al.*, 1977; Sedell and Swanson, 1982; Swanson *et al.*, 1982b; Triska *et al.*, 1982).

Early investigations of fish habitat in streams identified CWD as a major cover (Boussu 1954; Hunt, 1969; Tarzwell, 1936). Hartman (1965) observed that *O. kisutch* and *S. gairdneri* were associated with debris dams and that these salmonids decreased in winter where log cover was absent. Subsequent investigations have documented the use of wood habitat by fish in streams (Everest and Meehan, 1981; June, 1981; Lister and Genoe, 1979; Osborn, 1981).

In the Pacific Northwest, winter is a period of high flow, low stream temperature, and low light intensity. Stable winter habitat and refuges during high flow are critical for fish survival, and CWD is an important

source of cover and a major agent in channel stabilization. Fry and juveniles of *O. kisutch* and juvenile anadromous *S. gairdneri* (age 1+) used logs and upturned tree roots as their major source of winter cover in several streams on Vancouver Island, British Columbia (Bustard and Narver, 1975a). Juvenile *O. kisutch* in Carnation Creek, British Columbia, inhabited deep pools, log jams, and undercut banks with tree roots and debris in winter (Tschaplinski and Hartman, 1983). During winter, stream reaches with these habitat types retained higher populations of juvenile salmon than those without these habitats; furthermore, fewer fish were lost after freshets in reaches with abundant CWD. Logging did not result in a change in numbers of salmon that migrated out of Carnation Creek in the autumn or into the stream in the spring.

In addition to large, stable accumulations of CWD, lateral habitats outside the main channel (e.g., backwaters, sloughs, and side channels) are critical refuges for fish during floods and serve as rearing areas for juveniles. CWD, boulders, and living trees were the major structural features responsible for the creation and maintenance of backwaters and side channels in third-order streams in the Cascade Mountains (Moore, unpublished). Bustard and Narver (1975a,b) observed that juvenile *O. kisutch* moved into sidepools and small lateral tributaries during winter floods. Off-channel ponds in rivers of the Olympic Peninsula supported the majority of salmonid production in the drainage (Peterson, 1980). Side channels and terrace tributaries contained the highest biomass of juvenile *O. kisutch* in the Hoh River of the Olympic Peninsula (Sedell *et al.*, 1982). Bisson *et al.* (1982) found coho salmon fry predominantly in backwater pools in 19 stream reaches in Washington. In reaches above anadromous zones, backwater pools were the preferred habitat of the trout *Salmo clarkii*. Fry of *S. clarkii* in streams in the Cascade Mountains of Oregon occupied backwater habitats and were not found in the main channel until early fall; even then they remained in main channel habitats close to backwaters (Moore, unpublished).

The abundance of fish populations in streams and rivers is strongly related to the abundance of CWD. Wood debris was a major component of off-channel habitats in rivers of the Olympic Peninsula, and side channels with CWD supported eight times more juvenile *O. kisutch* than side channels without CWD (Sedell *et al.*, 1982). Densities of *Salmo trutta* in a Danish stream declined after removal of small wood debris (Mortensen, 1977). Lestelle (1978) observed numbers and biomass of resident *S. clarkii* declined in winter after removal of 85% of the wood volume in a stream in Washington. Import of wood from upstream reaches was associated with increases of trout numbers and biomass to the original amounts. Yearling anadromous *S. gairdneri* and *S. clarkii* of all ages preferred habitats with

abundant wood debris in streams in Washington (Bisson *et al.*, 1982). Densities of juvenile *O. kisutch* declined after removal of wood debris in two Alaskan streams (Bryant, 1982). In southeast Alaska, streams in clear-cut reaches supported higher biomass of young-of-the-year salmonids than streams with buffer strips or old-growth forests (Murphy *et al.*, 1985). However, streams with buffer strips contained significantly more yearling salmonids than streams flowing through clear-cuts or old-growth forests. Evidently, blowdown trees in the buffer strips provided an important source of cover that increased overwintering survival.

Spatial distribution of wood also influences the quality of fish habitat. Fish occupy three-dimensional space in the water column, and therefore the architectural arrangement of wood accumulations affects the potential use of that habitat. Little research has been completed on this aspect of fish habitat, but a recent study in streams in British Columbia found that fish abundance around wood debris increased as complexity of the accumulation increased (Forward, 1984). Intricate networks of logs, branches, roots, and small wood debris create a more complex, diverse array of cover and hydrologic features that may benefit fish populations.

3. Terrestrial Invertebrate Habitat

Vast numbers of terrestrial invertebrates use CWD for food, shelter, and as a site for breeding. Some rely entirely on the resources of a single tree species, while others are able to use many. Other invertebrate taxa found in CWD represent groups more commonly found in forest litter (Graham, 1925). This section reviews the major taxa that use CWD, how they use it, and the successional development of CWD in terms of invertebrate taxa.

a. Invertebrate Use of Coarse Woody Debris. Many invertebrates use wood in one form or another as food. Some invertebrates are only attracted to dying or very recently dead trees, while others require decayed wood. The part of a tree that can be eaten also varies between species. Some ingest the nutrient-rich inner bark, while others utilize the less nutritious wood (Parkin, 1940), and still other invertebrates eat the fungi decaying the wood rather than the wood itself. Within a dead tree, the nutrients and energy originating in the wood pass through many trophic levels (Savely, 1939).

Terrestrial invertebrates may also use CWD as protection from environmental extremes. For example, Lloyd (1963) found that slugs, snails, terrestrial isopods, centipedes, and earthworms migrated into branches during warmer weather, but lived in the litter layer during colder weather. Earthworms, slugs, snails, and centipedes have also been found in decayed *Pinus* and *Quercus* logs (Savely, 1939). Other invertebrates use

wood as a hibernation site. The carabid beetle *Feronia oblongopunctata*, normally a litter-inhabiting species, hibernates in winter as an adult in cells excavated in the wood and under the bark of logs, and aestivates in these same sites during the summer (Penney, 1967).

Some invertebrates, mainly insects, use wood as a nesting site. These include carpenter ants (*Camponotus*), termites (Isoptera), carpenter bees (Xylocopidae), and domestic honey bees (superfamily Apoidea). Some of the social wasps construct their "paper" nests from masticated wood fibers gathered from CWD.

Organisms spending much of their life cycle in CWD, such as bark beetles, wood-boring beetles, and some mites and collembolans, breed and reproduce there as well. Some organisms only use wood for a small portion of their life cycle. For example, the egg stage and instars I–III of the millipede *Cylindroiulus punctatus* are found under bark, while the later instars and adults are found in the litter layer (Banerjee, 1967).

b. Successional Relationships. The fauna associated with a tree changes as the tree's condition goes from living, to dying, to dead and decaying. During succession there is a shift from hostplant specificity to habitat specificity, so that by the end of succession, the decay state of CWD is more important than the tree species contributing the CWD (Howden and Vogt, 1951). Interest in the succession of insects in dead and dying trees extends back for some time. Some of the earliest workers in this field include Townsend (1886), Packard (1890), Felt (1906), Adams (1915), Blackman and Stage (1918, 1924), Graham (1925), and Savely (1939). More recent work has been conducted by Howden and Vogt (1951) on *Pinus* snags, Fager (1968) on *Quercus* logs, and Deyrup (1975, 1976, 1981) on the insect fauna of dead and dying *Pseudotsuga*. We will cover only the common points because an extensive review would be needed to cover succession of each tree species.

Bark beetles (Scolytidae) are among the first insects to occur in CWD, attacking weakened or recently killed trees. Bark beetles are often host specific and are usually limited in their occurrence to specific areas of the tree (Furniss and Carolin, 1977). An associated and often extensive guild of parasites and predators rapidly follows bark beetles into CWD. For example, Miller and Keen (1960) cited 16 insect species that preyed upon the western pine beetle (*Dendroctonus brevicomis*). Four species of parasitic Hymenoptera are associated with this beetle and 10 species of beetles (representing 6 families), 1 species of ant, and 1 species of snakefly (Raphidiidae) were reported as predators. The list of parasites and predators would be more extensive if mites had been included. Mites are often important egg predators, but no specific instances were reported for the western pine beetle. However, the authors do report larval predation by

mites, and this appears to be the case for many other bark beetle species as well (Rust, 1933).

Other wood-boring organisms follow shortly after the attack by bark beetles. The ambrosia beetles (Scolytidae), round-headed wood borers (Cerambycidae), flat-headed wood borers (Buprestidae), together with horn-tailed wasps (Siricidae) usually attack freshly killed trees. Some species are cambium or phloem feeders (some bark beetles and flat-headed borers), while others may start in the phloem and then tunnel into the heartwood (some round-headed borers, flat-headed borers, ambrosia beetles, carpenter worms, and horn-tailed wasps, among others). These species open up the wood to other decay organisms, either brought in with the insect or entering after an opening is created.

Termites and carpenter ants often enter decaying wood, but species have their own special requirements so far as moisture (e.g., dry- and damp-wood termites) and decay state are concerned. Termites and ants also have large groups of associated organisms that follow them into CWD, called termitophiles and myrmecophiles, respectively.

As the wood decays further, organisms unable to penetrate sound wood appear. A number of beetles are found in very decayed wood, including representatives of such families as Scarabaeidae, Lucanidae, and Passalidae. The larval stages of a number of families of flies are frequently found in very decayed wood, including the Tipulidae and Mycetophilidae. Many collembolans and mites also appear at this stage.

   c. *Major Taxa Using Coarse Woody Debris as Habitat.*

   i. *Bark beetles*. Bark beetles, or Scolytidae, play an important role in the creation and early stages of CWD decay. Stark (1982) recognized three stages in the life cycle of bark beetles: production (mating, gallery construction, oviposition, and brood development), dispersal (flight and host selection), and colonization (aggregation and overcoming host resistance). Only in the dispersal stage is the beetle away from CWD.

   Another type of scolytid is the ambrosia beetle. In North America, these beetles attack dead or dying trees (Stark, 1982) and have a symbiotic relationship with fungi. The beetles introduce the fungi into boles and their breeding galleries, where the fungi provide the insects food. Ambrosia beetles differ in their gallery construction from true bark beetles in that their galleries go deep into wood. The Platypodidae, a small family of beetles closely related to the Scolytidae, also are often called ambrosia beetles. They have habits similar to the scolytid ambrosia beetles, but confine most of their boring activities to heartwood (Furniss and Carolin, 1977).

   ii. *Wood borers*. A number of other beetle taxa bore into wood besides bark and ambrosia beetles. Two major families of wood-boring beetles are

flat-headed wood borers (Buprestidae) and round-headed wood borers (Cerambycidae). The large beetle family Curculionidae (weevils) also contains some wood-boring species.

The family Buprestidae contains a number of wood-boring species and most enter dying or dead trees (Furniss and Carolin, 1977). Many species are hostplant specific or at least confine their activities to closely related host species. Female buprestids lay eggs in cracks and crevices in the bark. The larvae bore into the cambium region first and then usually into the wood (Miller and Keen, 1960), forming flattened burrows that are packed with boring dust. Life cycles may last from one to many years.

The Cerambycidae function much like the Buprestidae by attacking weakened, dying, or recently dead trees. The eggs are laid in the cracks and crevices of bark or in holes created by the female beetle. The hatching larvae bore into the cambium layer and sometimes into the wood itself. Some species are quite large (adults 40–70 mm long) and create large burrows deep in the wood.

iii. Termites. Termites (order Isoptera) are an important group of wood-eating social insects occurring in many parts of the world. Although most abundant and diverse in tropical and subtropical regions, selected genera and species occur in cooler regions (Weesner, 1960, 1970). There are five living families of termites and more than 2000 species (Weesner, 1960). The more primitive families live in and eat wood, while the more advanced taxa make nests on the ground or in trees and may eat grass, dead leaves, and fungi. The primitive groups have symbiotic protozoa in their hindgut, enabling them to digest cellulose, whereas the more highly evolved groups derive their cellulases from bacteria in the gut or produce their own enzymes.

Termite excavations in wood are normally shielded from light and are usually longitudinal cavities. The cavities are frequently characterized by the presence of cylindrical pellets of excrement, although dry-wood termites may actually move these pellets outside the nest.

Damp-wood termites normally live in damp, generally rotten wood. *Zootermopsis angusticollis* (Hagen) is a common species in CWD along the Pacific Coast of North America (Furniss and Carolin, 1977). Dry-wood termites, as their name implies, enter and live in dry wood (Weesner, 1970). The subterranean termites often establish their colonies in the ground, but feeding frequently extends to wood above ground (Weesner, 1970). These termites build tubes to food sources, maintaining contact with the colony and preventing desiccation and exposure to light. Some of the species of subterranean termites show a preference for springwood, leaving the harder summerwood generally untouched (Furniss and Carolin, 1977).

iv. Carpenter ants. Carpenter ants, *Camponotus* Mayr, are a conspicuous group of wood-dwelling insects in most habitats containing CWD. Some members of the subgenus *Camponotus* nest in the soil and thus are not considered here. Carpenter ants are common in most northern boreal forests, and yet there is remarkably little information about most species, and even the taxonomy of the genus *Camponotus* is unsettled (Creighton, 1950).

Snags, logs, and stumps are used by carpenter ants as nesting sites, and although they chew the wood to excavate galleries, it is not ingested (Coulson and Witter, 1984; Furniss and Carolin, 1977). Most carpenter ants feed on honeydew produced by homopterans (Fowler and Roberts, 1980; Gotwald, 1968; Sanders, 1972; Tilles and Wood, 1982), but some are known to be predaceous (Ayre, 1963; Fowler and Roberts, 1980; Green and Sullivan, 1950; Myers and Campbell, 1976).

Life-history information on species of *Camponotus* in North America is limited and primarily based on the work of Pricer (1908) in Illinois and Sanders (1964) in New Brunswick, Canada. Articles by Eidmann (1929), Hölldobler (1944), and Marikovskii (1956) provide a similar basis for work on the Old World *Camponotus* species, *C. herculeanus*.

A colony of carpenter ants is normally established by one delated, fertilized queen (Mintzer, 1979). The colonizing queen is capable of boring into wood, but entry is commonly made through an existing opening such as that left by an emerging insect. Initially, colony formation often follows the burrows of wood-boring insect larvae (Breznak, 1982; Parkin, 1940). First-year colonies of *Camponotus* in Illinois contained a single queen and an average of 8.68–9.76 workers and 16.71–18.21 larvae (Pricer, 1908). It takes from 3 to 6 years before a colony produces winged females, at which time there would be ~2000 workers. Some colonies may be quite large. Sanders (1970) recorded a colony of *C. herculeanus* from Ontario that contained 12,240 workers, 1,059 females, 77 males, and 10,280 larvae. As colonies become older, they become decadent, producing large numbers of males but no winged females. Sanders (1970) suggests that a figure of 500 workers is characteristic of decadent colonies.

v. Other Hymenoptera. In addition to the Hymenoptera that are parasitic on other wood-inhabiting insects, two families are frequently found in CWD—the Siricidae, or horntail wasps, and the Xylocopidae, or carpenter bees. Most horntail wasps attack coniferous trees. Many species are polyphagous in the larval stage (Furniss and Carolin, 1977). Symbiotic fungi are reported to be associated with some species, and some larvae have been reported to feed on the fungi (Morgan, 1968). The Xylocopidae, or carpenter bees, often burrow into wood where they rear their young. The bee larvae develop in the cells constructed in the burrow.

vi. Lepidoptera. An enormous number of Lepidoptera are associated with trees; only a few taxa have wood-boring larvae. These include some Hepialidae, Cossidae, and Sesiidae. All of these have larvae that bore into living wood—most often into the phloem layer first—and then into the sapwood, and eventually into the heartwood (Furniss and Carolin, 1977).

vii. Diptera. The Diptera, or true flies, is a large group of insects, but comparatively few terrestrial species are associated with CWD and are chiefly in the immature stages. Teskey (1976) reported representatives of 45 dipteran families that had taxa associated with dead and dying trees. The larvae of some species of crane flies (Tipulidae) and fungus gnats (Xylophagidae) bore into rotten wood. Larvae of fungus gnats are often found beneath the loose bark of stumps and fallen trees where they feed on fungi. The larvae of some Asilidae are found in decaying wood where they prey on round-headed beetle larvae and other arthropods. Some species of Syrphidae have larvae that mine in the cambium layer, particularly of conifers (Furniss and Carolin, 1977). Larvae of the genus *Medetera* (Dolichopodidae) are important predators of bark beetle larvae and adults and some other wood-boring beetles.

viii. Mites. Wallwork (1976) studied the mite fauna of decaying twigs and branches of *B. lutea* and *Tsuga*. Three of the four wood-boring mite species occurred in both tree species. Two of the three species showed a preference for different parts of the branch. For example, *Steganacarus magnus* occurred most often in the heartwood of *B. lutea* and in the bark of *Tsuga*. A variety of fecal-feeding and predaceous mites also were found in both tree species. *Betula lutea* had a larger fauna (12 species) than *Tsuga* (6 species), but fewer total individuals per branch.

4. Influences on Aquatic Invertebrates

The distribution and abundance of aquatic invertebrates in streams are intricately linked to CWD. In addition to using wood directly as habitat or food, aquatic invertebrates are strongly influenced by channel structures created by CWD and the storage of inorganic sediments and organic matter (Anderson and Sedell, 1979; Meehan *et al.,* 1977; Sedell and Swanson, 1982; Triska and Cromack, 1980; Ward *et al.,* 1982). In this section, we examine the habitat relationships, feeding dynamics, and life-history strategies of aquatic invertebrates associated with CWD in streams. When CWD is abundant, a specialized fauna has evolved that is closely associated with wood debris. Dudley and Anderson (1982) listed over 50 taxa, representing five orders, as "closely associated" with wood and twice as many as facultative users. Almost all of these taxa were most common in headwater streams.

a. Habitat. Many invertebrates in streams and rivers use CWD surfaces opportunistically as a refuge. Other taxa bore, mine, and ingest decayed wood and associated microbes, feed on periphyton attached to the wood surface, use wood as an oviposition site or entry route into water, or use wood as an attachment site for filter feeding.

It is difficult to determine exactly where "aquatic" habitat ends. We have included floodplains subjected to infrequent flooding as well as the active channel. Species richness (especially of burrowers) is often greatest at the land–water interface, which is submerged during high water. Capillary movement of water allows streamside wood to remain fully saturated throughout most of the year.

Substrate quality is an important factor in aquatic invertebrate colonization of CWD. The species of wood, degree of waterlogging, and decay class are all important. The extent of microbial invasion has a considerable influence on its utilization by insects. Wood with surface decay is exploited by gougers (e.g., the beetle *Lara avara*), shallow tunnelers (primarily chironomids), and surface scrapers (e.g., the mayfly *Cinygma*), as well as taxa using it as an attachment site (e.g., black flies and net-spinning caddisflies). All of these species also occur on CWD with decay throughout. The many grooves, crevices, and cracks in the well-decayed CWD serve as refuges from predation and the abiotic environment. Other uses (oviposition, pupation, case-making, and emergence) also are greater on decayed CWD than on the firm, submerged pieces.

The absence of gallery formation and deep tunneling in submerged wood is a unique attribute of invertebrate–wood associations in aquatic environments (Cummins *et al.,* 1983). In terrestrial ecosystems, the abundance, diversity, and degree of social organization of insect taxa associated with wood are much greater than those found in freshwater ecosystems. In marine environments, insects are largely absent, but Annelida, Mollusca, and Crustacea are major inhabitants and decomposers of wood (Cummins *et al.,* 1983).

Wood is used as a feeding platform or attachment surface by invertebrates in streams or rivers with a shifting sand bed (Benke *et al.,* 1984; Cudney and Wallace, 1980; Dudley and Anderson, 1982; Nilsen and Larimore, 1973). Where CWD constitutes most of the stable substrate, it may be the setting for a significant amount of secondary production (Benke *et al.,* 1984). Cudney and Wallace (1980) found that submerged wood was the only substrate suitable for net-spinning caddisflies, in the Savannah River of Georgia. Snags in the Satilla River of Georgia were highly productive, not only for net-spinning caddisflies, but also for filter-feeding Diptera and other typical "benthic" insects (Benke *et al.,* 1984). Of the 100 taxa identified from snag, sand, and mud habitats, 63 occurred on

snags and 29 of these were "very common." Biomass of insects on snags was 20–50 times higher than in sandy habitats and 5–10 times greater than in mud habitats. Production estimates for the snag habitat are among the highest yet reported for stream ecosystems. The authors hypothesized insect production was limited by the availability of substrate rather than food.

The Elmidae, or riffle beetles, are commonly found on CWD in streams. *Lara avara* occurs in streams west of the Rocky Mountains and is the one obligate xylophagous elmid that has been studied (Anderson *et al.,* 1978, 1984; Steedman, 1983). Other genera of elmid beetles may be xylophagous, such as *Macronychus* and *Ancyronyx,* which are usually found on wood (White, 1982). *Macronychus glabratus* is reported to be a wood feeder (LeSage and Harper, 1976b). In Coast Range streams of western Oregon, the density of *Lara* larvae was 71 per m² of wood surface, with densities on coniferous wood about half that on deciduous wood (Steedman, 1983). Larvae were found in similar abundance on large and small sticks of wood in various states of decay (Steedman, 1983).

Wood is used for case construction by Trichoptera in several families and genera, but especially by the Limnephilidae. Of the 92 genera of case-making caddisflies discussed by Wiggins (1977), about one-quarter use bark or wood, at least occasionally, in case construction. Although most of these species add bark or wood chunks to their cases, *Amphicosmoecus* and *Heteroplectron* bore cavities in twigs and wood chips.

Pupation in moist or saturated wood is a common behavior for caddisflies and Diptera. Burrowing in CWD rather than attaching to stones may decrease mortality caused by predation, desiccation, or exposure to lethal temperatures when water level decreases. Burrowing into wood prior to pupation often occurs at or above the water line where oxygen concentration is high, but where the wood is still moist.

Wood is used as an oviposition site both above and below the water line. Many limnephilid caddisflies deposit egg masses on damp wood. Wisseman and Anderson (1984) found that in Coast Range watersheds, oviposition by *Ecclisocosmoecus scylla, Hydatophylax hesperus,* and some other species was concentrated on a few large logs overhanging the upper reaches of streams. Submerged branches are often used for oviposition by hydropsychid caddisflies. Eggs of the surface bugs *Gerris* and *Microvelia* are often glued to wood at the water's edge (Anderson, unpublished). On the same sticks, eggs of the free-living caddis, *Rhyacophila,* and the false cranefly, *Ptychoptera townesi* Alexander, were observed. Females of the xylophagous cranefly, *Lipsothrix nigrilinea* Doane, and of Chironomidae have also been observed ovipositing at or below the water line.

b. Wood Consumption. Xylophages consistently occur on or in woody debris and ingest wood particles. Diverse modes of feeding behavior and life-history strategies occur in this group, and all the major nonpredatory aquatic orders of aquatic insects have xylophagous representatives. Xylophages are less well represented in the hemimetabolous orders of insects than in the Holometabola, but some Plecoptera and Ephemeroptera ingest wood.

Plecoptera larvae can remove and ingest the soft, decayed surface of submerged wood by shredding or scraping, but few species have evolved as wood-feeding specialists. Gut-content analysis indicates the nemourids *Zapada* and *Visoka* and the peltoperlid *Yoraperla* are xylophages (Pereira *et al.*, 1982). In New Zealand, the austroperlid, *Austroperla cyrene* (Newman), was shown to be a wood feeder (Anderson, 1982).

Among the mayflies associated with wood, the tropical species *Povilla adusta* sometimes causes economic damage by burrowing into bridge pilings (Bidwell, 1979). This species is also abundant on submerged trees in African reservoirs (McLachlan, 1970; Petr, 1970). *Povilla adusta* burrows into wood or uses the galleries formed by terrestrial wood-boring beetles, but it feeds primarily on the periphyton attached to wood surfaces (Petr, 1970). The heptageneid mayfly, *Cinygma integrum* Eaton, is closely associated with wood debris in Pacific Northwest streams (Anderson *et al.*, 1984). Pereira (1980) reared *Cinygma* larvae using stream-collected wood as food. This species scrapes epiphytic autotrophs (algae) and heterotrophs (fungi and bacteria) from wood surfaces, and fungal mycelia are their primary food source (Pereira and Anderson, 1982).

The families of aquatic Coleoptera that consume wood include borers (Oedemeridae), scraper-collectors (Elmidae, Elminae; Psephenidae, *Acneus;* and Helodidae, *Cyphon,* and *Metacyphon*), and gougers (Elmidae, Larinae; and Ptilodactilidae, *Anchytarsus,* and *Anchyteis*). Scraper-collectors usually do not ingest significant amounts of wood fragments (Anderson, 1982; Pereira *et al.*, 1982). *Anchytarsus* is reported to be entirely xylophagous, but is rare throughout its range (LeSage and Harper, 1976a). Other ptilodactylids that may be wood feeders are also uncommon.

The oedemerid wharf-borer, *Nacerda melanura,* has been reported to be injurious to timbers of wharves along the California coast, and *Copidita 4-maculata* are known to bore into wet bridge and mine timbers (Essig, 1942). In Oregon and Washington, Dudley and Anderson (1982) found large numbers of larvae and adults of *Ditylus quadricollis* in a few submerged logs; where they occurred, the wood was riddled by their tunnels.

The Elmidae, or riffle beetles, are the most common xylophagous bee-

tles in stream habitats. *Lara avara* larvae feeding on *Alnus, Tsuga,* and *Pseudotsuga* wood that had been in a stream for 5 years produced feces at a mean rate of 9% of body weight per day (range 0–41%) (Steedman, 1983). Steedman calculated that the field population produced 1.1–2.5 g m^{-2} $year^{-1}$ of feces and removed 0.2–0.8% of the available CWD per year.

An investigation of feeding habits of Trichoptera in Oregon streams found that ~20 species ingested wood to some degree (Pereira *et al.,* 1982) and that many of the leaf shredders also feed on wood and associated microbes (Anderson *et al.,* 1978). The Calamoceratidae, Lepidostomatidae, and several genera of Limnephilidae are closely associated with wood in feeding. Some caddisflies listed as grazers by Wiggins and Mackay (1978), such as *Neophylax* and *Ecclisocosmoecus,* were also shown to fragment wood via their feeding activities. A New Zealand leptocerid caddisfly, *Triplectides obsoleta,* and a North American calamoceratid caddisfly, *Heteroplectron californicum,* both construct cases by hollowing out a twig and commonly tunnel into moist wood for pupation (Anderson, 1982). Though *Heteroplectron* consumes large quantities of wood, it cannot complete development with wood as its total diet (Anderson *et al.,* 1984).

The greatest diversity of aquatic and semiaquatic xylophages occurs in the Diptera. Most species are burrowers and collectively are probably the major wood decomposers in aquatic habitats. Dudley and Anderson (1982) listed 10 dipteran families that are closely associated with wood. Chironomidae (10 genera), Tipulidae (4 genera), and fungus gnats of the families Mycetophilidae and Sciaridae are the most common xylophages encountered. Only some genera of Chironomidae are fully aquatic, whereas the other taxa occur in moist wood at or above the water line.

The discovery that chironomid larvae live in decaying wood is fairly recent (Teskey, 1976), but several recent studies indicate wood-boring midges are widespread (Anderson *et al.,* 1984; Borkent, 1984; Cranston, 1982; Kaufman, 1983). Borkent (1984) reviewed the systematics and phylogeny of *Stenochironomus* and related genera and showed that the 65 species available for study were all highly modified for a mining mode of life, with a dorsoventrally compressed head capsule, expanded thoracic segments, and a long, flaccid abdomen. Most species of this genus were wood borers. Wood-mining *Stenochironomus* live in firmly anchored wood in lentic and lotic habitats. The larvae generally only mine angiosperm wood that has a clean surface and only occur in firm wood. The larval chambers are parallel to the wood surface under a layer of firm wood or thin bark. Other important wood-burrowing midges include four

genera of Orthocladiinae midges: *Chaetocladius, Orthocladius, Sympo-siocladius,* and *Limnophyes* (Anderson *et al.,* 1984).

A large xylophagous midge, *Xylotopus par,* burrows into soft, well-decayed wood (Kaufman, 1983). Growth rates of this midge were greatest in *Tilia* logs that were terrestrially decayed and then submerged for only 2 weeks. In submerged logs of *Fraxinus* and *Populus,* the density of *Xyloto-pus* exceeded 5000 larvae m^{-2}, and biomass increased exponentially from 70 mg m^{-2} in June to 5000 mg m^{-2} in August.

The large size of their larvae makes the Tipulidae the most conspicuous dipteran wood borers of semiaquatic habitats. Alexander (1931) listed 19 genera and 48 species of xylophagous tipulids on a worldwide basis, and Teskey (1976) recorded 30 Nearctic species associated with dead trees, but noted that his list was probably very incomplete. A succession of tipulid genera occurs in wood (Teskey, 1976). *Gnophomyia* larvae occur in fermenting sap beneath the bark before significant decay has commenced. *Ctenophora* and *Epiphragma* penetrate into relatively hard wood, while *Lipsothrix* larvae burrow into wood only where a portion of a log or branch is continuously immersed in a stream. Partitioning along the moisture gradient was observed in an Oregon stream in which *Austrolim-nophila badia* occurred primarily above the water line, whereas *Lip-sothrix* spp. occurred at and slightly below the water line (Anderson *et al.,* 1984; Dudley, 1982).

Life cycles and habitat preferences of the craneflies *Lipsothrix nigrili-nea* and *L. fenderi* differ in streams in western Oregon (Dudley, 1982). The nonadult stages are spent within soft logs in constant contact with water. *Lipsothrix fenderi* larvae are found in a wider variety of wood types, including solid wood, coniferous as well as deciduous species, and in marginal (drier) habitats.

  c. Life-History Strategies. Despite the number of examples of wood feeders discussed above, only a small fraction of aquatic insect taxa exploit wood debris as a food source. Life-history and feeding strategies of aquatic xylophages include some combination of the following: a long life cycle to compensate for low growth rates, high consumption rates, a symbiotic gut microflora to aid digestion and to furnish essential nutrients, and the ability to switch to high-quality food in later instars when rapid growth and lipid accumulation are required.

  A long life cycle is characteristic of most aquatic insects consuming wood. For example, the beetle *Lara* lives for more than 4 years, the caddisfly *Heteroplectron* has a generation time of 2 years or more, and the cranefly *Lipsothrix* requires 2 years or more to complete its life cycle. Xylophagous midges are apparently univoltine, whereas many of the collector-gatherers and algal feeding midges are multivoltine.

A symbiotic gut flora does not occur in the wood gougers *Lara* or *Heteroplectron* (Cummins and Klug, 1979; Steedman, 1983), which have a simple, straight gut without diverticula or a fermentation chamber to accommodate symbionts. The residence time of ingested particles in the gut of *Lara* is relatively short (~8 hrs); therefore, these insects consume large amounts of wood.

Increased consumption may compensate for low food quality (Cummins and Klug, 1979), but insects also may exhibit high rates of ingestion on optimum diets. High consumption rates are characteristic of the midge *Xylotopus* (Kaufman, 1983), wood-boring tipulids, and the caddisfly *Heteroplectron* (Anderson *et al.*, 1984).

Attached bacteria in the hindgut of wood-boring tipulids and in some other aquatic insects are assumed to be symbionts (Cummins and Klug, 1979). Kaufman (1983) described a thickening in the midgut region of *Xylotopus* that contained a dense arrangement of attached rods and filaments of a sporulating bacterium. In contrast to the more common situation where the bacteria are associated with the hindgut, this band in *Xylotopus* occurs on the posterior midgut wall, outside of the peritrophic membrane (Kaufman, 1983).

Concentration of N and other nutrients into a smaller volume by microbes is important to most xylophages. Steedman (1983) hypothesized that *Lara* passively absorbed molecules liberated by microbial enzymes and also digested contents of fungal, bacterial, and animal cells mechanically disrupted by feeding. Gougers and tunnelers as well as surface scrapers and shredders exploit the surficial layer of CWD enriched by microbes.

C. Importance of Coarse Woody Debris in Terrestrial Nutrient Cycles and Carbon Budgets

Coarse woody debris represents a substantial, yet little studied accumulation of energy, carbon, and nutrient elements in many forest ecosystems. Compared with other more commonly measured fluxes such as litterfall, the organic matter transfers into and out of the CWD compartment tend to be large. In this section, we compare the amount of nutrients stored in CWD relative to other ecosystem components and the flux of nutrients added to the forest floor in woody debris and leaf litter. A discussion of the mechanisms controlling the accumulation and loss of nutrients in CWD during decay then follows. Using simulation, we then

examine the role of CWD in nutrient cycling across the sequence of stand development and consider its impact on forest productivity.

1. Organic-Matter and Nutrient Storage

Despite over 20 years of ecosystem research, we were able to locate only eight terrestrial sites where amounts of organic matter and nutrients in CWD and other ecosystem components could be compared (Table 10). Overall, logs and snags accounted for 1–45% of total aboveground organic-matter storage, the two lowest values coming from mixed deciduous forests and the highest value coming from a young *A. amabilis* stand in which aboveground living biomass had not yet accumulated in large amounts. A second-growth tropical stand contained 23% of its aboveground mass in CWD, presumably left over from the previous stand. In contrast, two mature tropical forests contained 2–4% of their aboveground mass in CWD. CWD accounted overall for from <1 to nearly 20% of total ecosystem organic-matter storage, depending, in large part, on the amount of soil organic matter. For example, the 121-year-old *T. heterophylla* ecosystem from coastal Oregon has almost as much CWD as the old-growth *Pseudotsuga–Tsuga* ecosystem from the Oregon Cascades, and yet CWD comprises ~10% of the ecosystem total in the former case and ~17% in the latter case. The difference is primarily caused by the fact that soils in the coastal ecosystem accumulated ~6 times more organic matter than soils in the Cascade ecosystem.

Nitrogen and phosphorus in CWD account for 1–21% of the total aboveground storage (Table 10). In general, the proportion of ecosystem N stored in CWD is smaller than the proportion of organic matter stored, indicating that N concentration in CWD is lower than in other aboveground components. Two sites are exceptions to this pattern: the Virelles mixed-oak stand, where CWD accounted for a larger proportion of the N and P than of the aboveground biomass, and the old-growth conifer stand at H. J. Andrews Experimental Forest in Oregon, where CWD accounted for the same proportion of aboveground biomass and N.

Nutrient pools were measured across an age sequence of seven *Pseudotsuga*-dominated conifer stands in the Oregon and Washington Cascade Range (Table 11). The amount of N and P stored in CWD ranged from 100 to ~244 kg ha^{-1} and from 5 to 13 kg ha^{-1}, respectively, which is within the range reported for other ecosystems (Greenland and Kowal, 1960; Grier, 1976; Sollins *et al.*, 1980). Values were remarkably variable, however, and total storage in CWD showed little pattern with stand age. On average, the more advanced decay classes accounted for most of the N, P, and Ca stored in CWD, although two of the seven stands contained

Table 10

Biomass, Nitrogen, and Phosphorus Storage in Fallen Logs, Snags, and Other Ecosystem Components at Forest Sites throughout the World

Stand type	Item[a]	Fallen logs	Snags	Vegetation Above ground	Vegetation Below ground	Litter	Soil	System total	CWD (Percentage of aboveground)	CWD (Percentage of system total)	References
Tropical	DW	72	—[b]	236	54	2.27	44	408	23.4	17.8	Greenland and
second growth	N	230	—	1,469	316	35	4,605	6,650	13.3	3.5	Kowal (1960)
	P	19	—	95	22	1	13	150	16.5	12.6	
Mixed deciduous	DW	1.6	—	121	35	3.2	120	280.8	1.27	0.57	Duvigneaud
	N	11	—	406	127	33	4,480	5,060	2.44	0.22	and Denaeyer-
	P	0.5	—	32	12	1.4		45.9	1.47	1.09	DeSmet (1970)
Mixed deciduous	DW	3.9	—	122	34	25.6		185	2.57	2.10	Henderson and Harris (1975)
	N	9	—	388	104	265	5,080	5,850	1.36	0.15	Henderson et al. (1978)
Coastal *Tsuga*	DW	90	—	193	38	22	770	1,113	29.5	8.09	Grier (1976)
heterophylla	N	95	—	335	32	171	33,800	34,400	15.8	0.28	
(26 years old)	P	11	—	54	3	42	14	124	10.3	8.87	
Coastal *Tsuga*	DW	212	—	920	187	34	776	2,130	18.2	9.96	Grier (1976)
heterophylla	N	180	—	780	157	265	34,900	36,300	14.7	0.50	
(121 years old)	P	33	—	188	13	65	13	312	11.5	10.6	
Tropical montane rain forest	DW	11	—	492	63	10	330	906	2.14	1.21	Edwards and Grubb (1977)
Primary tropical forest	DW	18	—	406	67	6	248	745	4.19	2.42	Klinge (cited by Edwards and Grubb, 1977)
Old-growth	DW	190	25	718	152	51	133	1,270	21.9	16.9	Sollins
Pseudotsuga	N	190	25	539	197	260	3,720	4,930	21.2	4.36	et al. (1980)
menziesii	P	6.7	0.8	89.1	22.6	50.2	7.6	177	5.11	4.24	
Abies amabilis (23 years old)	DW	20	63	53	25	48	220	429	45.1	19.3	Grier et al. (1981)
Abies amabilis (130 years old)	DW	75	165	447	138	149	273	1,247	28.7	19.2	Grier et al. (1981)

[a] DW, dry weight (Mg ha^{-1}); N, nitrogen (kg ha^{-1}); P, phosphorus (kg ha^{-1}).
[b] Not available.

Table 11

Nutrient Storage in Coarse Woody Debris across a Chronosequence of
Pseudotsuga-Dominated Sites in the Oregon and Washington Cascade Range[a]

Location	Age (year)	DW[b] (Mg ha^{-1})	N[c]	P	K	Ca	Mg	Mn	Na
Bagby	250	115	244	12.4	21.9	223	28.8	9.5	5.5
H. J. Andrews 2	450+	79	143	7.5	15.3	153	17.8	7.8	3.4
H. J. Andrews 3	450+	115	227	12.3	24.0	237	28.9	12.7	5.3
Wind River	550	81	144	7.6	17.4	157	17.8	8.8	3.5
Squaw Creek	750	98	213	11.9	20.3	215	26.5	6.8	4.3
Mount Rainier 2	1000+	140	238	13.2	30.5	258	31.0	19.6	6.0
Mount Rainier 3	1000+	90	101	5.3	9.0	94	11.6	2.9	2.0

[a]From Sollins *et al.* (unpublished).
[b]DW, Dry weight.
[c]All elements are measured in kilograms per hectare.

a significant proportion of the total N and P in decay class III (Fig. 14). The amount of K stored in CWD tended to peak earlier in the decay sequence (class III or IV), which is to be expected given how quickly K leaches from CWD.

The significance of nutrient storage of CWD to the overall forest economy is difficult to judge. Compared with N stored below ground, the amounts stored in CWD are often relatively small indeed (Table 10). In *T. heterophylla* ecosystems, the soil contains ~200 times as much N as the logs. The soil of an old-growth *Pseudotsuga* ecosystem at H. J. Andrews was much less fertile, but the soil–log N ratio was still ~20. The amount of P stored in logs and soil is much more similar, especially if one includes only the readily extractable soil P in the comparison. Ratio of readily extractable soil P to P in logs ranged from 0.4 to 1.3 at the four sites where both were measured. The comparison requires caution, however, because there is much disagreement as to how to measure "readily extractable" soil P and because concentrations in the logs are near detection limits. At present, however, it appears that we lack the data to even roughly gauge the importance of P stored in CWD.

CWD and associated microbial communities greatly influence patterns of nutrient cycling in stream ecosystems. In a first-order stream in an old-growth coniferous forest in Oregon, the majority of the N was stored in coarse and fine woody debris (Triska *et al.*, 1984). CWD constituted 32% of the total N pool, while fine woody debris stored 18%. Fine particulate organic matter represented 40% of the total N stored, but a large fraction of this material may have been derived from CWD. Storage of a major
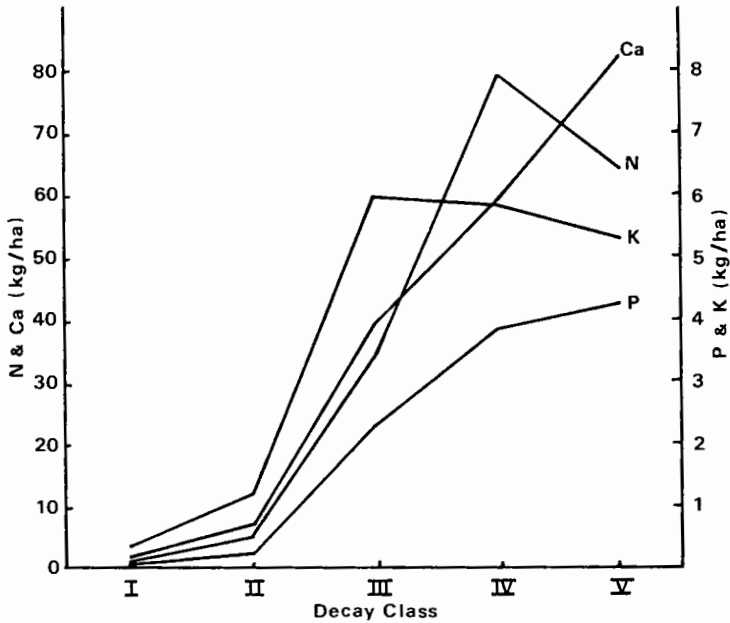
Fig. 14. Distribution of N, P, K, and Ca over decay classes in seven *Pseudotsuga menziesii*-dominated stands from the Cascade Range of Oregon and Washington.

fraction of nutrient capital in geomorphically stable, slowly decomposing CWD results in a persistent, stable nutrient supply for streams.

2. Input of Organic Matter and Nutrients to the Forest Floor

Input via tree death accounted for a substantial proportion of the total organic matter returned to the forest floor at the few sites where it was measured (Table 12). However, because leaf fall has higher nutrient concentrations than CWD, a larger proportion of nutrients return to the forest floor in foliage than in CWD.

Organic-matter transfer to the forest floor in fine and coarse wood are of similar magnitude. Together they account for 24–39% of total organic matter returning to the forest floor at five of the forest types, but for 60–74% of dry-matter return in the *Pseudotsuga* stands (Table 12). Why the latter ecosystems behave so differently is not known. Input of nutrients via fine wood has been measured in few ecosystems; at H. J. Andrews and Hubbard Brook, the two sites for which data could be obtained conveniently, fine woody litterfall accounted for 16 and 19%, respectively, of

Table 12

Annual Input of Organic Matter, Nitrogen, and Phosphorus in Falling Stems, Branches, and Foliage

Stand type	Stems and large branches			Fine wood			Foliage and miscellaneous			References
	DW[a] (Mg ha^{-1})	N (kg ha^{-1})	P	DW (Mg ha^{-1})	N (kg ha^{-1})	P	DW (Mg ha^{-1})	N (kg ha^{-1})	P	
Mixed northern hardwood	1	1.4	0	1.2	10.4	0.9	3.5	42.4	3.1	Gosz *et al.* (1972)
Liriodendron tulipifera	0.91	—[b]	—	0.12	—	—	3.3	—	—	Edwards (1972), Sollins *et al.* (1973)
Mixed deciduous/ pine	0.6–1.9	3.6[c]	—	0.5–0.7	—	—	3.4–4.1	34.0	—	Harris *et al.* (1973), Henderson and Harris (1975)
Pseudotsuga menziesii (20–90 years old)	2.61	1.32	0.19	0.84	—	—	2.38	21.3[c]	3.1[c]	Gessel and Turner (1976), Sollins (1982, unpublished)
Pseudotsuga menziesii (450+ years old)	7	3.9	0.6	1.1	3.8	0.5	2.9	16.0	4.0	Grier and Logan (1977), Sollins *et al.* (1980)
Populus tremuloides	0.45	—	—	0.85	—	—	3.1	—	—	Gosz (1980)
Abies amabilis (26 years old)	0.3	—	—	0.47	—	—	1.36	—	—	Grier *et al.* (1981)

[a]DW, Dry weight.
[b]Not available.
[c]Includes fine woody litterfall.

the total N returned in litterfall. In contrast, CWD accounted for 16 and 3%, respectively, of the total N returned to the forest floor. These two studies indicate that nutrient return in CWD can be ignored in some ecosystems, whereas return in fine woody debris definitely cannot. However, in forests where the CWD input rate is high, a large amount of nutrient transfer to the forest floor will be overlooked if CWD is not measured.

3. Nutrient Accumulation and Loss in Coarse Woody Debris

a. Input to Logs via Throughfall and Litterfall. Logs occupy a large portion of the land area—from 6 to 25% in conifer stands of the Pacific Northwest (Table 5). Consequently, they can potentially intercept a large proportion of incoming litterfall and throughfall. Nutrients normally added to the forest floor via these two pathways, may, therefore, accumulate within CWD. Grier (1978) found that Na accumulated in fallen logs near the Oregon Coast, whereas amounts of K decreased rapidly. Precipitation at this coastal site contained ~3 times as much Na as K, suggesting that rainfall provided the Na that accumulated during log decay. At other sites where precipitation does not contain unusually large amounts of Na, both Na and K concentrations decline roughly in parallel through time (Foster and Lang, 1982; Sollins and Cline, unpublished).

b. Input to Logs via N Fixation. The existence of asymbiotic N fixers in decayed wood was first postulated by Cowling and Merrill (1966), then demonstrated by Sharp and Milbank (1973) and Cornaby and Waide (1973). Estimates of annual N input average nearly 1 kg ha^{-1} year^{-1} across a wide range of forest types (Table 13). The lack of variation is deceptive, however, because lower rates at some sites were offset by larger biomass of CWD.

The organisms responsible for N fixation in decaying wood have received considerable study. Aho *et al.* (1974) isolated the obligate anaerobes *Klebsiella* and *Enterobacter* with nitrogenase activity from heart rot of living *A. concolor* trees. Spano *et al.* (1982) reported similar findings for fallen *Pseudotsuga* logs infected with *Fomitopsis pinicola*—obligate anaerobes were again responsible for the nitrogenase activity. Silvester *et al.* (1982) found, however, that the diazotrophic bacteria inhabiting fallen *Pseudotsuga* logs were microaerophiles, showing maximum activity at O$_2$ concentrations of ~5%. They explained the difference between their results and those of previous workers, noting that it was difficult to achieve complete anaerobiosis within the wood samples unless the samples were flushed with N$_2$ for several hours. With long flushing times,

Table 13

Acetylene Reduction and Estimated Nitrogen-Fixation Rates by Asymbiotic Organisms Inhabiting Coarse Woody Debris

Forest type	Acetylene reduction (nmol g^{-1} day^{-1})	CWD biomass (Mg ha^{-1})	Nitrogen fixation (kg ha^{-1} $year^{-1}$)	References
Mixed deciduous	25–37	11.8	0.9	Cornaby and Waide (1973)
Rocky Mountain mixed conifer	1–11	113	0.7	Larsen *et al.* (1978)
New England hardwoods	0–210	5–38	0.2–2.1	Roskoski (1980, 1981)
Intermountain *Thuja–Tsuga*	3–30	50	0.3	Larsen *et al.* (1982)
Rocky Mountain mixed conifer	36–230	—[a]	—	Spano *et al.* (1982)
Pacific Northwest *Pseudotsuga–Tsuga*	0–17	100	1.4	Silvester *et al.* (1982)

[a]Not available.

however, nitrogenase activity was zero, indicating that the organisms were not anaerobes.

The accuracy of current methods for measuring low-level N fixation by asymbiotes is subject to serious question. Only acetylene reduction was measured, not ^{15}N fixation, in five of the seven studies (Aho *et al.*, 1974; Cornaby and Waide, 1973; Larsen *et al.*, 1978; Sharp and Milbank, 1973; Spano *et al.*, 1982). Roskoski (1981) measured both processes and reported ratios of acetylene reduction to N_2 fixation ranging from zero to infinity, with a mean of 5.9, rather different from the theoretically expected ratio of 3.0. Excessive incubation time can lead to a substantial error in the ratio. Silvester *et al.* (1982) reported a mean ratio of 3.5 when incubations were kept <6 hrs, whereas ratios ranged from 4.55 to 6.01 when incubations were continued for 6–24 hrs. This confirmed work by David and Fay (1977) indicating that because acetylene inhibits N_2 fixation, amino N amounts in the diazotrophs will be depleted, in turn stimulating nitrogenase activity or synthesis.

Despite these methodological problems, it seems unlikely that N fixation in CWD amounts to more than a few kilograms per hectare per year. Such an input rate is much smaller than return in leaf fall and throughfall and is probably also smaller than return in root death. The N fixed in CWD, however, is a net input to the ecosystem; therefore it is more revealing to compare these rates to input by bulk precipitation and from N fixed elsewhere in the forest ecosystem. In an old-growth *Pseudotsuga* ecosystem, total input from external sources was estimated at 5 kg ha^{-1} year^{-1} (Sollins *et al.*, 1980), and an addition of even 1 kg ha^{-1} year^{-1} via fixation in CWD could be important. Input via precipitation is much greater at Hubbard Brook (22 kg ha^{-1} year^{-1}) (Likens *et al.*, 1977) and at the Oregon coastal sites studied by Grier (1978). At these two sites, the impact of a 1 kg ha^{-1} year^{-1} input via N fixation in CWD would be correspondingly less.

c. Input to Logs via Fungal and Root Colonization. Fungal rhizomorphs and vascular plant roots abound in rotten logs in all but the earliest stages of decay (see Section V,A). These interconnections with the "outside world" are likely the most important pathways by which N and other nutrients enter logs (Ausmus, 1977). There have been no quantitative studies of nutrient transfer into logs by fungi, although the ability of many fungi to translocate nutrients is well established (e.g., Bowen, 1973). Vascular plant roots may act similarly because as they grow into a matrix largely devoid of available nutrients, nutrients can presumably be mobilized from other portions of the plants and translocated into the roots that colonize the wood. Such roots might then die in place, adding nutrients to the wood.

d. Output from Logs via Fragmentation and Leaching. Although fragmentation is perhaps the dominant transfer of nutrients out of logs and snags, it remains the least studied. Lambert *et al.* (1980) and Sollins (1982) concluded that on a dry weight basis, fragmentation accounted for about half of the total loss from logs. The importance of fragmentation as a nutrient loss from logs and snags depends upon the behavior of the nutrient. For example, N concentrations tend to be highest in the most decayed material, which is most likely to fragment; consequently, the fragmented material is likely to be of higher N content than the more solid material that remains behind. Potassium concentrations, however, tend to be lowest in the most decayed material; fragmentation would therefore tend to be a much more important transfer of N than of K.

Leaching is in many ways the complement to fragmentation—where one is high, the other is low. Leaching accounts for major losses of K and Na from CWD, but is less important for N, P, and Ca losses. This is evident from the fact that K and Na concentrations decline much more rapidly during decay than do concentrations of the other elements (Foster and Lang, 1982; Graham and Cromack, 1982; Grier, 1978; Yavitt and Fahey, 1982). Unfortunately, no one has measured the amount of nutrients transferred from CWD via leaching or fragmentation.

e. Overall Pattern of Nutrient Accumulation and Loss. The above processes interact to control amounts of nutrients in CWD, and their occurrence is well documented even if their quantitative significance is not. One way to view the overall pattern of nutrient loss or accumulation in CWD is to plot proportion of the original nutrient and dry weight remaining through time. Typically, N and Ca remain above the dry weight curve, indicating that there is net transfer into the logs (Figs. 15–17). Potassium and P typically track below the dry weight line, indicating net transfer out of logs. These patterns appear to hold true regardless of wood species or ecosystem type (Foster and Lang, 1982; Graham and Cromack, 1982; Grier, 1978; Harris, 1978; Lambert *et al.*, 1980; Miller, 1983), except where precipitation contains unusually large concentrations of a particular element.

Nutrients probably also accumulate in decaying logs within aquatic ecosystems if patterns for fine wood are similar to CWD. In streams, N concentrations in twigs, chips, and bark of *Pseudotsuga* increased during the first 225 days of incubation (Triska and Cromack, 1980). Rates of increase in N content were greater in twigs and chips than in bark. Twigs and chips also decayed faster than bark. Nitrogen content of *Picea, Abies, Populus,* and *Alnus* wood chips increased with decay in streams of Quebec (Melillo *et al.*, 1983). The percentage of the original N content remaining generally leveled off after 3–12 months, depending on species.
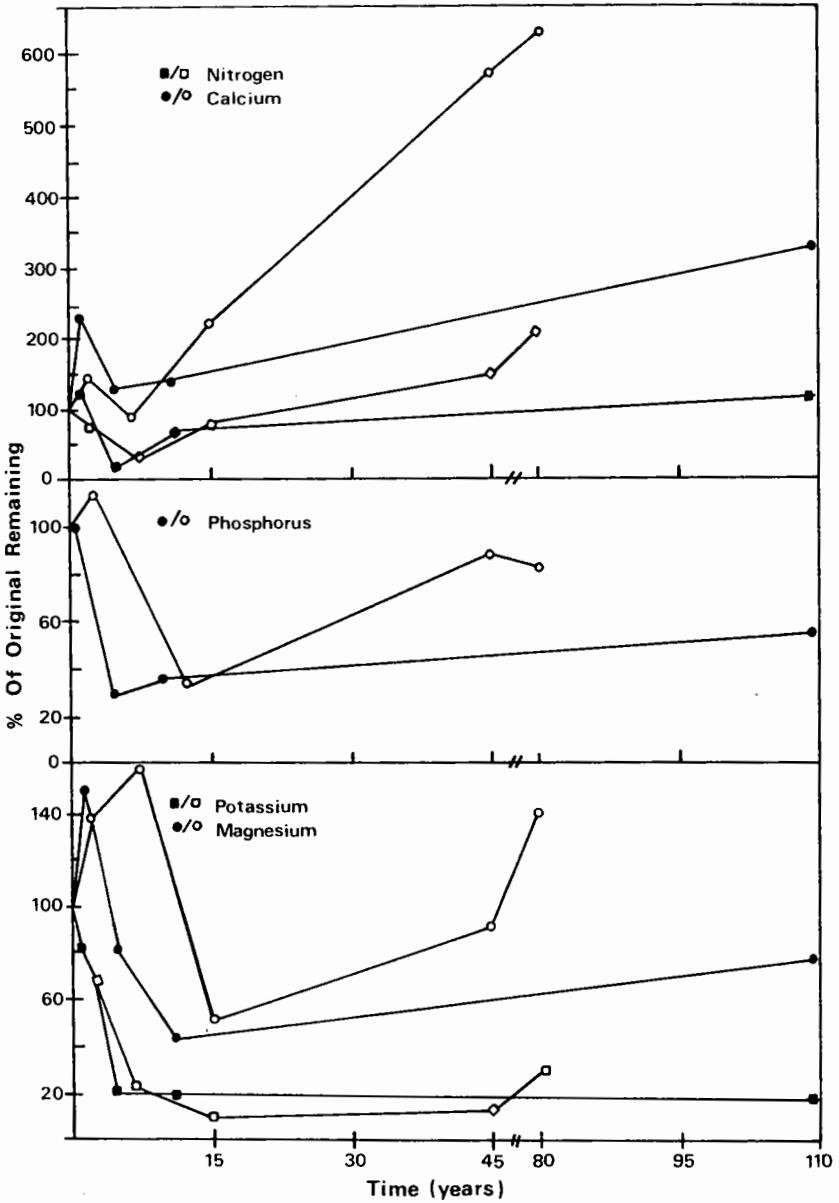
Fig. 15. Changes in nutrient content of root wood (2.6–5.0 cm diameter) with decay. Open versus closed symbols indicate different sites. After Yavitt and Fahey (1982).
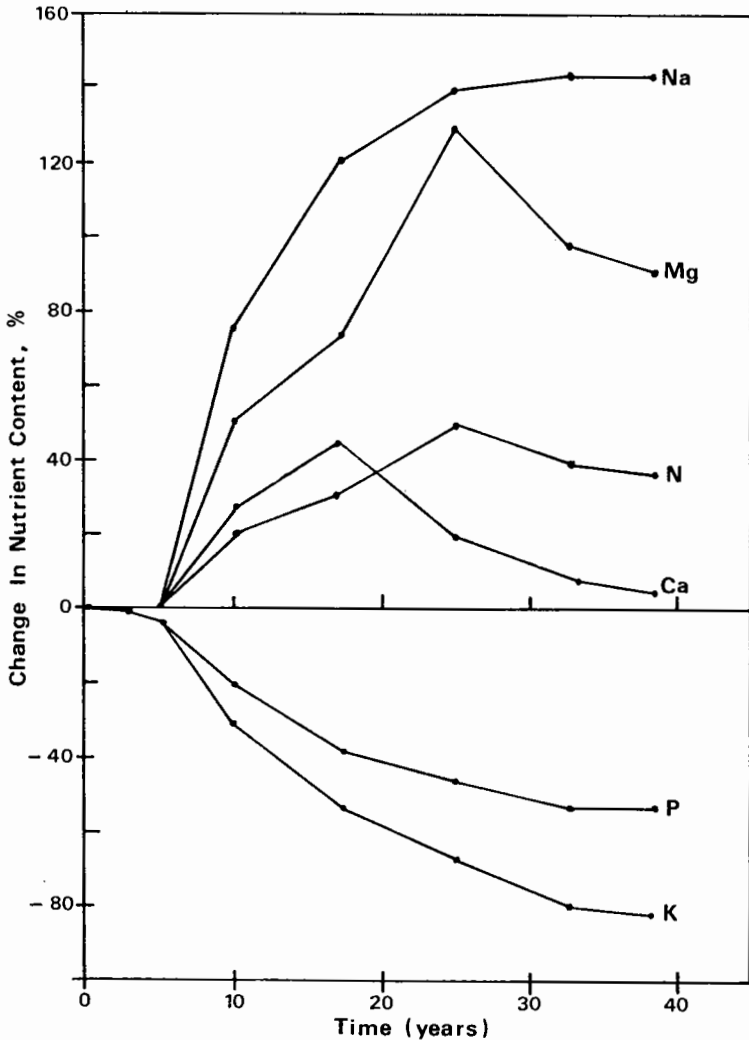
Fig. 16. Percentage accumulation or loss of nutrients in fallen logs as related to time since tree death. After Grier (1978).

The maximum amounts of N immobilized for *Alnus, Betula, Populus, Picea,* and *Abies* were estimated to be 4.06, 6.32, 5.43, 5.21, and 4.67 mg N g^{-1} of initial tissue. Nitrogen only accumulates on the surface of sub-merged CWD. For example, Anderson *et al.* (unpublished) found that the outer rind of microbially stained *Alnus* wood had ~5 times the N content of unstained wood. Abrasion of this outer N-rich layer by flowing water is
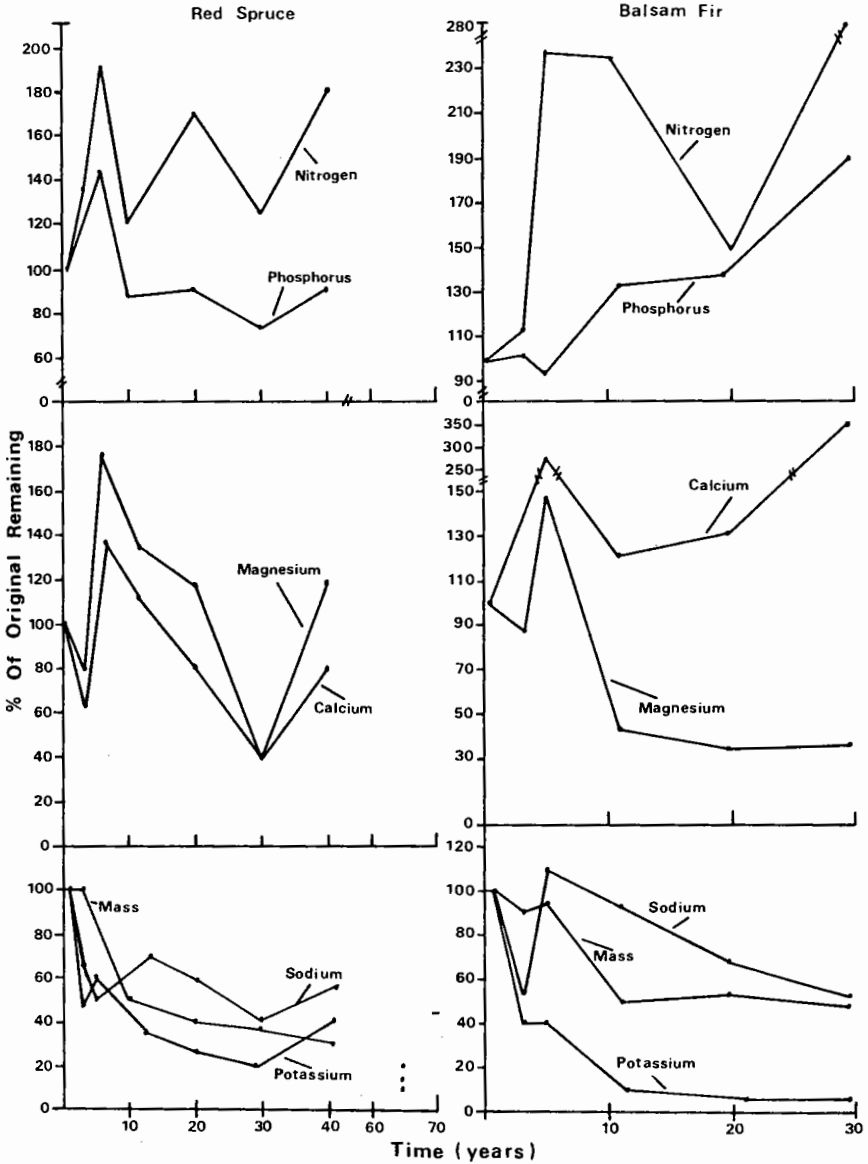
Fig. 17. Change in mass and nutrient content with decay of wood from 10–15-cm-diameter boles. The age 64 *Picea* value, from >25-cm boles, is shown to indicate potential long-term trends. After Foster and Lang (1982).

probably a major loss of N from logs in streams; however, the magnitude of this loss has not been estimated.

The overall nutrient accumulation and loss process can also be summarized as a "k" value—annual input of the element divided by amount in the CWD on the forest floor. An old-growth *Pseudotsuga* stand, where records of mortality span 30 years and ~40 ha, provides an example (Sollins, 1982). The k value is highest for Na (0.046 year^{-1}), and lowest for N (0.013 year^{-1}). The k values of the elements rank N < Ca < Mg < P < K < Na. Dry weight decay constant, k, in this ecosystem averaged 0.030 year^{-1}, which means that P, K, and Na were lost faster than dry weight; N, Ca, and Mg increased relative to dry weight.

4. Coarse Woody Debris as a Factor in Site Productivity

Effects of CWD on site productivity can be studied by simulating stand growth over several rotations with and without the initial accumulation of CWD provided by the old-growth stand. Here we use a computer model developed by Kimmins and Scoullar (1979, 1981) and modified to model growth of *T. heterophylla* (Sachs and Sollins, unpublished). The model, FORCYTE 10, considers N to be growth-limiting and decreases growth when available inorganic N is insufficient to permit stand growth at rates predicted from yield tables for unmanaged stands. The example site, on fertile land near the Oregon coast, had been cut once in the 1920s and the old-growth *P. sitchensis* removed; it was not burned, however, and large amounts of CWD survived into the current *T. heterophylla* stand.

The simulation begins by clear-cutting the existing stand and considers the impact of leaving or removing the old-growth CWD left over from the previous stand. Productivity was modeled over 17 30-year rotations without thinning, approximating the local management system for pulpwood production, or over six 90-year rotations, which approximates the least intensive, economically practical management regime at this site.

Merchantable yield decreased slowly under all scenarios, but more quickly if the old-growth CWD was removed initially from the stand (Fig. 18). Yield declined more under 30- than under 90-year rotation. Removal of the old-growth CWD caused short-term increases in yield relative to the control (CWD not removed). This occurred because CWD immobilizes N as it decomposes and makes the N unavailable for tree growth. CWD is thus a short-term N sink but a long-term N source.

Predicted differences in merchantable yield with and without old-growth CWD were perhaps small (about 5%), but the economic impact of
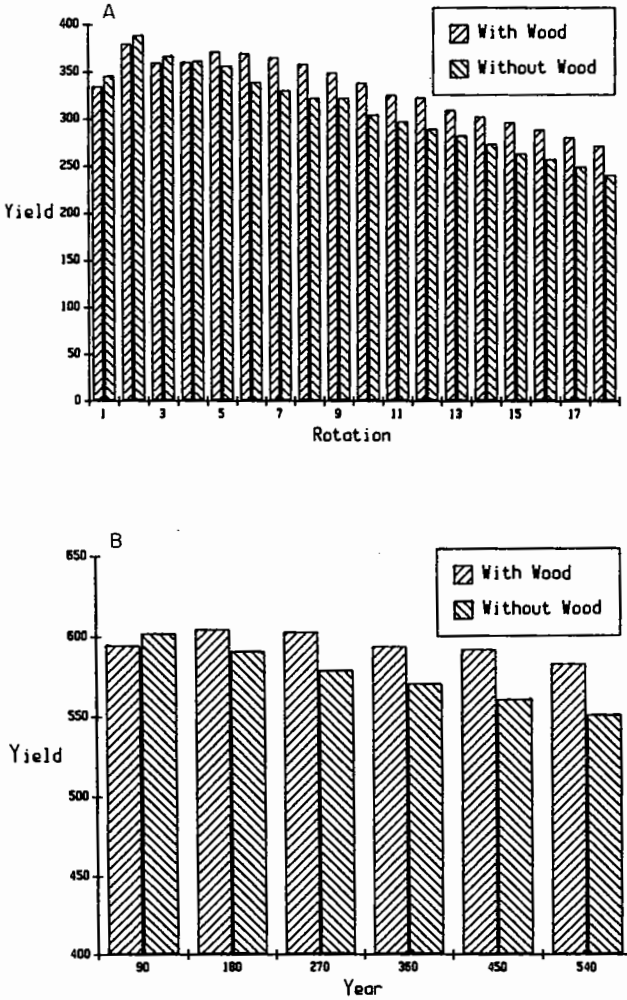
Fig. 18. Predicted effect of removal of CWD on subsequent yield in an intensively managed *Tsuga heterophylla* stand from coastal Oregon. Rotation lengths are 30 years (A) and 90 years (B) and predictions are based on the FORCYTE 10 model.

even these differences in merchantable yield could be substantial. Moreover, the site modeled here is one of the most N rich in the world (see coastal *Tsuga*, Table 10), and differences in yield after removal of CWD might be even greater at less fertile sites.

D. Geomorphic Functions of Coarse Woody Debris

The geomorphic roles of CWD can be grouped into effects on landforms and on transport and storage of soil and sediment. The importance of these roles differs between hillslopes and stream channels because the types and rates of soil and sediment transport as well as the mobility of CWD differ markedly between these environments. We will consider hillslopes and stream channels separately to highlight differences, but they intergrade in most landscapes.

1. Hillslopes

Geomorphic functions of CWD are rather poorly described and quantified for forested hillslopes. Effects of tree uprooting have received the greatest attention, while the effects of logs received the least.

a. Roots and Root-Throw. Tree uprooting creates microtopographic features and mixes soil. Microrelief of up to several meters is created on forested slopes by uprooted trees (Denny and Goodlett, 1956; Lyford and MacLean, 1966; Stephens, 1956). Stone's (1975) review found from 14 to 48% of the landscape was "visibly disturbed" by root-throw. The abundance of this landscape feature reflects the balance between processes creating and erasing this distinctive microtopography. Factors influencing root-throw potential of a site, such as topography, soils, and species wind firmness, as well as the size of the root systems upturned, strongly determine the rate microtopography is created. Surface erosion and soil creep obliterate pit-and-mound topography with rates dependent upon slope gradient and soil erodibility. Denny and Goodlett (1956) and Stephens (1956) estimate that pits and mounds can be distinguished from the surrounding forest floor for 300–500 years after their creation.

Root-throw and soil creep move soil at comparable rates. Denny and Goodlett (1956) calculate a soil transport rate of 1.5 mm year⁻¹ in the central Appalachian Mountains. Dietrich *et al.* (1982) estimate a rate of 2 mm year⁻¹ for a study area in the Tatra Mountains, Poland, using data from Kotarba (1970). Reid (1981) reports a soil movement rate of 1.8 mm year⁻¹ at a study site in the western Olympic Mountains, Washington. Swanson (unpublished) calculated a rate of 0.1 mm year⁻¹ for an old-growth *Pseudotsuga* forest in the western Cascade Mountains, Oregon.

The overall importance of root-throw to sediment production of a watershed has been examined using a sediment budget (Swanson *et al.*, 1982c). Reid (1981) estimated that 11% of sediment yield was derived from root-throw in a 10-km² basin on the west side of the Olympic Penin-

sula, Washington. In a 10-ha watershed forested with old-growth *Pseudotsuga* in western Oregon, Swanson *et al.* (1982a) calculated that soil transfer by root-throw accounted for ~2% of long-term sediment production in a landscape dominated by landslide erosion.

Root-throw can be an important process in soil genesis and patterning (Armson and Fessenden, 1973; Denny and Goodlett, 1956; Stephens, 1956; Stone, 1975). Uprooting and subsequent soil and litter transport and storage cause substantial soil mixing and heterogeneity. Although the annual turnover rate of surface soil is commonly slow—Swanson (unpublished) estimates a rate of 0.4% year^{-1} for an old-growth *Pseudotsuga* forest—the imprint of root-throw on soils is widespread because pits and mounds often persist for centuries.

b. Logs. Logs lying on the soil surface control the downslope movement of water, soil, and litter across the surface of the ground. In many forested environments, overland flow of water is rare, but downslope surface transport of particulate matter is well documented (Imeson and Von Zon, 1979; Swanson *et al.,* 1982a). The amount of sediment and organic matter stored upslope of logs in undisturbed forests, however, has not been studied. One would expect that the amount of storage would increase as slope increased and as the residence time of logs on the forest floor increased.

The influence of logs and other woody debris on surface erosion is well demonstrated in the landscape devastated by the May 18, 1980 eruption of Mount St. Helens, Washington. This eruption created a 50,000-ha zone of downed forest vegetation. CWD on and within the tephra deposits interrupted the surface and subsurface flow of water, and erosion rates on areas of downed forest were lower than areas clear-cut before the eruption (Collins *et al.,* 1983; Swanson *et al.,* 1983). Smith (1985) found that CWD stored significant amounts of tephra emplaced during the eruption, but stored little of the material transported by sheet and rill erosion.

2. Streams and Rivers

Recent interest in CWD in streams and rivers has stimulated consideration of its importance in controlling aquatic habitat and the movement of sediment and water. Controversy has often fueled this interest. On one hand, wood has been considered a hazard to navigation, life, and property during floods. CWD has also been cleared from rivers and streams to remove blockages to navigation and fish migration (Sedell *et al.,* 1984). This contrasts with the increasingly common practice of introducing and retaining CWD in streams for fish habitat improvement or channel stabilization. These conflicts in management objectives have triggered research on the behavior and functions of CWD in streams and rivers.

a. Channel Morphology. Steps in the channel longitudinal profile are created where a large log or accumulations of CWD form a dam that traps a wedge of sediment (Heede, 1972a,b; Keller and Swanson, 1979; Pearce and Watson, 1983). The tread of such a step is primarily composed of the stored sediment; the CWD accumulation forms the riser. Steps created by CWD reportedly vary widely in their importance to the channel profile. Marston (1982) evaluated effects of log steps in 13 watersheds of up to fifth order in the Oregon Coast Range. Steps created by CWD controlled 6% of total fall in the channels, but he argued that geologic factors, and not CWD, controlled the overall shape of the longitudinal profile. Stream reaches in other areas have much greater proportions of the channel fall occurring over CWD: 50–100% in the Rocky Mountains of Colorado and White Mountains of Arizona (Heede, 1972a,b, 1977); 30–60% in watersheds <5 km^2 in area and $<20\%$ in larger basins in Redwood Creek, California (Keller and Tally, 1979); 10–52% in the White Mountains, New Hampshire (Bilby, 1981); and 30–80% in the western Cascades, Oregon (Keller and Swanson, 1979; Swanson *et al.*, 1976). The degree to which CWD controls stream profile is related to abundance and size of CWD and the ability of channels to bypass obstructions. The importance of CWD in altering longitudinal channel profiles decreases with stream order. Bilby (1981), for example, observed that the percentage of channel drop formed by CWD decreased from 52 to 42 to 10% from first- to third-order channels in the Hubbard Brook Experimental Forest, New Hampshire.

CWD triggers abrupt changes in channel pattern and position by blocking flow in main channels and chronic changes by deflecting flow against banks, thus accelerating the lateral migration of streams. Entire sections of major rivers can be changed drastically, as was the case of the Red River in northern Louisiana, where an accumulation of CWD grew to a length of more than 300 km over $\sim$200 years (Lobeck, 1939). This jam blocked the main river and the mouths of tributary streams, forming lakes. Less dramatic changes are more typical, such as when CWD accumulates in channels and triggers oxbow cutoff of meander bends (Keller and Swanson, 1979).

Effects of CWD on channel geometry have been quantified over stream reaches and at sites of individual CWD accumulations. CWD partially or completely crossing a channel commonly deflects streamflow laterally or causes it to diverge. Sediment deposits upstream from the CWD as well as downstream in the case of low-gradient channels widen and decrease the depth of the channel (Keller and Swanson, 1979). Zimmerman *et al.* (1967) contrasted channel geometry, particularly channel width, between sod and forested stream banks in the Sleepers River basin, New Hampshire. Average channel width and variation in width was greater along