The Role of Wood Debris in Forests and Streams

Frank J. Triska and Kermit Cromack, Jr.

In the Pacific Northwest, old-growth forests and their associated streams contain large quantities of coarse wood debris. To date, such debris has been considered an impediment to reforestation and stream quality. Consequently, it has been virtually ignored in ecological studies, partly because man's need for wood fiber has resulted in the removal of debris from forests throughout the world but also because the extended period necessary for wood to decay makes it difficult to study nutrient recycling from such a process. In this paper, we shall attempt to correct that omission by exploring how wood debris is utilized in forest and stream ecosystems.

Such an exploration is timely in view of the diminishing amount of pristine forest. In the Pacific Northwest, the greatest accumulation of wood debris occurs from natural mortality and blowdown in such forests. Now that forests are being cut every 80 years instead of standing 250 to 500 years (the interval between natural catastropic fires), it is crucial that we determine the role of wood debris in pristine habitats and then incorporate that knowledge into existing management strategies for our forests and watersheds.

Our exploration will begin with determining the amounts of wood debris in various forest and stream ecosystems and its rates of accumulation in each. We shall then examine how debris modifies existing habitats and creates new ones. Next, we shall determine how rapidly coarse wood debris breaks down into its component elements and how its carbon and other elements are recycled. Finally, we shall discuss what implications these data have for the managers of forested watersheds in the Pacific Northwest.

WOOD BIOMASS AND ACCUMULATION

As we have indicated, debris accumulation must be considered over a period of about 500 years. Accumulation over such a cycle of secondary succession--from a nearly bare forest floor to the debris beneath a 450-year-old stand of Douglas-fir--is depicted in Figure 1. The diagram, which is a composite of data from three sites on the H. J. Andrews Forest near Eugene, Oregon, is not intended to represent any particular site. It does, however, reflect the fact that accumulations of debris are greater in the Pacific Northwest than elsewhere because of the larger biomass of the region's tree boles (Grier and Logan, 1977). In most cases, natural catastrophes would result in greater accumulations than depicted here (Franklin and Waring, 1980), but those that would result from clearcutting followed by yarding and burning are adequately portrayed.

In Figure 1, event 1 represents an increase in wood debris as a result of natural thinning following canopy closure. The increase in wood biomass is slight because such debris is finely divided and readily susceptible to decomposition. Event 2 represents a long period of accumulation as low branches are shed and the canopy increases in height. Event 3 represents a decrease in wood debris because of a litter brush fire. If trees were killed by such a fire, however, the accumulation of woody debris would increase.

Event 4 represents windthrow in a large old-growth stand. Event 5 represents the accumulation of large individual trees on the forest floor over an extended period. Toward the end of succession, even a single tree can introduce a large amount of organic matter. For example, the biomass of a tree 100 cm in d.b.h. equals 10 metric tons.

As the foregoing sequence implies, wood carbon entering the detritus pool of both the forest and its stream varies in decomposition rate according to stand age and history. For example, woody debris in young stands is finely divided and highly susceptible to microbial attack, whereas an equal amount of large woody debris with its low surface-to-volume ratio may have a decomposition period of hundreds of years. Furthermore, the wood component in litterfall is less than 10 percent in young stands but 70 percent in old-growth forests (Grier and Logan, 1977).

Few estimates exist of the quantity of wood debris in forests and their watershed streams. One site where data are available from both ecosystems is Watershed 10, a 450-year-old stand of Douglas-fir in the H. J. Andrews Forest. Biomass estimates of downed logs were made for the forested watershed by Grier and Logan (1977) and for the watershed streams by Froehlich et al. (1972). Log debris for the forest was estimated at 55 to 580 metric tons per hectare, whereas that for the stream channel was estimated at 298 metric tons per hectare. Plotting of these data on a map of standing and downed vegetation on Watershed 10 indicates a general decrease in wood debris from stream channel to ridgetop. This distribution results because the deep incisions in the basin cause trees to roll downhill toward the stream.

Quantities ranging from 55 to 580 metric tons per hectare represent a large pool of organic carbon. We now know that such pools of refractory (decomposition-resistant) carbon and other elements provide a nutrient source throughout secondary succession of ecosystems (O'Neill et al., 1975). Estimated wood debris in old Douglas-fir forests (Grier and Logan, 1977; MacMillan et al., 1977; Waring and Franklin, 1980) represents a larger aboveground pool of organic matter than the entire aboveground biomass of most current eastern deciduous forests (Day and Monk, 1974; Sollins and Anderson, 1971).

Although large wood debris (>10 cm in diameter) is more visible, fine wood debris also represents a substantial input and decomposes more rapidly both in streams and on land. Fine wood debris in Watershed 10 constituted only 13 percent of the biomass in the streams but decomposed faster, on the average, than coarse wood debris. The various litter inputs into the forest floor and streams of Watershed 10 are shown in Table 1.

Tables 2 and 3 indicate the biomass of wood debris in streams and on the forest

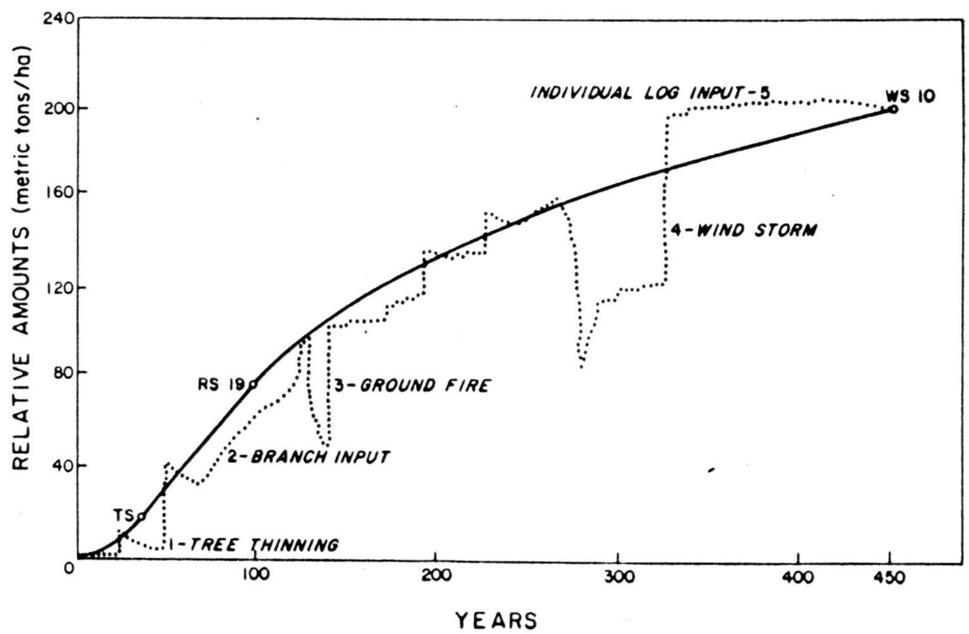

Figure 1. Accumulation of wood debris during the life of a hypothetical stand of Douglas-fir. The solid line indicates the overall increase of wood debris over time; included as reference points are data from the Thompson Site (TS), Washington Reference Stand 19 (RS 19), and Watershed 10 (WS 10), all on the H. J. Andrews Forest near Eugene, Oregon. The dotted line depicts major events (discussed by number in text) that affect debris accumulation.

floor of various old- and young-growth forests. By far the largest amount of wood debris occurs in streams draining old-growth redwoods and Douglas-fir/western hemlock. Even second-growth Douglas-fir/hemlock has more wood in its streams than do some old-growth sites in other parts of the country, partly because of the carryover of wood debris from the primeval forests. In old-growth forests in the Great Smoky Mountains of Tennessee, both spruce/fir and mixed hardwood stands have large quantities of wood debris in their streams.

Comparison of old- and second-growth forest types indicates that even in primeval forests, the amount of wood debris in the streams varied with species composition and environmental conditions. Regardless of these two factors, however, the quantity of such wood was probably much greater in many primeval forests than can be observed today. It follows that the biota of forested ecosystems and streams draining them evolved in a system where wood debris played a far larger role than it does today. Thus, wood debris has been removed in many parts of the world before man has fully understood its role.

One of the major difficulties in assessing the input rate of wood debris is the episodic nature of its accumulation. To date, the most successful methods have been dendrochronological, primarily the interpretation of tree scars (MacMillan et al., 1977; Swanson et al., 1976) or the assessment of dated successional sequences such as fir waves (Sprugel, 1976) in balsam fir forests (Lambert et al., in press). Permanent plots set aside for studies of tree growth and mortality afford another method of dating wood debris. While falling, trees may scrape against adjacent trees, resulting in the removal of bark and the decomposition of callus tissue in annual increments in the surviving trees. These increments or shock rings permit dating of the events (Shigo and Marx, 1977). Unfortunately, only a few trees leave such records of their deaths.

Dating the accumulation of large debris is especially difficult in third-order or larger streams. In first- and second-order streams, wood remains essentially where it falls. In the larger streams, however, it tends to be clumped by high water prior to decomposition, making it especially difficult to date the accumulations or to estimate decomposition rates or nutrient recycling. One can conclude that wood debris tends to exert a greater impact, in terms of amount, on the stream than on the surrounding forest and that this impact gradually diminishes as one proceeds downstream.

Table 1. Leaves and coarse and fine wood debris entering the forest floor and watershed stream at Watershed 10, H. J. Andrews Forest, prior to clearcutting[1]

Method of measurement	Leaf litter		Wood debris	
	Deciduous	Coniferous	Fine	Coarse
		$g/m^2/day$		
Litterfall	0.070	0.346	0.244	--
Lateral movement	.096	.143	.728	--
Scaling	--	--	--	0.548
Total	.166	.489	.972	.548
Percent composition	7.6	22.5	44.7	25.2

[1]Unpublished data from F. J. Triska, Dept. of Fisheries and Wildlife, Oregon State Univ., 1978.

MODIFYING AND CREATING NEW HABITATS

On both land and in water, wood serves as more than a large pool of refractory carbon. Its very presence in large quantities modifies habitats on the forest floor and in streams and creates new ones.

As habitat, wood debris represents an alteration in the physical structure of the forest, changing the nature of light reflection to the canopy and providing new types of habitat on the forest floor. Because wood accumulates irregularly, many different states of decay are present at a particular time. In natural stands, logs may be added to the forest floor and stream channel as intact boles after catastrophes such as windthrow and localized earth movements or after bankcutting or erosion. More highly decomposed wood may enter the forest floor or stream as snags.

To differentiate various states of wood decay and their effects on habitat, we have devised a classification system based on the findings of previous researchers (Table 4). The system is based on physical characteristics such as texture, shape, color, the presence or absence of bark or twigs, and propotion of the bole in contact with the ground. Trees alive when they fell to the forest floor or stream would usually be grouped in decay class 1, while snags would probably be in decay class 2 or 3.

Table 2. Estimated wood debris on the forest floor of selected old-growth and young-growth temperate forests.

Location	Forest type and age (years)	Logs[1]	Branches[2]
		metric tons/hectare	
Oregon[3]	Douglas-fir > 450	218	-
New York[4]	Spruce/birch > 300	42	-
New Jersey[5]	Mixed oak > 250	21.3	2.1
New Hampshire[6]	Mixed hardwoods > 170	34	-
New Hampshire[7]	Subalpine balsam fir ~ 80	71	33
North Carolina[8]	Mixed oak/hickory > 60	11.8	.7
Great Britain[9]	Mixed oak	-	2.0
Denmark[10]	Mixed oak	5	-
Poland[11]	Mixed spruce/basswood 200-400	22	-

[1]Logs assumed to include coarse woody debris > 7.5 cm in diameter.

[2]Branches assumed to range from 2 to 7.5 cm in diameter.

[3]MacMillan et al. (1977).

[4]McFee and Stone (1966).

[5]Lang and Forman (1978).

[6]Bormann and Likens (1979).

[7]Lambert et al. (in press); peak log biomass (> 8 cm in diameter) occurs at stand age 33 years.

[8]Cromack (1973).

[9]Swift et al. (1976).

[10]Christensen (1977).

[11]Falinski (1978); assumes a density of 0.35 for 63 m^3 of logs.

The role of large wood debris as habitat depends on its decay class (Fig. 2). For example, cover and nesting sites for terrestrial vertebrates depend on such factors as shape, texture, and presence of branches and twigs. Elton (1966), Winn (1976), and Maser et al. (1979) outlined some of the important features of coarse wood debris and noted how habitat role shifts with decay class.

Other factors which affect the role of wood as habitat for wildlife include size and orientation. Obviously, large logs provide greater cover for small vertebrates than do small ones (Ruben, 1976; Maser et al., 1979). Large logs are also more persistent features of the environment because they decompose slowly as a result of a low surface-to-volume ratio (MacMillan et al., 1977). The orientation which logs take also influences their capacity to serve as habitat. Logs oriented along a contour are most likely to serve as runways for small animals (Maser et al., 1978) and to capture soil and organic debris, which slows erosion and maximizes nutrient retention.

Physical distribution is also important. Generally, the more even the overall distribution, the greater the habitat diversity and utilization (Winn, 1976; Maser et al., in press). Large blowdowns may provide excellent cover and concealment for smaller animals such as porcupines (Taylor, 1935) while interfering with the passage of larger wildlife such as deer (Lyon, 1976) and wild boar (Falinski, 1978). On the other hand, large areas devoid of wood debris lead to reduction or elimination of those species dependent on it for some stage of their life cycle.

In addition to serving as animal habitat, downed wood debris also serves an important function for the plant community. As log debris decomposes, its internal moisture and nitrogen concentration in-

Table 3. Estimated coarse wood debris in first- and second-order streams draining old- and young-growth temperate forests.

Location	Forest category	Wood[1]
	OLD-GROWTH	kg/m^2
Oregon[2]	Douglas-fir/hemlock	25-40
Idaho[2]	Spruce/lodgepole pine	7
New Hampshire[2]	Spruce/fir	4
Tennessee[3]	Spruce/fir	10
Tennessee[3]	Mixed hardwoods	13
Southeastern Alaska[4]	Spruce/hemlock	5
California[4]	Redwoods	45-80
	YOUNG-GROWTH	
Michigan[5]	Mixed hardwoods	4-8
Oregon[5]	Douglas-fir/hemlock	20-25

[1] > 10 cm in diameter

[2] Unpublished data from J. R. Sedell and F. J. Swanson, Dept. of Fisheries and Wildlife and Dept. of Forest Engineering, Oregon State Univ., 1978.

[3] Unpublished data from S. V. Gregory, Dept. of Fisheries and Wildlife, Oregon State Univ., 1978.

[4] Unpublished data of F. J. Swanson and G. W. Lienkemper, Dept. of Forest Engineering, Oregon State Univ., 1978.

[5] Unpublished data of J. R. Sedell, Dept. of Fisheries and Wildlife, Oregon State Univ., 1977.

Table 4. Decay classes of Douglas-fir, after Fogel et al. (1973), MacMillan et al. (1977), and Maser et al. (1979).

	Class				
Characteristic	1	2	3	4	5
Bark	Intact	Intact	Sloughing	Detached or absent	Detached or absent
Structural integrity	Sound	Sound	Heartwood sound, supports own weight	Heartwood rotten, does not support own weight, branch stubs pull out	None
Twigs < 3 cm	Present	Absent	Absent	Absent	Absent
Texture of rotten portions	Intact	Mostly intact, sapwood partly soft	Hard, large pieces	Soft, small blocky pieces	Soft, powdery when dry
Color of wood (except in portions with white rot)	Original color	Original color	Reddish brown or original color	Reddish or light brown	Red-brown to dark brown
Invading roots	Absent	Absent	Sapwood only	Throughout	Throughout
Vegetation	None	None surviving	Conifer seedlings	*Tsuga* < 15 cm DBH; smaller shrubs, moss	*Tsuga* up to 200 cm DBH: shrubs, some large; moss
Fungal fruiting	Fungal colonization, few large fruiting bodies	*Cyathus*, *Tremella*, *Mycena*, *Collybia*, *Polyporus*, *Fomitopsis*, *Pseudohydnum*	*Polyporus*, *Polyporellus*, *Pseudohydnum*, *Fomitopsis*	*Cortinarius*, *Mycena*, *Marasmius*	*Cortinarius*, *Collybia*, *Cantharellus*
Mycorrhizae[1]	Absent	Absent	Mycorrhizal colonization	*Boletus*, *Corticium*, *Hydnotria*, *Lacaria*, *Piloderma*, *Rhizopogon*	*Boletus*, *Corticium*, *Hydnotria*, *Lacaria*, *Piloderma*, *Rhizopogon*

[1] J. M. Trappe, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Corvallis, Oregon, 1979.

crease (Place, 1950; Rowe, 1955). In the Pacific Northwest, decomposing logs eventually serve as nursery sites for hemlock, the climax species in moist Douglas-fir habitat (Franklin and Dyrness, 1973). Thus, by serving as plant habitat, downed logs influence forest succession (Jones, 1945; Rowe, 1955).

Besides providing habitat, wood debris also modifies the forest floor. If coverage of the forest floor is extensive, a large area may be taken out of production for extended periods. If wood is in contact with the ground, some physical and biological properties of the soil beneath may be modified significantly. Ausmus (1977) reported that soil under logs in a deciduous forest increased 4-fold in organic matter, 8-fold in adenosine triphosphate or ATP (which is a measure of microbial biomass), 18-fold in nematode density, more than 2-fold in root biomass, and 5-fold in calcium concentration. In the Pacific Northwest, preliminary data by K. Cromack, Jr., and D. H. McNabb (Dept. of Forest Science, Oregon State Univ., 1978, personal communication) indicate that Ceanothus velutinus undergoes a significant increase in nodulation (for fixation of nitrogen) in soil under old logs. B. Bormann (Dept. of Forest Science, Oregon State Univ., 1979, personal communication) has reported that nodulation of red alder occurred beneath burned logs on a clearcut in western Washington.

In watershed streams, the accumulation of coarse wood debris also modifies the stream channel and provides specialized habitat (Figs. 3-5). The amount and relative role of wood increases dramatically as one proceeds upstream. For example, in the first-order stream called Devil's Club Creek on the H. J. Andrews Forest (Table 5), wood completely inundates the channel. In fact, at summer low-flow there is more water in the decaying wood tissue than is free-flowing in the stream channel. Under these circumstances, wood plays a strong role in directing water flow and sediment storage.

In the smallest streams, wood debris is especially valuable in creating habitat, where, because of high streambed gradients, it might not otherwise exist. Small, steep watershed streams have extensive areas of bedrock except where sediment is entrained by wood debris (Figs. 4-5). At these sites, small riffles and pools are formed behind debris, thus facilitating the establishment of a biological community. Because small streams do not have enough hydrologic force to remove debris, wood-created habitat in these streams is most often formed by individual pieces of debris or minor accumulations. The biological community in these small

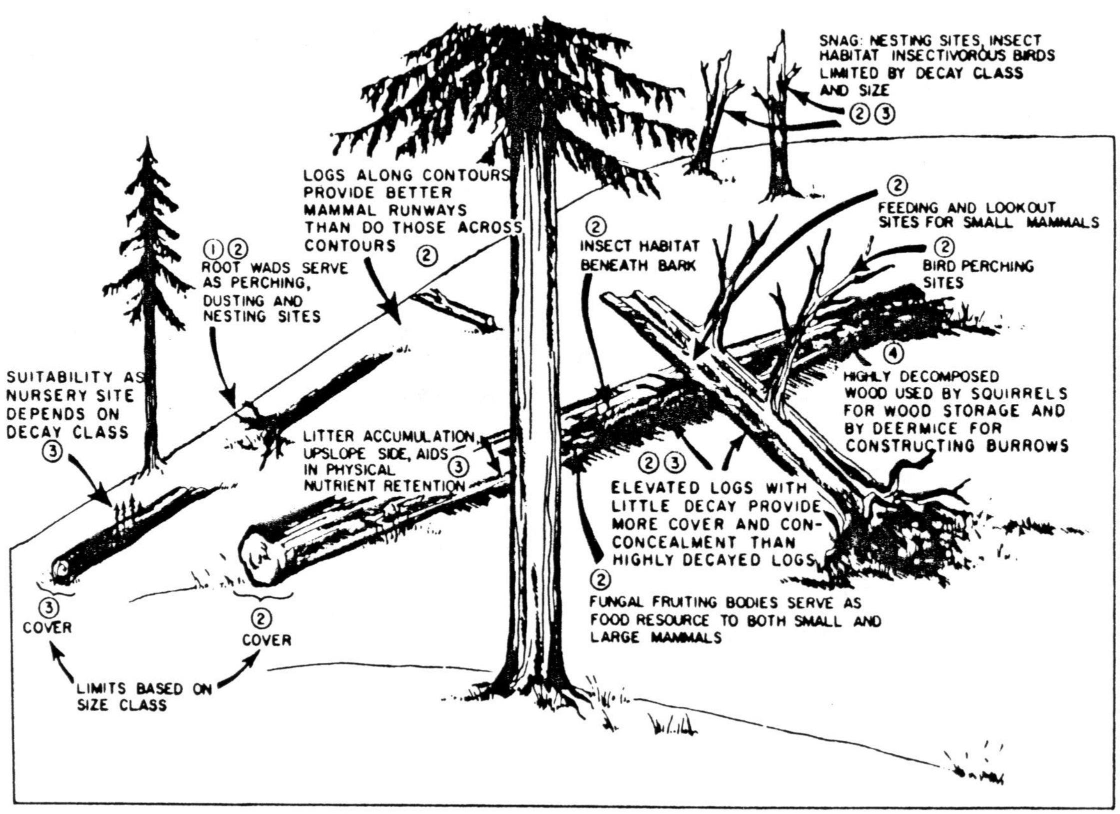

Figure 2. Role of coarse wood debris as habitat on the forest floor. Habitat role is dependent on decay class, size, amount, and orientation of debris. Circled numbers indicate decay classes.

streams, although not tremendously productive, is effective at processing particulates and even at altering certain nutrient concentrations of the water before it reaches a second-order stream (S. Gregory, Dept. of Fisheries and Wildlife, Oregon State Univ., 1978, personal communication).

First-order streams in old-growth forests are thus effective ecosystems because of the retentiveness of wood-created habitat. Time gained by slowing and directing water flow and by increasing biologically and chemically active surfaces facilitates chemical exchange with organic and mineral surfaces, as well as promoting microbial colonization and invertebrate consumption of organic particulates. Retention is particularly important for litter processing because microbial colonization is a prerequisite to invertebrate consumption of wood and other litter (Triska, 1970; Anderson and Grafius, 1975).

Although most extensive in first-order streams, wood-created habitat is most visible in third- to fifth-order streams. In these larger streams, heavy discharges exert enough hydrologic force to clump debris. These clumps entrain large amounts of organic matter and sediment, which form areas of rich biological habitat. In streams larger than fifth-order, coarse

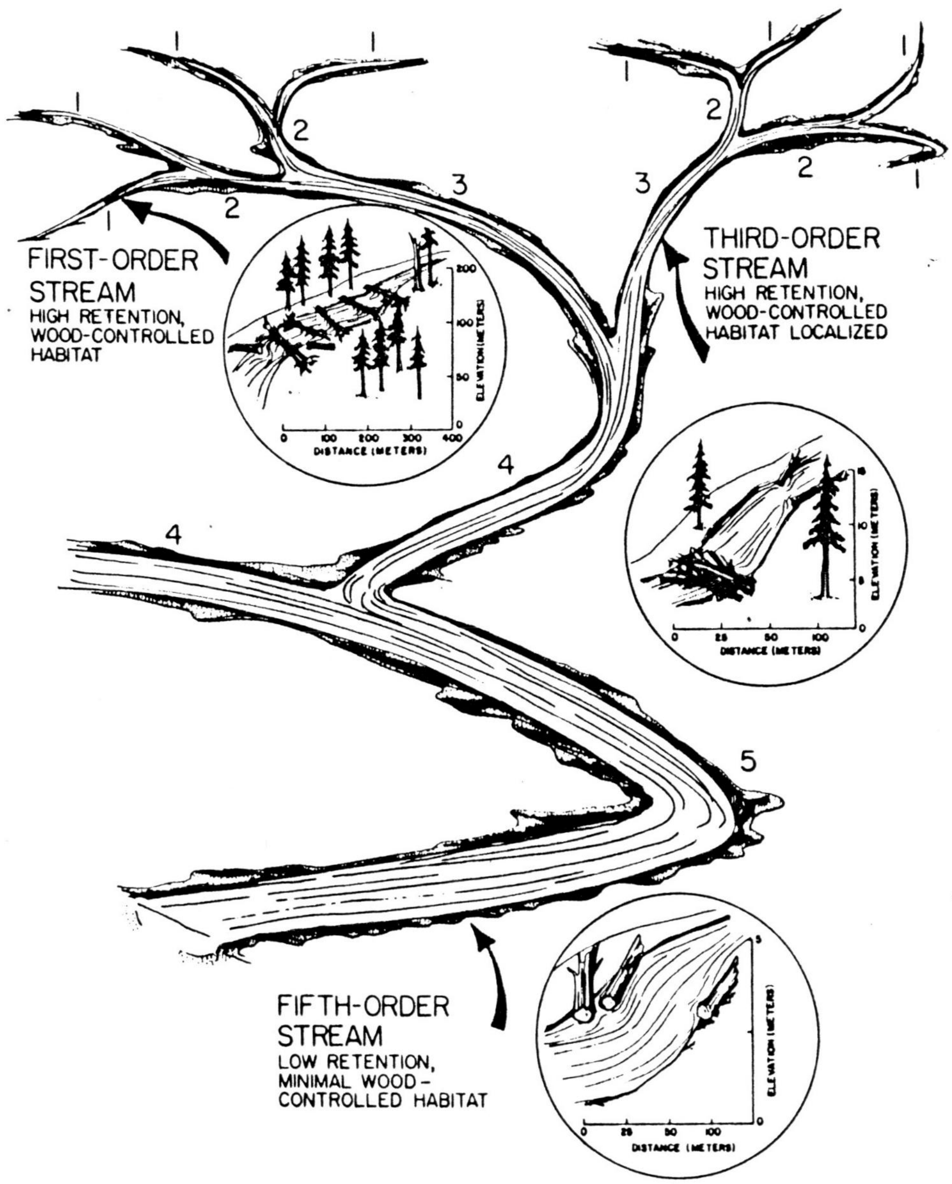

Figure 3. Role of wood in the various watershed streams of a drainage network. Note that the amount of wood-created habitat decreases as one proceeds downstream. Circled numbers indicate stream order.

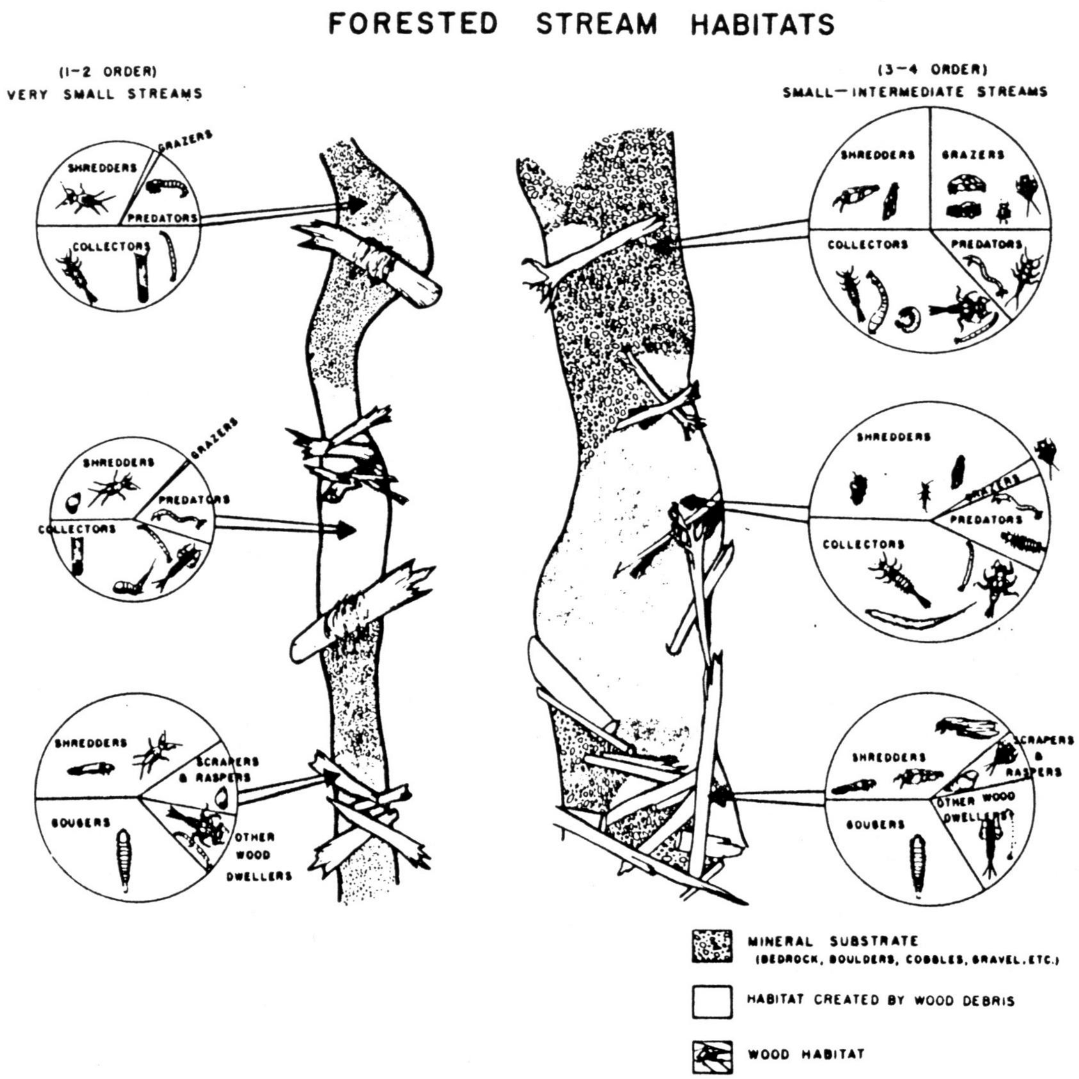

Figure 4. Formation of wood-created habitat and its influence on the invertebrate community of first- through fourth-order streams. Life functions of various invertebrate groups based on Cummins (1974) and Anderson et al. (1978). Size of segments in each chart based on proportional role of indicated functional group.

Table 5. Estimates of coarse and fine wood debris from selected streams of increasing watershed area within and adjacent to the H. J. Andrews Forest.

Stream	Stream order	Watershed area	Gradient	Coarse wood debris[1]	Fine wood debris
		km²	percent	kg/m²	
Devil's Club Creek	1	0.05	35	40.89	1.11
Mack Creek	3	5.35	20	28.50	0.61
Lookout Creek	5	60.20	12	11.65	.08
McKenzie River	7	1,642.00	9	.07	.08

[1] > 10 cm in diameter.

wood debris is found along banks or deposited in the riparian zone and thus plays a minor role in habitat formation.

Although the smallest streams have the most extensive wood-created habitat, they also have the lowest invertebrate biomass. Anderson et al. (1978) describe 38 taxa of invertebrates, mostly insects, associated with wood in Oregon streams. However, only a few of these insect species are truly xylophagous (wood-consuming): Lara anova (gouging), Heteroplectron californicum (boring), and Lipsothrix spp. (tunneling). For the others, wood serves an incidental role--for example, as an attachment site for feeding or pupation; for oviposition; as a nursery area for early instars; or for nesting, molting, or emergence (Fig. 5).

These incidental associations can have a direct influence on the structure of the stream's invertebrate community, as evidenced by Grafius's (1977) population estimates for the leaf-consuming caddis, Lepidostoma unicolor, in various aquatic habitats. L. unicolor consumes Douglas-fir needles after they have been conditioned by microbial colonization (Sedell et al., 1975). To test the suitability of various habitats, Grafius determined larval densities of Lepidostoma in three stretches of a watershed stream--a stretch draining a clearcut, one draining an area of old-growth Douglas-fir, and one behind a debris dam (Fig. 6). In the clearcut stretch, Lipidostoma larvae were scarce because of the absence of suitable litter. Larval density was higher in the stretch draining the old-growth area, where litter had been retained among pieces of coarse wood debris. There were 15 times more larvae behind the debris dam, however, because the coarse wood had captured large amounts of litter, thus facilitating microbial conditioning and expanding the amount of available habitat. Thus, wood debris sometimes plays an important role completely unrelated to its own utilization as an energy or nutrient source.

The effect of coarse wood debris on fish habitat (Fig. 5) has been summarized by Hall and Baker (1977) and Baker (1979). Overall, wood debris seems to have a direct influence on the size of fish populations but only an indirect influence on their metabolisms. Actual habitat value of debris dams is dependent on such factors as the stability of the structure and the diversity of habitat created behind it. The most important function of wood debris is to provide cover and protection from predation. For underyearling salmon and trout, debris provides not only cover but also protected rearing areas (Hartman, 1965; Coulter, 1966; Sheridan, 1969; Meehan, 1974), particularly during overwintering (Hartman, 1965; Bustard and Narver, 1975). Adult salmon often inhabit pools formed by coarse wood debris (James, 1956; Larkin et al., 1959; Sheridan, 1969). At two sites in the Oregon Coast Range, Baker (1979) found that fish biomass was significantly higher behind debris dams than either upstream or downstream.

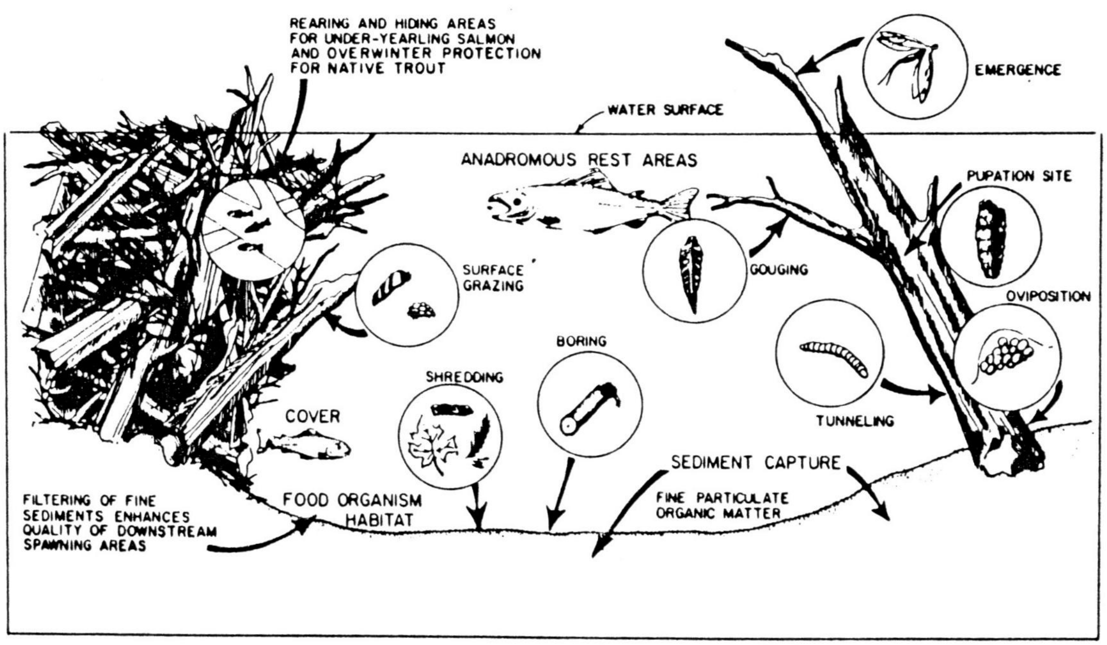

Figure 5. Role of coarse wood debris as habitat in a watershed stream. Habitat role is dependent on decay class, size, amount, and orientation of debris.

Accumulations of coarse wood debris also function as filtering devices (Hall and Baker, 1975). Bishop and Shapley (n.d.) found that the amount of fine sediments was significantly reduced and oxygen concentration was increased in gravel areas downstream from such accumulations. As pointed out previously, this filtration can increase the production of fish food organisms.

WOOD DECOMPOSITION AND NUTRIENT CYCLING

As mentioned at the outset, decomposition of coarse wood debris requires several hundred years. This persistence of debris is related to its size, shape, and nutrient composition (Fogel and Cromack, 1977; MacMillan et al., 1977; Lambert et al., in press). Because of the extended periods involved, investigators have devised broad classifications for wood decay, such as the one outlined previously in Table 4. A major problem with such schemes, however, is that a single log can contain wood in various stages of decay. This condition often arises because of (1) greater soil contact at one end than the other, (2) partial decomposition prior to contact with the forest floor, (3) distinct decay zones related to plant, animal, and microbial activity, (4) waterlogging of debris in the stream channel, and (5) significantly different diameters at the base and the tip. By later stages of log decomposition, wood texture is so soft that increased streamflow will disintegrate the softest portions and sweep them downstream as fine particles. On land, logs with advanced decay can exist for more than 500 years (MacMillan et al., 1977).

The process of water logging is depicted in Figure 7, which represents 50 years of decomposition in a single log whose length spans three distinct habitats--streams, riparian, and terrestrial. This log exhibits five stages of decay resulting from the varying environmental factors to which it has been subjected.

In streams, the decay of intact logs seems to occur primarily from the periphery of the log toward the interior, and the process is slower than on land. In small streams, for example, logs do not always have permanent contact with the water. If this contact occurs only during the rainy seasons or when the stream is at its highest, decay is likely to be retarded. And even when the log is submerged or has continuous contact with the water, waterlogging prevents oxygen diffusion deep within the woody tissue. Consequently, because most cellulolytic and lignin-decomposing fungi are aerobic, decomposition of major structural tissue is retarded.

Because decomposition of wood in streams begins on the periphery, physical processes such as scouring play a more important role than on land. Decomposition from the outside inward is also evident in the action of invertebrates within waterlogged debris. Of the 38 insect taxa reported by Anderson et al. (1978) in such debris, only two were tunneling as opposed to surface species. Of these, only *Lipsothrix* spp. were present in substantial numbers, which were described as occurring "in tunnels in decayed alder wood that was so soft it could be broken apart by hand."

Unlike the decay process in streams, wood decay on land can occur both from the outside inward and from the center to the

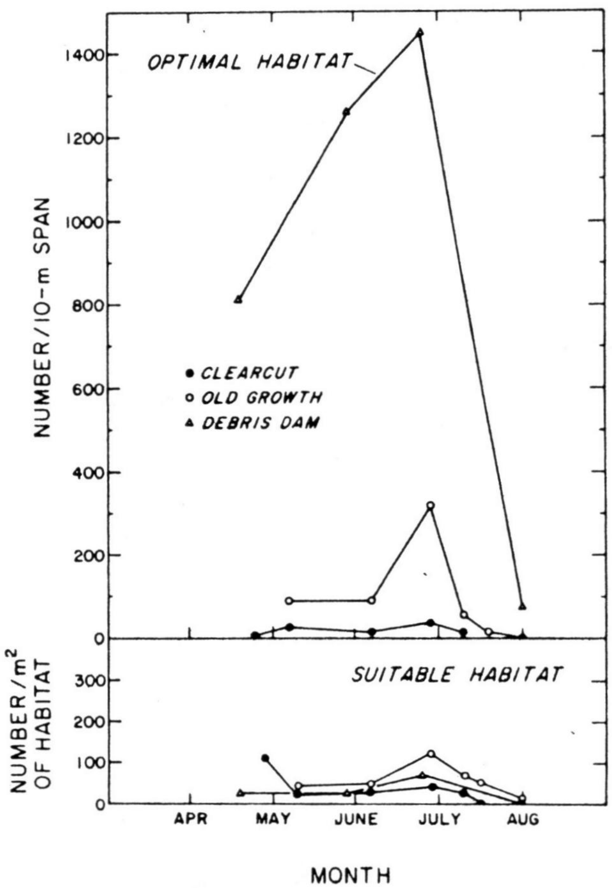

Figure 6. Density of Lepidostoma unicolor larvae in three stretches of Mack Creek -- one stretch draining a clearcut, one draining an old-growth area, and one behind a debris dam--within the H. J. Andrews Forest. Upper graph depicts larval density along a 10-m span, whereas the lower graph depicts larval density per square meter of suitable habitat. (From Grafius, 1977).

outside. On land, moisture content of decomposing coarse debris increases with age (Fig. 8), but logs rarely achieve the waterlogged, spongy state observed in the final stages of decomposition in water. The greater moisture content in wood debris on land in fact facilitates decomposition by preventing drying out during the warm, droughty summers characteristic of the Pacific Northwest. Thus, the terrestrial log acts as a perched water table, encouraging not only decomposition but also invasions by burrowing mammals and tunneling invertebrates. Common invertebrates such as termites, carpenter ants, and wood-boring beetles are well known for their ability to operate within the wood matrix (Elton, 1966). This activity in turn further enhances aeration.

Because wood on the forest floor remains permanently in place with ever-increasing soil contact as time progresses, mycorrhizal associations sometimes act as sources of nutrients to promote wood decay. Harvey et al. (1976) demonstrated the importance of decaying logs as sites for colonization by ectomycorrhizal fungi. Such fungal activity promotes carbon mineralization and the immobilization and fixation of nitrogen (Larsen et al., 1978; Silvester, 1978), thereby decreasing the carbon/nitrogen ratio of decomposing tissues and providing sources of nutrients and water for the establishment of nursery hemlocks on decaying logs. These colonizing seedlings in turn lead to further fragmentation and aeration as their roots penetrate the decomposing wood.

As log decay advances, there is a progressive increase in the concentration of essential nutrients such as nitrogen and phosphorus (Fig. 8). This is due primarily to the fact that carbon is mineralized at a greater rate than most other essential elements during initial stages of decay. The net result is that other essential elements are conserved for recycling within the forest ecosystem.

As log decay advances, there is a progressive decrease in wood density. In a study on the H. J. Andrews Forest (MacMillan et al., 1977), Douglas-fir logs were estimated to lose about 75 percent of their density after about 220 years. As such logs become less dense, their habitat value for tunneling invertebrates and small mammals increases. Unfortunately, similar estimates are not available for logs in stream channels.

Although large debris is the most visible wood component on land and in streams, fine wood contributes substantially to energy flows and nutrient cycling throughout the course of secondary succession. Average decomposition periods for fine wood are faster than those for coarse debris (Fogel and Cromack, 1977; MacMillan et al., 1977; Grier, 1978; Sollins et al., in press). The large nutrient pool provided by fine wood is intermediate in availability between those of leaf litter and coarse wood debris.

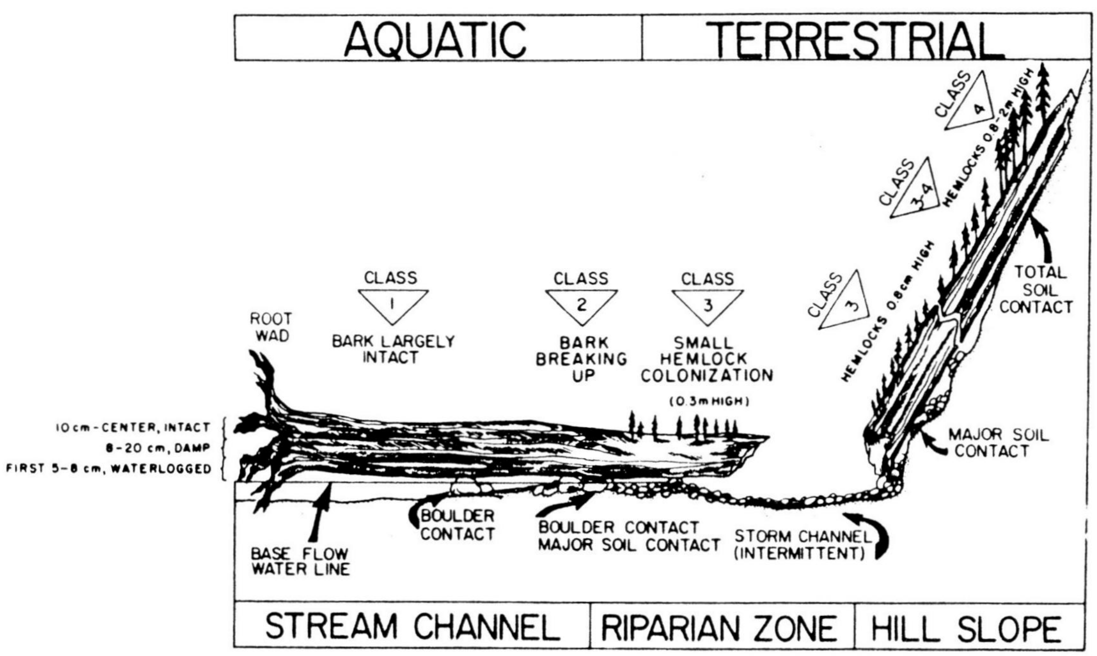

Figure 7. Decomposition over a 50-year period in a single log whose length spans three habitats. Note that five decay classes are represented within the log.

Branches and twigs also play an important role in providing habitat and a food source, particularly in aquatic environments. Anderson et al. (1978) report that the majority of invertebrate organisms they collected from seven streams in Oregon were found on wood 1 to 10 cm in diameter. Because most of the aquatic invertebrates on wood are associated with surfaces, it is reasonable that they would be associated with debris providing a large surface-to-volume ratio as well as ample sites for attachment.

The role of wood as habitat and as a source of carbon and other nutrients varies not only be debris size but also by debris species. Tunneling invertebrates which use rotten wood as a nutrient source prefer intermediate-sized debris (1 to 10 cm in diamter) of deciduous species. When wood is intermediate in size, waterlogging in streams apparently does not cause an acute diffusion problem, as it does in large debris.

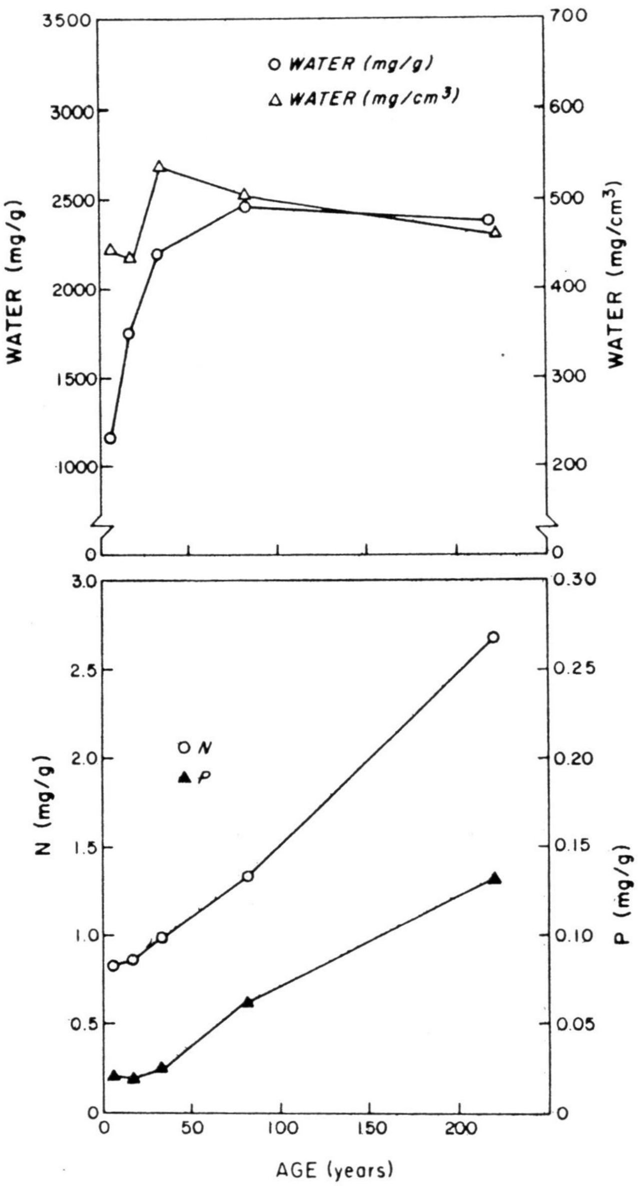

Figure 8. Water, nitrogen, and phosphorus contents in relation to age of wood debris at a mid-elevation stand of Douglas-fir in the H. J. Andrews Forest. (From MacMillan et al., 1977).

Little is known about how wood of small to intermediate size is decomposed in the terrestrial environment. Accordingly, this process is being studied at Mack Creek and on the forest floor of the H. J. Andrews Forest. Five types of fine wood substrates of Douglas-fir have been placed both on the forest floor and in the stream. Data analyzed to date indicate that fine wood debris decomposes faster in the aquatic than in the terrestrial environment (Fig. 9). The largest difference between decomposition in the two habitats was observed in chips, which have the largest surface-to-volume ratio. The next greatest difference was in twigs, which are sapwood and therefore the second most decomposable substrate. Bark and heartwood sticks, which one would expect to be the least susceptible to microbial breakdown, exhibited the smallest differences between decomposition on land and in water and also the lowest incidence of decay.

As noted previously, in large wood debris decomposition is accompanied by an increase in nitrogen concentration. The same process was observed in the fine wood substrates (Fig. 10). As with weight loss, the greatest increase in nitrogen concentration and the largest difference between reactions in the terrestrial and aquatic environments were observed in the least refractory substrates--chips and twigs. Because the data analyzed to date cover only 220 days, long-term trends, or even seasonal trends related to temperature, are not yet known.

One of the major obstacles to the decomposition of wood debris is its extremely high carbon/nitrogen ratio (322 for twigs, 357 for bark, 1,175 for heartwood chips, and 1,382 for heartwood blocks of Douglas-fir). Nitrogen fixation could play an important role in the early stages of decomposition by initially decreasing the carbon/nitrogen ratio. Therefore, acetylene reduction, as a chemical assay of nitrogen fixation (McNabb and Geist, 1979), was studied in the five substrates to determine if fixation contributes to the observed increase in nitrogen concentration. Acetylene reduction was observed at some time in all five substrates. As one might expect from previous data, acetylene reduction was

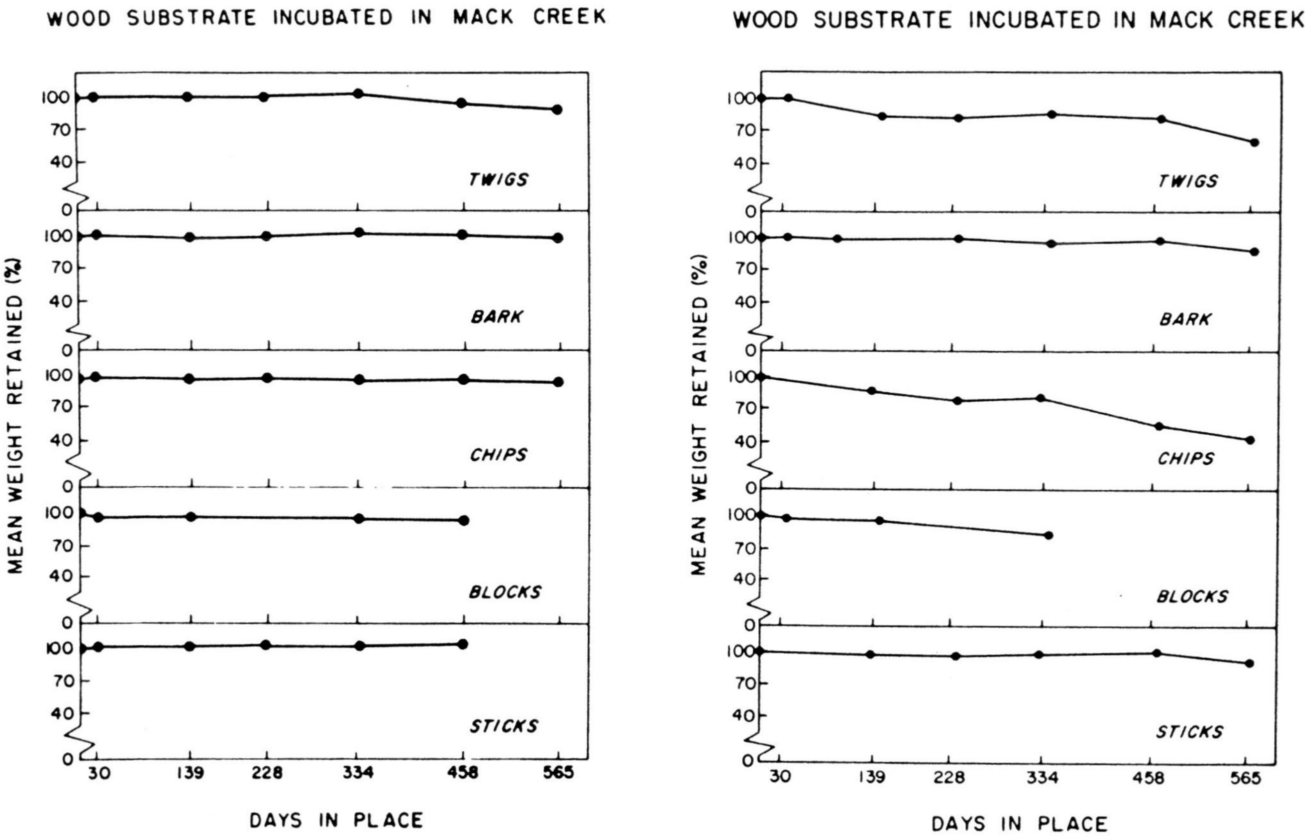

Figure 9. Weight loss in five fine wood substrates of Douglas-fir placed on the forest floor and in Mack Creek on the H. J. Andrews Forest. Each point is the mean of three samples.

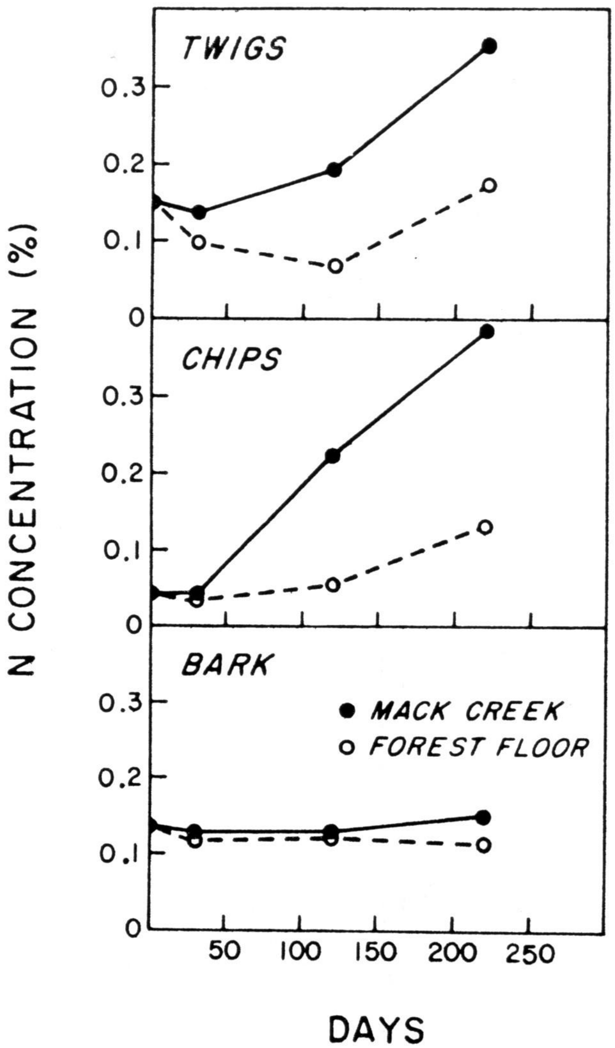

Figure 10. Change in nitrogen concentration in three fine wood substrates placed on the forest floor and in Mack Creek on the H. J. Andrews Forest.

greatest in the stream in the least refractory samples--chips and twigs--and lowest among samples on the forest floor (Fig. 11).

Factors such as temperature and moisture are important in influencing the nitrogen fixation rate and the rates of diffusion of nitrogen and oxygen to nitrogen-fixing bacteria. A general relationship between temperature and nitrogen fixation rates has been noted in the literature (Cromack et al., 1979; Kallio et al., 1972; Paul, 1975). Acetylene reduction has also been detected in large log debris and in small-sized wood (Cornaby and Waide, 1973; Sharp and Millbank, 1973; Sharp, 1975; Roskoski, 1977; Larsen et al., 1978). Through nitrogen fixation, logs may not only serve as an important source of habitat but may also facilitate their own decomposition and perhaps even contribute significant quantities of nitrogen to the forest floor.

MANAGEMENT IMPLICATIONS

Wood debris functions as an integral component of forest ecosystems. Concerted efforts to conserve wood debris will be needed if managed forests are to maintain the diversity of plant, animal, and microbial habitats currently present in unmanaged, primeval forests. On forest land, woody debris (slash) should be maintained over approximately 10 percent of clearcut areas (Maser et al., 1979). It would be desirable to leave several logs of decay classes 1 and 2 per hectare; these could be culled from logs of less desirable timber quality. As many logs as possible of classes 3, 4 and 5 (which have little or no commercial value) should be retained. In some instances, a portion of the woody debris could be utilized locally as firewood. Logs could be physically rearranged on the landscape to ensure optimal density and physical stability as part of the routine logging operations and site preparation (Maser et al., 1979).

The removal of natural, stable woody debris from streams can damage both the stream channel and streamside riparian habitat. Consequently, such material should be left in place when possible. In cases where massive accumulations occur, either as a result of logging or catastrophic events such as debris avalanches, significant wood removal may be necessary. In such cases, the advice of competent stream ecologists and geomorphologists should be sought before removal of massive debris jams are attempted. The general goal for wood management in streams should be to maintain well-established debris so that it can continue to function both as habitat and as a long-term nutrient source to stream organisms.

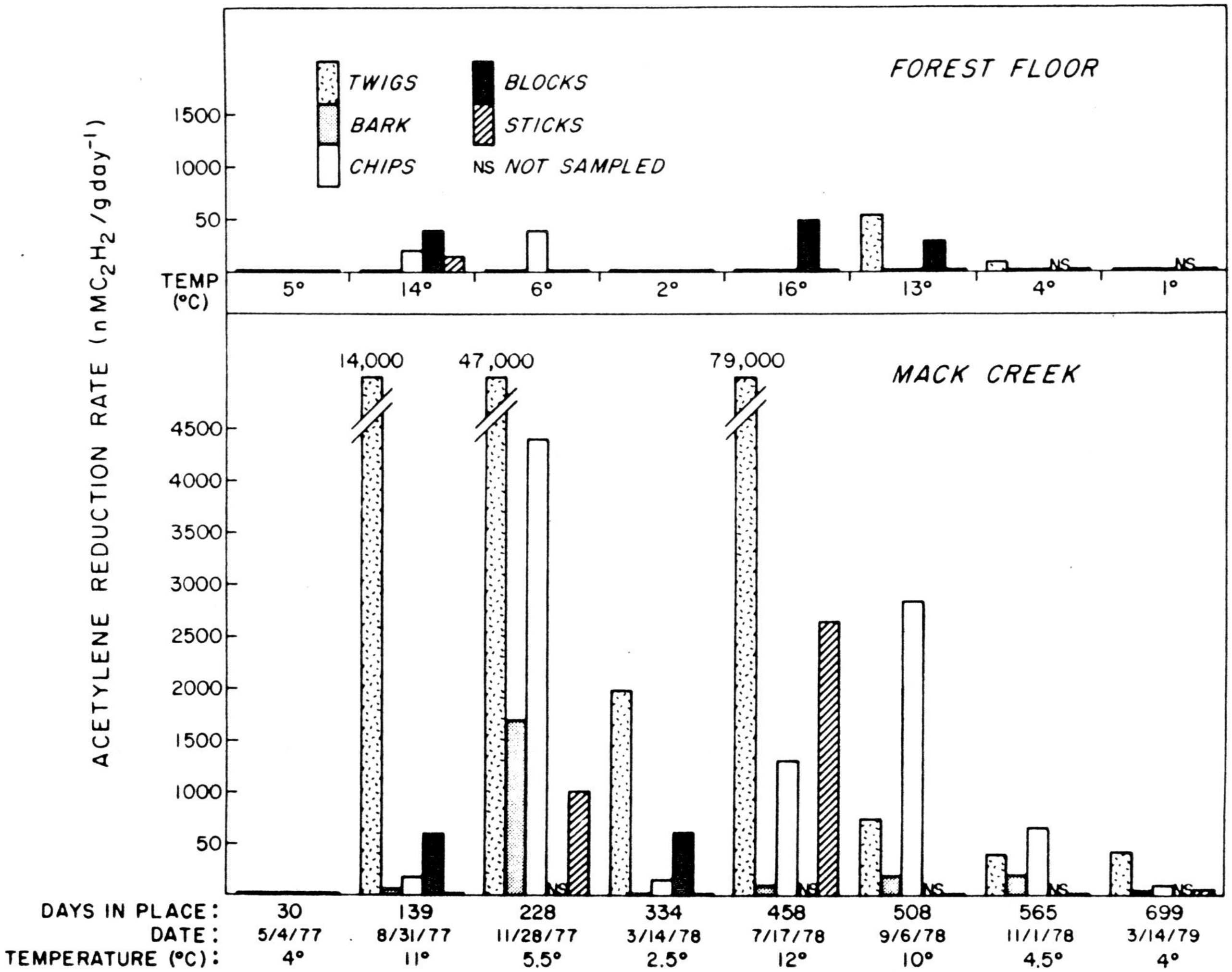

Figure 11. Rates of acetylene reduction in five fine wood substrates placed on the forest floor and in Mack Creek on the H. J. Andrews Forest.

ACKNOWLEDGEMENTS

We acknowledge National Science Foundation Ecosystems Grants No. DEB-76-21402 and DEB-77-06075 for support of our work. We appreciate the help of the following people from Oregon State University: for technical assistance, J. Anders, B. Buckley, G. Hawk, P. MacMillan, C. Mallonie, S. Phillip, and L. Roberts; for the use of unpublished data, C. Baker, B. Buckley, T. Dudley, R. Fogel, E. Grafius, G. Hawk, G. Lienkaemper, P. MacMillan, M. Ogawa, J. R. Sedell, F. Swanson, and J. Trappe. Additional suggestions and assistance in this work have come from P. Sollins, Oregon State University, and from J. Means and J. F. Franklin, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station.

LITERATURE CITED

Anderson, N. H., and E. Grafius. 1975. Utilization and processing of allochthonous materials by stream Trichoptera. Verh. Internat. Ver. Limnol. 19:3083-3088.

Anderson, N. H., J. R. Sedell, L. M. Roberts, and F. J. Triska. 1978. Role of aquatic invertebrates in processing wood debris in coniferous forest streams. Am. Midl. Natur. 100: 64-82.

Ausmus, B. S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. In Soil Organisms as Components of Ecosystems, edited by U. Lohm and T. Persson. Proc. 6th Int. Colloq. Soil Zool., Ecol. Bull. (Stockholm) 25:180-192.

Baker, C. O. 1979. The impacts of logjam removal on fish populations and stream habitat in western Oregon. M.S. thesis, Oregon State Univ., Corvallis.

Bishop, D. M., and S. P. Shapley. n.d. Effects of log debris jams on southeastern Alaska salmon streams. Unpublished report, Inst. of Northern Forestry, Pac. Northwest Forest and Range Experiment Sta., Juneau, Alaska.

Bormann, F. H., and G. E. Likens. 1979. Patterns and Processes in a Forested Ecosystem. New York: Springer-Verlag.

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

Christensen, O. 1977. Estimation of standing crop and turnover of dead wood in a Danish oak forest. Oikos 28:177-186.

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

Coulter, M. W. 1966. Ecology and management of fisheries in Maine. Ph.D. thesis, State Univ. College of Forestry at Syracuse, N.Y.

Cromack, K., Jr. 1973. Litter production and decomposition in a mixed hardwood watershed and a white pine watershed at Coweeta Hydrologic Station, North Carolina. Ph.D. thesis, Univ. of Georgia, Athens.

Cromack, K., Jr., C. C. Delwiche, and D. H. McNabb. 1979. Prospects and problems of nitrogen management using symbiotic nitrogen fixers. In Symbiotic Nitrogen Fixation in the Management of Temperate Forests, edited by J. C. Gordon, C. T. Wheeler, and D. A. Perry, pp. 210-223. Forest Res. Lab., Oregon State Univ., Corvallis.

Cummins, K. W. 1974. Structure and function of stream ecosystems. BioScience 24:631-641.

Day, F. P., Jr., and C. D. Monk. 1974. Vegetation patterns on a southern Appalachian watershed. Ecology 55: 1064-1074.

Elton, C. S. 1966. The Pattern of Animal Communities. New York: John Wiley and Sons, Inc.

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

Fogel, R., and K. Cromack, Jr. 1977. Effects of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Can. J. Bot. 55:1632-1640.

Fogel, R., M. Ogawa, and J. M. Trappe. 1973. Terrestrial decomposition: a synopsis. Conif. For. Biome Rep. 135.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service Pac. Northwest Forest & Range Experiment Stn. Gen. Tech. Rep. PNW-8.

Franklin, J. F., and R. H. Waring. 1980. Distinctive features of the northwestern coniferous forest: development, structure and function. (In this volume).

Froehlich, H. A., D. McGreer, and J. R. Sedell. 1972. Natural debris within the stream environment. Univ. of Washington, USIBP Internal Rep. 96, Conif. For. Biome.

Grafius, E. J. 1977. Bioenergetics and strategies of some Trichoptera in processing and utilizing allochthonous materials. Ph.D. thesis, Oregon State Univ., Corvallis.

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

Grier, C. C., and R. S. Logan. 1977. Old-growth Pseudotsuga menziesii communities of a western Oregon watershed: biomass distribution and production budgets. Ecol. Monogr. 47:373-400.

Hall, J. D., and C. O. Baker. 1975. Biological impacts of organic debris in Pacific Northwest streams. In Logging Debris in Streams, Workshop II. Oregon State Univ., Corvallis.

Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). J. Fish. Res. Board Can. 22:1035-1081.

Harvey, A. E., M. J. Larsen, and M. F. Jurgensen. 1976. Distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. Forest Sci. 22:393-398.

James, G. A. 1956. The physical effect of logging on salmon streams of southeast Alaska. USDA Forest Service, Alaska For. Res. Cent. Stn. Pap. 5.

Jones, E. W. 1945. The structure and reproduction of the virgin forests of the north temperate zone. New Phytol. 44:130-148.

Kallio, P., S. Suhonen, and H. Kallio. 1972. The ecology of nitrogen fixation in Nephroma arcticum and Solorina crocea. Rep. Kevo. Subarctic Res. Stn. 9:7-14.

Lambert, R. L., G. E. Lang, and W. A. Reiners. 1980. Weight loss and chemical change in boles of a subalpine balsam fir forest. Ecology (in press).

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

Larkin, P. A., and others. 1959. The effects on freshwater fisheries of man-made activities in British Columbia. Can. Fish. Cult. 25:27-59.

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

Lyon, L. J. 1976. Elk use as related to characteristics of clearcuts in western Montana. In Proceedings of the Elk-logging-roads Symposium, edited by S. R. Hieb, pp. 69-72. Univ. of Idaho, Moscow.

MacMillan, P. C., J. E. Means, G. M. Hawk, K. Cromack, Jr., and R. Fogel. 1977. Douglas-fir log decomposition in an old-growth Douglas-fir forest. Northwest Sci. (abstr.), p. 13.

Maser, C., J. M. Trappe, and D. C. Ure. 1978. Implications of small mammal mycophagy to the management of western coniferous forests. In Trans. 43rd North Am. Wildl. and Nat. Resour. Conf. Wildlife Manage. Inst., pp. 78-88. Washington, D. C.

Maser, C., R. G. Anderson, K. Cromack, Jr., J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. In Wildlife Habitats in Managed Forests -- the Blue Mountains of Oregon and Washington, edited by J. W. Thomas, pp. 78-95. USDA Forest Serv. Agric. Handbook 553.

McFee, W. W., and E. L. Stone. 1966. The persistence of decaying wood in the humus layers of northern forests. Proc. Soil Sci. Soc. Amer. 30:512-516.

McNabb, D. H., and J. M. Geist. 1979. Acetylene reduction assay of symbiotic N_2 fixation under field conditions. Ecology 60:1070-1072.

Meehan, W. R. 1974. The forest ecosystem of southeast Alaska. 3. Fish habitats. USDA Forest Serv. Pac. Northwest Forest & Range Exp. Stn. Gen. Tech. Rep. PNW-15.

O'Neill, R. V., W. F. Harris, B. S. Ausmus, and D. E. Reichle. 1975. A theoretical basis for ecosystem analysis with particular reference to element cycling. In Mineral Cycling in Southeastern Ecosystems, edited by F. G. Howell, J. B. Gentry, and M. H. Smith, pp. 28-40. ERDA Symp. Series (CONF-740513).

Paul, E. A. 1975. Recent studies using the acetylene reduction technique as an assay for field nitrogen fixation levels. In Nitrogen Fixation by Free-living Micro-organisms, edited by W. D. P. Stewart, pp. 259-269. New York: Cambridge University Press.

Place, I. C. M. 1950. Comparative moisture regimes of humus and rotten wood. Can. Dep. Resour. & Dev., Forestry Branch, For. Res. Div., Silvicultural Leaflet 37.

Roskoski, J. 1977. Nitrogen fixation in northern hardwood forests. Ph.D. thesis, Yale Univ., New Haven, Conn.

Rowe, J. S. 1955. Factors influencing white spruce reproduction in Manitoba and Saskatchewan. Can. Dept. of Northern Affairs and Nat. Resour., Forestry Branch, For. Res. Div. Tech. Note 3.

Ruben, J. A. 1976. Reduced nocturnal heat loss associated with ground litter burrowing by the California red-sided garter snake, Thamnophis sirtalis infernalis. Herpetologica 32:323-325.

Sedell, J. R., F. J. Triska, and N. S. Triska. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. I. Weight loss in associated invertebrates. Verh. Internat. Ver. Limnol. 19:1617-1627.

Sharp, R. F. 1975. Nitrogen fixation in deteriorating wood: The incorporation of and the effect of environmental conditions on acetylene reduction. Soil Biochem. 7:9-14.

Sharp, R. F., and J. W. Millbank. 1973. Nitrogen fixation in deteriorating wood. Experientia 29:895-896.

Sheridan, W. L. 1969. Effects of log debris jams on salmon spawning riffles in Saginaw Creek. USDA Forest Service, Alaska Region.

Shigo, A. L., and H. G. Marx. 1977. Compartmentalization of decay in trees. USDA Forest Service Agric. Inf. Bull. 405.

Silvester, W. B. 1978. Nitrogen fixation and mineralization in Kauri (Agathis australis) forest in New Zealand. In Microbial Ecology: Proceedings in Life Sciences, edited by M. W. Loutit and J. A. R. Miles, pp. 138-143. Berlin: Springer-Verlag.

Sollins, P., and R. M. Anderson, eds. 1971. Dry weight and other data for trees and woody shrubs of the southeastern U.S. ORNL-IBP-71-6 Rep., Oak Ridge Natl. Lab., Oak Ridge, Tenn.

Sollins, P., C. C. Grier, F. M. McCornison, K. Cromack, Jr., R. Fogel, and R. L. Fredriksen. 1980. The internal element cycles of an old-growth Douglas-fir forest in western Oregon. Ecol. Monogr. (in press).

Sprugel, D. G. 1976. Dynamic structure of wave-generated Abies balsamea forests in the northeastern U.S. J. Ecol. 64:889-912.

Swanson, F. J., G. W. Lienkaemper, and J. R. Sedell. 1976. History, physical effects and management implications of large organic debris in western Oregon streams. USDA Forest Service Pac. Northwest Forest & Range Exp. Stn. Gen. Tech. Rep. PNW-56.

Swift, M. J., I. N. Healey, J. K. Hibberd, J. M. Sykes, V. Bampoe, and M. E. Nesbitt. 1976. The decomposition of branch-wood in the canopy and floor of a mixed deciduous woodland. Oecologia 16:139-149.

Taylor, W. P. 1935. Ecology and life history of the porcupine (Erethizon epixanthum) as related to the forests of Arizona and the southwestern U.S. Univ. of Arizona Biol. Sci. Bull. 3,6:5-177.

Triska, F. J. 1970. Seasonal distribution of aquatic hyphomycetes in relation to disappearance of leaf litter from a woodland stream. Ph.D. thesis, Univ. of Pittsburgh, Pa.

Waring, R. H. 1980. Vital signs of forest ecosystems. (In this volume).

Winn, D. S. 1976. Terrestrial vertebrate fauna and selected coniferous forests habitat types on the north slope of the Unita Mts. USDA Forest Service Region 4, Wasatch Natl. Forest, Salt Lake City, Utah.