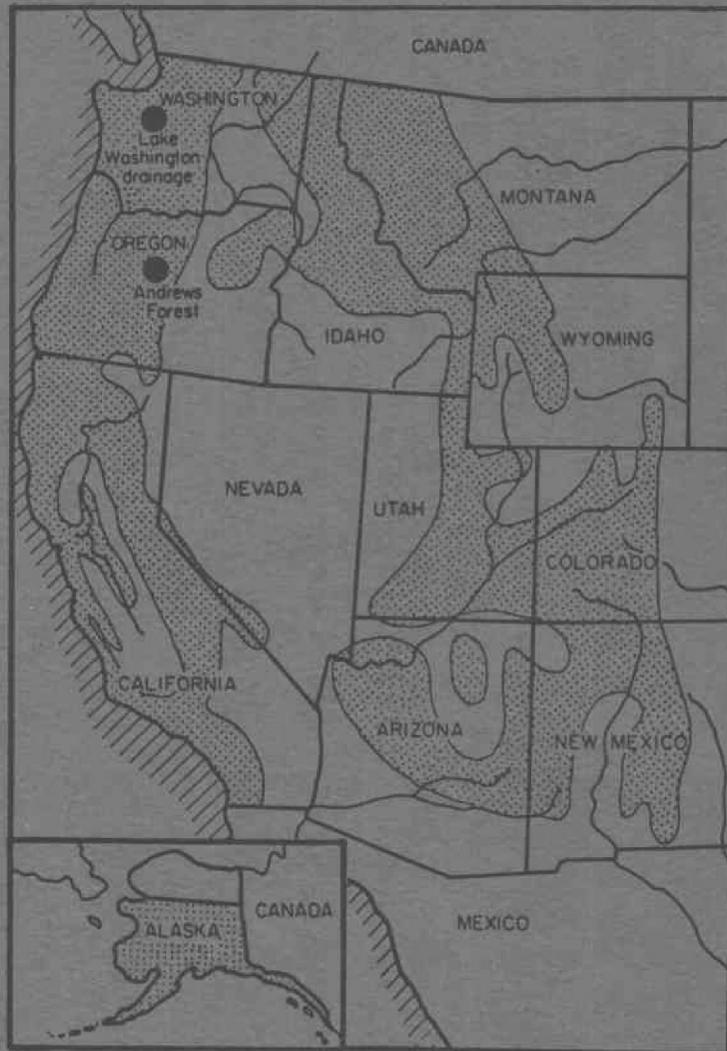


S. P. Hessel



CONIFEROUS FOREST BIOME

ECOSYSTEM ANALYSIS



PROPOSAL FOR 1975 TO 1977
VOLUME II
MARCH 1974

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3. STRUCTURE AND DYNAMICS OF CONIFEROUS FOREST ECOSYSTEMS

This volume represents a synthesis of many of the results of the Coniferous Forest Biome program to date, particularly with reference to the structure and function of terrestrial and aquatic ecosystems within the Douglas-fir region of the Pacific Northwest. Emphasis is placed on the structure of ecosystems along environmental gradients; carbon, water, and nutrient cycling; and the role of consumers, decomposers, and succession. Some data from terrestrial ecosystems outside the Douglas-fir region are presented but we have not synthesized many of these data. We have had a unique opportunity in this Biome to examine interfaces between aquatic and terrestrial systems involving both streams and lakes, and the results are presented below.

Most data discussed in this volume were obtained from the intensive research sites: the old-growth H. J. Andrews Experimental Forest in the Oregon Cascade Mountains, and the Cedar River--Lake Washington drainage in the Washington Cascade Mountains. Research at the latter site was conducted on four lakes (Washington, Sammamish, Chester Morse, and Findley), in the young-growth Douglas-fir ecosystems near the A. E. Thompson Research Center, and in the Findley Lake watershed. Descriptions of these sites are presented in section 2.2. Additional sites near Fairbanks, Alaska; Missoula, Montana; Priest River, Idaho; Fort Collins and San Juan Mountains, Colorado; Berkeley, California; Flagstaff, Arizona; and Logan, Utah, were also used.

Modeling has been used as a major synthesis mechanism, and process and ecosystem models are discussed throughout this volume. Part 4 is devoted to a discussion of what we have learned from our modeling studies.

Our proposed work in 1975-1977 will be focused on expansion of our studies in space and time and on the behavior of ecosystems in response to stress and manipulation, such as insect consumption and disease. Part 5 presents some data on what we have learned to date about the effects of certain of these stresses and manipulations.

No attempt was made to synthesize all the data we have collected in the last three years. That will be accomplished in 1974 and will be published as a volume in the U.S./International Biological Program series.

3.1. Terrestrial Ecosystems

This section represents a synthesis of results to date on the structure and dynamics (function) of natural terrestrial ecosystems in the Coniferous Forest Biome. The major emphasis in the Biome program has been on the Douglas-fir (*Pseudotsuga menziesii*) region and an attempt has been made here to synthesize data collected on the Biome research sites prior to the initiation of the Biome with data collected by Biome researchers. This synthesized information has given us a deeper understanding of the structure (section 3.1.1) and dynamics (section 3.1.2) of coniferous ecosystems and has enabled us to develop penetrating hypotheses to be investigated in the 1975-1977 period.

Although a smaller emphasis has been placed on obtaining data from other regions in the Biome, the coordinating sites and the environmental grid programs have enabled us to prepare a preliminary comparison of the structure and function of coniferous forest ecosystems across the Biome (section 3.1.3).

3.1.1. Structure of coniferous ecosystems in the Douglas-fir region

The Douglas-fir region is considered to be that area in the Pacific Northwest in which Douglas-fir occurs (Figure 3.1). It is a geographic region encompassing coastal and interior mountain ranges, coastlines, and interior valleys and basins, and is generally considered to enclose the area west of the Cascade Crest in British Columbia, Washington, and Oregon. Douglas-fir does occur on the east side of the Cascades, but the structure and dynamics of those forests will not be discussed here.

3.1.1.1. Structure of the Douglas-fir region (environmental features and biological components). The description of the vegetation in the region follows that used by Franklin and Dyrness (1969, 1973). They have used zones as basic organizational units for the vegetational communities, where zones are areas in which a single tree species is the major climax dominant, e.g., Tsuga heterophylla. Within each of the forest zones there can be several associations, each of which represents a climatic climax.

Zones may occur as sequential belts on mountain slopes, but generally they interfinger, with lower elevational limits in valleys and highest limits on ridges. As a result species occupying modal sites in one zone may occur on moist, cool habitats in an adjacent warmer drier zone. Zonal schemes reflect plant responses to strong macroclimatic gradients in temperature and moisture. In some cases, however, unusual physical or chemical soil properties may override climatic factors and modify zonal patterns.

Forested zones in the Douglas-fir region are shown in Table 3.1. These are in the coastal Picea sitchensis zone, the widespread Tsuga heterophylla zone, the Abies amabilis zone, and the subalpine Tsuga mertensiana zone. Typical tree species and their zonal occurrence in western Washington are listed in Table 3.2. The basic vegetation descriptions below are from Franklin and Dyrness (1969, 1973) but the detailed descriptions of the structure in the research areas represent a synthesis of the results of many individual Biome research projects on the intensive research sites (the Cedar River watershed in Washington and the H. J. Andrews Experimental Forest in Oregon), which are described in part 2.

The Picea sitchensis (Sitka spruce) zone. This coastal zone has received little attention in the Biome and will be given only a passing mention. The zone is generally only a few kilometers in width, except where it extends into river valleys and down the west side of the Olympic Peninsula (Figure 3.1). It is generally found below 150 m but may extend to 600 m when mountains are close to the coast. This zone has a mild climate, and annual precipitation averages 2000-3000 mm. Fog drip adds more precipitation. Major soil groups are brown laterites, reddish brown

Table 3.1. Forested zones in the Douglas-fir region.

Zonal groups	Zone
Xerophytic	<u>Juniperus occidentalis</u> ^a <u>Pinus ponderosa</u> ^a <u>Pseudotsuga menziesii</u>
Temperate	<u>Picea sitchensis</u> <u>Tsuga heterophylla</u> <u>Abies amabilis</u>
Subalpine	<u>Tsuga mertensiana</u>

^aGenerally not considered to be important west of the Cascades but there are xerophytic areas in the Puget Trough province.

Table 3.2. Representative tree species and their relative importance in both seral and climax communities in forested zones of western Washington (from Franklin and Dyrness 1969).

Species	Zones ^a			
	<u>Picea</u> <u>sitchensis</u>	<u>Tsuga</u> <u>heterophylla</u>	<u>Abies</u> <u>amabilis</u>	<u>Tsuga</u> <u>mertensiana</u>
<u>Abies amabilis</u>	m	m	M	M
<u>Abies grandis</u>	m	m	m	
<u>Abies lasiocarpa</u>			m	M
<u>Abies procera</u>			M	m
<u>Chamaecyparis nootkatensis</u>			m	M
<u>Picea sitchensis</u>	M	m		
<u>Pinus monticola</u>		m ^b	m	m
<u>Pinus contorta</u>	m	m ^b	m	m
<u>Pseudotsuga menziesii</u>	M	M	M	m
<u>Tsuga heterophylla</u>	M	M	M	m
<u>Acer macrophyllum</u>	m	m		
<u>Alnus rubra</u>	M	M		
<u>Thuja plicata</u>	M	M	m	

^aM = major species, m = minor species.

^bExcept major species in the Puget Trough province.

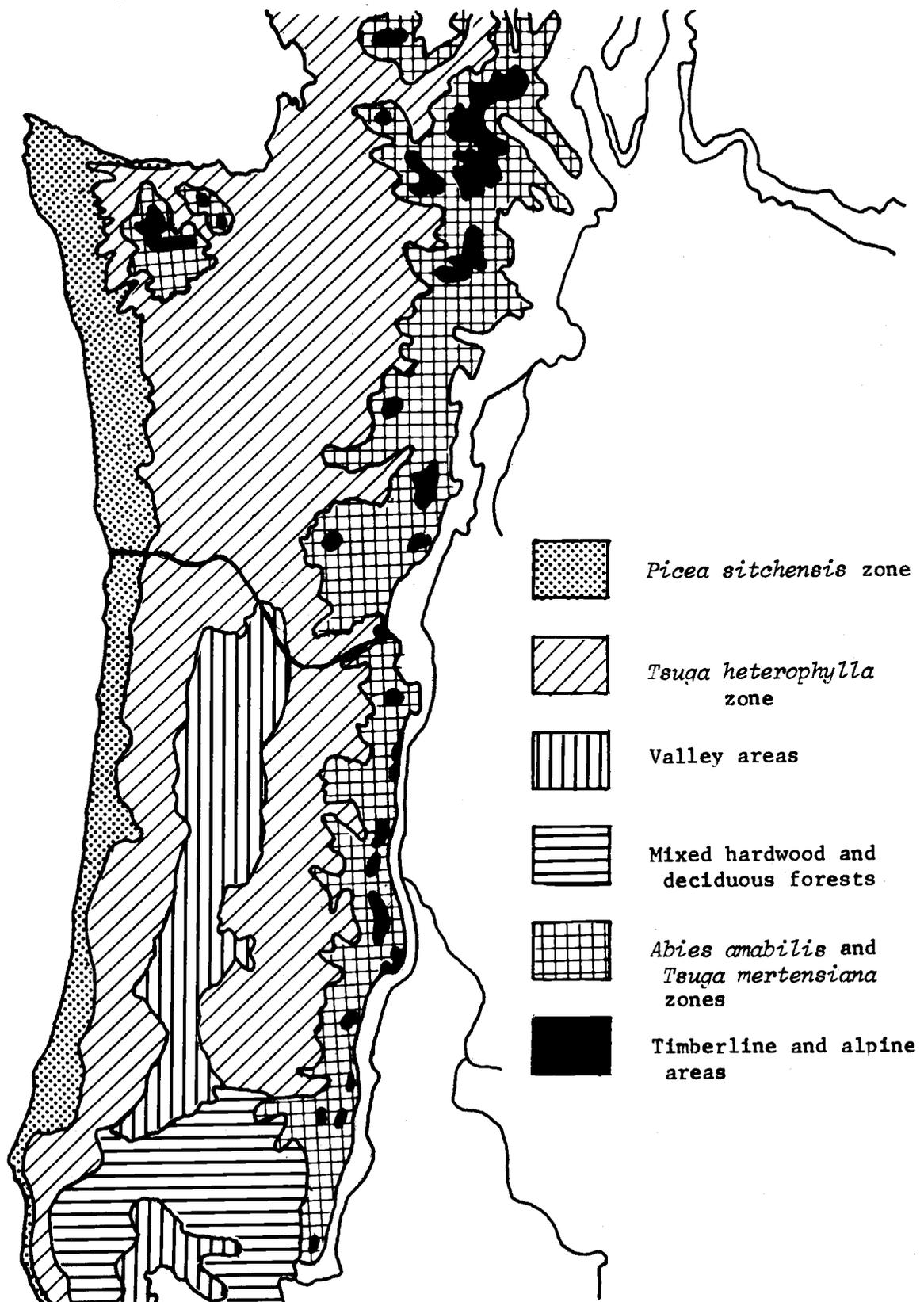


Figure 3.1. Generalized vegetation map of the Douglas-fir region of western Oregon and Washington (after Franklin and Dyrness 1969).

laterites and sols bruns acides. Surface soils are strongly acid (pH 5.0-5.5), high in organic matter (15%-20%) and total nitrogen (0.5%), and low in base saturation (10%).

The major tree species are Picea sitchensis, Thuja plicata, Tsuga heterophylla, Pseudotsuga menziesii, and Alnus rubra; the first three are the most common. Mature forests have lush understories of shrubs, herbs, ferns, and cryptogams. Specific communities included in this zone are the sand dunes, tidal marshes, prairies, and forested swamps. No information is included here on the insects, birds, and animals associated with this zone.

The Tsuga heterophylla (western hemlock) zone. The Tsuga heterophylla zone is the most extensive vegetation zone in western Oregon and Washington (Figure 3.1). It is the most important for timber production. This zone extends south from British Columbia through the Olympic Peninsula, Coast Ranges, Puget Sound area, and the Cascades. In Oregon it is split into two major segments, the Coast Ranges and Cascades. The southern limits are shown in Figure 3.1.

The zone ranges in elevation in the Cascades from sea level to 600-700 m at 49°N and from 150 to 1000 m at 45°N. In the Olympics it ranges from 150 to 550 m on western slopes and from nearly sea level to 1125 m on eastern slopes.

Although it is called the Tsuga heterophylla zone, large areas in the zone are forested with Pseudotsuga menziesii, since it is the dominant species in seral stands that have developed after logging or burning. Even old-growth stands frequently maintain a major component of Douglas-fir.

Because of the importance and extensive area of the Tsuga heterophylla zone in the Douglas-fir region, the Biome intensive research sites were located in it. The Washington intensive site, which is the Cedar River watershed, consists largely of seral stands of Douglas-fir and grades into the Abies amabilis zone at higher elevations. The H. J. Andrews Forest (the Oregon intensive site) includes two major zones, the Tsuga heterophylla zone and the Abies amabilis zone, as well as a transition zone between these two (Zobel et al. in press).

The Tsuga heterophylla zone has a wet, mild, maritime climate (Table 3.3), but it includes a number of climatic variations. Annual precipitation averages 1500-3000 mm and occurs mainly during the winter. Summers are relatively dry, with only 6%-9% of the total precipitation. Detailed climatological data are available for the Andrews Forest (Zobel et al. 1973b, Fredriksen 1972) and the Thompson site (Fritschen 1972, 1973b).

The soils in the Tsuga heterophylla zone are derived from a wide variety of parent rocks, yet they do have some common features. Soil profiles are generally moderately deep and of medium acidity. Surface horizons are well aggregated and porous. Organic matter content ranges from moderate in the Cascades to high in portions of the Coast Ranges and the Olympic Peninsula. Most soils in the zone are of medium texture

Table 3.3. Climatic data from representative stations within the Tsuga heterophylla zone (from Franklin and Dyrness 1969).

Station	Elev (m)	Lat	Long	Temperature (°C)				Precipitation			
				Av ann	Av Jan	Av Jan min	Av Jul	Av Jul max	Av ann (mm)	Jun- Aug (mm)	Av ann snow- fall (cm)
Darrington, Wash.	168	48°15'	121°36'	9.7	1.0	-3.3	17.4	25.7	2045	154	120
Greenwater, Wash.	521	47°09'	121°39'	7.4	-1.2	-3.7	15.8	22.6	1487	138	198
Castle Rock, Wash.	36	46°17'	122°54'	10.4	2.9	-0.2	17.6	26.7	1453	109	27
Wind River, Wash.	351	45°48'	121°56'	8.8	0	-3.7	17.5	26.9	2528	119	233
Detroit, Oreg.	485	44°44'	122°09'	9.3	0.9	-3.2	17.9	27.5	1929	110	156
McKenzie Bridge, Oreg.	419	44°10'	122°10'	10.1	1.6	-2.6	18.9	29.4	1789	106	
Valsetz, Oreg.	346	44°50'	123°40'	9.6	2.4	-0.7	16.6	25.6	3207	144	38

Source: U.S. Weather Bureau

ranging from sandy loam to clay loam. Soil types range from sols bruns acides and reddish brown lateritic soils in the Coast Ranges and Olympic Peninsula to brown podzolic soils and reddish brown laterites in the Cascade Range.

Soils on the Thompson Research site are formed from glacial outwash, which is common in the Puget Sound area, and are brown podzolics. Descriptions of the two major soil series (Alderwood and Everett) are shown in Table 3.4. The moister soils are the Alderwood Series. Parent material in this area tends to be acid in nature whereas the parent material on the H. J. Andrews Forest tends to be basic in nature. The soils are podzolic-lateritic intergrades and have higher potassium and calcium than the Thompson site soils. Brown and Parsons (1973b) have characterized the soils of the 19 reference stands in the H. J. Andrews Forest. Soils of the reference stands are primarily brown podzolic and podzolic-lateritic intergrades. A typical soil profile in reference stand 1 (Pseudotsuga menziesii/Holodiscus discolor community) at an elevation of 480-500 m is shown in Table 3.5.

Biological components of the zone. The information on the structure of biological components of the Tsuga heterophylla zone provides a necessary input for calculating standing biomasses of all ecosystem components including trees, understory vegetation, birds, insects, fungi, lichens, and mammals and for determining spatial distribution patterns. This information is vital to our modeling efforts particularly in connection with carbon, water, and nutrient cycling.

Major forest tree species in this zone are Pseudotsuga menziesii, Tsuga heterophylla, and Thuja plicata. Abies grandis, Picea sitchensis, and Pinus monticola occur sporadically. Abies amabilis is common near the upper altitudinal limits or even well within the Tsuga heterophylla zone in the northern Cascades and Olympics.

Except on recently disturbed sites or specialized habitats (e.g., riparian sites) hardwoods are not common and are subordinate. Alnus rubra, Acer macrophyllum, and Castanopsis chrysophylla are the most widespread. Populus trichocarpa, Fraxinus latifolia, Acer macrophyllum, and Alnus rubra are found along the major water courses.

Scientists in the Coniferous Biome have studied the forest communities in detail at both intensive sites. Seral stands on the Cedar River watershed in Washington have been classified by Scott and Long (1973). As a result of fires, logging, or both, much of the Puget Sound region is dominated by Douglas-fir and alder rather than the climax western hemlock. The species cover and constancy for three young-growth forest communities in the area of the Thompson Research Center are presented in Table 3.6. Three forest community types can be delineated. These seral communities are, in order of increasing soil moisture and, coincidentally, decreasing total area: Douglas-fir/salal (Pseudotsuga menziesii/Gaultheria shallon), Douglas-fir/sword fern (P. menziesii/Polystichum munitum), and alder/sword fern (Alnus rubra/P. munitum). The alder/sword fern community occurs on soils of the Alderwood Series. Although stands of the Douglas-fir/sword fern community are dominated

Table 3.4. Description of major soil profiles occurring at the Thompson research site.

Horizon	Depth (cm)	Alderwood profile	Horizon	Depth (cm)	Everett profile
Forest floor	2.5	Acid, dark brown, partially decomposed forest litter	Forest floor	2.5	Undecomposed mosses, twigs, needles
A1	0.0	Decomposed organic matter Brown sandy loam; moderate medium granular structure; friable; scattered concretions, clear, wavy boundary; many roots; pH 4.6	A1	0.0	Decomposed organic matter Black brown gravelly, sandy loam; weak granular structure; friable; clear wavy boundary; many roots; pH 5.4
B1	12.5	Pale brown sandy loam, weak medium subangular blocky structure; friable; scattered concretions; clear wavy boundary; many roots; pH 5.0	B21	8	Dark brown gravelly, sandy loam; massive to very weak structure; very friable; clear wavy boundary; many roots; pH 5.6
B21	30.0	Light yellowish-brown gravelly, sandy loam; weak medium subangular blocky structure; friable; clear, wavy boundary; roots present; pH 5.25	B22	24	Brown gravelly, loamy sand; massive structure; very friable; a abrupt wavy boundary; many roots; pH 5.85
B22	60.0	Very pale brown gravelly, sandy loam; moderate medium subangular blocky to massive structure; friable; roots present; pH 5.25	C1	45	Yellow brownish gray very gravelly sand; single grain structure; friable; clear wavy boundary; few roots; pH 5.85
B3	72.5	Dark gray gravelly, sandy loam; strong medium blocky structure to massive; roots rare; pH 5.0	C2	72	Variegated colored very gravelly sand; single grain structure; friable; no roots

Table 3.5. Soil profile description for reference stand 1, pit 1, H. J. Andrews Forest (from Brown and Parsons 1973^b).

<u>Horizon</u>	<u>Depth (cm)</u>	<u>Description</u>
011	3-2	Needles, twigs, cones, etc.
012	2-0	Partially decomposed needles, twigs, cones, etc.
A1	0-16	Very gravelly loam, granular structure, friable, clearly wavy boundary, 55% pebbles, pH 6.3.
A3	16-44	Very gravelly loam, subangular blocky structure, very friable, clear straight boundary, 55% pebbles, pH 6.2.
B1	44-73	Very gravelly loam, subangular blocky structure, very friable, clear straight boundary, 55% pebbles, few pumice grains, pH 6.6.
B2, B3	73-132	Very gravelly loam, subangular blocky structure, very friable, clear straight boundary, 55% pebbles, few pumice grains, pH 6.2.
C	132-154	Very gravelly loam, massive structure, very friable, grain straight boundary, 60% pebbles, few pumice grains.
IIR	154-184+	Highly fractured reddish breccia bedrock.

Table 3.6. Species cover (%) and constancy (%) for three forest communities in the area of the Thompson Research site (after Scott and Long 1973).

	Douglas-fir/ Salal		Douglas-fir/ sword fern		Alder/ sword fern	
	Cover	Constancy	Cover	Constancy	Cover	Constancy
OVERSTORY TREE LAYER						
<i>Acer macrophyllum</i>			Tr	13	8	58
<i>Alnus rubra</i>			1	13	75	100
<i>Prunus emarginata</i>	Tr	9	1	13	1	17
<i>Pseudotsuga menziesii</i>	76	100	75	100	3	50
<i>Thuja plicata</i>	1	18	3	20	1	17
<i>Tsuga heterophylla</i>	5	54	11	87	Tr	8
SMALL TREE AND TALL SHRUB LAYER						
<i>Abies grandis</i>					Tr	8
<i>Acer circinatum</i>	4	54	2	80	8	83
<i>Acer macrophyllum</i>			Tr	7		
<i>Alnus rubra</i>					Tr	8
<i>Cornus nuttallii</i>	Tr	9	1	20	Tr	8
<i>Corylus cornuta</i> var. <i>californica</i>	1	18			Tr	8
<i>Holodiscus discolor</i>	3	45				
<i>Menziesia ferruginea</i>			Tr	7		
<i>Oplopanax horridum</i>			1	40	1	33
<i>Prunus emarginata</i>					Tr	8
<i>Rubus parviflorus</i>			Tr	7	Tr	8
<i>Rubus spectabilis</i>			1	33	2	50
<i>Sambucus racemosa</i>			1	20	1	50
<i>Symphoricarpos albus</i>					Tr	8
<i>Thuja plicata</i>	Tr	9	2	53	Tr	8
<i>Tsuga heterophylla</i>	6	82	10	100	3	75
<i>Vaccinium membranaceum</i>			Tr	7		
<i>Vaccinium parviflorum</i>	3	91	3	87	1	75
LOW SHRUB LAYER						
<i>Berberis nervosa</i>	3	75	6	27	4	33
<i>Gaultheria shallon</i>	56	100	3	67	2	50
<i>Menziesia ferruginea</i>	Tr	9				
<i>Rosa gymnocarpa</i>	Tr	9				
<i>Rubus ursinus</i>	3	91	3	93	11	100
HERB LAYER						
<i>Achlys triphylla</i>			Tr	7	1	25
<i>Actaea rubra</i>			Tr	27	TR	8
<i>Asarum caudatum</i>			Tr	7	Tr	8

Table 3.6. Species cover (%) and constancy (%) for three forest communities in the area of the Thompson Research site (after Scott and Long 1973) (continued).

	Douglas-fir/ Salal		Douglas-fir/ sword fern		Alder/ sword fern	
	Cover	Constancy	Cover	Constancy	Cover	Constancy
<i>Athyrium filix-femina</i>			Tr	33	1	42
<i>Blechnum spicant</i>			1	47	Tr	33
<i>Campanula scouleri</i>	Tr	9			Tr	8
<i>Chimaphila menziesii</i>	Tr	36	Tr	7		
<i>Circaea alpina</i>			Tr	13	Tr	8
<i>Corallorhiza maculata</i>	Tr	9	Tr	7		
<i>Dicenta formosa</i>					1	33
<i>Digitalis purpurea</i>					Tr	8
<i>Dryopteris austriaca</i>			1	7		
<i>Equisetum arvense</i>					Tr	8
<i>Festuca sp.</i>			Tr	7	Tr	17
<i>Galium triflorum</i>	Tr	9	1	53	1	50
<i>Goodyera oblongifolia</i>	Tr	9	Tr	7		
GRASSES						
<i>Hieracium albiflorum</i>			Tr	7	2	42
<i>Hypopitys monotropa</i>	Tr	9				
<i>Linnaea borealis</i>	6	64	6	33	Tr	8
<i>Luzula parviflora</i>	Tr	18	Tr	27	Tr	42
<i>Maianthemum unifolium dilatatum</i>			1	40	1	25
<i>Montia sibirica</i>			Tr	7	4	75
<i>Polystichum munitum</i>	4	91	43	100	58	100
<i>Pteridium aquilinum</i>	8	91	2	80	8	58
<i>Smilacina stellata</i>			Tr	20	Tr	8
<i>Streptopus amplexifolius</i>	Tr	9				
<i>Tiarella trifoliata</i>			Tr	20	Tr	8
<i>Tiarella unifoliata</i>			Tr	7	1	17
<i>Tolmiea menziesii</i>					1	17
<i>Trientalis latifolia</i>	Tr	36	Tr	40	Tr	8
<i>Trillium ovatum</i>	Tr	27	1	87	Tr	8
<i>Viola sempervirens</i>	1	64	2	40	Tr	8
MOSS LAYER						
<i>Dicranum fuscescens</i>	Tr	9	Tr	13	Tr	25
<i>Eurhynchium oregonum</i>	44	100	22	93	9	92
<i>Hylocomium splendens</i>	3	54	7	53	1	25
<i>Mnium insigne</i>	1	54	1	87	1	75
<i>Mnium spinulosum</i>	Tr	18	Tr	20		
<i>Plagiothecium undulatum</i>	1	64	1	80	Tr	42
<i>Polytrichum juniperinum</i>	Tr	9	Tr	7		
<i>Rhytidiadelphus loreus</i>	Tr	9	Tr	20	Tr	42
Number of stands examined	11		15		12	
Ages of stands examined (yr)	35-73		31-50		30-50	

by Douglas-fir, hemlock is an important component. This community has more species present and is more diverse than either of the other two forest communities.

The Douglas-fir/salal community represents the most extensive community on the lower watershed and is found characteristically on moderate slopes and on soils of the Everett Series.

Forest communities in the old-growth Andrews Forest in Oregon are also arranged along moisture gradients. For example, sites characterized by understories of Holodiscus discolor (ocean spray) or salal are dry. Mesic sites are typified by Berberis nervosa (Oregon grape) and Acer circinatum and moist sites by sword fern at the Thompson Research site. The composition of three old-growth community types representative of this spectrum on the western slopes of Oregon's Cascade Range are presented in Table 3.7. Comparison of understories in Tables 3.6 and 3.7 reveals that the same types of understories are found in young-growth and old-growth stands in the zone.

Detailed mapping of the vegetation on several of the watersheds on the H. J. Andrews Forest has been completed (Dyrness and Hawk 1972, Hawk and Dyrness 1972, Hawk 1973). For example, Hawk (1973) using a 25-m grid system, mapped the vegetation into seven plant communities occurring on watershed 10 (Figure 3.2).

Checklists of lichens (Pike 1972) and fleshy fungi (Rhoades 1972) on the H. J. Andrews Forest have been compiled along with a list of microfungi and associated substrates (Sherwood 1973). Epiphytic mosses and lichens in particular are an important component of old-growth forests (Denison 1973, Pike et al. 1972) and their role in nutrient cycling is discussed in section 3.1.2.3.

A great variety of insects is found in young-growth forests especially associated with dead and dying Douglas-fir. Table 3.8 shows a checklist of predaceous and parasitic Hymenoptera occurring on dead Douglas-fir on the Cedar River watershed. Diptera are presented in Table 3.9. The relationships to their host and habitat are shown (M. A. Deyrup, pers. commun.).

Daterman et al. (1973) have produced an inventory of invertebrate terrestrial consumers in the H. J. Andrews Forest. Approximately 500 different species of insects were captured including the western spruce budworm. Krantz et al. (1973) also conducted a survey of the spiders, insects, and nematodes of watershed 10, but the details of these surveys are not presented here. A minimum of 50 families and 60 genera of mites are present, the majority are Cryptostigmata. Population estimates vary from 5000 to 350,000 per square meter. Nine categories of nematodes are present, most belonging to the saprozoic, dorylaimoid, aquatic, and monchoid groups. Population estimates vary from 400,000 to 2,000,000 per square meter.

Surveys of vertebrate consumer (mammal and bird) populations have been conducted at the Thompson site (Miller et al. 1972). Table 3.10 shows

Table 3.7. Abundance of selected species in three associations found in the *Tsuga heterophylla* zone of the western Oregon Cascade Range (from Franklin and Dyrness 1969).

Species	Association		
	<i>Pseudotsuga</i> <i>/Holodiscus</i>	<i>Tsuga</i> / <i>Berberis</i>	<i>Tsuga</i> / <i>Polystichum</i>
<u>Trees</u>			
<i>Pseudotsuga menziesii</i>	Abundant	Common	Occasional
<i>Tsuga heterophylla</i>	Rare	Common	Common
<i>Thuja plicata</i>	--	Occasional	Common
<i>Acer macrophyllum</i>	Occasional	--	Rare
<i>Libocedrus decurrens</i>	Occasional	--	--
<i>Pinus lambertiana</i>	Occasional	--	--
<i>Arbutus menziesii</i>	Rare	--	--
<i>Taxus brevifolia</i>	Common	Common	Occasional
<u>Shrubs</u>			
<i>Acer circinatum</i>	Common	Common	Occasional
<i>Holodiscus discolor</i>	Common	--	--
<i>Gaultheria shallon</i>	Abundant	Occasional	Rare
<i>Corylus cornuta californica</i>	Common	--	Rare
<i>Vaccinium parvifolium</i>	Common	Common	Common
<i>Rhododendron macrophyllum</i>	Rare	Common	Rare
<i>Symphoricarpos mollis</i>	Common	Rare	Rare
<i>Berberis nervosa</i>	Common	Common	Common
<i>Rubus ursinus</i>	Common	Common	Common
<u>Herbs</u>			
<i>Linnaea borealis</i>	Common	Common	Occasional
<i>Whipplea modesta</i>	Common	Rare	--
<i>Synthyris reniformis</i>	Common	Rare	--
<i>Polystichum munitum</i>	Rare	Occasional	Abundant
<i>Coptis laciniata</i>	Rare	Common	Occasional
<i>Viola sempervirens</i>	Occasional	Common	Occasional
<i>Vancouveria hexandra</i>	Rare	Rare	Common
<i>Tiarella trifoliata</i>	--	Rare	Common
<i>Disporum smithii</i>	--	--	Occasional
<i>Trillium ovatum</i>	Occasional	Occasional	Occasional
<i>Hieracium albiflorum</i>	Common	Rare	--
<i>Galium triflorum</i>	--	Occasional	Common
<i>Oxalis oregana</i>	--	Rare	Common
<i>Struthiopteris spicant</i>	--	--	Occasional
<i>Asarum caudatum</i>	--	--	Occasional
<i>Festuca occidentalis</i>	Common	--	--
<i>Iris tenax</i>	Common	--	--
<u>Mosses, Liverworts and Lichens</u>			
<i>Eurhynchium oreganum</i>	Occasional	Abundant	Common
<i>Homalothecium megaptilum</i>	Occasional	Occasional	Rare
<i>Hylcomium splendens</i>	Occasional	Rare	Occasional
<i>Rhytidiadelphus loreus</i>	Common	Occasional	Occasional
<i>Rhacomitrium canescens</i>	Occasional	--	--
<i>Mnium insigne</i>	--	--	Common
<i>Peltigera aphthosa</i>	Common	--	--
<i>Dicranum fuscescens</i>	Common	Common	Occasional
<i>Hypnum circinale</i>	Common	Common	Common
<i>Cladonia</i> spp.	Occasional	Rare	--
<i>Scapania</i> spp.	--	Rare	Occasional

Source: Unpublished data on file at Forestry Sciences Laboratory, Pacific Northwest Forest & Range Exp. Sta., Forest Serv., U. S. Dep. Agr., Corvallis, Oregon.

Table 3.8. Predaceous and parasitic Hymenoptera on dead Douglas-fir in the Cedar River watershed (after M. Deyrup, unpubl.).

Species	Abundance	Host in watershed	General habitat
<u>Leptothorax acervorum</u>	Abundant	General predator; invades scolytid galleries	Usually in clearing
<u>Lasius niger</u>	Abundant	General predator	Clearing and shade
<u>Camponotus herculeanus</u>	Moderately abundant	General predator	Clearing and shade
<u>Formica truncicola</u>	Abundant	General predator	Clearing and shade
<u>Pristaulacus minor</u>	Abundant	<u>Melanophila drummondi</u>	Unshaded areas
<u>Codrus similis</u>	Rare	Staphylinids	Shaded areas
<u>C. placidus</u>	Moderately abundant	Staphylinids	Shaded areas
<u>C. serricornis</u>	Rare	Staphylinids	Shaded areas
<u>Roptrocerus xylophagorum</u>	Abundant	<u>Pseudohylesinus nebulosus</u>	Shaded areas
<u>Orussus occidentalis</u>	Rare		Unshaded areas
<u>Eurytoma tonici</u>	Moderately abundant	<u>Pseudohylesinus nebulosus</u>	Shaded areas
<u>Heydenia unica</u>	Moderately abundant	<u>Pseudohylesinus nebulosus</u>	Clearing and shade
<u>Cheiropachus brunneri</u>	Moderately abundant	<u>Pseudohylesinus nebulosus</u>	Clearing and shade
<u>Cecidostiba thomsoni</u>	Abundant	<u>Pseudohylesinus nebulosus</u>	Clearing and shade
<u>C. acuta</u>	Abundant	<u>Pseudohylesinus nebulosus</u>	Clearing and shade
<u>C. dendroctoni</u>	Rare	<u>Dendroctonus pseudotsugae</u>	Clearing and shade
<u>Aplomerus robustus</u>	Rare	Buprestids	Clearing
<u>Odontocolon dichrous</u>	Rare	Cerambycids	Shaded areas
<u>Xorides cincticornis</u>	Rare		Shaded areas
<u>Coleocentrus manni</u>	Moderately abundant		Standing trees in shade
<u>Apistephialtes dentatus</u>	Rare	<u>Enoclerus spegeus</u> , <u>Thanasimus undatulus</u>	Clearing
<u>Dolichomitus pygmaeus</u>	Rare		Shaded areas
<u>D. foxleei</u>	Rare	<u>Melanophila drummondi</u>	Unshaded areas
<u>D. terebrans</u>	Abundant	<u>Pissodes fasciatus</u>	Shaded areas
<u>Rhyssa lineolata</u>	Moderately abundant	<u>Urocerus albicornis</u>	Shaded areas
<u>R. alaskensis</u>	Moderately abundant		Clearing
<u>Megarhyssa nortoni</u>	Rare	<u>Urocerus albicornis</u>	Clearing
<u>Helconidea necydalis</u>	Abundant	Cerambycids	Shaded and open areas
<u>Spathius sequoiae</u>	Abundant	<u>Pseudohylesinus nebulosus</u>	Shaded areas and clearing
<u>Ecphylyus sp.</u>	Rare	<u>Cryphalus pubescens</u>	
<u>Eubadizon strigitergum</u>	Abundant	<u>Pissodes fasciatus</u>	Shaded areas
<u>Atanycolus anocomidis</u>	Moderately abundant	<u>Melanophila drummondi</u>	Unshaded areas
<u>A. longifemoralis</u>	Abundant	<u>Melanophila drummondi</u>	Unshaded areas
<u>Coeloides brunneri</u>	Abundant	<u>Dendroctonus pseudotsugae</u>	Shaded areas and clearing
<u>Neocatolaccus n.sp.</u>	Rare	<u>Melanophila drummondi</u>	Unshaded areas

Total number of species of Hymenoptera (including siricids) found on dead and dying Douglas-fir in Cedar River watershed, 38; number of species of Hymenoptera associated with dead and dying Douglas-fir not found in Cedar River watershed, 36; number of genera from Cedar River watershed, 27; number of genera not found in Cedar River watershed, 12.

Table 3.9. Diptera associated with dead and dying Douglas-fir in the Cedar River watershed (after M. Deyrup, unpubl.).

Species	Abundance	Role
<u>Medetera aldrichii</u>	Abundant	Predator of scolytid larvae
<u>M. caerulescens</u>	Rare	Predator of scolytid larvae
<u>Medetera</u> sp.	Abundant	Predator of scolytid larvae
<u>Xylophagus fasciatus</u>	Abundant	Subcortical; general predator
<u>X. gracilis</u>	Abundant	Subcortical; general predator
<u>Odinia betulae</u>	Abundant	Associated with <u>Trypodendron lineatum</u>
<u>Chymomyza</u> sp.	Abundant	Associated with ambrosia beetles
<u>Lonchaea corticis</u>	Common	Associated with <u>Dendroctonus pseudotsugae</u>
Sciaridae	Common	Scavenger in scolytid galleries
<u>Forcipomyia</u> sp.	Common	Subcortical in fermenting sap
<u>Pseudogaurax dubius</u>	Rare	Associated with <u>Scolytus unispinosus</u>

Table 3.10. Birds, mammals, reptiles, and amphibians occurring on the Cedar River watershed.

Scientific name	Common name	Scientific name	Common name
BIRDS		MAMMALS	
<u>Bombycilla cedrorum</u>	Cedar waxwing	<u>Castor canadensis</u>	Beaver
<u>Bonasa umbellus</u>	Ruffed grouse	<u>Canis latrans</u>	Coyote
<u>Bubo virginianus</u>	Great horned owl	<u>Cervus canadensis</u>	Elk (wapiti)
<u>Colaptes cafer</u>	Red-shafted flicker	Chiroptera	Bats
<u>Columba fasciata</u>	Band-tailed pigeon	<u>Eutamias townsendi</u>	Townsend's chipmunk
<u>Corvus brachyrhynchos</u>	Common crow	<u>Lepus americanus</u>	Snowshoe hare
<u>Corvus corax</u>	Common raven	<u>Lutra canadensis</u>	River otter
<u>Dendragapus obscurus</u>	Blue grouse	<u>Lynx rufus</u>	Bobcat
<u>Dendrocopos villosus</u>	Hairy woodpecker	<u>Microtus oregoni</u>	Oregon vole
<u>Dendroica nigrescens</u>	Black-throated gray warbler	<u>Mustela erminea</u>	Shorttail weasel
<u>Empidonax spp.</u>	Empidonax flycatchers	<u>Mustela frenata</u>	Longtail weasel
<u>Hyalocichla ustulata</u>	Swainson's thrush	<u>Neotoma cinerea</u>	Bushytail woodrat
<u>Ixereus naevius</u>	Varied thrush	<u>Neurotrichus gibbsi</u>	Shrew-mole
<u>Junco oreganus</u>	Oregon junco	<u>Odocoileus hemionus</u>	Black-tailed deer
<u>Loxia curvirostra</u>	Red crossbill	<u>Ondatra zibethica</u>	Muskrat
<u>Molothrus ater</u>	Brown headed cowbird	<u>Peromyscus maniculatus</u>	Deer mouse
<u>Oporornis tolmiei</u>	MacGillivray's warbler	<u>Procyon lotor</u>	Raccoon
<u>Parus rufescens</u>	Chestnut-backed chickadee	<u>Sorex trowbridgei</u>	Trowbridge shrew
<u>Passerella iliaca</u>	Fox sparrow	<u>Sorex vagrans</u>	Vagrant shrew
<u>Perisoreus canadensis</u>	Gray jay	<u>Sorex obscurus</u>	Dusky shrew
<u>Pipilo erythrophthalmus</u>	Rufous-sided towhee	<u>Tamiasciurus douglasi</u>	Chickaree
<u>Piranga ludoviciana</u>	Western tanager	<u>Ursus americanus</u>	Black bear
<u>Regulus calendula</u>	Ruby-crowned kinglet	<u>Vulpes fulva</u>	Red fox
<u>Regulus satrapa</u>	Golden-crowned kinglet	<u>Zapus trinotatus</u>	Jumping mouse
<u>Selasphorus rufus</u>	Rufous hummingbird		
<u>Sitta canadensis</u>	Red-breasted nuthatch	REPTILES	
<u>Sphyrapicus varius</u>	Yellow-bellied sapsucker	<u>Charina bottae</u> ^a	Rubber boa
<u>Spinus pinus</u>	Pine siskin	<u>Gerrhonotus coeruleus</u> ^a	Northern alligator lizard
<u>Troglodytes troglodytes</u>	Winter wren	<u>Thamnophis orinoides</u>	Northwestern garter snake
<u>Turdus migratorius</u>	Robin	<u>Thamnophis sirtalis</u>	Common garter snake
<u>Vermivora celata</u>	Orange-crowned warbler		
<u>Vireo gilvus</u>	Warbling vireo	AMPHIBIANS	
		<u>Ambystoma macrodactylum</u>	Long-toed salamander
		<u>Bufo boreas</u>	Western toad
		<u>Hyla regilla</u>	Pacific tree frog
		<u>Rana aurora</u>	Red-legged frog
		<u>Taricha torosa</u>	Western newt
		<u>Plethodon spp.</u> ^a	Red-backed newt
		<u>Rana catesbiana</u> ^a	Bull-frog

^aAnticipated presence, not actually observed.

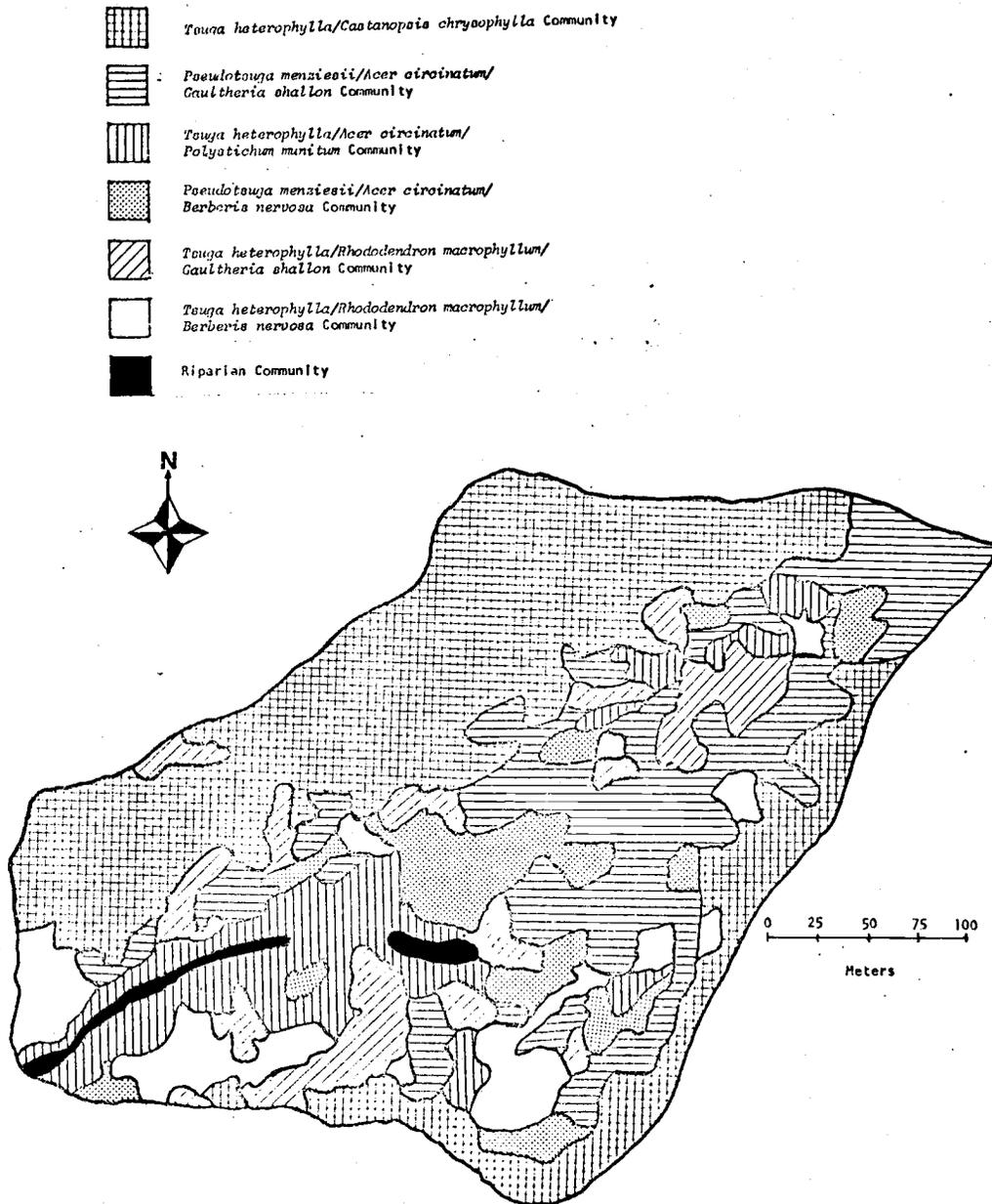


Figure 3.2. Plant community distribution on watershed 10, H. J. Andrews Experimental Forest (from Hawk 1973)

species lists including large mammals. Information on vertebrate consumers on the H. J. Andrews Forest has been collected but is not yet available (R. Nussbaum, pers. comm.).

The Abies amabilis (Pacific silver fir) zone. The Abies amabilis zone lies between the temperate mesophytic Tsuga heterophylla zone and the subalpine Tsuga mertensiana zone. It occurs on the western slopes of the Cascade Range from British Columbia south to about 44°N at elevations from 1000 to 1500 m in Oregon and 600 to 1300 m in northern Washington. Where local conditions are favorable, it occurs on the east side of the Cascades.

Environmental features. The Abies amabilis zone is wetter and cooler than the adjacent Tsuga heterophylla zone and receives considerably more precipitation in the form of snow (Table 3.11), much of which accumulates in winter snowpacks of as much as 1-3 meters. The complex of soil-forming processes leads toward podzolization. This trend is less pronounced in the south of the zone and more pronounced in the north, where true podzols are typical. Organic matter accumulations are of the mor or duff-mull type, which average only 5-10 cm thick except in northern Washington, where accumulations up to 30 cm may be encountered.

Both the Cedar River watershed and H. J. Andrews Forest include areas in the Abies amabilis zone. Table 3.12 shows a typical soil profile in the Findley Lake basin representing soils of mixed materials, one of the three soil groups found in these areas (Bockheim and Ugolini 1972). Other groups are soils of talus and residual soils of ridges. The soil profile is interrupted by several layers of volcanic ash and mineral horizons. The soil parent material consists of lava and breccia flows, interstratified boulder conglomerates, and subordinate volcanic sandstone (Hammond 1963). Mechanisms of ionic leaching in the soil tend to be different from those at the Thompson research site, and this is discussed in detail in section 3.1.2.3. The accumulation of litter on the forest floor at Findley Lake (Table 3.12) should be contrasted with the smaller accumulation on the Thompson research site (Figure 3.3).

Reference stand 12 on the H. J. Andrews Forest is located in the Abies amabilis zone at 980-1000 m. Table 3.13 shows a typical soil profile in this stand. The litter layer here is also thicker than the litter layer in reference stand 1, which is in the Tsuga heterophylla zone (Table 3.5).

Biological components of the zone. Forest composition in the Abies amabilis zone varies widely, depending upon stand age, history, and locale. Typical tree species are Abies amabilis, Tsuga heterophylla, Abies procera, Pseudotsuga menziesii, Thuja plicata, and Pinus monticola. Understories are dominated by ericaceous genera such as Vaccinium and Rhododendron. Communities vary markedly in composition from very dry to very moist sites and there is considerable geographic variation within the zone.

Vegetation of the Findley Lake basin in the Cedar River watershed is shown Figure 3.3 (Del Moral 1973). The distribution of dominant vascular plants along moisture gradients is presented in Table 3.14. The dominance

Table 3.11. Climatic data from representative weather stations within the Abies amabilis zone (from Franklin and Dyrness 1969).

Station	Elev. (m)	Lat	Long	Temperature (°C)					Precipitation		
				Av ann	Av Jan	Av Jan min	Av Jul	Av Jul max	Av ann (mm)	Jun- Aug (mm)	Av ann snow- fall (cm)
Snoqualmie Pass, Wash.	991	47°25'	121°25'	5.5	-3.2	-6.6	14.4	21.1	2656	227	982
Spirit Lake, Wash.	1063	46°16'	122°09'	5.6	-2.0	-4.4	14.9	22.3	2253	140	718
Government Camp, Oreg.	1280	45°18'	121°45'	5.6	-1.7	-4.9	14.0	20.8	2190	190	792

Source: U.S. Weather Bureau

Table 3.12. Description of soil profile in an Abies amabilis/Tsuga heterophylla/Gaultheria shallon community near Findley Lake (after Bockheim & Ugolini 1972).

Horizon	Depth (cm)	Description
O1	6-5	Fresh needles and other litter
O2	5-0	Partially decomposed litter
A2	0-9	Light-gray loamy sand, structureless, very friable, clear irregular boundary, few fine roots, volcanic ash
A2--B	9-20	Yellowish red loamy sand, structureless, very friable, abrupt broken boundary, few fine roots, volcanic ash 0-10 cm
IIB21hir-- IIB21ir	20-60	Yellowish red gravelly loam, massive, friable, few fine roots. --IIB21lr, dark reddish brown gravelly loam to gravelly silt loam --IIB2hir, contains weakly cemented lenses of ortstein, few fine roots, 50% of volume, clear wavy boundary, volcanic ash(?)
IIB22hir-- IIB22ir	60-92	Yellowish red very cobbly loam, massive, friable--IIB22ir, dark reddish brown very cobbly loam, massive firm, 20% of volume--IIB22hir contains weakly cemented "lenses" of ortstein, 50% of volume, diffuse smooth boundary, volcanic ash(?)
IIB23 or IIB3	92-127	Strong brown very cobbly loam, massive, friable, few fine roots 60-70% cobbles by volume, volcanic ash(?)

Table 3.13. Description of soil for reference stand 12, pit 2, H. J. Andrews Forest (from Brown and Parsons 1973b).

<u>Horizon</u>	<u>Depth (cm)</u>	<u>Description</u>
011	14-15	Needles, cones, twigs, etc.
012	13-10	Partially decomposed needles, etc.
013	10-0	Partially decomposed wood & bark.
A1	0-29	Gravelly sandy loam, granular, very friable, clear wavy boundary, 45% pebbles; abundant pumice grains, pH 5.4
B2	29-58	Very gravelly sandy loam, blocky, very friable, grain wavy boundary, 55% pebbles, abundant pumice grains, pH 6.0.
B3	58-81	Very gravelly loam, blocky friable, clear wavy boundary, 50% pebbles etc., abundant pumice grains, few charcoal chips, pH 6.4
IIC1	81-107	Very gravelly loam, friable, grain wavy boundary, 60% pebbles etc., abundant pumice grains, pH 6.4

Table 3.14. Distribution of dominant vascular plants in the Findley Lake basin. Community types are arranged in order of the inferred moisture gradient: I, wet meadow; II, shrub type; III, *Abies* forest; IV, mixed forest; V, *Tsuga* forest; VI, mesic meadow; VII, dry meadow. The body of the table is composed of prominence values. P = present, but not in sample quadrats (from Del Moral 1973).

Species	Community type						
	I	II	III	IV	V	VI	VII
<i>Elymus hirsuta</i>	25.0
<i>Caltha biflora</i>	17.5
<i>Carex</i> #1	7.0
<i>Trisetum</i> sp.	6.0
<i>Sanguisorba sitchensis</i>	4.5
<i>Dodecatheon jeffreyi</i>	4.0
<i>Carex</i> #2	2.8
<i>Habenaria saccata</i>	2.5
<i>Equisetum hyemale</i>	2.0
<i>Ludwigia palustris</i>	1.0	2.1	..
<i>Osmorhiza chilensis</i>	0.5	5.0
<i>Senecio triangularis</i>	6.0	0.3	0.1
<i>Viola adunca</i>	1.5	2.0	..	0.1
<i>Aconitum columbianum</i>	11.0	..	0.7	0.6
<i>Valeriana sitchensis</i>	1.5	1.0	0.8	0.2
<i>Saxifraga punctata</i>	1.0	1.0	4.1	0.2
<i>Tiarella unifoliata</i>	P	7.5	2.9	0.4	0.2	0.6	..
<i>Smilacina stellata</i>	1.5	3.5	1.6	1.7	P	1.5	..
<i>Veratrum viride</i>	0.5	2.5	2.0	0.5	..	0.5	..
<i>Acer circinatum</i>	29.0
<i>Alnus sinuata</i>	71.0
<i>Ribes lacustre</i>	4.5
<i>Ribes bracteosum</i>	25.0	3.0
<i>Rubus spectabilis</i>	19.0	1.4	0.5
<i>Menziesia ferruginea</i>	8.5	3.5	3.5	11.5
<i>Blechnum spicant</i>	3.5	3.0	0.1	1.5
<i>Trillium ovatum</i>	6.6	1.0	0.1	P	1.0	..
<i>Vaccinium membranaceum</i>	1.0	6.3	24.5	13.5	12.0	..
<i>Achlys triphylla</i>	1.0	5.5	0.1	11.0	1.0	..
<i>Sambucus callicarpa</i>	3.0	7.1	3.5	..
<i>Tsuga heterophylla</i>	3.5	0.1
<i>Rubus pedatus</i>	6.5	0.8
<i>Abies amabilis</i>	83.2	68.9	33.0
<i>Tsuga mertensiana</i>	14.3	29.9	67.0
<i>Clintonia uniflora</i>	12.5	5.7	2.2
<i>Vaccinium deliciosum</i>	14.8	10.0	P	2.5	..
<i>Vaccinium scoparium</i>	P	7.5	6.0	P	..
<i>Cryptogramma crista</i>	1.1	0.5	..	5.5	..
<i>Xerophyllum tenax</i>	9.5	29.5	40.1	16.0	23.0
<i>Rubus lasiococcus</i>	4.4	7.1	9.0	10.0	1.4
<i>Pyrola secunda</i>	2.1	1.0	2.0
<i>Chamaecyparis nootkatensis</i>	1.1
<i>Rhododendron albiflorum</i>	69.7	16.0
<i>Sorbus sitchensis</i>	30.3	84.0	100.0	..
<i>Rubus parviflorus</i>	0.2	2.5	0.3	..
<i>Lupinus polyphyllus</i>	1.8	P	4.5	1.0
<i>Phyllodoce empetriformis</i>	P	22.5	2.2
<i>Luetkea pectinata</i>	P	P	4.0
<i>Phlox diffusa</i>	P	P	2.0
<i>Spirea densiflora</i>	9.5	..
<i>Pachystima myrsinites</i>	4.0	..
<i>Juniperus communis</i>	P	3.1
<i>Amelanchier alnifolia</i>	33.0
<i>Arctostaphylos uva-ursi</i>	4.1
<i>Lomatium</i> sp.	23.0

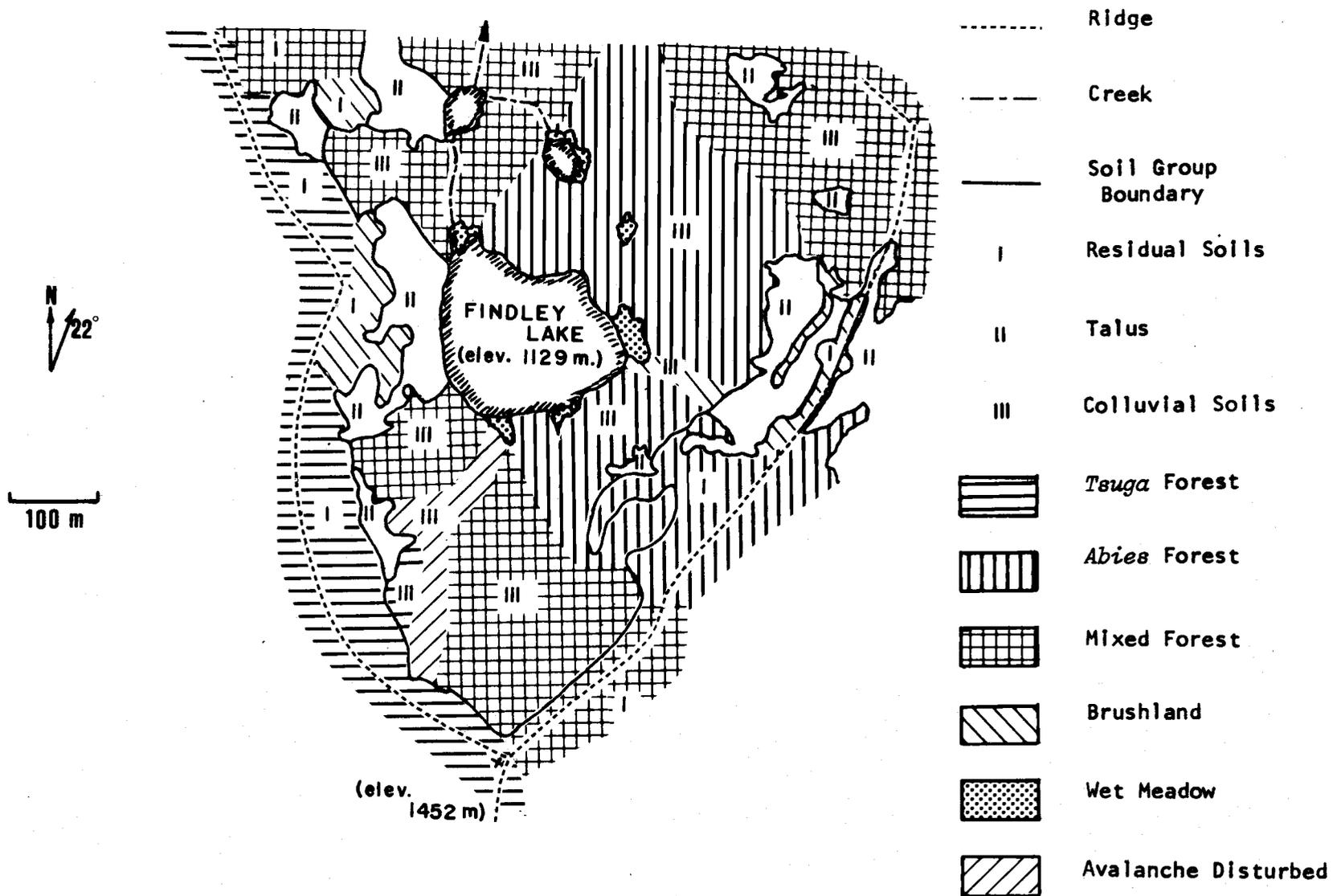


Figure 3.3. Vegetation and soils of the Findley Lake Basin.

of Abies amabilis increases from the dry ridgetops to the mesic slopes of the basin.

The Abies amabilis zone occurs at higher elevations in the H. J. Andrews Forest. A more detailed discussion of the forest communities in this area is presented in section 3.1.1.2.

Information on the animals, insects, birds, and microfauna in this zone is available, but as yet it has not been fully analyzed and is not presented here.

Tsuga mertensiana (mountain hemlock) zone. This zone is the highest forested zone in the Douglas-fir region. Very little attention in the Biome program has been given to it, so a brief description will suffice. Elevational limits of the zone are between 1300 and 1700 m in the Washington Cascades and between 1700 and 2000 m in the southern Oregon Cascades. It is the wettest and coolest of the forested zones, with precipitation ranging from 1600 to 2800 mm. Snowfall ranges from 400 to 1400 cm. Soils within the zone are podzolic.

Forest composition varies with locale and relatively few species are found as dominants. Tsuga mertensiana dominates old-growth forests and Abies lasiocarpa or Pinus ponderosa dominates seral or drier stands. Understory species are mainly Ericaceae, Rosaceae, and Compositae. No description of the biological components of this zone is given here.

3.1.1.2. Distribution of forest communities along environmental gradients. One of the objectives of the Biome program is to understand the processes that affect forest composition. Such an understanding can be obtained through modeling studies; but to model processes effectively, a meaningful method of classifying forest communities in relation to environmental conditions must be used.

To serve the needs of an integrated research program, a classification scheme that uses something other than species composition must be used. A more useful classification would relate forest communities to environmental gradients (Zobel et al. in press). They have classified the 23 communities on the H. J. Andrews Forest along temperature and moisture gradients (Figure 3.4). As pointed out by Waring et al. (1972), however, most previously defined environmental gradient schemes cannot be directly applied outside the region in which they were developed.

Fortunately, a foundation for a process-oriented approach was laid by Mason and Langenheim (1957), who introduced the idea of an "operational environment" that recognizes specific plant response to environmental stimuli; i.e., it is more important to assess the availability of water to plant roots than the origin of that water. This distinction greatly reduces the number of factors that must be considered; e.g., altitude, slope, and the like may be ignored if the mode of action can be identified and measured.

The plant responses we wish to measure must be related to the entire plant but they must be closely identified with specific environmental

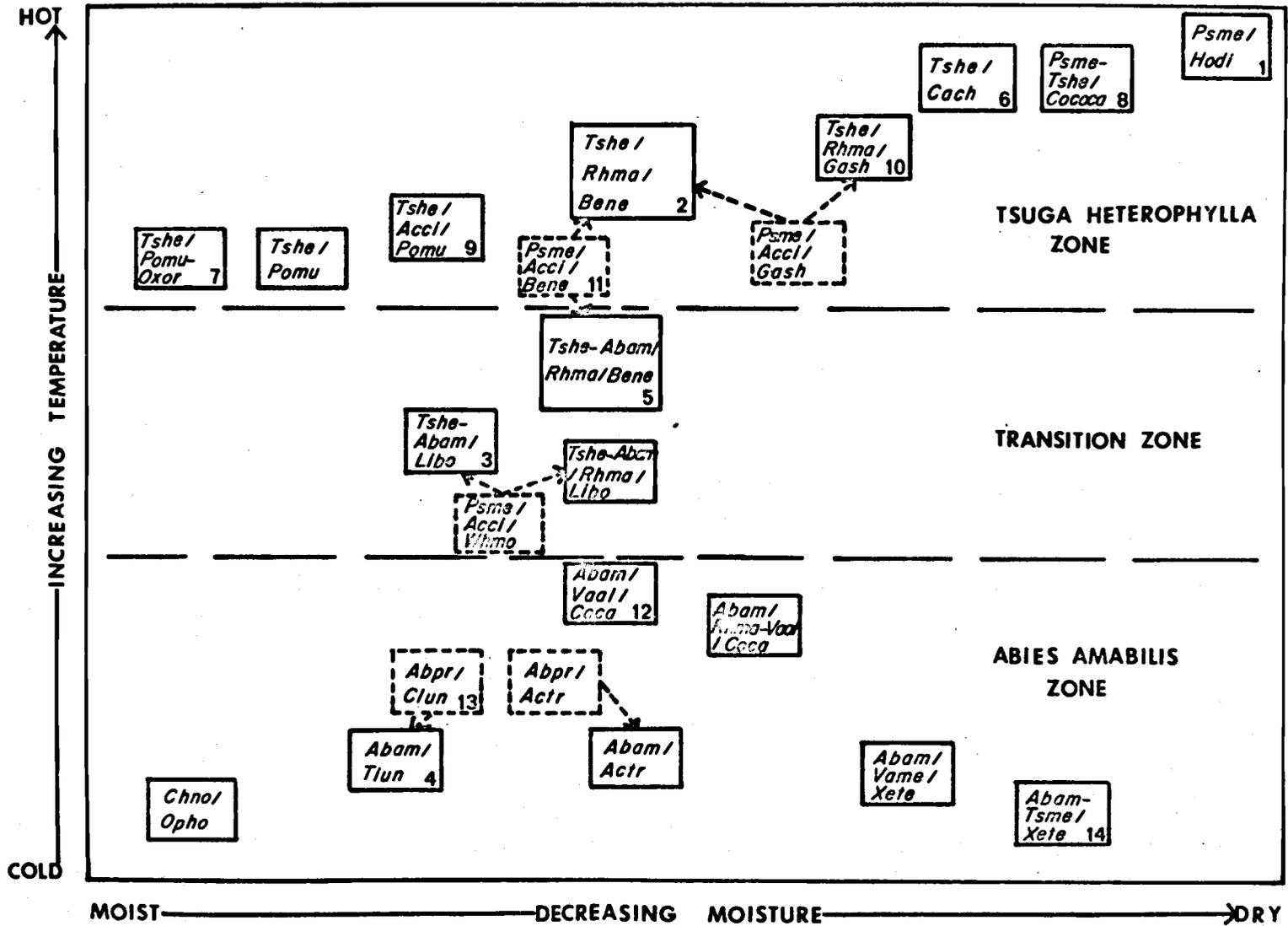


Figure 3.4. Plant community distribution on the H. J. Andrews Experimental Forest along temperature and moisture gradients (from Zobel et al 1974).

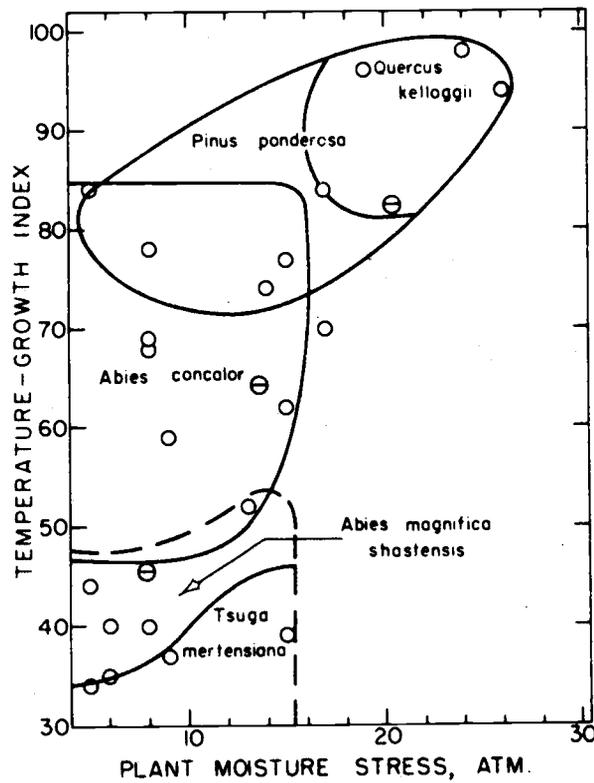
stimuli. Waring et al. (1972) have suggested that phenology, carbon dioxide exchange, plant moisture stress, stomatal resistance, and foliar nutrition are suitable plant responses to measure. Phenological development reflects past environment; carbon dioxide exchange provides a ready means of quantifying the effects of light and temperature upon photosynthesis; plant moisture stress before dawn is an excellent measure of how plants respond to soil water status; stomatal resistance reflects the influence of evaporative stress and soil drought; and foliar nutrition indicates the interaction between supply of nutrients in the soil and nutrient demand.

During the past 10 years, studies have been carried out in southwestern Oregon in many forest stands. In many of these stands, environmental data on air and soil temperature, radiation, humidity, soil moisture, and soil fertility were recorded. Site environment was defined and quantified by measuring and/or simulating growth, transpiration, photosynthesis, or moisture stress (Cleary and Waring 1969, Emmingham 1971, Reed 1971, Waring and Cleary 1967, and Waring and Major 1964). The indexes produced by these measurements or simulations locate ecosystems within an environmental grid and permit certain ecosystem characteristics such as productivity and plant species composition to be predicted (Waring et al. 1972). These ordinates also are used in the stand succession model being developed by K. L. Reed, E. R. Hamerly, and W. H. Emmingham, which is discussed in section 3.1.2.5.

To visualize this information more effectively, the distribution of selected conifers in the Siskiyou Mountains in southern Oregon is presented in relation to two rather simple plant response indexes, temperature-growth index, and plant moisture stress (Figure 3.5; Waring et al. 1972). The distributional patterns closely reflect the adaptation of the various conifers. The plant response indexes were predicted correctly from knowledge of plant distributions for three validation stands as indicated by the circles in Figure 3.5. It is significant that such predictions are possible without physiological observations on species other than reference plants. Once such relationships are established, understanding of the operational environment can be achieved without additional measurements of any kind.

The ordinates discussed above were tested on communities at the H. J. Andrews Experimental Forest (Zobel et al. 1973a, Zobel et al. in press). The maximum predawn moisture stress and the calculated temperature-growth index effectively separate the previously classified communities in the study area (Figure 3.6). The range of environmental indexes measured in this area is very similar to that in the eastern Siskiyou Mountain forests. Other indexes currently being tested include year day of selected phenophases, a photosynthesis simulation (results of which are presented in section 3.1.2.2, which describes carbon cycling), nutritional quality, and decomposition.

It is thought that differences in nutrient concentration between new and old foliage might be interpreted as an indication of site nutritional quality. Samples taken before budbreak on 1972 Douglas-fir foliage had



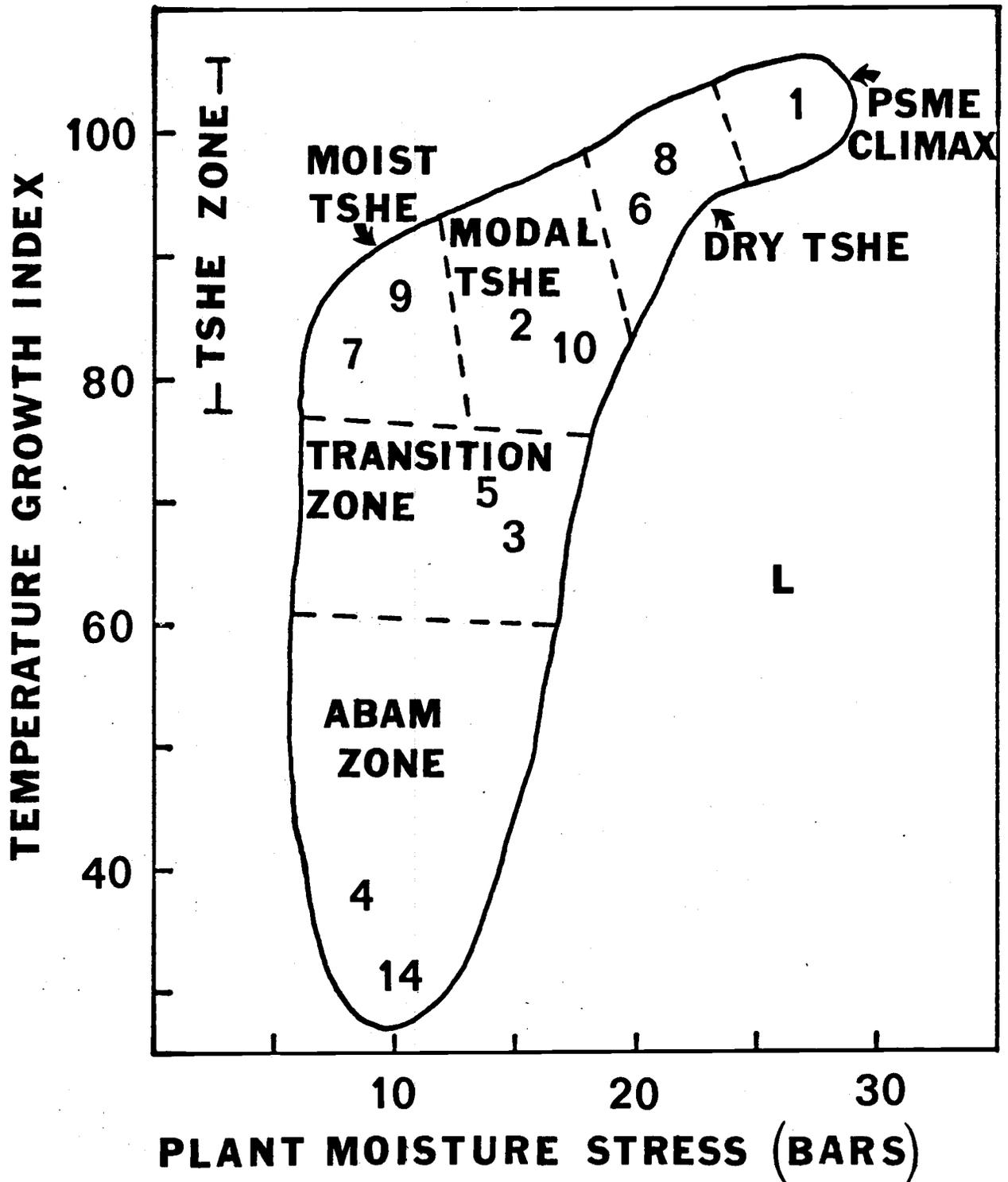


Figure 3.6. Distribution of vegetation zones in the H. J. Andrews Experimental Forest in relation to moisture and temperature defined by plant response indices. ABAM = *Abies amabilis*, PSME = *Pseudotsuga menziesii* and TSHE = *Tsuga heterophylla* (from Zobel et al 1974).

nitrogen levels less than one percent. This rose to 1.1% to 1.2% by the end of the growing season. In 1974 we will continue to seek a method for quantifying the nutrient status of forest sites. Litter trap and litterbag studies, undertaken in 1973, will be used to produce comparable data on turnover time and yearly and seasonal decomposition rates. Chemical analyses are planned to help establish litter decomposition in selected ecosystems.

Until 1973 environmental grid studies were confined to forested communities in the state of Oregon. Sites have now been set up at several of the coordinating sites in the Biome and these are discussed further in section 3.1.3.

3.1.2. Dynamics of coniferous ecosystems in the Douglas-fir region

The functioning of relatively undisturbed coniferous forest ecosystems in the Douglas-fir region was studied to gain a better understanding of how these systems operate in both space and time, and to investigate specific questions of interest to Biome researchers. Examples are shown in Table 3.15. We have just begun to study stressed or manipulated systems and we propose to continue this work in 1975-1977. Our findings to date concerning stressed or manipulated systems are presented in part 5.

Our major focus has been on water, carbon, and nutrient cycling, and, most recently, succession. The processes involved and the differences and similarities between ecosystems revealed by our studies to date are discussed here. Many of our results are integrated into models, and these are also discussed in section 3.1.2. Section 3.1.2.4 is devoted entirely to discussion of stand and watershed modeling of water, carbon, and nutrient cycling.

Most data have been acquired from individual tree process studies (photosynthesis, evapotranspiration) and stand level studies (leaching, throughfall, litterfall, biomass) in the young-growth Douglas-fir and alder stands near the A. E. Thompson site on the lower Cedar River watershed, from studies in the 175-year-old Pacific silver fir stands near Findley Lake in the upper Cedar River watershed, and from stand and watershed studies in the old-growth (450 years) Douglas-fir stands in the H. J. Andrews Experimental Forest. Some additional information is available from ecosystems outside the Douglas-fir region, but it is not yet fully analyzed. Greenhouse and laboratory studies have been conducted to determine the effects of various environmental regimes on photosynthesis, nutrient ion leaching, and plant uptake.

The individual tree process and stand level studies at the Thompson site are aimed at determining the relationships between processes, stand level material cycling, and environmental factors. Waterflow and nutrient ion transport have been studied at this site for some time by intercepting and sampling solutions at a number of levels within the stand (Cole and Gessel 1965). Individual studies on evapotranspiration and photosynthesis have been greatly aided by the installation of a 28-m-high Douglas-fir tree in a weighing lysimeter (Fritschen et al. 1973), which consists of

Table 3.15. Examples of specific questions to be investigated by Coniferous Forest Biome scientists and modelers concerning the dynamics of coniferous forest ecosystems.

-
-
1. What are the most important processes to be included in stand level water cycling models?
 2. How do these processes vary as functions of environmental conditions?
 3. Can results from stand level water, carbon, and nutrient cycling models be applied to regions in the Biome other than the one for which each was developed?
 4. Can unstratified watershed models for water cycling be applied in all coniferous forest watersheds across the Biome?
 5. How do the carbon and nutrient budgets and yearly fluxes vary throughout the Biome as functions of cover type, age, and site quality?
 6. How do the important processes involved in carbon and nutrient cycling, photosynthesis, transpiration, uptake, weathering, respiration, and decomposition vary as functions of environmental conditions across the Biome?
 7. What is the variation in rates of photosynthesis in different parts of the crown of the same tree?
 8. What mechanisms control internal redistribution of water in coniferous species?
 9. Is the mechanism of ionic leaching similar through soils in all coniferous forest ecosystems across the Biome?
 10. What is the relationship between net assimilation, transpiration and water stress, and environmental variables throughout the year?
 11. What is the relationship between nutrient internal retranslocation and uptake in various species in relation to their requirements?
 12. Are some species more efficient with respect to nutrient use?
-
-

a 3.7-m-diameter by 1.2-m-deep soil container constructed around the root ball of the tree. The weighing lysimeter has been used to test meteorological techniques for comparing predicted evaporation against observed values.

Studies of ecosystem dynamics at Findley Lake have focused on nutrient cycling, including weathering, and ecosystem interaction between terrestrial and aquatic systems. Interaction studies are discussed in section 3.3.

Studies of small watersheds are a major part of the research program in the H. J. Andrews Forest. Bormann and Likens (1967) have summarized adequately the contributions of these studies to our understanding of ecosystem cycles. Watersheds are easily definable landscape units and can be used to calculate hydrological and nutrient budgets, which include weathering and erosional losses. Internal cycling processes and perturbations can be examined through paired watershed techniques. The weaknesses of this approach are due to the assumptions that most of the outflows pass through the weirs, that leakages if they occur are the same for paired watersheds, and that the material cycles within the paired watersheds are the same.

The watershed studies on coniferous ecosystem dynamics at the Andrews Forest have examined (1) storage and accumulation rates of carbon and nutrients in the vegetation and forest floor; (2) transfer of nutrients in solution from forest floor to soil; (3) nutrient content of soil solutions and available soil nutrients; (4) the path of waterflow on slopes; (5) the velocity of waterflow through soil and mean turnover time of the soil solution; (6) sources of nutrients to streams for watershed components including the canopy, soil mantle, and stream system; (7) storage of soil in debris jams in creek channels, their age, and stability; and sources of cations and silica from mineral weathering and weathering reactions.

By integrating the results of the diverse studies, we have gained a better understanding of the dynamics of undisturbed coniferous ecosystems in the Douglas-fir region. This has been one of the basic aims of the Biome program, and it has been achieved to a great degree through the use of simulation models. Individual process models have been developed for waterflow in trees and soil, uptake, transpiration, photosynthesis, and growth (Reed et al. 1973, Hatheway et al. 1972a, b, Waring et al. 1973b, Reed and Waring 1974). Many of these process models have been incorporated into a homogeneous stand level model being developed by Sollins and Swartzman for carbon, water, and nutrient cycling, which is described in section 3.1.2.4. Watershed level models have been developed for waterflow (Brown et al. 1972, Overton and White 1974, Shih et al. 1973). These models are currently being modified by S. G. Rogers (pers. commun.) to take into account spatial heterogeneity. Future plans are to develop watershed level models for carbon and nutrient cycling. The internal structure of these models will be based on the current stand level cycling models. A stand successional model that predicts long-term stand compositional and growth changes (J. L. Reed, pers. commun.) and a regional successional model have been developed. These models are discussed in section 3.1.2.5.

3.1.2.1. Water cycling processes. Water cycling studies have been conducted with the major objective of generalizing the hydrologic behavior of stands and watersheds. Stand level process models have been developed from studies of water movement in the soil-plant-atmosphere system, i.e., representing movement of water in the sequence including precipitation, movement through the canopy, stemflow, flow through unsaturated soil, uptake by the roots, conduction of water through the vascular system to the leaves, and transpiration and evaporation from the leaves to the atmosphere.

The downward flow of water through soil profiles has been measured at the Thompson site for many years by the tension lysimeter system (Cole and Gessel 1965). P. Machno (pers. commun.) added an extra dimension to these studies by investigating the effects of simulated rainfall on wetting fronts in the rooting zone. The simulated rainfall was provided both above and below the canopy with a sprinkler system. Hatheway et al. (1972a) applied Richards' (1931) soil flow model to the Thompson site soil with some success (Figure 3.7). Observed and predicted values are in agreement although discrepancies occur.

The Richards model is shown below:

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left(D \frac{\partial \theta}{\partial z} \right) + \frac{\partial K}{\partial z}$$

$$D = K \frac{\partial \psi}{\partial \theta}$$

where K is the hydraulic conductivity (cm/min), ψ is the soil water pressure or suction (hydraulic head, cm), θ is the soil water content (volume of water per unit volume of soil), and z is the height above datum (reference level) of the point under consideration (cm). Since the gravelly sandy loam is extremely variable, it is felt the initial results on flow should not be extrapolated beyond that local area. The variation in soil properties has resulted in a 25% discrepancy between predicted and observed peak flows.

Tree water status studies have been conducted including measurements of heat pulse velocities, stomatal behavior, xylem water potentials, dimensional fluctuations, and lysimeter tree weight changes. In connection with these studies, standard meteorological data were collected above the canopy, including solar radiation, net radiation, dew point, windspeed and direction, air and soil temperatures, and precipitation.

Models currently being developed include one that describes the flow of water in the stem of a tree, one that links flow in the soil to flow in the tree, and one that simulates flow in a stratified soil. Governing equations are commonly partial differential equations of the parabolic type. Careful attention is given to boundary conditions and to physical interpretation of exchange coefficients. The stemflow model predicts change in circumference and sap flow velocity. Outputs agree with field measurements of Lassoie (1973), but we are not yet satisfied that the boundary conditions used are entirely correct.

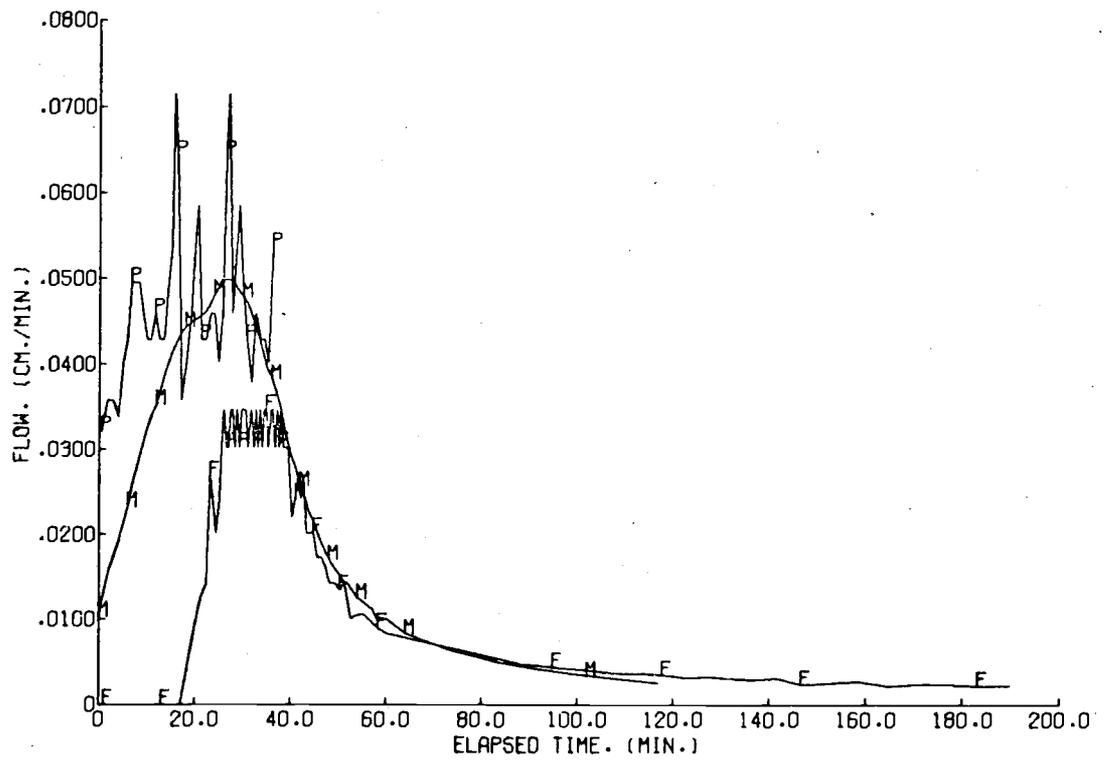


Figure 3.7. Precipitation (P), observed soil water flow (F) and modeled soil water flow (M) at 11 cm. Lysimeter suction was 50 cm of water (from Hatheway et al 1972a).

Investigations of temporal and spatial variations in Douglas-fir stem circumferences (SC) and water status have been conducted at the Thompson site in conjunction with the net assimilation (NA) studies of D. J. Salo and J. W. Leverenz, whose data are discussed in section 3.1.2.2. Automated band dendrometers were attached to various trees at different heights along their stems and continuously monitored from March 1973. Tree water status was characterized by measurements of stomatal infiltration pressure (P_{stom}), scholander bomb pressure (P_s), and heat pulse velocity (HPV). Measurements of transpiration (TR) and calculations of leaf temperature were available from the cuvette studies. Trees from different crown classes were examined. Data were collected periodically during the year, usually starting before sunrise and continuing until late afternoon or evening. Meteorological and lysimetric data are available from L. J. Fritschen.

Data representative of dominant trees (601, the lysimeter tree, and 637) on a sunny day when soil moisture (SM) was relatively low, evaporative demand was high, and NA (see Figure 3.12) peaked early in the morning are shown in Figure 3.8. Decreases in SC were evident at all band locations starting in the morning, as transpirational water loss and P_s increased. The greatest decreases occurred in the stem near midcrown (637 at 24 m). At this level, morning shrinkages and subsequent afternoon recoveries began earlier than at breast height because of the greater tissue sensitivity to changes in tree water status (Lassoie 1973). The general trends of actual TR and HPV in the lysimeter tree were similar, and rates decreased around noon because of complete stomatal closure and/or the artificial increase in humidity inside the cuvette cylinder. Predawn P_s values were significantly higher in the lysimeter tree, but midday maxima were similar for both individuals. The significantly shorter period of time required to reach maximum P_s in the lysimeter tree suggested relatively earlier hydroactive stomatal closure and limitation of water loss. Slight stomatal opening was evident after humidifying the cylinder.

Similar data taken on a day characterized by high SM, moderate evaporative demand, and high NA (see Figure 3.13) are shown in Figure 3.9. Stem shrinkage patterns in 637 were similar to those observed earlier but no significant decreases in SC occurred in the lysimeter tree. Presumably, increasing SM by irrigating the lysimeter on 6 September eliminated the demand for internally stored water, even though TR values were high. General TR and HPV trends were quite similar. Predawn P_s values were lower than those observed earlier because of the increased SM following irrigation and light precipitation, but midday maxima were similar. The duration of high stress in the lysimeter tree, however, was much less than that observed under low SM conditions. The absence of hydroactive stomatal closure allowed rapid and high transpirational water losses to occur.

Daily changes in SC were accumulated throughout the summer and examined in relation to tree water status. Typical sigmoidal trends were observed in all trees with growth usually proceeding rapidly from mid-April through mid-July. The greatest growth rates occurred near midcrown. A late-summer net decrease in size was observed in all trees except 601. This

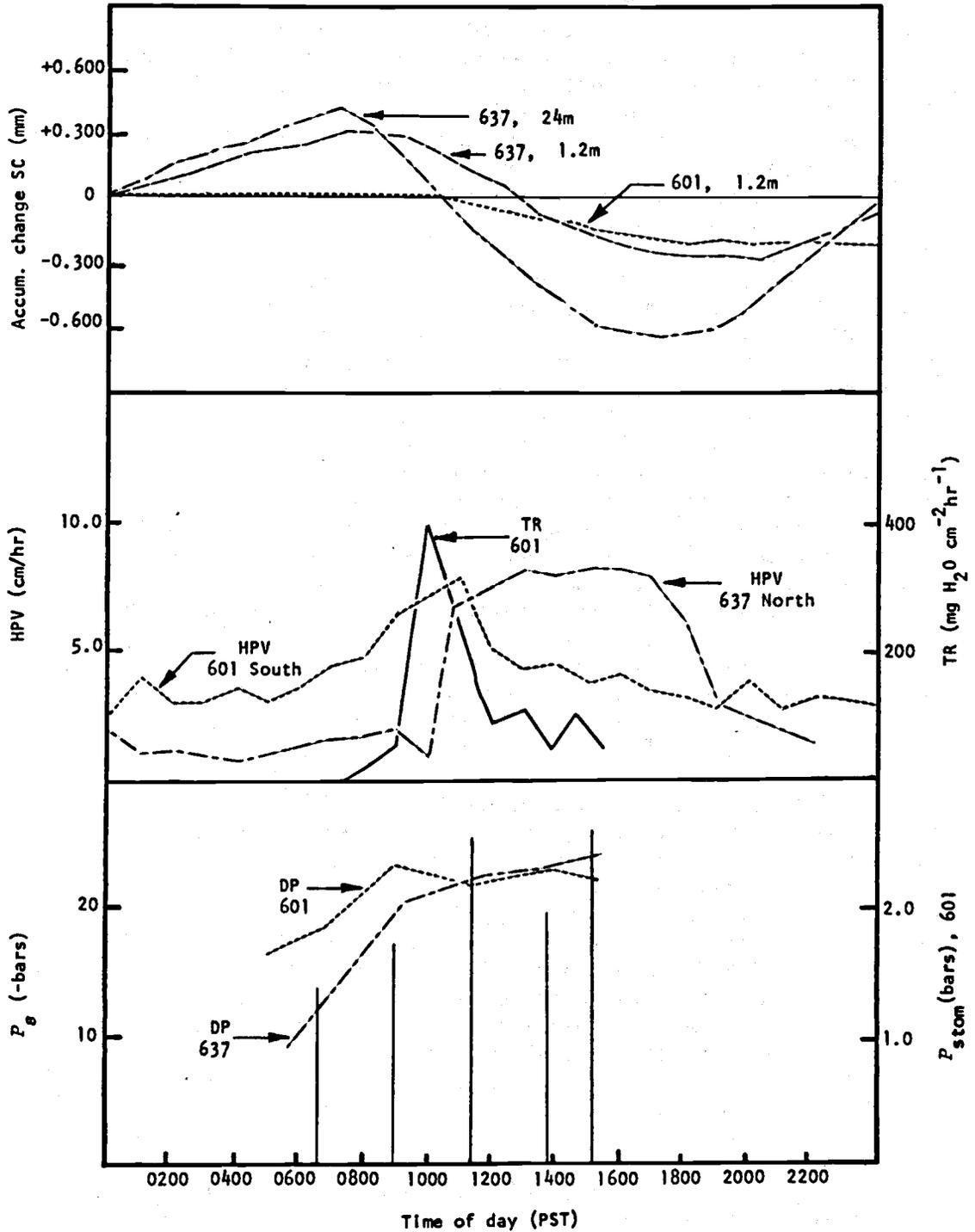


Figure 3.8. Accumulative change in stem circumference (SC), heat pulse velocity (HPV), transpiration (TR), Scholander bomb pressure (P_s) and stomatal infiltration pressures (P_{stom}) on two dominant Douglas-fir trees (601 and 637) at the Thompson site on 22 August, 1973.

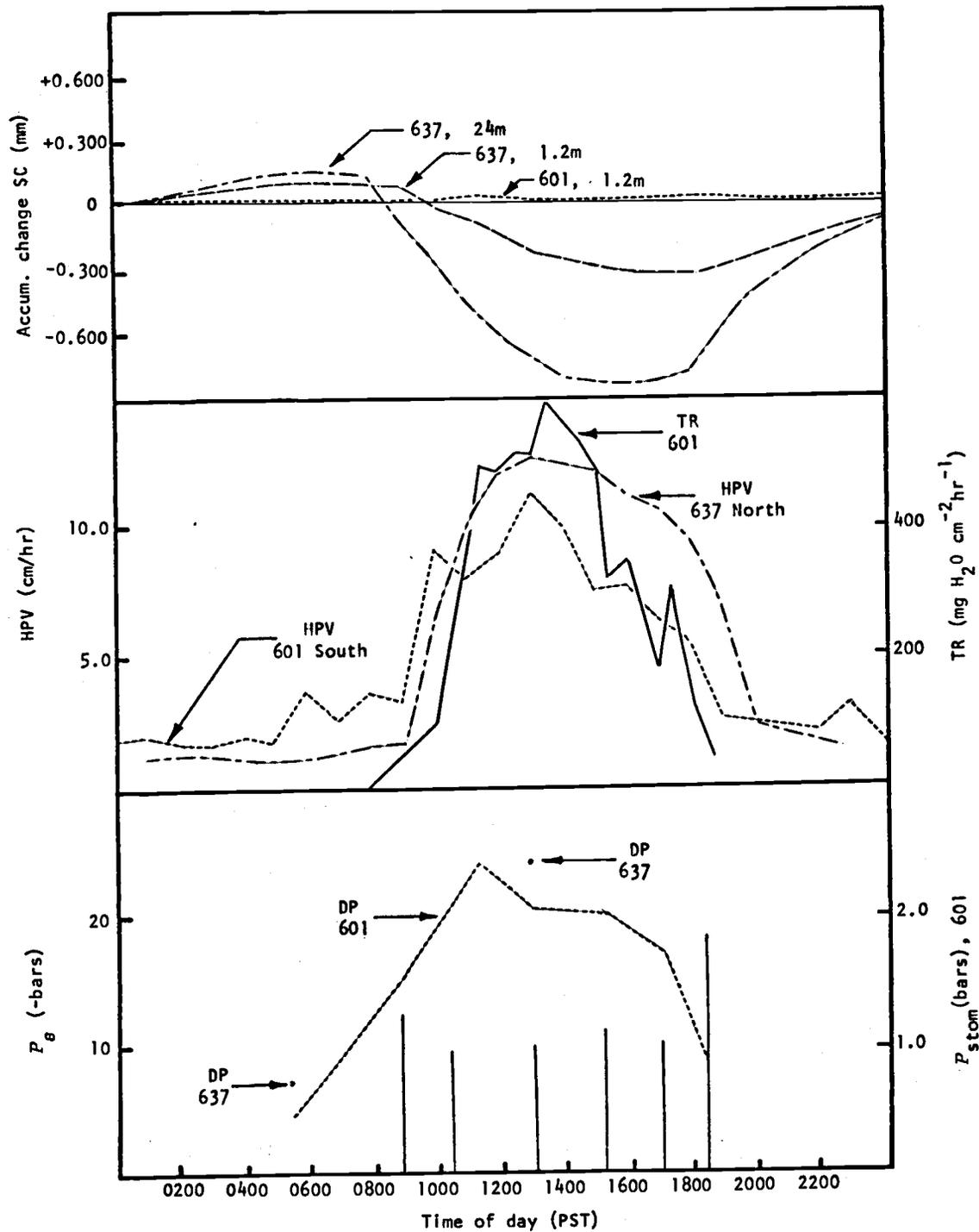


Figure 3.9 Accumulative change in stem circumference (SC), heat pulse velocity (HPV), transpiration (TR), Scholander bomb pressure (P_s) and stomatal infiltration pressures (P_{stom}) on two dominant Douglas-fir trees (601 and 637) at the Thompson site on 8 September, 1973.

corresponded to low seasonal SM levels and high predawn P_g values. The lost increment was required following the recharge of the soil by heavy rains in early fall. This resulted in decreased predawn P_g readings and the recharging of dehydrated stem tissues. No prolonged late-summer shrinkage occurred in the lysimeter tree (601), since SM usually remained low for relatively short periods of time. During the summer, however, three distinct peaks in predawn stresses, corresponding to periods of reduced tree growth, were evident. Maximum predawn P_g values during 1973 were higher than those observed during 1972 in both 601 (-18 bars versus -9 bars in 1972) and 637 (-13 bars versus -8 bars in 1972). Predawn P_g readings in a suppressed Douglas-fir were significantly higher throughout the summer than those observed in other crown classes.

Lysimeter tree weight changes as a function of time are shown in Figure 3.10. Increase in weight in the early morning hours is due to dew, which may be as much as 19% of the hydrologic balance on summer days (Fritschen and Doraiswamy 1973). Evaporation calculated from lysimeter tree data is shown in Table 3.16 for a period in May 1972. Leo J. Fritschen and co-workers (pers. commun.) have been testing aerodynamic models to predict evapotranspiration from meteorological variables, thus far unsuccessfully. Eddy correlation techniques will be evaluated in 1974.

3.1.2.2. Carbon cycling processes. Carbon cycling and accumulation have received considerable attention in the Coniferous Forest Biome because prediction of the productivity of coniferous ecosystems is one of the major goals of the Biome. In contrast to the generally closed nutrient cycling systems in coniferous forests, carbon cycling is open; i.e., atmospheric carbon dioxide is assimilated in tree and understory species and respired by plants, animals, and decomposers.

Carbon standing crops (biomass), litterfall, and net annual production in young- and old-growth Douglas-fir, 35-year-old alder, and 175-year-old Pacific silver fir ecosystems are presented in Table 3.17. Total carbon on the old-growth Oregon site is over twice that on the young-growth site. The difference is due to the large amount of carbon accumulated in the branches, stems, roots, and large litter components at the old-growth site. The carbon in overstory foliage, however, is similar. The understory components in the old-growth stand have considerably larger biomass. Litterfall on the old-growth site is more than on the young-growth site particularly in the log and branch category; and productivity is less on the old-growth site because the trees are expending most of the captured energy in maintenance. Complete data are not available from the alder and Pacific silver fir ecosystems but it should be noted that the overstory species in the alder ecosystem have considerably less foliage than the understory. Pacific silver fir has considerably more overstory foliage than the other ecosystems and this is due in part to the fact that needles are retained on the trees for up to eight years in comparison with four to five years for the Douglas-fir at the Thompson site and one year for the alder.

Studies on aboveground biomass of understory and overstory species in different ages of Douglas-fir stands by J. Long and J. Turner (pers. commun.) have provided interesting information on stand dynamics with

Table 3.16. Net radiation R_n , evaporation from the lysimeter tree E , and evaporative flux on a stand basis LE for 3-4 May 1972 at the Thompson Research Center (after Fritschen and Doraiswamy 1973).

Hour ending	3 May 1972			4 May 1972		
	R_n (ly/min)	E (ℓ /hr)	LE (ly/min) ^a	R_n (ly/min)	E (ℓ /hr)	LE (ly/min) ^a
0100	-0.033	0.00	0.00	-0.048	1.47	0.08
0200	-0.037	0.00	0.00	-0.042	2.21	0.13
0300	-0.035	0.42	0.02	-0.044	2.31	0.13
0400	-0.022	0.52	0.03	-0.036	2.10	0.12
0500	0.023	3.26	0.19	-0.006	1.79	0.10
0600	0.108	0.00	0.00	0.123	-3.36	-0.19
0700	0.306	-5.57	-0.32	0.316	-3.68	-0.21
0800	0.495	-2.00	-0.11	0.500	-4.20	-0.24
0900	0.660	-0.52	-0.03	0.660	-1.26	-0.07
1000	0.717	-0.63	-0.04	0.771	-1.68	-0.10
1100	0.860	-1.16	-0.07	0.862	-1.47	-0.08
1200	0.849	-2.00	-0.11	0.882	-3.68	-0.21
1300	0.664	-2.94	-0.17	0.852	-2.63	-0.15
1400	0.556	-3.68	-0.21	0.750	-5.57	-0.32
1500	0.516	-4.20	-0.24	0.604	-4.73	-0.27
1600	0.389	-4.73	-0.27	0.424	-4.20	-0.24
1700	0.200	-4.73	-0.27	0.212	-5.78	-0.33
1800	0.010	-4.73	-0.27	0.016	-7.04	-0.40
1900	-0.053	-3.89	-0.22	-0.051	-3.68	-0.21
2000	-0.051	-1.68	-0.10	-0.044	-1.37	-0.08
2100	-0.048	0.00	0.00	-0.042	-0.52	-0.03
2200	-0.044	0.21	0.01	-0.042	-0.32	-0.02
2300	-0.047	0.52	0.03	-0.020	0.10	0.01
2400	-0.049	1.47	0.08	-0.037	0.95	0.05
Summation	R_n (ly)	E (ℓ)	LE (ly)	R_n (ly)	E (ℓ)	LE (ly)
Daily total	356	-36.06	-124	394	-44.24	-149
Negative period total	-25	-42.46	-146	-25	-55.17	-189
Positive period total	331	6.40	22	369	10.93	37
$[\Sigma (+LE)/\Sigma (-LE)]$ x 100			15			20
Bowen ratio $[\Sigma R_n - \Sigma (-LE)]/\Sigma (-LE)$			1.44			1.13

^aEvaporative flux is based on the assumption that one tree occupies 17.49 m².

Table 3.17. Carbon standing crops (kg/ha), annual production, and litterfall in old growth (A), and young-growth (B) Douglas-fir, alder (C) and Pacific silver fir (D) ecosystems.

	A (Watershed 10) 450 yr	B (Thompson site) 42 yr	C (Thompson site) 35 yr	D (Findley Lake) 175 yr
Overstory				
Foliage	8,906	9,100	4,100	15,698
Branches	48,653	22,200	19,400	17,711
Bole	472,593	140,100	151,600	265,011
Roots	74,380	33,100	34,300	
Total overstory	604,480	204,500	209,400	
Understory				
Large shrubs				
Foliage	1,604			
Stems	4,834			
Small shrubs				
Foliage	1,991			
Stems	270			
Herbs	65			
Total understory	8,764	1,000	9,500	
Epiphytes	1,100			
Total forest floor	98,550	22,800	66,300	
Soil (0-100 cm)	150,000	111,600	158,500	
TOTAL ECOSYSTEM	862,894	339,900	488,000	

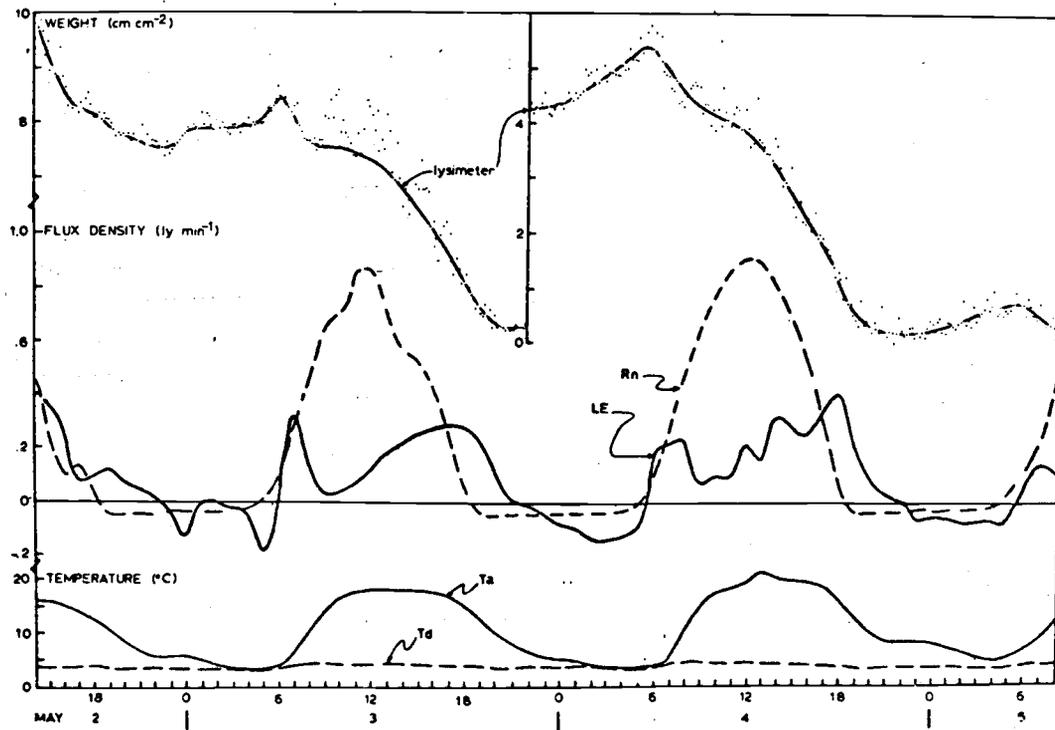


Figure 3.10. Lysimeter weight referenced to a dummy standpipe, net radiation R_n , evaporative flux density LE , air temperature T_a , and dew point T_d for 2-5 May, 1972 at the Thompson Research Center^d (from Fritschen and Doraiswamy 1973).

respect to carbon cycling. With increasing age up to age 73, all overstory components are increasing in weight with age while the total understory biomass is decreasing. Based on the estimates of foliage biomass reviewed by Turner and Cole (1973), crown and foliage weight of conifer stands becomes constant at an early stage in development, usually within a few years of crown closure. This figure is approximately 10^4 kg/ha for foliage in temperate forests; it increases with site quality but is independent of stand density. Higher stand density appears to shorten the time before the foliage weight becomes constant. Figure 3.11 is a comparison of the development of foliage biomass with age in plantations and natural stands. The plantation foliage weight appears to be leveling off, and the weight at which this is occurring is similar to the foliage weight of the natural stand. We might assume that an approximate foliage weight of $8.5-9.0 \times 10^3$ kg/ha is an upper limit for this site quality (site quality 4). Foliage biomass leveled off at approximately age 60 in the natural stand at the Thompson site but before age 36 in the plantation because of high initial planting density (2160 stems/ha) and subsequent earlier crown closures in the plantation. The overstory foliage biomass on watershed 10 of the Andrews Forest is 8900 kg/ha and watershed 10 is of similar or perhaps slightly higher site quality than the Thompson site. Overstory foliage biomass thus appears to be more or less constant from early in the stand life to as long as 450 years. Understory foliage biomass, however, is considerably more at watershed 10.

With increasing age there is an increase in the diversity of both the overstory and understory. While this increase is due in part to increased species richness, it is also due to changes in the evenness of component of diversity. That is, the relative importance of Douglas-fir diminishes as individuals of other tree species such as western hemlock increase in size and understory shrubs regain prominence.

Studies of net assimilation at the Thompson site have been conducted with thermoelectrically cooled assimilation chambers since August 1972 by D. J. Salo and R. G. Amundson. Data collected during two- to three-day periods throughout the year illustrate the effect of various environmental conditions on net photosynthesis. Cuvettes were also attached to branches of the lysimeter tree (601) while it was enclosed in a plastic cylinder during the study conducted by L. J. Fritschen in August-September 1973 (section 5.3).

Typical data collected during 1973 included CO_2 differentials, relative humidity (RH), leaf temperature (T), photosynthetically active radiation (PAR), stomatal infiltration pressure (P_{stom}), and Scholander bomb pressure (P_g). Data representative of a sunny day when soil moisture (SM) was low, leaf resistance (r_L) was moderate to high, and insolation and temperature were both high are plotted in Figure 3.12. Net assimilation (NA) peaked in the early morning and rapidly declined with increasing temperature and leaf resistance. Transpiration (TR) increased with evaporative demand but was also limited by leaf conductance and decreased markedly as resistance increased to high levels.

Measurements made on a day characterized by moderate water stress and temperatures and low leaf resistance and light are illustrated in

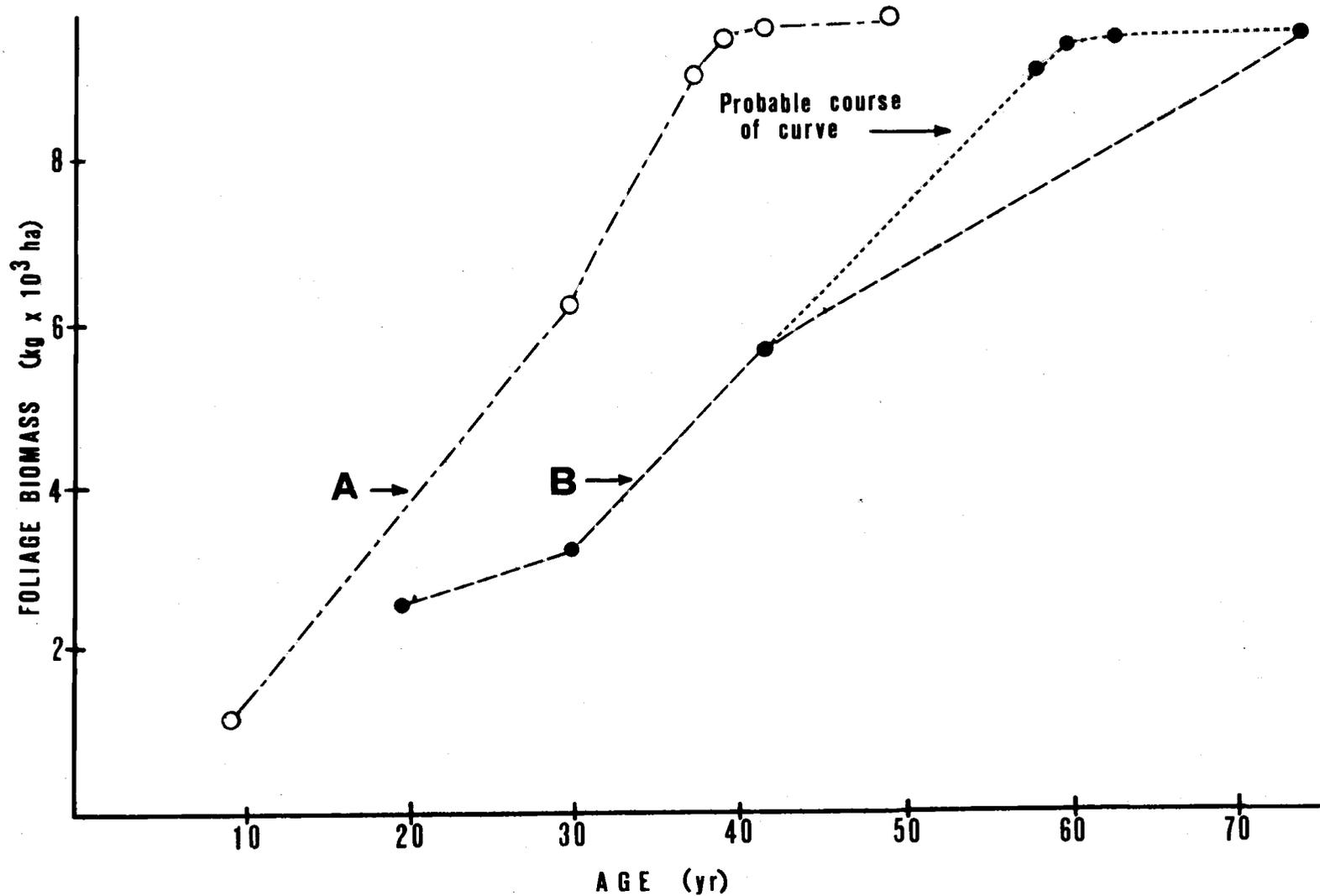


Figure 3.11. Foliage biomass as a function of age at the Thompson site in a plantation (A) and a naturally regenerated stand (B) (from Long and Turner ----).

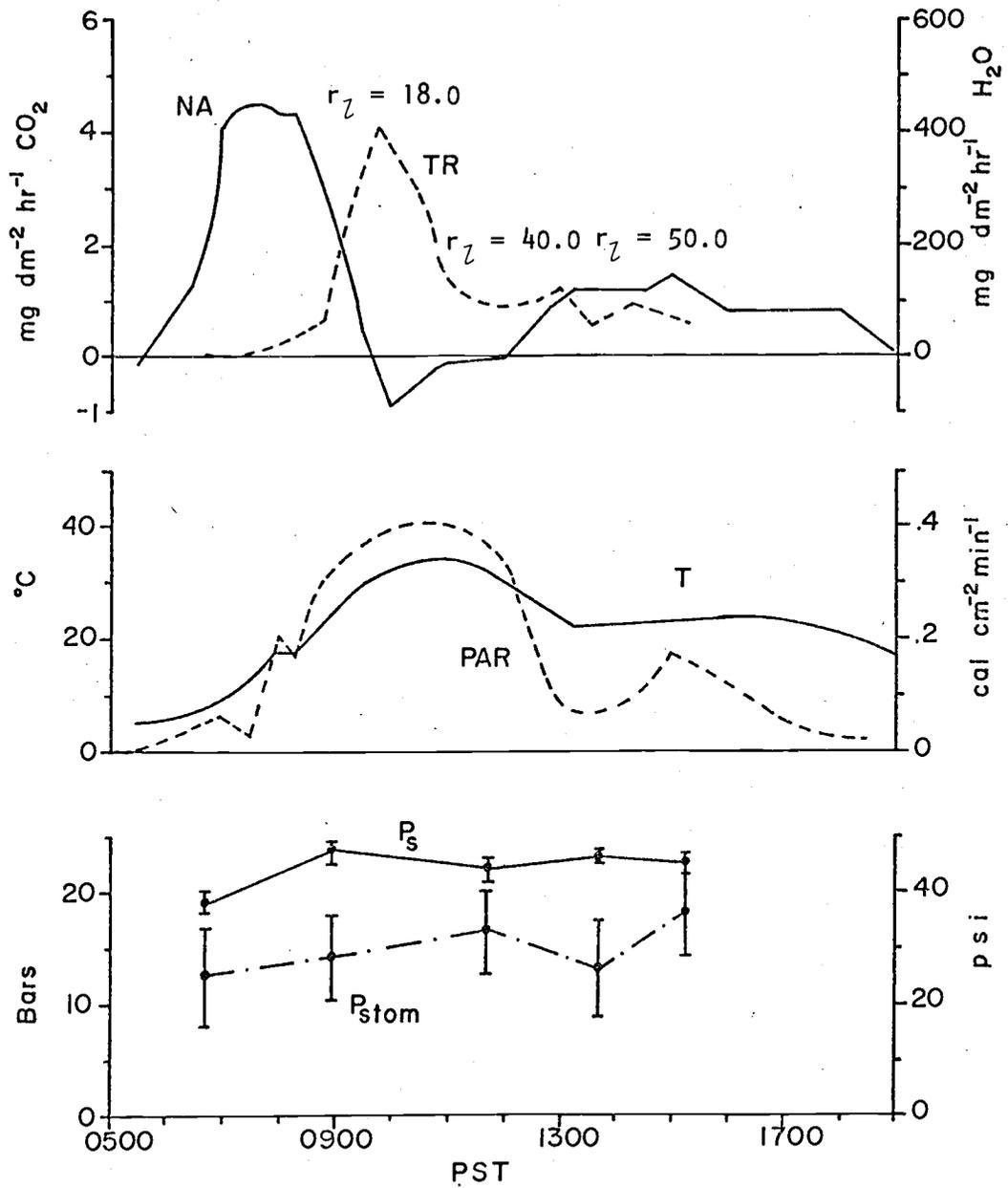


Figure 3.12. Net assimilation (NA), transpiration (TR), light (PAR), leaf temperature (T), xylem water pressure (P_s , bars), stomatal infiltration pressures (P_{stom} , psi) and stomatal resistance (r_z , sec/cm) on the lysimeter tree at the Thompson site on 22 August, 1973.

Figure 3.13. Though light was limiting, total net CO₂ assimilation exceeded that of the hot day mentioned above. Data plotted in Figure 3.13 illustrate the high total net assimilation values that can occur under relatively high water stress conditions when SM is also high. They were collected following irrigation of the lysimeter with 1000 liters of water and show that under these conditions net photosynthesis is primarily limited by temperature and light since leaf resistance was low to moderate all day.

Wintertime net assimilation rates were lower than those measured during the spring, summer, and fall. On one occasion in February 1974 a rate less than one-half maximum values was recorded even though light and leaf resistance did not appear limiting and daytime temperatures were moderate. During a two-week cold period in January 1974, stomata remained closed, pressure bomb values were extremely high ($P_g \leq -40$ bars), and no detectable transpiration or assimilation occurred even though sunny conditions prevailed and daytime leaf temperatures exceeded 0°C; however, stem temperature at 1.5 m was approximately -4°C.

A major gap in our perception of in vivo coniferous forest canopy processes has been the lack of knowledge of the correlation between patterns of net photosynthesis and transpiration rates and branch and/or shoot hierarchy. Several people have alluded to such a correlation (Phillips 1967, Woodman 1968).

Using small, uncooled, stirred cuvettes in an open gas exchange system, J. W. Leverenz (unpubl. data) examined differences between net assimilation rates in current year foliage on primary, secondary, and tertiary shoots in two branch systems at midcrown in a dominant Douglas-fir tree (637) near the weighing lysimeter installation. This study took place in August and September 1973. Data from two representative days are presented in Figure 3.14 and 3.15. Figure 3.14 shows an overcast day when net photosynthesis rates were essentially equal in a primary and a nearby secondary shoot on the same branch. Net photosynthesis on this day closely followed irradiance; however, differences in the diurnal patterns of stomatal (leaf) conductance can be seen.

The following day was clear with high light intensities and larger vapor pressure deficits. Stomatal conductance in both shoots was lower than the previous day and net assimilation rates and stomatal conductances were reduced to a much greater extent in the secondary shoot. In this study not all secondary or tertiary shoots were affected to the same degree. Lateral shoots closest to terminal shoots had the greatest reduction in gas exchange rates.

Many attempts have been made at modeling photosynthesis in plants (Brown 1969, Duncan et al. 1967, Lommen et al. 1971). Hatheway et al. (1972a) considered and incorporated aspects of these already published models in their model for terrestrial primary production. Reed et al. (1973) have carried on from there and have developed a steady-state model that expresses net photosynthesis as a function of light, temperature, CO₂ concentration, and stomatal resistance. This model, although it has

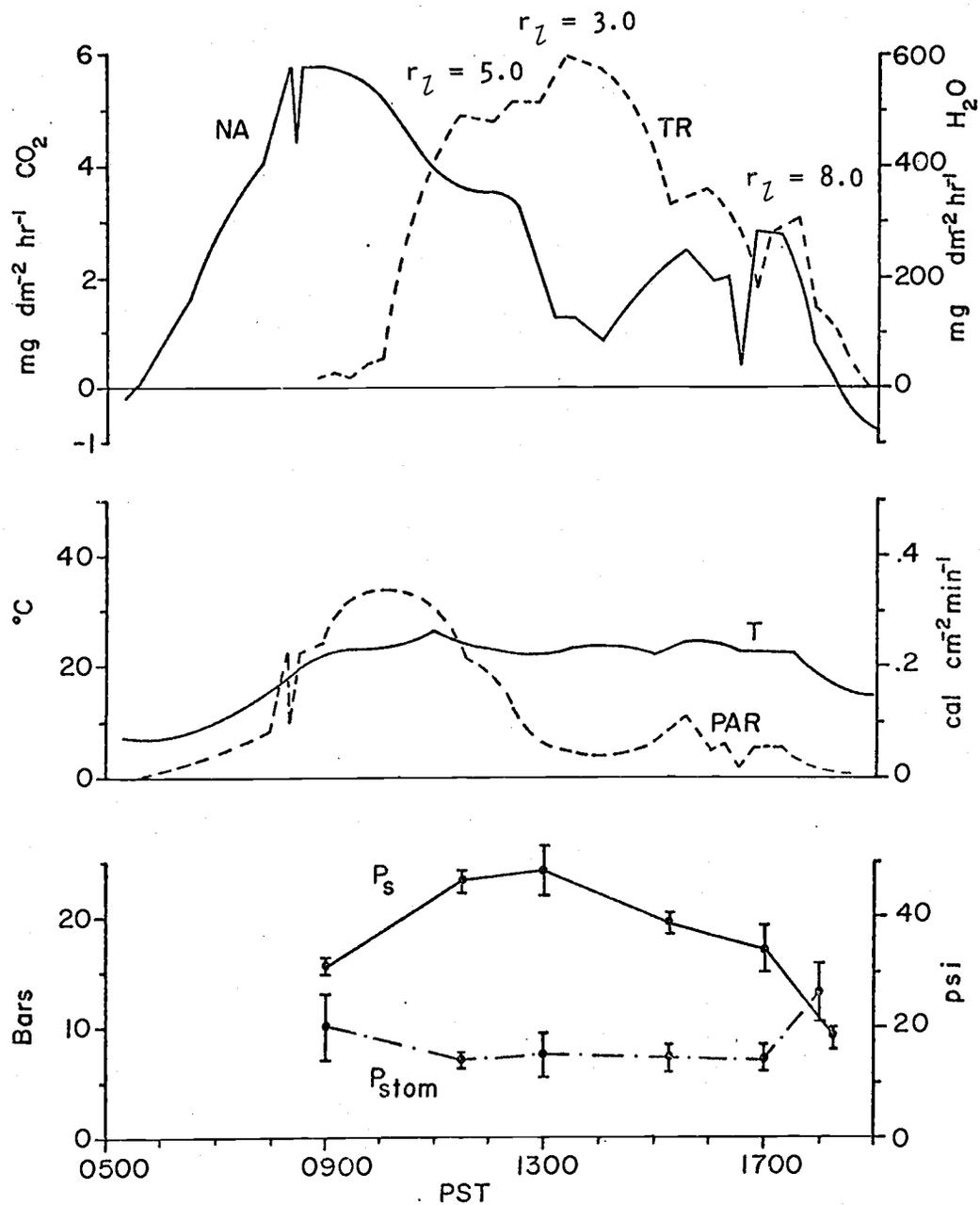


Figure 3.13. Net assimilation (NA), transpiration (TR), light (PAR), leaf temperature (T), xylem water pressure (P_s , bars), stomatal infiltration pressures (P_{stom} , psi) and stomatal resistance (r_L , sec/cm) on the lysimeter tree at the Thompson site on 8 September, 1973.

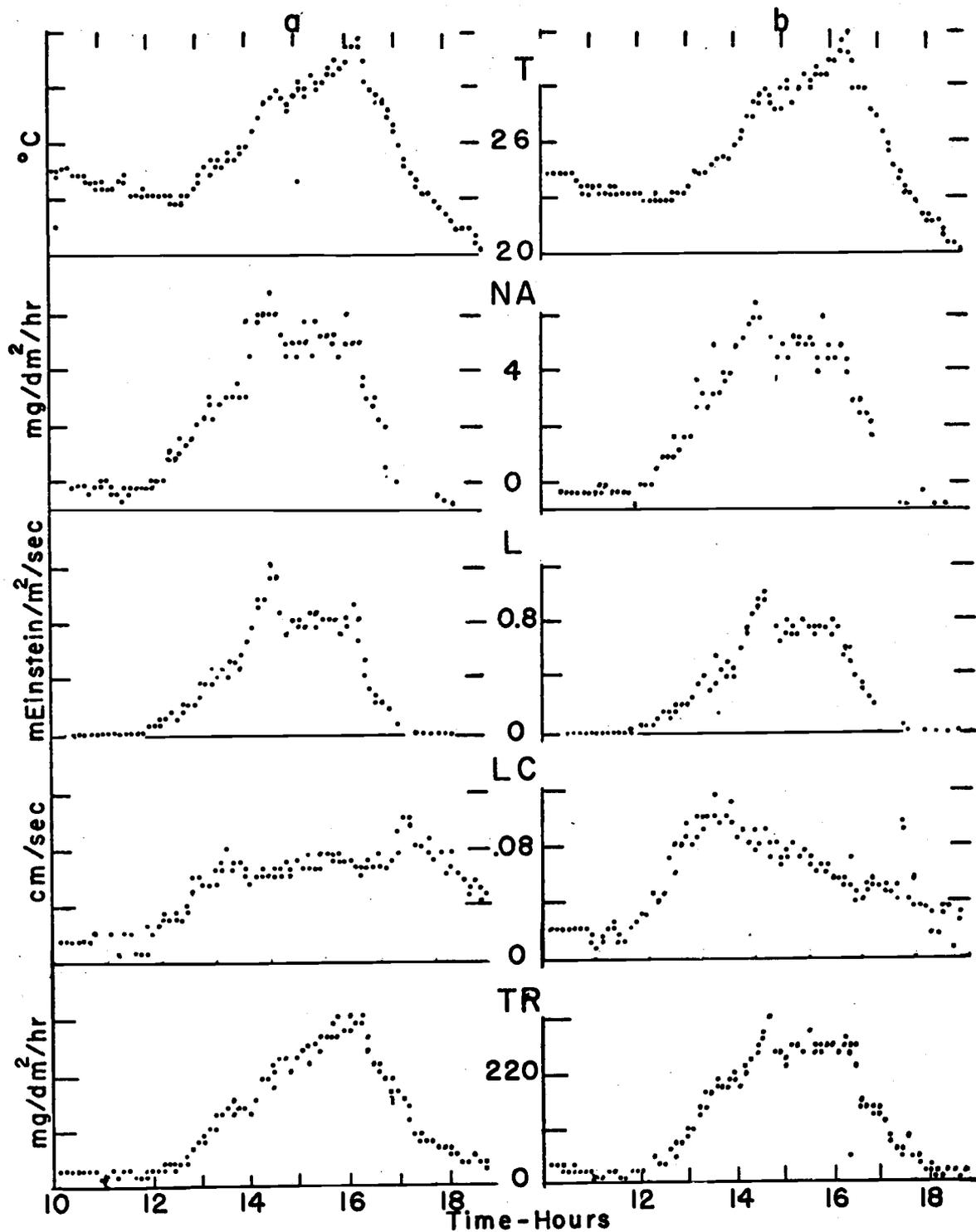


Figure 3.14. Leaf temperature (T), net assimilation (NA), light (L), leaf conductance (LC) and transpiration (TR) for current years foliage on a primary shoot (a) and secondary shoot (b) on a dominant tree at the Thompson site on 10 August, 1973.

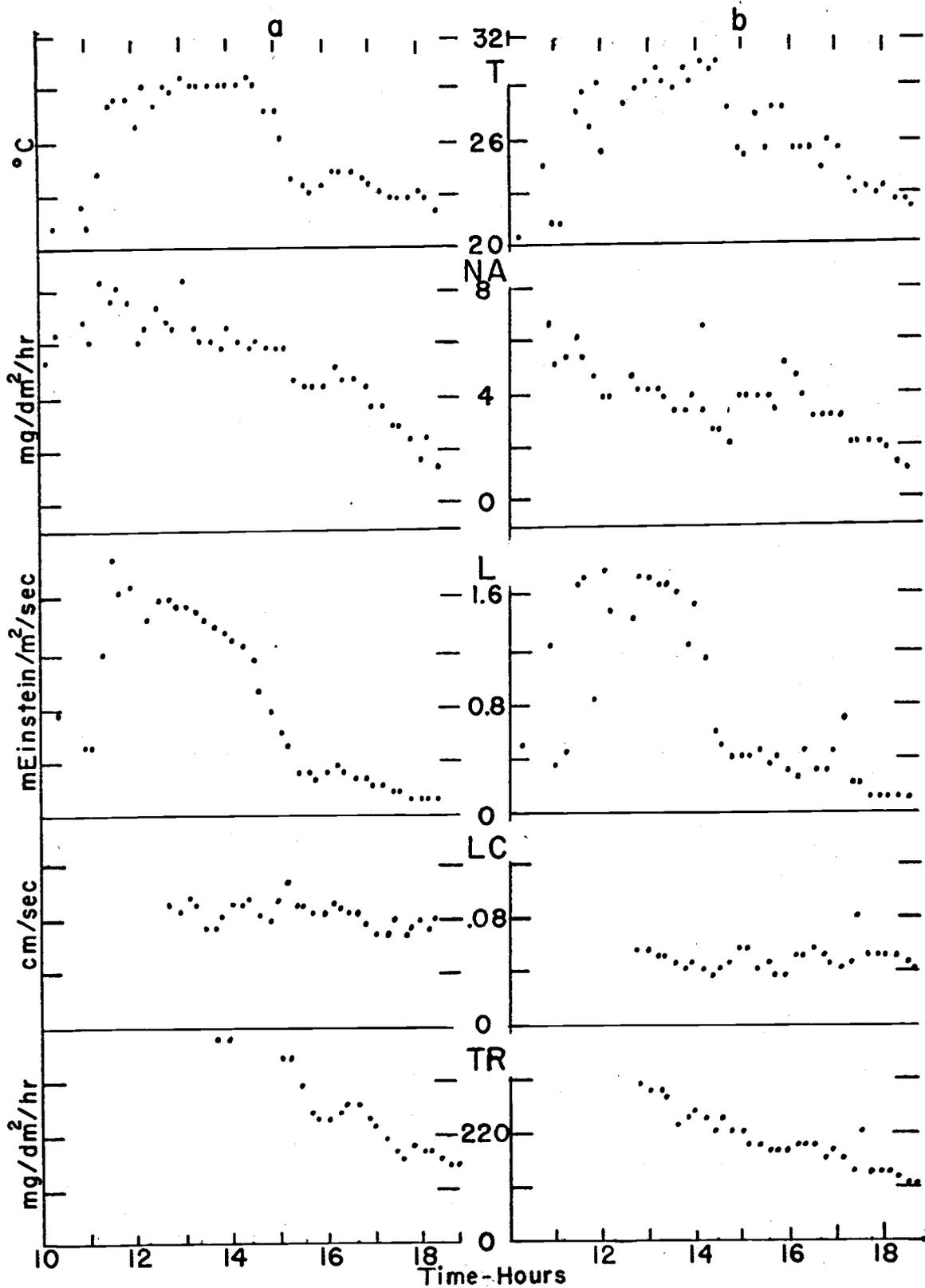


Figure 3.15. Leaf temperature (T), net assimilation (NA), light (L), leaf conductance (LC) and transpiration (TR) for current years foliage on a primary shoot (a) and secondary shoot (b) on a dominant tree at the Thompson site on 11 August, 1973.

weaknesses, does give good approximations of diurnal fluctuations in net photosynthesis. Figure 3.16 shows model output compared with photosynthesis data for Liriodendron tulipifera (tulip poplar). Douglas-fir data from D. J. Salo and J. W. Leverenz are currently being incorporated into this model. P. Sollins has also developed functions for photosynthesis and respiration that depend on daily values of driving variables appearing in the equations below.

$$PSN = [B_1(DL)(B_2 - T)^{B_4}(T - B_3)(LC)] * \left[\frac{\frac{L}{60(DL)}}{B_5 + \frac{L}{60(DL)}} \right] * \frac{1}{r_L^2}$$

where PSN is net daily photosynthesis (mg CO₂/dm²), DL is day length (hr), T is average day temperature (°C), r_L is average leaf resistance (sec/cm), L is total radiation (ly/day), B₁ is 0.0097 (mg CO₂ per hr per dm² [°C^{-(B₄+1)] sec/cm), B₂ is 45 (°C), B₃ is -5 (°C), B₄ is 1.1 (dimensionless), and B₅ is 0.1 (ly/min).}

$$R = -B_6 * (1 - DL) * \exp B_7 TN$$

where R is respiration (mg CO₂/dm²), TN is average night temperature (°C), B₆ is 0.1 (mg CO₂ per dm² per hr), and B₇ is 0.2 (1/°C). The results from both equations are added to give net daily CO₂ fixation.

W. H. Emmingham (pers. commun.) has incorporated data from the Thompson site (D. J. Salo and J. Leverenz) and California (J. Helms) into this model and has simulated photosynthesis for needles near the canopy top. Potential photosynthesis throughout the year has been calculated using light and average ambient temperature values for three locations in Oregon: on a southeast slope at 600 m in the Coast Range near Corvallis, in the Willamette Valley near Corvallis, and at 1000 m near Mt. Hood. Results of this simulation are shown in Figure 3.17. The highest potential occurs in the Coast Range and photosynthesis is considerably reduced at high elevations.

From field studies we know that frost, cold soil temperatures, and moisture stress prevent trees from attaining their potential photosynthesis. This information has been included in the simulation and Figure 3.17 indicates how much of the potential is reached at each location. At the Coast Range site only about 40% of the potential is reached, whereas 56% and 58% potential are reached in the mountain and valley sites, respectively. A considerable portion of the loss at the Coast Range site is due to summer drought. This points out a potential for the use of forest irrigation to improve moisture conditions and capture some of the loss due to drought.

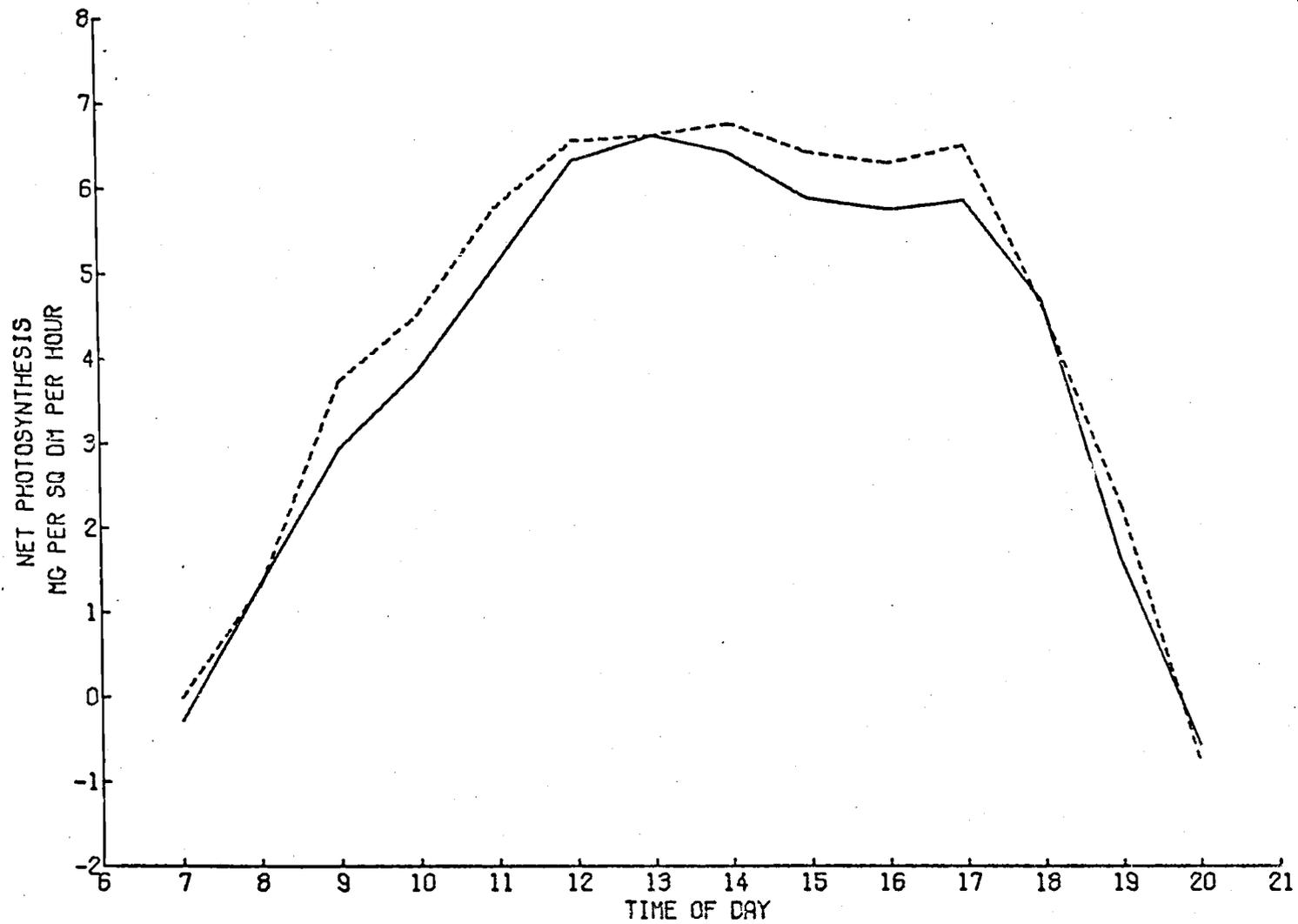


Figure 3.16. Comparison of predicted (dashed line) to observed net photosynthesis (solid line) in Liriodendron tulipifera on 19 August, 1971 (from Reed et al 1973).

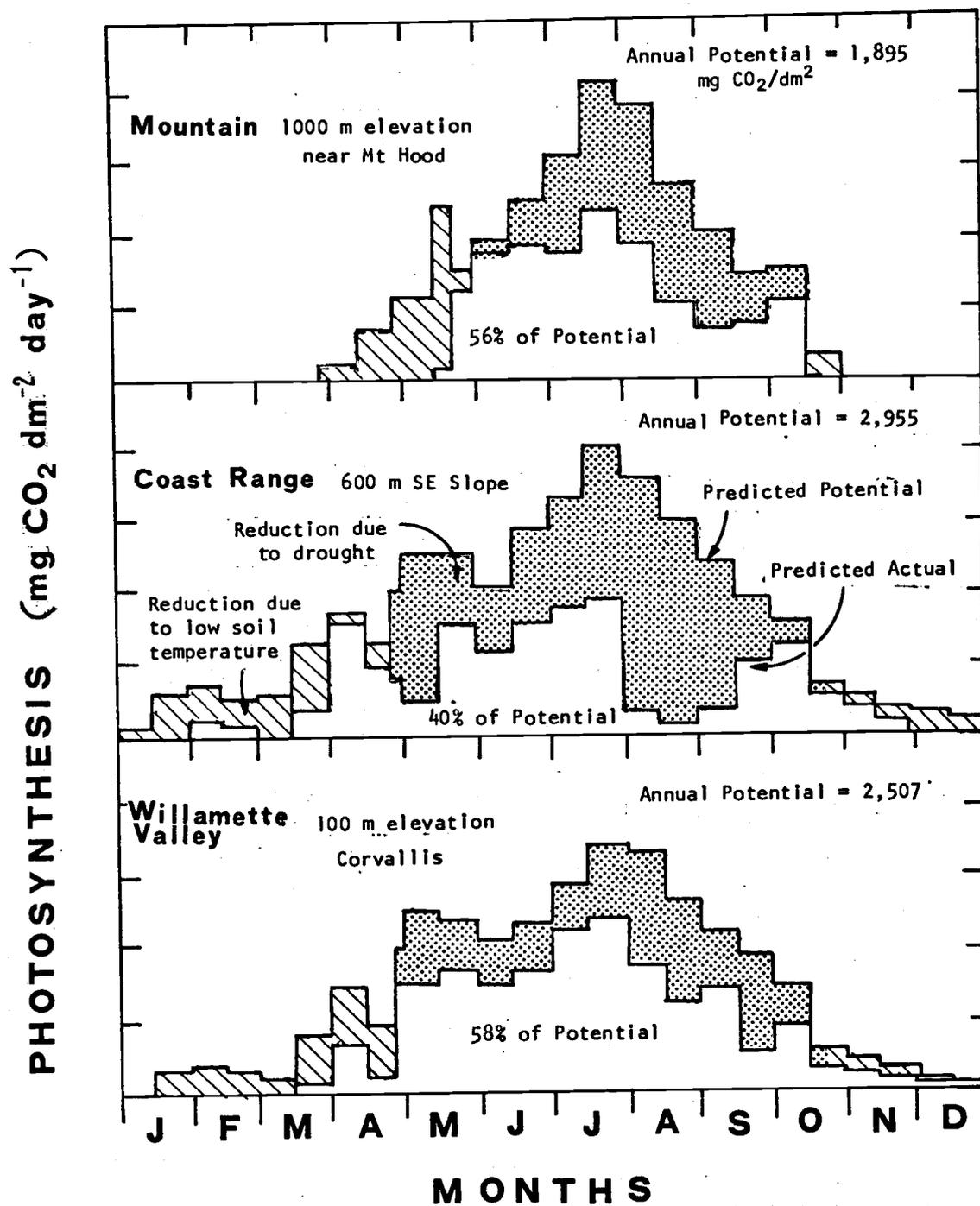


Figure 3.17. Predicted potential and actual photosynthesis in Douglas-fir, for three locations in Oregon; a mountain site, a coast range site and a Willamette valley site (W.H. Emmingham, pers. commun.).

Our efforts this year (1974) will be on modeling in detail the relation between leaf resistance, plant moisture stress, vapor pressure deficit, and soil moisture status, building on the models developed by Reed, Hatheway, and Sollins. A simplified version of the model will then be incorporated into the coarser resolution unit area model being developed by Sollins and Swartzman (section 3.1.2.4).

3.1.2.3. Nutrient cycling processes. In general terms, our objectives in nutrient cycling research are: (1) to establish annual nutrient budgets for the major forest ecosystems of the Biome; (2) to study nutrient cycling at the process, stand, and watershed levels in order to understand the mechanisms governing cycling in various ecosystems in the Douglas-fir region; (3) to determine changes in cycling associated with changes in stand development, productivity, succession, and ecosystem manipulation; (4) to develop conceptual and simulation models of nutrient cycling as a means of extending our understanding of ecosystems; and (5) to evaluate the effects of manipulation or stresses such as defoliation and fertilization on nutrient cycling. This last objective is discussed in part 5.

This section represents a discussion of integrated results involving nutrient inventories and fluxes. A discussion of modeling of nutrients is contained in the next section (3.1.2.4), which describes the linkages between water, carbon, and nutrient cycling at the stand level.

For forest growth, 13 mineral nutrients are essential (Gessel et al. 1973). These are accumulated by trees in various quantities from about 1% oven-dry weight for a variety of elements to several parts per million (ppm) for copper. The approach taken by the Biome in studying the role of nutrients has been to examine the magnitude of the various nutrient pools (soil, litter, trees, and understory) and the rates at which the nutrients are cycling within different coniferous ecosystems.

Discussion here is limited to four nutrients, nitrogen, phosphorus, potassium, and calcium. These nutrients were selected because of their distinctive patterns of movement and use within the system. Nitrogen is relatively mobile and is deficient in the glacially derived soils of the Douglas-fir region. Phosphorus is cycled mostly within the plants, while potassium is highly soluble and is lost rapidly from trees, although it is replaced rapidly (Riekerk 1967). Calcium accumulates in tissue with age.

The natural coniferous forest ecosystem approaches a closed system with respect to nutrient cycling. There is very little elemental loss by leaching and little input each year by precipitation and weathering, except in the case of calcium at the Andrews Forest and at Findley Lake, as shown in the nutrient budgets in Table 3.18. This large calcium loss is mainly due to bedrock weathering. An explanation for this closed system can be obtained by examining the mechanisms governing leaching in coniferous forest ecosystems.

Mechanisms governing leaching. In soils most plant macronutrients are available primarily as positively charged ions (cations) including nitrogen, which is usually present as NH_4^+ . Exceptions are phosphorus

Table 3.18. Comparison of annual inputs, losses, and balances of nitrogen, phosphorus, potassium, and calcium at the Thompson site and Findley Lake (Washington) and watershed 10, Andrews Forest (Oregon), in kilograms per hectare.

	N	P	K	Ca
Thompson site (young-growth Douglas-fir)				
Input (precipitation)	1.1	trace	0.8	2.8
Loss (leached beyond root zone)	<u>0.6</u>	<u>0.02</u>	<u>1.0</u>	<u>4.5</u>
Forest stand balance	+0.5	-0.02	-0.2	-1.7
Findley Lake (Pacific silver fir)				
Input	1.3	0.04	0.8	0.6
Loss	<u>2.1</u>	<u>1.0</u>	<u>5.5</u>	<u>11.2</u>
Forest stand balance	-0.9	-0.96	-4.7	-10.6
Watershed 10 (old-growth Douglas-fir)				
Input (precipitation)	2.3	0.9	0.3	3.1
Loss (runoff)	<u>1.1</u>	<u>1.4</u>	<u>1.1</u>	<u>61.3</u>
Unit watershed balance	+1.2	-0.5	-0.8	-58.2

and sulfur, normally present in anion form, and nitrogen when it is present as nitrate.

The major carrier for nutrient ions is water. Water brings in nutrients through precipitation, leaches nutrients from tree components, reaches the forest floor in throughfall and stemflow, and transports ions through the forest floor and soil horizons. Water is also essential for transporting nutrients in the tree and for release of nutrient ions from parent material (weathering). A further mechanism involves litterfall from trees and its decomposition.

Mechanisms involving nutrient ion leaching in the soil have been examined at the Thompson site and at Findley Lake. Nutrient ions are not simply flushed through the Douglas-fir ecosystems by percolating water. That would mean that the greatest rates of transfer would occur in the peak rainfall periods in the winter. Rates of transfer are highest, however, in the fall (Figure 3.18).

Two separate processes are involved in ionic leaching. First, most nutrients must be changed to ionic form through decomposition or weathering, but even then they are not free to move through the soil. They are either taken up by the plant or bound to electrically charged exchange sites on the soil colloids. For any positively charged ion (cation) to leach through the soil, it must be accompanied by an equivalently charged negative ion (anion). In general a deficiency of anions exists in forest soils of the temperate regions (Nye and Greenland 1960). In our studies at the Thompson site, which are representative of lowland forests of the Douglas-fir region, we have found that the principal anion is the bicarbonate ion, although an increasing amount of the sulfite ion has been found.

The bicarbonate ion operates in the following manner. Respiration and decomposition result in CO_2 production. A small part of the CO_2 that accumulates in the soil atmosphere and soil solution hydrolyzes to carbonic acid, which then ionizes to hydrogen ions and bicarbonate (HCO_3^-) or carbonate ions. This hydrolysis is strongly pH dependent, with an equilibrium pH of 4.5; i.e., below pH 4.5 it remains in undissociated form (H_2CO_3).

The hydrogen ions in the soil solution can replace readily available cations from the colloid exchange sites, which are then transported along with the HCO_3^- ions through the soil. This mechanism is particularly active during the passing of a wetting front as a result of a storm in the summer and fall, when CO_2 production is high (McColl 1972).

One of the questions we are attempting to answer is whether bicarbonate leaching is the dominant mechanism in all ecosystems in the Douglas-fir region, since any process that adds anions to the system behaves in the same way.

At the high-elevation Findley Lake site, which is dominated by Pacific silver fir stands, concentration of leachates in the soil solution is less than at the Thompson site (D. Johnson, pers. commun.). Annual

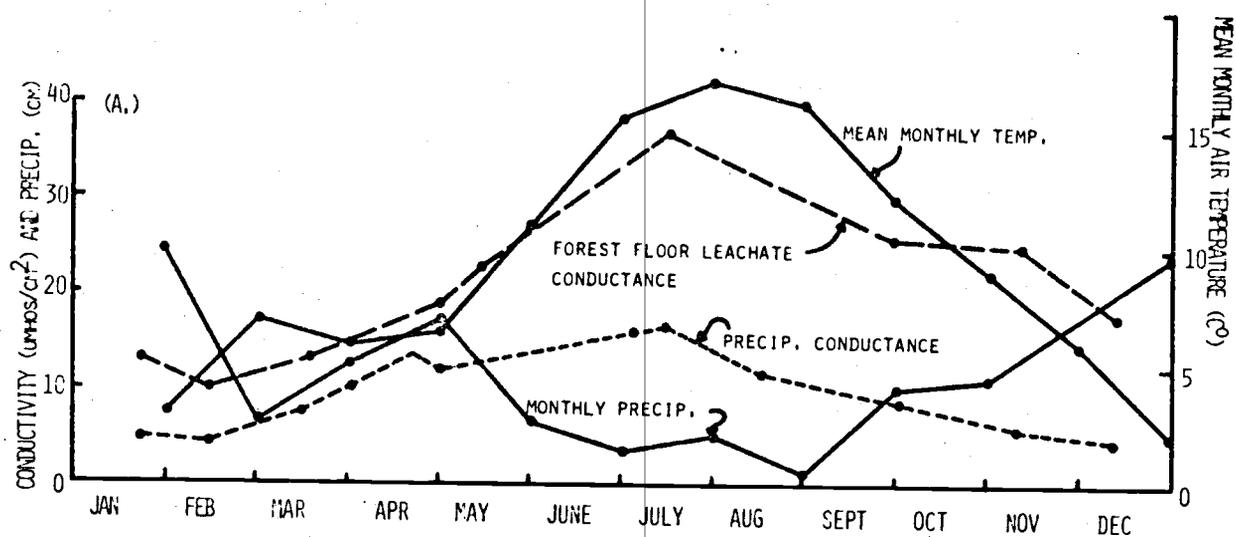


Figure 3.18. Mean monthly precipitation, air temperature, and specific conductance of precipitation and forest floor leachates for the Thompson site during 1970 (from Grier and Cole 1972).

leaching from these stands, however, is similar (Table 3.18) because of the higher rainfall at Findley Lake. Our research has suggested that organic acids (humic or fulvic) dominate leaching in the upper soil horizons. Carbon dioxide production is low because of low rates of decomposition due to low temperatures. Soil solution pH values are lower than those at the Thompson site and are very close to equilibrium pH (4.5) for carbonic acid. It is interesting to note that at the Thompson site the forest canopy serves to raise the pH of incoming precipitation whereas at Findley Lake it lowers it. In the lower horizons, organic acids appear to be removed from dominance in the solution and leaching is again dominated by CO₂ hydrolysis, so that most cations leaving the system probably do so accompanied by bicarbonate ions. The hypothesis that has emerged from our studies is that the carbonic acid mechanism is responsible for soil leaching in temperate western coniferous forests, but that in colder and more northern zones organic acids dominate.

Nutrient ion uptake in Douglas-fir seedlings is currently being investigated in greenhouse studies. Soil columns were established in a controlled environment to investigate the leaching processes in a typical forest soil, an Indianola loamy sand. The columns were set up with and without six-month-old seedlings, and with the A00 and A0 layers and all stones greater than 2 mm removed.

The columns were leached initially with distilled water until a constant amount of potassium was leached each time. Leachates were analyzed for ammonium, potassium, magnesium, calcium, nitrate, phosphate, and sulfate ions, and for conductivity, alkalinity, and pH. Water loss was also evaluated.

Treatments given to the columns were warm and cold temperate regimes and nutrient additions. Figure 3.19 shows data for two nutrient additions to the columns in two temperate regimes, warm and cold.

The loss of potassium from the columns with seedlings is greatly reduced compared with the columns without seedlings. The effect of seedlings in reducing potassium leaching is evident throughout the leaching process and is probably due to potassium uptake by the seedlings. During the warm regime water loss is considerably greater in the columns with seedlings than in those without, presumably because of evapotranspiration. When the cold regime was imposed evapotranspiration was reduced, and water loss was similar in all columns. The amount of potassium leached from the columns with seedlings is greater in the cold regime than it is in the warm regime. This increased potassium movement could be due to reduced uptake by plants.

Information gathered from these soil columns will be used to quantify some of the parameters influencing movement of ions through the soil-plant system, in particular the influence of plants on the soil leaching process, and temperate effects. The data will be used in the nutrient cycling model being developed by Sollins and Swartzman which is discussed in section 3.1.2.4.

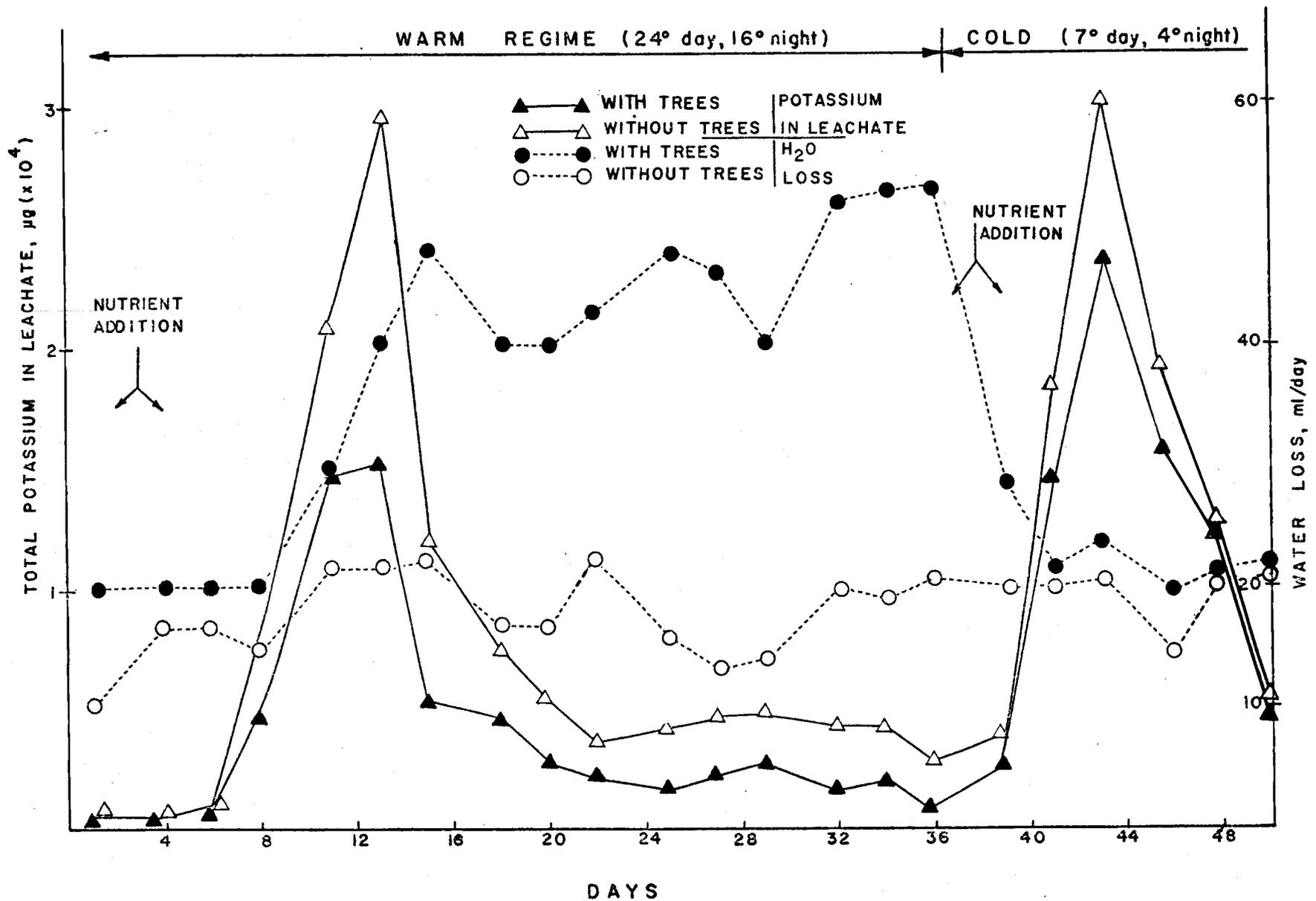


Figure 3.19. Potassium leachate and water loss from laboratory soil columns with and without Douglas-fir seedlings in two temperature regimes (after R.W. Rains and C. Bledsoe, pers. commun.).

Mineral weathering is a continuous and positive source of base nutrients to the elemental cycle. Studies determining the rate of weathering have been conducted at Findley Lake. Data so far collected are not sufficient to derive conclusions on rate of leaching, ionic concentration in the leachates, ionic distribution, and seasonal changes with respect to the pedological and geochemical cycles.

Comparisons between Douglas-fir ecosystems of varying ages. Questions related to changes in nutrient cycling associated with age can be answered only by comparative studies. In this discussion we wish to relate nutrient cycling to precipitation, litterfall, throughfall, stemflow, decomposition, leaching, and uptake. Redistribution in the plant in relation to annual nutrient requirements is also discussed.

A comparison of nutrient cycling data from the young-growth Douglas-fir ecosystems at the Thompson site and the old-growth ecosystems in the H. J. Andrews Forest can be placed in better perspective if we compare annual fluxes and nutrient capitals of nitrogen, phosphorus, potassium, and calcium as shown in Figures 3.20 and 3.21. Detailed nutrient capitals are shown in Tables 3.19 and 3.20 in comparison to biomasses for the two sites. These figures show nutrient pools or capitals as circles. Fluxes between the pools are shown by arrows. Outputs from the old-growth system represent stream output from the watershed and thus include weathering losses. Inputs, outputs, and balances of nitrogen and potassium are similar at both sites in spite of major differences in stand age, size, and nutrient capitals.

The greater input of phosphorus at the Andrews site is probably due to atmospheric input from fertilized farmland. Groundwater analysis indicates that the large calcium output from watershed 10 at the H. J. Andrews Forest is a consequence of bedrock weathering rather than loss from the biological zone. Soils in the H. J. Andrews Experimental Forest are derived from basic rocks with relatively high potassium and calcium contents, whereas soil parent material at the Thompson site is acidic in nature. It appears that the mechanisms regulating nutrient retention and loss are similar at the two sites despite the differences in structure, soil age, stand maturity, and geographic location.

In view of the similarities between nutrient input and output budgets and the major differences between organic matter and nutrient accumulations on the two sites, one would expect to find substantial differences in internal nutrient cycling between the two sites. Nutrient fluxes in the text to follow will be discussed by major category (e.g., litterfall, throughfall and stemflow, decomposition and leaching, and uptake) with details of each at the two sites.

Nutrient return in litterfall. Nutrient return in litterfall is shown in Figures 3.20 and 3.21. Total litterfall at each site is quite different although total tree foliage biomass is similar (Tables 3.19 and 3.20). Litterfall in the 45-year-old stand at the Thompson site is currently about 2900 kg per ha per yr, of which about 75% or 2200 kg per ha per yr is foliage. In contrast, litterfall in the 450-year-old stand

Table 3.19. Nitrogen, phosphorus, potassium, and calcium contents of the vegetation, soil, and litter in a young-growth Douglas-fir ecosystem on the Thompson site.

System component	Dry Wt (kg/ha)	Nutrient Content			
		N	P	K	Ca
Overstory					
Foliage	9,100	102	29	62	73
Branches	22,100	61	12	38	106
Bole	140,000	125	19	96	117
Roots	33,000	32	10	24	37
Understory	1,000	6	6	7	9
Total Vegetation	205,200	326	76	227	342
Litter layer					
01 and 02	16,500	156	23	20	112
logs	6,300	19	3	12	25
Soil (0-60 cm)	111,600	2,809	3,878	234	741
TOTAL ECOSYSTEM	339,900	3,310	3,980	493	1,220

Table 3.20. Nitrogen, phosphorus, potassium, and calcium contents of the vegetation, soil, and litter in an old-growth Douglas-fir ecosystem on watershed 10, H.J. Andrews Forest.

System component	Dry wt. (kg/ha)	Nutrient content (kg/ha)			
		N	P	K	Ca
Overstory					
Foliage	8,906	74.8	20.4	69.5	92.6
Branches	48,543	48.6	10.2	48.6	243.3
Bole	472,593	189.0	11.8	122.8	283.5
Roots	74,328	62.4	5.2	20.8	96.6
Understory					
Large shrubs					
Foliage	1,604	16.8	2.2	5.3	10.1
Stems	4,834	8.3	3.3	7.1	20.8
Small shrubs					
Foliage	1,991	17.0	2.1	8.6	11.0
Stems	270	0.7	0.2	0.6	0.8
Herb layer	65	0.9	0.3	1.4	0.7
Epiphytes	1,100	13.5			
Total vegetation	614,344	432.0	55.7	284.7	759.4
Litter layer					
01 + 02	43,350	433.5	61.1	49.8	363.3
logs	55,200	132.5	8.6	20.1	80.1
Soil (0-100 cm)	79,250	4300.0	29.0 ^a	1200.0 ^b	5500.0 ^b
TOTAL ECOSYSTEM	792,144	5298.0	154.4	1554.6	6702.8
Annual litterfall					
Foliage					
Overstory	1,480	2200.0			
Understory	1,800				
Logs and branches	3,100	700.0			
TOTAL LITTERFALL	6,380	2900.0			

^aExchangeable phosphorus.

^bAmmonium acetate extracted.

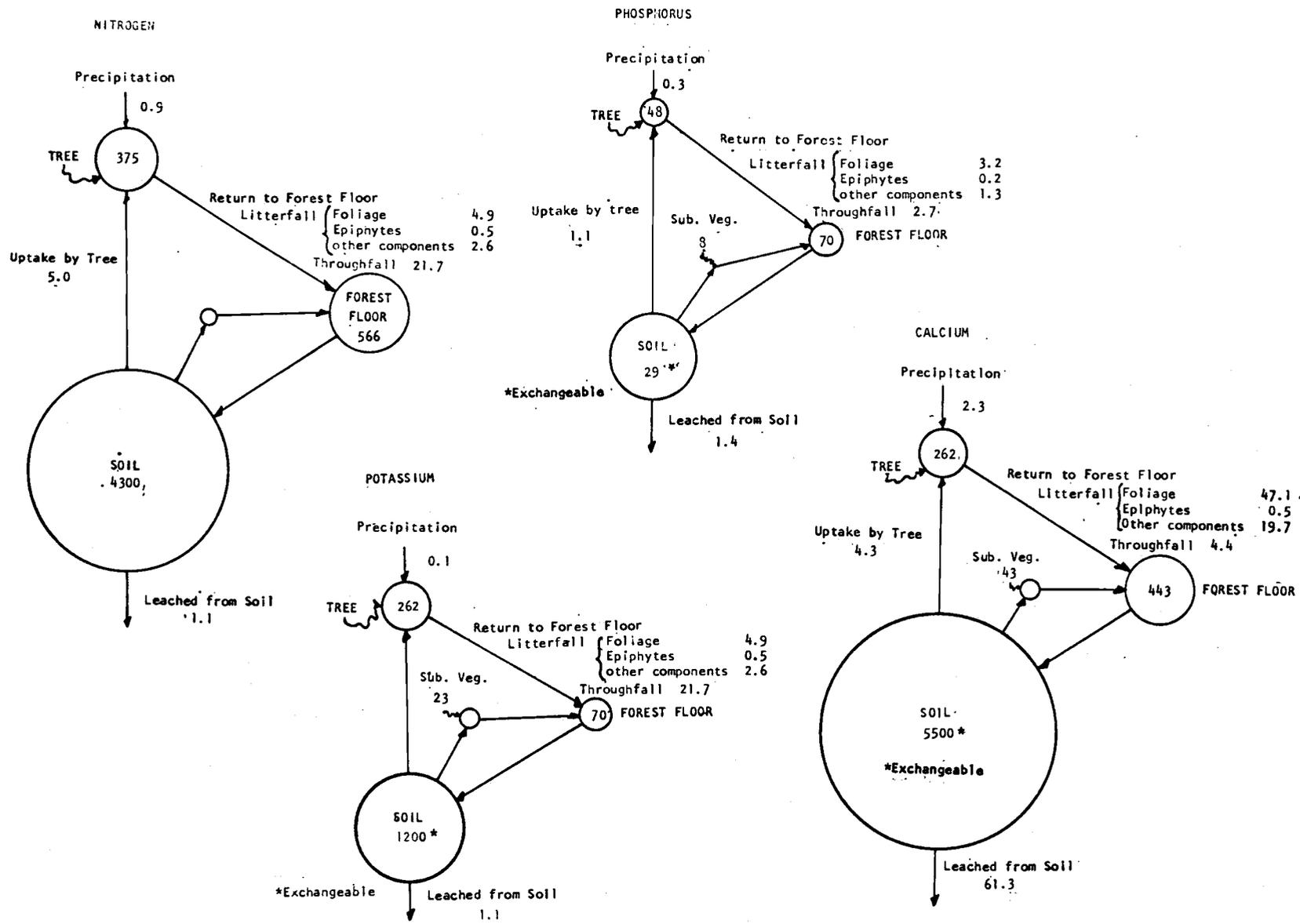


Figure 3.20. Distribution and cycling of nitrogen, phosphorus, potassium and calcium in an old-growth Douglas-fir ecosystem (Watershed 10) on the H.J. Andrews Experimental Forest. Nutrient capitals and flows are kg per ha and kg per ha per year, respectively.

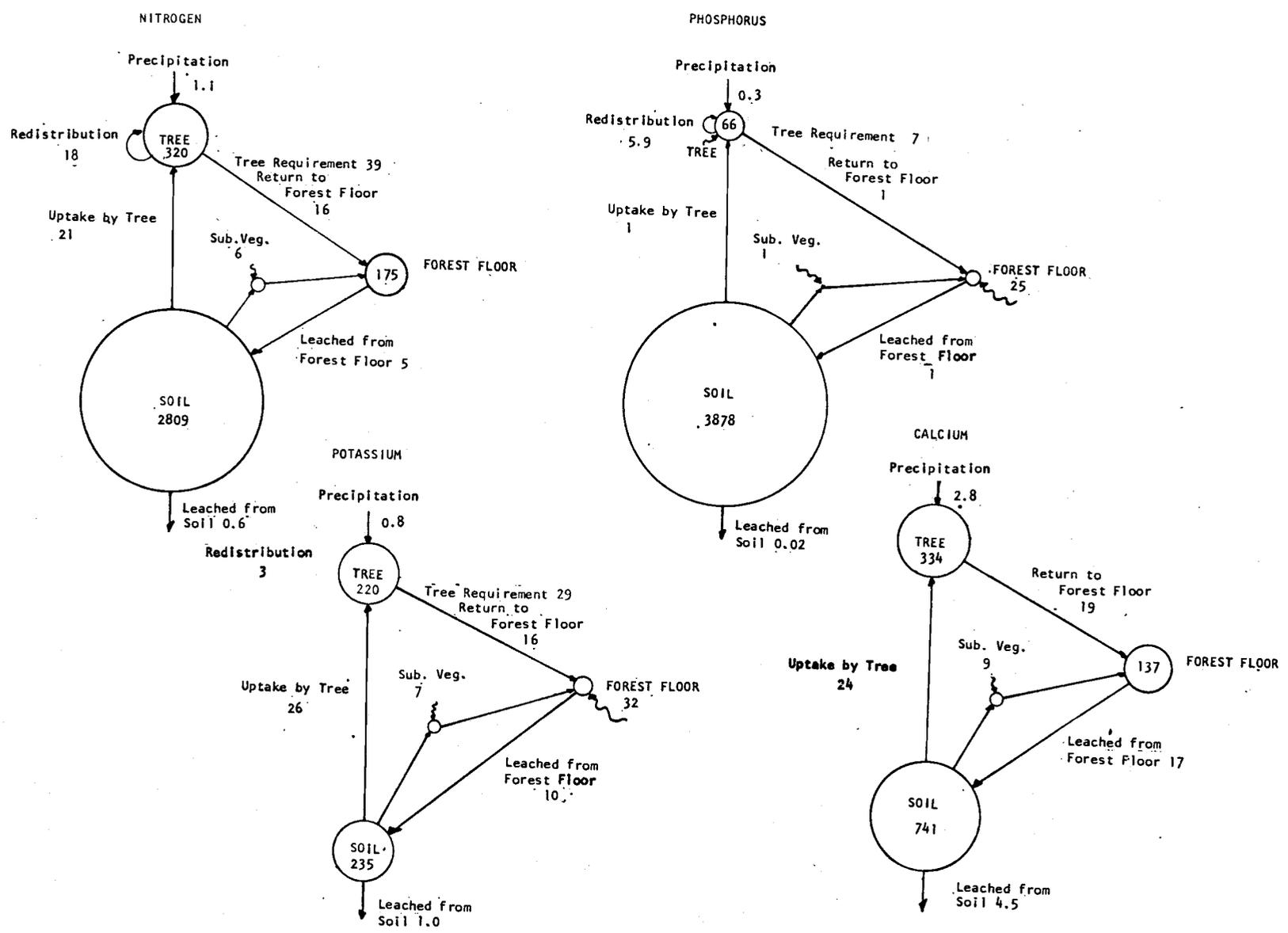


Figure 3.21. Distribution and cycling of nitrogen, phosphorus, potassium and calcium in a young-growth Douglas-fir ecosystem at the Thompson site. Nutrient capitals and flows are kg per ha and kg per ha per year, respectively.

on watershed 10 averages 6380 kg per ha per yr, of which only 47% or 3000 kg per ha per yr is foliage. The difference between foliage litterfall at the two sites is due to the presence of arborescent deciduous and evergreen hardwoods in the lower canopy of watershed 10. Arborescent hardwoods are virtually absent from the Thompson site. At the Thompson site, over 90% of all nutrients in litter are returned in the foliage component of the litter. In contrast, on watershed 10, 48% nitrogen, 69% phosphorus, 61% potassium, and 70% calcium are returned annually in foliage litter (Grier et al. in press). Also in contrast to the Thompson site, over half the nutrient cycling is taking place in subordinate vegetation, assuming that nutrient content is proportional to dry weight. Turnover time is six years for the overstory litter but only two years for the understory litter.

Another important difference in comparing litterfall between the two sites is the difference in nutrient return via epiphyte-fall. On watershed 10, epiphytes on branches alone amount to a dry weight of 1100 kg/ha and contain 13.5 kg/ha nitrogen. Many lichens fix atmospheric nitrogen and, because of this and the possible role in absorbing and desorbing nutrients in precipitation and throughfall, further studies of the role of epiphytes in nutrient cycling are planned. On watershed 10, annual nutrient return by epiphyte-fall is 6.7% nitrogen, 3.6% phosphorus, 5.6% potassium, and 0.7% calcium of total nutrient return by litterfall. Epiphytes are a negligible component of litterfall at the Thompson site (Grier et al. in press).

A portion of nutrient return by litterfall is in the form of fine organic matter such as insect frass, spores, pollen, and dust. This material is overlooked in many nutrient cycling studies in spite of the high nutrient concentrations and high-energy carbon compounds it contains. This microlitter has a strongly seasonal input to the litter layer (est. 3.8 kg per ha per yr of nitrogen) and studies of microlitter input and turnover are currently in progress (Grier et al. in press).

Nutrient return in throughfall and stemflow. Nutrient return by throughfall for the two sites is also shown in Figures 3.20 and 3.21. As can be seen from these data, there are differences between the two sites for most nutrients. These differences are not entirely due to differences in foliage mass, but rather are due to the much larger component of hardwood species in the overstory of watershed 10. Greater precipitation on watershed 10 may also play a role, however. Some of the differences observed may be due to the greater branch mass of the plant communities on watershed 10 and may also reflect changes in solution chemistry resulting from leaching of epiphytes by precipitation.

Stemflow measurements are currently in progress on the intensive study plots at the Thompson site and from the 15 mapping units on watershed 10. Some interesting results are coming from this work. Earlier studies of stemflow in old-growth Douglas-fir stands (Rothacher 1963) indicated only 0.27% of total precipitation reached the soil surface by stemflow; but this study included only trees greater than 28 cm diameter at breast height (dbh). Our results in similar, nearly adjacent stands and based on trees greater than 5 cm dbh show that 2%-4% of total precipitation

returns to the soil as stemflow. This indicates that small stems may carry a disproportionate share of total stemflow in old-growth stands and, further, that stemflow estimates based strictly on tree basal area may be inaccurate.

Return of nutrients to the soil by stemflow is not strictly proportional to stemflow water volumes. Data from the Thompson site indicate that of the total nutrient return in solution, 12% nitrogen, 25% phosphorus, 24% calcium, and 13% potassium are returned to the soil annually by stemflow representing less than 10% of yearly precipitation (Grier et al. in press).

Nutrient return by both stemflow and throughfall is sensitive to climatic factors and probably also to the phenological stage of the vegetation. Figure 3.22 shows how potassium return in stemflow for a single tree differs between a cool spring (1970) and a warm spring (1971) at the Thompson site.

Nutrient return through decomposition and leaching. Over 88% nitrogen, 33% phosphorus, 18% potassium, and 70% calcium reaching the soil surface in the Douglas-fir forests under study do so by litterfall. Thus studies of litter decomposition, nutrient mineralization, and nutrient transfer to the soil are a vital component of nutrient cycling studies in the Coniferous Biome. Work is currently in progress at both intensive sites examining the factors involved in litter decomposition and the relationship between decomposition and nutrient mineralization.

Decomposition studies centered on watershed 10 have emphasized determination of rates of decomposition over habitat types ranging from wet to dry and from cold to warm on a variety of substrates both woody and nonwoody. Litter temperatures and moisture are being monitored, as well as the chemical quality of litter including nutrient elements, lignin, and cellulose.

Data on nutrient mineralization during decomposition are being provided from two sources, tension lysimetry and analysis of litterbags. Tension lysimetry provides integrated mineralization data for the total litter mass, while litterbag studies provide mineralization data for the specific substrates. Results indicate that in the first six months of decomposition, weight loss of green needle litter is 17%, while potassium, magnesium, and calcium concentrations decrease 75%, 75%, and 15%, respectively; nitrogen and phosphorus concentrations show no change (Grier et al. in press). Similar data are now available for a wide variety of substrates. For example, weight loss of fallen conifer needles and moss (Isotrichum stoloniferum) is 10% in the first year, while the nitrogen-rich lichens lose 50%-60% of their weight in one year. Between 800 and 1600 kg/ha of lichens are supported on old-growth Douglas-fir branches and stems at the Andrews Forest. From 35% to 40% of the total lichen crop falls each year, constituting an addition of 5.6-12.8 kg per ha per yr of nitrogen to the forest floor (Grier et al. in press).

Studies involving decomposition of Douglas-fir sapwood stakes at the litter surface, at the soil-litter interface, and buried in the soil

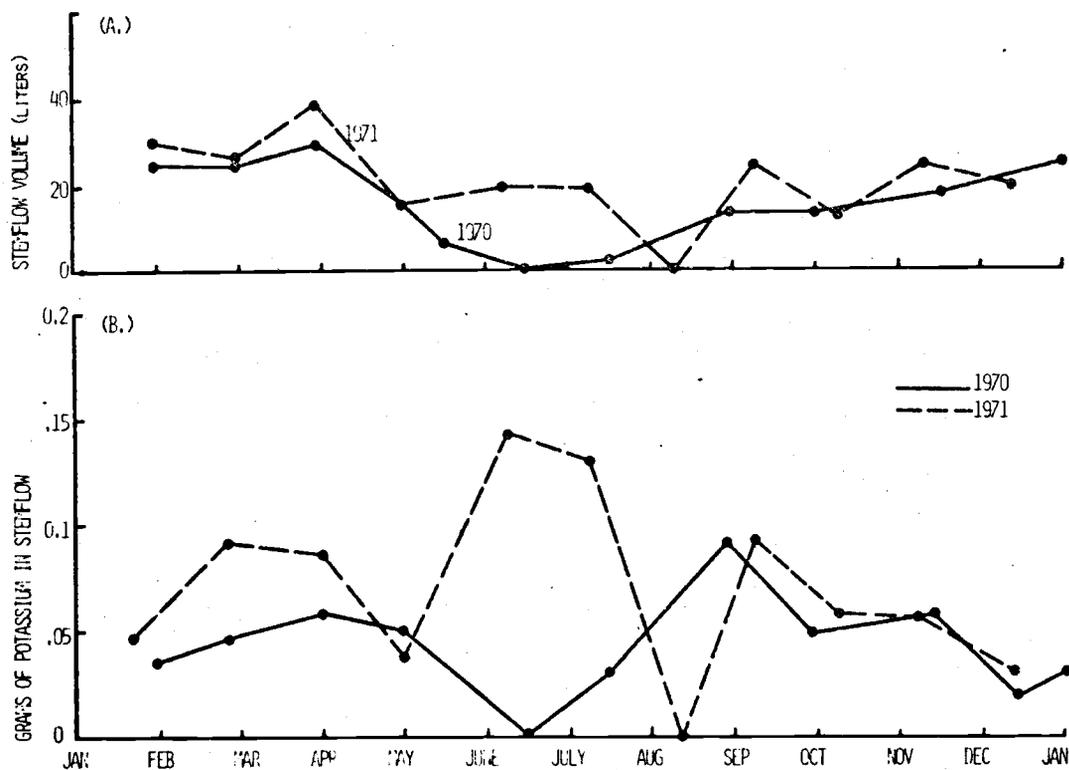


Figure 3.22. Volume of stemflow (A) and quantity of potassium transferred to the soil (B) from a 15-cm diameter Douglas-fir during two successive years at the Thompson site.

at the Thompson site and watershed 10 show that decomposition proceeds in a stepwise manner (Minyard and Driver 1973). During the first month of exposure, short-chain polysaccharides and other materials soluble in cold water are leached or utilized by nondecay microorganisms. As decomposition progresses, the wood constituents celluloses, hemicelluloses, and lignins are depolymerized by decay fungi. The by-products of such processes are leached into the soil, utilized by soil microorganisms, or both, and ultimately become part of the soil organic matter. The mechanisms of leaching through the soil were discussed earlier.

Nutrient return through uptake and nutrient requirements. To this point, the discussion has been focused mainly on movement of nutrients from standing vegetation to the soil. Nutrient uptake and utilization by standing vegetation complete the internal cycle of nutrients in coniferous forests.

Nutrient uptake figures for the Andrews Forest and Thompson site are shown in Figures 3.20 and 3.21. Uptake at the old-growth site is considerably less than in the young-growth site.

Nutrient requirements for both sites are low compared with stands in other parts of the world. For example, Nelson et al. (1970) report 34.2 kg/ha nitrogen, 4.7 kg/ha phosphorus, 18.9 kg/ha potassium, and 22.0 kg/ha calcium accumulated by five-year-old loblolly pine (Pinus taeda L.) in producing 9400 kg/ha of organic matter during one year. Nutrient requirements for the old-growth forest are substantially below those of the 42-year-old stand of the Thompson intensive site in spite of the threefold greater biomass accumulation on watershed 10. The lower demand for nutrients by the old-growth forest may indicate a successional trend in decreased nutrient demand that will be continued into climax Tsuga heterophylla stands typical of this area.

The watershed 10 ecosystem cycles large amounts of calcium in comparison with that of the Thompson site. Evidence of this may be seen in the large calcium outflow in drainage water (Figure 3.20) and the greater calcium return by litterfall in the old-growth stand of watershed 10.

Nutrient requirements for stand growth in coniferous forests are not provided exclusively from sources in the soil; instead, approximately 50% of nutrient requirements are met by translocation of nutrients within individual trees. A major contribution of mineral cycling research in the Coniferous Forest Biome has been quantification of the amounts of nutrients supplied by the soil and by translocation. Table 3.21 shows nitrogen uptake and translocation in stands ranging from 9 to 95 years old on the same soil series at the Thompson site. Obviously from these data the proportion of nitrogen taken annually from the soil remains nearly constant during this period in the stand development.

Another interesting trend can be seen by expressing annual nitrogen requirement as a percentage of the total in the overstory (Table 3.21). Here, a slight peak in nitrogen annual requirement is suggested somewhere between 35 and 73 years of age. Extending this trend to the old-growth stands of watershed 10, we find that requirement/total is 0.65% of

Table 3.21. Changes in the dynamics of nitrogen uptake, requirements, and accumulation for a series of ages of Douglas-fir (after Cole et al. in press b).

Age (yr)	Total tree accum. (kg/ha)	Tree req. (kg/ha)	Tree uptake (kg/ha)	Req./total tree (%)	Uptake/total tree (%)	Uptake/req. (%)
9	33	4	2	12	6	55
35	288	39	21	14	7	54
73	297	42	22	14	7	53
95	362	35	19	10	5	53

Table 3.22. Comparison between alder, Douglas-fir, and true fir regarding the dynamics of nitrogen uptake, requirements, and accumulation (after Cole et al. in press b).

Tree	Total tree accum. (kg/ha)	Tree req. (kg/ha)	Tree uptake (kg/ha)	Req./total tree (%)	Uptake/total tree (%)	Uptake/req. (%)
Alder (age 34)	589	152	82	39	20	54
Douglas-fir (age 35)	288	39	21	14	7	54
True fir	320	22	10	7	3	44

accumulation in the tree. An interesting question, as yet unanswered, is whether this pattern of nutrient utilization will be continued as Tsuga heterophylla succeeds the present Pseudotsuga menziesii overstory. These data indicate that early successional stages place larger nutrient demands on a site than do later stages (Cole et al. in press b).

Comparison of ecosystems dominated by alder, Douglas-fir, and Pacific silver fir. To obtain some concept of differences in nutrient cycling in ecosystems dominated by different species, nutrient cycling in red alder and Douglas-fir at the Thompson site and Pacific silver fir at Findley Lake can be compared in Figures 3.21, 3.23, and 3.24. The higher soil nitrogen in the alder ecosystem is due in part to the symbiotic fixation relationship between alder and microorganisms. It has been determined that 35-40 kg per ha per yr of nitrogen can be fixed in this way at the Thompson site. Soil values in the Pacific silver fir stand are also considerably higher in nitrogen than Douglas-fir stands. This stand is considerably older than the other stands (175 years) and a considerable amount of nitrogen is returned to the soil through litterfall, throughfall, and decomposition.

The alder and Douglas-fir stands, although of similar age and biomass, have accumulated greatly differing amounts of nutrients. Alder has fixed greater amounts of nitrogen but is lower in other nutrients.

There is a decreasing annual uptake of nitrogen as we progress from a pioneering (alder) to a climax forest ecosystem (Pacific silver fir). In addition, the forest becomes more dependent on internal cycling for nitrogen, depending less on the soil as a supplier. The rate of cycling (as can be seen from the comparison between uptake and total tree accumulation, Table 3.22) also decreases as we progress through this successional series.

It is apparent that the principal mechanism affecting the rate of cycling and uptake by a given species is the length of time foliage is retained. In the above example, obviously alder retains its foliage but for a single growing season while true fir foliage can be retained for upward of 12 years. That, however, does not explain what relative ecological advantage or disadvantage such behavior provides. While confirming data have not been collected, it would appear that tree species associated with slower rates of elemental cycling and uptake are associated with sites of relatively slow rates of organic decomposition. For example, the true fir area has a thick organic accumulation obviously suggesting extremely slow rates of organic mineralization. A tree species requiring a high rate of available nutrients would not be ecologically suited to this site.

3.1.2.4. Stand and watershed modeling of water, carbon, and nutrient cycling. The discussions in the previous section have treated water, carbon, and nutrient cycling as somewhat independent functions. In reality they are not independent but are closely coupled; the carbon and water act as the principal carrier for nutrients. The linkage and the interactions between these cycles can be effectively examined only by models. We have constructed a simulation model consisting of coupled

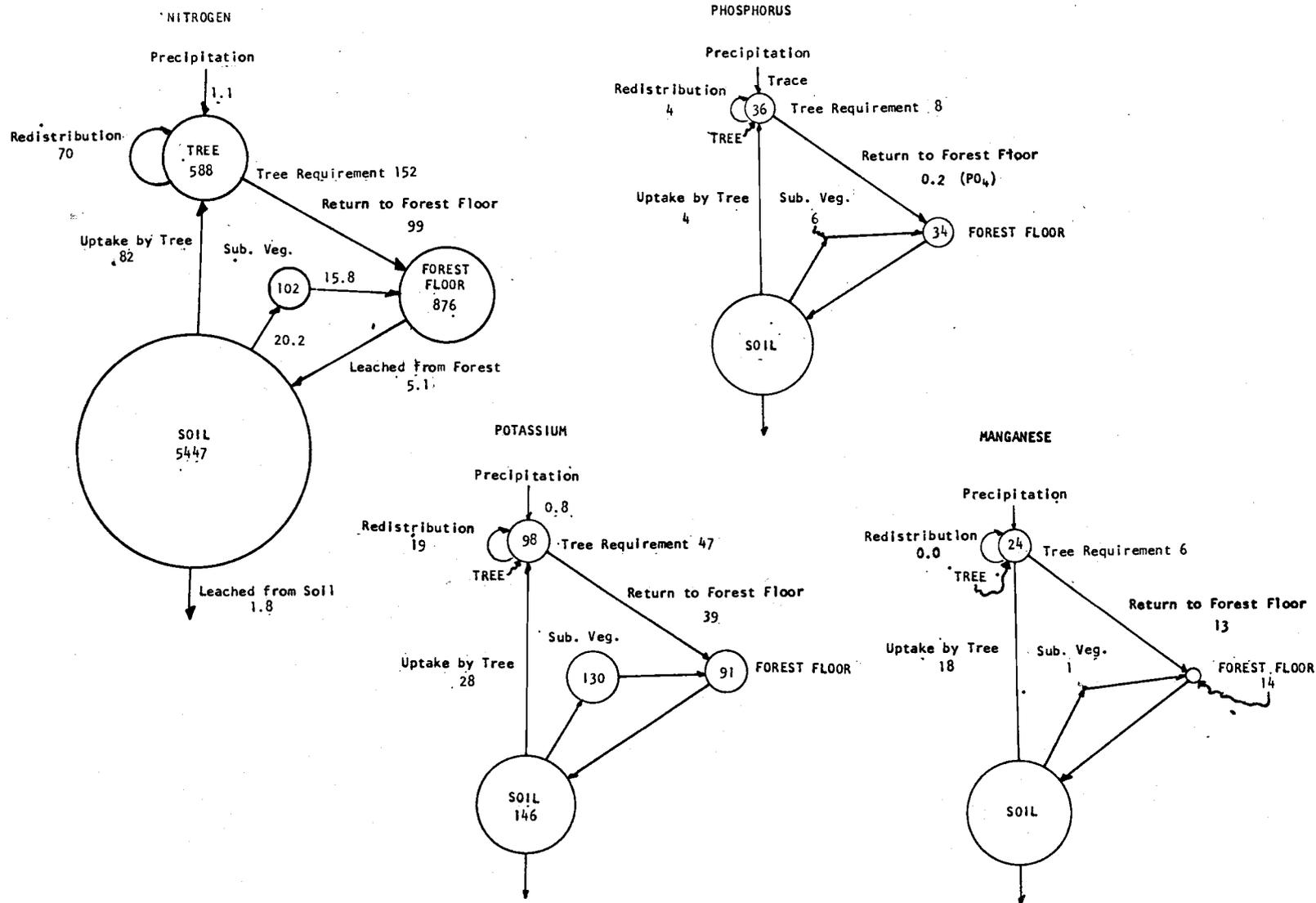


Figure 3.23. Distribution and cycling of nitrogen, phosphorus, potassium and manganese in a 35 year-old red alder ecosystem at the Thompson site. Nutrient capitals and flows are kg per ha and kg per ha per year, respectively.

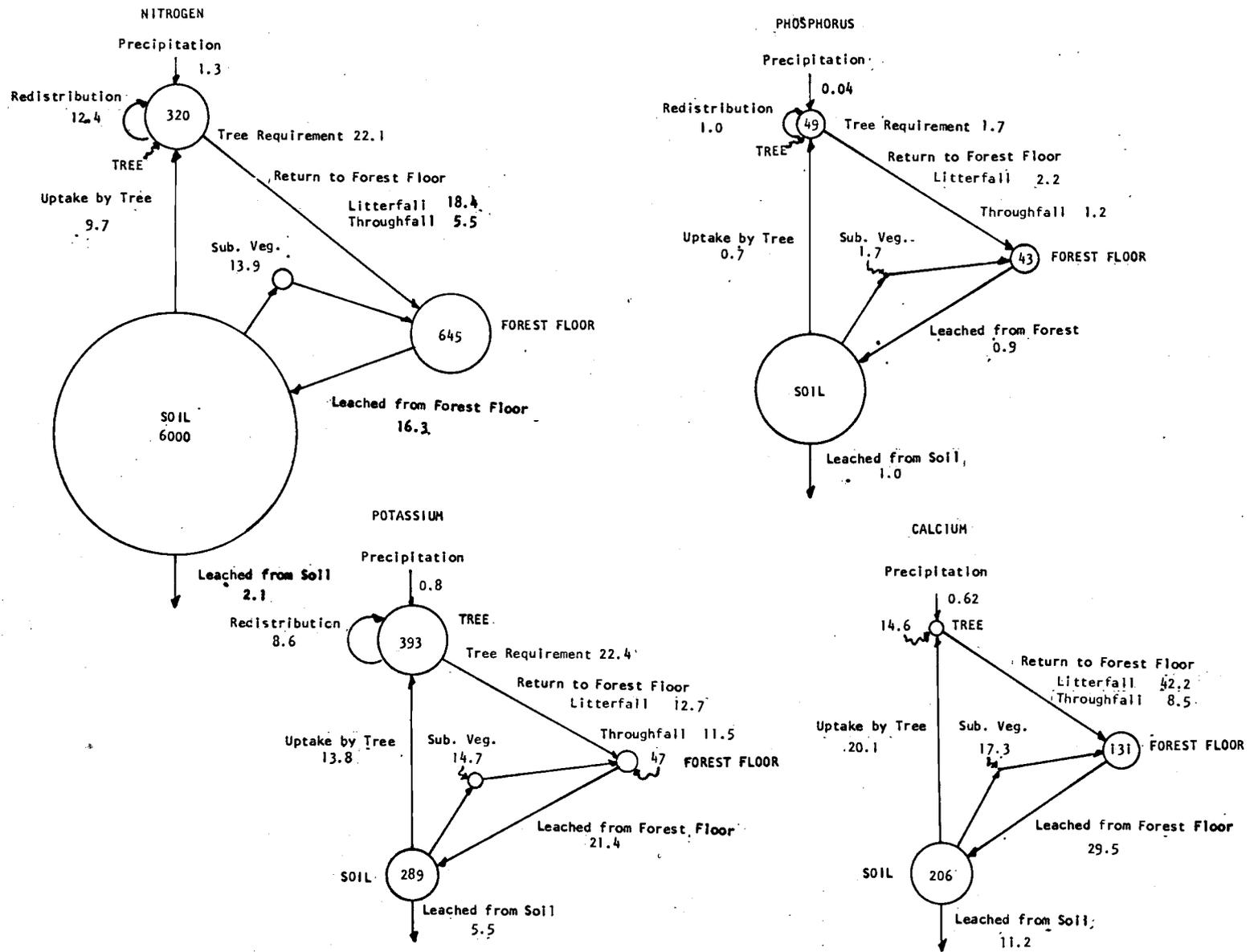


Figure 3.24. Distribution and cycling of nitrogen, phosphorus, potassium and calcium in a 175 year-old Pacific silver fir ecosystem at Findley lake. Nutrient capitals and flows are kg per ha and kg per ha per year, respectively.

submodels of carbon, water, and nutrient cycles. The models are relatively simple and, for example, in the case of nutrient cycling, individual nutrients are not considered separately but all are lumped into anion and cation elements with the exception of H^+ and HCO_3^- , which are considered separately.

The model consists of a set of coupled difference equations describing flow of materials between compartments representing storages in various substrates, positions, and species groups. The method has been described by Reichle et al. (in press) and Sollins et al. (in press), and is an outgrowth of earlier work by Olson (1965) and Odum (1971). The submodels for water, carbon, and nutrients are coupled through interactions among their respective flow functions.

Conceptual models of the subsystems, consisting of box-and-arrow diagrams, are presented in Figures 3.25-3.28. Annual budgets of accumulation and transfer among different components of the system were determined and data voids were noted. By assuming material balance, unmeasured transfers were calculated. From the budget data and information on factors affecting rates of processes, dynamic simulation models were constructed enabling us to study both ecosystem dynamics and behavior of these systems under stress or manipulation.

The growth of primary producers and the chemistry and amount of water as functions of time are the outputs of prime interest. The model structure has been designed to accommodate the impact of stresses and manipulation (including fertilization, defoliation, clearcutting, and climatic changes) on ecosystem behavior.

The modeling approach presently restricts us to areas of land that are assumed to be homogeneous with respect to soils, topography, climate, species composition, and age of vegetation. Spatially homogeneous areas can be modeled by subdividing each area into smaller, homogeneous units.

Overall model structure. As previously mentioned, our ecosystem model is conceived as a hierarchical structure in which the first level consists of modules for different substances. These are carbon, water, and four groups of nutrient elements in ionic form, namely, H^+ , other cations, HCO_3^- , and other anions. Material balance is maintained strictly in all except the H^+ and HCO_3^- modules. Driving variables of the model consist of air temperature, precipitation, vapor pressure deficit, solar radiation, and concentrations of all four element groups in the precipitation. Day length and soil and litter temperature are calculated. Transfers are calculated at intervals of one day for the water module and one week for the carbon module. Nutrient transfers are calculated at daily or weekly intervals depending on whether they are calculated as part of a water or a carbon transfer, respectively.

Section 6.2 describes model documentation, and many of the model equations are presented there. Examination of these equations reveals the range of realism adopted in our approach. In cases where the process

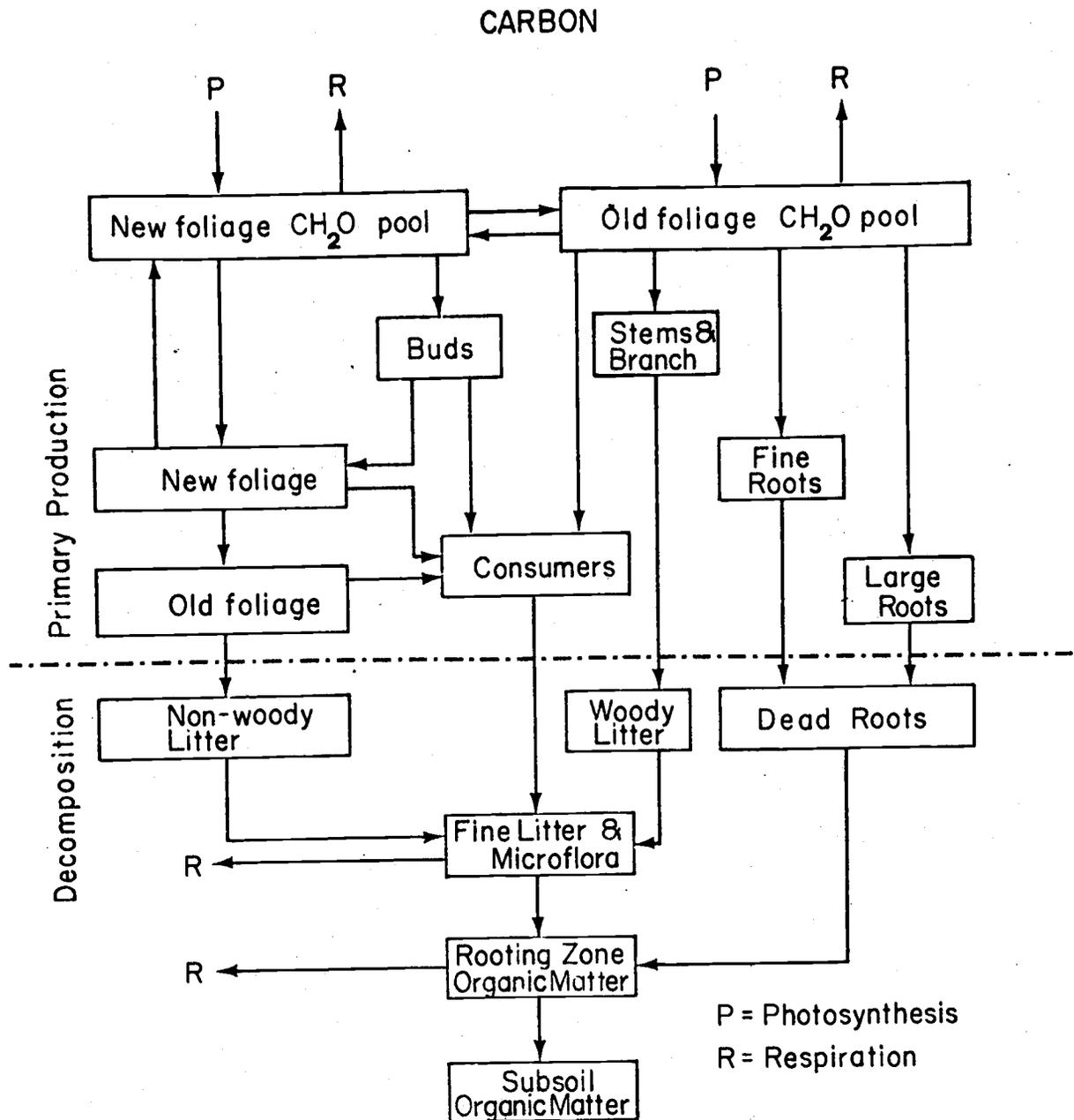


Figure 3.25. Flow diagram for the carbon module.

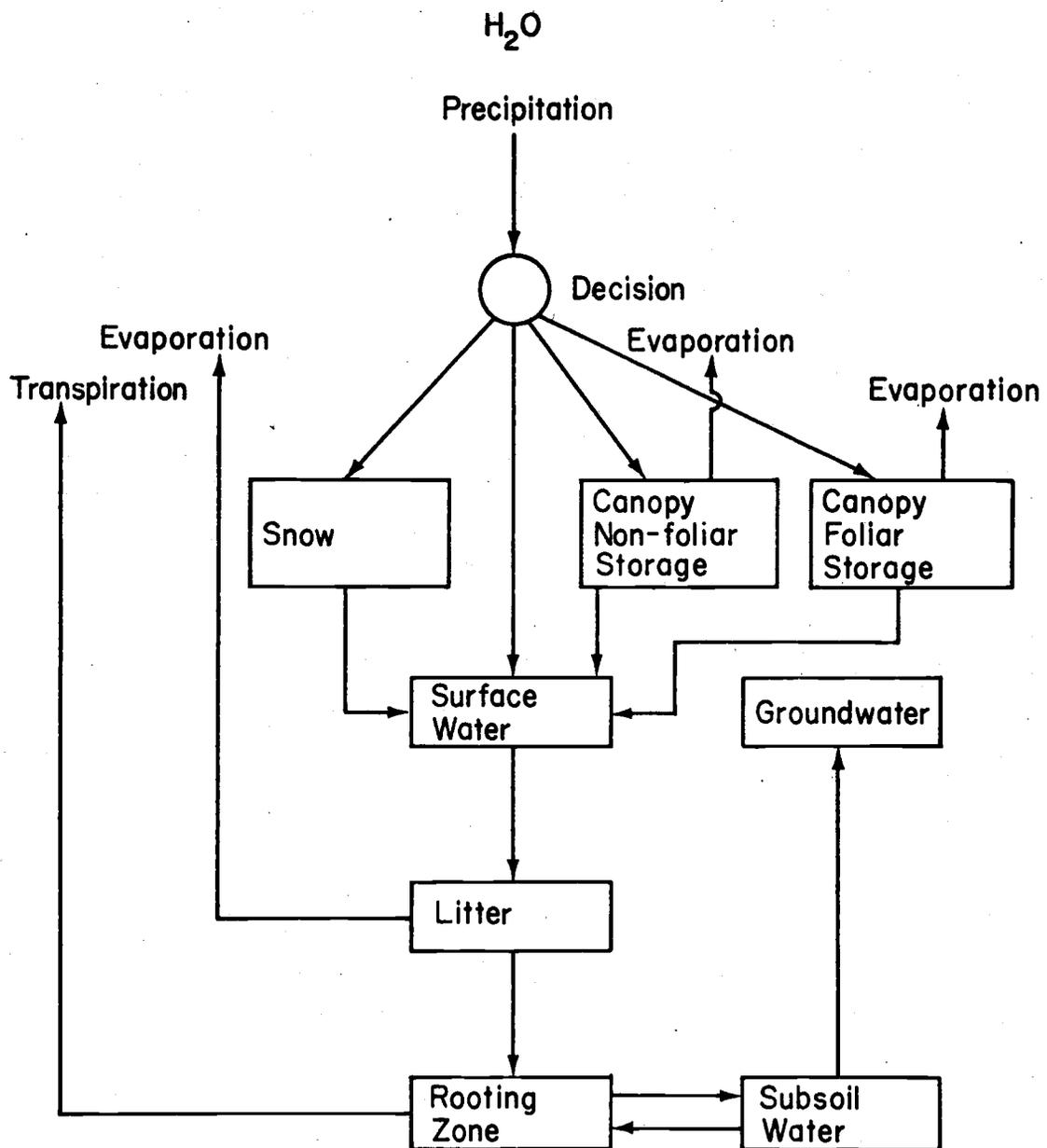


Figure 3.26. Flow diagram for the water module.

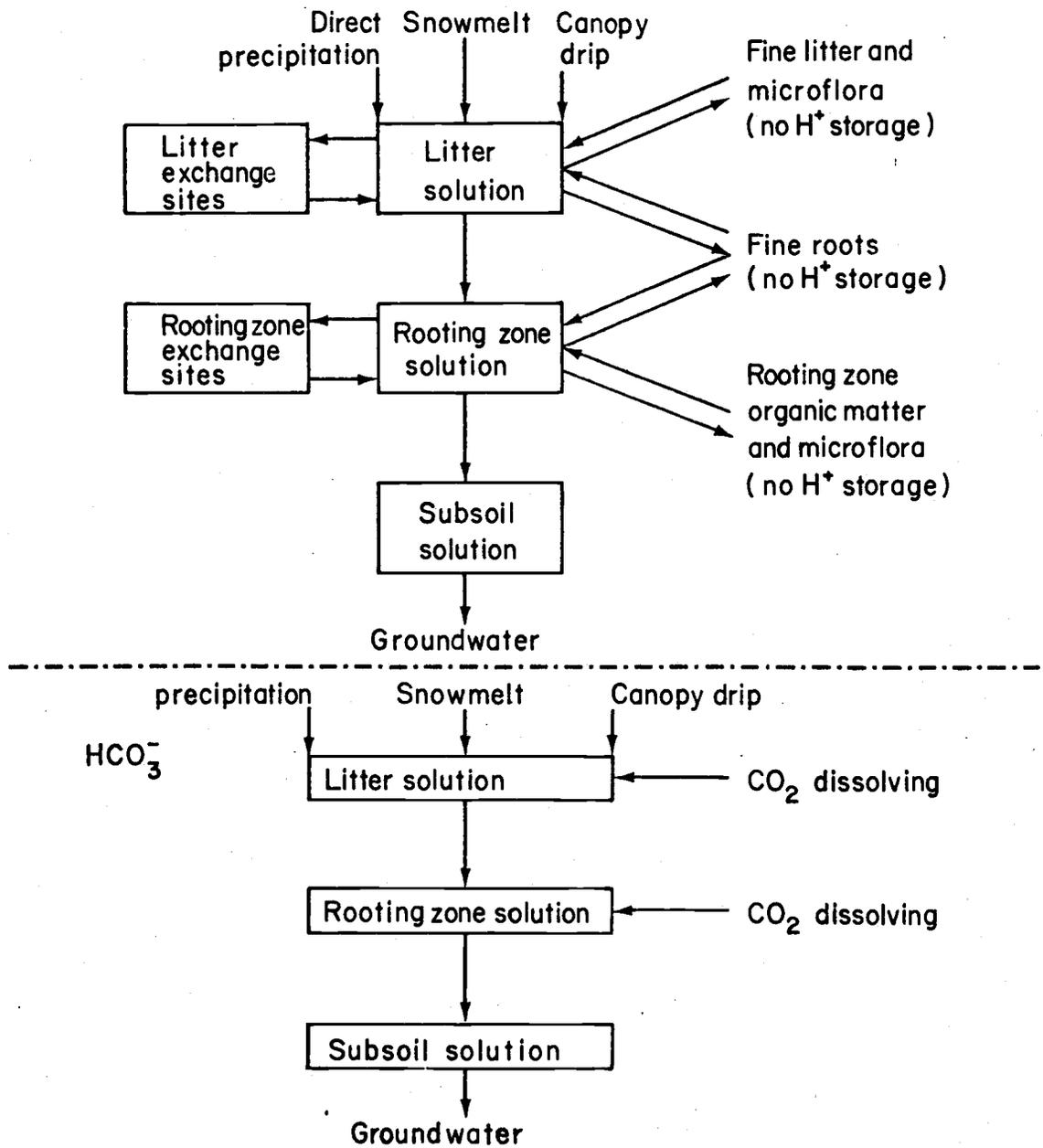
H⁺

Figure 3.27. Flow diagram for the H⁺ and HCO₃⁻ section of the nutrient module.

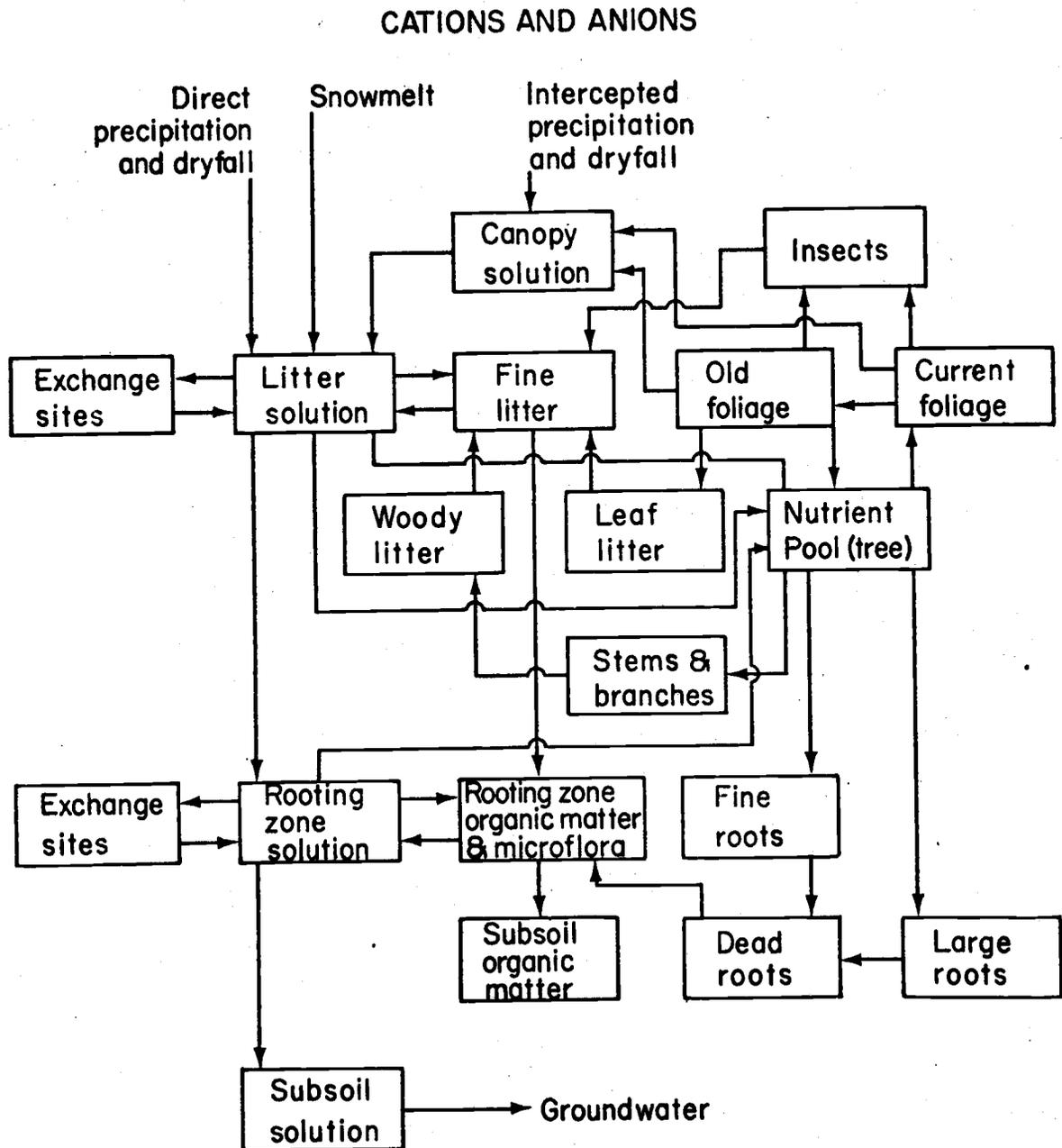


Figure 3.28. Flow diagram for the cation and anion section of the nutrient module.

is not well studied or definitive data are lacking, linear donor control is used. For example, decomposition of dead roots is expressed as:

$$F_{62,21} = B_{38}G_{60}X_{62}$$

where $F_{62,21}$ refers to the transfer from the dead root compartment X_{61} to the rooting zone organic matter compartment X_{21} , B_{38} is a parameter obtained by curve-fitting, G_{50} is a function of rooting zone soil temperature, and X_{62} is the carbon content of the dead root compartment. The expression for net daytime photosynthesis G_3 is more complex and is based on simple assumptions regarding light filtering through a canopy and the photosynthetic response of individual leaves to temperature, light, and foliage resistance (see Sollins et al. in press). The equation presented has been validated by comparison with a detailed mechanistic model developed from basic gas-exchange data.

$$G_3 = \frac{-B_4 Z_3 G_2 X_2}{B_6 (X_2 + X_3) G_{26}^2} \ln \frac{B_5 + Z_4 \exp -B_6 (X_2 + X_3)}{B_5 + Z_4}$$

where

$$G_2 = \begin{cases} B_7 Z_2 (44 - Z_2)^{0.35}, & 0 < Z_2 < 44 \\ 0 & , \text{ otherwise} \end{cases}$$

and Z_3 is day length (fraction of the day); G_2 is the air temperature effect on photosynthesis; Z_2 is air temperature ($^{\circ}\text{C}$); B_7 is a factor such that $G_2 = 1$ for $Z_2 = 22^{\circ}\text{C}$; X_2 is new (current year) foliage biomass (tons carbon per hectare); X_3 is old foliage biomass; B_6 is the light extinction coefficient (hectares per ton); G_{26} is current foliage resistance averaged over a week (seconds per centimeter); B_4 is the maximum photosynthesis rate at some temperature, day length, foliage resistance, and foliage biomass; B_5 is the light intensity at which photosynthesis is one-half the maximum rate at those conditions; and Z_4 is incident shortwave radiation (langleys per minute) averaged for the week.

The photosynthesis expression exemplifies the sorts of functions we would like to develop (but obviously have not) for all transfers. It is, we claim, physiologically reasonable, testable in the field (at least part by part), and includes (except for the nutrient effect, which is not shown) all factors expected to be of importance. Our modeling approach permits us to substitute more realistic expressions as they

become available. The structures of the carbon, water, and nutrient modules are described in the next paragraphs and selected outputs from the model are presented in a following section.

Structure of the carbon module. The carbon module divides logically into three parts (Figure 3.25), primary production, consumers, and decomposition. The decomposition part includes litter, dead roots, standing deadwood, soil organic matter, and the associated free-living organisms. The consumer section is at present only a single compartment but should be adequate for initial studies of effects of consumers on primary producers. A more complex food chain model (Strand in press) will eventually be substituted for this compartment to study effects of changes in food supply on consumers. Interactions between different vegetation components can be investigated by using parallel models for shade-intolerant overstory species, shade-tolerant overstory species, understory species, and subordinate vegetation.

The arrangement of the compartments within the primary producer carbon model builds on previous studies by Sollins et al. (in press). They divided the vegetation into three parts--a photosynthetic layer, an uptake layer, and a massive but relatively inert layer of supporting and conducting tissue interposed between. Ideally each of these layers then would be divided into a structural and a labile component. The structural part includes protein, cellulose, and lignin, while the labile part includes sugars, starch, and amino acids. The labile pool associated with the foliage is very small and transitory, however, and the current version of the model contains no stored carbohydrate. The labile pool associated with the fine roots, on the other hand, has been included with the larger pool associated with stems, branches, and large roots.

Another feature of this model is the presence of a bud compartment that limits the possible leaf production during a growing season (Sollins et al. in press). In addition, fine roots include the associated mycorrhizae, and standing deadwood is included in the woody litter compartment. The structure of the decomposition module is routine (see Sollins et al. in press) except for the inclusion of a fine-litter compartment.

Immediately beneath the litter is a layer termed the "rooting zone." It typically corresponds to the A or A1 horizon but is defined as that region of the mineral soil from which uptake occurs and in which fine roots are found. The name is misleading, however, since we allow, even in the model, for uptake in the litter by fine roots. A better term is lacking.

Structure of the water module. The water module (Figure 3.26) is based on a watershed model developed by Overton and White (1974). The philosophy of this model is unusual compared with previous hydrologic models (e.g., Huff 1968, Brown et al. 1972, Goldstein and Mankin 1972) in that it attempts a realistic representation of biological phenomena such as interception and transpiration.

The model has been modified to include more biology and to be more suitable for coupling with the carbon and the various nutrient modules. For example, a litter moisture compartment (omitted from Overton and White's model because of its nearly inconsequential storage capacity) is included here because of the dependence of litter decomposition on litter moisture content and because various functions in the nutrient modules require this information. The model describes water cycling on a homogeneous land area rather than a watershed and neglects the effects of horizontal waterflow.

Couplings with other modules include the use of foliage biomass to calculate interception and transpiration and use of litter standing crop to calculate the water storage capacity of the litter. Litter temperature is used in calculating evaporation from the litter and rooting zone temperature is used in calculating transpiration.

The major objective of the stand and watershed hydrologic studies is to prepare a model that will provide predictions of the hydrologic state of a coniferous watershed at any desired place at any desired time, where state is defined by the input needs of other submodels or systems, particularly primary producers. Several attempts at developing watershed models have been made (Brown et al. 1972, Overton and White 1974, Shih et al. 1973). Particular attention has been paid in the development of these models to subsurface waterflow, which of course is not considered in stand level models. In current models the internal structure of watersheds is conceptualized in Figure 3.29 as being homogeneous, but the models are capable of predicting streamflow with reasonable accuracy (Figure 3.30). A model is currently being developed by J. J. Rogers (pers. commun.) to include topographical stratification based on compartment boundaries along stream courses and vegetative type map boundaries arranged into riparian, midslope, and ridgetop zones as conceptualized in Figure 3.31.

Modelers from the USDA Forest Service, Flagstaff, Arizona, have developed a model for their study area using the structure and modeling programs developed for watershed 10 (J. J. Rogers pers. commun.).

Structure of the nutrient modules. The nutrient modules (Figures 3.27 and 3.28) are based on the separation of the nutrient elements into four ionic groups, H^+ , other cations, HCO_3 , and other anions. What we do hope to study is the overall mineral cycle, the role of the vegetation therein, and the various mechanisms that might lead to increased nutrient loss in the groundwater. The vegetation is included primarily for completeness and is viewed as a pump (or perhaps a waterwheel), which draws nutrients out of the rooting zone and then allows them to return some-time later in the form of litterfall and root death. Because we have included foliar nutrient compartments as well as an overall plant nutrient pool, however, we should be able to predict changes in these compartments under different manipulations and stresses and perhaps infer relationships between these changes and corresponding changes in carbohydrate production and wood formation.

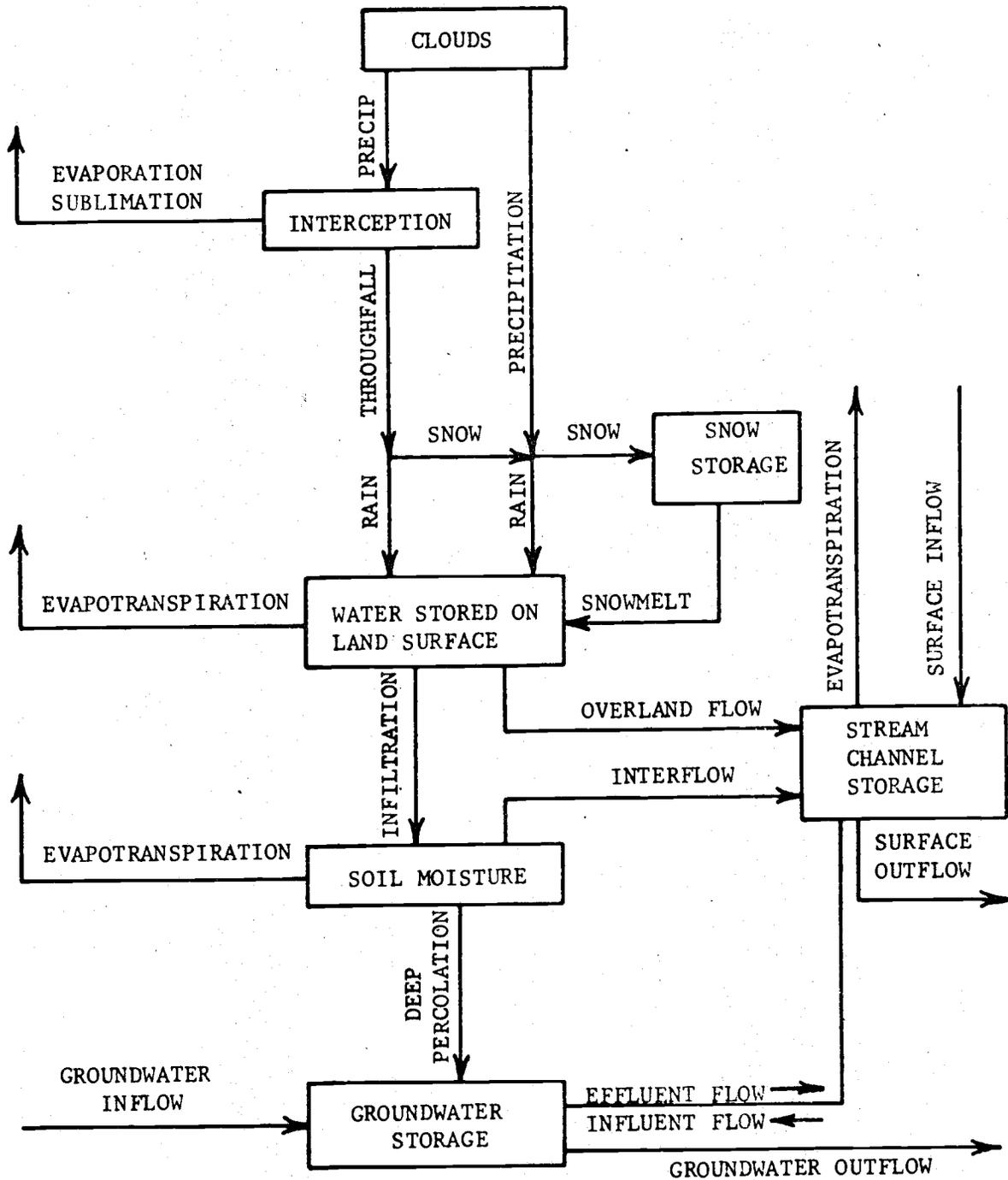


Figure 3.29. A flow diagram of the hydrologic system within a typical watershed area (from Brown et al 1972).

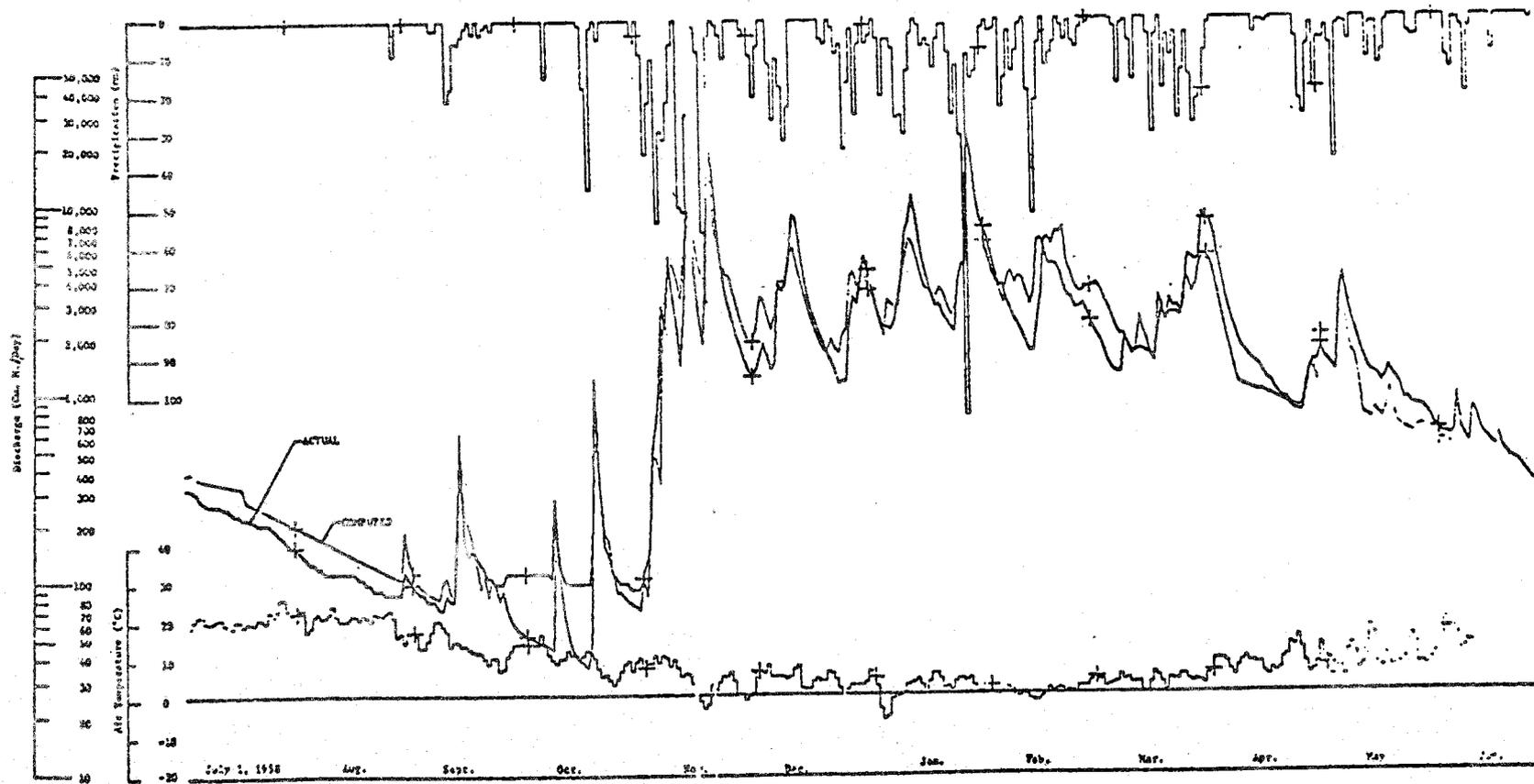


Figure 3.30. Actual and computed water discharge from Watershed 2, H.J. Andrews Experimental Forest (from J.P. Riley and G.B. Shih, P. 32-34 in Waring et al 1973).

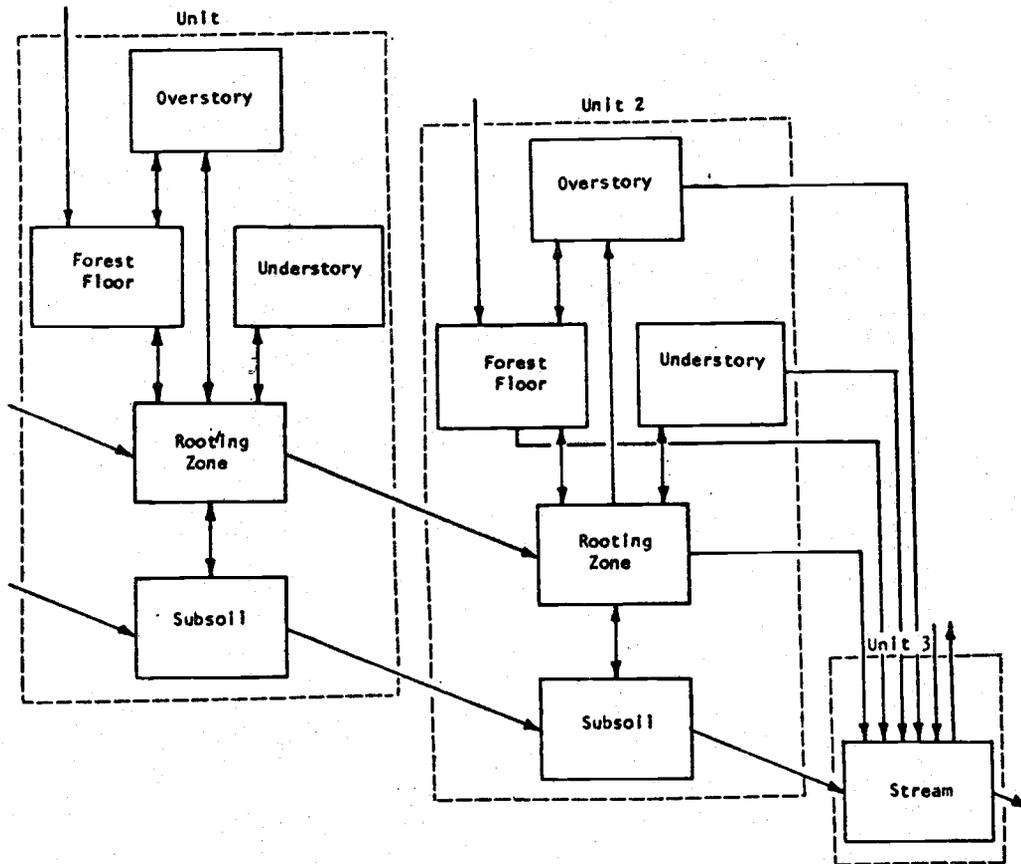


Figure 3.31. Structural diagram of Watershed 10, H. J. Andrews Experimental Forest showing internal stratification.

The transfer of nutrients among the nutrient modules occurs either in the solution phase (e.g., uptake) or in a phase associated with carbon transfer. Except within the vegetation component, most processes involve solution phases. Each solution compartment corresponds to a compartment in the water module (Figure 3.26), i.e., any transfer of water also results in transfer of dissolved nutrients. Uptake, however, is assumed to be an active process dependent on fine-root biomass, nutrient concentration, and temperature. Uptake is limited as the soil dries. An explanation of ionic leaching mechanisms in forest soils of the Coniferous Biome is covered in section 3.1.2.3 (Cole et al. in press a), and these mechanisms are included in the model.

The second group of nutrient transfers involves those associated with carbon transfer in the carbon module. Each storage compartment in the carbon module (Figure 3.25) has a corresponding compartment in the nutrient module. Many transfers are analogous, e.g., litterfall, foliage consumption by insects, and incorporation of nutrients in stemwood and branches in proportion to carbon incorporation.

A material balance of anions and cations is maintained, but this is not the case for H^+ and HCO_3^- since they are not followed through the vegetation. Any movement of these components through the vegetation is considered to be unimportant. Since uptake of cations and anions may not exactly balance, we maintain a balance of charge through appropriate transfers of H^+ .

Couplings between the nutrient modules and the carbon and water module are many and complex. Many transfers are assumed to be directly proportional to transfers of carbon or water. Other coupling variables include dependence of uptake by roots on fine-root biomass, a relation between exchange capacity and organic matter content, and the effect of rooting zone CO_2 production on input of HCO_3^- to the rooting zone solution. This last process may be affected by rooting zone water content in two ways. (1) The dissociation of H_2CO_3 is modeled as an equilibrium reaction and is thus dependent on HCO_3^- concentration, which is affected by water content. (2) Rooting zone water content affects the volume of the rooting zone atmosphere and thus the partial pressure of CO_2 in the rooting zone atmosphere.

Behavior of the coupled carbon-water model. Parameters of the carbon-water model have been calculated for watershed 10 on the H. J. Andrews Forest using 1973 biomass estimates based on recent stem map data and climatic data for 1958-1959. The nutrient cycling modules are currently being set up, and output is not yet available. All figures show the behavior of model variables graphed against time in Julian days.

Behavior of the hydrologic compartments of the carbon-water model corresponds for the most part to that of the Overton and White (1974) model upon which it is based. The snowpack (Figure 3.32) persists until day 120, resulting in constant litter temperatures during that period. Water intercepted by foliar and nonfoliar components of the canopy fluctuates widely (Figure 3.33) reflecting drying between storm events.

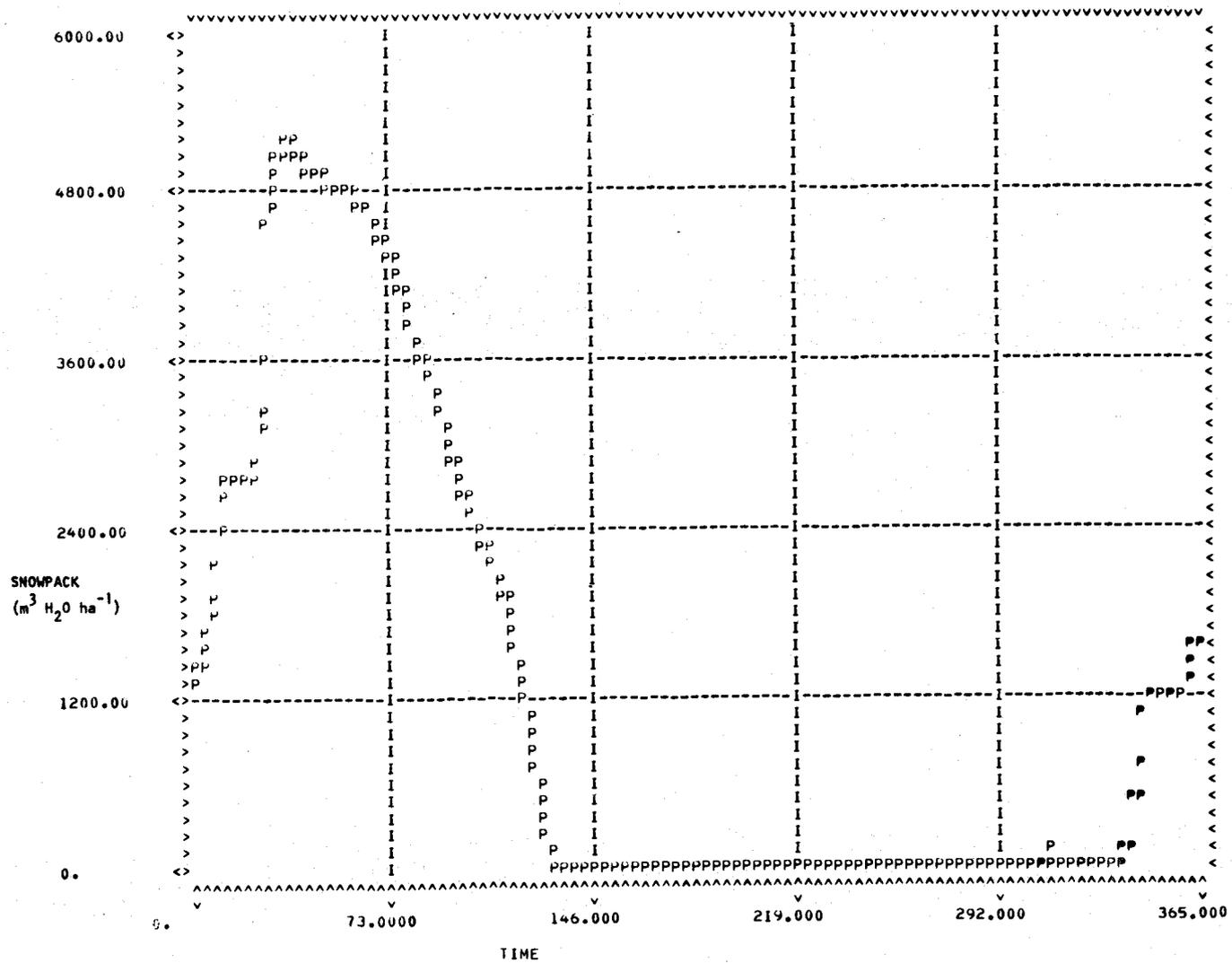
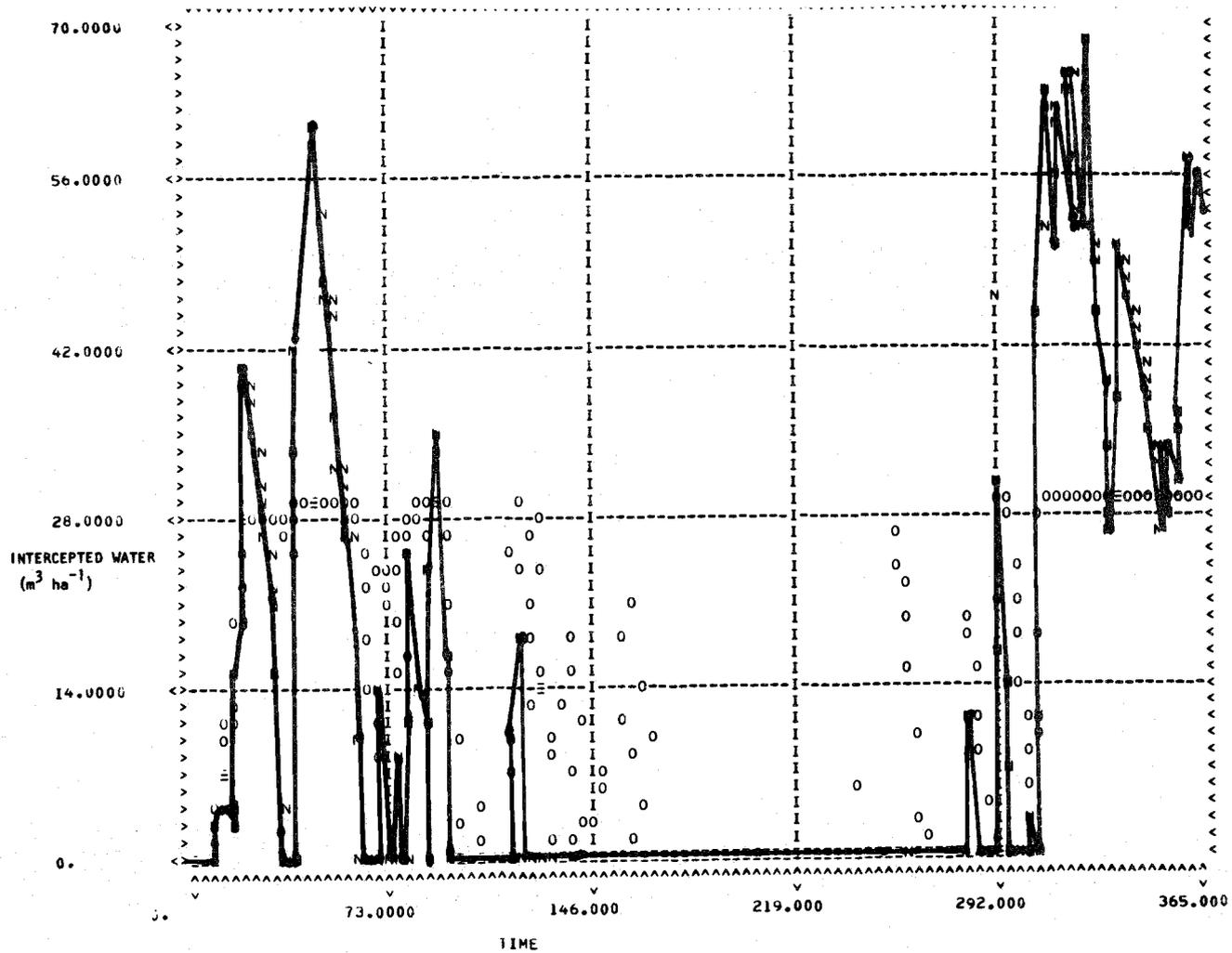


Figure 3.32. Predicted snowpack.



SOLID LINE SHOWS INTERCEPTION BY FOLIAGE; 'O's INDICATE INTERCEPTION BY OTHER SURFACES

Figure 3.33. Predicted intercepted water.

Litter moisture (Figure 3.34) decreases markedly in late summer causing corresponding decreases in decomposition rates. Rooting zone moisture (Figure 3.35) also decreases during the summer. In the current function for calculating plant moisture stress, 2570 cubic meters/ha is the point at which resistance to gas transfer (stomatal resistance) begins to increase and 1819 cubic meters/ha is the point at which transfer effectively stops. These limits are shown in Figure 3.35 and may be compared with the behavior of the carbon compartments discussed below.

The carbon module operates at a weekly interval and uses average weekly weather data as driving variables. Because of this, curves are much smoother, and most discontinuities are artifacts of the plotting program. The growing season extends from day 126 when budbreak occurs to day 280 when, in this version of the model, new foliage becomes old foliage. Patterns of new and old foliage development are shown in Figures 3.36 and 3.37, respectively. The behavior of the carbohydrate pool (Figure 3.38) reflects primarily the behavior of the foliage compartments and climatic factors. The sharp decline in reserves following budbreak is caused by utilization of reserves for new leaf growth. The leaves quickly become self-supporting, however, and the export of the surplus photosynthate to the pool causes an increase in reserves. Unfortunately moisture limitations soon restrict photosynthesis (Figure 3.35) and reserves decline sharply. A brief period of adequate moisture and warm temperatures allows renewal of reserves in the early fall.

Growth of stems and large roots (Figures 3.39 and 3.40) shows some interesting lag effects. In some months root growth lags behind stem growth because of a corresponding lag in soil temperature behind air temperature. Also of interest is a very small increase in stem growth early in the growing season caused by the extremely high carbohydrate levels. Previous models of tree carbohydrate dynamics (Sollins et al. in press) failed to predict early season stem growth. Any substantial moisture stress in a successful system implies very high early-season carbohydrate levels, which may be a partial explanation of the cause of early stem growth. Behavior of the forest floor compartments is affected mainly by litter temperature and moisture content.

Analysis of the response of the carbon-water model to changes in annual climate uncovered many interactions between the water and carbon cycle and is discussed in section 5.9.

3.1.2.5. Succession. The basic descriptions of succession in the three zones (Tsuga heterophylla, Abies amabilis, and Tsuga mertensiana) covered by our succession models are presented below. The material was obtained from Franklin and Dyrness (1969, 1973). Succession in the Picea sitchensis zone is not discussed here. These descriptions are followed by discussion of the stand and regional models developed by Biome modelers.

The Tsuga heterophylla (western hemlock) zone. The early stages of succession following logging have been the subject of a number of studies. These studies generally have been limited to the first five to eight years and detailed patterns for the entire successional period have not been worked out.

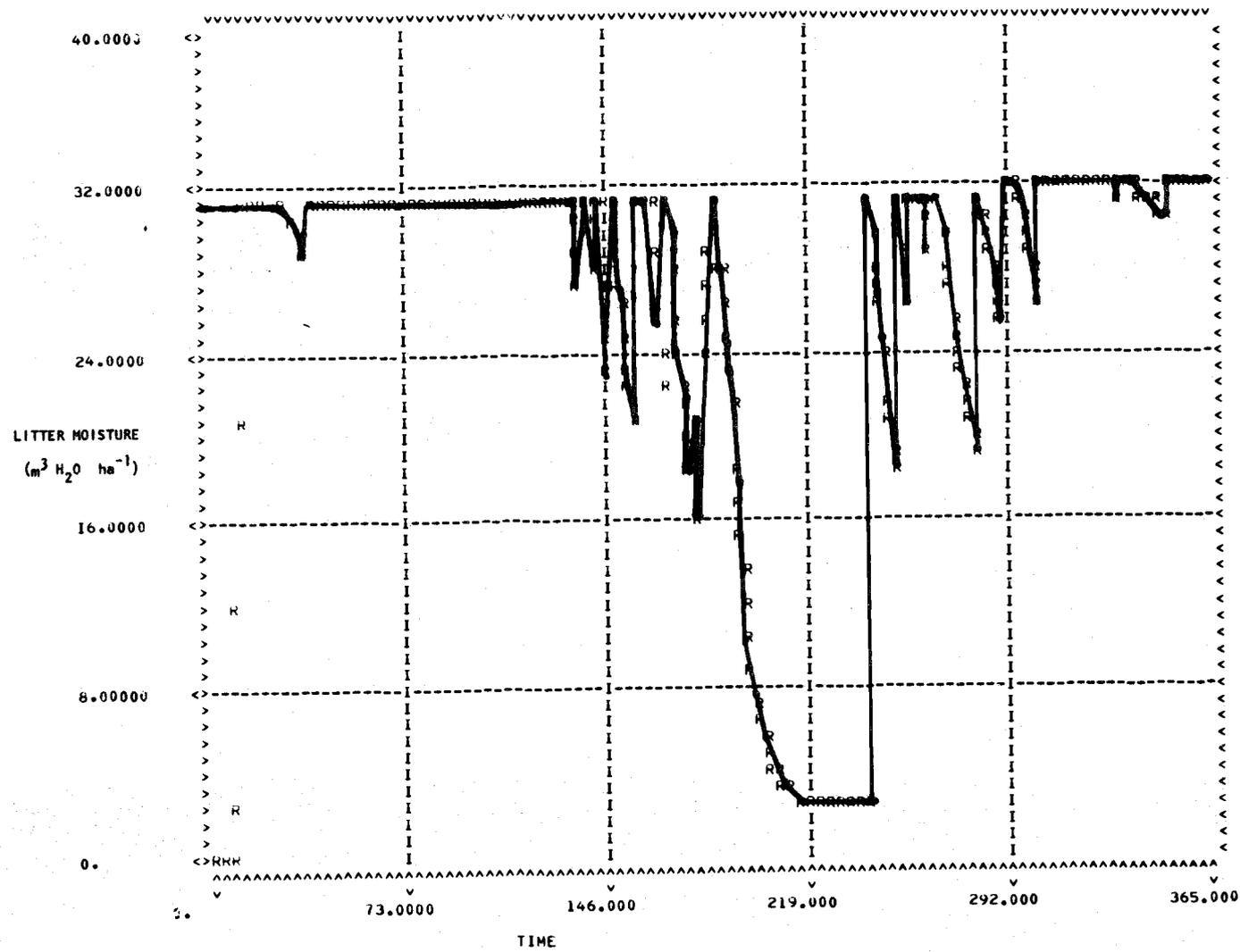


Figure 3.34. Predicted litter moisture.

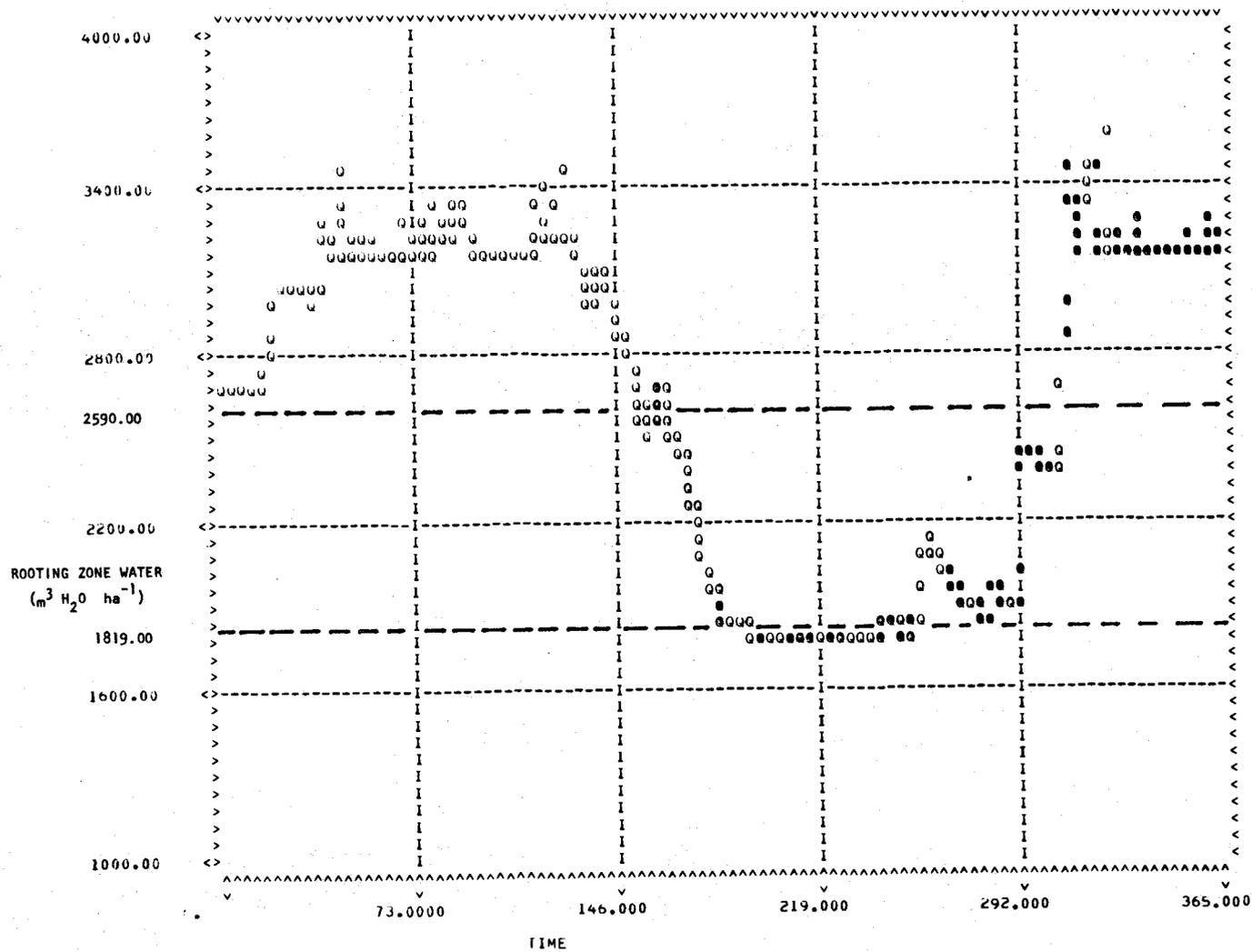


Figure 3.35. Predicted rooting zone moisture.

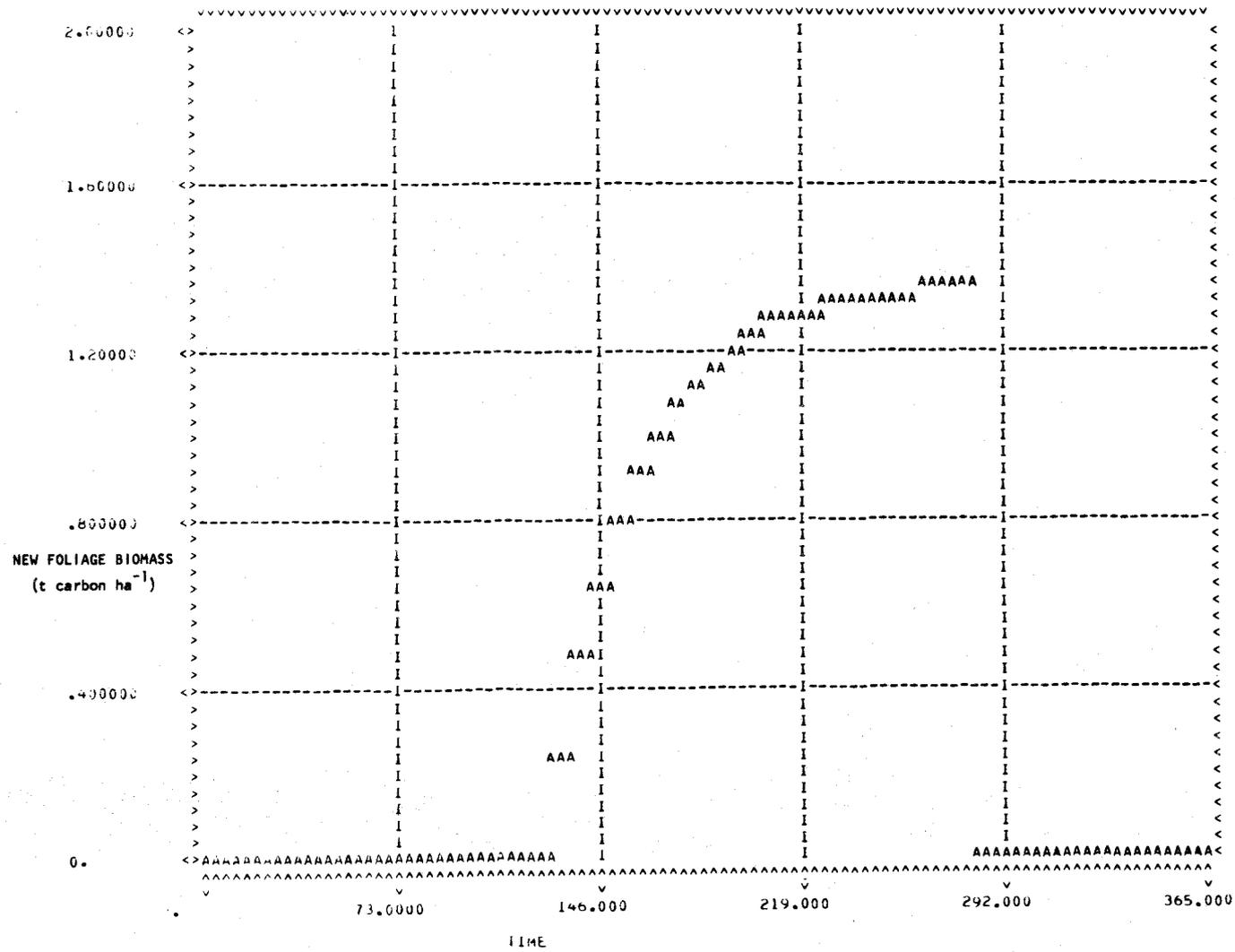


Figure 3.36. Predicted new foliage biomass.

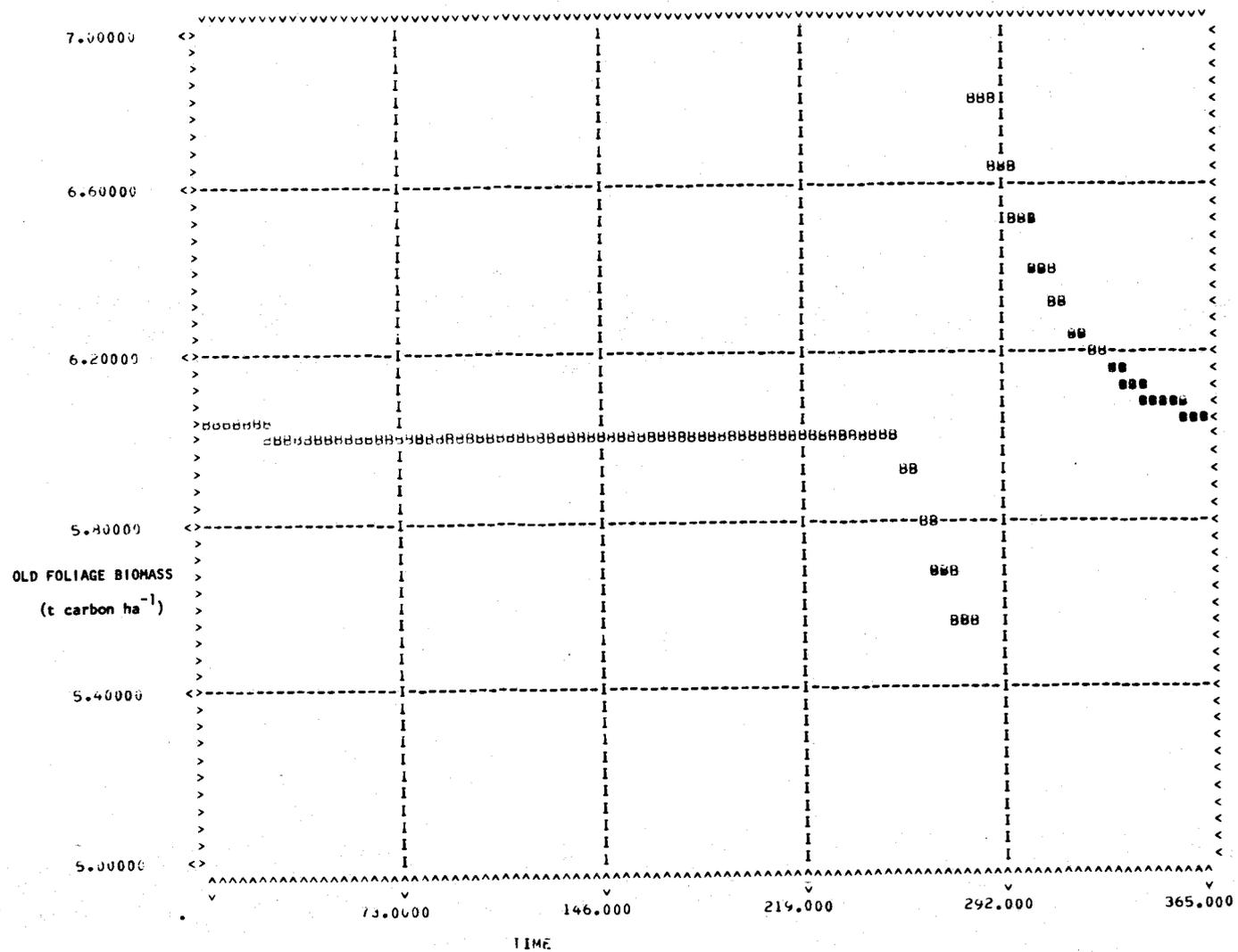


Figure 3.37. Predicted old foliage biomass.

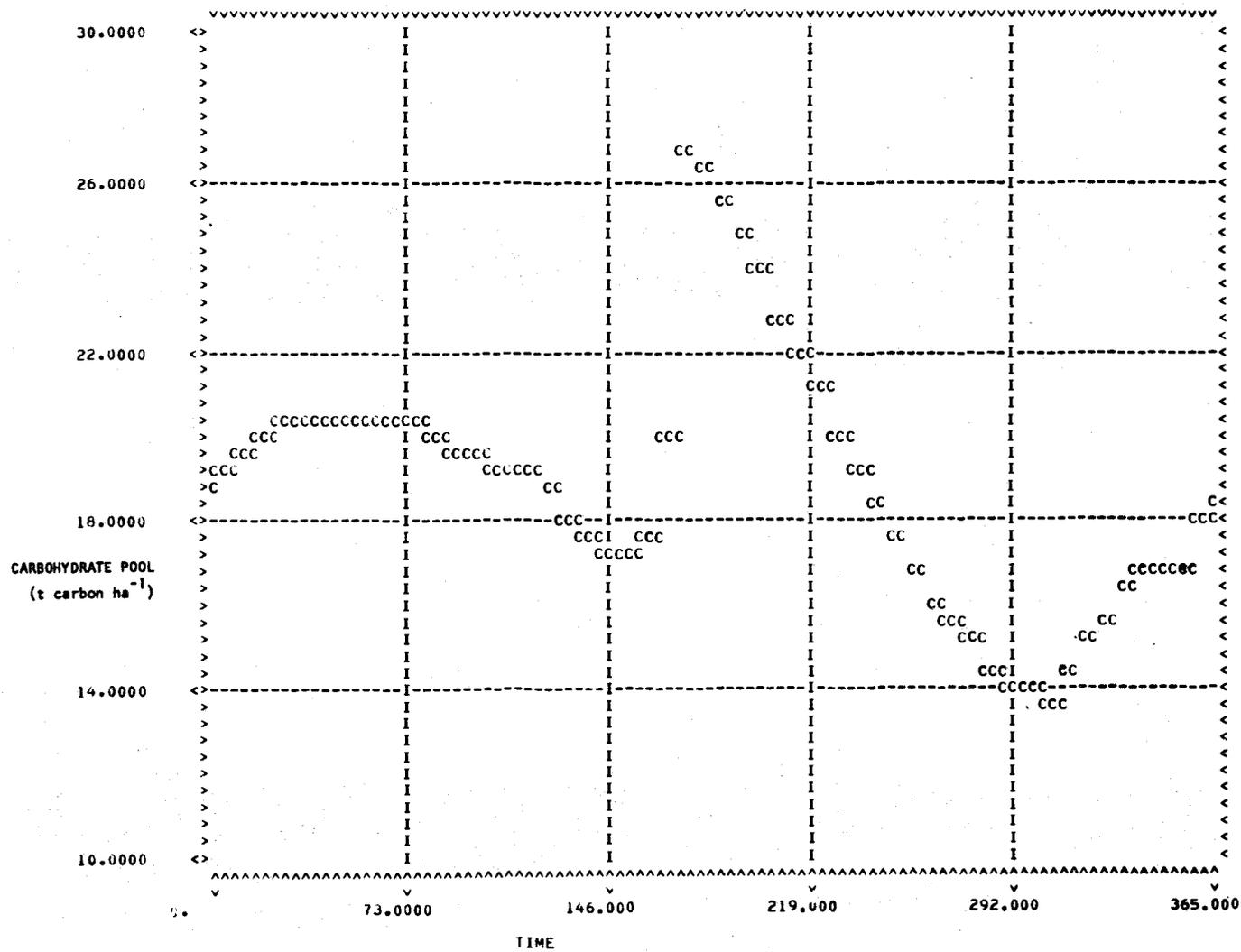


Figure 3.38. Predicted carbohydrate pool.

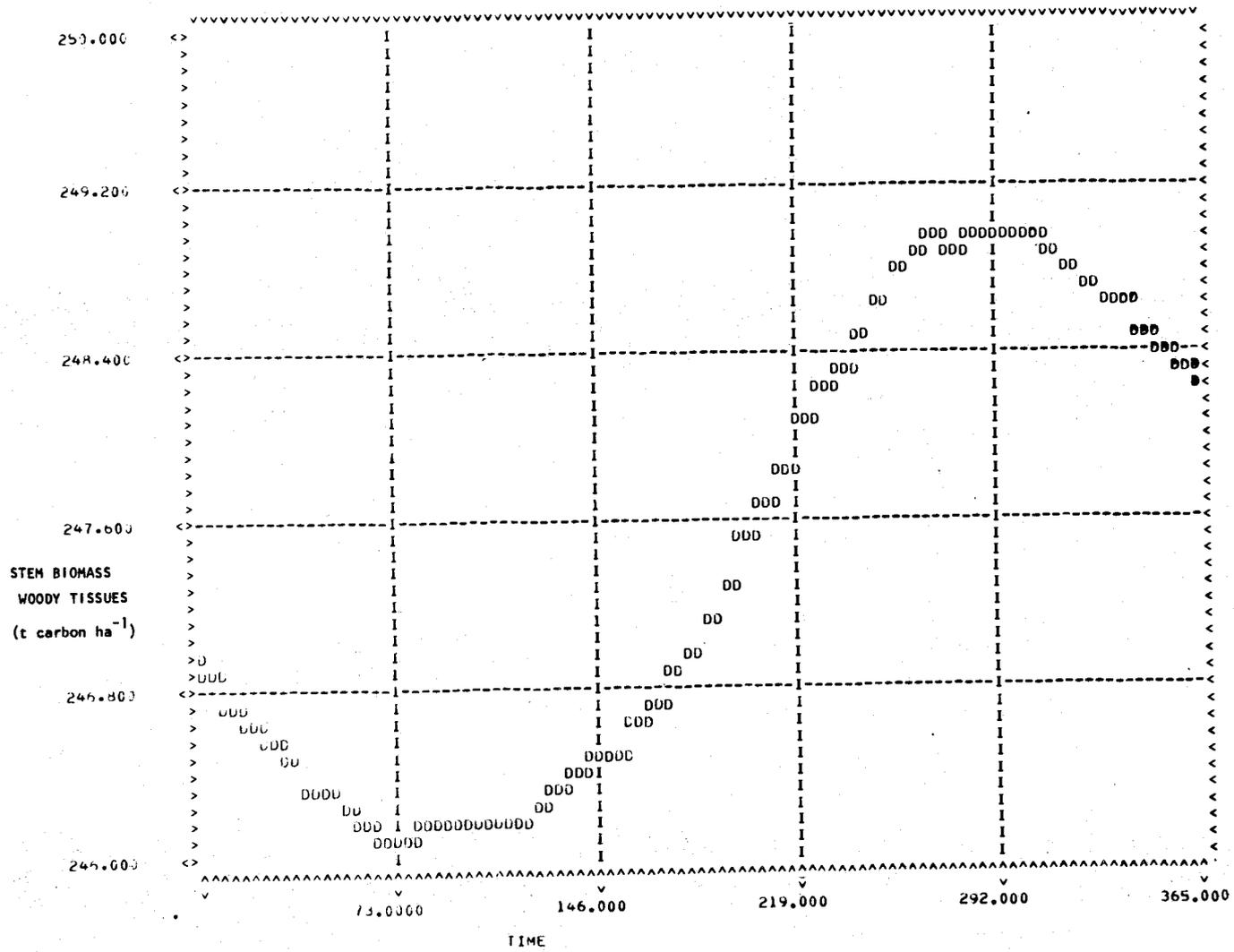


Figure 3.39. Predicted stem biomass - woody tissues.

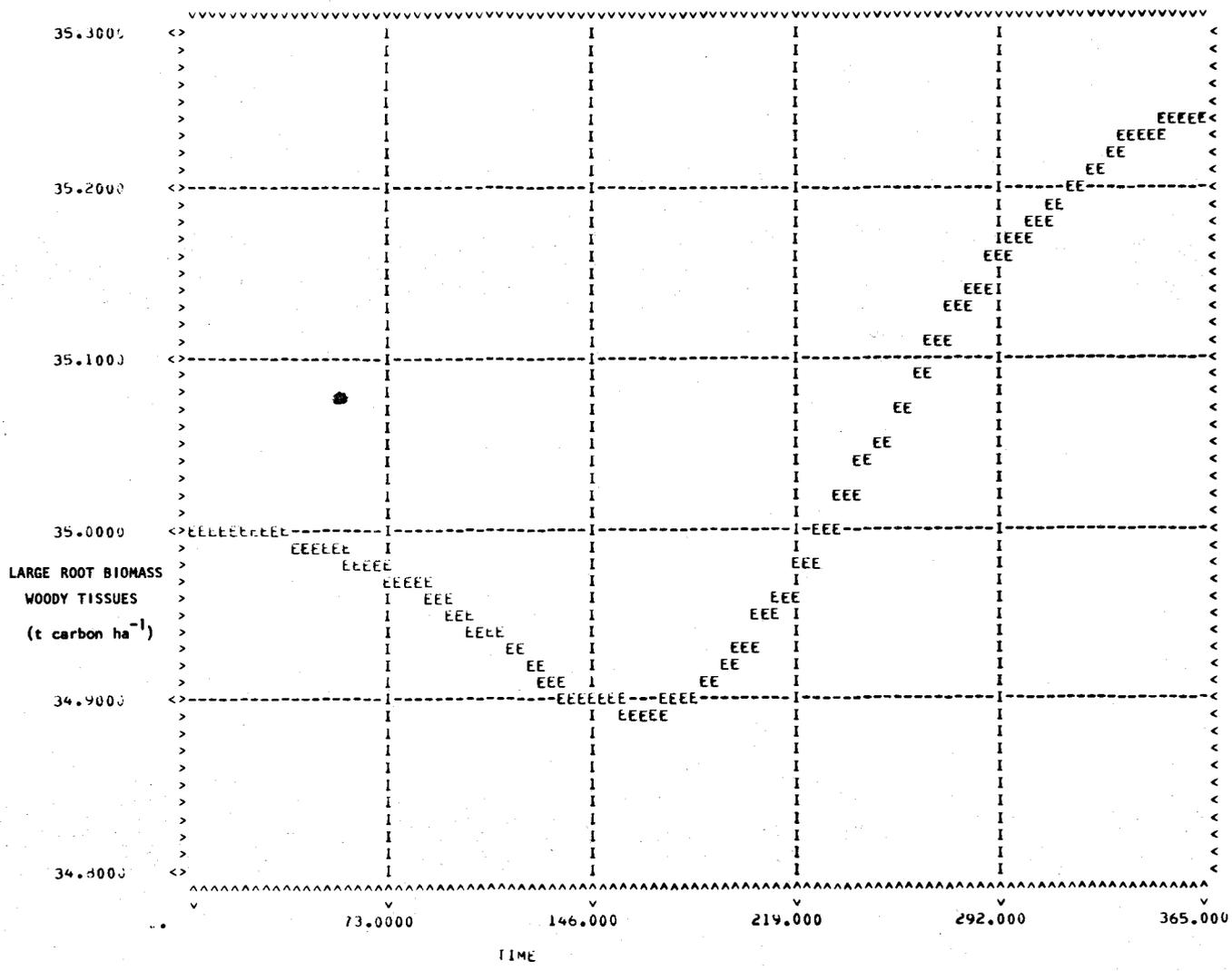


Figure 3.40. Predicted large root biomass - woody tissues.

During the first growing season after burning, residual species from the old stand, invading herbs such as Senecio sylvaticus, Epilobium angustifolium and E. paniculatum, and a moss-liverwort stage occur. Second-year vegetation consists largely of herbaceous species dominated by S. sylvaticus, which is present in only small amounts in subsequent years. Perennial invading species including Pteridium aquilinum also begin to build up until the fourth or fifth year.

This initial "weed" stage gradually gives way to stands including the residual species Acer circinatum, Rubus ursinus, Berberis nervosa, Rhododendron macrophyllum, and Gaultheria shallon, and the invaders Ceanothus velutinus and Salix spp. These shrubs dominate the site until they are overtopped by tree saplings, generally of Douglas-fir.

Late successional stages have received less study, but 20 years after fire in the Coast Range of Oregon seral vegetation can be classified into six associates that are related to environmental factors. These associates range from Vaccinium parvifolium/Gaultheria shallon on relatively xeric sites to Alnus rubra/Polystichum munitum on mesic sites. In general, the composition and density of seral forest stands is dependent on the type of disturbance, available seed source, and environmental conditions. A very common occurrence is the development of dense, nearly pure, essentially even-aged Douglas-fir stands, which are often dense enough to eliminate most of the understory vegetation in the first 100-150 years. At this stage, mortality begins to open up the stand. Understory species and western hemlock then begin to invade. Other situations that can occur are: (1) open stands of Douglas-fir with a persistent understory of Gaultheria shallon or Acer circinatum, (2) stands dominated by Alnus rubra, or (3) stands dominated from the beginning by western hemlock or western redcedar (in the wetter parts of the zone).

True climax forests are rare, but relatively old-growth forests (400-600 years old) do occur and from these conclusions can be drawn about what potential climaxes may be. On very dry sites, western hemlock is absent and Douglas-fir is the climax species. On wet sites western redcedar and western hemlock are the climax species, and on medium sites western hemlock appears to be the sole climax species.

It is of interest to point out that there are large areas differing from the surrounding western hemlock zone in the Puget Sound area, and in talus communities. In the Puget Sound basin, prairie, oak woodland, and pine forest are encountered, mainly because of differences in climate and soil types.

The Abies amabilis (Pacific silver fir) zone. The major climax species in this zone is Abies amabilis. A typical successional sequence begins with site invasion by Douglas-fir or noble fir (Abies procera) or both. Both these species fail to reproduce and the Pacific silver fir is usually the last to invade the site, but it can function as a pioneer species. Western hemlock may be established initially or may develop under the forest canopy. Western hemlock is a minor climax species especially at lower elevations.

The Tsuga mertensiana (mountain hemlock) zone. Early stages in succession have not been studied in depth, but they often involve domination of a site by fire-resistant understory species, e.g., Vaccinium membranaceum and Xerophyllum tenax. Successional sequences of tree species vary geographically. On moist sites noble fir and Pacific silver fir can function as pioneer species, but on dry sites seral forests of Pinus contorta or Abies lasiocarpa develop. In Washington and northern Oregon, Pacific silver fir is the major climax species in closed forests.

Succession models. The major objectives of the modeling program involving succession were: (1) to develop a stand (community) level model that can predict species composition and biomass for each component in the community using the Botkin et al. (1970) model as an example; (2) to develop a regional model to predict changes in area occupancy of various communities over long time periods; and (3) to develop these models with a structure that will allow investigation of the effects of manipulations and incorporation of process level models.

Stand level succession model. The approach used in the development of the stand level succession model is based on the concept of environment set forth by Hutchinson (1957), where environment is described as an n -dimensional Cartesian space, the ordinates of which are environmental factors or variables. Reed and Waring (1974) suggested that the indices of E -space Θ be defined as a relation between a set of physical variables H , and organism response parameters B .

$$\Theta = R(H, B)$$

where $H = \eta_1, \eta_2, \dots, \eta_n$ and $B = \beta_1, \beta_2, \dots, \beta_n$.

This concept is in general agreement with environmental definitions proposed by Mason and Langenheim (1957) and discussed by Vandermeer (1972) and Levandowsky (1972a, 1972b) among others.

This basic relation of physical environment to plant response poses problems of measurement: It is difficult to measure environment as organisms sense it. A common approach is to define orthogonal ordinates based on canonical or other multivariate analysis of physical variables and population response. Because plants are so strongly coupled to environment, it is possible to simulate stimulus-response variables from physiological models (Reed and Waring 1974). These ordinates are strongly related to growth of plants. Hence, in the case of plants, niche can be defined in terms of growth in lieu of population. Indeed, population of tree species is a poor criterion for environmental suitability because stand density is related to other nonenvironmental factors. The use of frequency in the case of herbs and forbes, however, will still be necessary.

Our definition of environment, then, is an n -dimensional metric space with indices Θ . Vandermeer (1972) describes a fundamental niche as that locus in E -space where a given tree species or taxonomic unit growth exceeds some minimum growth level without direct competition from other species. The realized niche is that locus where growth occurs in the

presence of other species. The distinction between fundamental and realized niches is sometimes unclear. Further, the relation given in the equation must be defined for a given reference species; it is impossible to define θ in terms of each species. Plant growth is tightly coupled to environment, and vice versa; therefore it is necessary to consider the feedback between forest growth and environment.

Plant succession can be thought of as a drift of an ecosystem point through E -space. Community structure is the result of the point's passing through the various plant niches. The direction of the drift and its velocity are a function of plant growth rates, frequency of disturbance, climatic changes, and so on. The impacts of man and natural perturbations can be visualized easily as a rapid movement of the ecosystem through E -space. Determination of movement is the target of the successional model. Requirements of the succession model are:

1. A growth model for trees (height)
2. A growth model for perennial brush (biomass)
3. A growth model for herbaceous annuals (biomass)
(the growth models are all functions of θ)
4. A seeding-establishment model
5. A mortality model
6. Models of environmental changes with growth

The succession model is in the process of development, and the goal for 1974 is the completion of the interactive succession program, which includes preliminary models of stand growth related to light, temperature, and moisture; and then a rigorous testing of the growth model by simulating effects of defoliation on individuals.

The height growth of Douglas-fir in an optimum total environment of light, temperature, and moisture has been simulated by K. L. Reed (pers. commun.) and is presented in Figure 3.41. Figure 3.42 shows height growth as a function of the total environment simulated over a 250-year period. At age 250 with an optimum environment height growth would be 100 m, but with $R = 0.5$ height growth would amount to only about 40 m.

K. L. Reed (pers. commun.) has been able to define environmental regions or niches for various site qualities of Douglas-fir in terms of light (percentage of sunlight), temperature (optimum temperature days), and moisture (transpiration ratio). Figures 3.43-3.45 quantify the observation that as environmental parameters approach optimum for growth niche area decreases. The other requirements of the model are as yet in the development phase.

Regional succession model. The rationale and a possible methodology for modeling succession at the regional level developed for eastern forests (Shugart et al. 1973, Johnson 1974) were selected as the approach for modeling succession in western forests. A major reason for choosing this already-developed technique was the opportunity to compare long-term events between two plant formations using similar modeling methods. Eastern deciduous forests typically have short-lived "pioneer" species

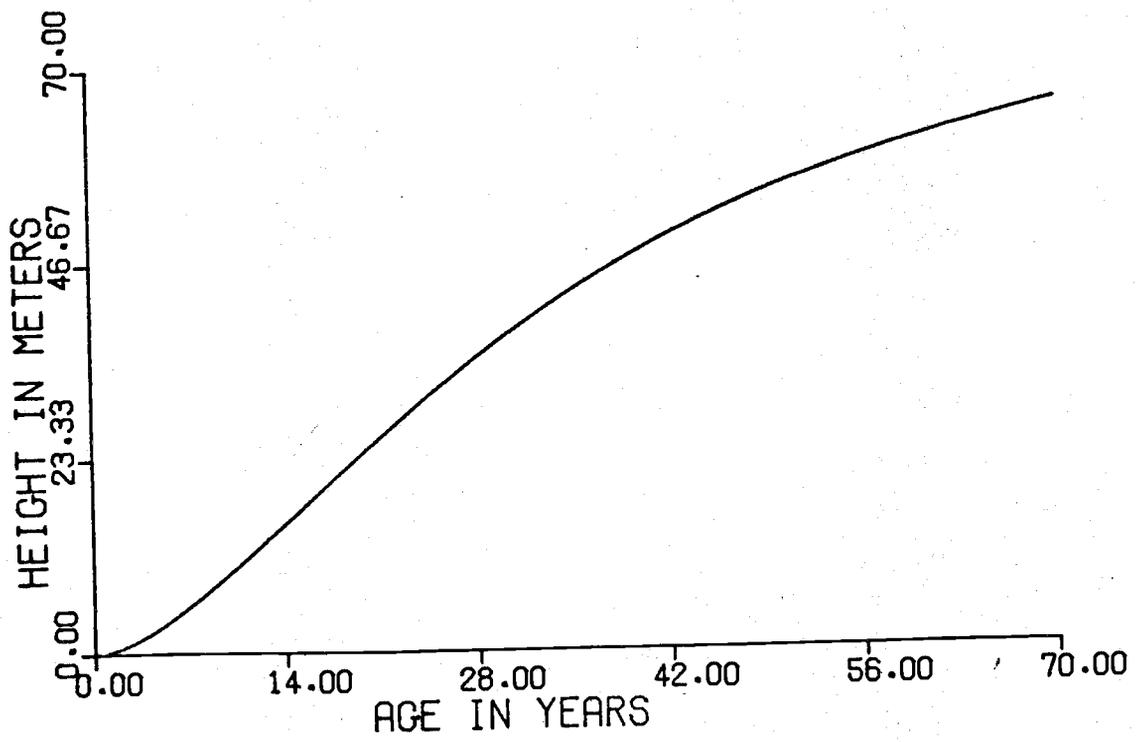


Figure 3.41. Predicted cumulative height growth of Douglas-fir in an optimum environment.

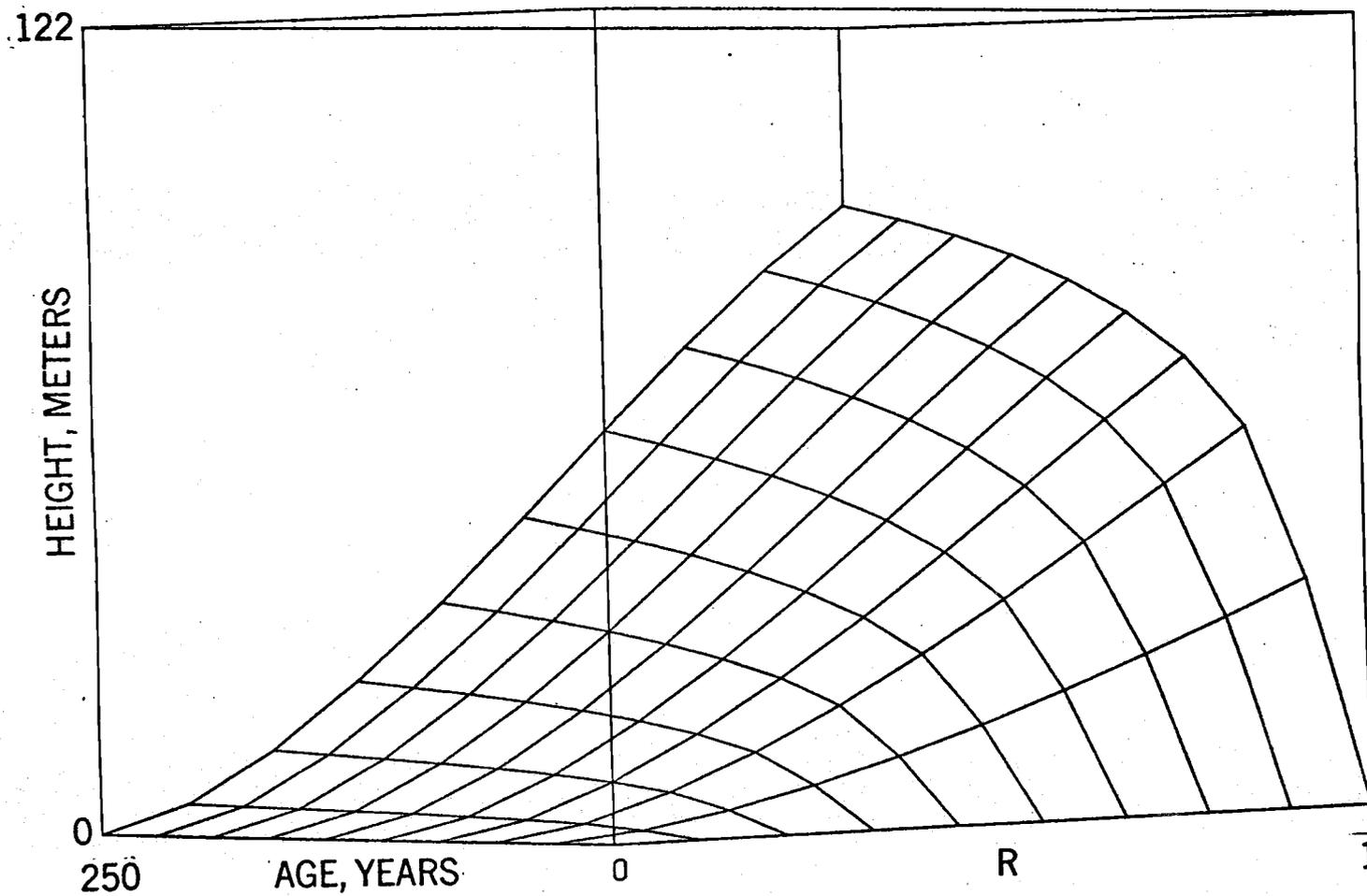


Figure 3.42. Predicted cumulative height growth of Douglas-fir as a function of total environment, R.

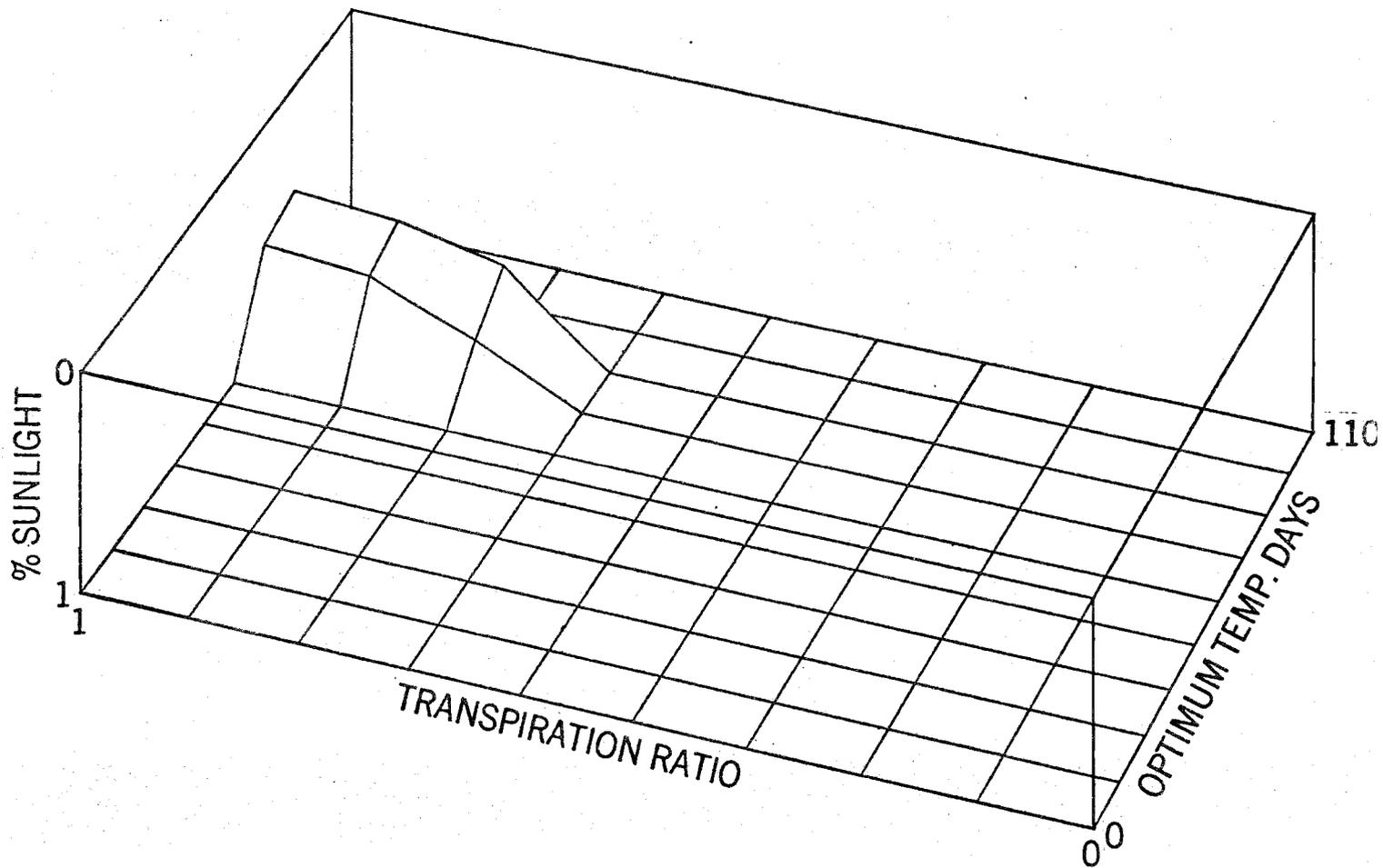


Figure 3.43. Environmental region defined by percent sunlight, transpiration ratio and optimum temperature days in which Douglas-fir grows 35 m in 50 years.

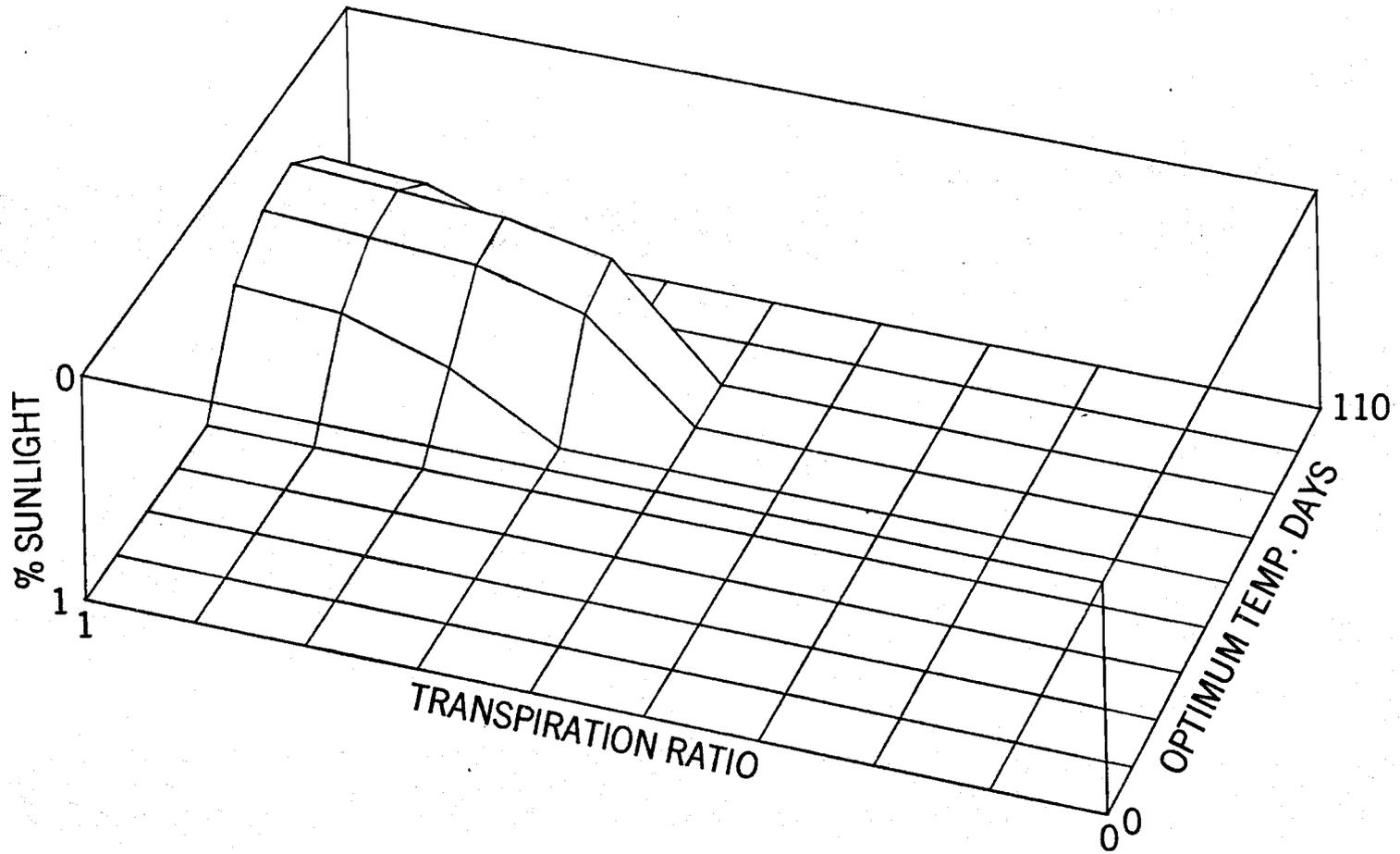


Figure 3.44. Environmental region defined by percent sunlight, transpiration ratio and optimum temperature days in which Douglas-fir grows 23 m in 50 years.

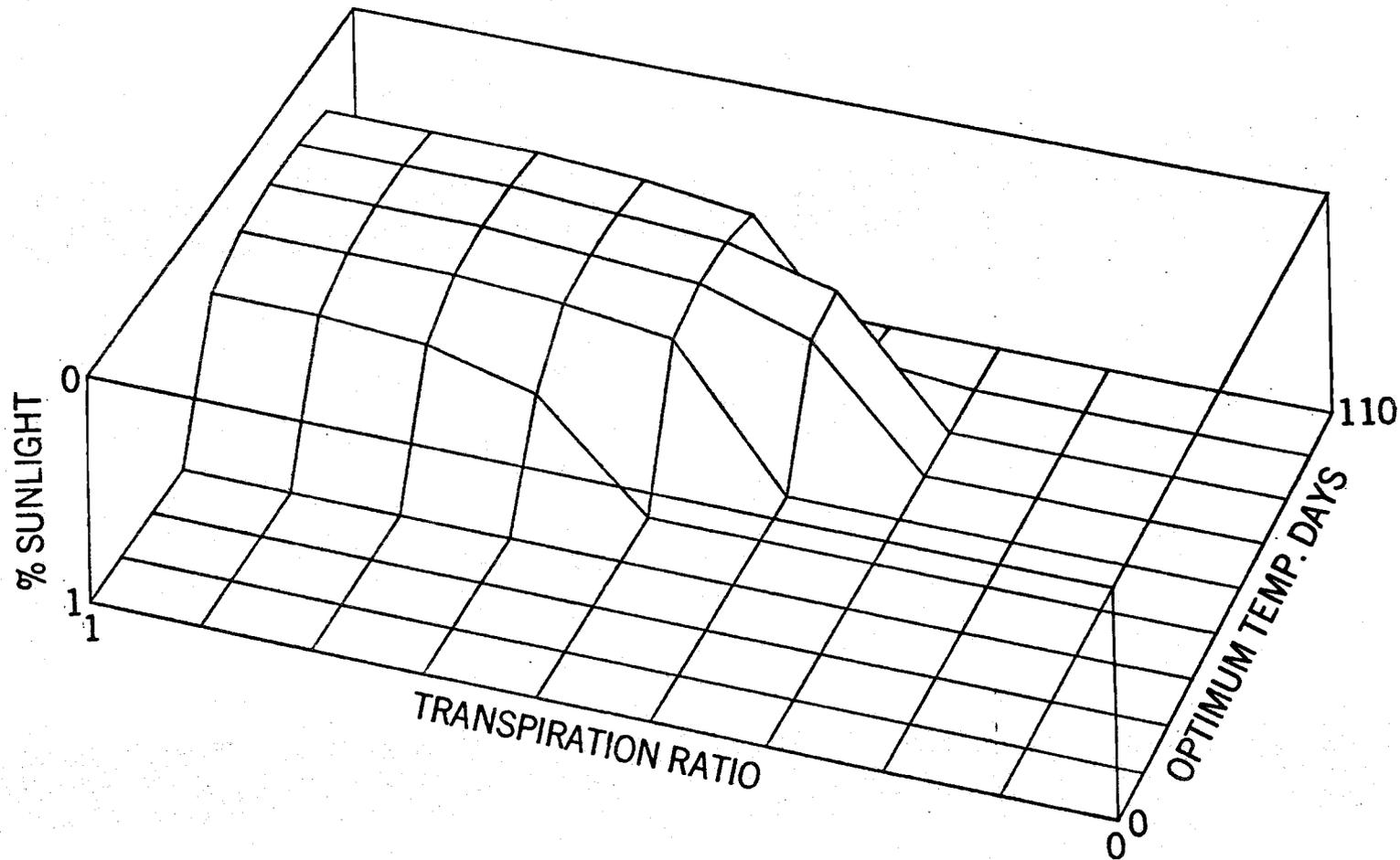


Figure 3.45. Environmental region defined by percent sunlight, transpiration ratio and optimum temperature days in which Douglas-fir grows 6 m in 50 years.

such as aspen (Populus spp.) or Virginia pine (Pinus virginiana), with life expectancies generally less than 100 years. Western coniferous forests often have long-lived "pioneer" species such as Douglas-fir, with a life span of over 650 years. One of the results of these different life cycles is that eastern forests appear to reach an equilibrium (if mature communities are considered at equilibrium) in 250 years (Shugart et al. 1973, Johnson 1974) while it may take 1000 years in the Douglas-fir region of western North America.

Joan Hett (pers. commun.) has developed for the H. J. Andrews Experimental Forest a regional model that transfers areas of land from one forest cover type to another. The Andrews Forest was selected for a number of reasons: It has a well-defined political boundary; the data collected within the area are available from the USDA Forest Service and IBP studies; there is a good understanding of the successional sequence in this region of the Oregon Cascade Mountains; and as the IBP watershed studies are inside the boundaries of the forest, it is possible the succession model will be able to add another dimension, long-term effects of selected management policies, to these studies.

Figure 3.46 shows the successional pattern based on elevation and habitat. The compartments inside each forest type module represent size classes based on diameter at breast height (dbh). These are (1) seedlings and saplings (less than 10.16 cm), (2) pole timber (10.16-30.48 cm), (3) standard timber (30.48-76.2 cm), and (4) "super" standards (greater than 76.2 cm). It should be explained, the fourth size class is missing in the high-elevation communities since diameters at breast height greater than 76 cm are seldom reached.

Parameters used in the model were gathered from many sources. Franklin and Dyrness (1969, 1973) provided initial conditions for each compartment and estimated transfer times T_1 and T_2 as well as the percentages of land area (P) suitable for the successional sequence at each elevation and habitat. Growth rates (obtained mainly from the literature or IBP studies) were used to obtain transfers from one size class to the next (T_2). Results from the first simulation of the successional sequences in the transition and fir zones can be seen in Figures 3.47 and 3.48. It should be noted that these results are only preliminary and have not been checked against actual data. Also, as there are no feedbacks in the model, it cannot be considered realistic.

Plans for 1974 include tuning this model to ensure more accurate transfer rates and incorporating ongoing vegetation mapping results as initial conditions. Also, the area used as "clearcut" in this model includes all areas that have been clearcut and still do not have a closed forest canopy. These areas are in reality in all stages of succession and should not be treated as a homogeneous unit. It is hoped that more realistic clearcut parameters can be determined. Once the model is simulating acceptable changes through time, several management policies will be incorporated. The first will be the effects of various cutting routines such as selection cutting versus clearcutting, and changing the number and frequency of hectares cut per year.

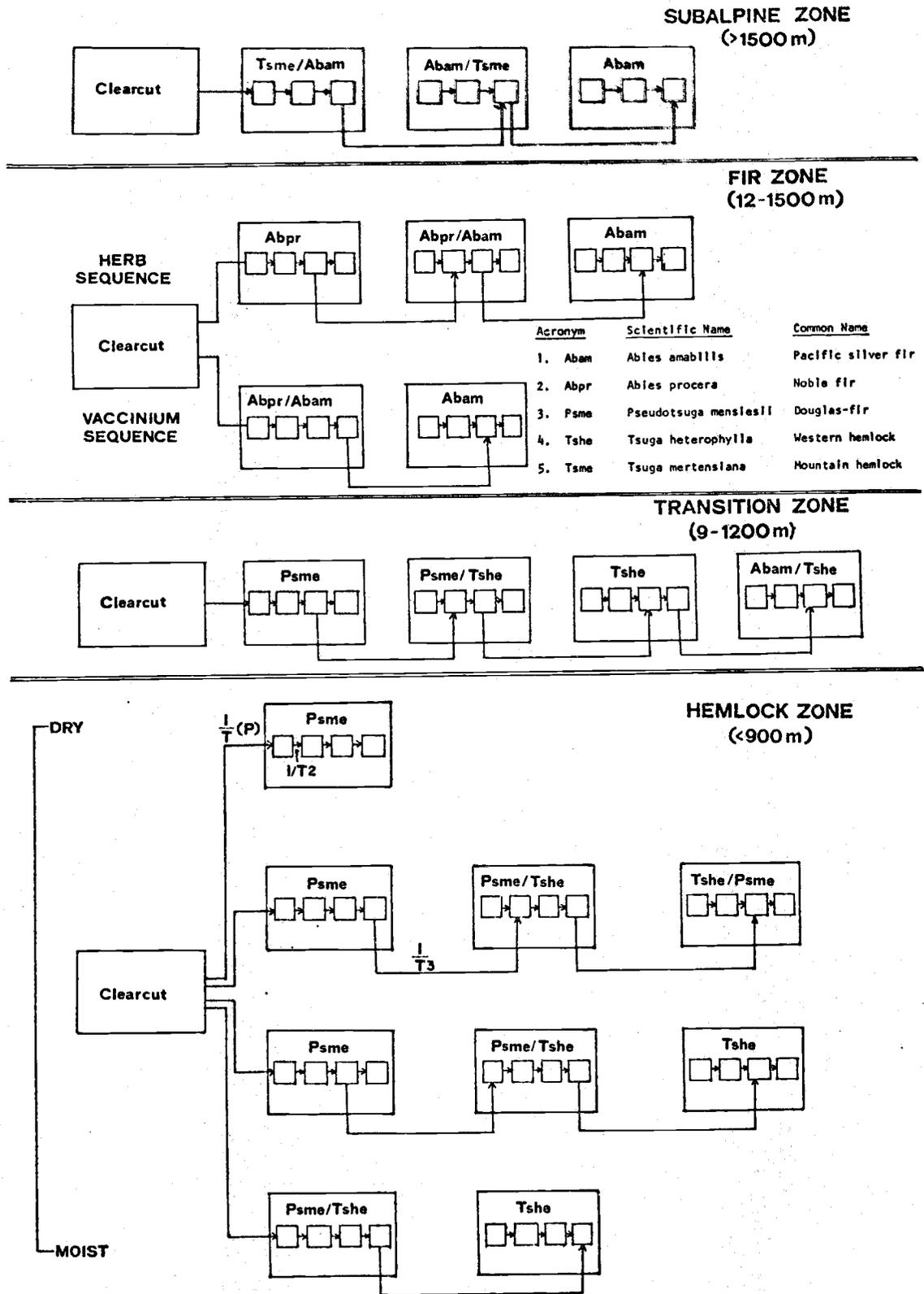


Figure 3.46. Successional patterns in the subalpine, fir transition and hemlock zones based on elevation and habitat.

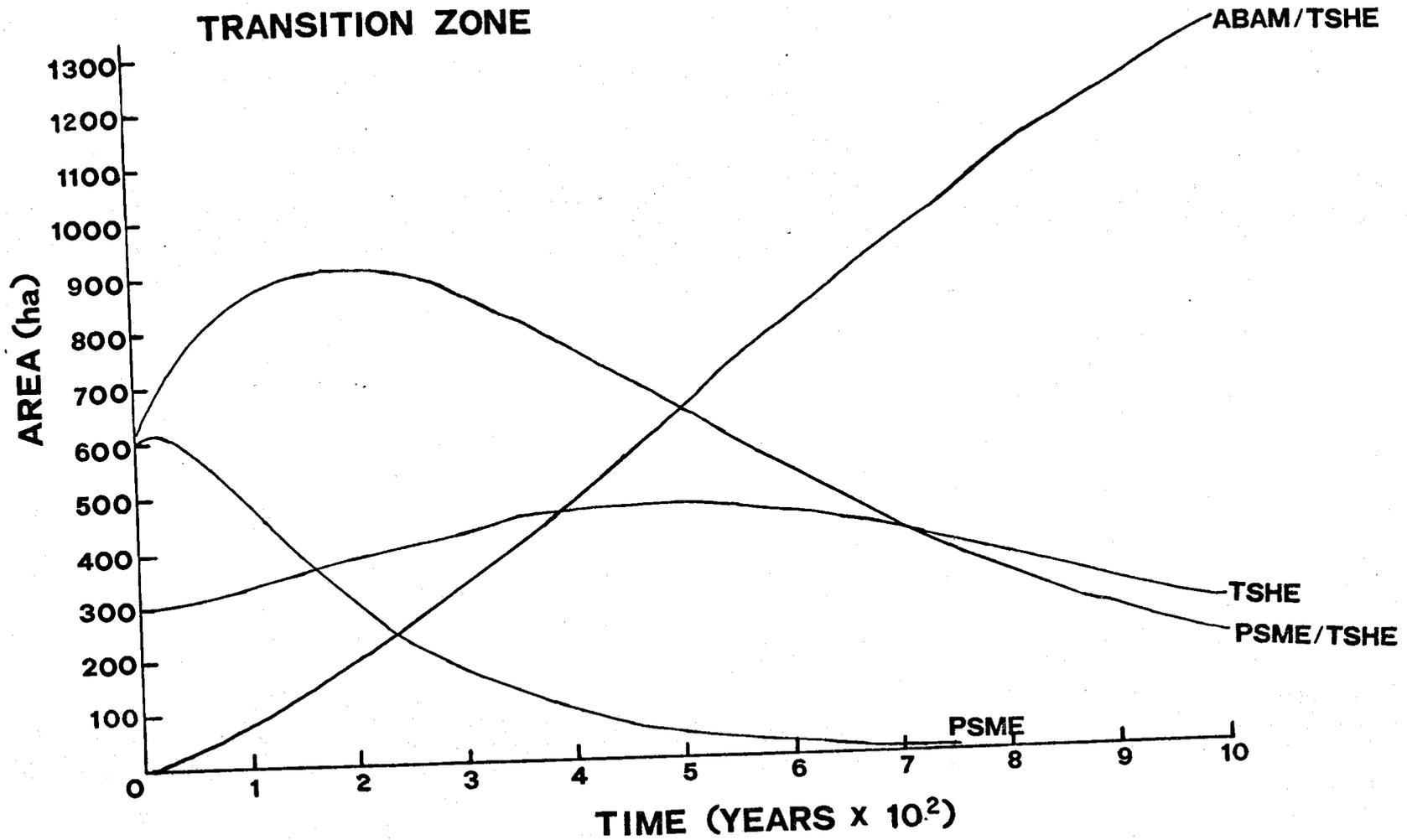


Figure 3.47. Successional sequence in the transition zone.
 ABAM = Abies amabilis, PSME = Pseudotsuga menziesii and TSHE = Tsuga heterophylla.

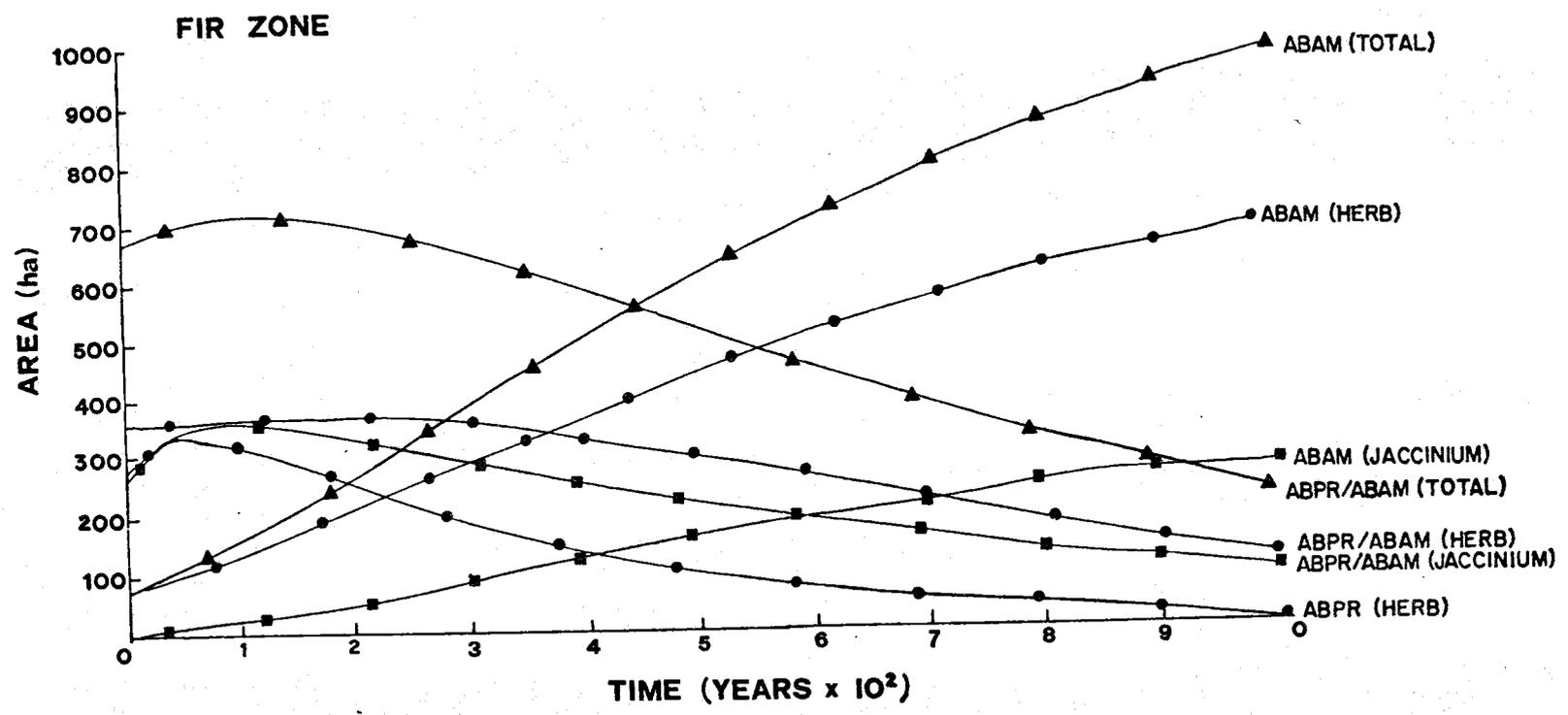


Figure 3.48. Successional sequence in the fir zone. ABAM = Abies amabilis and ABPR = Abies procera.

3.1.2.6. The role of consumers. The basic objectives of consumer research were to determine in both young-growth and old-growth Douglas-fir ecosystems: (1) the biomass of consumer groups, (2) the distribution of these groups (small and large mammals, birds, and insects) with respect to their foraging strata (litter layer, canopy, etc), and (3) their role in carbon and nutrient cycling, and accordingly, forest succession. Consumers make up only a small percentage (<0.01%) of the total biomass of coniferous forest ecosystems (Table 3.23) in both the Cedar River watershed and the Andrews Forest. Small-mammal biomass observed on the Thompson site was 0.2 kg/ha (Miller et al. 1972). Estimates of large-mammal biomass 50-55 years after logging in Douglas-fir forests range from 5 to 11 kg/ha (Taber 1973). Bird biomass fluctuates seasonally; the largest bird biomass observed at the Thompson site is 0.04 kg/ha in the summer (Miller et al. 1972). Bird biomass for the Andrews Forest is slightly higher (0.25 kg/ha; Strand in press). Standing biomass of canopy insects is higher (1.3 kg/ha) than bird biomass at the Andrews Forest (Strand in press). The distribution of these consumer groups and their roles are discussed below.

Small and large mammals. Eighteen species of mammals occur at the Thompson site (Table 3.24; Miller et al. 1972). Secondary consumers (eating mostly animal material) are relatively numerous in the small-mammal population, pointing to the abundance of invertebrate food in the litter and soil. Of the primary consumers (eating mostly plant material) only Rocky Mountain wapiti and black-tailed deer were found to form seasonal populations potentially capable of influencing plant productivity and succession on a regional scale. Fifteen years ago wapiti were unknown in the Cedar River watershed. J. Schoen and B. Bradley (pers. commun.) have indicated that the high populations of wapiti (0.6/ha) now occurring on the Cedar River watershed are capable of consuming 164 kg/ha during a three-month winter period. Wapiti use the watershed in a highly irregular manner, avoiding certain areas and concentrating in others. Several wapiti have been radio-tracked to obtain data on movement patterns as shown in Figure 3.49. Preferred habitats appear to be alder--sword fern flats associated with river drainages in the winter and the higher elevations in the summer. Deer concentrations as high as 0.5/ha would consume 0.6 kg per hectare per day during periods of peak concentrations. This consumption is considerably less than that of the wapiti.

The impact of ungulate browsing on forest regeneration has long been recognized as significant in the Douglas-fir forests of the Pacific Northwest (see Black et al. 1969, for example). Of the deer and wapiti, deer are considered the more important, because regionwide they are much more abundant and more difficult to control through manipulation of hunting-pressure. In a continentwide survey (Taber 1963), it was estimated that the increase in hunter-harvest necessary to stabilize populations would be white-tailed deer 200%, mule deer 80%, and wapiti 5%. Damage to forest regeneration is naturally linked to seasonal populations and relative preference among the available forage strata. The population dynamics state of knowledge of the two ungulates in western Washington can be stated as follows:

Table 3.23. Biomass (in kilograms per hectare) of consumer groups at the H.J. Andrews and Thompson sites in comparison with total ecosystem biomass.

	Andrews site	Thompson site
Small mammals		0.2
Large mammals		5-11
Birds	0.25	0.04
Insects	1.3	
Total ecosystem	862,894	339,900

Table 3.24. Names, foraging strata, and consumer roles of mammals of the Thompson site, Cedar River watershed, Washington (from Miller et al. 1972).

Scientific name	Common name	Foraging stratum ^a	Consumer role ^b
<u>Canis latrans</u>	Coyote	G	II°
<u>Cervus canadensis</u>	Elk (wapiti)	G, S	I°
Chiroptera	Bats	C	II°
<u>Eutamias townsendii</u>	Townsend's chipmunk	G, S	I°
<u>Lepus americanus</u>	Snowshoe hare	G, S	I°
<u>Lynx rufus</u>	Bobcat	G	II°
<u>Microtus oregoni</u>	Oregon vole	G	I°
<u>Mustela erminea</u>	Shorttail weasel	G	II°
<u>Mustela frenata</u>	Longtail weasel	G	II°
<u>Neotoma cinerea</u>	Bushytail woodrat	G, S	I°
<u>Neurotrichus gibbsi</u>	Shrew-mole	B, L	II°
<u>Odocoileus hemionus</u>	Black-tailed deer	G, S	I°
<u>Peromyscus maniculatus</u>	Deer mouse	L, G	I°
<u>Sorex trowbridgii</u>	Trowbridge shrew	L	II°
<u>Sorex vagrans</u>	Vagrant shrew	L	II°
<u>Tamiasciurus douglasii</u>	Chickaree	G, S, C	I°
<u>Ursus americanus</u>	Black bear	L, G, S	I°
<u>Zapus trinotatus</u>	Jumping mouse	G	I°

^aB = soil layer; L = litter layer; G = ground layer, under 30 cm; S = shrub layer, 30 to 180 cm; C = crown layer, area occupied by living crowns of forest overstory.

^bI° = primary consumer, eats mostly plant material; II° = secondary consumer, eats mostly animal matter.

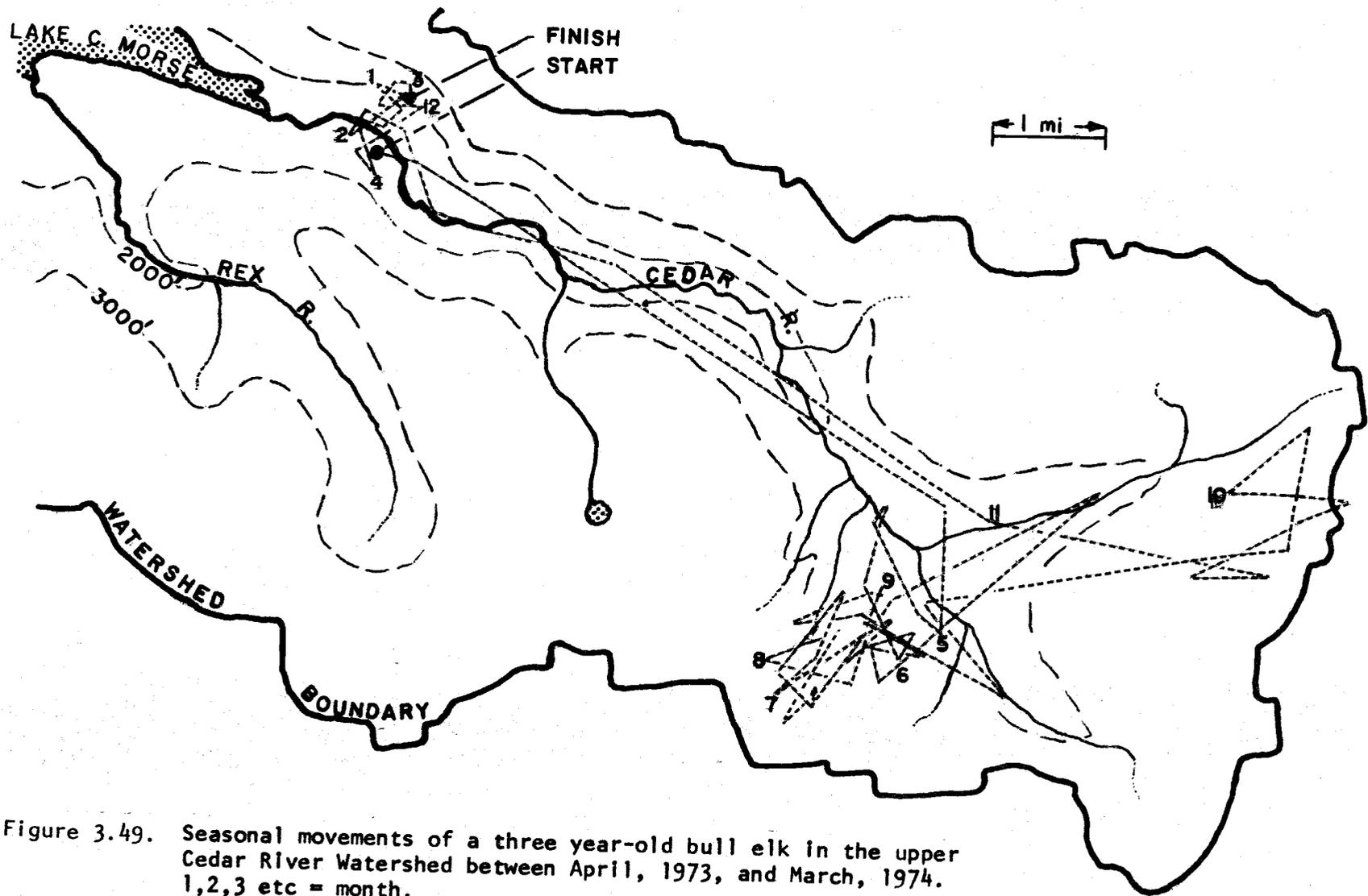


Figure 3.49. Seasonal movements of a three year-old bull elk in the upper Cedar River Watershed between April, 1973, and March, 1974. 1,2,3 etc = month.

Overall populations--deer stable, wapiti increasing
 Degree of concentration--deer dispersed, wapiti concentrated
 Knowledge of ecology--deer good, wapiti poor

The role of elk in acting as a stress on the system is discussed further in part 5.

No quantitative data are available in this Biome on the role of mammals in carbon or nutrient cycling. There is no doubt, however, that the larger mammals must at least be responsible for preparing certain materials for the decomposers, thus potentially regulating the rate of carbon and nutrient cycling. Productivity of preferred species could be reduced by continued browsing by increasing wapiti populations.

The influence of small mammals on reforestation also has been recognized. Many small mammals cause regeneration problems because they eat seeds and damage young seedlings. Succession patterns also can be affected by small mammals, e.g., the snowshoe hare has a decided preference for Douglas-fir over western hemlock in the western Oregon Cascades (Black 1965). Encounter and preference tests for various combinations of seeds for tree species offered to two species of shrew (Sorex trowbridgii and S. vagrans) indicate that Douglas-fir seeds are preferred above those for the true firs (Abies amabilis and A. procera). Differences in preferences were noted between the shrew species and shrew moles for all tree seeds. Results of trapping indicate a noticeable seasonal difference between small-mammal populations, with numbers higher in summer than in winter.

Birds. Forty-one species of birds were identified as spring and summer residents of the five study plots near the Thompson site. Only 22 of these species, however, composed the breeding community. Table 3.25 shows the foraging strata and consumer roles of 32 of the bird species. The bird survey in the H. J. Andrews Forest revealed 23 species in 11 stand types and as many as 15 species in one location. At watershed 10, seven species of omnivorous birds were found. The annual consumption by these seven species of birds totals 6.2 kg/ha (Table 3.26).

Birds consume very little of the vegetative biomass, so their effect on carbon and nutrient cycling is likely to be negligible. Their effect on regeneration and succession through selective removal of seeds and their consumption of reproductive plant parts may be considerable, however, and data on these aspects are presently being collected.

Invertebrates. The number of species of invertebrates captured in three Douglas-fir stands in the H. J. Andrews Forest is presented in Table 3.27. In all, 696 species of invertebrates were captured (W. P. Nagel, pers. commun.). The annual consumption by grazing insects is estimated to be 42.5 kg/ha or about 1.6% of total primary production (Strand in press).

Studies of invertebrates at the Thompson site have focused on the population dynamics and host selection behavior of the Douglas-fir beetle (Dendroctonus pseudotsugae). Coniferous forest insects normally do not consume a great deal of biomass (as indicated by Strand) but they do

Table 3.25. Names, foraging strata, and consumer roles of birds of the Thompson site, Cedar River watershed, Washington (from Miller et al. 1972).

Scientific name	Common name	Foraging stratum ^a	Consumer role ^b
<u>Bombycilla cedrorum</u>	Cedar waxwing	C	I°
<u>Bonasa umbellus</u>	Ruffed grouse	L, G, S, C	I°
<u>Bubo virginianus</u>	Great horned owl	G	II°
<u>Colaptes cafer</u>	Red-shafted flicker	G, C	II°
<u>Columba fasciata</u>	Band-tailed pigeon	L, S, C	I°
<u>Corvus brachyrhynchos</u>	Common crow	G	II°
<u>Corvus corax</u>	Common raven	G	II°
<u>Dendragopus obscurus</u>	Blue grouse	L, G, S, C	I°
<u>Dendrocopos villosus</u>	Hairy woodpecker	S, C	II°
<u>Dendroica nigrescens</u>	Black-throated gray warbler	S, C	II°
<u>Empidonax spp.</u>	Empidonax flycatchers	S, C	II°
<u>Hylocichla ustulata</u>	Swainson's thrush	L, G	II°
<u>Ixereus naevius</u>	Varied thrush	L, G	II°
<u>Junco oreganus</u>	Oregon junco	L, G	I°
<u>Loxia curvirostra</u>	Red crossbill	C	I°
<u>Molothrus ater</u>	Brown-headed cowbird	G	I°
<u>Oporornis tolmiei</u>	MacGillivray's warbler	S, C	II°
<u>Parus rufescens</u>	Chestnut-backed chickadee	S, C	II°
<u>Passerella iliaca</u>	Fox sparrow	G	I°
<u>Perisoreus canadensis</u>	Gray jay	G, C	II°
<u>Pipilo erythrophthalmus</u>	Rufous-sided towhee	G	I°
<u>Piranga ludoviciana</u>	Western tanager	S, C	I°
<u>Regulus calendula</u>	Ruby-crowned kinglet	C	II°
<u>Regulus satrapa</u>	Golden-crowned kinglet	C	II°
<u>Selasphorus rufus</u>	Rufous hummingbird	G, S	I°
<u>Sitta canadensis</u>	Red-breasted nuthatch	S, C	II°
<u>Sphyrapicus varius</u>	Yellow-bellied sapsucker	S, C	I°
<u>Spinus pinus</u>	Pine siskin	C	I°
<u>Troglodytes troglodytes</u>	Winter wren	G, S	II°
<u>Turdus migratorius</u>	Robin	L, G	II°
<u>Vermivora celata</u>	Orange-crowned warbler	S, C	II°
<u>Vireo gilvus</u>	Warbling vireo	S, C	II°

^aB = soil layer; L = litter layer; G = ground layer, under 30 cm; S = shrub layer, 30 to 180 cm; C = crown layer, area occupied by living crowns of forest overstory.

^bI° = primary consumer, eats mostly plant material; II° = secondary consumer, eats mostly animal matter.

Table 3.26. Annual consumption by the canopy bird population while in residence at watershed 10 (WS 10) (Nussbaum, personal communication; after Strand, in press).

Bird	Days at WS 10 per year	Annual consump- tion of insects (kg/ha)	Total consumption (kg/ha)
Chestnut-backed chickadee	365	1.7	2.1
Golden-crowned kinglet	365	1.7	1.8
Hammond's flycatcher	112	0.2	0.2
Hermit warbler	88	0.3	0.3
Stellar's jay	365	0.2	1.2
Western flycatcher	100	0.3	0.3
Western tanager	145	0.3	0.3
TOTAL		4.8	6.2

Table 3.27. Number of species of invertebrates captured in three Douglas-fir stands (Nagel, personal communication; after Strand (in press)).

Invertebrate class	Number of species
Herbivores feeding on:	
Any plant	166
Herbs	6
Trees and shrubs	63
Lower plants	<u>24</u>
	259
Predators:	150
Parasites feeding on:	
Invertebrates	94
Vertebrates	<u>1</u>
	95
Saprophores feeding on:	
Plant material	78
Animal material and feces	<u>14</u>
	92
General scavengers:	<u>100</u>
TOTAL	<u><u>696</u></u>

perform critical roles. They prepare and condition dead and dying materials for decomposers and under certain conditions become important factors in controlling ecosystem stability. Insect populations can switch from endemic to epidemic populations in response to host conditions which then is reflected in beetle host selection behavior. This regular change in population status has led us to postulate that, to maintain stability at equilibrium, a forest system may require periodic stress such as a modest insect attack in order to release nutrients and maintain the existing species composition.

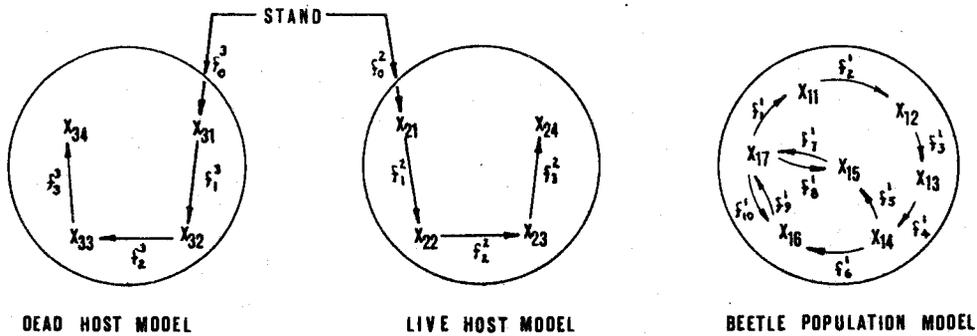
The Douglas-fir beetle can condition the dead or dying host for invasion by decomposers and in some cases the beetles readily kill healthy trees. Trees under the greatest moisture stress are quickly located and killed by bark beetles. Vigorous trees, however, are capable of overcoming beetle attacks by filling egg galleries with resin. In locating their hosts, insects respond to host- and insect-produced volatiles. Early-emerging adults orient their flight toward host volatiles in contrast to the late-emerging adults, which orient their flight toward the insect-produced pheromones in combination with host volatiles.

Douglas-fir bark beetle population model. The model is constructed to predict beetle population and stand host dynamics. Beetle populations are expressed in numbers of individuals per hectare represented by seven state variables; the stand model uses nine state variables to represent the live and dead host material and soil moisture (Figure 3.50). The stand model characterizes host material in terms of surface area (square meters) and number of trees per hectare. Processes being modeled are death, birth, maturation, host selection behavior of the beetles, tree mortality, and availability of live hosts in the stand.

At present the model has all the relationships in Figure 3.50, defined and is coded for simulation runs. The model simulations so far have tested predicted behavior with field observations. The maturation relationships, when simulated using average air temperature to predict development times, are quite consistent with the field observations of Schmitz and Rudinsky (1968). This same comparison run had a brood survival rate of 35% which compares favorably with the 34%-40% survivorship, observed by Schmitz and Rudinsky (1968) at normal population levels. A hypothetical data set was constructed to test annual behavior. The model produced one to one and one-half generations annually, which is consistent with the beetles' life cycle.

A data set is yet to be compiled with respect to a particular site, but it appears that data exist for both watershed 10 and the Cedar River watershed. With a site data set, the attack behavior of the model can be tested for consistency. The attack model will also undergo modification.

When the data sets are compiled and an updated attack model is completed, we will be able to conduct simulation runs, on both monthly and annual bases, to test host material--population level interactions and environmental patterns inducing host-population dynamics. Then it will be possible to identify critical stand-population levels necessary for epidemic-endemic cycle conditions, and to hypothesize various patterns



VARIABLES	MODEL PROCESS	RELATIONS
X_{21} - Live Host Available		
X_{22} - Initial Attack Phase		
X_{23} - Secondary Attack Phase		
X_{24} - Final Attack Phase		
X_{31} - Dead Host Available		
X_{32} - Initial Attack Phase		
X_{33} - Secondary Attack Phase		
X_{34} - Final Attack Phase		
X_{11} - Number of Eggs		
X_{12} - Number of Larva(all Instars)		
X_{13} - Number of Pupa(Includes Prepupa)		
X_{14} - Callow Adults		
X_{15} - Pioneer Adults(attracted To new host material)		
X_{16} - Follower Adults(attracted To new gallery)		
X_{17} - Gallery Adult		
	BEETLE	LIVE HOST
	f_1^1 - Oviposition by Gallery Adult	f_0^2 - Availability of Living Host[uses transpiration model; running and working]
	f_2^1 - Hatching	f_1^2 - Transfer of New Attack Host From Available
	f_3^1 - Pupation	f_2^2 - Transfer of Initial Attack Host To Secondary
	f_4^1 - Emergence	f_3^2 - Transfer of Secondary Attack Host To Final
	f_5^1 & f_6^1 - Partitions Mature Adults Into Pioneers or Followers	
	f_7^1 - Host Selection by Pioneers	DEAD HOST
	f_8^1 - Emergence From Gallery by Pioneer	f_0^3 - Stand Mortality
	f_9^1 - Host Selection by Follower	f_1^3 - Transfer of New Attack Host From Available
	f_{10}^1 - Emergence From Gallery by Gollower	f_2^3 - Transfer of Initial Attack Host To Secondary
		f_3^3 - Transfer of Secondary Attack Host To Final

Figure 3.50. Flow chart, variables and model process relations in the Douglas-fir bark beetle population model (R. Rydell, pers. commun.).

of annual behavior based on environmental data to test the consistency of the model in comparison with long-term field observations.

If the model is adequate in describing site dynamics for the Douglas-fir bark beetle, we then can use it to compare sites. By using the mathematical characterization generated during simulation runs, it will be possible to develop data that will relate beetle population and stand mortality to stand condition and stand location in various environments.

Because of the model formulation, it can be used as a canonical form to model any bark beetle. Thus it is possible to use the model to generate a subsystem of the food chain, in particular the functional group of bark beetles. Again using the mathematical formulation of the model, a single model (of the functional group) can be constructed from the several models representing the beetle species.

Decomposition of large woody material is initiated and enhanced by the action of invading insects. Density of attack on felled material is not evenly distributed; the highest densities are on the lower half of the material and lowest densities on the top half. The insects provide entry places for fungal mycelia and spores, thus increasing the rate of decomposition and nutrient cycling. A great deal of information has been gathered on the complex interaction between the various groups of insects invading the moribund or dead host (Deyrup in press).

Nutrient cycling is also enhanced by soil and litter invertebrates. Particular attention has been given to the banana slug (Ariolimax columbianus), which is capable of returning nitrogen, phosphorus, and potassium to the soil in readily available form. Slugs are capable of consuming as much as 30% of their body weight in 24 hours (K. Richter, pers. commun.).

Integration of consumer processes. To this point the discussion of the role of consumers has considered the role of consumer groups separately. Just as the processes we discussed earlier in connection with carbon, water, and nutrient cycling do not function independently, neither do consumer processes function independently. Strand (in press) has integrated canopy food chain processes in an old-growth Douglas-fir watershed in a simulation model. This model can be directly linked to the model of carbon, water, and nutrient cycling developed (P. Sollins and G. Swartzman, pers. commun.). The carbon module contains a term for foliage consumption by insects and Figure 3.51 shows the main routes of energy transfer between the nine functional groups identified (Strand and Nagel 1972). In other words, the food chain has been conceptualized as consisting of grazing vertebrates, grazing insects, sucking insects, seed and cone insects, predaceous birds, parasitic invertebrates, predaceous invertebrates, omnivorous birds, and nest predators. Surveys of the watershed fauna have shown that these functional groups are complex and may contain large numbers of species.

A complete energy budget for all compartments has not yet been completed but a partial budget has been constructed (Figure 3.52). The grazing insects are probably the major foliage consumers in the canopy food

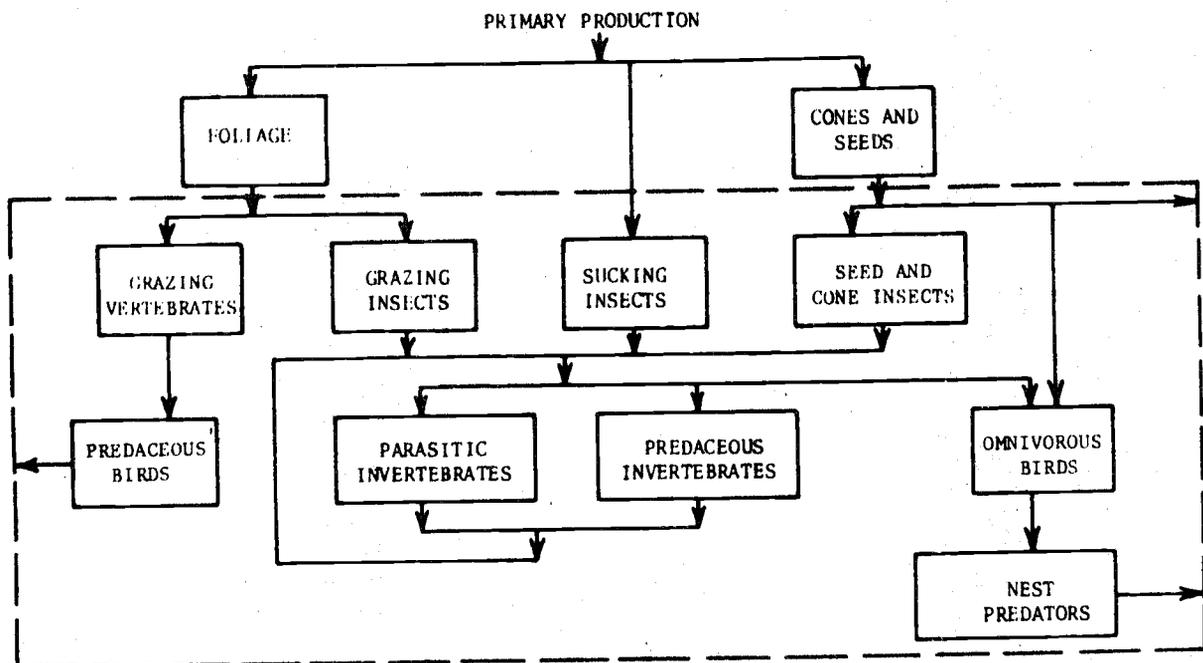
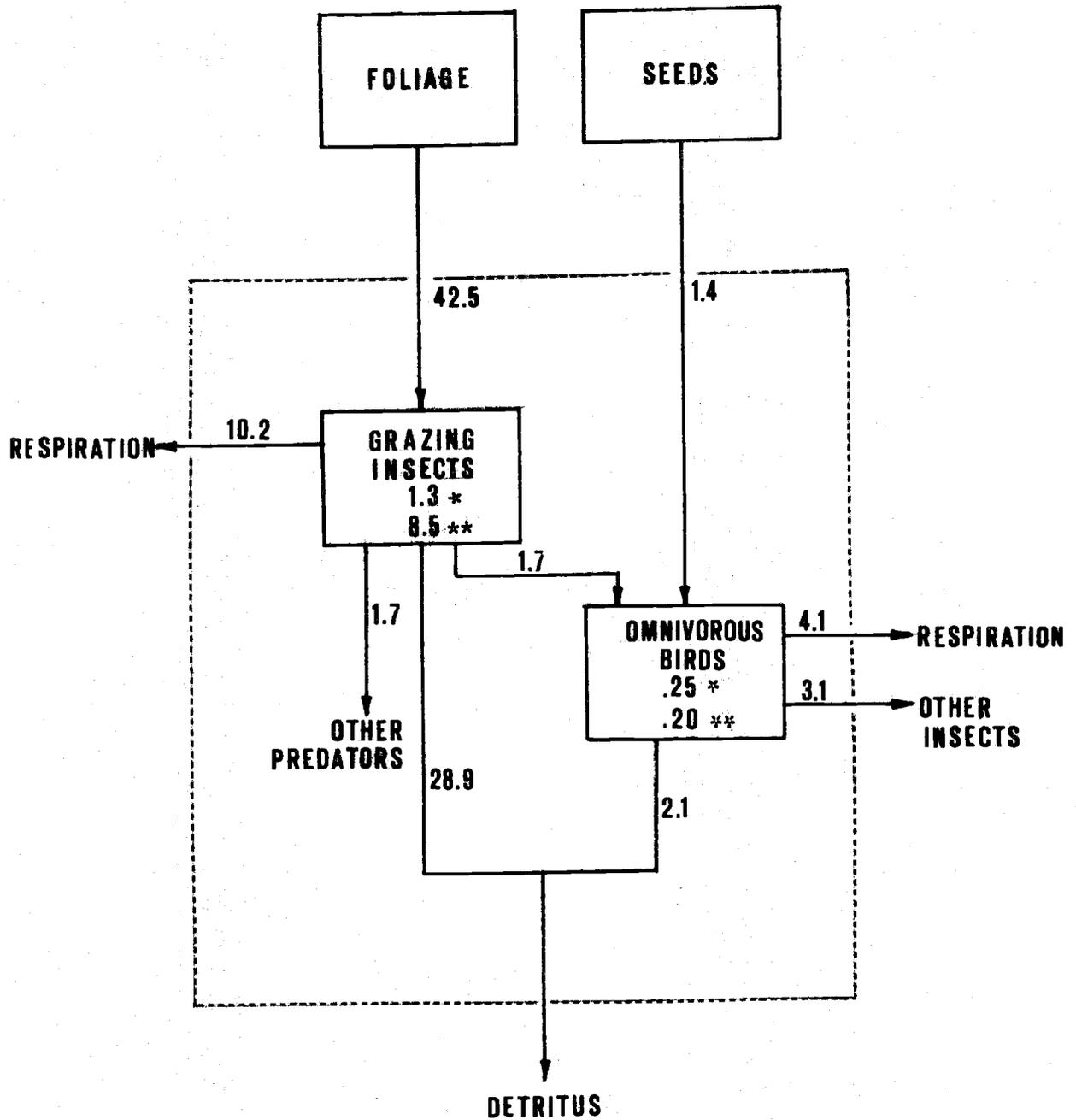


Figure 3.51. The major energy pathways between the components of the forest canopy food chain (from Strand and Nagel 1972).



* mean standing crop during spring and summer(kg/ha)

** annual secondary production(kg/ha)

Figure 3.52. The energy flux through two functional groups in the canopy food chain. Standing crops are kg/ha and fluxes are kg per ha per year.

chain. The annual consumption by grazing insects on the watershed is estimated to be 42.5 kg/ha or about 1.6% of primary production. This percentage compares favorably with consumption of Liriodendron foliage (Reichle et al. 1973).

At current population levels, the canopy food chain uses a relatively small amount of energy. Some grazing and sucking insects, however, have the capacity for extreme population fluctuations that can make them major energy users. In fact Keene (1952) lists 14 species of such insects that have been reported as economic pests in Douglas-fir forests.

Conclusions. Our results to date indicate that consumers are only a small component of the total biomass of both old-growth and young-growth Douglas-fir ecosystems. Under stable population conditions, consumers do not contribute greatly to the amounts of carbon and nutrients cycling through coniferous ecosystems. Populations of certain large mammals (such as wapiti) and certain groups of foliage consuming insects (such as the tussock moth), however, are capable of expanding rapidly and causing considerable changes in the rates of carbon and nutrient cycling and perhaps temporary losses in productivity. Rafes (1970), however, has indicated that increment losses are negligible when consumption is less than 50%. Insect population explosions are thought to act as controllers of total ecosystem stability.

3.1.2.7. The role of decomposers. Nutrient cycling and energy flow are two ecological processes which delineate the structure and dynamics of ecosystems. In terrestrial ecosystems an important set of energy flows and nutrient transfers result from litter fall and the subsequent decomposition of the litter.

Our decomposition studies have attempted to determine changes in nutrient content and weight loss of woody and non-woody substrates on a seasonal basis to test the hypothesis that decomposition rate will reflect differences between habitat types in the Coniferous Forest Biome. The habitat types selected are representative of stands located in environments ranging from wet to dry and from cold to warm. Simultaneous tests have also been made of the hypotheses that substrate chemical quality affects decomposition (Alexander 1961) and that temperature and moisture are the major abiotic environmental factors affecting decomposition in this Biome, as is the case in other terrestrial Biome regions (Witkamp 1971). Approximately 7100 litter bags containing various substrates were placed in different habitats during 1973 to evaluate these hypotheses (Fogel and Cromack in press). Other approaches have included field measurement of litter respiration (C. T. Youngberg and M. Phillips pers. commun.), laboratory assessment of the effects of available carbon and temperature on litter respiration (Gilmour et al. 1973), and biochemical studies of wood and needle litter decomposition (Minyard and Driver 1972a, b; 1973).

Preliminary results (Fogel and Cromack in press) from the approximately eight-month-old litter bag experiments indicate that cumulative weight loss of green Douglas-fir needles, presented for Reference Stand 2, H. J.

Andrews Experimental Forest, showed almost no weight change during the summer months (Figure 3.53). Respiration data (C. T. Youngberg and C. M. Gilmour pers. commun.) confirmed the low biological activity. This was attributed to the low precipitation during this period. Weight loss data for green Douglas-fir needles (Figure 3.54) showed no significant differences between habitat types over a six-month period. Data for Douglas-fir cones, branches and bark (not shown here) also indicated no significant differences between habitat types, although weight loss of these woody materials was less than that of needles. This difference could be due to substrate quality. There is a general trend ($r^2 = 0.56$) showing lower decomposition rates associated with higher lignin content (Figure 3.55) or C/N ratio ($r^2 = 0.49$) of litter substrates. Data for other nutrients (N, P, K, Ca, Mg, Fe, Mn, Cu, Zn, and Na) are currently being collected and statistically reduced.

The work of Gilmour (1973) shows that rates of carbon loss for forest floor litter components may be expressed for various undecomposed litter substrates and also for more stabilized humus fractions. Composite forest litter samples exhibit experimental k carbon rate loss values depending upon the degree to which decomposition has previously proceeded under field conditions. The method of Olson (1963) is used in the calculation of k loss rate values. For example, the more stabilized humus fractions should exhibit the lowest turnover rate. Initial litter decomposition, representative of newly fallen needles, has the highest turnover time.

Biochemical changes have been examined by determining the solubility of Douglas-fir needles and sapwood in cold water, hot water, alcohol/benzene, and 1% sodium hydroxide at various intervals after placement on the Thompson Research site. Minyard and Driver (1972a) indicate that during the first six months the cuticle of Douglas-fir needles is degraded and in the next six months cellulose and saccharides are increasingly solubilized.

Similar studies on Douglas-fir sapwood stakes placed at various levels in the soil shows that wood decomposition exhibits a similar stepwise response pattern (Figure 3.56). During the first month of exposure short-chain polysaccharides, soluble in cold water, are leached or used by microorganisms. During the second month hot water extracts increase, decomposition of longer chain polysaccharides such as starches, lignin or cellulose has started. Solubility in 1% NaOH also indicates that cellulose decomposition has increased slightly in the second month. Ethanol/benzene soluble materials such as resin, acids, fats, and oils do not become available until the fourth month. Decomposition of large Douglas-fir boles (Table 3.28) has been assessed by examining nutrient and organic constituents of various log decay classes (Fogel and Cromack in press, Fogel et al. 1973). Leachates from the solubility tests are currently being analyzed for nutrient content.

3.1.3. Comparison of structure and function of coniferous ecosystems across the Biome.

One of our objectives is to compare ecosystems across the Biome. However,

Table 3.28. Nutrient contents and composition of logs on the H.J. Andrews Experimental Forest.

Stage of log decay ^a	Percentage						Parts per million				
	N	C	Non-cell-wall	Lignin	Cellulose	Ash	P	K	Ca	Na	Mg
1	0.12	52.6	20.3	57.6	22.0	0.06	157	360	1041	15	61
2	0.24	56.4	6.5	86.6	6.7	0.23	155	365	1451	42	240
3	0.37	53.2	15.0	72.7	11.4	0.99	236	141	2347	44	366

^aDecay condition where: 1 is least decomposition, bark still intact; 2 is log rotted throughout, but still retaining recognizable structure; and 3 is log integral with forest floor.

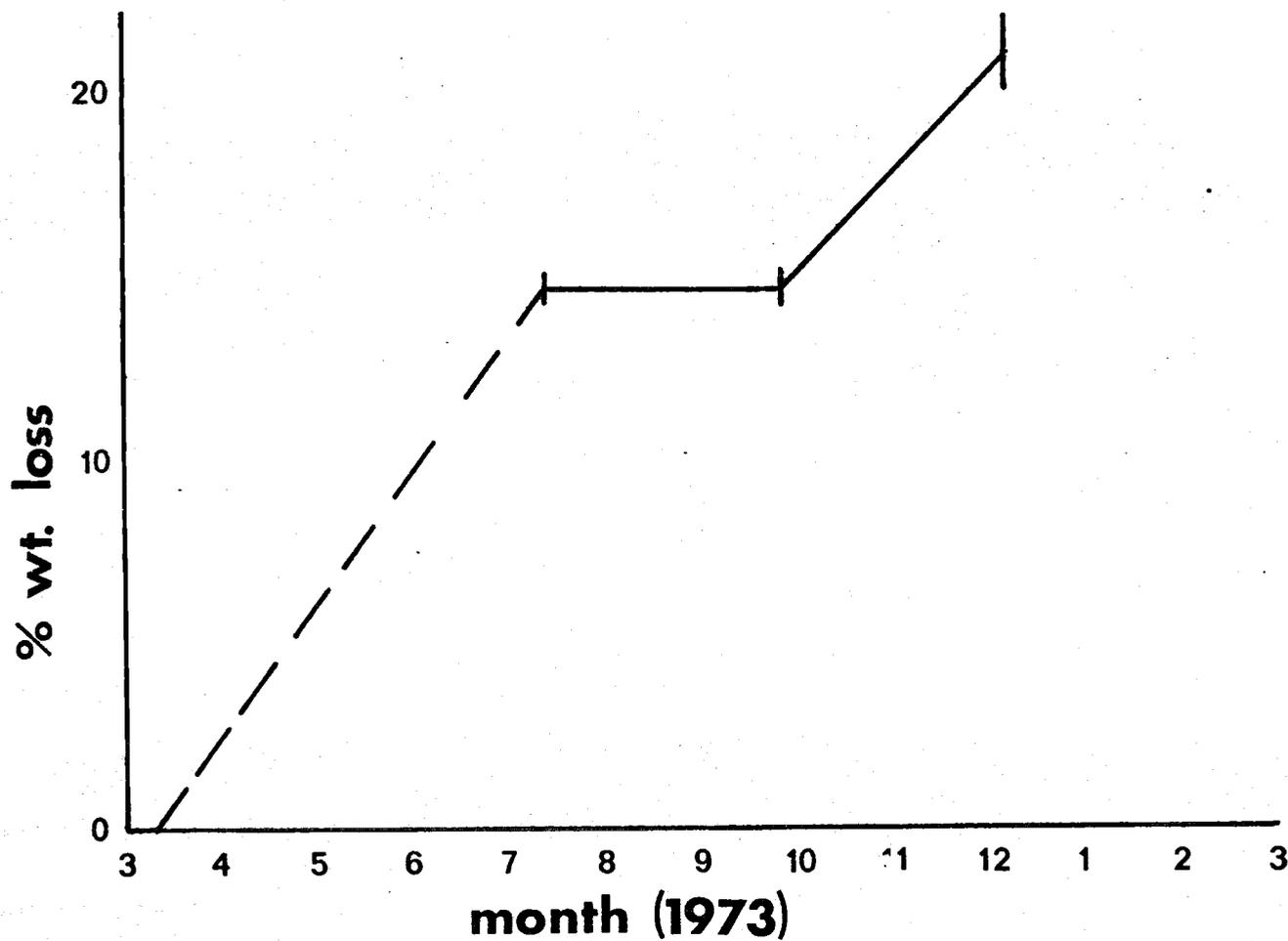


Figure 3.53. Weight loss of Pseudotsuga menziesii needles in the Rhododendron macrophyllum/Berberis nervosa habitat type in Reference Stand 2, H. J. Andrews Experimental Forest. 95% confidence limits are shown.

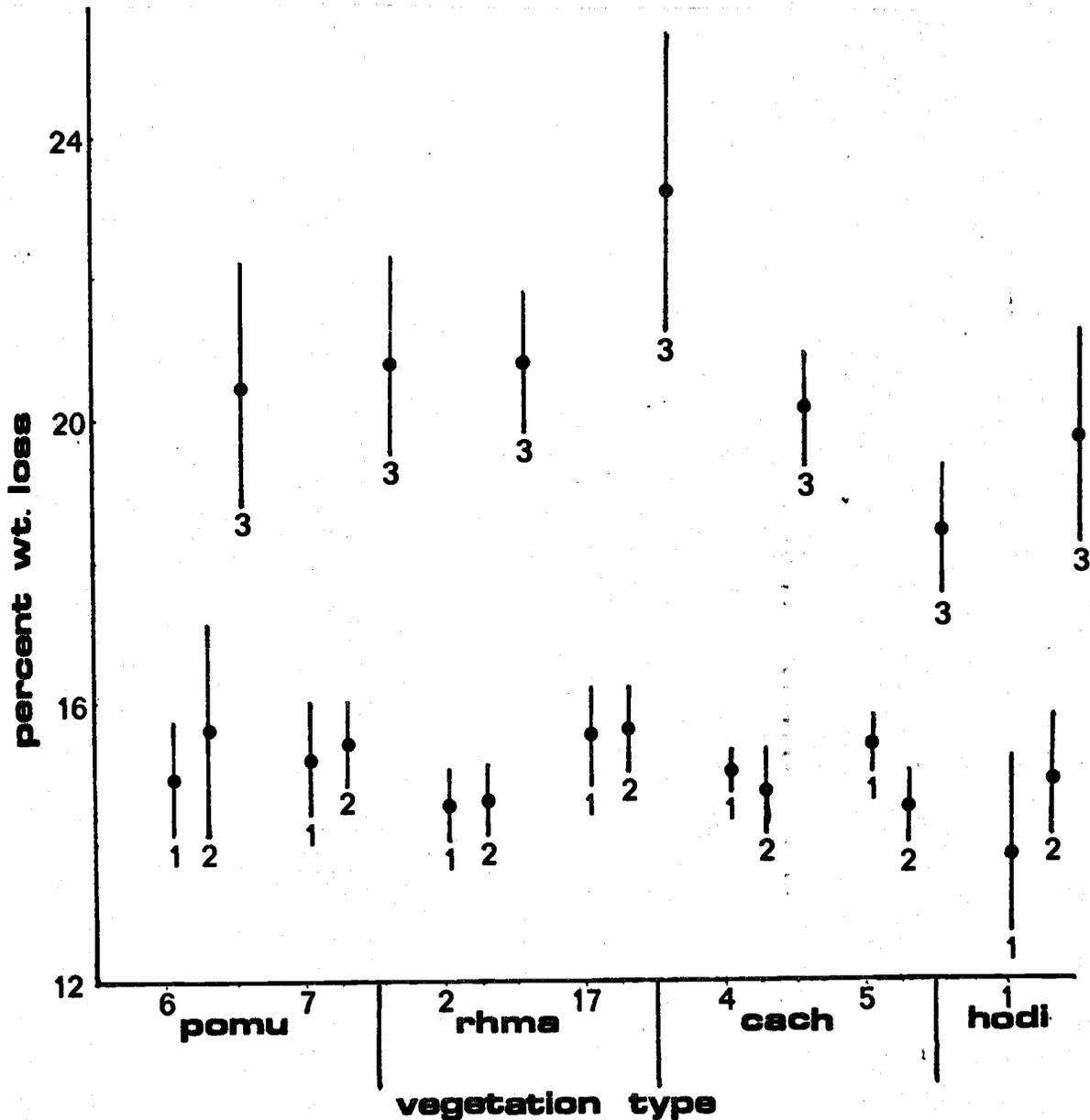


Figure 3.54. Weight loss of green *Pseudotsuga menziesii* needles in four vegetation types in the H. J. Andrews Experimental Forest after 4 months (1), 6 months (2) and 9 months (3) beginning 10 March, 1973. pomu = *Polystichum munitum*, rhma = *Rhododendron macrophyllum*, cach = *Castanopsis chrysophyllum*, and hodi = *Holodiscus discolor*. 95% confidence limits are shown.

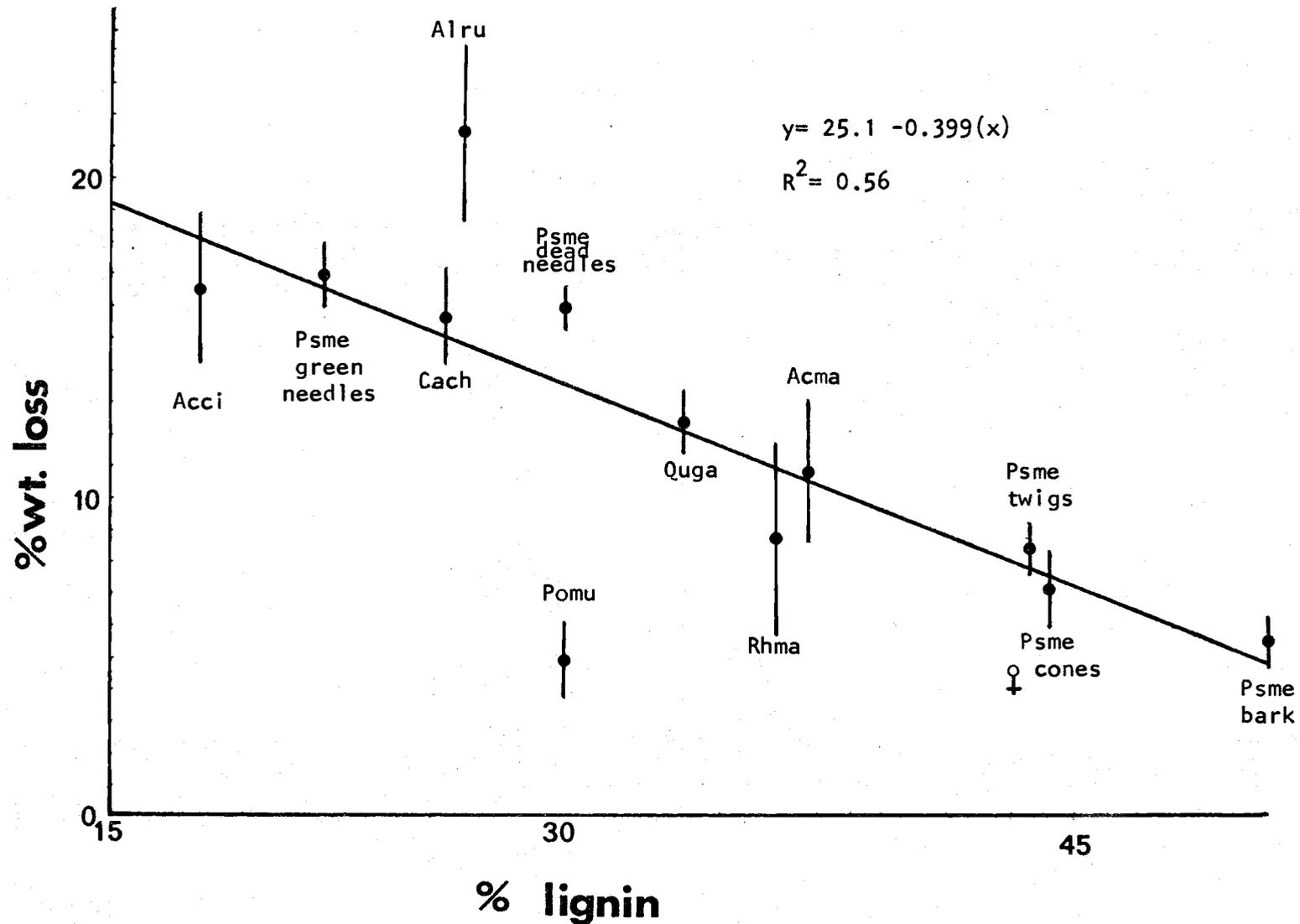


Figure 3.55. Weight loss of substrates as a function of their lignin content in Reference Stand 2, H. J. Andrews Experimental Forest after a 6 month period beginning 29 May, 1973. Acci = Acer circinatum, Acma = Acer macrophyllum, Alru = Alnus rubra, Cach = Castanopsis chrysophyllum, Pomu = Polystichum munitum, Psme = Pseudotsuga menziesii, Quga = Quercus garryana and Rhma = Rhododendron macrophyllum. Substrates are needles unless otherwise indicated. 95% confidence limits are shown.

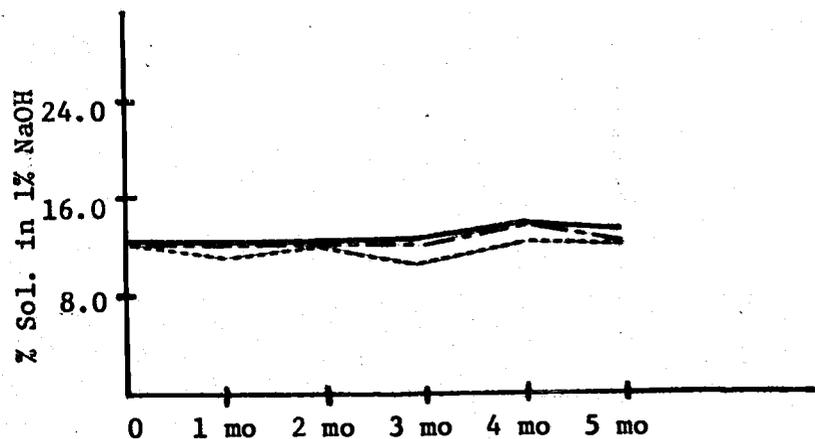
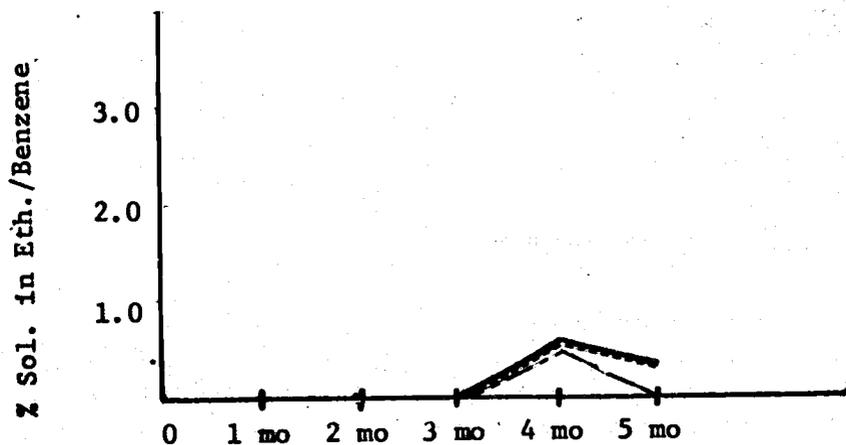
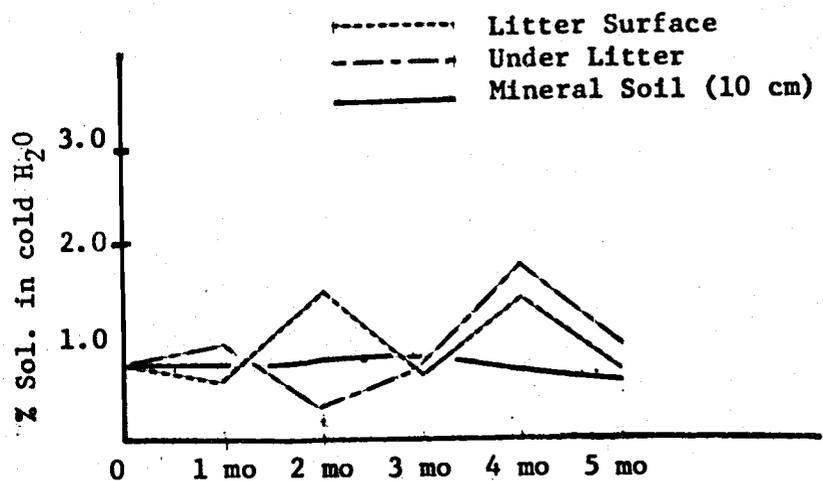
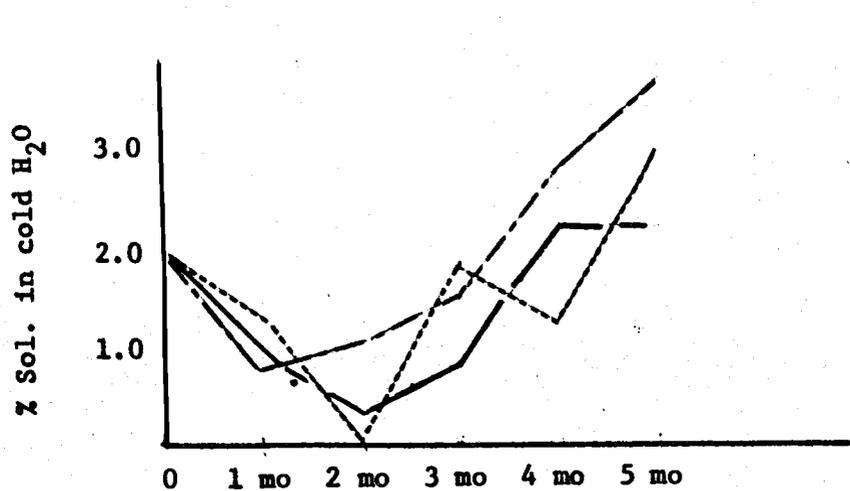


Figure 3.56. Solubility evaluations of Douglas-fir sapwood illustrating the initial stages of decomposition.

few of the data now being synthesized are available but they will be included in the Biome synthesis volume.

Preliminary biomass data are available from a black spruce ecosystem near Fairbanks, Alaska (K. Van Cleve pers. commun.), from a lodgepole pine ecosystem in Colorado (Moir 1972), and from the cooperative study between the Japanese IBP and the Coniferous Forest Biome (C. C. Grier pers. commun.). Turner and Cole (1973) have reviewed biomass information from the literature and have summarized some trends in biomass distribution and amounts. They do point out, however, that it is difficult to compare directly the results of one study with another because of differences in sampling techniques and site qualities, etc.

Recognizing these problems an attempt has been made here to compare some of the preliminary data. Table 3.29a compares biomass of lodgepole pine and black spruce ecosystems to the biomass of the Douglas-fir ecosystems at the intensive sites. If total above-ground biomass is plotted against age for each stand, the lodgepole pine and spruce data do not deviate greatly from a straight line drawn between the data points for the two Douglas-fir ecosystems. However, the distribution of the biomass in the ecosystem components does differ between ecosystems. The spruce ecosystem has nearly double the non-living material found in the much older Douglas-fir ecosystem in Oregon.

Satoo (1967) noted that in Pinus densiflora stand stem biomass is a function of age, and branch biomass is a function of age and stand density. Leaf biomass was found to be constant after crown closure. We wish to investigate if Satoo's findings apply across the Biome to a variety of species. Table 3.29b presents data for the components of overstory biomass (foliage, branches, and bole) for several stands in Oregon, Washington, Colorado, and Alaska. The Oregon stands show an increasing bole biomass with age with the exception of Watershed 10. These data tend to support Satoo's observations. The exception is probably due to poorer site qualities on Watershed 10 and the different stratification techniques used in determining overstory and understory. Satoo's finding concerning relationships between age and branch biomass also appears to apply to these data. His conclusion about foliage biomass is untestable with these data. However, Turner and Cole (1973) indicate that there appears to be an upper limit of foliage biomass in the Douglas-fir ecosystems they have examined of about 8-10 t/ha, and a limit of about 30 t/ha for crown biomass. The data in Table 3.29b would indicate, however, that this upper limit does not apply to all species and there is evidence (C. C. Grier pers. commun.) that it may not apply in all Douglas-fir ecosystems.

Yoda (1968) found that foliage/bole ratios increased with increasing elevation in Nepal. A comparison of this ratio with elevation cannot be examined with accuracy from our preliminary data, but a rough comparison can be made. The sitka spruce and western hemlock ecosystems are from the mid-elevation western hemlock zone, and the noble fir is from the Pacific silver fir zone at a high elevation. Foliage/bole ratios for these ecosystems are; 0.009, 0.140, 0.065, 0.019, and 0.02, respectively. This does not support Yoda's observations.

Table 3.29. (a) Biomass (metric tons/ha) of the above- and belowground components of Douglas-fir, lodgepole pine, and black spruce ecosystems. (b) Biomass (metric tons/ha) of the aboveground components of western hemlock, Douglas-fir, lodgepole pine, sitka spruce, noble fir and black spruce ecosystems.

(a)	Douglas-fir ^a		Lodgepole- pine ^b	Black spruce ^c
	Washington (35 yr)	Oregon (450 yr)	color (77 yr)	Alaska (130 yr)
Overstory	171.1	530.0	274.6	117.4
Subordinate vegetation	1.0	8.8	0.0	2.4
Dead + litter	10.7	98.5	40.1	161.1
Aboveground	182.8	637.3	278.6	280.9
Roots	33.0	74.3	96.8	51.7
Soil	123.0	150.0		475.0
TOTAL	338.8	861.6		807.6

(b)	Western hemlock Oregon (26 yr) ^d	Douglas-fir Washington (35 yr) ^a	Lodgepole pine Colorado (77 yr) ^b	Sitka spruce Oregon (100 yr) ^a	Noble fir Oregon (120 yr) ^a	Black spruce Alaska (130 yr) ^c	Douglas-fir Oregon (450 yr) ^a
	Foliage	21.1	9.1	17.4	7.7	17.7	9.2
Branches	20.7	22.0	40.4	53.2	66.2	15.2	48.6
Bole	150.9	140.0	216.8	828.0	861.0	86.4	472.5
TOTAL	192.7	171.1	274.6	888.9	944.9	110.8	530.0

^aC. C. Grier (pers. commun.)

^bMoir (1972)

^cK. Van Cleve (pers. commun.)

^dFujimoru (1971)

Nitrogen and phosphorus budgets for the Douglas-fir ecosystems at the intensive sites and the 130 year-old black spruce stand in Alaska are presented in Table 3.30. Total system nitrogen is not very different in all three ecosystems, but the distribution in the above ground components differs. In particular there is a larger amount of nitrogen in the dead and litter component in the spruce ecosystem than either of the Douglas-fir ecosystems. This would indicate that there is an accumulation of nitrogen in the non-living ground components in this northern ecosystem. Phosphorus data show the same trend. However, total system phosphorus is much lower in the spruce ecosystem.

These preliminary data indicate that there are differences in the total amounts and distributions of biomass and nutrients in coniferous ecosystems across the Biome which need further examination.

Table 3.30. Budgets and distribution of nitrogen and phosphorus in Douglas-fir ecosystems in Washington and Oregon, and a black spruce ecosystem in Alaska.

	Budgets (kg/ha)						Distribution (%)					
	Douglas-fir Washington (35 yr)		Douglas-fir ^a Oregon (450 yr)		Black spruce ^b Alaska (130 yr)		Douglas-fir Washington (35 yr)		Douglas-fir ^a Oregon (450 yr)		Black spruce ^b Alaska (130 yr)	
	N	P	N	P	N	P	N	P	N	P	N	P
Overstory	271	66	312	42	223	29	60	71	34	38	26	26
Understory	6	1	44	8	25	4	1	1	5	7	3	4
Dead + litter	175	26	566	61	604	78	39	28	61	55	71	70
Aboveground	452	93	922	111	852	111	100	100	99	100	100	100
Roots	32	10	62	5	71	8						
Soil	2809	3878	4300		2363	1642						
				29 ^c		4 ^c						
Total	3383	3981	5284		3286	1761						
				146 ^c		123 ^c						

^aC. C. Grier (personal communication).

^bK. Van Cleve (personal communication).

^cExchangeable N and P.

3.2. The Structure and Dynamics of Lake Ecosystems in the Douglas-fir Region

The analysis of freshwater ecosystems in the Coniferous Forest Biome has centered on the comparative productive capacity of lakes. Ecosystems under study by University of Washington scientists include Lake Washington, Lake Sammamish, Chester Morse Lake, Findley Lake, and Fern Lake. Coordination studies have been completed at Castle Lake, California, by the University of California at Davis. The principal objective of the Coniferous Forest Biome aquatic program is to develop an understanding of the functional aspects of energy, organic matter, and minerals within aquatic ecosystems and to assess their dependence upon external and internal sources of energy, organic production, and physiochemical events. Current research and modeling activities are incorporating quantitative relationships among nutrient cycling, decomposition, primary production, and consumer feeding and production for the purpose of simulating and to predict if possible, responses of aquatic systems to natural and man-induced perturbations.

3.2.1. Lake ecosystems of the Lake Washington drainage basin

Lake ecosystems research on the Lake Washington drainage basin near Seattle, Washington, involves the development of a basic understanding of carbon and nutrient changes within lacustrine environments by studying lakes in different trophic states. Research and process model development are centered on physical and chemical features, allochthonous input and communities of phytoplankton, zooplankton, limnetic fish, benthic-littoral fish, and benthic organisms.

Lakes of the Lake Washington drainage basin (1299 km²) are located in two distinct subdrainages: Issaquah Creek--Lake Sammamish drainage (855 km²) including Lake Sammamish, Lake Washington, and Cedar River Valley (466 km²) which includes Chester Morse and Findley Lakes. These subdrainages exhibit contrasting patterns of land use, morphometric features, and budgets for water, nutrients, and energy. Principal flow of the Sammamish system is at a low elevation through Lake Sammamish (12 m elevation, 19.8 km², 31 m deep), a mesotrophic lake subjected to urbanization and limited agricultural practices. The Cedar River system originates at higher elevations in the Cascade Mountains with nutrient inputs mainly from forested ecosystems. The upper watershed of the Cedar River includes two oligotrophic lakes, Findley Lake (1131 m elevation, 0.09 km², 30 m deep), and Chester Morse Lake or reservoir (473 m elevation, 6.54 km², 38 m deep), which are part of the controlled-access municipal water supply area of the City of Seattle. The Cedar River enters the southern end of Lake Washington and the Sammamish Slough enters the northern end. Lake Washington (8.6 m elevation, 87.6 km², 64 m deep), which is currently recovering from eutrophication (Edmondson 1972), drains west through Lake Union and the Hiram Chittenden Locks into Puget Sound.

Information obtained in Findley and Chester Morse Lakes has been compared with Lakes Washington and Sammamish based on the hypothesis that a better understanding of biotic-abiotic interactions could be achieved

by studying lakes with different trophic conditions. These four lakes form a graded series with respect to altitude, morphometry, productivity, and amounts of human interference with the surrounding watershed. The altitude differences alone are responsible for extreme climatic variance between the lower and the upper lakes. But the degree of human settlement of the locale probably has had the most pronounced effect on the degree of eutrophication.

The land surrounding Lake Washington is heavily settled; the watershed of the north, west, south, and parts of the east shores is completely urbanized. The remainder of the east shore is suburban in character. Trunk sewer lines completely surround the lake so that no sewage flows into Lake Washington. The Lake Sammamish shore is predominantly suburban on the west and south shores, except for the small village of Issaquah to the south. The east shore of Sammamish is predominantly rural in character. The west and south and parts of the eastshore watershed are provided with sewer lines and most of the residences are connected. Chester Morse and Findley Lakes are located in a regulated watershed so that the only major disturbance of nature has been the extensive logging operations in the Chester Morse drainage area. No man-made disturbances have occurred in the Findley watershed. A comparison of several trophic status indicators in these four lakes is presented in Table 3.31.

Both Lakes Sammamish and Washington have been described extensively by other investigators. Lake Sammamish has been closely monitored for biological and nutrient changes both before and after the diversion of sewage effluents in 1968 (Welch and Spyridakis 1972, Emery 1972, Isaac et al. 1966). Lake Washington has also been closely watched for changes resulting from the diversion of sewage effluents (Edmondson et al. 1956, Edmondson 1966, 1972).

3.2.1.1. Plankton and nutrient relationships. Plankton-nutrient cycling research (1971-1973) on Lakes Washington and Sammamish, and Chester Morse and Findley Lakes has examined seasonal patterns of phytoplankton productivity, biomass, respiration, growth kinetics, phytoplankton cell size, composition, light conditions and nutrient supply, and uses modeling to simulate and evaluate the temporal-spatial dynamics of plankton production. Model development is linked to research by laboratory and field studies on needed functional components. Controlled experiments are designed in conjunction with modeling, for example, definition of relationships between light, temperature, nutrient concentration, and carbon uptake rates by algae. Field measurements of solar radiation, nutrients, temperature, and depth to which algal photosynthesis occurs are made to define ambient changes and the results incorporated in the submodels. Studies are also made of zooplankton feeding rates and production and these are to be tied to the phytoplankton production and limnetic fish submodels through transformation of algal food material into animal biomass.

In Lake Washington oxygen production rather than carbon assimilation has been the principal means of estimating phytoplankton productivity.

Table 3.31. Comparison of trophic status indicators of four lakes in the Cedar River drainage system.

Lake ^a	Year	Total P ($\mu\text{g}/\ell$)	PO_4P ($\mu\text{g}/\ell$)	$\text{NO}_2+\text{NO}_3\text{-N}$ ($\mu\text{g}/\ell$)	Si ($\mu\text{g}/\ell$)	Chl α ($\mu\text{g}/\ell$)	Produc. (mg C m^{-2} day^{-1})	Secchi (m)
Findley	1972	11.4	3.1	5.41	1780	0.6	220	16.4
Chester Morse	1972	6.9	2.1	9.36	3220	1.1	262	8.3
Sammamish	1971	48.0	7.0	86.0	1100	7.1	499	3.5
Washington	1971	18.7	1.1	56.5		9.5	1070	2.3

^aData for Lakes Chester Morse, Sammamish, and Washington are mean values for the May through August growing period. Findley Lake values are means for the July through October growing season. Nutrient and chlorophyll α values were derived from surface concentrations in Lakes Washington and Sammamish (Welch and Spyridakis 1972), while in Findley and Chester Morse they are derived from the weighted mean concentrations of the photic zone.

In order to compare the productivity of Lake Washington with the productivities of the upper three lakes, it was necessary to convert the values derived by the light and dark bottle oxygen method into the same terms used for the upper three lakes.

Calculations based on data supplied by Edmondson (Welch and Spyridakis 1972) show that Lake Washington has a mean primary productivity of 1070 mg carbon per m² per day during the May to August growing season. This compares with 499 mg carbon per m² per day in Sammamish, 260 mg carbon per m² per day in Chester Morse, and 220 mg carbon per m² per day in Findley.¹ The mean chlorophyll a concentrations during the growing season indicate a substantial phytoplankton biomass gradient exists among these lakes; it is 9.5, 7.1, 1.1, and 0.6 µg chlorophyll a per liter in Washington, Sammamish, Chester Morse, and Findley, respectively (Hendry 1973).

Findley Lake is a dimictic, subalpine cirque lake located in a small (260 ha) watershed. Seasonal changes in phytoplankton productivity are regulated primarily by light. For approximately eight months of the year it is snow covered, and phytoplankton production is insignificant because of lack of light. The four-month growing season was characterized by the rapid development of a phytoplankton bloom following clearing of snow from the lake surface. At 12 m, which includes 90% of the total lake volume, the autotrophic capacity of the 25-m water column was 36 g carbon per m² per year, and total lake production was 530 kg carbon per year (Hendry 1973).

The Secchi disk transparency of Findley Lake ranged from 11.5 to 19.5 m with a vertical extinction coefficient range of $K = 0.13$ to $K = 0.24$. Transparency is inversely correlated to chlorophyll a content, with a correlation coefficient of -0.77 at the 0.05 level of significance.

Chester Morse Lake is a natural glacial valley lake that has been dammed to increase its elevation by approximately 10 m. The lake is dimictic and was completely frozen over in February 1972.

The concentrations of available nitrogen ranged from 18 to 127 µg/l, and orthophosphorus ranged from 1 to 14 µg/l. The productivity of Chester Morse Lake was shown to be limited by the depletion of available phosphorus during the April to October period of thermal stratification. During the rest of the year, high turbidity reduced light penetration, and mixing deep into the water column caused light to be growth limiting. Productivity ranged from 24 to 1681 mg per m² per day, with a May through August mean of 569 mg carbon per m² per day. The autotrophic capacity of the lake water was 47 g carbon per m² per year, and total annual production was 2.89×10^5 kg of carbon.

The Secchi disk transparency of Chester Morse Lake ranged from 3.3 m to 9.9 m, with a mean value of 8.8 m during the growing season. The

¹July through October mean productivity in Findley Lake.

vertical extinction coefficient ranged from $K = 0.230$ to $K = 0.58$. There was no significant correlation between transparency and chlorophyll *a* content, and it appears that turbidity caused by silt from the Rex and Cedar Rivers is primarily responsible for variation in potassium.

Interrelationships between light, nutrient availability, and productivity.

The interrelationships between light intensity, nutrient availability and the productivity of natural phytoplankton communities were studied. The physiological condition of the entire phytoplankton community was examined by normalizing the productivity values to remove the variation in productivity caused by light intensity and biomass concentration. A normalized productivity index (production per biomass per insolation, $[P/B]/I$) was obtained by dividing productivity by an estimate of the carbon biomass and by daily insolation. The $(P/B)/I$ also had a tendency to increase over time following an actual production peak, so that a $(P/B)/I$ peak occurred later in the growing season.

Another method used to investigate the effect of light and nutrient availability on productivity was in vitro incubations of natural phytoplankton communities at various light and nutrient treatment levels. Several models describing the effect of light intensity and nutrient availability on P/B , the production/biomass quotient, were examined. The function

$$\mu = \mu_m \frac{S}{k_t + S} \frac{R}{R_o} \exp(1 - R/R_o)$$

where μ is P/B , μ_m is maximum P/B , S is P concentration, k_t is S at $\frac{1}{2} \mu_m$, R is lux, R_o is optimum lux, was found to describe experimental results at the 0.05 level of significance, with a high degree of correlation (Hendry 1973).

It was initially hypothesized that the k_t values of natural phytoplankton populations were related to the productivity of the ambient waters in such a fashion that as productivity increases so does k_t . The half saturation constant k_t reflects the relative ability of phytoplankters to use low levels of nutrients. The k_t values obtained were 0.17, 0.36, 0.42, and 2.84 $\mu\text{g P/l}$ for Findley, Chester Morse, Sammamish, and Washington, respectively. By comparing these k_t values for the four lakes, the direct correlation between the trophic status and k_t confirms this hypothesis for natural phytoplankton communities in lacustrine environments.

Another result of these experiments was that the phytoplankton from oligotrophic to mesotrophic lakes were all stimulated by phosphorus concentrations as low as 1 $\mu\text{g P/l}$. The light treatments had less effect than was anticipated; the greatest response to light intensity was found at the lowest nutrient concentrations. It appears that cells grown at higher nutrient concentrations achieve their maximum growth response regardless of light intensity because of light adaptation, while cells at lower nutrient concentrations, being relatively nutrient starved, are unable to make physiological adaptations to varying light regimes.

Relation of size-classes of phytoplankton to lake productivity. Another objective of this research was to investigate the relative contributions of three size-classes of the phytoplankton to lake productivity in four lakes of contrasting trophic state. The hypothesis that the relative contributions of the various size-classes of the phytoplankton communities are related to the overall productivity of the lake is supported by both observations in nature and experimental research.

Some of the routine in situ carbon-14 productivity samples were fractionated by selective filtration into net-, nano-, and ultraplankton by passing the carbon-14-labeled sample through a stacked series of three filters of 50, 5, and 0.45 μm nominal porosity. The results for the ultraplankton were not entirely successful because of filtering characteristics of the 5 μm nominal porosity Millipore filter that was used to separate the nano- from the ultraplankton. It was concluded that data relating to ultraplankton obtained by this technique should be interpreted cautiously since the carbon assimilation values may be either too high because of the passage of labeled debris from cell rupture on the coarser filters or too low because of excessive retention of the 5- μm filter.

Except in Findley Lake, the contribution of the net plankton to the productivity of the whole community increased in a nearly linear fashion with lake productivity. An explanation for the seemingly anomalous results in Findley is that the lack of disruptive circulation there allowed the inclusion of cells in the net plankton, which in the other lakes would have passed into the nannoplankton. In all four lakes the relative contributions of the net plankton to productivity were at a maximum early in the growing season in response to increased temperature during a period of relatively high nutrient concentration.

Growth kinetics of the net and nannoplankton were studied in conjunction with the nutrient enrichment experiments on Lake Washington. The half-saturation constants and optimal light intensities were, for the net plankton, $k_t = 4.6 \mu\text{g P/l}$, $R_0 = 4329 \text{ lux}$, and $\mu_m = 0.135/\text{hr}$. For the nannoplankton the values were $k_t = 2.8 \mu\text{g P/l}$, $R_0 = 1585 \text{ lux}$, and $\mu_m = 0.167/\text{hr}$. These results indicate that the nannoplankton cells were able to maintain a higher maximum specific growth rate at lower levels of available nutrients than were the net plankton. This extends to lakes the conclusions of other investigators in marine waters (Dugdale 1967) that competition for available nutrients in oligotrophic waters would result in the dominance of species with low k_t values (Hendry 1973).

Studies involving the respiratory electron transport system. During 1973 we have continued monitoring the respiratory electron transport system (ETS) activity distribution in Lake Washington and Lake Sammamish. In addition, we have initiated the study of ETS activity distribution in Chester Morse and Findley Lakes. These studies have been designed to answer specific questions we feel are important to the understanding of an aquatic ecosystem, such as the following: (1) What is the relative importance of the phytoplankton, zooplankton, and bacterial respiration? (2) How much of the primary productivity of the phytoplankton community is oxidized by that community to meet cellular energy requirements? (3) Which is more important in the cycling of nutrients, bacteria or

zooplankton? (4) What are the relationships between ETS activity and carbon-14 uptake, ETS activity, chlorophyll concentrations, and the like? (5) What are the cycles of ETS activity both diel and temporal? In order to construct a realistic simulation model of the carbon flow, designed to predict the influence of both natural and man-induced perturbations of an aquatic ecosystem, these questions must be answered.

Figures 3.57 and 3.58 show the integrated ETS activity in the euphotic zone of the four lakes as a function of time. Both Findley and Chester Morse Lakes have low ETS activity when compared with the other two lakes. Findley Lake shows a minimum in August, while Chester Morse displays a maximum. Averaged over the sampling period the integrated ETS activity at Findley Lake is slightly less than that at Chester Morse, both of which are considerably lower than that of either Lake Washington or Lake Sammamish, which show a maximum in July. The average and range for each of the lakes is shown below in descending order:

<u>Lake</u>	<u>Average</u>	<u>Range</u>
Findley	9 mg O ₂ per hr per m ²	17-4 mg O ₂ per hr per m ²
Chester Morse	13 mg O ₂ per hr per m ²	22-8 mg O ₂ per hr per m ²
Washington	55 mg O ₂ per hr per m ²	80-29 mg O ₂ per hr per m ²
Sammamish	62 mg O ₂ per hr per m ²	93-30 mg O ₂ per hr per m ²

This is presumably owing to the more oligotrophic nature of the two lakes in Chester Morse watershed, along with possible man-induced inputs into Lakes Washington and Sammamish. In fact, based on a study near the White's Point sewage outfall of Los Angeles, Packard and Harmon (1972) have suggested that in vivo incubation measurements to determine BOD can be replaced by the in vitro ETS determination. If this approach proves reliable, one could consider Lake Sammamish the most polluted of the four lakes, with Findley and Chester Morse Lakes much "cleaner."

Vertical profiles of carbon-14 uptake and ETS activity in Lake Washington have been compared. The ETS activities have been converted to carbon equivalents using an R/Q of 0.85. It is interesting to note that of the total integrated carbon-14 uptake, approximately 28% and 57% are respired within the nannoplankton community on 4 May and 13 June, respectively.

Respiration, ammonia, and phosphate regeneration rates for the euphotic zone netplankton have been calculated from ETS activities. The respiration rate was obtained by multiplying the ETS activity by 1.96, an experimentally determined factor (Packard et al. in press). The nutrient regeneration rates were calculated from the respiration rates using a factor of 4.47×10^{-3} for ammonia, and 0.395×10^{-3} for phosphate. These factors are based on the relationship between respiration and ammonia excretion as derived by Conover and Corner (1968), and the relationship between ammonia and phosphate excretion as derived by Beers (1964). A combination of these studies yields an O:N:P ratio of 226:11:3.1 by atoms. We have calculated the turnover time of these nutrients in

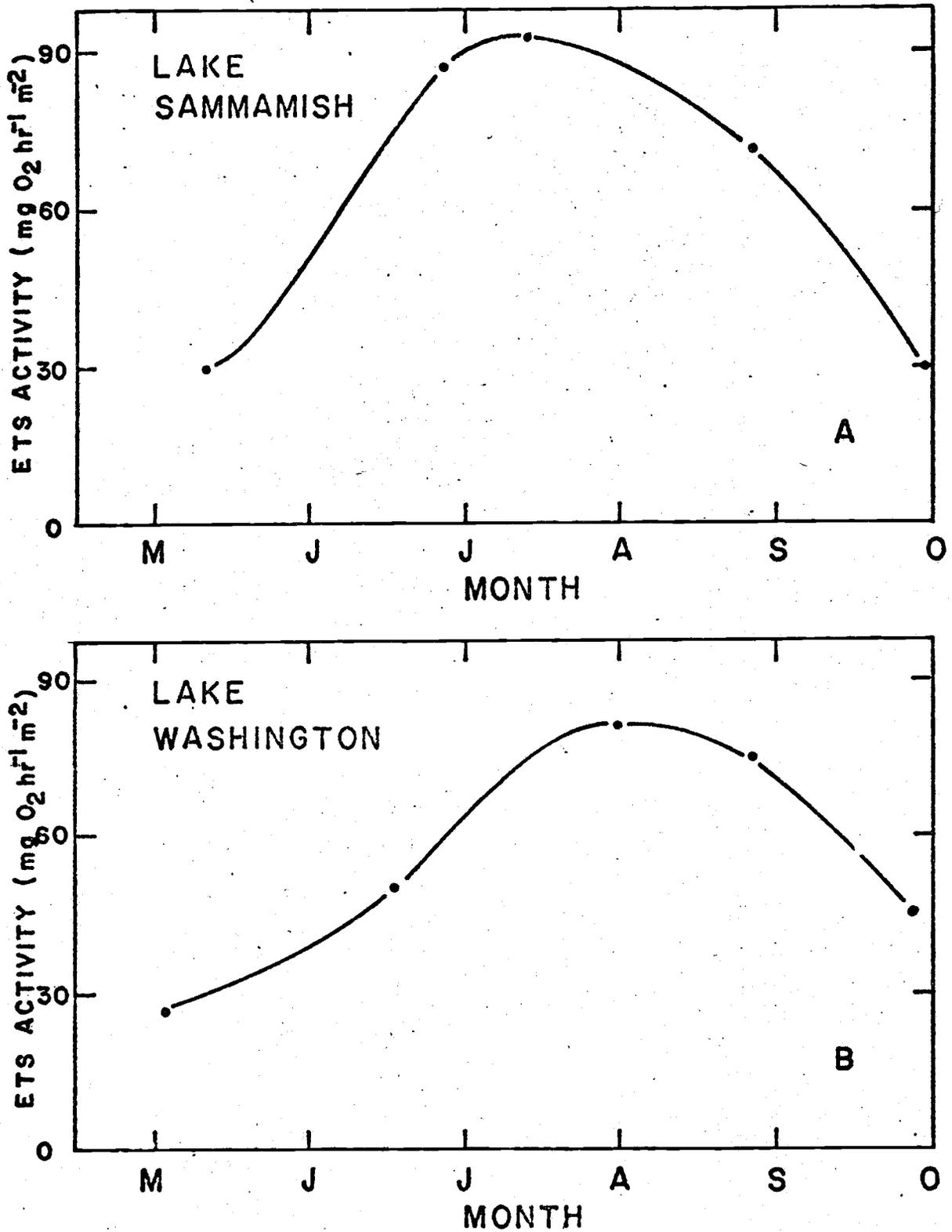


Figure 3.57. Integrated respiratory electron transport activity in the euphotic zones (100-1% light levels) in Lakes Washington and Sammamish as a function of sampling date.

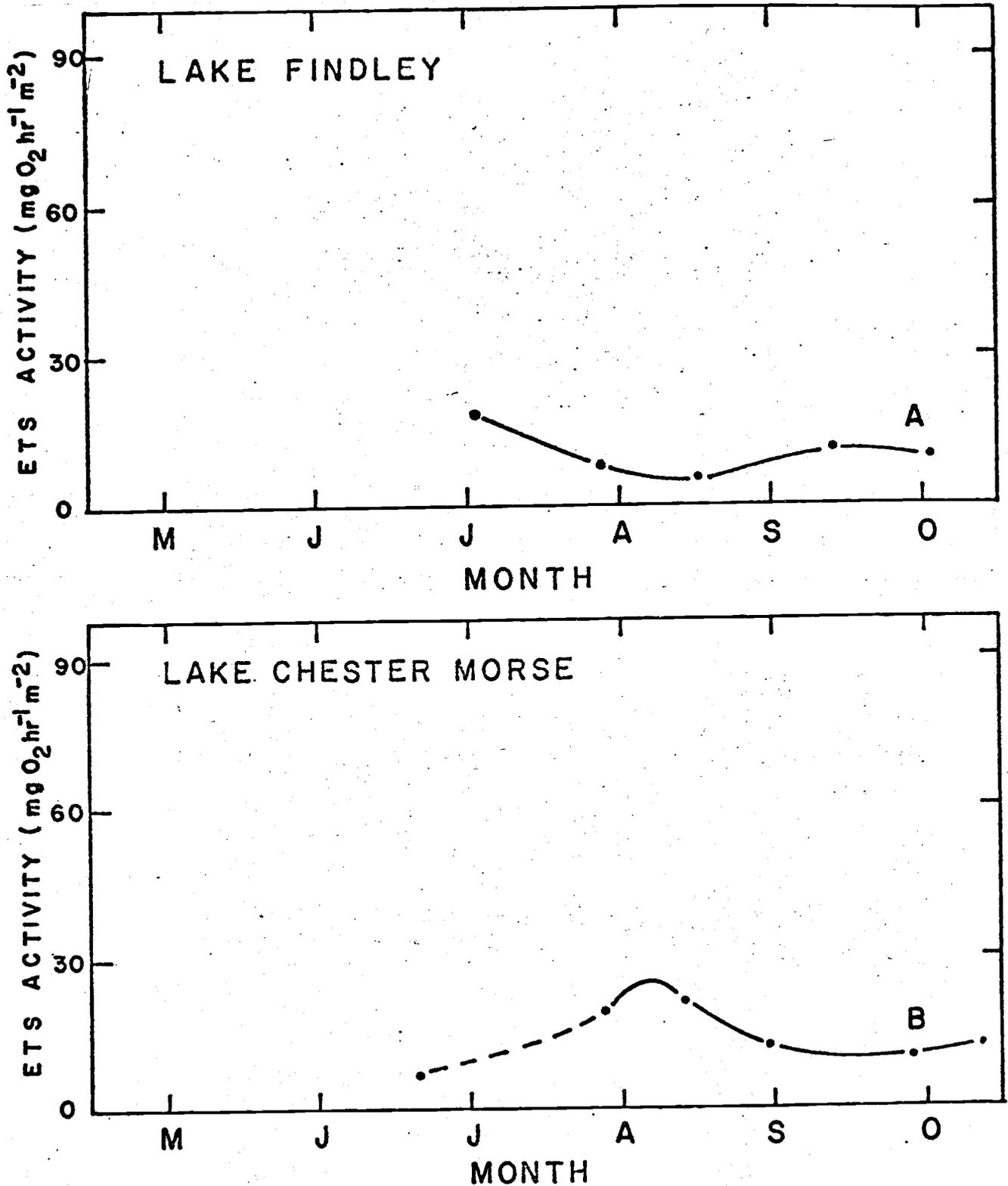


Figure 3.58. Integrated respiratory electron transport activity in the euphotic zones (100-1% light levels) in Lakes Findley and Chester Morse as a function of sampling date.

Findley Lake assuming a steady state and that net plankton respiration is the major pathway of nutrient regeneration. We calculated turnover times of ammonia and phosphate of 68 and 10 days, respectively. This indicates that phosphate is cycled approximately seven times faster than ammonia. It must be emphasized here that these estimates are based on some very bold assumptions and much more detailed analysis is needed. They do, however, serve to demonstrate the type of data analysis we plan to undertake when the other necessary data become available.

Nitrogen fixation rates were determined periodically by the acetylene reduction technique at three depths in each of the lakes. Fixation began in June in Lakes Washington and Sammamish and peaked during July and August. Chester Morse and Findley Lakes did not exhibit acetylene reduction activity until August and the rates encountered were much lower than in the other two lakes. Nitrogen fixation in the lakes correlates closely with the concentrations of blue-greens.

The need to quantify the dependence of lake productivity and in general the lake water quality upon nutrient supply in the lakes of the Cedar River watershed necessitated the extension and expansion of past years' nutrient monitoring program to include sediment nutrient regeneration and sedimentation studies. As an integral part of the original charge of this project the monitoring program initiated in 1970 to evaluate the forms and amounts of nutrient compounds in Findley and Chester Morse Lakes and Lake Sammamish was continued to the present and was extended to include Lake Washington. The data of this extensive monitoring have been entered in the information bank, available for Biomewide use, and will not be elaborated on here.

3.2.1.2. Zooplankton. Zooplankton grazing rates and life history stage densities for secondary production estimates were determined in 1972 and 1973. Eight copepod species, seven cladoceran, and nine rotifer species were identified. No one species of cladoceran or copepod occurred in all the lakes, but the rotifers are common throughout. Copepods in the lakes showed no clear diel vertical migration, while two cladocerans did migrate. Copepods were most important numerically in the lakes. Some principal members were Diaptomus ashlandi, which reached a seasonal maximum adult density of 11/l (mean of water column) in Lake Sammamish and Limnocalanus in Chester Morse which reached a maximum of 0.7/l. Two Diaptomus species are important in Findley Lake. Densities averaged about 10 times greater in Sammamish than in the two oligotrophic lakes. Data on population dynamics from the egg ratio technique are given for the common cladocerans of Findley Lake (Table 3.32).

Grazing rates (in situ) were partitioned for three phytoplankton size classes (same sizes as previously described) to assess the effect of feeding on particle size and to relate to concurrent studies on fractionated phytoplankton productivity and nutrient responses. Zooplankton grazing appeared to account for a considerable proportion of the loss of nanoplankton in all lakes except for more eutrophic Lake Sammamish, where blue-greens and net plankton are more frequent and detritus feeders are favored (Table 3.33). Grazing of phytoplankton by zooplankton stimulated photosynthetic carbon uptake in the light in excess of 200% over ungrazed

Table 3.32. Birth and death rates, population change rate, and mean number of eggs/♀ for cladocerans in Findley Lake, 1972.

Sampling interval	Holopedium				<u>Daphnia rosea</u>			
	b	r	d	E	b	r	d	E
11 Jul						0.147		0
25 Jul		-0.124		0	0.104	0.125	-0.021	1.500
1 Aug		0.441		0	0.223	0.187	0.036	1.529
8 Aug	0.095	-0.192	0.287	0.644	0.140	-0.056	0.196	0.812
15 Aug	0.542	0.011	0.531	3.750	0.086	0.017	0.069	0.667
29 Aug	0.191	0.086	0.105	0.800	0.239	0.078	0.161	1.373
14 Sep	0.058	-0.120	0.178	0.353	0.095	-0.038	0.133	0.620
6 Oct	0.095	-0.026	0.121	1.187	0.020	-0.147	0.167	0.273
21 Oct	0.182	-0.025	0.207	2.889	0.004	0.080	-0.076	0.083
4 Nov	0.300	0.040	0.260	5.571		0.117		
12 Nov	0.166			3.636				
	avg 0.204				avg 0.114			

Table 3.33. Phytoplankton loss rates through zooplankton grazing and the relative size of producers present and percent of growing season productivity in the Cedar drainage lakes in 1972-1973.

Lake	Date	Loss rate	Algal size		Productivity (%)
			Present	Grazed	
SPRING					
Chester Morse	5/1/73	617	nano	ultra nano	235
Sammamish	4/10/73	125	net	net	21
	4/20/73	302	net	ultra nano	50
SUMMER					
Findley	9/22/72	35	nano	nano ultra	16
	8/26/73			nano ultra	
Chester Morse	7/9/72	51	nano	nano	20
Sammamish	7/24/72	266	nano	nano	44
	8/27/72	14	nano	net	2

loss rate - mg C/m³ day assuming C/chl α = 50.

net > 50 μ m; nano 50-5 μ m; ultra \times 5 μ m.

populations. Phytoplankton loss rates from grazing ranged from 0.002 to 0.268 μg chlorophyll a per animal per day. Feeding was found to be maximum at low concentrations of algae. These rates account for from 2%-247% of the average growing season productivity in the lakes. Net plankton ($>50 \mu\text{m}$) were seldom grazed and, since that size fraction and algal mass in general increased with mean productivity and nutrient content in the lakes, such decreasing efficiency in food transfer is seen as a major effect of eutrophication.

3.2.1.3. Fishes. The major limnetic fishes of Lake Washington (sockeye, smelt, stickleback), Lake Sammamish (sockeye, kokanee, chinook), and Chester Morse Lake (pigmy whitefish, Dolly Varden, rainbow trout) are being studied to develop data sets for implementation of limnetic fish models. Estimates of population abundance, biomass, production, mortality, and growth for each major pelagic fish population have been completed in Lake Washington and Lake Sammamish and will be included in the model after completion of successful simulations for sockeye salmon. In addition, a bimonthly field study of sockeye feeding on zooplankton has also been completed in Lake Washington. Emphasis is placed on sockeye salmon because it feeds on zooplankton, and zooplankton constitutes the major link with primary producers. This information and zooplankton community studies of Lake Washington by W. T. Edmondson of the University of Washington are providing a basis for models of trophic relations of limnetic fish.

Investigations of the limnetic fish populations of Lake Washington were continued through 1973. Population estimates were established through the acoustical procedures developed under the Sea Grant program and were used in conjunction with biological information obtained from midwater net sampling to obtain point estimates of abundance and biomass. From these, growth rate and production of the different species were determined (Table 3.34). Seasonal patterns in population parameters and changes in the horizontal and vertical distributions of the major pelagic species and year classes in the lake were analyzed also. A high correlation was found between the distribution of densities of the 1971 year classes of sockeye salmon and longfin smelt, and was hypothesized to be due to physical factors acting simultaneously on the two species. A comparison of the vertical distributions of the major pelagic species provided a highly significant multiple correlation coefficient, perhaps indicating that the same factors controlled the vertical distribution of each species.

Periodic monitoring of the size of the adult sockeye salmon population in Lake Washington by acoustical methods is being continued through 1973 and 1974. A series of 11 surveys over an identical transect pattern was completed during the months of June through November for estimation of the time and rate of movement into the lake, the total adult sockeye salmon escapement, and the rate of migration up the Cedar River. The estimate of escapement was similar to the estimate based on counts at the Chittenden Locks by the Washington State Department of Fisheries.

Estimates of the abundance of presmolt sockeye salmon in the lake were used in conjunction with estimates of adult escapement for further

Table 3.34. Fish population parameters for Lake Washington of the 1971 year classes of sockeye salmon and longfin smelt and the 1971 and 1972 year classes of threespine stickleback.

Fish group	Date	Mean weight w (g)	Inst. growth rate G (per mo)	Stock numbers N ($\times 10^6$)	Biomass B		Biomass B (kg)	Production P		
					(kg)	(kg/ha)		(kg/mo)	(kg) interval total	(kg/ha) interval total
<u>1972</u>										
Sockeye salmon 1971 year class	7 Mar	0.17		0.646	0.110	0.013				
			0.391				100	39	53	0.006
	17 Apr	0.29		0.325	90	0.010	2,270	2204	4,040	0.461
			0.971							
	11 Jun	1.72		2.585	4,450	0.508	8,195	4338	10,264	1.171
			0.529							
	21 Aug	6.01		1.987	11,940	1.363	17,250	4554	10,019	1.144
		0.264								
26 Oct	10.75		2.098	22,560	2.575	28,100	3344	5,461	0.623	
		0.119								
14 Dec	13.06		2.576	33,640	3.840	27,260	-818	-1,636	-0.187	
		-0.030								
<u>1973</u>										
	12 Feb	12.30		1.698	20,899	2.384	23,186	2231	3,494	0.399
			0.096							
	1 Apr	14.33		1.782	25,483	2.909				
							Totals		31,695	3.617
<u>1972</u>										
Longfin smelt 1971 year class	7 Mar	1.57		0.101	160	0.018				
			0.159				180	29	40	0.005
	17 Apr	1.95		0.104	200	0.023	4,540	3668	6,723	0.767
			0.808							
	11 Jun	8.58		1.035	8,880	1.014	8,675	1596	3,776	0.431
			0.184							
21 Aug	13.27		0.638	8,470	0.967	15,175	1988	4,374	0.500	
		0.131								
26 Oct	17.70		1.236	21,880	2.497	15,745	-472	- 771	-0.088	
		-0.030								

Table 3.34. Fish population parameters for Lake Washington of the 1971 year classes of sockeye salmon and longfin smelt and the 1971 and 1972 year classes of threespine stickleback (continued).

Fish group	Date	Mean weight w (g)	Inst. growth rate G (per mo)	Stock numbers N ($\times 10^6$)	Biomass B		Biomass B (kg)	Production P			
					(kg)	(kg/ha)		(kg/mo)	(kg) interval total	(kg/ha) interval total	
<u>1972</u>											
Longfin smelt	14 Dec	16.84	0.036	0.570	9610	1.097	7380	266	532	0.061	
<u>1973</u>											
	12 Feb	18.09	-0.004	0.285	5150	0.588	2762	-10	-15	-0.002	
	1 Apr	18.05		0.021	378	0.043					
							Totals		14,749	1.674	
<u>1972</u>											
Three-spine stickleback 1971 and 1972 year classes	7 Mar	1.54		1.198	1850	0.211					
			0.037				1350	50	68	0.008	
	17 Apr	1.62		0.525	850	0.097					
				0.058				540	31	57	0.007
	11 Jun	1.80		0.130	230	0.026		a	a	a	
				a							
	21 Aug	0.70		0.655	460	0.053					
			0.312				1365	426	937	0.107	
	26 Oct	1.39		1.630	2270	0.259					
			0.086				2775	239	390	0.045	
	14 Dec	1.60		2.050	3280	0.374					
			0.131				3535	463	926	0.106	
<u>1973</u>											
	12 Feb	2.08		1.822	3790	0.433					
			-0.051				2511	-127	-199	-0.023	
	1 Apr	1.94		0.635	1232	0.141					

^aThese values were not computed since two different populations, the 1971 and 1972 year classes of threespine stickleback, were represented by the June and August estimates, respectively.

definition of the spawner-recruit relationship for the Lake Washington sockeye salmon run. A major goal in the continuing work on the spawner-recruit model is to develop the capability to predict escapement accurately from acoustic estimates of smolts prior to outmigration.

Studies on the feeding ecology of fish have been continued with the objective of determining the quantity of food consumed each day by juvenile sockeye salmon (Oncorhynchus nerka) in the limnetic zone of Lake Washington to better understand the elements of the trophic level next beyond the zooplankton. This information is essential to the current comprehensive modeling studies of energy transfer in the Lake Washington ecosystem.

Diel sampling of the 1971 year class was conducted in February and April 1973; however, the presmolts were unavailable to the sampling gear in April. Previously, successful diel sampling had been conducted in June, August, October, and December 1972. The first three of these dates coincided with the primary lacustrine growing period of the juvenile sockeye salmon. A 5.5-m herring trawl was fished from the research vessel MV Commando, and echo-sounding gear was used to help locate the fish and determine depths to be sampled. Miller high-speed plankton nets were sent down with some of the trawl hauls to secure simultaneous plankton samples.

The amount of food consumed, size of fish, and time of year were noted. Estimates of the rate of gastric evacuation were made by length group of fish from nighttime samples (Fig. 3.59). Inherent in the procedure was the assumption that no feeding occurs at night and that the volume of stomach contents decreases exponentially with time. The results indicated a decrease in the rate of gastric evacuation with increasing size of fish and with advancing time of year, the latter probably as a result of decreasing night temperature of residence. The daily ration was computed by length group of fish from samples collected throughout the 24-hr sampling period. The procedure assumed that on the average the rate of food consumption equals the absolute value of the rate of gastric evacuation. The amount of food consumed increased with increasing size of fish; however, expressed as a percentage of body weight, it decreased. Food consumption reached a peak in autumn. Comparisons of stomach contents with the simultaneously collected plankton samples indicated selection of the larger prey species. Some differences in diet with respect to size of fish were noted in summer.

Seasonal abundance estimates of the 1971 year class of sockeye salmon have been made on Lake Sammamish. These estimates incorporate age 0 kokanee along with age 0 migratory sockeye. Seasonal abundance estimates of resident kokanee and residual (age 1+) chinook also have been completed. Catch data indicated that the 1970 year class of fall chinook, which entered the pelagic zone at least by July, constituted a major proportion of the large fish targets enumerated acoustically throughout the remainder of the year (Berggren 1974).

Estimates of biomass and production, distribution, and food habits of the 1971 year class of sockeye and other limnetic fish were made for Lake

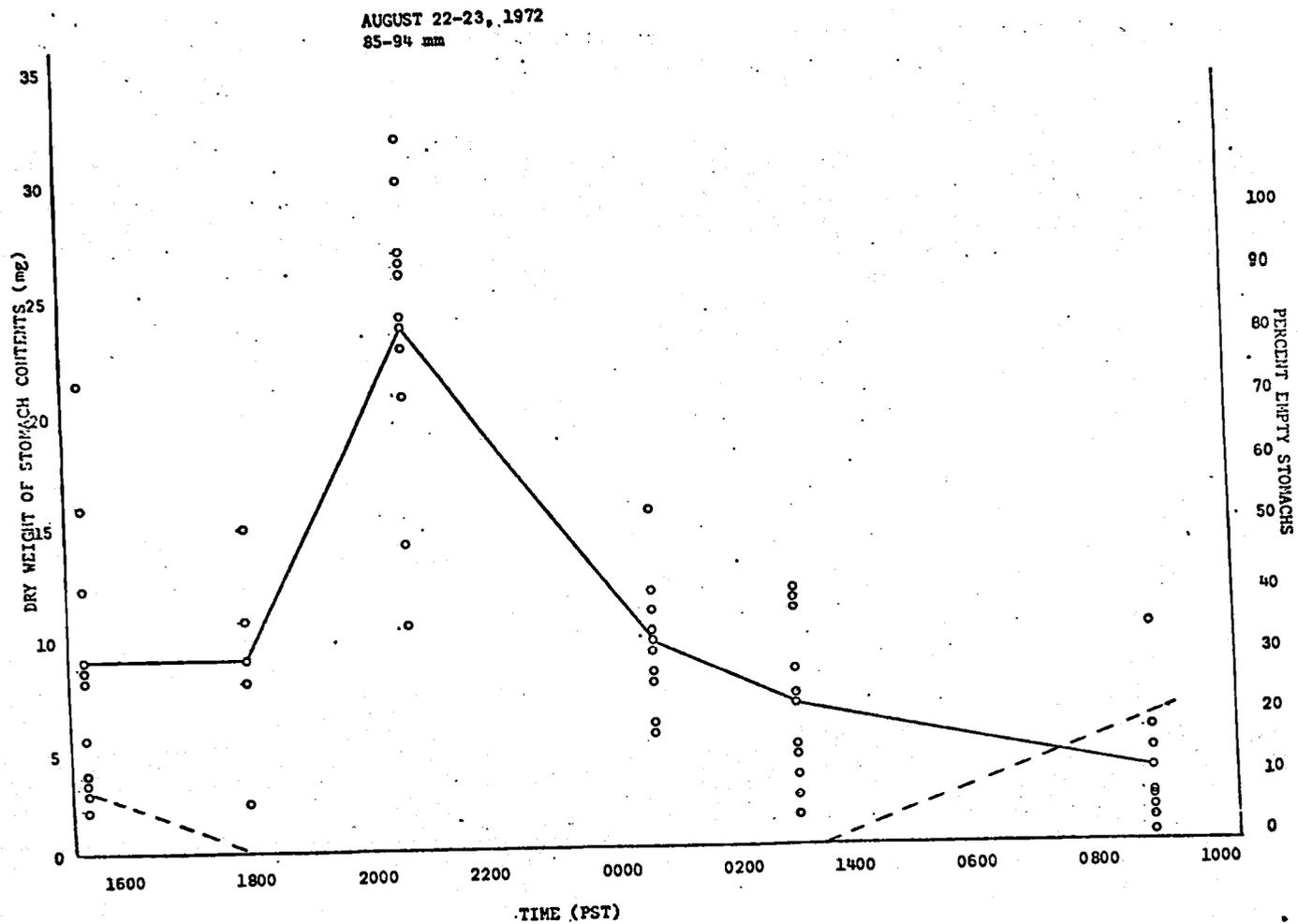


Figure 3.59. Estimate of rates of gastric evacuation for the 85 to 94-mm length group of juvenile sockeye salmon.

Sammamish. Biomass and production are shown in Table 3.35. The resulting biomass and production per hectare were greater than Lake Washington's (Traynor 1973), indicating a large 1971 year class of sockeye in Lake Sammamish. The population approached approximately one-half the density per unit volume of the 1969 year class of sockeye salmon in Lake Washington, the largest year class observed since 1969 when monitoring of the lake began. Horizontal and vertical distributions reflected the effects of limitation of habitat by oxygen deficiency in the hypolimnion. Minimum differential feedings of juvenile sockeye salmon was observed between 10-mm length groups. Daphnia was the predominant food item during most of the year although ostracods were utilized during the winter at a time when feeding was reduced.

The Chester Morse Lake study is designed to determine the population sizes, age and growths, length-weight relationships, fecundity, sex ratios, mortality rates, and feeding habits of rainbow trout (Salmo gairdneri) and Dolly Varden (Salvelinus malma). Biomass and production of the two species are being estimated from this information.

Peterson estimates from the August data result in population estimates of $4650 \leq 8138 \leq 15,752$ rainbows and $1684 \leq 3015 \leq 6147$ ($\alpha = 0.05$) Dolly Varden. A Schnabel estimate over the eight-month sample period results in population estimates of 9830 rainbows and 1305 Dolly Varden. Age determinations are being completed to calculate age distributions of sampled populations.

The feeding habits of pygmy whitefish, Prosopium coulteri and the age, growth, and fecundity are being incorporated in the discussion of this significant food item of Dolly Varden. Rainbow data will be used in the basic population dynamics model.

At present, the limnetic fish model consists of a feeding dynamics and energy budget model for sockeye salmon in Lake Washington. Other major limnetic fish such as stickleback and smelt will be included after completion of successful simulations for sockeye. Emphasis is placed on sockeye because of its unique feeding behavior on "entirely" zooplankton. This model provides a useful structure for analysis of growth in sockeye salmon and relates to other sockeye salmon producing systems with widely differing zooplankton population characteristics. Optimal foraging theory allows one to predict which segment of the zooplankton population encountered by the salmon that will be eaten. This strategy is provided by a vector of (P_i) , which maximizes expected total energy ingested per time spent foraging.

The effects of the external variables such as light and water temperature are provided in the model. These allow us to study energetic implications of the observed feeding behavior of salmon, which include diel vertical migration and the limitation of feeding to hours of dusk and dawn. The model is tied to the wider ecosystem structure through two major couplings. These are species specific grazing rates on zooplankton and release of carbon, nitrogen, and phosphorus through excretion of metabolic wastes.

Table 3.35. Seasonal biomass and production estimates for Lake Sammamish of the 1971 year class of sockeye salmon (surface area of lake is 1980 ha).

Date	Mean weight (g)	Stock numbers	Biomass		Mean biomass (kg)	Interval length (mo)	Inst. growth rate (mo)	Production			
			(kg)	(kg/ha)				Monthly		Total interval	
								(kg/mo)	(kg ha ⁻¹ mo ⁻¹)	(kg/int)	(kg ha ⁻¹ int ⁻¹)
<u>1972</u>											
20 Feb	0.45	138,590	62.37	0.032	177.56	1.64	0.377	66.94	0.034	109.78	0.055
10 Apr	0.84	348,506	292.75	0.148	394.94	1.19	0.377	148.89	0.075	177.18	0.089
16 May	1.32	376,615	497.13	0.251	1,943.44	1.24	0.377	732.68	0.370	908.52	0.459
23 Jun	2.11	1,606,523	3,389.76	1.712	5,519.04	2.86	0.377	2,080.68	1.051	5,950.74	3.005
18 Sep	6.19	1,235,592	7,648.31	3.863	9,306.16	1.38	0.377	3,508.42	1.772	4,841.62	2.445
30 Oct	10.41	1,053,218	10,964.00	5.537	11,237.79	2.53	0.081	910.26	0.460	2,302.96	1.163
<u>1973</u>											
15 Jan	12.88	893,756	11,511.58	5.814	8,552.36	1.18	0.070	598.67	0.302	706.43	0.357
20 Feb	13.99	399,795	5,593.13	2.825	4,335.84	0.98	0.065	281.83	0.142	276.19	0.139
22 Mar	14.91	206,476	3,078.56	1.555							
TOTAL PRODUCTION						13.00				15,273.42	7.71

3.147

The current benthic and littoral fish model is based on biomass or energy flow. The first part of the model is a simulation of biomass flow and distribution in the lake by regions and time. The temporal-spatial movement of fish in Lake Washington by season has been documented for the three most abundant fish, peamouth, yellow perch, and northern squawfish. The peamouth (*Mylocheilus caurinus*) was chosen as the first species to be used in developing the model because of the availability of data. For example, estimates of biomass and production for peamouth indicate that production occurs in the first years while in later years the biomass loss is greater than production (Table 3.36). The biomass movement model is driven by temperature and time and simulates migration of peamouth in Lake Washington by season. Biomass in closed bands of constant water depths roughly paralleling the lakeshore were chosen as the four state variables. Biomass was calculated from relative fish numbers using natural mortality rates and an independent numbers estimate of one age group.

The second part of the model includes population and biomass dynamics by species. The model attempts to simulate changes in the age structure, standing crop, and production or loss as reproduction, death, and growth rates vary. Repeated for each species, the model will allow changes in the relative species composition, biomass, and production. The calculated values for state variables, such as standing crop or production, can be apportioned to the lake regions based on the output of the energy flow and distribution model. Additional information on peamouth, squawfish, and perch for use in examining relationships between variables is being completed by several Coniferous Biome projects.

3.2.1.4. Benthic processes. Development of studies on benthic processes is based on distinct couplings with the plankton community and between internal compartments of benthic communities. The benthic community of a lake is being considered as dependent upon transfers of energy, carbon, and nutrients from sedimented organic and inorganic matter into paths of substrate burial, chemical oxidation, microbial-macroinvertebrate metabolism, fish predation, and insect emergence. Sedimentation; exchange of carbon, nitrogen, and phosphorus; and carbon fixed by periphyton are linked to the available carbon, nitrogen, phosphorus, and microflora-meiofauna components of the benthic community. Carbon fixation (net production), respiration, and biomass of periphyton are being assessed in several of the lakes. Sedimentation measurements include inputs of major cations, heavy metals, and dissolved and particulate carbon, nitrogen, and phosphorus from endogenous organic matter production and organic-inorganics from exogenous sources. Exchange of carbon, nitrogen, phosphorus, and oxygen by the benthic community occurs during chemical oxidation, oxygen consumption, microbial mineralization, and macroinvertebrate respiration. One of the research projects on Lake Sammamish is considering the effect of both oxygen concentrations and temperature on the rate of diffusion of oxygen and reducing compounds across an enclosed in situ sediment-water interface. Oxygen consumption or total community metabolism has been assessed in all four lakes. Nutrients released and oxygen uptake rates are being studied in an effort to explain oxygen depletion, nutrient-cycling, and levels of chemical oxidation.

Table 3.36. Yearly production by age groups of peamouth in Lake Washington.

Age	Wt. (μ m)	Inst. growth rate G	Stock nos. N_t	Biomass @ B_1	Inst. Mort. Coeff. Z	Mean Biomass B	$P \sim$ kg
2 t ₁	63.3	0.557	112,646	7130.4	1.699	13,318	+7418.1
t ₂	110.0		20,580				
3 t ₁	110.0	0.393	20,580	2263.8	1.699	-1,263.7	-496.7
t ₂	163.1		3,760				
4 t ₁	163.1	0.379	3,760	612.8	1.699	-340.2	-128.9
t ₂	238.0		687				
5 t ₁	238.0	0.228	687	163.5	1.696	-85.7	-19.5
t ₂	299.0		126				
6 t ₁	299.0	0.083	126	37.7	1.700	-18.7	-1.5
t ₂	325.0		23				
7 t ₁	325.0	0.080	23	7.5	1.749	-3.6	-0.3
t ₂	300.0		4				
							6771.2 kg

The measurement of sediment metabolism in Lake Washington was performed by Pamatmat and Bhagwat (1973). They reported that the rate of total oxygen uptake by the sediment represents the sum of aerobic plus anaerobic metabolism in a surface layer of indeterminate thickness. In situ rates of anaerobic metabolism in the sediment column can be determined by means of a triphenyltetrazolium chloride (TTC) method of total dehydrogenase assay. In Lake Washington, which has had a long and well-documented history of eutrophication and deposition of sewage effluent, anaerobic metabolism by bacteria alone in the sediment column far exceeds total metabolism as estimated by the rate of total oxygen uptake by undisturbed cores. The total oxygen uptake (biological and chemical) ranged from 0.16 to 0.45 calories per core per hour while the dehydrogenase activity (TTC) ranged from 0.37 to 4.7 calories per core per hour.

Mineralization of organic compounds in the benthic community by bacteria may be the principal biotic process of the available carbon, nitrogen, and phosphorus microbial components in sediments. Current studies are investigating the dynamics of the benthic microbiota by assessing the mineralization rates of [^{14}C]glucose and possibly cellulose and chitin. Sediment samples have been collected and analyzed from Lakes Washington, Sammamish, Findley, and Chester Morse. The fine bacteria-rich sediments at the sediment-water interface were collected with a suction type sampling device, refrigerated, and returned to the laboratory. At the time of sampling, a temperature profile of the lake from surface to bottom was taken. The rate of glucose mineralization by the bacteria was measured by incubating sediment and uniformly labeled [^{14}C]glucose at the in situ temperature. In each lake sampled, the bacteria associated with the shore sediment were more numerous and exhibited a higher rate of glucose mineralization than those found in the sediment of deepwater stations. In all lakes the glucose mineralization rate was greater in summer, decreased in fall, and attained a minimum value in winter and early spring. Sediment samples collected in winter were incubated at the in situ temperatures prevailing at other seasons of the year. The rate of glucose utilization or turnover time fell very close to the rates obtained at the different seasons. Samples collected during the summer and tested under conditions prevailing during colder periods also gave excellent results. These data indicate that the temperature in the environment has a great influence on the activity of the bacteria responsible for mineralization.

As of August 1973, data were collected for one year for the four lakes. Glucose mineralization rates determined during 1973 are very similar to those obtained for the same period one year ago. In many of the lakes significant differences occur in the glucose mineralization rate at the various stations sampled; however, sediments collected within 33 m at the same depth were not found to be different, showing the lack of variation for a given depth and sediment type.

Aerobic and anaerobic bacterial plate counts were run on the sediments collected. Counts obtained with anaerobic incubation, which enumerates anaerobes and facultative anaerobes, were one order of magnitude lower than aerobic counts. Sediment samples collected from deep water were also about one order of magnitude lower than those obtained from shallow

or shore stations. In addition, the numbers of organisms capable of digesting chitin or cellulose were estimated by adding reprecipitated chitin (0.6%) or reprecipitated cellulose (0.1%) to the medium. Chitinoclastic or cellulolytic bacteria were easily detected on the medium by a clear zone or plaque that appeared around the colonies hydrolyzing the complex molecules. The highest bacterial counts were obtained with aerobic incubation. Bacteria capable of digesting chitin were found in all stations sampled in the four lakes. All but one chitinoclast tested were obligate aerobes. As with total bacterial counts, the total chitinoclast biomass and the percentage of total aerobic chitinoclasts counted were higher for shallow or shore samples than for the deeper stations. There appeared to be an increase in numbers of chitinoclasts in the winter months over the summer months. Studies on the four lakes showed that the highest numbers of chitinoclasts were found in the shore stations of Chester Morse and Findley Lakes; however those organisms isolated from Lakes Washington and Sammamish were more rapid in hydrolyzing chitin.

Cellulolytic bacteria have been isolated from Lakes Sammamish and Washington and no doubt play a part in the role of cellulose decomposition in the lake systems. The strains of cellulolytic bacteria isolated are obligate anaerobes; however, they have not been identified.

Additional work includes a detailed study of chitin in the four lakes. This material coming from insect exoskeletons, zooplankton, and crustaceans has not received the attention given to chitin in the environment. The rate of bacterial mineralization of chitin is being assessed with emphasis on the enzyme systems involved.

Through expansion of the above research on bacteria and subsequent modeling, we plan to address such questions as what changes occur in mineralization rates with different temperatures and sedimentation rates for within and between lakes. If mineralization rates of organics differ for lakes but not for temperatures and sediments, will the variation be related to proportions and differences in availability of carbon, nitrogen, and phosphorus in various organic substrates? Or, more specifically, how does the availability of organic nutrients limit utilization of carbon compounds?

Similar questions are to be addressed in studies of allochthonous inputs to the particulate organic matter (woody) components of the benthic community in Findley Lake. This interface program and detrital inputs and decomposition are scheduled to be expanded and linked to mineralization studies. Litterbags used in the decomposition study are to be subsampled to measure differences in mineralization rates for substrates in different stages of decomposition.

Pollen, diatom, and sedimentary chlorophyll analysis of Findley Lake indicates distinct relationships between the aquatic and terrestrial environments. Any severe disturbance of the terrestrial environment caused shifts in the aquatic ecosystem. These changes often involved a sequence of changes in the dominant diatom present. Further, the pattern of changes in the aquatic ecosystem seemed to be related to

the type of disturbance in the surrounding watershed, for example, forest fires. Sedimentary chlorophyll either did not change significantly or varied in relation to changes in the number of conifer needles in the sediment.

Sediment patterns were measured in the four lakes of the Lake Washington drainage basin. More extensive treatment of sediment fluxes were made in Findley Lake and sediment nutrient regeneration from in situ Lake Sammamish experiments.

Sediment of detritus through the water column was measured by sediment traps at pelagic and nearshore zones at three-week to two-month intervals in the four lakes from April 1972 up to the present. Sediment traps were placed at two to three different depths in the water column corresponding to trophogenic and thermocline zones of the lakes. Only the sedimentation rates measured at two meters off the sediment bottom will be discussed. Sediment aliquots were analyzed for total carbon (99% organic carbon), phosphorus, nitrogen, and iron and a number of trace metals.

The rate of sedimentation of autochthonous and allochthonous material to the bottom of the four lakes for comparable time periods is presented in Table 3.37. It is difficult to generalize from these results, for each of the four lakes represents distinct local characteristics. Thus station 2 in Lake Washington is strongly influenced by inputs from the Evergreen Point Bridge. Basic differences in the lakes are shown by elemental fluxes, percent contents, and ratios of carbon:nitrogen, nitrogen:phosphorus, and carbon:phosphorus. Thus, the sediment trap data indicate that a major input to Findley Lake is allochthonous organic while in Chester Morse Lake inorganic inputs from either bottom sediment resuspension or from allochthonous sources are predominating. The sedimentation data from Lake Sammamish indicates the relative importance of inputs, especially phosphorus and iron, from sediments brought about by the reduction of Fe^{3+} and dissolution of phosphorus in the oxygen-depleted sediment-water interface.

With regard to total sedimentation there is little relative difference between the lakes with the exception of Findley Lake, which shows appreciably smaller sediment flux. Also with the exception of Findley Lake, where large allochthonous carbon inputs are occurring, there is little difference in carbon fluxes measured for the lakes. The nitrogen fluxes in Chester Morse and Findley Lakes are approximately half those of Lakes Sammamish and Washington, reflecting the nitrogen poor watershed environment. In contrast to low nitrogen content, the phosphorus content of sedimented material in Findley Lake is relatively high but not appreciably different from those of Lakes Washington and Chester Morse. Lake Sammamish shows both the highest flux and content of phosphorus, emphasizing the importance of the bottom sediment--derived phosphorus through Fe^{3+} reduction. Both phosphorus and iron are redeposited in Lake Sammamish hypolimnion upon oxydation of Fe^{2+} and precipitation of ferric hydroxyphosphates. The significantly higher iron contents of sedimented material in Chester Morse Lake further indicate the possibility of sediment resuspension. No generalization can be made relative to C:N and

Table 3.37. Total sediment, C, N, P and Fe fluxes in milligrams per square meter per day, percentage of C, N, P, and Fe contents, and C:N, N:P, and C:P ratios of sedimented material 2 m off bottom at nearshore and pelagic stations of Lakes Chester Morse (CM), Findley (F), Washington (W) and Sammamish (S) during the year 1973 (P. B. Birch, R. S. Barnes, personal communication).

Lake and station	Depth (mm)	Date	Total sediment	C		N		P		Fe		Ratios of		
				(flux)	(%)	(flux)	(%)	(flux)	(%)	(flux)	(%)	C:N	N:P	C:P
CM-1	23	22 Apr- 15 Sep	685	41.4	6.1	4.9	0.72	1.02	0.15	31.0	4.5	8.5	4.8	41
CM-2	28	22 Apr- 25 Sep	657	53.6	8.1	6.8	1.03	1.67	0.26	34.0	5.1	7.8	4.1	32
F-1	12	13 Apr- 27 Sep	263	78.9	30.0	2.9	1.09	0.52	0.20	2.5	0.9	28.0	5.5	153
F-2	24	13 Apr- 27 Sep	165	47.2	28.6	3.0	1.81	0.47	0.29	4.8	2.3	16.0	6.3	100
W-4	11	19 Apr- 7 Sep	463	30.2	6.1	4.9	1.06	0.73	0.16	8.8	1.9	6.1	6.7	41
W-2	60	28 Apr- 6 Sep	953	56.2	5.9	9.9	1.04	1.60	0.17	25.0	2.6	5.6	6.2	35
S-1	17	18 May- 21 Sep	247	45.9	18.6	4.9	2.00	1.50	0.61	4.5	1.8	9.4	3.3	31
S-2	28	7 Apr- 8 Oct	582	43.9	7.5	7.2	1.24	1.71	0.29	13.3	2.3	6.2	4.2	26

C:P ratios in the traps except that in Findley Lake these ratios are two to four times higher than in the other lakes, indicating the high allochthonous organic inputs in the former lake. The N:P ratios are significantly higher in Lake Sammamish as a result of phosphorus dissolution from bottom sediments. Seasonal plankton sedimentation data not depicted in Table 3.37 rank the lakes in the same order relative to productivity as measured by carbon-14 assimilation: Lake Washington \geq Lake Sammamish > Chester Morse > Findley Lake.

Analysis of sediment trap samples for lead, copper, and zinc has confirmed substantial inputs of these elements to the lake sediments. In Lake Washington, the lead input as measured by the traps indicates that the floating bridges and associated highway traffic are primary causes of high lead concentrations in the sediments. In more remote areas of the lake lead concentrations drop to 100-200 ppm, about one-tenth of that of the bridge site. Lake Sammamish values of 50-250 ppm, are very similar to Lake Washington nonbridge levels. Chester Morse lead levels of 63-150 ppm are slightly lower than those in Lake Sammamish and may be attributed to lessened urban intensity. Findley Lake, on the other hand, has much higher lead values than either Chester Morse or Lake Sammamish--possibly attributable to local mineralization but more likely due to effects of research activity on this small, remote lake.

Zinc data also show strong evidence of anthropogenic inputs near the bridge in Lake Washington, but even the background values away from the bridge are higher than those in other lakes. Chester Morse and Lake Sammamish values are similar although the range of values is considerably greater in Chester Morse. Findley Lake zinc levels are generally about half that of Chester Morse (55-184 ppm). Copper levels show patterns similar to zinc, with the ranges in the larger three lakes almost identical and Findley levels about a factor or two lower (16-70 ppm).

Tables 3.38 and 3.39 present detail bottom sedimentation data for Findley Lake by season and station in mg per m² per day (Table 3.38) and in g per m² per growing season 28 June-27 September (Table 3.39). An estimated annual daily sedimentation rate was computed and presented in Table 3.38. On the basis of this sedimentation rate (174 mg per m² per day) and assuming that sedimented material at the lake bottom has a density of 1.05 g per cm³ and contains 90% water, a sedimentation rate of about 0.40 mm per year was calculated. This rate compares well with the 0.27 mm per year rate calculated by Adams (1973) from pollen analysis. Tables 3.40 and 3.41 show some of the physical and chemical characteristics of the Findley Lake sediments (10 cm deep). Comparison of C:N ratios of sedimented material with those of surrounding soils of the watershed indicates that a certain nitrogen enrichment occurs in sediment. Nitrogen immobilization in Findley Lake may be due to nitrogen uptake by microbial organisms on litter during late summer and fall, when relatively energy rich material is entering the lake. Such nitrogen immobilization, if it actually occurs, could explain the low inorganic nitrogen levels measured in the lake in late fall and could be responsible for the nitrogen enrichment of sediments.

The sediment nutrient regeneration studies in Lake Sammamish involved the incubation of six sediment-water columns in enclosed cylinders in

Table 3.38. Total sediment, C, N, and P fluxes in milligrams per square meter per day, percentage of C, N and P contents, and C:N, N:P, and C:P ratios of sedimented material 2 m off bottom as a function of season and station in Findley Lake during the year 1973 (Birch, 1974, R. S. Barnes pers commun.)^a

Stn.	Depth (m)	Date	Total sediment	C		N		P		Ratios of		
				(Flux)	(%)	(Flux)	(%)	(Flux)	(%)	C:N	N:P	C:P
ICE-COVERED PERIOD												
1	12	3-27 Mar	109	8.1	7.5	0.86	0.78	0.11	0.10	9.4	7.8	73.6
1	12	27 Mar-13 Apr	100	34.1	34.1	0.86	0.86	0.11	0.11	39.7	7.8	310.0
1	12	13 Apr-24 May	87	24.3	23.3	1.92	2.21	0.28	0.32	10.6	6.9	72.5
Station average ^b			96	19.4	20.2	1.40	1.45	0.19	0.20	13.9	7.4	102.1
2	24	13 Apr-24 May	26	8.5	32.7	1.02	3.93	—	—	8.3	—	—
Stn. 1 & 2 period average			61	14.0	23.0	1.21	1.98	0.19	0.20	11.6	7.4	102.1
ICE-MELTING PERIOD												
1	12	24 May-28 Jun	639	262.0	41.2	4.47	0.70	0.59	0.09	58.6	7.6	444.1
2	24	24 May-28 Jun	416	141.0	33.9	5.44	1.31	0.69	0.16	25.9	7.9	204.4
Stn. 1 & 2 period average			528	201.5	38.2	4.96	0.94	0.64	0.12	40.6	7.8	314.8
SUMMER												
1	12	28 Jun-27 Sep	199	35.3	17.7	2.67	1.34	0.59	0.30	13.2	4.5	59.8
2	24	28 Jun-30 Jul	112	20.7	18.5	2.95	2.63	0.37	0.33	7.0	8.0	56.0
2	24	30 Jul-27 Sep	156	33.2	21.3	2.92	1.87	0.41	0.26	11.4	7.1	81.0
Station average			140	28.8	20.5	2.93	2.09	0.40	0.28	9.8	7.3	72.0
3	12	28 Jun-30 Jul	74	13.7	18.6	2.02	2.73	0.28	0.38	6.8	7.2	48.9
3	12	30 Jul-27 Sep	316	37.3	11.8	4.13	1.31	0.83	0.26	9.0	5.0	44.9
Station average			232	29.1	12.5	3.40	1.47	0.64	0.28	8.6	5.3	45.5
4	6	28 Jun-27 Sep	214	26.5	12.4	2.55	1.19	0.36	0.17	10.4	7.1	73.6
Stn. 1, 2, 3, & 4 period average			196	30.0	15.3	2.89	1.47	0.50	0.25	10.4	5.8	60.0
ESTIMATED ANNUAL DAILY SEDIMENTATION, MARCH 1973-MARCH 1974^c												
All stations			174	39.1	22.5	2.38	1.37	0.40	0.23	16.4	6.0	97.8

^aWeights are given on oven-dried (105°C) basis. ^bAll average values are time weighted. ^cFor this estimation it was assumed that daily sedimentations for the periods 27 September-15 November and 15 November (lake freezing) to 3 March 1974 were the same as station 3 (30 Jul-27 Sep) and station 1 and 2 (3 Mar-24 May), respectively.

Table 3.39. Summer autochthonous (AT), allochthonous (AL) and total (T) sedimentation fluxes in grams per square meter, C, N and P contents, and C:N, N:P and C:P ratios of sedimented material at 2 m off bottom as a function of station in Findley Lake, 28 June-27 September 1973.^{a,b}

Type of Flux	Total Flux	C		N		P		Ratios of		
		(Flux)	(%)	(Flux)	(%)	(Flux)	(%)	C:N	N:P	C:P
<u>DEEP SUBBASIN, STATION 2 (22 m deep)</u>										
Total	12.7	2.60	20.5	0.27	2.13	0.040	0.32	9.6	6.8	65
AT		1.44		0.24		0.034		6.0	7.0	42.4
AL		1.16		0.03		0.004		40.0	7.0	290.0
<u>DEEP SUBBASIN, STATION 1 (12 m deep)</u>										
Total	18.1	3.21	17.7	0.24	1.33	0.054	0.30	13.4	4.4	59.4
AT		1.14		0.19		0.027		6.0	7.0	42.2
AL		2.07		0.05		0.007		40.0	7.0	295.7
<u>DEEP SUBBASIN, AVERAGE OF STATION 1 and 2</u>										
Total	15.4	2.91	18.9	0.26	1.69	0.047	0.31	11.2	5.5	61.9
AT		1.29		0.22		0.031		6.0	7.0	41.6
AL		1.62		0.04		0.006		40.0	7.0	270.0
<u>SHALLOW SUBBASIN, STATION 3 (12 m deep)</u>										
Total	21.1	2.65	12.6	0.31	1.47	0.058	0.28	8.6	5.4	45.7
AT		1.72		0.29		0.041		6.0	7.0	42.0
AL		0.93		0.02		0.003		40.0	7.0	310.0
<u>OUTLET SUBBASIN, STATION 4 (6 m deep)</u>										
Total	19.5	2.41	12.4	0.23	1.18	0.033	0.17	10.5	7.0	73.0
AT		1.20		0.20		0.029		6.0	7.0	41.4
AL		1.21		0.03		0.004		40.0	7.0	302.5
<u>WHOLE LAKE AVERAGE, ALL STATIONS</u>										
Total	17.9	2.66	14.9	0.27	1.51	0.046	0.26	9.9	5.9	57.8
AT		1.43		0.24		0.034		6.0	7.0	42.1
AL		1.23		0.03		0.004		40.0	7.0	307.5

^aFor original data see Table 3.

^bThe proportion of total deposition to autochthonous and allochthonous was based on the assumption that the autochthonous C:N:P and allochthonous C:N:P ratios were 42:7:1 and 280:40:1, respectively.

Table 3.40. Eh and pH values, moisture contents, particle size distribution, and cation exchange capacity of Findley Lake surface (10 cm deep) sediments (Lanich 1972).

Station	Depth (m)	pH	Eh (volts)	Moisture content (%)	Size distribution (%)			CEC (meq/100 g) ^a
					Sand	Silt	Clay	
1	25	6.5	+0.350	87	25	43	32	22.7
4	7	6.0	+0.355	86	28	51	21	3.9
5	9	6.7	+0.425	74	34	33	33	7.2
2	5	6.1	+0.280	66	77	14	9	8.7
3	14	6.5	+0.205	86	48	30	22	12.1

^aExpressed on oven-dried (105°C) weight.

Table 3.41. Carbon, nitrogen, phosphorus, and iron contents of Findley Lake surface (10 cm deep) sediments (Bauer 1971, Horton 1972)^a.

Station	Depth (m)	Total C (%) ^b	Exchangeable	Total N (%)	Total P (%)	C:N ratio	N:P ratio	C:P ratio	Fe (%)	Fe:P ratio
			NH ₄ -N (μg/g)							
1	25	11.5	72	0.72	0.14	16.0	5.1	82	2.7	19.3
4	7	7.0	11	0.56	0.08	12.5	7.0	88	1.6	20.0
5	9	3.5	4	0.26	0.12	13.5	2.2	29	4.4	36.7
2	5	11.5	10	0.61	0.08	18.9	7.6	144	2.0	25.0
3	14	9.0	54	0.64	0.10	14.1	6.4	90	1.6	16.0

^aExpressed on oven-dried (105°C) weight.

^bInorganic C was less than 0.1%.

situ. Starting in the fall of 1972, water samples were removed from the columns at irregular intervals over a 180-day period and analyzed for total phosphorus and total soluble phosphorus, total and soluble iron, dissolved oxygen, and alkalinity. Specific conductance, pH, temperature, total nitrogen, total soluble nitrogen, NO_3 -plus- NO_2 -N and NH_4 -N were also monitored. This experiment was repeated in the spring of 1973 employing the same methods, except sampling was at 10-day intervals over a 30-day period.

Representative results of the release of total soluble phosphorus and iron, and total phosphorus and iron from the Lake Sammamish sediments into two in situ incubated lake water--sediment columns are presented in Figures 3.60 and 3.61 (F. C. Monahan pers. commun.). The oxygen depletion data are also depicted. Figure 3.60 represents data for the fall 1972 to spring 1973 incubation study while Figure 3.61 represents results from the 30-day spring 1973 experiment. Differences in the rates of phosphorus and iron release as well as oxygen depletion depicted in these two figures are easily attributable to the distinct temperature regimes observed in the lake water during the winter and spring incubations. There was approximately 10°C difference in the water temperature between the two experiments; the lowest and highest temperatures measured were 7°C (winter 1973) and 15° to 18°C (spring 1973), respectively.

The oxygen content of the columns was depleted relatively rapidly. The oxygen level decreased from initial levels at about 6-10 to less than 3 mg/l within 30 days and subsequently dropped to as low as 0.7 mg/l in some columns. The measured oxygen values may have been higher than actual levels because of sampling difficulties. No differences were observed in the oxygen levels in opaque and transparent columns indicating photosynthetic processes were either absent or insignificant. The loss of oxygen was accompanied by increases in phosphorus, iron, and nitrogen contents. Conductivity and alkalinity increased while pH decreased to 6.8 in most cases.

Total phosphorus increased in most of the columns to about $200\ \mu\text{g/l} \pm 20\ \mu\text{g/l}$, while soluble phosphorus increased to $140\ \mu\text{g/l} \pm 10\ \mu\text{g/l}$. Total iron increased in most of the columns to $2.1\ \text{mg/l} \pm 0.2\ \text{mg/l}$, while soluble iron increased to $1.50\ \text{mg/l} \pm 0.1\ \text{mg/l}$. Generally, the total phosphorus and total soluble phosphorus curves paralleled each other, coinciding with reduction of Fe^{+3} . Purging the columns with N_2 affected the rate of oxygen depletion and subsequent rate of release of nutrients but not the magnitude of release. The high iron content measured in the columns under nearly complete anoxic conditions increased the sensitivity of the systems to any possible oxygen intrusion. Thus, in some of the column systems, iron and phosphorus were found to decrease following their peak concentrations as a result of the precipitation of ferric hydroxy and/or ferric hydroxyphosphate compounds.

With respect to nitrogen, NO_3 -plus NO_2 -N generally decreased on the columns but did not disappear. In most cases NH_4^+ -N was initially increased to between 150 and 180 $\mu\text{g/l}$ before decreasing to values less than 100 $\mu\text{g/l}$. In general it was found that total inorganic nitrogen increased 20%-25% above the initial levels followed by a marked decrease

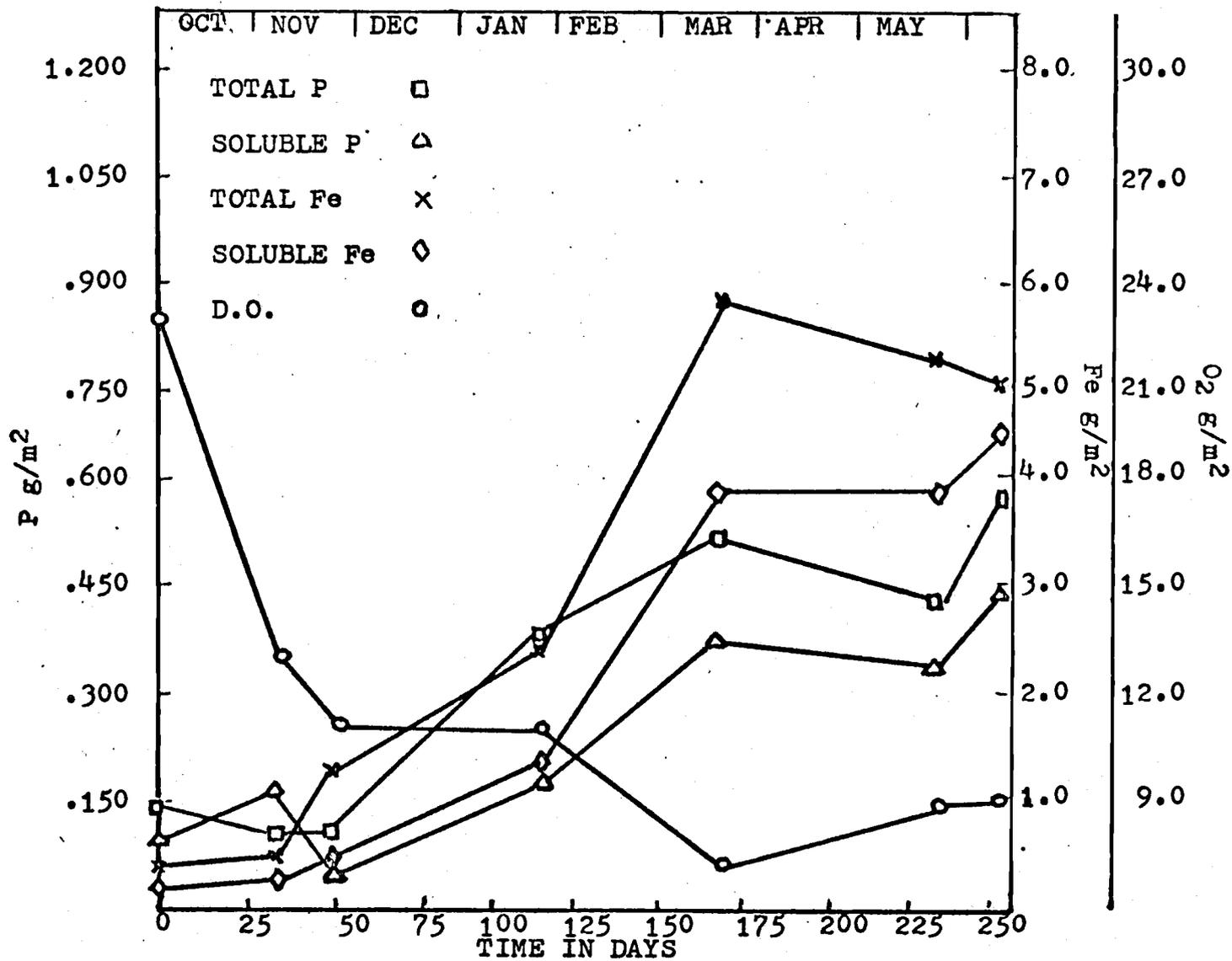


Figure 3.60. Replicate for sediment phosphorus release and associated iron and oxygen data for Lake Sammamish sediments from October 1972 to May 1973.

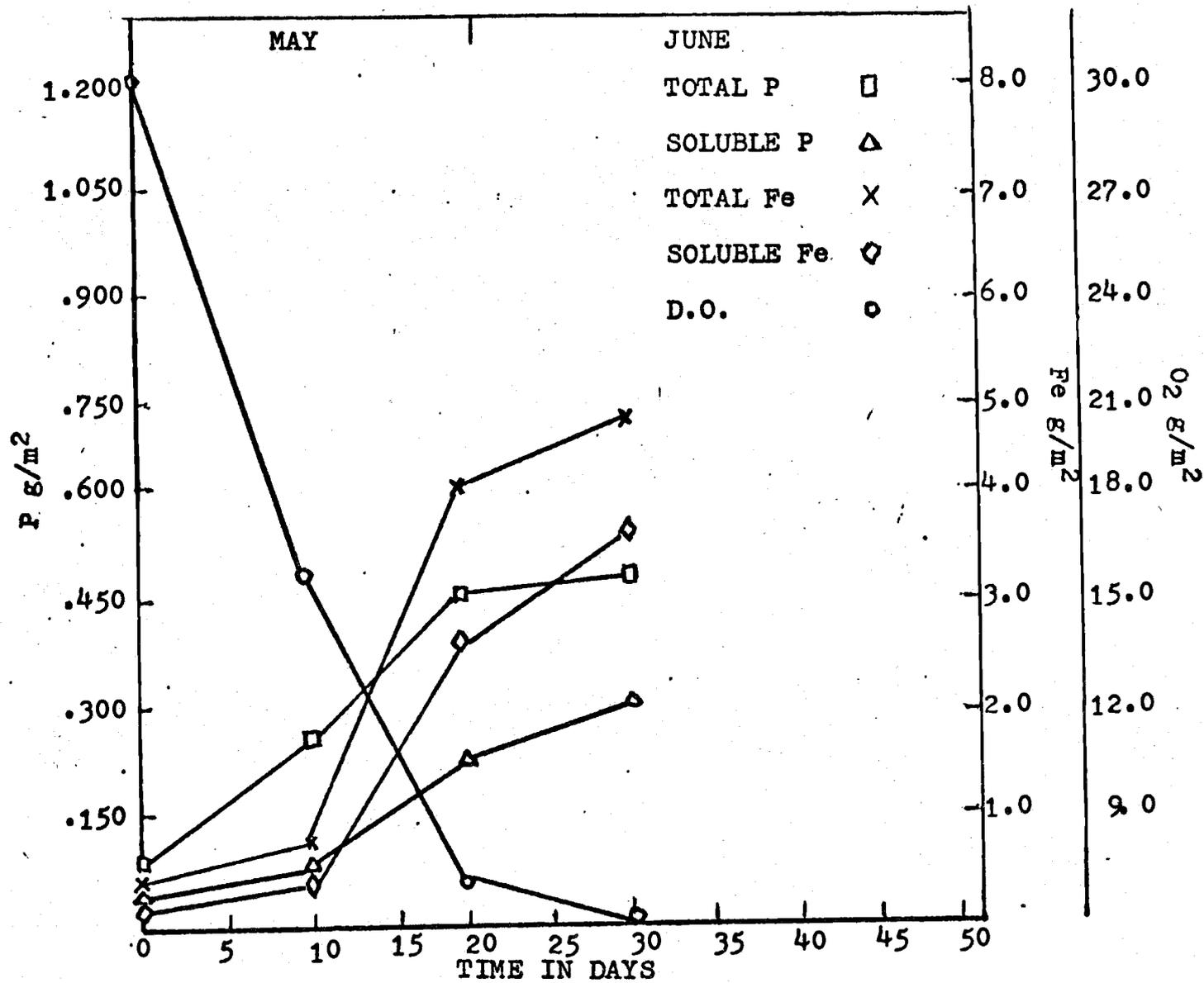


Figure 3.61. Replicate for sediment phosphorus release and associated iron and oxygen data for Lake Sammamish sediments in May and June, 1973.

in the later stages of incubation. This decrease represented a 40%-50% loss of the initial inorganic nitrogen contents. It appeared that as the anoxic conditions became more pronounced, there was a loss of nitrogen from the system by biological and/or chemical denitrification.

The maximum rates of phosphorus release were from 4-6 mg per m² per day at temperatures between 6° and 10°C and increased to 11-15 mg per m² per day at temperatures between 10° and 18°C. The maximum amount released was not a function of temperature.

The release of phosphorus in the columns increased to a maximum between 550 and 600 mg/m² for total phosphorus and 350 and 400 mg/m² for total soluble phosphorus. These values compared well with those obtained for the lake but were 50%-60% lower than those in a laboratory experiment conducted at 25°C under completely mixed and anaerobic conditions.

Despite this discrepancy in the magnitudes of release, the soluble phosphorus/total phosphorus and soluble iron/total iron ratios compared well for the in situ and laboratory experiment, further emphasizing the role of the ferrous-ferric iron coupling in the control of phosphorus concentrations. In all three systems, lake, in situ, and laboratory, the relations of soluble phosphorus/total phosphorus to soluble iron/total iron were similar.

Comparison of the maximum amounts of phosphorus in the in situ column and in 30-m-deep lake water column to the surface (10 cm deep) sediment phosphorus contents revealed that as much as 19%-20% of the sediment phosphorus was released in both cases. The corresponding maximum iron values in the water columns represented 4%-5% of the amount of iron in the surface sediments.

It can be concluded that sediment phosphorus release is a primary input factor in the dynamics of phosphorus in the lake. The release of phosphorus from the sediments could supply enough phosphorus to support summer production in Lake Sammamish provided that a lake mixing mechanism were available to supply hypolimnetic phosphorus to the photic zone. About 75% of the total phosphorus released into the hypolimnion of the lake is supplied by the sediments, on the basis of the in situ column study results. The lack of response in the trophic status of Lake Sammamish following sewage diversion in 1968 could very well be attributed to this demonstrated ability of lake sediments to supply large amounts of nutrients to the lake water column. It will be difficult to anticipate any changes in the nutrient status of the lake within a time period comparable to that observed in Lake Washington case, as long as hypolimnetic oxygen deficits continue during stratified periods.

The significance of the in situ study is that it indicated that comparisons can be drawn between laboratory and in situ studies. If the laboratory studies are done under comparable conditions, the results can be extrapolated to the natural system.

The macroinvertebrate populations of the benthic community are being defined. The objective is measurement of energy and carbon flow with

field estimates of biomass, density, species composition, life cycles, and literature values for assimilation, mortality, respiration, and the like. The research includes assessing the relationship of macroinvertebrate biomass, density, and distribution to the standing crop and distribution of detritus. Preliminary information indicates that the major standing crop of detritus and benthic organisms is at the mouth of inlet streams and rivers of all four lakes. A concurrent study of aquatic insects has found the highest emergence for insects in Findley Lake near inlet areas of high detrital standing crops. These data will be used to evaluate the hypothesis that a significant portion of fish production is supported by the detrital food chain. In addition, this information will serve as input to a model on overall lake productivity.

Chironomid larvae are the dominant organisms in the profundal areas of all lakes but Chester Morse, where Pontoporeia affinis is the dominant species. Other groups found commonly in the profundal zone are oligochaetes and sphaerids. Of lesser importance are ceratopogonids, gastropods, and leeches. Littoral areas show increased species diversity as expected with sialids, tricopterans, ephemeropterans, and water mites, in addition to the groups mentioned above.

A length-weight relationship has been established for chironomids and similar relationships for P. affinis, oligochaetes, and sphaerids are being explored. Preliminary estimates of chironomid larval mortality and growth rates show predation pressure in the spring and fall coincident with their primary growth periods. Stratification over the summer limits predation and growth because of lack of oxygen on the bottom. Temperature drops over the winter reduce metabolic activity of both predator and prey, with mortality and growth leveling off. Emergence occurs in the spring with very high mortality in the pupal stage due to increased visibility from migrations to the surface.

Fish-feeding on benthic organisms has been shown to be selective. Preliminary evidence indicates a preference for chironomid larvae and pupae. Chironomids in the lakes studied have a nutritional makeup of approximately 60% protein, 10% ash, 22% carbohydrate, and 8% fat. Whether they are preferred as a food type because of greater availability to the predator or nutritional value is unknown.

The productivity of benthic organisms has been shown to depend heavily on primary production, allochthonous input, lake sedimentation rates, fish feeding, and several physical properties (temperature, mixing, depth, oxygen concentration, etc.). Correlations with these parameters when the data become available are planned.

The production of macroinvertebrates and fish in the Cedar River is under investigation as part of the studies of streams in the Coniferous Forest Biome. The Cedar River system is unique by virtue of its multiple use. The free-flowing river is divided into three rather discrete reaches. The upper reach, immediately above Chester Morse Reservoir, is relatively unaffected by man's activities except for well-controlled logging. The middle reach, immediately below the dam, is directly influenced by the reservoir and fluctuating discharge due to hydroelectric

generation. The lower reach, extending to Lake Washington, is delineated by the City of Seattle water supply diversion at Landsburg. This diversion limits the upstream extent of migration of anadromous fish, of which sockeye salmon are the most numerous. The watershed above the diversion is a source of municipal and industrial water supply for metropolitan Seattle, and has unexploited resident fish populations.

Initially, quantitative macroinvertebrate and water quality samples were collected from the three river reaches over a 17-month period. This is being followed by a quantitative study of the fish populations through electrofishing methods. Preliminary estimates of the fish populations indicate a general increase in biomass downstream and a predominance of rainbow trout or rainbow-steelhead trout (Salmo gairdneri) at each station during the summer sampling period. Significant numbers of chinook (Oncorhynchus tshawytscha) and coho (O. kisutch) salmon were also found below the Landsburg diversion. Water quality analysis was also conducted, and an increase was found in total alkalinity, pH, conductivity, hardness, and temperature from upstream to downstream. The contribution of plankton from Chester Morse Reservoir to the river below has resulted in a proliferation of filter feeders in the benthic community, represented by forms such as Hydropsyche and Simuliidae. The production of Simuliidae was estimated to increase by about two orders of magnitude immediately below the reservoir. Further work is being devoted to production estimates of Plecoptera, with the assistance of Dr. Arden Gaufin, University of Utah. Ephemeroptera, Trichoptera, and Diptera, as well as the input of allochthonous material in the stream system.

Research on the trophic dynamics of lakes in 1974 will concentrate on synthesis of past data into a general model comparing the several IBP lakes and using this model to guide extensive diel and bloom period sampling. This sampling will concentrate on Lake Washington, with supersynoptic type measurements in the other lakes. These data will be incorporated into a finer resolution model of a Lake Washington water column and to update the comparative, cross-lake model. The sampling will attempt to elucidate several of the key mechanisms regulating lakes. Thus research will concentrate on the quantitative relations between nutrient cycling and production, extent, and factors affecting material and energy transfers between trophic levels, population dynamics of some aquatic organisms, importance of physical transport processes, and the response of an aquatic system to exogenous perturbations. Couplings to higher trophic levels will be provided by several fish studies.

Lake research outside the Lake Washington drainage basin but supported by the Coniferous Forest Biome has been completed. Results of the Fern Lake research by the College of Fisheries were synthesized into an ecosystem model during 1973 (Fowler 1973). Submodels for hydrology, nutrients, phytoplankton, and zooplankton were combined into a simulation model that uses temperature and climatological data as driving variables to predict the levels of various other components of the ecosystem. Predictions from all portions of the model have been compared with those observed in data collected at Fern Lake. An example of the manipulations now possible with

this model were considered. Conceptually, most of the components of this ecosystem may be partitioned into major interacting sections represented both in the model and in nature:

1. The hydrological section of the model incorporates the dynamics and interactions of evaporation and transpiration as these variables affect precipitation and soil water in the watershed. This section also simulates the flow of water into the lake (via the inlet stream) through its dependence on the water content of the soil.
2. The nutrient model is patterned after work by Johnson et al. (1969). In this section the stream's contribution to the nutrients of the lake is simulated as it depends upon the rate of flow of the stream.
3. Biological models are included as they represent the primary producers (as measured by chlorophyll a) and zooplankton. These models are based on logistic population growth models and Michaelis-Menten consumption models. Through these equations, and additional functional terms to include the interactions between the phytoplankton and zooplankton, as well as their environment, this biological sector is imbedded within the model as it predicts their environmental conditions. The level of nutrients, the flushing action of the stream, and temperature are major components of this environment in the model.
4. Temperatures in the stream and temperatures at various levels in the lake are simulated through relationships with the climatological variables. Lake temperatures in the model reflect the physical properties of water and its vertical transferral of heat.

Predictions from all portions of the model are compared with those observed in the data collected at Fern Lake. An example of the manipulations now possible with this model is presented and discussed.

Consideration is given to the implications of the model concerning the function of the ecosystem at Fern Lake. Several variables are identified with respect to their importance in the function of the system. Precipitation is seen to be of major importance in its flushing action on the lake. Air temperature and sunlight are found to be of significance in their influence on the temperature of the stream and lake. The behavior and structure of the model imply that there is a marked effect by the zooplankton on the phytoplankton abundance.

The course of future work and possible directions it should take as indicated by this model are discussed. The development of this model could have benefited from more extensive information concerning specific nutrients and specific phytoplankton species. The weekly time scale was found to be quite adequate for most cases and is recommended for such rapidly changing aspects of the ecosystem as the streamflow, phytoplankton levels, and zooplankton levels.

Modeling and research on the phosphorus dynamics (Richey in press) and heat budgets in Castle Lake, California, were completed in 1973. This study identified important phosphorus parameters and developed a methodology to measure them in the lake. Expected rates of phosphorus fluxes were estimated by the use of isotope measurements and phosphorus pool sizes were assessed through chemical determinations and from calculations of phytoplankton, bacteria, and zooplankton carbon masses and transfers. The heat budget of Castle Lake was considered as an accounting system for energy flux and a physical framework that governs a majority of biological processes. The heat budget encompasses the important abiotic phenomena of lake stratification, absorption of net radiation, heat storage and loss, net advection of energy into and out of a lake, turbulence, and light regimes (C. R. Goldman, pers. commun.).

3.3. Linkages Between Terrestrial and Aquatic Ecosystems

Examination of the linkages between terrestrial and aquatic ecosystems in the Coniferous Forest Biome has been an important aspect of the program. Our studies have focused on land-streams systems in the H. J. Andrews Experimental Forest in Oregon, and land-lake systems at Findley Lake in the Cedar River--Lake Washington drainage in Washington.

3.3.1. Land-stream systems

The idea that most streams not significantly altered by man are predominantly heterotrophic has been well substantiated by stream biologists over the past few years. That is, the maintenance of stream community structure and function is dependent upon the import of organic matter from autotrophically dominated terrestrial communities. Woodland streams can be compared with soil litter communities and the benthic communities of lakes in that they are detritus based and dependent upon export of production from other systems.

Part of the work under way in Oregon under the Coniferous Biome program is designed to study the interrelations between the terrestrial and aquatic components of small watersheds. Under investigation in the stream ecosystem are large stream/small stream decomposition rates, detrital processing by invertebrates, stream particulate organic matter budgets, forest and clearcut stream production, and process modeling.

3.3.1.1. Large stream/small stream decomposition. Some of the mechanisms involved in the degradation of vascular plant tissue in stream environments have been the subject of recent studies (Kaushik and Hynes 1971; Vannote 1970; Triska 1970; Cummins et al. 1972, 1973; Fisher and Likens 1972). The functional relationships among vascular plant tissue, dissolved organic matter, microbial organisms (fungi and bacteria), and animals have not been clearly defined, however.

The present study assessed the sources and magnitude of various particulate organic matter inputs and their fates in two Cascade Range streams. The three main objectives of this study were: (1) to estimate litterfall biomass and lateral movement of detritus into a stream running through an old-growth forest; (2) to estimate the rates of litter breakdown in two coniferous forest streams of different flow; and (3) to obtain a data base for construction of an organic material budget and for later systems modeling of energy or mineral cycling.

These studies were conducted in the H. J. Andrews Experimental Forest. The drainage is characterized by steep topography, with about one-fifth of the study area consisting of more gentle slopes or benches. Mack Creek and the stream draining Watershed 10 were the two streams in the drainage basin that were studied intensively. Mack Creek with a slope of 44% is one of the three major streams draining the entire H. J. Andrews Forest. The overall slope of the stream channel in Watershed 10 is 45%. However, side slopes and headwall range up to 90%.

Litter input. Monthly collection of litterfall for a full year indicated

a dominance of coniferous needles (Figure 3.62). Approximately 65% by weight consisted of litter from Douglas-fir and western hemlock. Needle fall occurred to some extent throughout the year, but was particularly heavy from the conclusion of the rainy season in June until the return of autumn rains in November. As expected, major inputs of deciduous leaf material occurred from mid-October through November. Deciduous inputs consisted primarily of vine maple and bigleaf maple. Insect frass falling through the canopy during dry summer months constituted a significant energy input whose role remains to be clarified. Highly refractory material (twigs, bark, and wood) constituted 10% of the energy input. On a yearly basis, Watershed 10 averaged a daily input of 1.0 g per m². This value is low compared with the finding of Abee and Lavender (1972) who estimated 1.5 g per m² per day for homogenous reference stands of the same forest.

The first three months of lateral movement sampling (March-May) indicate that the amount of organic material entering the stream from the bank is approximately 1.5 times the litterfall. Thus, approximately 2.5 g per m² per day entered Watershed 10 in the form of litter. This value is in the low-middle range of a series of values for input of large particulate detritus (<1mm) from several eastern streams reported by Cummins et al. (1973).

Litter breakdown. There were significant differences between streams and among species in the rate of disappearance of leaf material from leaf packs containing conifer needles (Douglas-fir and western hemlock), and vine maple, bigleaf maple and red alder leaves. Mixed leaf packs consisting of bigleaf maple and red alder were placed in Mack Creek. All species broke down more rapidly in Mack Creek than in Watershed 10. In the single-species packs, coniferous needles disappeared most slowly and alder and vine maple most rapidly. Mixed packs of leaf species that decomposed at different rates, fast for alder and slow for bigleaf maple, resulted in a decay coefficient higher than that of either species individually. This suggests that naturally occurring mixtures of leaves may decompose faster than monospecies leaf packs.

Linear trends of the data on weight loss of vine maple and conifer packs (Figure 3.63) indicated that regression analysis would be a valid technique for comparing weight losses from the leaf packs for both streams. All regression lines were highly significant ($P < 0.01$). Vine maple packs in Mack Creek lost 50% of their initial weight in 36 days as compared with 123 days in Watershed 10. Conifer packs in Mack Creek required 89 days to lose 50% of their weight as compared with an estimated 465 days in Watershed 10.

The differences in disappearance rates for the same leaf species between the two streams might be explained in part by the difference in the number of shredding invertebrates found in the two streams. There were greater numbers and biomass of invertebrates in Mack Creek compared with Watershed 10. The ratio of invertebrate biomass to leaf-pack biomass was also significantly greater in Mack Creek than in Watershed 10 (Figure 3.64). A large percentage of the invertebrate biomass on the conifer packs in

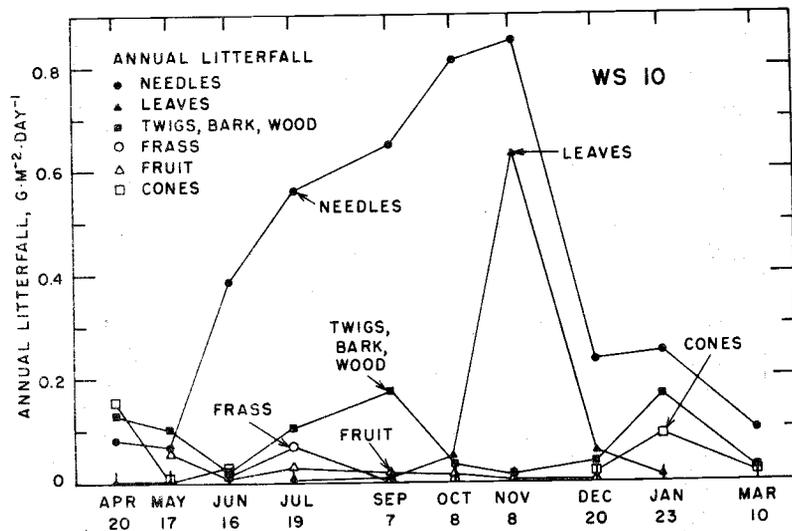


Figure 3.62. Annual litterfall in Watershed 10 by litter type.

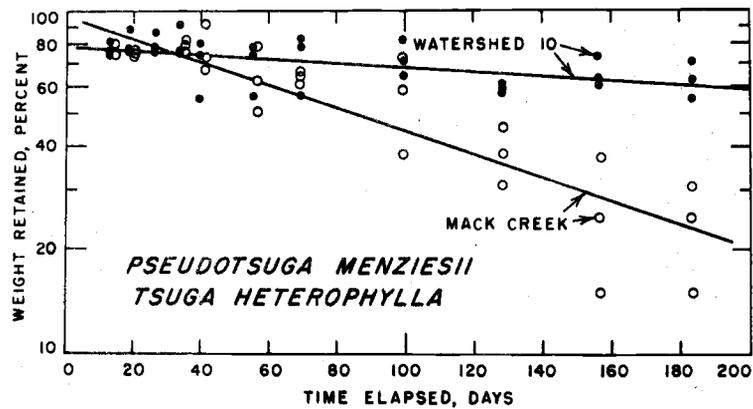
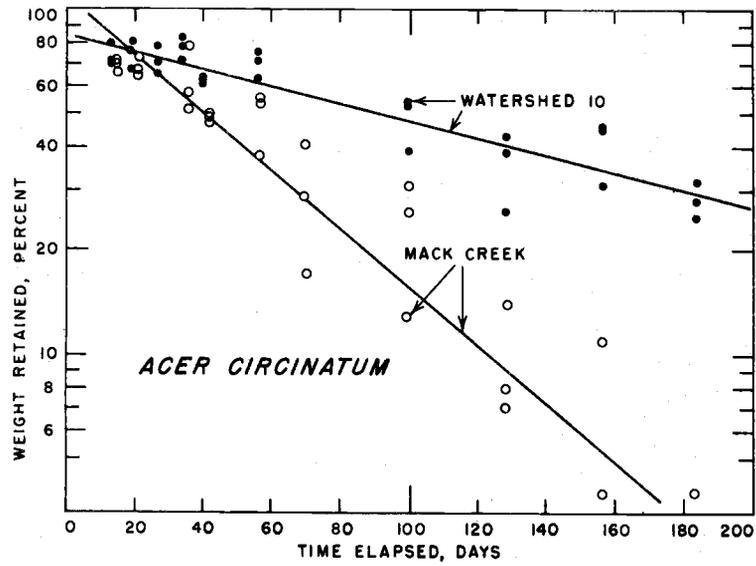


Figure 3.63. Disappearance rates by weight loss of vine maple (*Acer circinatum*) leaf packs, and Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) needle packs in Mack Creek and the Watershed 10 stream.

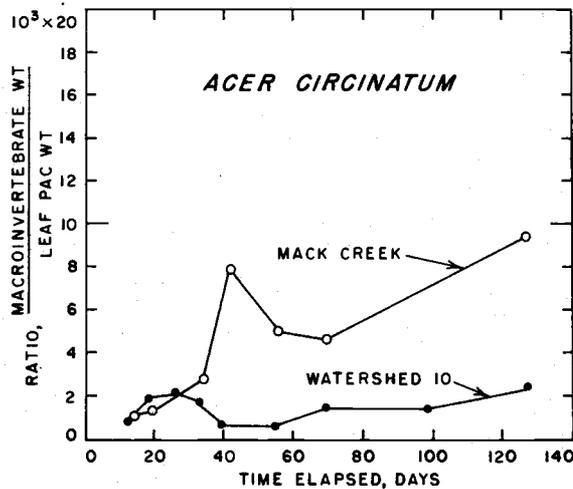
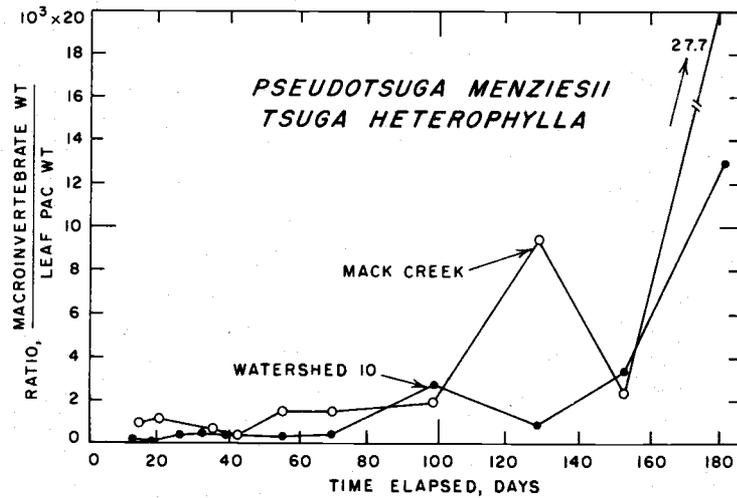


Figure 3.64. Ratio of macroinvertebrate biomass to mean leaf pack weight for Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) needle packs, and vine maple (*Acer circinatum*) leaf packs in Mack Creek and the Watershed 10 stream.

Watershed 10 was composed of small snails. The two Watershed 10 ratios that rise above the Mack Creek ratios were due to large numbers of snails that appeared in the packs after 90 days incubation.

The range of rates among leaf species is not surprising in that different leaf species become conditioned by microbial activity at different rates and, thus, more readily acceptable as food for shredding invertebrates (Triska 1970, Boling et al. in press). Needle litter, generally considered highly refractory, was expected to be exported from the Watershed prior to decomposition and to provide only a minor food source for invertebrates. Conifer packs incubated in Mack Creek, indicate, however, that after 120 to 200 days in the stream, needle litter became palatable to shredding insects (Figure 3.65). After the conditioning phase, needle packs were heavily grazed by Lepidostoma sp. until entirely consumed. Prior to conditioning, needles were grazed minimally by insect detritivores.

A comparison of the decay coefficients in this study with other values reported in the literature shows that decay rates in Mack Creek for vine maple, alder, and the mixed pack are much higher than the fastest rates ($K=0.22$) reported by investigators in Michigan (Boling et al. in press). The slow decay rates of conifer and bigleaf maple from Mack Creek are in the middle range of their values. The decay rates of conifer needles and bigleaf maple in Watershed 10 are lower than the lowest Michigan values. Approximate decay rates calculated for red maple, tulip poplar, and white oak in Tennessee (Thomas 1970) fall within the range of decay coefficients from Mack Creek.

The comparison of decay coefficients between Michigan and the Cascade streams is of great interest in that the water temperatures of the streams in these two regions were roughly the same. The temperatures of the Michigan streams ranged from 0.1-11°C with a mean temperature over the fall-winter season between 3-4°C (R. Peterson, pers. commun.). The stream temperatures in the Andrews Forest ranged from 0.1-8°C, with a mean temperature also about 4°C. The decay rates from Tennessee were determined from a stream whose temperature ranged between 10-16°C.

Many of the problems in interpreting leaf pack studies in forests have been discussed by other investigators, including Minderman (1968) and Anderson (1973). Leaf accumulations in streams are subject to breakdown processes analogous to those in the terrestrial litter. On land, abiotic fragmentation occurs from animal activity when the litter is wet. Leaf accumulations decomposing in streams are subject to freshets, which result in increased fragmentation and reduced animal consumption. As the water level drops and abiotic fragmentation diminishes, animal feeding increases. Conifer needles, being small and compact, with a tight vein network, resist fragmentation more than vine maple or alder. Thus, as Anderson (1973) points out, one would expect different leaf species to have various degrees of susceptibility to mechanical breakdown.

Since weight loss is a measure of leaf disappearance rather than decomposition, the biochemical parameter of lignin composition was used to obtain an additional index of microbial activity to help separate biotic from

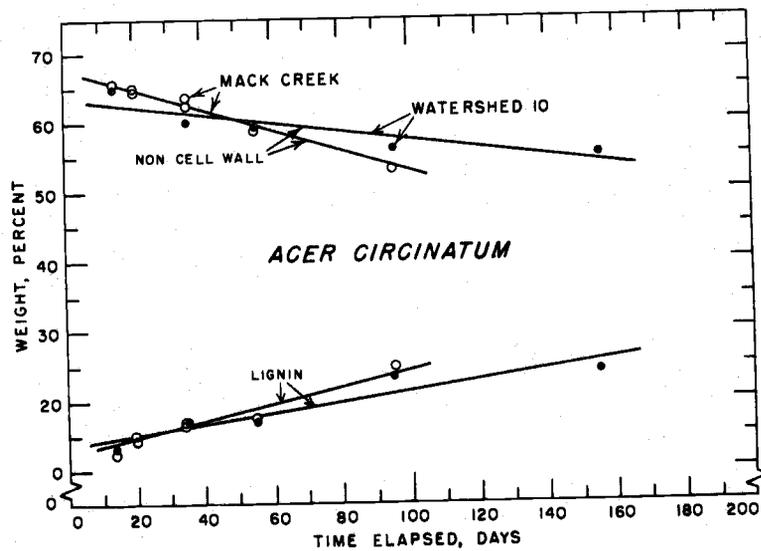
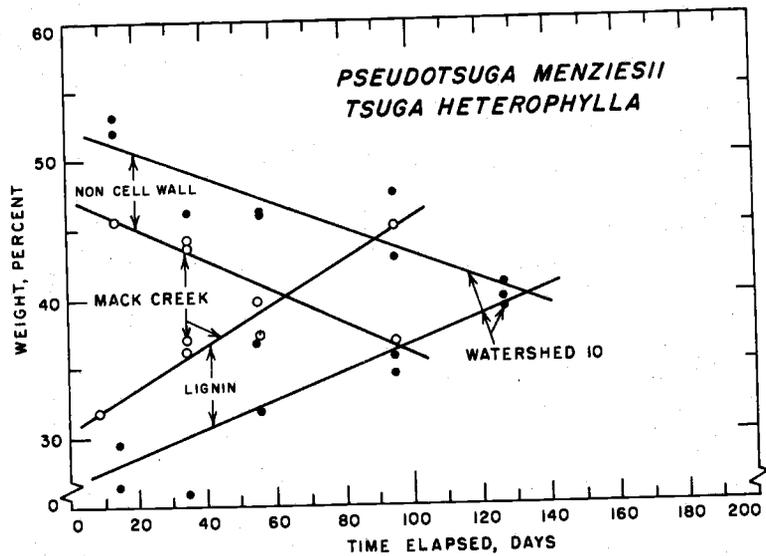


Figure 3.65. Percent changes of noncell wall constituents and lignin composition for Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) needle packs and vine maple (*Acer circinatum*) leaf packs in Mack Creek and the Watershed 10 stream.

abiotic processes. Lignin was chosen since it is the leaf constituent most resistant to decomposition, and therefore increases in percent composition as decomposition proceeds. Changes in lignin were compared to decreases in the most labile fraction, the noncell wall constituents. Alexander (1961), Peevy and Norman (1948), and Pinck et al. (1950) have indicated that changes in lignin composition may provide a good relative prediction of litter decomposition rates. In addition, Cromack (1973), working in a wet hardwood forest and white pine plantation, found that the rate of change of lignin content may be the best single criterion predicting leaf litter decay rates.

In our study, increase in percentage of lignin and decrease in percentage of noncell wall constituents (NCWC) were consistent with the weight loss data for conifer and vine maple packs (Figure 3.66). NCWC consists of soluble carbohydrates, soluble protein, organic acids, nonprotein nitrogen, hemicellulose, and additional soluble organic material. The slower increase in percentage of lignin and the slower loss of NCWC in Watershed 10 than in Mack Creek indicated that decomposition was occurring at a slower rate in the smaller stream. Preliminary data on respiration rates of litter from the two streams also confirm greater microbial activity in Mack Creek.

Changes in litter quality may have proceeded at a slower rate in Watershed 10 due to fluctuating water levels that occasionally left leaf packs exposed to air. Although leaf packs remained wet continually, intermittent exposure to air could have altered bacterial and fungal communities. In Mack Creek all leaf packs were continually submerged. For whatever reason, leaf packs "conditioned" move slowly in Watershed 10.

The differences in processing rates of leaf litter material were also reflected in the chemical constituents of the litter. Throughout the experiment concentrations of nitrogen and phosphorus for all leaf substrates were higher in Mack Creek than in Watershed 10. A comparison of nitrogen concentrations is provided in Figure 3.67. Most leaf packs lost some nitrogen due to leaching during the first 20 days. For conifer, pine, and maple, nitrogen concentration exceeded preleaching levels. In Watershed 10, nitrogen concentrations were always lower than Mack Creek, but usually approached initial concentrations as decomposition proceeded. These results probably indicate microbial immobilization.

This factor of nitrogen immobilization has commonly been observed in agricultural research (Richards and Norman 1931; Waksman and Gerretsen 1931, and Alexander 1961). Similar increases in nitrogen concentration as decomposition proceeds have also been observed for many leaf species in forest soils (Caldwell and DeLong 1950; Saito 1957; Ivarson and Sowden 1959; Bocock et al. 1960; Gilbert and Bocock 1960; and Bocock 1963, 1964). In fact, Gilbert and Bocock (1960) and Bocock (1964) have reported absolute increases in nitrogen content as litter decomposes.

Increases in nitrogen concentration may enhance the value of "conditioned" litter as a source of this nutrient for shredding invertebrates. The effect of conditioning time, temperature, and food density on consumption of litter by shredding invertebrates are being investigated.

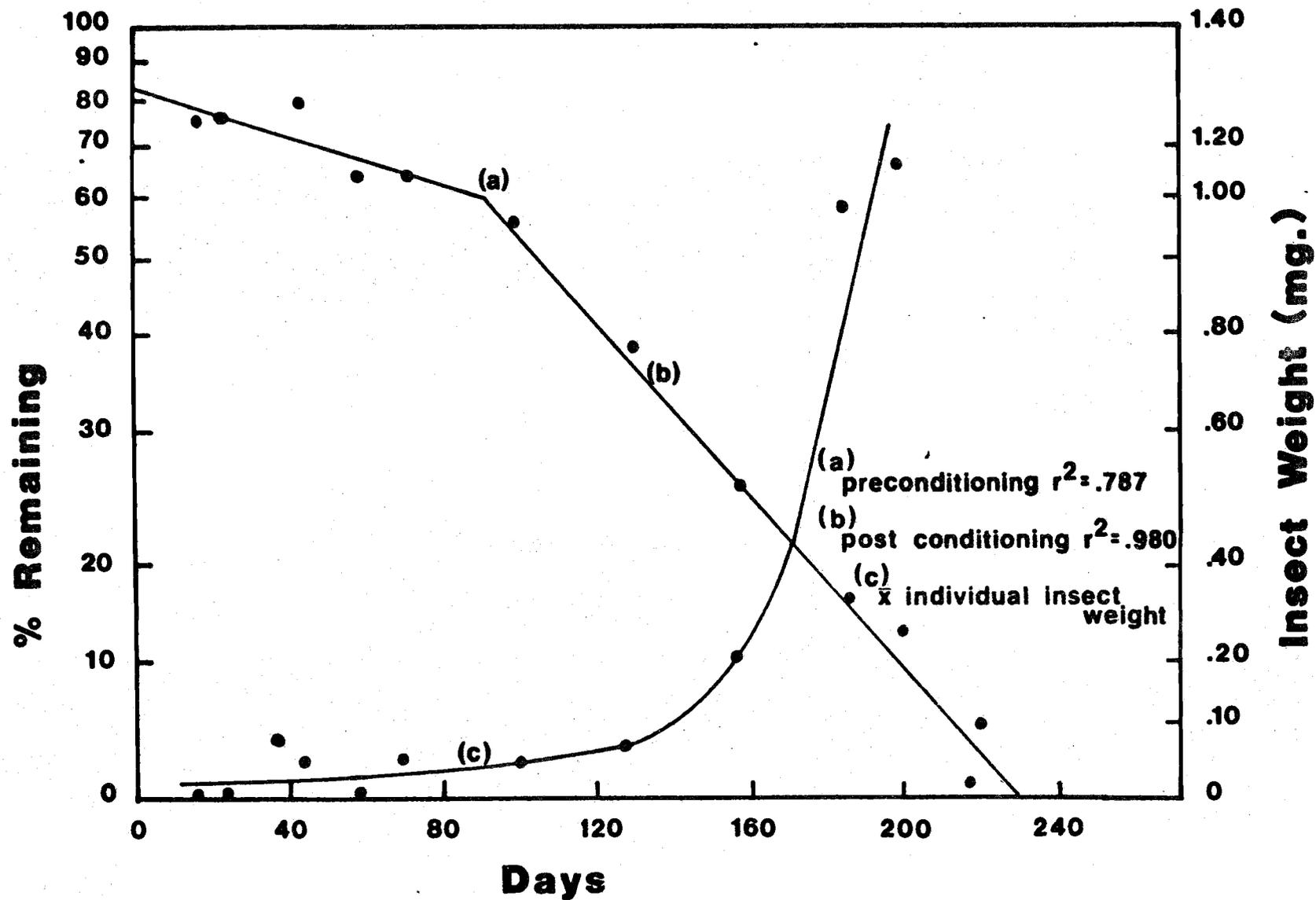


Figure 3.66. Needle pack weight loss of Douglas-fir and western hemlock in Mack Creek. (a) Weight loss during preconditioning period (0-100 days). (b) Weight loss during post-conditioning (130-220 days) by insect consumption and microbial decomposition. (c) Mean individual weight of Lepidostoma sp. associated with leaf packs.

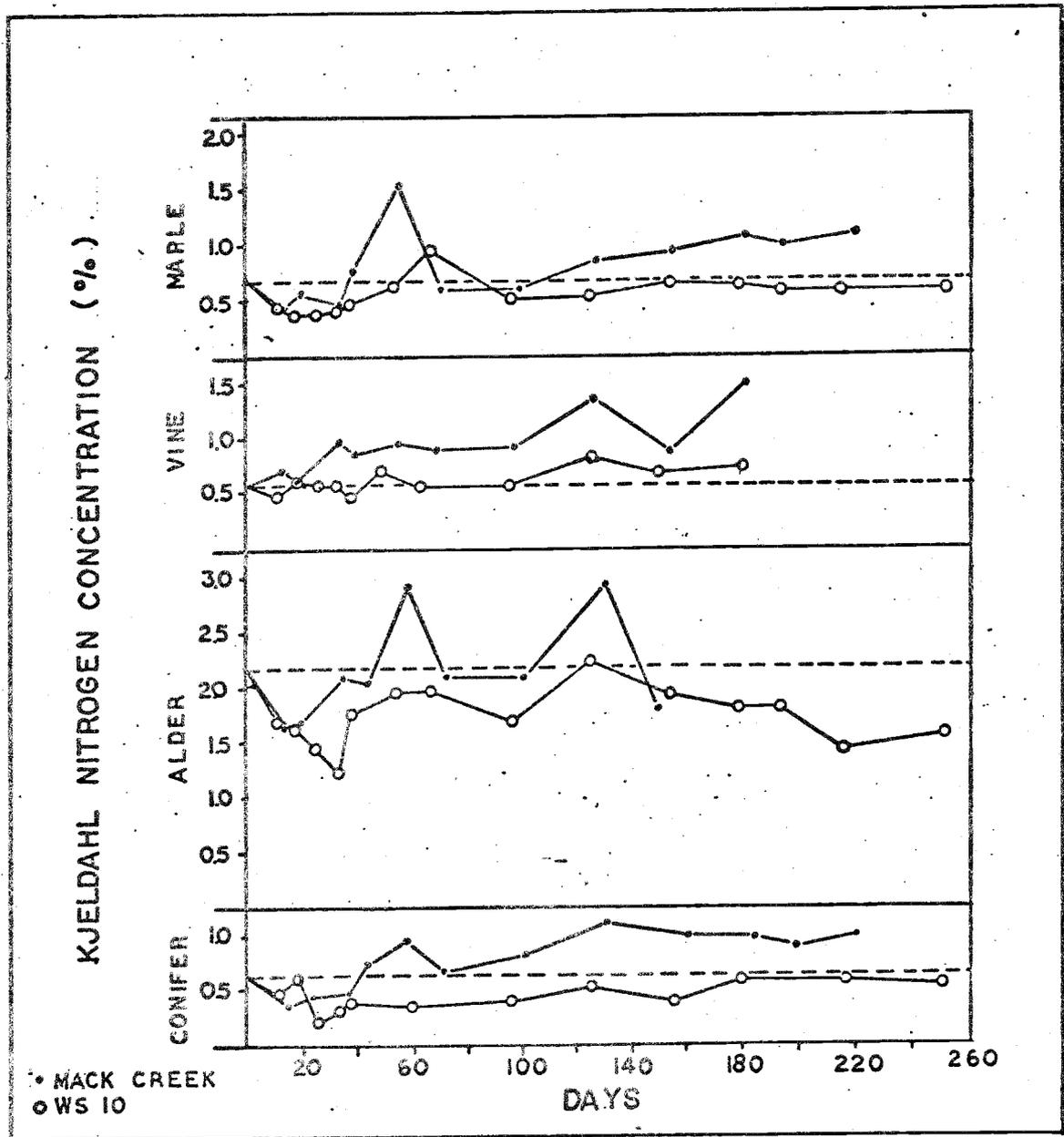


Figure 3.67. Nitrogen concentration of decomposing leaf litter in Mack creek and watershed 10, H. J. Andrews Experimental Forest.

3.3.1.2. Detrital processing by invertebrates. Investigation of the role of caddis larvae as shredders in the stream ecosystem has led to qualitative and quantitative studies of their food habits. Rather than becoming involved in a large scale program of gut-content analysis, we have been screening for species that occupy different feeding niches and that could then be used for laboratory studies. To date we have no complete quantitative consumption studies for a full life cycle, but several experiments demonstrated the importance of caddisflies as processors of allochthonous and autochthonous material in the stream system.

The data will be incorporated into the general stream model as an insect feeding sub-model, with the basic equation being:

$$C = F + N + R + G \quad (1)$$

This states that consumption (C) results in fecal production (F), nitrogenous excretion (N), respiration (R), or growth (G) (production).

Effects of leaf conditioning. Alder leaves were incubated in mesh bags in Oak Creek for periods of up to 46 days. The leaves were then brought into the laboratory and feeding and fecal production by Lepidostoma quercina were measured for three days. Figure 3.68 shows the consumption rates versus leaf age, with each point representing one replication involving 12-15 insects. It is apparent from these results that leaf conditioning, due to microbial colonization for 2-3 weeks, has a marked effect on leaves as a food source.

Feeding rate and body size. Feeding rate versus body weight is shown in Figure 3.69 for L. quercina. Each point represents a replication containing four insects fed on alder leaves for two days. The same insects were tested in a Gilson respirometer for respiration rate versus body size at 5, 15, and 20°C. Within this size range there was no apparent difference in respiration rate ($\mu\text{l O}_2$ per mg per hr) between the different sizes of insects, although respiration increased with temperature as expected. From equation 1, assuming fecal production and nitrogenous excretion to be proportional to consumption, growth efficiency (the proportion of consumption that is utilized as growth) must decrease with increasing size of the insect, and with increasing temperature.

Population density - food density relationships. Laboratory feeding experiments with L. quercina were set up to obtain data on food consumption and growth rate at various food densities. These data are required to test the hypothesis that benthic insects are food limited. Figure 3.70 shows a portion of the results obtained from an experiment with 600 insects measuring consumption of alder leaves, fecal production, and growths of L. quercina fed on three different food densities and at three different temperatures. At all temperatures the low food density limited consumption and the high food density allowed unrestricted feeding. As expected consumption increased with increasing food density and temperature. Consumption rate was limited unless food was available in excess of 1.5 times the maximum consumption per day.

Discussion. The above data can now be used to begin preliminary modeling

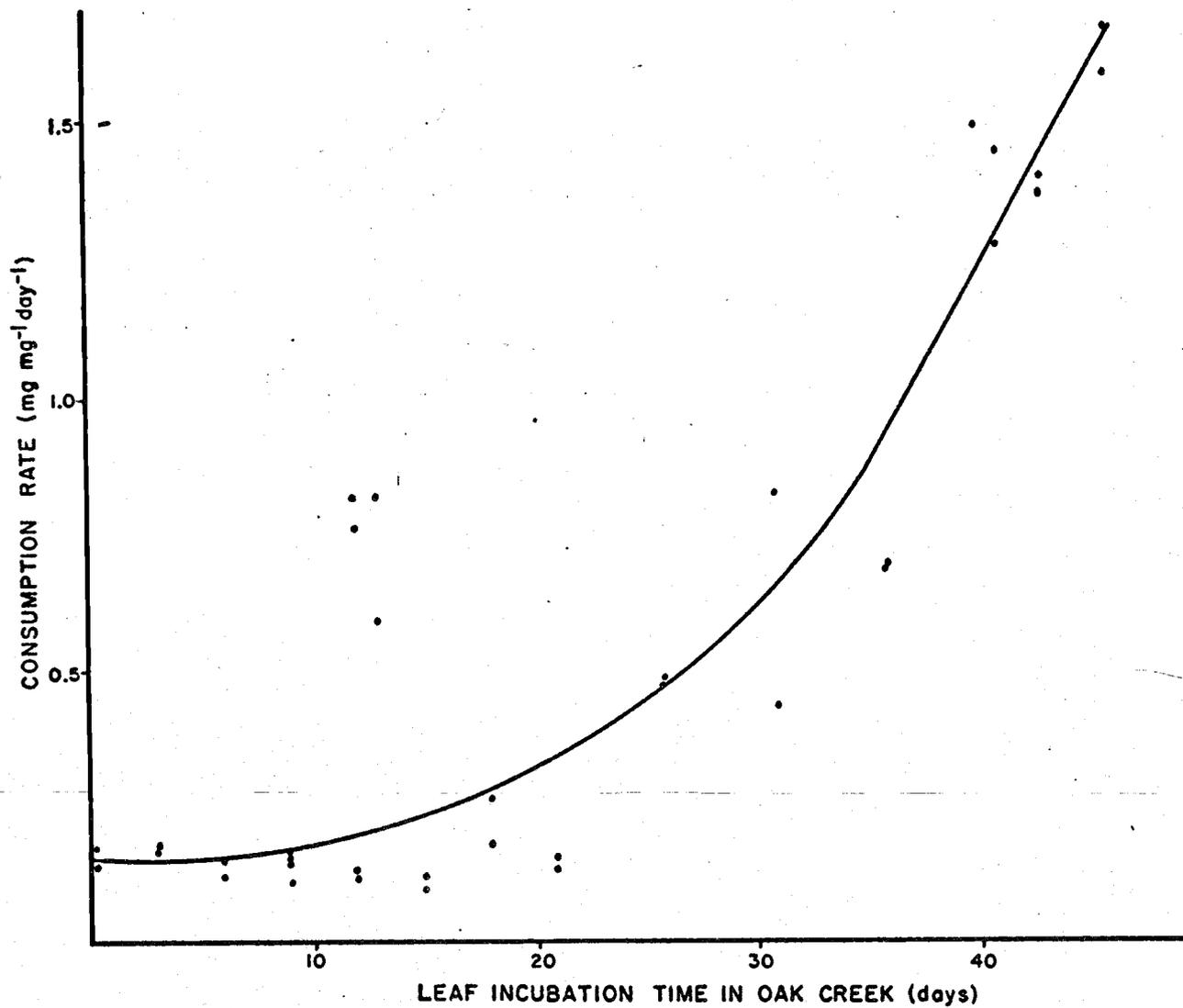


Figure 3.68. Consumption rate of alder litter by Lepidostoma sp. as a function of conditioning time in Oak Creek.

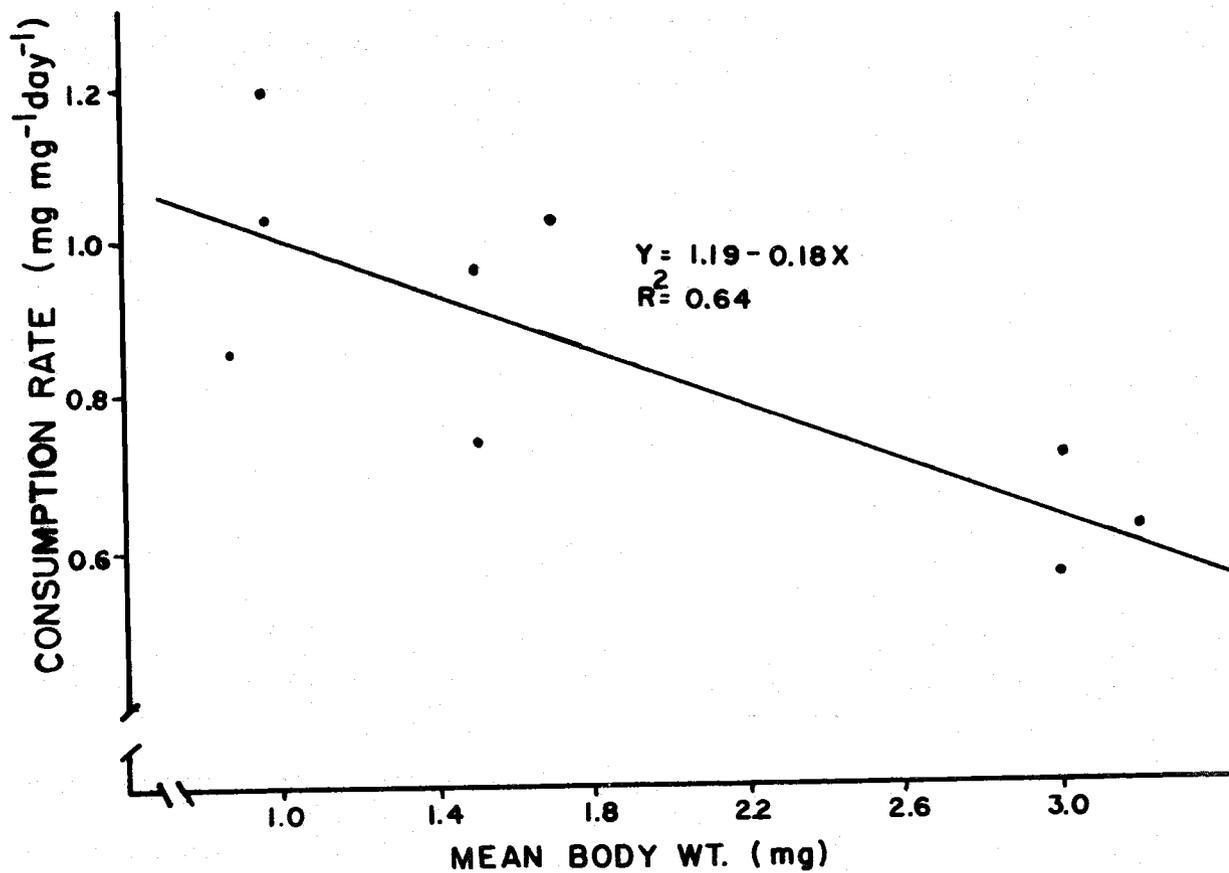


Figure 3.69. Consumption rate of Lepidostoma sp. larvae fed on alder (Alnus sp.) leaves as a function of body weight.

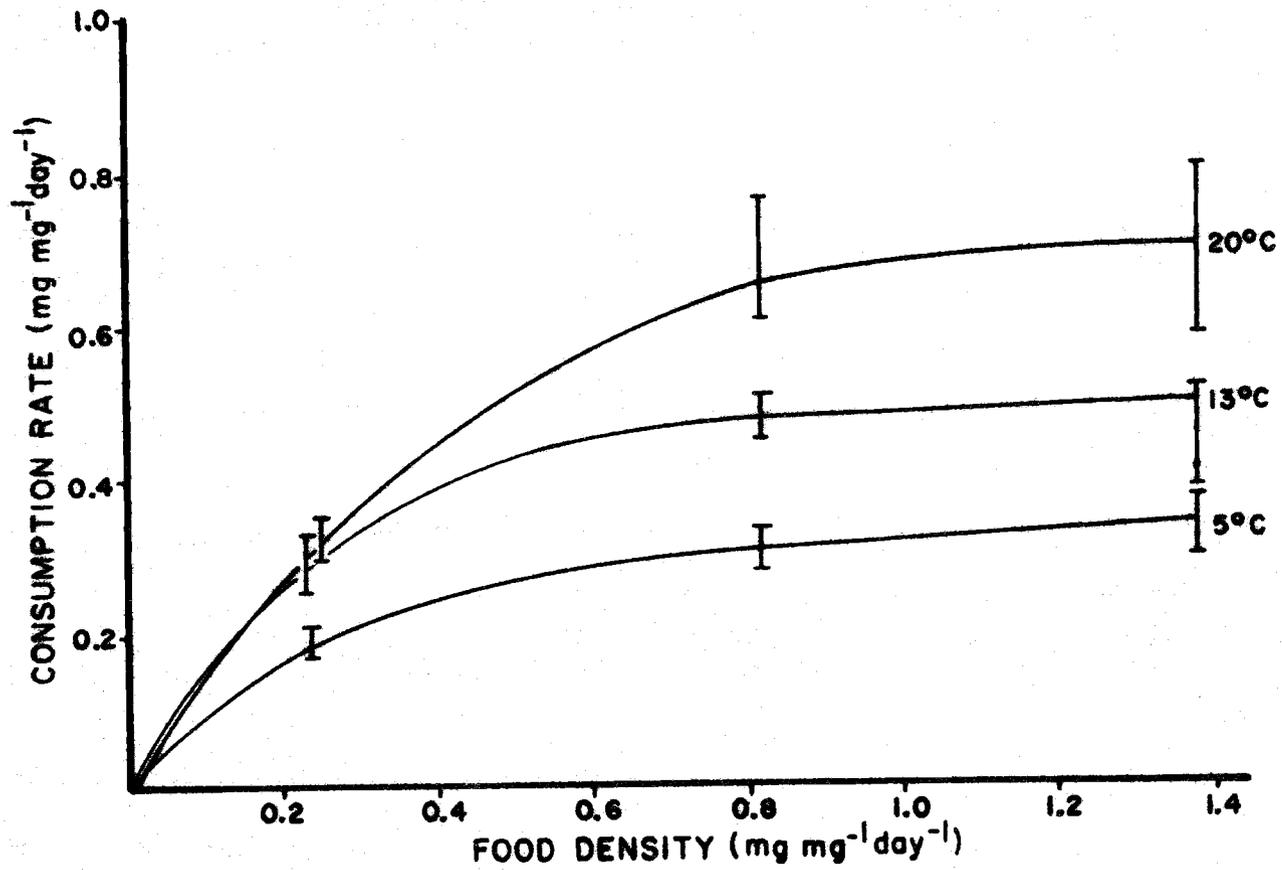


Figure 3.70. Consumption rate of *Lepidostoma quercina* larvae fed on alder (*Alnus* sp.) leaves as a function of food density at three different temperatures. 95% confidence levels are shown.

of food utilization, based on equation 1, for early to mid-final instar L. quercina. This portion of the life cycle has the highest consumption and growth. Another series of experiments on late-final-instar larvae is in progress to provide additional data, particularly on the effects of size and physiological age.

Similar experiments will also be done to examine the processing and utilization of conifer needles. As a food for shredders, these differ from deciduous leaves both in time of availability and in relative attractiveness. However, after several months of microbial conditioning, conifer needles are readily consumed by L. unicolor. From preliminary experiments, we know that feeding rates on fir needles by this species can be as high as three to four times the body weight per day. This extremely high consumption rate indicates that in order to obtain sufficient nutrient from the low quality food source, the larvae must process large quantities of material. In this respect, comparisons will also be made with consumption rates of periphyton-grazers, glososomatid caddisflies, that are utilizing a high quality food source.

Fecal production studies have been conducted for several species of caddisflies. If assimilation efficiency is known, measurement of fecal production is one of the easiest ways of estimating food consumption. However, the more important objective of these studies is to understand the degradation process of allochthonous material within the stream system.

Chemical degradation during the shredding process was studied by comparing the composition of the leached leaf food source and the feces. The latter are about 16% lower in non-cell-wall constituents, and higher in lignin (9%), cellulose (5%), and ash (2%). In other words, the larvae have utilized some of the microbial component (fungi and bacteria) and perhaps some of the readily digestible leaf components. There is a corresponding increase in the feces of the more refractory components--the lignin, cellulose and ash.

In addition to this chemical degradation, there is the physical component of shredding process. The feces are a finely divided compost-like material with a large surface area for further microbial colonization. This mechanical change in structure, which provides a food source for filter feeders and sediment feeders, is one of the significant pathways in the nutrient cycling in the stream system.

3.3.1.3. Particulate organic budget for Watershed 10. The data gained from the lateral movement decomposition and insect biomass and feeding studies provided an opportunity to construct a first-approximation particulate organic matter budget (Figure 3.71). All values were measured independently rather than by difference; however, the results must be interpreted with caution because many of the estimates have been based on short-term sampling.

The stream bottom area was estimated at 300 m². Measurements of input were litterfall, lateral movement, throughfall, algal production, and moss

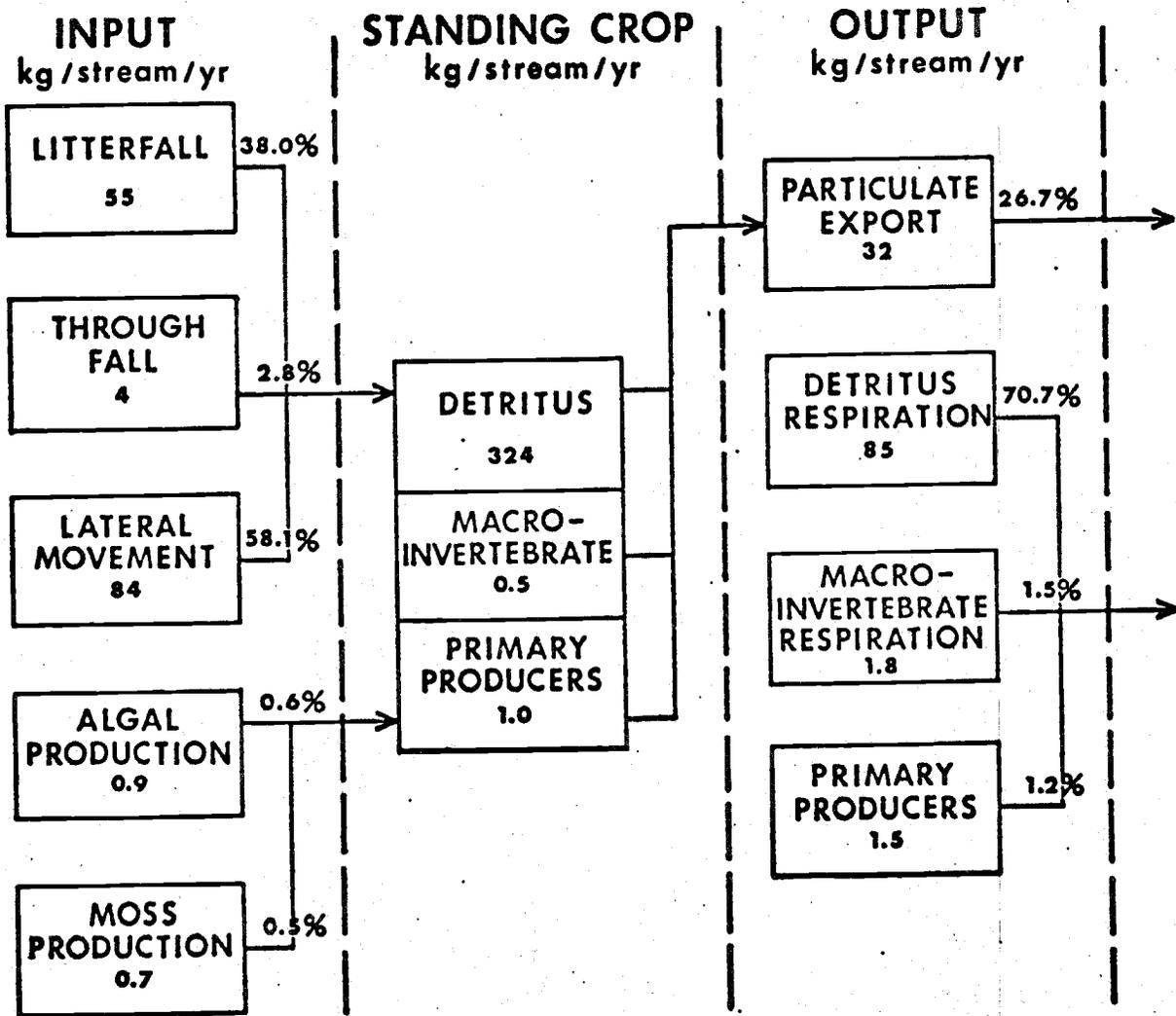


Figure 3.71. Particulate organic budget for watershed 10, H. J. Andrews (1972-1973) Experimental Forest.

production. Throughfall was estimated by G. Carroll (pers. commun.) at 0.1 g per m^2 per day based on a three-day sample. Algal biomass was estimated at 0.33 g/m^2 by chlorophyll extraction; turnover time was assumed to be 40 days. Moss production was estimated at 2.1 g per m^2 per yr from Fisher (1970). Standing crop of detritus was calculated from 20 core samples, 15 cm in diameter. Macroinvertebrate biomass was based on an averaging of two different methods. The first was a single standing crop estimate (ten 15-cm cores), with production estimated at 3.5 times standing crop (Waters 1969). Standing crop by this method was calculated to be 1.3 g/m^2 , with an annual production of 4.55 g/m^2 . The second method used was year-round emergence data from Watershed 10 and indicated a standing crop of 2 g/m^2 . This value was obtained by assuming emergence was one-fourth of the average standing crop (Anderson 1974). Annual production was calculated to be 7 g/m^2 , using Waters' 3.5 turnover ratio. Respiration of detritus was based on 100 measurements of five size classes of detritus at 10°C . Caloric content was assumed at $16.7 \times 10^3 \text{ Joules/g}$ (4000 cal/g).

A net accumulation of 24.3 kg occurred in the water year 1972-1973. This water year was particularly dry, which could have resulted in less export and less microbial respiration. Detrital respiration accounted for about 70% of the loss of particulate organic matter, suggesting the need for more accurate assessment of this process.

The same general approach has previously been used by Fisher and Likens (1972) to construct an organic budget for a stream in New Hampshire. This stream has a relatively low gradient (14% streambed slope), receives the bulk of its litter input in the autumn, and has a fairly evenly distributed precipitation pattern of about 123 cm/yr. The Fisher and Likens organic budget assumed the stream was in steady state, that is, the inputs equaled the outputs. In addition, their largest component of the particulate organic output (microbial respiration) was obtained by difference. Watershed 10 is a high-gradient stream (45% slope), receives the bulk of its litter input over the summer and fall, and receives precipitation of 240 cm/yr, 90% of which falls in a six-month period between October and March. Nonetheless, for both systems, 99% of the particulate organic input is detritus or litter, and 1% or less is contributed by the primary producers. For both streams, about two-thirds of the detrital inputs were processed by organisms in the stream. Only about one-third of the detrital input was exported out of these small streams (Figure 3.72). Such data indicate small woodland streams are indeed significant biological processing units.

Reichle (in press) has compared some computed metabolic parameters of several different terrestrial ecosystems. The object of his comparison was to demonstrate consistent patterns that could be extrapolated between systems. One such ratio discussed by Reichle is ecosystem maintenance efficiency. This ratio represents the cost of production in an ecosystem and is defined as the ratio of autotrophic respiration to gross primary production. For purposes of comparison, one could assume that detrital input to a stream system is analogous to gross primary production in a terrestrial system. Both represent nearly all the gross energy input

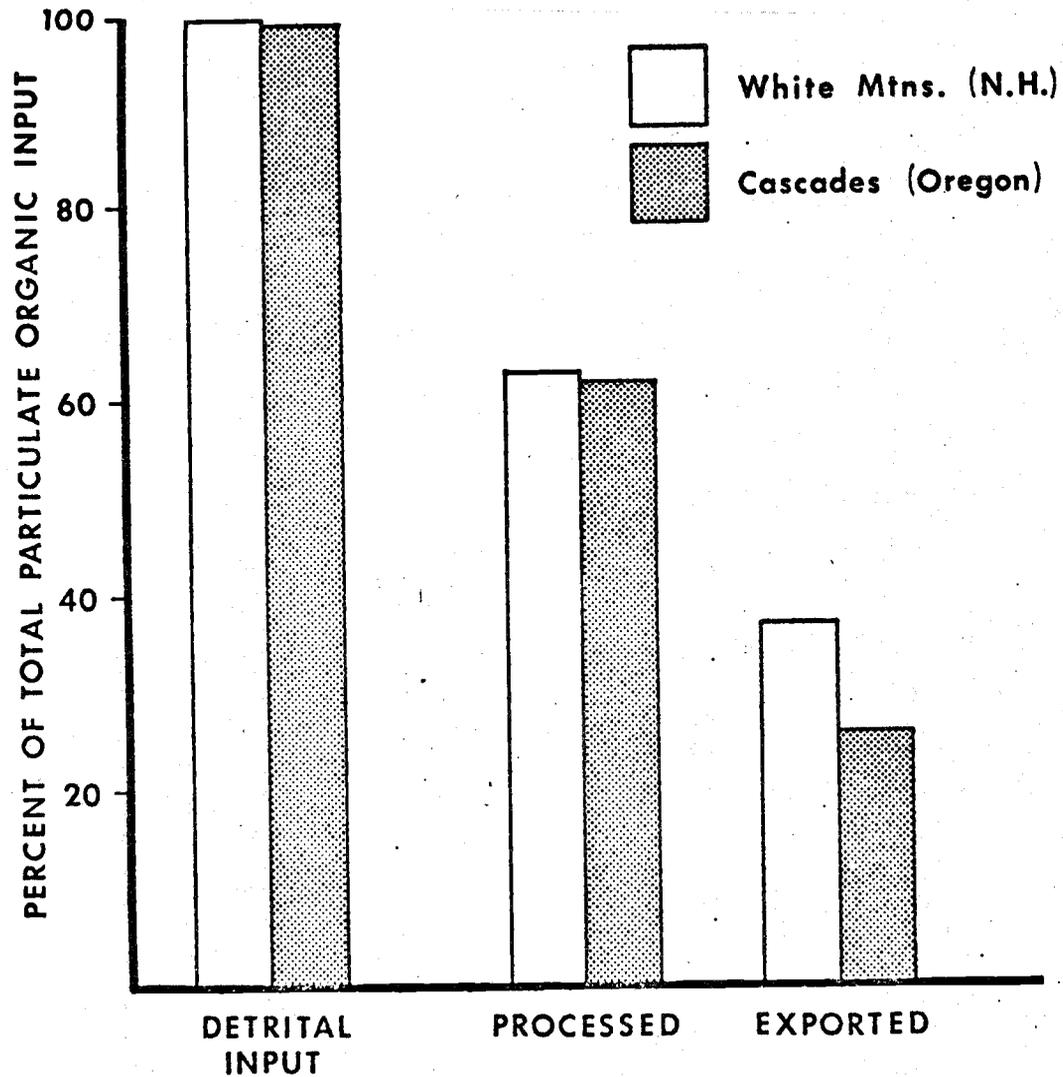


Figure 3.72. Comparison of particulate organic material input, processing, and export for two small mountain streams, Bear Brook in the White Mountains of New Hampshire, and watershed 10 in the Oregon Cascades.

to their respective systems. Likewise, detrital respiration in streams could be substituted for autotrophic respiration in calculating analogous ratio for stream ecosystems.

For three terrestrial systems (coniferous forest, deciduous forest, and grassland) the maintenance efficiencies ranges from 0.53 to 0.62 (Reichle in press). The corresponding values for the Oregon and New Hampshire streams were 0.59 and 0.63 respectively. These values suggest an unsuspected similarity between terrestrial and aquatic systems.

3.3.1.4. Forest and clearcut stream production. Autotrophic production in streams is controlled by the interrelationships between light, nutrients, and temperature. Light intensity, light quality, and temperature are controlled by the degree of shading from the surrounding terrestrial vegetation. The principal sources of nutrients for aquatic plants in streams are groundwater and throughfall, both of which are strongly affected by the biological activity of the terrestrial ecosystem. Therefore all factors that regulate primary production in streams are influenced greatly by the surrounding vegetation. Determining effects of different land ecosystems on both primary and secondary production is one of our aims.

Studies of community structure of primary producers, standing crop, and colonization rates of algae onto stream substrates were conducted on three streams of different size in the H. J. Andrews Experimental Forest: Watershed 10, Mack Creek, and Lookout Creek. Watershed 10 is a small, heavily shaded stream; Mack Creek is an intermediate, third-order stream with forested and clearcut sections; and Lookout Creek is a large, third-order stream that is forested but very open.

Effects of changes in light and forest cover on primary production. Distinct shifts in the community structure of primary producer occurred as the light intensity increased. The dominant primary producer in the heavily shaded stream was an aquatic moss. The periphyton community in the forest section of the intermediate stream was composed principally of diatoms, shifting to a mixed community of diatoms, Prassiola, and Zygnema in the clearcut section. The filamentous diatom Melosira was found in the largest stream. Similar shifts to green, filamentous algae have been found with increased light intensity by Butcher (1946), Dever (1962), Hansmann (1969), and McIntire and Phinney (1965). Opening of the canopy either naturally with increasing stream size, or artificially by land manipulations, changes the community structure of primary producers.

Standing crop of algae and colonization rates of algae onto stream substrates increased as light increased (Table 3.42). On the three stream systems alone this could have been interpreted as the effect of several variables other than light intensity such as stream morphology or water chemistry. However, the drastic differences in the standing crop and colonization rates in the clearcut and forest sections of the same stream indicate that light intensity has a great effect on autotrophic production. McIntire (1966) demonstrated that primary production increased as light intensity increased in a laboratory stream at 10°C in Oregon. We feel that the great differences in light intensity on streams in the coniferous forest leads to different rates of primary production in these streams.

Table 3.42. Standing crop and colonization rates of algae in three streams in the H.J. Andrews Experimental Forest (April-September 1973).

Stream	Mean standing crop (g/m ²)	Mean colonization rate (mg m ⁻² day ⁻¹)
Watershed 10	0.3	3.5
Mack Creek forest section	1.6	11.2
Mack Creek clearcut section	2.3	25.8
Lookout Creek	14.1	135.3

Table 3.43. Physical characteristics of clearcut and forest sections on Mack Creek.

	Clearcut	Forest
Length (m)	204.0	203.0
Mean width of water surface (m)	2.82	2.83
Mean stream width (m)	4.87	5.37
Water surface area (m ²)	575.3	574.5
Pool area (m ²)	89.0	147.9
Number of pools	33	30
Pool to riffle and cascade ratio	0.183	0.347
Mean depth (cm)	10.3	9.6

This hypothesis that light is the major limiting factor of primary production in coniferous forest streams will be tested in 1975 to 1977.

Of the possible limiting plant nutrients, carbon dioxide, nitrates, and phosphates, only nitrates were distinctly different between the streams we have studied. Research on primary production in open, artificial streams by Weyerhauser has indicated that at certain seasons primary production can be increased by increasing nitrate concentration when light is not limiting. To determine the effect of different nitrate concentrations on streams that are limited by shading, we plan to place three artificial stream channels on a low nitrate stream that is shaded by a forest. Various nitrate concentrations will be maintained in two of the channels and the third will be used as the control stream. The effect of nitrate concentration on primary production in streams where light is limited will be examined in this way.

As previously noted, Mack Creek had both clearcut and forested sections. The clearcut was nine years old and therefore was not subject to the catastrophic effects of scouring, lethal temperatures, and siltation that are prevalent in recent clearcuts. Thus, both sections of stream were stable and represented a heterotrophic system in the forest and an autotrophic system in the clearcut.

Studies on the algae, terrestrial debris, insect populations, and cutthroat trout populations in both the clearcut and the forest allowed us to determine the effect of this shift between heterotrophy and autotrophy on the productivity of the stream. The standing crop of algae in the forest was 1.6 g/m^2 and 2.3 g/m^2 in the clearcut (Table 3.42). Standing crop of algae alone tells little about the production of algae, therefore the rate of colonization of algae onto bare substrates was examined in both sections of the stream. The algal colonization rate in the forest averaged $11.2 \text{ mg per m}^2 \text{ per day}$ and $25.8 \text{ mg per m}^2 \text{ per day}$ in the clearcut. This increase in algal production was accompanied by an increased standing crop of typical grazing insects such as Chironomidae, Glossosomatidae, and Baetis.

Since terrestrial vegetation was drastically different in the two sections, the amount of organic debris in the two sections was also different. Standing crop of coarse debris in the forest was 19.3 kg/m^2 and only 0.7 kg/m^2 in the clearcut. The fine debris standing crop in the forest was 0.7 kg/m^2 and 0.3 kg/m^2 in the clearcut. Many of the typical detritivores such as Leuctridae, Nemouridae, Pteronarcidae, Chloroperlidae, Lepidostomidae, and Limnophilidae had greater standing crops in the forest as opposed to clearcut.

The response of the insect community to the differences in the forest and the clearcut was consistent with the change in the energy base in the two sections. To determine if insect production was also different between the heterotrophic and autotrophic system, insect emergence was measured in the clearcut and the forest. Insect emergence was four times greater in the clearcut ($6.0 \text{ mg per m}^2 \text{ per day}$) than in the forest ($1.54 \text{ mg per m}^2 \text{ per day}$). The mean size of emergent insects in the clearcut (0.86 mg) was also greater as opposed to the forest section

(0.54 mg). If the insect productivity was indeed greater in the autotrophic system, this should also be reflected in the production of cutthroat trout in the two systems. To this end an intensive cutthroat study was initiated on the clearcut and forested sections of Mack Creek.

Trout production. Cutthroat occur in many small streams in the Coniferous Forest Biome. Present land management practices, including logging, may significantly alter the stream environment and affect the trout populations. Hall and Lantz (1969) report increased water temperature and reduced dissolved oxygen in a small coastal stream following clearcut logging. During the first two post-logging years, the cutthroat trout population was estimated to be approximately 25% of pre-logging levels. In addition to changing physical environmental conditions, it is reasonable to assume long-range effects of clearcutting may be reflected through alterations of the food resource. A population and food habits study of the cutthroat trout is being conducted in both an eight-year old clearcut and an adjacent forested section of Mack Creek, a tributary of Lookout Creek which drains the H. J. Andrews Forest.

A two-hundred meter study section was established in the clearcut and the forested segments of the stream. The lower boundary of the forested section was approximately 250 meters upstream from the upper boundary of the clearcut section. Both study areas were selected so as to contain two relatively large pools with the remainder in small pools, riffles, and cascades.

The estimated physical characters of the two study sections are included as Table 3.43. The sections are similar in mean width, surface area, and mean depth. Slightly greater pool area existed in the forest section. The temperature and flow data have not been fully analyzed. Generally the clearcut was characterized by slightly higher summer temperatures with wider fluctuations.

The bimonthly estimates of trout population size as calculated by the removal method of population estimation are shown in Figure 3.73. The apparent increases in numbers over time cannot be satisfactorily explained by immigration, since no tributaries or other locations suitable for emigration exist. General movement in Mack Creek was impaired by the precipitous nature of the stream. Recapture of tagged trout while conducting population estimates and collecting stomach content samples indicate little trout movement occurred. All upstream movement of trout from Lookout Creek was precluded by a debris dam located below the clearcut study section. It was reasonably hypothesized that the trout were within the study areas, but at the time of the population estimates certain segments of the population were unavailable for capture.

The proposed hypothesis led to a reanalysis of the data. Since all trout greater than 70 mm in length captured during April and June population estimates were tagged and could be later identified by tag number, a mark and recapture method of population estimation was employed. All tagged trout, whether captures or recaptures composed the marked group for the date of the estimate. Any "marked" trout subsequently recaptured

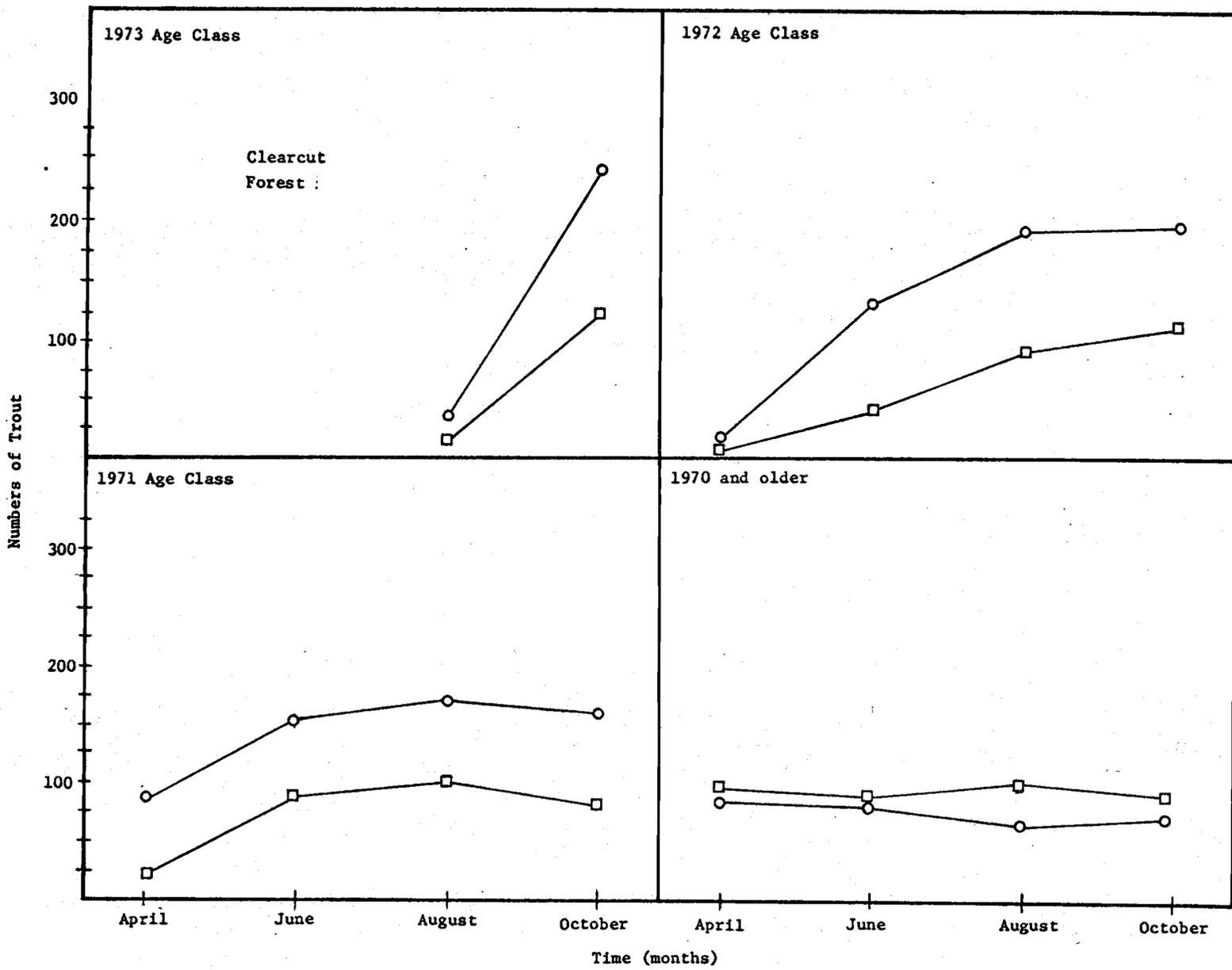


Figure 3.73. Estimated numbers of cutthroat trout by age class in the clearcut and old-growth forest study areas of Mack Creek.

during the following bimonthly removal estimate was considered a recapture in forming the capture (C) to recapture (R) ratio of the Peterson population estimation equation:

$$\frac{\text{Population } (\hat{N})}{\text{No. marked } (M)} = \frac{C}{R}$$

The usual assumptions of no mark loss, differential mortality, and differential recapture rate were made.

An estimate of population size at time of marking is shown in Figure 3.74. The procedure yields realistic mortality curves which tend to support the original hypothesis. Estimates were not possible for 1973 and 1972 age classes since these trout were normally less than 70 mm in length, the minimum tagging size. The results of the population estimates, regardless of method of computation, indicate that the clearcut section supported a higher number of trout than the forested section.

The length frequency distributions of trout captured while conducting the population estimates were used to estimate the mean length of the year classes in both study sections. From Figure 3.75 it can be seen that trout in the clearcut were consistently larger than forest residing trout. The magnitude of the difference increases with trout age up to the last age category, which represents a composite of age classes.

The trout stomach contents are presently being analyzed, with attention being focused on differences in diet between the trout captured in the clearcut and forested areas. By the end of 1974, the sorting should be complete and data will be available on the diet composition.

The relocated laboratory feeding experiments relating to prey and predator size, density, and consumption have been unsuccessful primarily due to the refusal of the trout to feed after human disturbance. An analysis of prey and predator size from stomach contents revealed no consistent regression of predator size on mean prey size. Mean prey length and width and estimated mean volume have been used as dependent variables with fish length the independent variable. Small trout were found not to consume large prey, but large trout did consume small prey. On a numerical basis, large prey composed only a small percentage of prey consumed by large trout. No apparent differences existed between the sizes of prey consumed in the clearcut and forested sections. More work with an altered experimental design eliminating human disturbance is necessary to begin to understand prey selection by stream dwelling trout.

Our studies to date indicate that the numbers and biomass (6 g/m²) of cutthroat trout in the forest are less than the numbers and biomass (12 g/m²) in the clearcut. These results suggest the hypothesis that consumer production increases as the heterotrophic-autotrophic nature of streams shifts towards autotrophy. We propose to examine this hypothesis in 1975 to 1977.

3.3.1.5. Process modeling. In January 1973, an interdisciplinary group

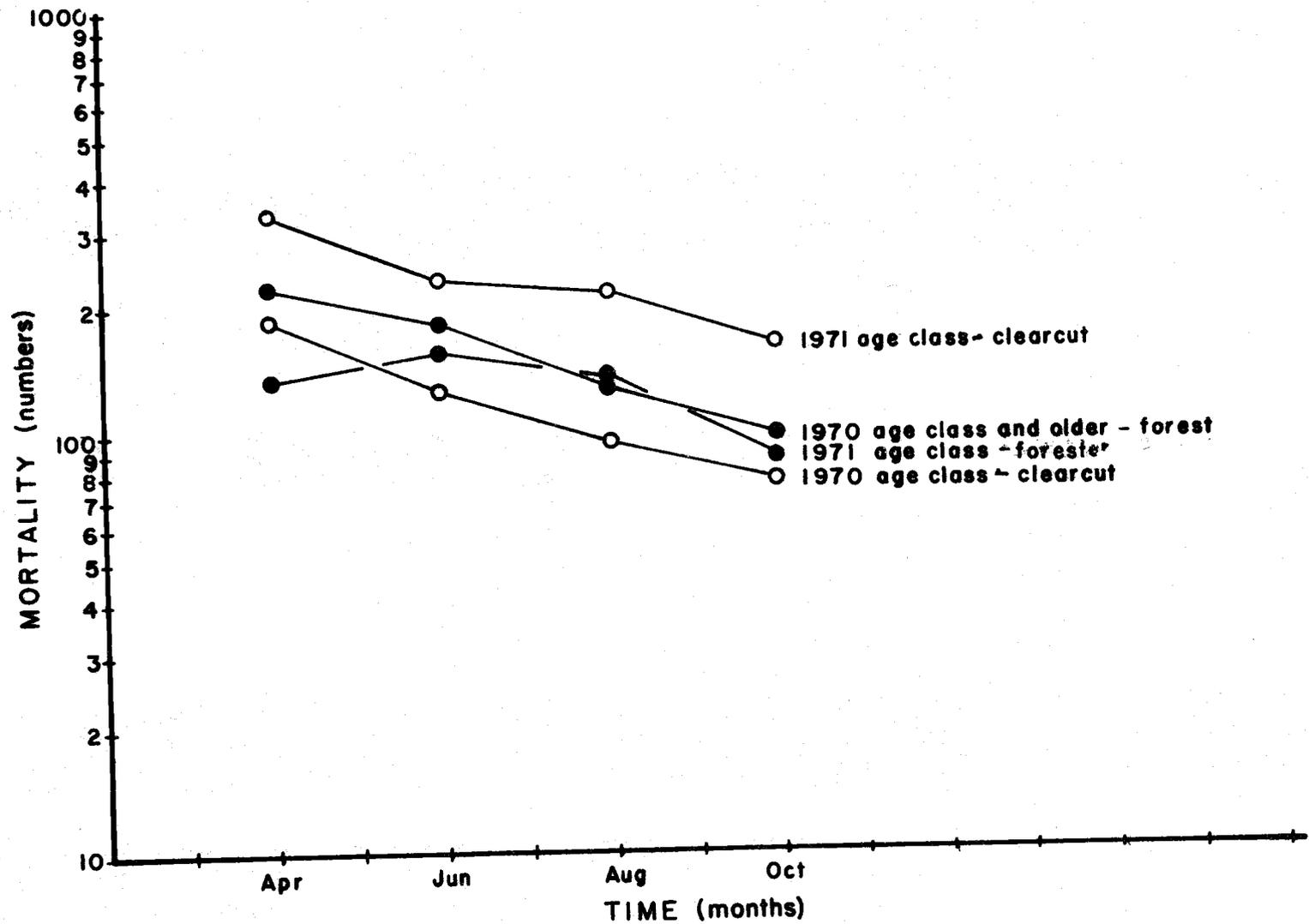


Figure 3.74. Mortality of cutthroat trout in the forest and clearcut obtained by mark and recapture method for 1971 and 1970 and old age groups.

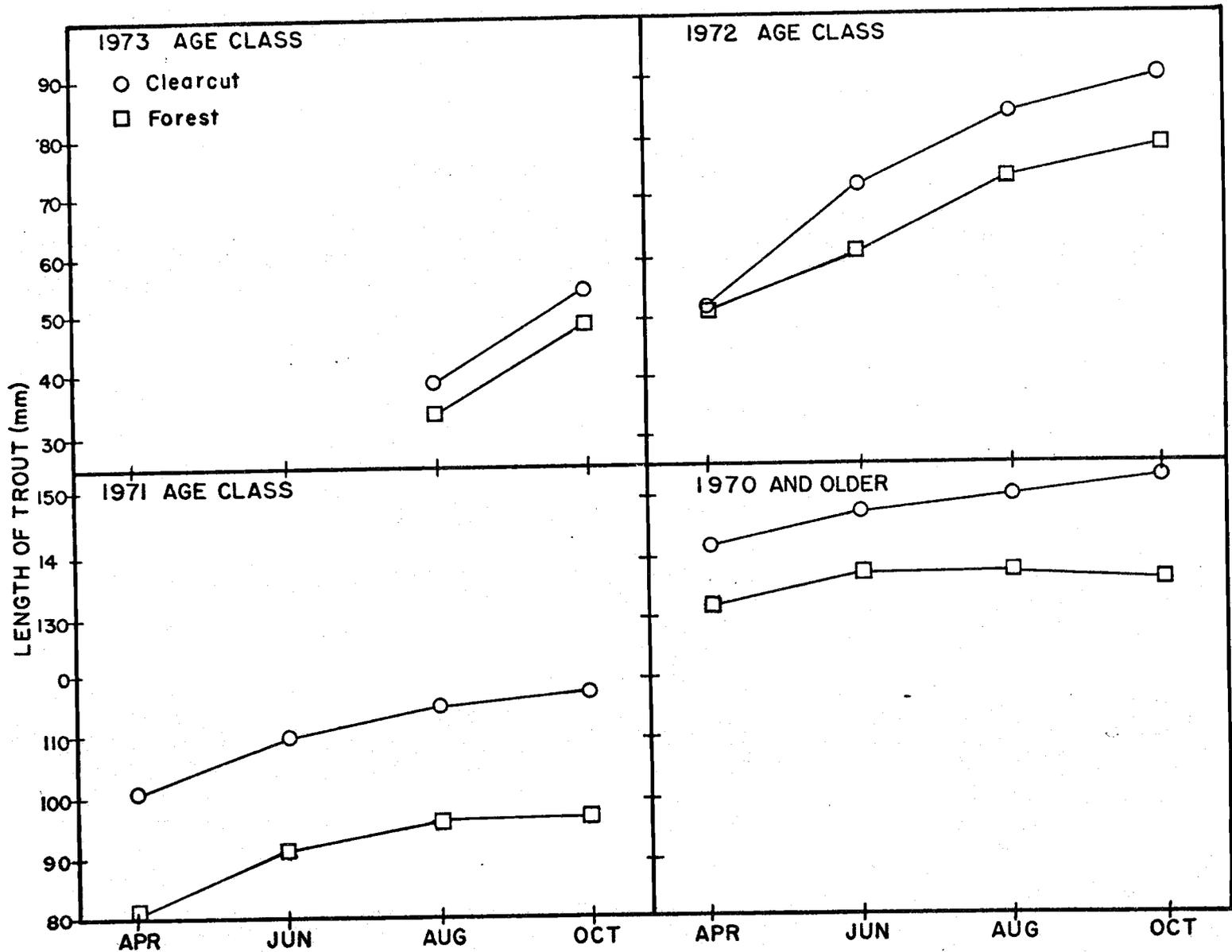


Figure 3.75. Mean length of cutthroat trout by age class in the clear-cut and old-growth forest study areas of Mack Creek.

of scientists at Oregon State University initiated discussion sessions that were primarily concerned with the development of a general conceptual model of small lotic ecosystems. This group consisted of specialists interested in such diverse areas as insect ecology and physiology, fisheries biology, primary production and phycology, the consumption and decomposition of allochthonous organic material, data synthesis, and model development. After a series of meetings that extended through the summer of 1973, the group adopted the following modeling strategy for streams of the Coniferous Forest Biome: (1) The stream model will develop as an expansion of an earlier model of periphyton dynamics which was based on experimental observations from work with laboratory streams; (2) The emphasis of the stream model will be on the total stream subsystem and its couplings with the terrestrial and hydrologic subsystems of the coniferous forest ecosystem; (3) The stream model will be concerned primarily with the major processes and functional groups in lotic systems rather than the dynamics of individual species populations; (4) A Universe-Coupling structure will be used in the construction of the hierarchical, modular system of stream processes; (5) The model of the stream subsystem will be programmed in FLEX, a general model processor patterned after Klir's General Sequential System Paradigm (Klir 1972); (6) The model eventually will be converted to a form compatible with REFLEX, a multi-level, hierarchical model processor capable of mixed resolution; (7) An analysis of model properties and documentation will be conducted concurrently with model development.

A simple and an expanded model of periphyton dynamics in lotic environments were described in a recent publication (McIntire 1973). The simple model included one level variable, the biomass of the periphyton assemblage, and four rate variables: primary production, community respiration, and two export fractions. In the expanded model three level variables and eight rate variables were added to the simple model to introduce the effects of allochthonous organic matter and grazing activities by an aquatic snail. In general, computer output from the expanded model supported the hypothesis that the relatively low biomasses of periphyton observed in the small streams of western Oregon are the result of grazing activities by aquatic animals, high silt loads during the fall and winter months, and the effects of a dense canopy of terrestrial vegetation on light penetration. Moreover, the model indicated that it is bioenergetically feasible for a periphyton biomass of about 10 g/m^2 to support a grazer biomass of 150 g/m^2 or more if the productive capacity of the system is sufficient. This model provided an analytical way of synthesizing the results of a number of experiments with periphyton assemblages in laboratory streams. It also identified weaknesses in the experimental data and provided insights into the dynamics of periphyton assemblages that could not be obtained by intuition alone or by examining the results of individual experiments.

In the fall and winter of 1973, the expanded model of periphyton dynamics was converted to the FLEX form and expanded further to include the conditioning and processing of needle and leaf packs and the process of shredding (i.e., the consumption of needle and leaf detritus by insects). The snail was temporarily retained as a state variable in this model to represent the processes of grazing and collecting, processes involving the consumption of periphyton and fine particulate organic

matter, respectively. Parameter estimations associated with these new components of the model were based on field data obtained by personnel supported by the Biome and on other data from the literature. A complete card file containing a description of each mathematical function and the values and source of each parameter estimate is maintained and updated concurrently with model development. This filing system is compatible with both the FLEX and REFLEX model processing systems.

A study of model behavior in early 1974 stimulated a number of interesting biological questions and provided motivation for some future research activities. The question of whether or not insect populations are limited in size by food was particularly intriguing and will be included as part of the research program next year. Without the inclusion of separate processes of grazing, collecting, and predation, the model channels a considerable amount of energy through the snail population. In contrast, biomasses of other state variables are more realistic relative to natural streams in the Biome. In any case, properties of the present model suggest that we are probably underestimating the export of fine particulate organic matter and other components of the stream biota, particularly at times of high stream flow.

During the rest of 1974, the stream modeling effort will be directed toward the introduction of the grazing, collecting, and predation processes as separate components of the model. In addition, we will refine and make some adjustments in the components of the present version, especially in parts dealing with hydrologic processes and insect respiration.

3.3.2. Land-lake systems at Findley Lake.

Findley Lake is a unique and well-suited area for studying the interactions between forest and lake ecosystems because of the relative simplicity and stable location of the land-lake interface. Within the framework of the Findley Lake program the following questions concerning these interactions have been pursued: (1) What are the internal mechanisms of carbon and nutrient conservation in the watershed? (2) What is the relative importance of detritus versus groundwater pathways of carbon and nutrient transfers with respect to the overall productivity of the lacustrine system? (3) Where are the actual terrestrial-aquatic interface boundaries for the different mineral elements located and what processes control these?

3.3.2.1. General description. Findley Lake is a subalpine lake located in the Cascade Mountains, approximately 60 km east of Seattle, Washington. The lake is at an elevation of 1129 m and, with two smaller ponds, occupies a 250 ha cirque basin drained by Findley Creek, a tributary of the upper Cedar River. Vegetation and soils are shown in Figure 3.76. The vegetation consists mainly of Pacific silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) forests with brush-covered avalanche and active talus slopes. The geologic substrate consists of thick lava flows and boulder conglomerates of the Cougar Mountain Formation covered with several volcanic ash deposits and overlying fractured Snoqualmie granodiorites. The oligotrophic lake covers 9 ha with a maximum depth of 27.5 m and mean depth of 7.8 m. Major bottom types are the debris-covered littoral zone, ooze-covered pelagic zone, and the north-south ridge of mixed deposits

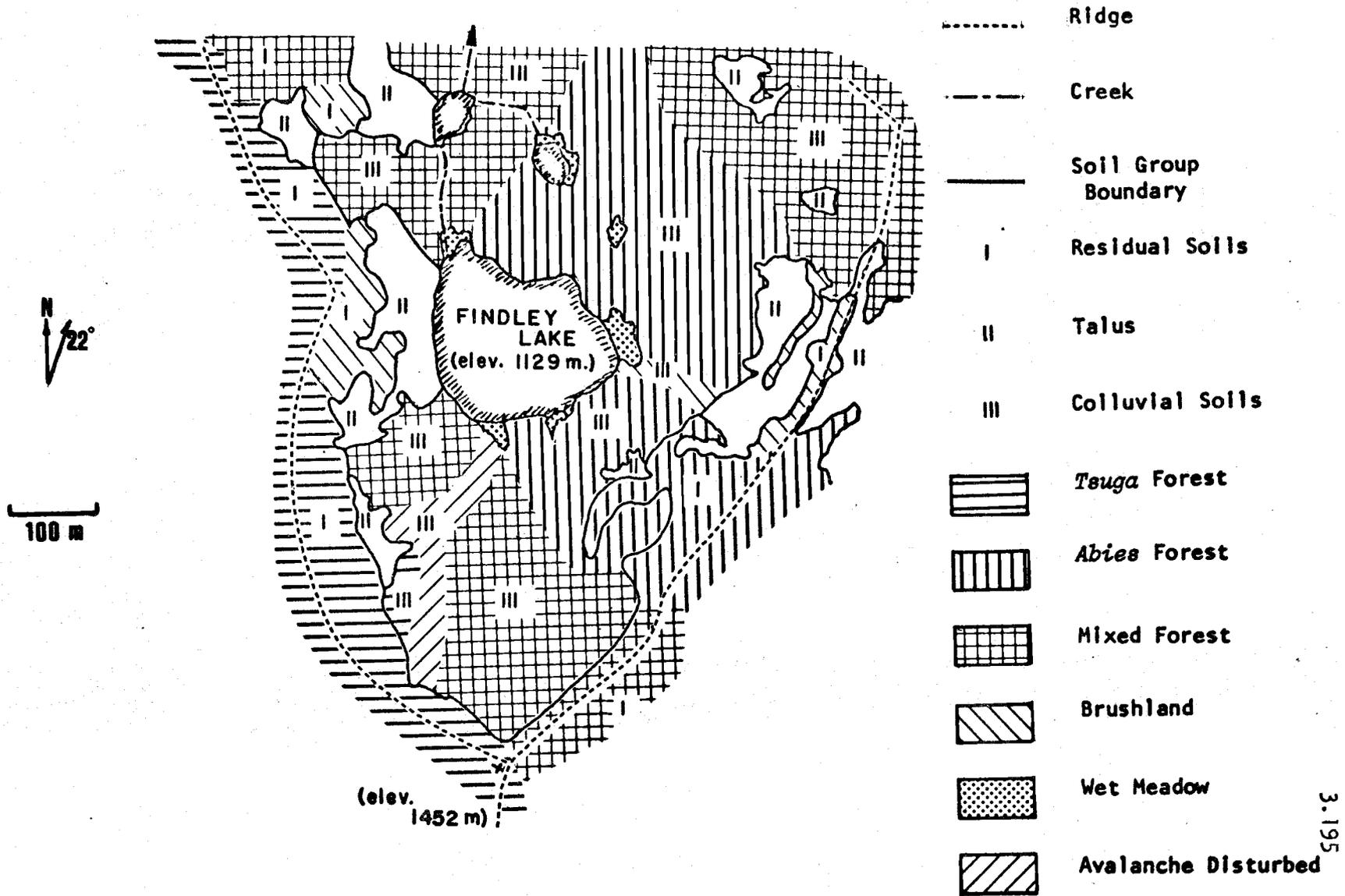


Figure 3.76. Vegetation and soils of the Findley Lake Basin.

through the middle (Figure 3.77). Temperatures of pelagic sediments vary between 4° and 5° C during the year. The lake is snow-covered (up to 7 m thick) for most of the year and has an ice-free season of about 150 days.

3.3.2.2. Terrestrial processes. The major event affecting the land-lake interface appears to be the flushing of accumulated organic debris and dissolved mineral nutrients into the lake with the snowmelt and stream runoff during early summer (Figure 3.78). The more pedestrian transport processes across the interface during the summer-autumn months are litterfall and nutrient dissolution in ground and streamwaters.

Nutrient element dynamics. The earlier vegetation and soil mapping work has been phased into process studies of mineral cycling, ion transport, and soil solution dynamics. D. W. Cole and J. Turner (see section 3.1.2.3 and Figure 3.24) studied the nutrient balance of a Pacific silver fir forest nearby the research station as part of a comparative study focused at the Thompson Research Center. The data primarily indicated a high retention of mineral elements in the thick litter layer, suggesting that slow decomposition is a controlling factor in nutrient conservation. Withdrawal of nutrients from foliage prior to abscission was also noted, which is particularly important with reference to high storage capacity created by a long needle retention time (up to 20 yr). These forest data are used in conjunction with the studies of litterfall into the lake by R. I. Gara and G. Rau as discussed below. D. W. Cole and D. Johnson also collected crownwash and soil solution information on anion contents (carbon and sulfur) for a test of the ion transport theory as developed on the Thompson Research Center. It appears that acid breakdown products from the slow and partial decomposition play an important role.

F. Ugolini, M. Singer, and R. Minden studied the soil solution dynamics at the same location to assess the processes of soil formation, rate of weathering, and critical elemental gradients in the profile. The data established (for the first time) that the podzolization process is operative in this soil (Singer and Ugolini 1973), and that the edaphic cycle (forest-soil) is rather sharply defined by the lower B horizon (Table 3.44). This work, together with the groundwater information from H. Riekerk, raised the question as to how the edaphic cycle is related to the large-scale and long-term geochemical cycle of the watershed.

Hydrology. D. Wooldridge and S. Burges developed the basis for estimates of the hydrological balance of the Findley Lake drainage. The preliminary data indicated that snowmelt had a profound influence on the lake biology (Figure 3.78). Refinements in snow characteristics, groundwater and inlet streamflows, and loss estimates have been identified and are being implemented by more careful documentation.

3.3.2.3. Aquatic processes.

Fate of allochthonous material. Allochthonous inputs from the forest into a 10 m wide littoral zone of the lake by litterfall and streamflow have

Table 3.44. Findley Lake ecosystem average nutrient concentration data (in parts per million).^a

Solution	Total N	Total P	K	Ca	Si	Date	Investigators
Precipitation	0.49	0.01	0.2	0.2	0.2	7 Jun-7 Sep 1973	Singer
Snow							
forested lake	0.23	0.18	0.4	0.2	0.4	20 Mar 1972 2 Mar 1973	Singer Rau
Litterfall							
forested lake	0.30 0.16					4 Oct 1973 4 Oct 1973	Rau Rau
Crownwash	0.22	0.05	0.5	0.3	0.1	7 Jun-7 Sep 1973	Singer
Soil solutions						7 Jun-7 Sep 1973	Singer
litter	0.74	0.04	2.0	1.3	6.6		
A horizon	0.43	0.12	1.2	1.2	5.0		
B2 horizon	0.24	0.05	0.5	0.6	3.2		
B3 horizon	0.25	0.11	0.7	0.6	2.0		
Groundwater	0.23	0.003	0.3	1.7		18 Oct-29 Nov 1973	Riekerk
Springs	0.04	0.004	0.2	1.5		1 Nov-29 Nov 1973	Riekerk
Inflows	0.10	0.008	0.2	2.5	4.2	17 May 1973-17 Jan 1974	Singer, Rau Riekerk
Lake water						7 Jun-13 Aug 1973	Wissmar, et al.
5 m depth	0.10	0.011			1.6		
15 m depth	0.10	0.010			2.2		
25 m depth	0.11	0.014			2.6		
Outflow	0.14	0.008	0.2	2.5	3.1	17 May 1973-17 Jan 1974	Singer, Rau Riekerk
Upper Cedar River	<0.05	<0.01		7.9	4.7	1 Apr-10 Nov 1972	Seattle Water Quality Lab.

^aThese preliminary data have large errors ($\pm 80\%$).

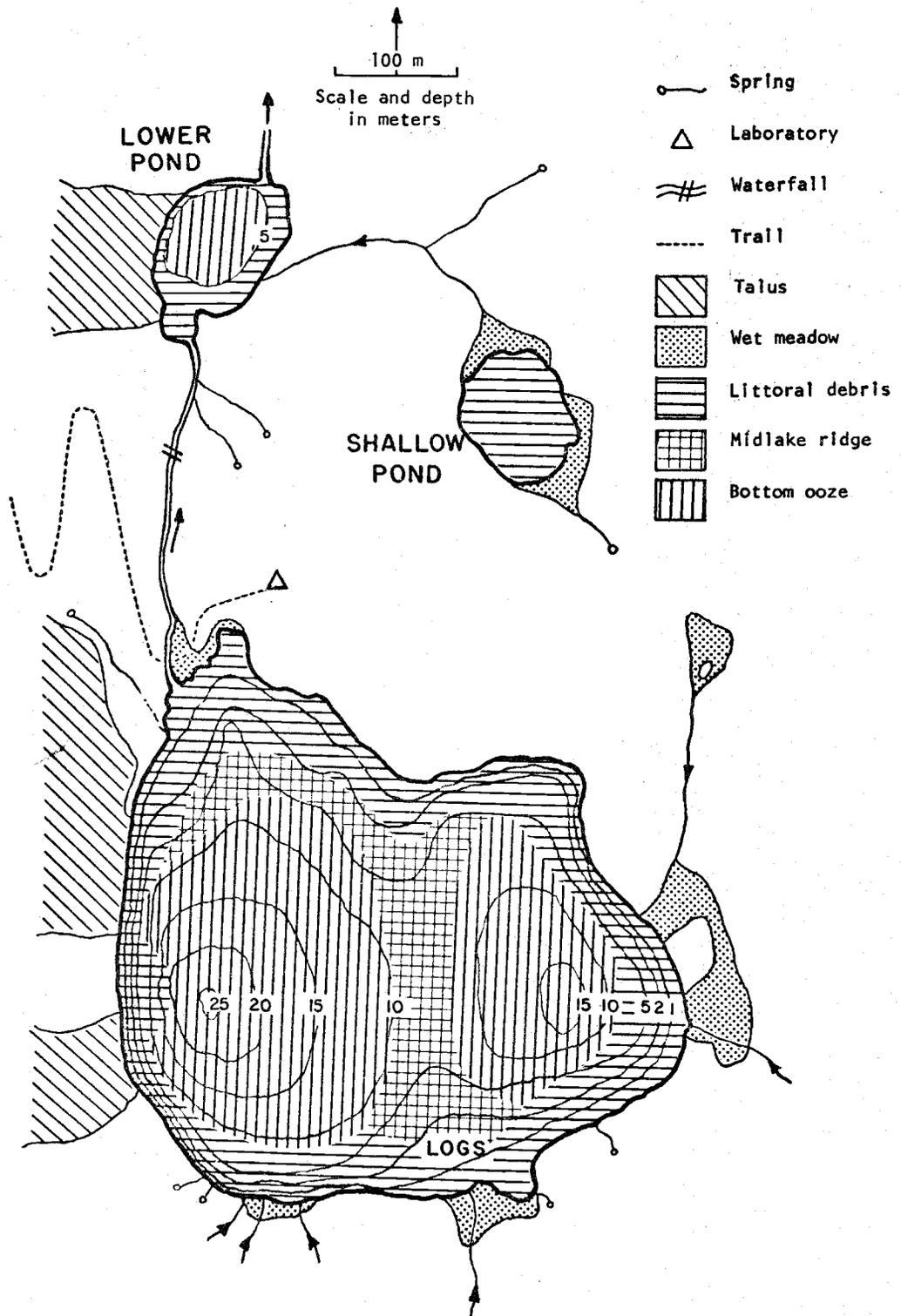


Figure 3.77. Physiographic features and biological zones of Findley Lake.

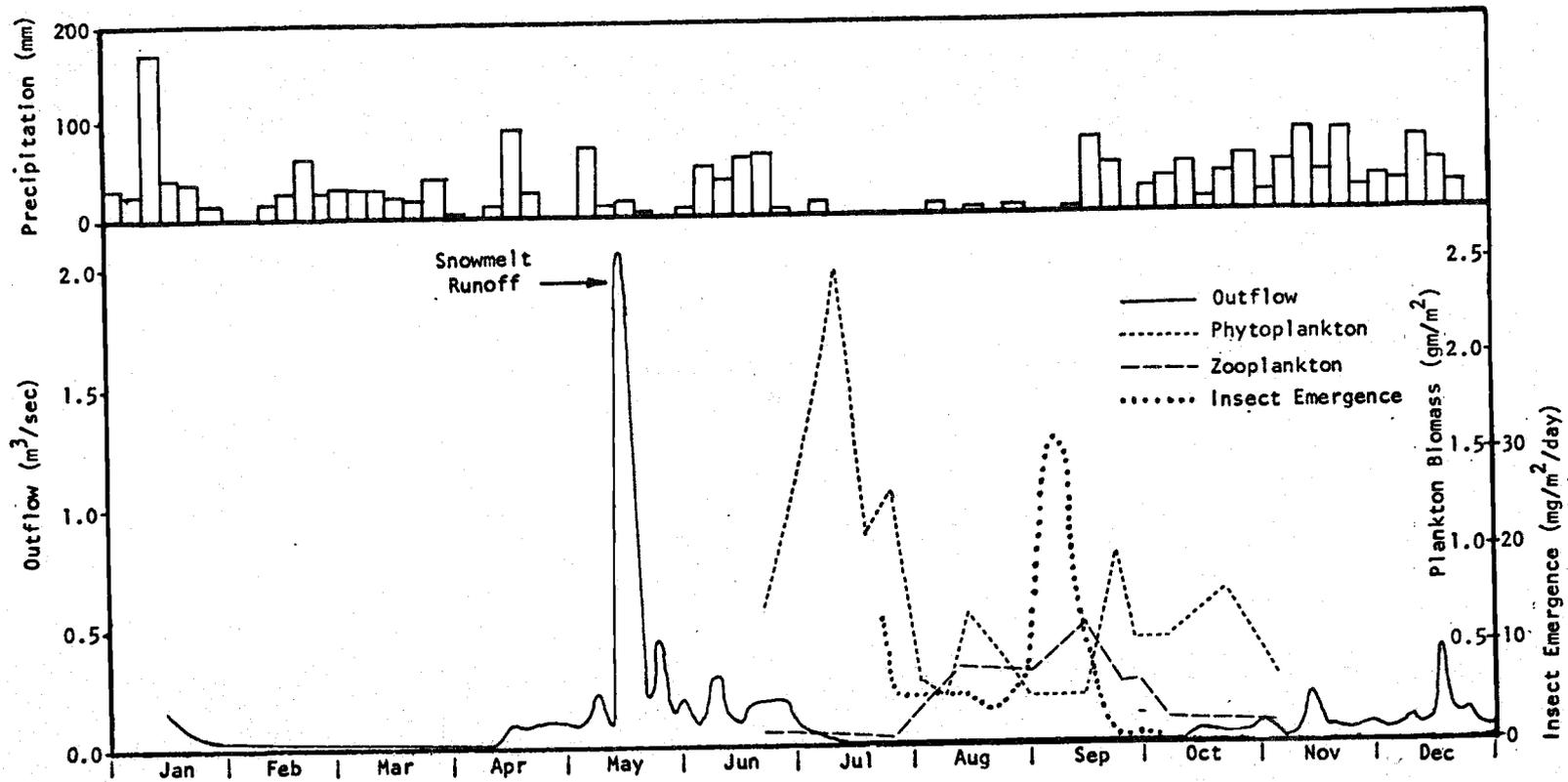


Figure 3.78. Precipitation, lake, outflow, phytoplankton and zooplankton production, and insect emergence at Findley Lake during 1973.

been estimated by R. I. Gara and G. Rau using screens and transects across the interface. The greater part of the litterfall and streamflow detritus entering the lake (42 mg C per m² per day) was in the littoral zone, as compared with 5 mg C per m² per day in the pelagic zone, an average of 7 mg C per m² per day for the total lake. The total input of carbon from these sources over a 150-day ice-free season was 95 kg. The carbon input from snowmelt was estimated at 148 kg, which may be high because of the lack of data on detritus loss from the lake through the outlet stream during snowmelt.

Additional research on the fate of detritus being completed or in progress includes pollen analysis and dating of the lake sediments (M. Tsukada); lake sedimentation rates; allochthonous composition and carbon, nitrogen, and phosphorus content (D. Spyridakis); decomposition (weight loss) and succession of associated invertebrates (J. Matches); mineralization by sediment bacteria (J. Staley); total benthic community metabolism by oxygen uptake experiments (T. Packard and A. Devol); macroinvertebrate (insect) production of benthos (F. Taub); insect processing of detritus (shredding of allochthonous material), (R. Wissmar and R. I. Gara); and insect emergence rates, biomass, and composition (T. Sherk).

Water column and bottom processes. In order to assess the significance of particulate carbon inputs to the nutrient recycling and biological production in Findley Lake it is important to follow the particulate carbon flux through the water column to the sediments. The partitioning of sedimenting particulate carbon into allochthonous and autochthonous carbon forms will be indicative of which carbon forms are available to the benthic community. The availability of particulate carbon and associated nutrients to the benthic community may be dependent upon the amount of particulate carbon received from phytoplankton carbon versus the more refractory terrestrial carbon.

A possible indicator of phytoplankton particulate carbon falling to the bottom can be taken as the difference between particulate carbon collected at the surface and at the bottom of the lake. Comparison of field estimates with simulated phytoplankton carbon lost or sedimented, predicted by the water column carbon model of R. Wissmar and J. Richey indicates that there is considerable agreement between observed and predicted figures. The sediment trap estimates of phytoplankton carbon reaching the bottom indicate 0-15 mg C per m² per day, respectively. Terrestrial carbon sedimented before the snowmelt averaged 5-30 mg C per m² per day, which increased to 200 mg C per m² per day during snowmelt over two to three weeks. Subsequent sedimentation decreased to 10 to 20 mg C per m² per day for the remainder of the summer, with slight increases caused by litterfall, which begins in late summer and continues through the fall. Particulate carbon sediment inputs by stream runoff coincide with snow and icemelt, and increase to greater than 3000 mg C per m² per day at the peak of the snowmelt period. Total sedimentation in the lake for the 150-day ice-free season amounted to 243 kg C from terrestrial sources (allochthonous) and 49 kg C from phytoplankton sources (autochthonous). Of this total 176 kg C was buried, 27 kg C emerged as insects, and 89 kg C was respired by the benthic community.

Particulate carbon and associated nutrients received at the lake surface, mainly in the form of needles, can vary in C:N from 40 to 100 depending upon the age and decomposed state of the materials. Once the terrestrial materials are in the lake the ratio drops to 13 to 15. Sediment C:N ratio of 15 may indicate that, with the above sedimentation rates for Findley Lake and at apparent low levels of sediment mineralization, considerable nitrogen and perhaps carbon may be lost in burial.

As discussed previously, the dominant event affecting the biological water column processes is snowmelt and subsequent increase in light levels and nutrient availability. Phytoplankton biomass immediately increases from 600 to 2400 mg C/m², then drops back to about 400 mg C/m² (Figure 3.78). The average phytoplankton carbon fixation for the total lake was two orders of magnitude greater than that by the periphyton. These estimates compare favorably with Experimental Lakes Area lakes in Canada having similar water chemistry (Schindler 1973). Total carbon in the lake fixed by phytoplankton and periphyton amounted to 491 kg for the 150-day ice-free growing season.

Nutrient concentration increased during the winter through regeneration by zooplankton excretion and decomposition. During snowmelt, with increases in light levels the phytoplankton rapidly increased and nutrients were rapidly depleted. Nitrate decreased from 800 to 150 mg/m² in 20 days, phosphate was depleted from 100 to 0 mg/m² in 40 days, and ammonium from 400 to 0 mg/m² almost immediately. At the time that zooplankton biomass was increasing (maximum of 500 mg C/m² about 60) phosphate and particularly ammonium inventories increased, while nitrate remained low. Curiously, after building to 600 mg/m², ammonium concentrations decreased to about 200 mg/m², while phosphate continued to increase.

To relate the changes in the phytoplankton and zooplankton communities to observed nutrient changes, the following approach was taken (R. Wissmar and J. Richey pers. commun.). The amount of a nutrient present at a time $t + 1$ is a function of the amount of the nutrient present at the previous time (N_t), plus the amount of the nutrient regenerated in that time interval (N_{reg}), minus the amount consumed through photosynthetic and other biological uptake processes (N_{uptake}):

$$N_{t+1} = N_t + N_{reg} - N_{uptake}$$

Assuming initially that uptake is solely via photosynthetic demand, the amount of phosphorus needed is approximately by 0.01 CA and the nitrogen by 0.13 CA where CA is photosynthetic carbon uptake. Initially zooplankton excretion will be assumed to provide the major regeneration mechanism as given by a function of the electron transport system (ETS) respiration (A. Devol and T. Packard, pers. commun.). Solution of equation (1) for phosphate and nitrogen ($NO_3 + NH_4$) was calculated by using field values for the initial conditions and the approximations for uptake and regeneration. Results are given in Figure 3.79.

For both nitrogen and phosphate the observed decline in nutrients during the first month is predicted almost exactly by the model of equation (1).

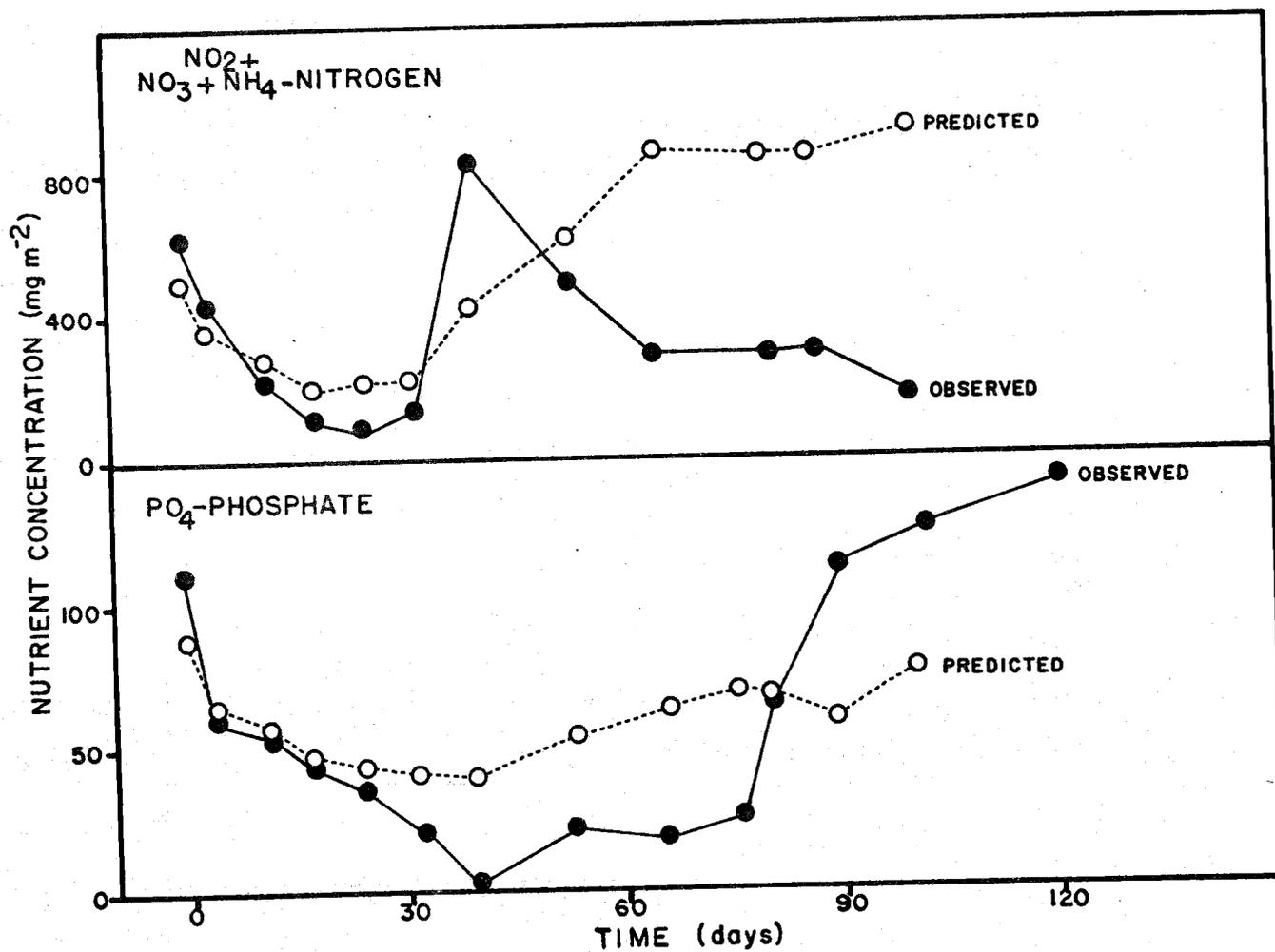


Figure 3.79. Predicted and observed values of nitrogen and phosphate concentrations in Findley Lake after snowmelt in 1973.

This implies that indeed photosynthetic uptake and zooplankton excretion are the major mechanisms affecting nutrient supply. The minimum observed value of phosphate is below the limits of detection of the chemical methods, thus, the error between observed and predicted is not significant.

The increase in phosphate in the latter part of the season is matched in trend but not in magnitude by the predicted model, which implies that another source of phosphate regeneration, perhaps autolysis from dead organisms, is important. In the case of nitrogen, however, the predicted levels were much higher than the observed, and completely missed the downward trend of the observed nitrogen. It appears that a significant uptake mechanism was left out of the model. Nitrification is possible, but no observed increase in NO_3 was observed. Luxury consumption by phytoplankton is possible, but was not observed in the case of phosphate. A likely explanation is immobilization of ambient nitrogen by the bacterial and fungal communities associated with allochthonous needle litter. Further support for this theory is the decrease in the C:N ratio for incoming litter 40-100:1 to 15:1 in the sediments, implying that carbon was lost or nitrogen was gained. Further work must be done to elucidate what the important nitrogen immobilization mechanism might be.

4. MODELING IN THE CONIFEROUS FOREST BIOME OF IBP

The Coniferous Forest Biome's models consist of representations of the structure and function of systems ranging from highly mechanistic models of single processes at a time resolution of minutes (photosynthesis modeling, tree energy balance, ONAR lake model) to less mechanistic stand level, watershed level, and lake and stream level "whole system" models at a time resolution of days and weeks, to long-term succession models at a time step of a year or even 10 years. The orientation in most of these models has been to replicate the flow of various elements through a system by functionally representing the behavior of various flow controlling processes, and their response to environmental changes including both biotic and abiotic elements of the system.

The discussion is organized into several topic areas: (1) organization of modeling resources and personnel, (2) the modeling process, (3) hypothesis testing and an ecosystem theory, and (4) model evaluation.

4.1. Organization of Modeling Resources and Personnel

Modeling, like any other synthetic activity, does not take place in a vacuum. There are several prerequisites needed for a modeling program to be successful. First, a nucleus of modelers is needed to coordinate research, and there must exist a common framework for communication, be it a common jargon, diagram framework, or mathematics. There must be parallel level information exchange; that is, information must flow to all areas where collaboration is extant so that the "wheel is not reinvented," rather than information moving only up the hierarchical chain of command. The modeler and biology team must be sufficiently expert in the areas of biology being studied that they have a good grasp of the relevant literature. Finally, they must use a method of display and documentation of their information that will result in effective peer education and encourage peer review.

A great deal of effort has been spent in 1973 and 1974 toward bringing together a group that makes viable active modeling possible within the Coniferous Forest Biome. New modeling personnel have been added (J. Richey, P. Sollins, G. Swartzman, and J. Rogers), and we now have a total of six modeling personnel. Programmer support has been enlarged from two to three and one-half programmers devoted to modeling activities. Flow and process oriented simulation languages (FLEX and REFLEX, Overton et al. 1973; and SIMCOMP, Hamerly 1973c) are being used to facilitate and broaden the interaction between modelers and the computer, effectively producing more active modelers by simplifying the mechanics of modeling. A series of modeling workshops, some already held and some planned, have brought the previously disparate modeling activities into closer collaboration and coordination. Interaction between Oregon State University and University of Washington modeling personnel has expanded, owing largely to the efforts of the new modeling persons. The group has developed or is developing a rigorous documentation procedure also used in model development, which is adding considerably in transfer of the contents of the models to biologists as well as allowing for direct communication of the model assumptions and equations to researchers

operating on different computers. This documentation technique is a modification of the flow control diagram (Swartzman and Newton 1973) and FLEXFORM (Overton et al. 1973), and is described in section 6.2.

The documentation is used with only minor modifications for publication of the model assumptions and display of results. In the burgeoning literature in ecological modeling there is a general hodgepodge of display formats. We feel that a standard is sorely needed and find our documentation procedure complete, conversational, and simple to follow, although we are open to better alternatives if they are offered.

4.2. The Modeling Process

Separate from the question of personnel and organization of a large-scale modeling effort is the question of how models are built. How are the many-faceted ideas about the system or the processes involved placed in a quantitative, concisely stated framework?

This topic is touched on partly because modeling has been oversold in the past and we want to put into clearer perspective what modeling can and cannot do. First, let us claim that ecological modeling is not like physical modeling, where experiments can be replicated and causal links are well understood. We are trying to represent fairly large ecosystems by breaking them down into convenient parts and developing (usually simple) hypotheses about how these parts interact to produce a reasonable facsimile of the behavior of the whole system. We are dealing with very large and complex systems and it is generally necessary to represent the systems in a simple fashion so that we can understand them.

The first of the representations (or transformations of the real system) is called dimension collapse, which allows examination of the system as a spatial average. This simplification is commonly carried out although real ecosystems may be spatially heterogeneous. Another common dimension collapse is to treat system changes as though they occurred at discrete time intervals rather than continuously. The changes are assumed to occur at an average rate over the time interval. All the models developed within the Coniferous Biome include dimension collapse. For example, the time step chosen for the stand level water-carbon nutrient flow model is variable--daily for water and nutrient flows and weekly for carbon flows. The model treats a spatially heterogeneous coniferous stand as a spatially homogeneous average. The farthest move in our models toward including spatial heterogeneity explicitly is that of dividing a watershed up into three different spatially homogeneous subunits based on position.

All ecological modeling is based on simplification. Recognizing that real ecosystem processes respond to a myriad of environmental parameters, ecological modeling asserts that one can simplify the description of process behavior by representing the response to only the most important factors and still be able to represent the process and indeed to represent a whole system made up of such simplified process representations. Akin to simplification is system definition, in which the biota in the system are broken down into groups, classes, or elements. This corresponds to the choices of state variables in a model. For example, in the insect

population dynamics model, the insect population is broken down into age classes containing individuals assumed to have the same system response properties within each age class. System definition excludes explicit use of experiments performed at a higher level of resolution than that chosen for the model.

Another transformation involves generalization. It results from the fact that equal information is not available about each of the processes within a given system. Since a holistic representation is desired, it is often necessary to extract information about a process from the same process on related systems (e.g., using assumptions about root death in Douglas-fir based on root death information for yellow poplar). Generalization, when judiciously applied, is based on the similarity of behavior of related life forms.

Further system transformation occurs through analogizing. An example is the inference of the behavior of one process from the response of a similar process. In our nutrient cycling model, we infer temperature response of cation exchange in the litter from analogous response relationship noted in the soil.

Also used is resolution shifting, where a particular process behavior is explained by resorting to an understanding of the process at a greater degree of resolution than that represented in the model. For example, information about individual plant physiological response may be used to justify a curve relating photosynthesis to temperature even though the physiological mechanisms are not explicitly stated in the photosynthesis-temperature curve.

Unit standardization is another transformation. Since one must keep track of units, it is preferable to use comparable units for all flows. For example, the unit chosen for waterflow in one model was cubic meters per hectare and carbon flow was in metric tons per hectare. What assumptions are made when transforming units? It is not a simple problem of keeping track of dimensionality, but rather a problem of how to relate carbon to energy or biomass, for example. The ratio of carbon to biomass changes, depending upon where in the system the carbon is and what time of the year it is.

A final transformation is paradigm filtering. In paradigm filtering, the modeler looks not at the system itself but at a picture of the system based on experiments, hypotheses, and literature, which range widely in their information content and relevance. It is probably the haziest transformation and is the most subtle in its effect. It is natural that the information available to a modeling team often depends on the resource personnel accessible to the team. Thus the evidence relating to a given process becomes a function of the past history of research development relevant to that process as well as the ability of the modeling team to relate this information (filter it) to the modeled representation of that process.

For example, the literature on biotic succession has resulted in a multiplicity of hypotheses concerning changes in biotic structure and

function and abiotic structure during succession. The vastness of the literature as well as the paucity of testable hypotheses makes paradigm filtering a difficult task for succession modelers.

The system transformations often appear in the output of the models through model artifacts. They usually manifest as a typical system behavior that can be traced back to a transformation in model development. For example our waterflow models showed large monthly jumps in transpiration because of a monthly factor used in computing potential evapotranspiration.

Naturally the transformations are not conducted independently of the system nor are they often a choice of the modeler. They are often dictated by the size of the system, the time available to work on the model, and information available and obtainable about the system. Needless to say, with greater transformation of the system, we lose resolution of the output. We cannot trace back from the model information lost in making the transformations, since these are not reversible transformations. You cannot relate what you saw (with your eyes) during a half-hour period if your eyes are closed. It is important to recognize that, without transformation, ecosystem modeling would not be feasible at all. Also it is important to understand that many questions cannot be explored with the model because of the transformations on the system.

Our ability to examine these questions falls through the cracks (usually unnoticed) because of the transformations, and that illustrates one of the shortcomings of the approach. This points to the need for developing clear objectives for the model and determining the questions you wish to ask the model to investigate in advance. Planning can then be a payoff between objectives of the modeler and constraints to the model development (time and money limits, lack of information, and so on). It has fallen through the cracks during a modeling transformation.

Given the first alternative, we are left with trying to supply a more accurate hypothesis about a process when very little may be known about the process. We are then trying to reevaluate the function of the process. Under the latter alternative we must return to the planning phases and reexamine the structure of the model. Present-day modeling efforts usually deal with systems that are large and complex and generally models do not represent (adequately) the function of the systems. As our models progress, however, we believe that we will be able to form a body of ecosystem hypotheses.

Our present-day models bring forth hypotheses about individual processes and enable us to examine these processes in a variety of conditions. Whole-system questions can be examined using the model and new experimental programs can be developed to examine the dynamic holistic behavior with respect to these questions.

The hypotheses and structures we have incorporated in our present models are unique to ecosystem modeling and contribute to knowledge about ecosystems. In the stand level water-carbon-nutrient flow models, we have included a labile carbohydrate pool for new leaves and one for the rest of the tree as a structural component. This pool is used as a

regulator to supply growth and respiration demands to plant tissue. This we feel provides a more accurate picture of actual plant response than conceptualizing labile pool as a part of the plant tissue within the various plant parts.

4.3. Hypothesis Testing and Ecosystem Theory

Transformations placed on a system representation (model) to make it tractable may reduce the ability of the model to predict quantitative response under many perturbations of interest. Can we then learn anything new at all about a system from a model? Can we formulate and examine meaningful hypotheses about system behavior and can we move toward formulation of an ecosystem theory using models? The definitive answer to this question (if one exists at all) must wait for the future--we can only speculate at this time.

The first thing of note is that a model actually consists of groups of hypotheses or in some cases axioms about how the processes within a system behave under a variety of environmental conditions. These process oriented hypotheses generally are geared to operation in combination with each other in order to generate whole-system environmental response, and as such cannot be treated as separate units. Nevertheless, there are still modules or subsystems that can be separated out and examined independent of whole-system behavior. It may be asked how well the representation of process behavior may be generalized in a hypothesis in relation to other systems. There has been considerable interchange on the use of various formulations to represent several processes. A good example of such a hypothesis is the response of plant photosynthesis to temperature. Experimental evidence on a variety of natural and cultivated plant species has indicated that photosynthesis response to temperature can be represented as in Figure 4.1. Our models, then, consist of a large group of hypotheses of this type. The hypotheses cannot be validated through the use of the model as they are accepted as the axioms of the model. It may be shown, however, that the axioms lead to counterintuitive behavior of the whole system.

One might think that all that is necessary in developing a whole-ecosystem theory is to find the proper set of ecosystem axioms and the rest will fall into place. The problems are that (1) the whole-system behavior is not easily observable; (2) models are designed to represent not whole systems but specific systems; (3) the way in which the axioms are combined to prove the theorems is not clear (we have no clear deductive rules for ecosystem mathematics as we do for geometry); and (4) the level of resolution to be used for the axioms is not clear.

For example, if a model fails to display reasonable system behavior, one can assume either that some axiom is wrong or that the structure interrelating the axioms is inadequate to bring the proper system interactions into play. If the error is in an axiom, the offender may often be traced; but if it is in the model structure, it cannot be traced using the model itself.

In our nutrient model we are tracing the flow of H^+ , HCO_3^- , and anions (lumped) and cations (lumped) through the litter and soil. To our

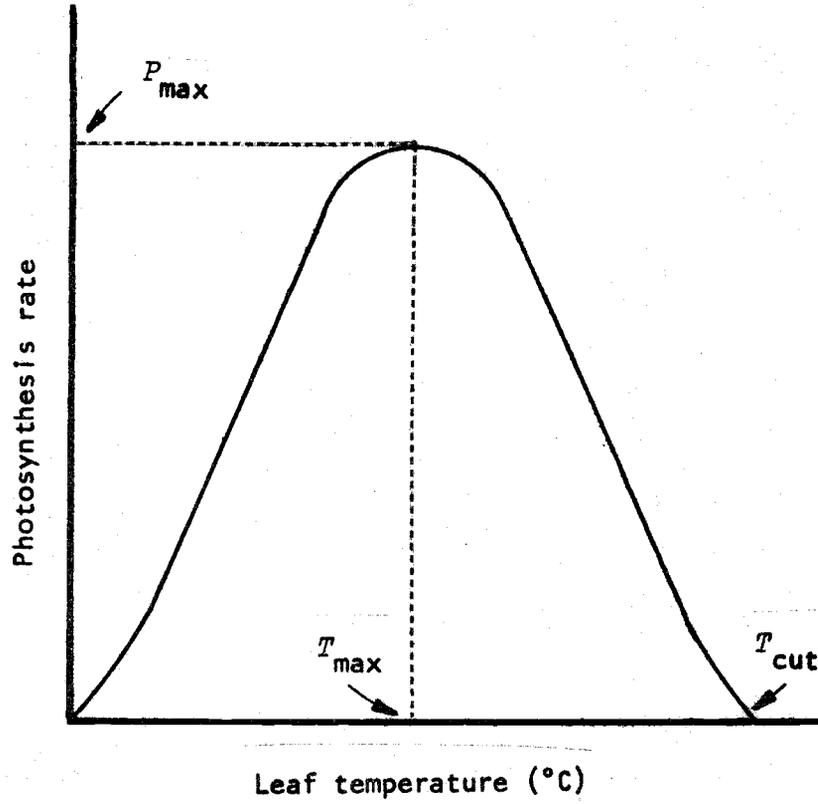


Figure 4.1. Generalized photosynthesis response to leaf temperature.

knowledge this is the most detailed account of soil and plant mineral processes yet attempted and may lead to a series of preliminary hypotheses about the role of minerals in plant growth processes in vivo.

Again, we emphasize the limitations of present models in handling directed questions about the whole system, because of transformations. For example, we know that our present model of carbon, water, and nutrient flow through a mature Douglas-fir dominated stand cannot allow us to examine the effects of clearcutting. This is because all plant growth processes in the model revolve around and depend upon the carbohydrate pool, which would cease to exist when the stand is clearcut. Since reproduction by seeds plays only a minor role in mature stands over a short timespan of one to five years, it was neglected in the formulation of model structure. Thus the filter or transformation removing sexual reproduction results in inability to question the model about the effect of certain important (to man) perturbations.

One model that we see as exceptionally promising for testing and formulating hypotheses about ecosystem behavior is the long-term mechanistic succession model of K. Reed. In this model the niches of most common species in the coniferous zone are defined and the succession scenario is played out as individual trees are established, grow, and die according to their response to the environment. Feedback is introduced as the trees change their environment through their own growth and thereby feed back on their own future survival probability.

Because the model treats individual species and is not tied to a specific site, questions of succession under different environmental conditions can be investigated. Also hypotheses about the long-term alteration of the environment during succession can be investigated. Furthermore, various adaptive strategies for species can be tried out to see whether different species are playing different adaptive strategies, and how strategy change affects a species' chances for survival.

4.4. Model Evaluation

There are five areas where we see that evolution of modeling activities is necessary. These are: (1) Technical. How well structured is the model in terms of its ability mathematically to represent and interrelate the processes comprising the model? How good is the translation of the ideas of the biological researchers to the modelers? How good a grasp of the tools germane to modeling (such as time phasing, curve fitting, parameter activities, computer programming, and the like) did the modelers have? (2) Developmental process. Did the modeling involve and stimulate the persons involved? Was it a medium for mutual education? (3) Display and documentation. Were the model assumptions clearly explained and was it possible for an independent person to replicate the model, given the documentation? (4) Expertise. Did the modeler use the information from experimentation and the literature in model formulation? (5) Usefulness. Did the model prove useful in examining questions about the system and did it stimulate further research in the area?

Evaluation of modeling activity from these standpoints is a difficult if not impossible task. How can we know if all the relevant information has been included? Where does one learn about the modeling process? Who knows whether a model is technically adequate, since almost all model computer programs can be improved in retrospect? Indeed, we are a long way from good evaluation procedures. In some areas all models to date are insufficient. For example, documentation, even when (or perhaps especially when) a computer listing is included, requires hours of hard backtracing to recover the initial assumptions if they are recoverable at all. Sources of information are most poorly documented and these are most important in the consideration of expertise. Much of the lack of progress in moving toward a uniform ecosystem theory may be in the poor evaluation procedure that we presently have in modeling. Mar and Newell (in press), in their report on visits to various sites to conduct modeling under the National Science Foundation's RANN (Research Applied to National Needs), attempted to evaluate some of the less tangible aspects of modeling programs (working conditions, technical ability) and have some interesting ideas, although they are admittedly preliminary in nature.

We did not include validation, or how well a model fits the system behavior (data), an evaluation criterion for a model. This is because it is almost always possible, with the proper manipulation of parameters, to replicate any system behavior desired. It would be better to develop a model that did not replicate system behavior but resulted in some new areas of research in those processes incorrectly understood and in further collaboration among the researchers, than one that "had it all together" and was developed in a vacuum of interaction.

4.5. Improvement of Present Coniferous Modeling Efforts

We must increase collaboration along presently existing networks and we feel that we have enough flexibility in this respect to handle our needs in the years to come. The three areas where the greatest improvement can be expected are in (1) adequate time for planning and coordination of modeling activities with each other and with the field data collection and experimental effort; (2) display, documentation, and publication of model assumptions and results; and (3) more interaction of biologists with the modeling itself through the development at the University of Washington of an interactive, terminal-oriented modeling language analogous to REFLEX developed by the modeling groups at Oregon State University. We feel that REFLEX, developed by Scott and Overton at Oregon State University, offers a powerful tool for modular model development and we will continue with its use there.

Until recently there has been difficulty in coordinating some of the modeling groups with field researchers. The problem has been due partly to lack of sufficient modeling personnel and partly to lack of established collaboration links. The situation is improving with the institution of various working seminars and small working groups of biologists and modelers. The improvement must continue and the initiation of task or problem oriented research should help in that direction by replacing large general discussion meetings with small intensively interacting work cadres.

Data, which supply the cement to modeling work, must continue to be synthesized in the information bank. Work to bring information bank procedures into line with the Ecosystem Analysis Programs' (Biomes') pledge to serve as an archive for ecosystem research should expand in the future, and we hope to hire a person to ensure that the collection continues smoothly at an increased pace.

Plans for 1974 call for the development over the next four months of an interactive ecosystem model oriented simulation language related both to REFLEX (Overton et al. 1973) and to a simulation language developed for population dynamics by R. Rydell (pers. commun.) at Oregon State University. This language will be simple enough that only basic FORTRAN knowledge will be necessary to implement it. Time phasing, input and output formatting, and variable updating all will be provided by the language (as they are by the two languages developed at Oregon State University).

It is important to involve biologists in actual modeling work since they are most familiar with the system behind the model and will never lose track of it in their work. They are free of the stigma that the model can become a system in itself after one has looked at it long enough.

With respect to display and documentation, mention already has been made of the documentation scheme we have developed. We are working toward having a documentation notebook on each model available in our work area in the Center for Quantitative Science at the University of Washington, for information exchange purposes. We hope over the next year to publish these documentation "books" in their entirety as Biome bulletins. In journal articles we will probably have to content ourselves with a complete structural description of the model as well as an outline for the function of the processes and discussion of some of the more interesting relationships along with display of output and discussion of relevance to questions asked about the system (e.g., output under varying perturbations). More speculative parts of the model should be published so that suggestions from peers can be obtained.

We will experiment with graphical display to highlight and clarify discussions about models, and we will attempt sensitivity analysis especially on the more speculative functions so that future research needs can be underlined.

4.6. Ongoing Modeling Activities

Table 4.1 summarizes the modeling activities presently ongoing under US/IBP Coniferous Forest Biome auspices. The table gives information about the modeling personnel mainly responsible for development of the model. While most of these models had many collaborators, especially biologists, an exhaustive list for each model would be too long. The development time gives an idea, when combined with number of flows and state variables, of the magnitude of the task and how far along the model is in its development. The time step for the model gives an idea of the type of data and information to which the model is tied. Simulation language use gives an idea of how our models are implemented to the computer. The data base category gives an idea of how closely tied the various models are to relevant data and information.

Table 4.1. Ongoing modeling activities in the Coniferous Forest Biome

Model name	Principal developer	Develop. time (to date)	State variable flows	Time step	Data bases ^a	Simulation language	Comments
Watershed hydrology	Overton, White	8 man-mo	7/16	day	2, 4	FLEX/REFLEX	Used to test FLEX/REFLEX processor
Carbon-water stand level, WS-10	Sollins Swartzman	4 man-mo	24/48	day/week	2, 3, 4	SIMCOMP/FLEX	Based on previous model
Carbon, H ₂ O, nutrient, Cedar River	Sollins Swartzman	2 man-mo	75/127	day/week	1, 2, 3, 4	SIMCOMP	Based on previous model
Lake dynamics	Richey	5 man-mo	~100-225 ~200-300	hourly/daily	2, 3, 4		Largely data oriented
Fish population dynamics & biomass production	Bartoo	6 man-mo	~50/~150	annual	2		A thesis topic
Insect population dynamics	Rydell, Gara	16 man-days	15/20	biweekly	2, 4	SIM*	*SIM is a special population dynamics oriented simulation language
Stream modeling	McIntire, Colby	3 man-mo	9/20	daily	2, 4	FLEX/REFLEX	
Aquatic phosphorus model	Richey	2 man-yr	9/19	hourly	2, 3, 4	FLEX/SIMCOMP	Ph.D. thesis at Univ. Calif. Davis adapted to Lake Washington.
Stand succession model	Reed, Hamerly	6 man-mo	~400/~800	annual	2, 4		Coordinated with environmental grid program
Photosynthesis model	Reed, Hamerly	7 man-mo	2/4	hourly	2, 3, 4		
Lithnetic fish growth & behavior model	Eggers	2 man-yr	12/36	hourly/ monthly	1, 2, 3, 4		Includes literature search & field collection time; a thesis topic
Regional succession	Hett	1 1/2 man-mo	81/81	10 yearly	2	SIMCOMP	Includes adaptation of SIMCOMP
Fire ecology	Kickert	1/2 man-mo	7/16	daily	4		Based on watershed hydrology model & carbon model
Elk population dynamics & migration	Miller, Hatheway	2 man-mo	14/36	yearly	4		Partly associated with a class project
Physical process tree waterflow model	Hatheway, Winter	2 man-mo	diffusion flow	continuous	2, 4		
Erosion model	Swanston	1 man-mo	12/15				Still in conceptual phase
Leaf resistance model	Farnum	1 man-mo	10/20	continuous	3, 4		Data from lysimeter tree

^aThe four categories used in this table are: (1) process studies (controlled experiments on individual processes), (2) field measurements for validation purposes, (3) parameter estimation from field data on processes under natural field conditions, and (4) literature and hypotheses.

5. BEHAVIOR OF CONIFEROUS ECOSYSTEMS RESULTING FROM MANIPULATIONS AND STRESSES

The major thrust of our past studies has been toward understanding the structure and function of relatively undisturbed coniferous forest ecosystems. One of the objectives of our proposed research in the 1975-1977 period is to understand how the systems we have been studying will behave when perturbed, either by stress, which we have defined as being naturally generated (e.g., a sudden increase in defoliation by insects), or by manipulation, which we define as man generated (e.g., thinning or pollution).

We began only a few perturbation studies in the IBP period but we have been able to gain some insights into system behavior from an experimental and modeling viewpoint. The preliminary results presented below indicate that there is much to be learned about the behavior of perturbed systems, and have enabled us to focus our 1975-1977 efforts on certain key stresses and manipulations that will provide information for the development of ecosystem theory. The information also will be directly available for application to land management problems.

The stresses and manipulations on terrestrial systems considered here are fertilization, harvesting, drought and irrigation, fire, air pollution, erosion, and invertebrate consumers. The effects of water pollution and certain forest manipulations on aquatic systems are considered, as are effects of changing climate. No attempt has been made here to present an exhaustive literature review of these topics; rather, highlights are presented, and relevant literature is used where possible. One aspect that stands out from a survey of the literature is that perturbation studies rarely have been given a holistic approach to ecosystems, but rather have considered only a part (e.g., effects of fertilization on tree growth).

5.1. Fertilization

Fertilization, defined as addition of essential elements to a system, has been studied in the field, in the laboratory, and by model-building. These studies, supplemented with data from the literature, will form the base for fertilizer manipulation research in 1975-1977. Fertilizer application to the coniferous ecosystem is proving to be a very useful tool in learning how the ecosystem functions, as well as increasing ecosystem productivity. The following discussion outlines the progress made in understanding the effect of fertilization on ecosystem functioning.

In contrast to short-rotation agricultural crops, forest fertilization studies are relatively recent and the processes are less well understood. Research in the Northwest was started in the 1950s (Gessel et al. 1951, Walker et al. 1955). Early studies involved both greenhouse work and application of fertilizers in the field, with subsequent measurement of growth as estimated by increase in height, diameter at breast height, and volume. Many current fertilizer research programs involve these same measurements of response (Gessel et al. 1969, Forestry Commission 1972, Atkinson 1973, J. N. Woodman, pers. commun.). In general the

reports demonstrate an increased growth rate following nitrogen application to Northwest conifers; regression analysis is often used to clarify this correlation, since variability is high. Nitrogen is considered to be the principal element limiting Northwest forest growth and the optimum application is 150-300 kg/ha (Gessel et al. 1969).

It has always been difficult to measure growth response to fertilization in a way that minimizes biological variability; thus it is not surprising that scientists evaluating fertilizer responses would look less for variable indicators than increases in height or volume. Current research is focusing on the following indicators of nitrogen deficiency: total foliar nitrogen, foliar amino acid levels, needle length, nitrogen distribution within the foliage, foliar rates of photosynthesis and respiration, and foliar chlorophyll contents. Brackett (1965) reported that Douglas-fir foliar nitrogen percentage increased (from 1.3% to a maximum 1.75% nitrogen) with increasing nitrogen application (200-300 kg/ha is optimal). Similar results were reported by Canadian researchers (Beaton et al. 1964, Lee 1971). Lavender (Lavender and Carmichael 1966, Lavender 1970), however, pointed out that foliar nutrient concentrations vary greatly with foliage age, crown position, time of year, crown class, and elevation. He recommends collections in the late fall from the upper crown. Large increases in amino acid concentration also follow nitrogen fertilization; arginine in particular increases (R. Van den Driessche pers. commun.). Considering arginine's high nitrogen content (four nitrogens/molecule) and its role as a storage nitrogen compound in cellular physiology, this result is expected.

Nitrogen fertilizer increased the photosynthesis rate of new Douglas-fir shoots, but not older shoots, in the first year of treatment (Brix 1971). The difference could be observed only during periods of rapid growth (July-November, March-April), and was less apparent in the second year after treatment. Fertilization increased both total foliar nitrogen and chlorophyll content in new and older foliage, but these results should be used with caution, since the photosynthetic effect was found only in the new shoots.

The previous paragraphs have dealt with fertilization effects on primary production (e.g., growth, foliar nitrogen, photosynthesis). Recent research on forest fertilization has taken another direction--toward understanding fertilization effects on biogeochemical cycling. The role of the soil in tree growth and its interaction during fertilizer manipulations is now recognized (Gessel et al. 1973). An extensive research program on the Thompson site (Cole and Gessel 1968) has been exploring links in the mineral cycle--from the litter through the soil to the plant roots and back again. Little nitrogen is lost by leaching or volatilization (Cole and Gessel 1968, Crane 1972). The Thompson site research also has shown that redistribution of essential elements within the tree plays a major role in the mineral requirements of the foliage (Cole et al. in press b). Thus the Coniferous Biome fertilization research in 1975-1977 can rely on a strong background of soil-fertilizer interaction information.

During 1974 the Coniferous Forest Biome mineral cycling group has begun to develop a nutrient cycling model, adapted from an earlier model

(Sollins et al. in press). Model building has stimulated interdisciplinary cooperation and organization of ideas. The model is now being calibrated against existing data; future manipulation is planned (G. Swartzman, pers. commun.) as the data from the 1975-1977 fertilizer studies become available.

5.2. Clearcutting

The issues that have received most attention with respect to clearcutting of forest ecosystems are (1) effects on water quantity, (2) loss of nutrient elements from the system, (3) effects on stream biology, and (4) erosion.

In 1965, 15.8 ha on the Hubbard Brook Experimental Forest in New Hampshire was completely deforested in an experiment designed primarily to determine the effect of vegetation elimination on water yield (Hornbeck et al. 1970). All trees and woody vegetation were cut and left in place; herbicides were applied over the next three years to prevent regrowth. After this treatment, however, discharge of some nutrients, in particular nitrate-nitrogen and calcium (Bormann and Likens 1970), were found to be high.

Reinhart (1973) has contrasted the Hubbard Brook study with several other studies conducted in east coast forests to determine if the concerns expressed about clearcutting in light of the Hubbard Brook study were correct. He concluded that after clearcutting in New Hampshire forests, losses of nitrogen and calcium may amount to about 2% and 4%, respectively, of the capital available. Nutrient losses following clearcutting in the central and southern Appalachians, however, appear to be negligible. Differences seemed to be related to the nature of podzol soils in New Hampshire. Timber and harvest clearcutting did not result in reduced water quality in any of the studies.

Although initial losses were considerable in the New Hampshire experiments, a study by Marks and Bormann (1972) shows how forest regrowth tends to minimize nutrient losses and promote "a return to steady-state cycling characteristics of a mature forest."

How do these results from eastern forests relate to the effects of clearcutting in western coniferous forests? Leaching in the Douglas-fir region appears to be dominated by the bicarbonate anion (see section 3.1.2.3). Research from our Thompson site indicates that nutrient leaching increased little after clearcutting (Cole and Gessel 1965). This is not surprising since the increased CO₂ production caused by increased decomposition does not result in greatly increased bicarbonate levels. The only way significant losses could occur would be through the addition to the system of mobile anions such as nitrate or sulfate (Gessel et al. 1973). The potential impact of sulfate pollution on coniferous ecosystems is discussed in section 5.5.

Losses from Hubbard Brook were mainly in the anion form of nitrogen (nitrate). Although nitrate can form biologically through the nitrification of ammonia, few instances have been reported of any significant occurrence of this reaction in the temperate forest region (Gessel et

al. 1973). One likely source of these anions in the Hubbard Brook region is air pollution (Fisher et al. 1968).

Although our studies indicate that nutrient losses, particularly nitrogen and phosphorus, are relatively low from forest ecosystems after clearcutting, particularly when revegetation occurs rapidly, concentrations of nitrate and phosphorus in streams may increase 20- to 100-fold for a period of one to three years after clearcutting (Sedell et al. in press). Also, stream temperatures increase after clearcutting and, coupled with nutrient increases, the impact on algal growth and the rates of decomposition of organic debris are quite significant. After clearcutting the stream switches from a detrital to an algal energy base. Even though algae are present at low biomass, turnover ratios (annual production/mean biomass) are high. Very little algae can thus support a large consumer biomass. During logging operations, however, excess debris appears to have diverse effects on fish populations.

The stream biology model being developed in the Coniferous Biome has been used to study further the effects of clearcutting. It has become obvious that any useful model of a stream ecosystem must be coupled with terrestrial models involving carbon, water, and nutrients.

Many questions regarding the impact of clearcutting on the whole coniferous ecosystem, however, remain to be answered. For example, do our observations concerning nutrient losses from clearcuts apply to other regions in the Biome? Reinhart (1973), in his review of old and more recent literature, indicates that soil disturbance and erosion associated with logging have a greater impact than tree cutting by itself. A more detailed account of erosion studies is presented in section 5.6.

Our proposed studies in 1974 and 1975-1977 will continue to investigate questions involved with the behavior of coniferous forest ecosystems when clearcut.

5.3. Drought and Irrigation

L. J. Fritschen, D. R. M. Scott, and R. Walker conducted studies in 1972 and 1973 on the effect of irrigation and drought upon second-growth Douglas-fir. Data were collected on evapotranspiration in relation to soil water potential and the atmospheric evaporative demand. Stomatal resistances and "Scholander bomb" pressures were determined at the same time. During the summer of 1973, a plastic container was built around the lysimeter tree. The plastic bag was opened at the top. Sensors located at the inlet, outlet, and in the plastic container permitted the determination of evapotranspiration under different environmental conditions. The soil moisture content was very low at the start of these studies, then the soil was irrigated. Data were collected while the soil was wet and during the drying processes. Photosynthesis data with stomatal resistances were collected by means of cuvettes inside the container by D. J. Salo, along with "bomb" pressure data. The data are yet not completely analyzed.

Partial analyses of the data concerning transpiration and net assimilation indicate that during the periods of high water stress before irrigation on 6 September, net assimilation and transpiration rates were

much lower than they were following irrigation. These experimental data support results from the photosynthesis simulation model of P. Sollins modified by W. H. Emmingham, which show that photosynthetic capacity is considerably reduced by drought stress in the summer in three locations in Oregon. The implication from these simulations is that summer irrigation would substantially increase net assimilation.

5.4. Fire

The fire ecology project in the Coniferous Forest Biome has focused its work toward analyzing the most important problems of ecologic effects of fire as natural processes in the functioning of coniferous ecosystems. Three interdependent activities have been initiated in this analysis: a question survey, an extensive literature search, and systems modeling.

From contacts made with 411 scientists and land managers from Alaska through New Mexico, a variety of research needs have been disclosed. The perspective is to examine the effects of various quantifiable fire attributes on characteristics of ecosystem structure and function.

FIRE ATTRIBUTES  ECOSYSTEM STRUCTURE & FUNCTION

The feedback processes concerned with the effects of ecosystem structure and function on fire behavior are part of the focus of the Northern Forest Fire Laboratory, USDA Forest Service, which is a cooperating agency in this project effort.

The question survey has revealed greater understanding on this overall problem area in several ways. It has revealed that in conceptualizing system models to study fire effects on ecosystems, the investigator must consider a variety of fire attributes as inputs to the system: transient, transcendental, geometric, and temporal. Transient fire attributes include radiation intensity, temperature gradients, radiation spectral composition, and gradients in smoke concentration. Transcendental attributes include quantity of biomass reduction by species and size class, and the degree of biomass disfiguration, such as charring of stems. Geometric fire attributes include fire density (number of discrete burn areas per unit time), spread rate, burn area size and shape, flame height and width, and burn area location vis-a-vis topography and watershed drainage pattern. Temporal attributes include the natural frequency distribution of reburning of a given ecosystem, and the timing of a fire vis-a-vis the stage in an organism's life cycle or seasonal phenology.

The question survey has also helped to identify the nature of the ecosystem problems characterized by a high demand for better understanding.

At the regional scale for example, a land manager in New Mexico has asked, "What are the long-range effects of many small open parks, being allowed to reseed naturally with spruce, fir, and pine, on ungulate browsers in the food chain?"

At the watershed scale, a scientist in Idaho has asked, "Does a unit watershed have critical areas with respect to fire effects?"

Regarding aquatic ecosystems, a scientist in Alberta, Canada, has asked, "What are the long- and short-term effects of forest fire on the nutrient levels in mountain lakes? Is productivity affected significantly? What changes occur in the planktonic, benthic, and shoreline communities? What changes occur in the input of terrestrial insects that would serve as imported fish-food organisms?"

Fire effects on productivity are emphasized in a typical question from a land manager in Montana, "Is the fuel accretion process in dry forest sites one of diminishing accretion with time or unlimited accretion when fire has been excluded?" and, "Without fire, either wild or prescribed, will the forest slowly choke on its own waste?"

The ecological process of competition in the context of fire is exemplified by a scientist in Arizona: "On sites where Arizona fescue becomes established, ponderosa pine is excluded. Is this a permanent condition? Will the fescue disappear after a length of time, or is it necessary for fire to prepare the site before the pine can reestablish itself? In the Pinus ponderosa--Festuca arizonica association in the Southwest, which is the climax species?"

With regard to food chains and predation in view of fire attributes, most of the questions are directed at the response of the density of a particular animal population in terms of the habitat niche. None of our respondents focused on the trophic niche or hypervolume niche. This gap has made evident the potential importance of the following problem: How does species diversity of dietary preference of carnivores in bird, mammal, insect, and reptile food chains change with fire of different degrees of fuel reduction and area size?

Nutrient cycling--fire relations research needs are typified in the problem posed by a scientist: "How are levels and types of soil microorganisms affected by fire? Does occasional low intensity burning increase soil microbial activity and allow for retention of nutrients in the ecosystem, or are the released nutrients lost to runoff and deep percolation?"

An increase in fire frequency with respect to plant species diversity is emphasized by a scientist in Idaho: "Do repeated burns tend to influence the species composition of the subsequent plant communities in coniferous forested areas as found in north central Idaho?"

A scientist in Montana emphasized a commonly identified succession-fire problem: "What is the adjustment in ecological successional state, in given plant communities, in response to fire of varying intensity and character? In plant communities, which have for eons of time been maintained by fire, what is the probable biological terminus if fire could be indefinitely omitted?"

Another ecological issue related to succession is stability. It was observed that no scientists or land managers identified explicit problems dealing with stability-fire relations. This omission is interpreted as indicating an area of strong importance for further theoretical investigation.

In the process of surveying the literature on the ecological effects of natural fire in coniferous ecosystems, we have implemented a set of computerized literature retrieval programs called FAMULUS, with 3000 citations. Searches through this literature file reveal the proportionate quantities of literature for various aspects of ecosystem structure and function based on our file of 3000: 39 unit watershed response, 10 lake ecosystems, 66 stream ecosystems, 36 fish response, 1379 coniferous forest, 163 shrubland (seral community), 154 grassland (meadows), and 153 deciduous (aspen).

With regard to fire impact at various levels of biological organization, especially ecosystem level, we find the following proportional quantities of literature, out of our file of 3000: ecosystem structure, 53 species diversity, 23 mosaic, 19 zonation, and 9 ecotone; ecosystem function, 431 abiotic response (microclimate, hydrology, soil), 100 nutrients, 266 ecological processes (biomass accumulation, decomposition, competition, succession, stability, disease, dispersion, grazing), 27 population structure, 290 population dynamics, and 151 plant organs.

It is evident that the literature base for this total research area is meager for aquatic system response, terrestrial ecosystem structure, population structure response, and nutrient cycling response. While it is not directly evident from these figures, literature is virtually nonexistent on how terrestrial food chains respond to various fire events. Neither could we uncover any research reports treating the quantitative response of regional-scale ecosystems to variations in fire density or fire frequency.

The Fire Ecology Modeling Workshop, held in Missoula, Montana, during November 1973 assisted in the identification of system model structures for examining the behavior of fire as an ecosystem process. Conceptual and flow chart models were examined and proposed as tools to investigate the following questions: (1) Are forest fires a form of nature's regulation of insect and disease populations? (2) What might be the effect of different snag densities on the bird and rodent populations and consequently the availability of seeds for revegetating the burned area? (3) What are the effects of various temporal and spatial patterns of fires as seen in the spatial distribution of deer, rodent, and bird populations? (4) In stands of various natural fire frequencies, what is likely to be the effect of fire exclusion on the buildup and decomposition of dead organic matter on the forest floor? (5) In semiarid inland forests, are there conditions under which natural forest fires contribute to the stability of stream productivity over the long term?

Modeling activities also have enabled close inspection as to where fire attributes integrate with the structure of waterflow and carbon flow. The Biome's models for these systems have been examined in this light.

Preliminary results indicate that the waterflow model will have to be used in a distributive sense, and will have to be modified to include state variables for water, in addition to carbon, in various biomass compartments, before meaningful fire ecology simulations can be achieved.

5.5. Air Pollution

Although we have not carried out any studies on the direct impact of air pollutants on the biological components of coniferous ecosystems, we have been in a position to examine the effect of pollution-induced acidic rainfall on cation leaching in a Douglas-fir ecosystem (D. W. Johnson, pers. commun.). The emphasis on cation leaching does not indicate that we are disinterested in the serious problem of direct air pollution impact in the Douglas-fir region. Evidence from southern California (Miller 1973) has shown that air pollutants are capable of causing physical damage to trees and can change successional patterns.

Since the Swedish report on air pollution across national boundaries to the 1972 United Nations Conference on the Human Environment (Engstrom et al. 1971), much concern has been expressed over the effects of acid rainfall on both urban and rural areas. There are now several papers available on this subject (Fisher et al. 1968, Hoeft et al. 1972, Johnson and Reynolds 1972, Lazrus et al. 1970).

At the Thompson research site in Seattle's Cedar River watershed the mechanisms of cation leaching in coniferous forest soils have been studied. A detailed discussion of this mechanism was discussed in section 3.1.2.3. Bicarbonate and accompanying hydrogen ions produced as a result of litter decomposition and hydrolysis are the principal leaching agents at the Thompson site. The hydrogen ions displace nutrient ions from the soil exchange sites and these ions, accompanied by bicarbonate ions, are able to leach through the soil. Any anion (such as sulfate) added to the soil potentially can act in a similar way to the bicarbonate ion. Acidic precipitation (principally due to sulfuric acid) has been recorded at the Thompson site for about five years. In 1973 we began to assess the effects of this acid input and its associated anions on the cation leaching in this carbonic acid--dominated system. Both rainfall and tension lysimeter samples were analyzed for the anions sulfate, bicarbonate, and nitrate. Conductivity and pH also were measured.

At this time a full year's data on H^+ and SO_4^{2-} input and movement are not yet available, but it appears that atmospheric sulfate input may account for about one-third of the total yearly cation removal at the Thompson site (Table 5.1). The estimate may be a little high since chloride was not monitored; however, as chloride usually enters the system as a salt (e.g., NaCl rather than HCl) its effects on cation removal from the system are probably not nearly so pronounced as those of SO_4^{2-} and HCO_3^{2-} .

It is not known whether incoming sulfate passes directly through the soil or whether it is taken up and recycled first. In any case Table 5.1 indicates that as much sulfate leaves the system as enters it.

Table 5.1. Total leaching of bicarbonate (HCO_3^-) and sulphate (SO_4^{2-}) from 20 February 1973 to 6 November 1973 at the Thompson site.

Sampling station	Total HCO_3^- (equiv/ha)	Total SO_4^{2-} (equiv/ha)
Precipitation	149	164
Throughfall	195	210
Forest floor	844	396
A horizon	458	196
B horizon (50 cm)	487	186

The sulfate-bicarbonate interaction is complicated. Sulfate and bicarbonate input via precipitation are quite variable throughout the year. In terms of equivalents per hectare, however, sulfate input is rather steady regardless of the amount of rainfall. This suggests a relatively constant concentration of SO_2 or SO_4^{2-} in the atmosphere above this site, perhaps resulting from smelting operations.

Since sulfate input is often associated with low pH values, which suppress bicarbonate formation, it is not surprising that from June through October sulfate and bicarbonate inputs are often inversely correlated. On several occasions, significant inputs of nitrate were noted along with low precipitation pH values; however, the incoming nitrate did not penetrate the forest canopy at all. Perhaps it was taken up by the canopy microorganisms.

Sulfate and bicarbonate leaching (throughfall) in the forest canopy are about equal at all times (Table 5.1). Low pH (<4.0) precipitation is often buffered to a higher pH (75.0) upon leaching, so that HCO_3^- formation is not suppressed. Although sulfate plays an important role in canopy leaching, bicarbonate leaching dominates in the forest floor and soil (Table 5.1) where pH values never fall below 6.

In general it appears that the leaching action of acid rainfall (due to sulfuric acid) takes place in the forest canopy with a small amount of leaching in the forest floor. It is not known what increasing the current amounts of sulfuric acids would do to soil leaching but our evidence indicates that extremely large amounts would be needed before the bicarbonate mechanism ceases to be dominant.

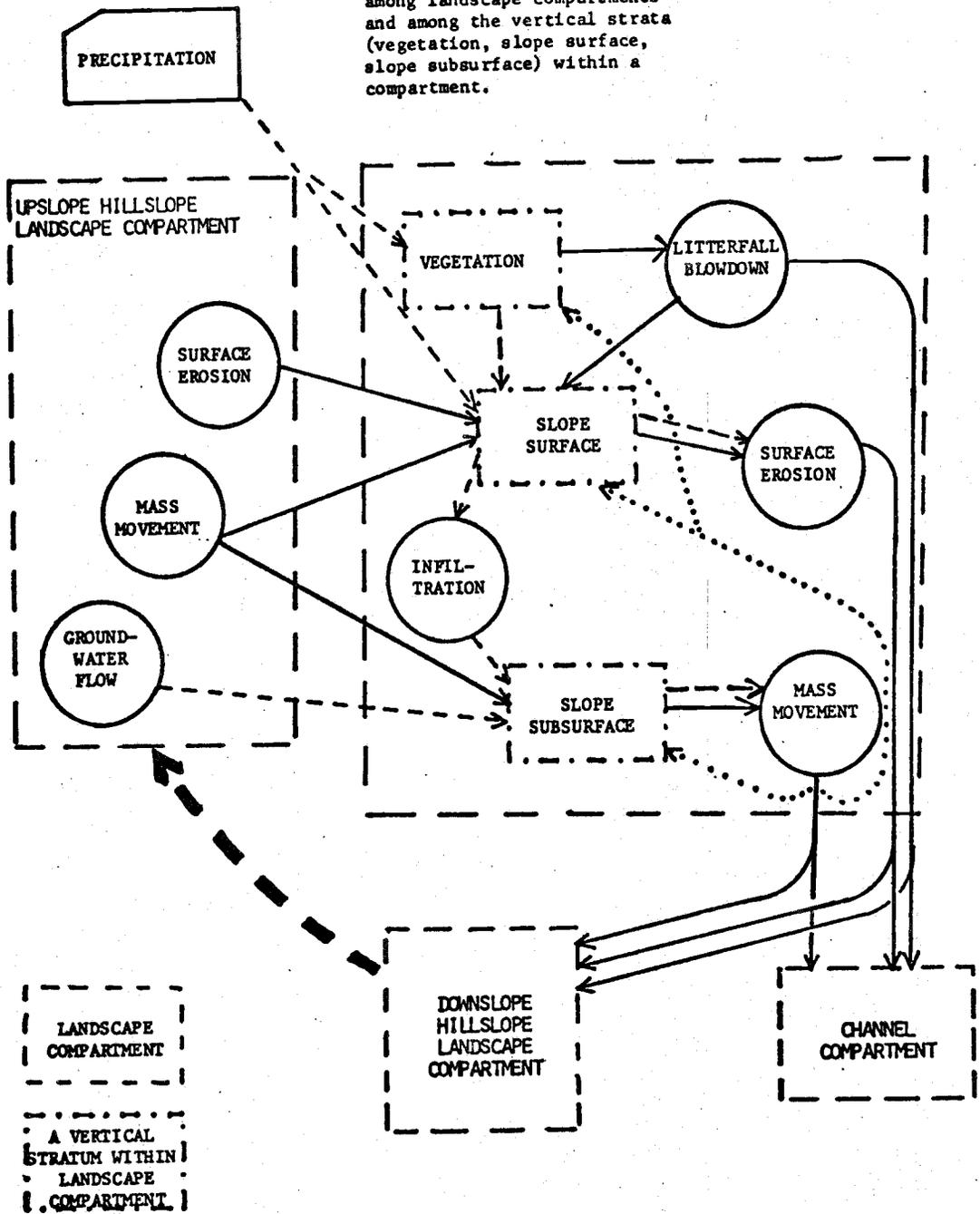
5.6. Erosion

Only recently have studies in the Coniferous Forest Biome been focused on erosion. Scientists interested in nutrient cycling as well as those charged with the management of forested lands are becoming increasingly concerned with gaining a better understanding of long-term consequences of erosion processes. Questions being asked are: What is the magnitude of soil losses due to erosion? How do rates of erosion compare with soil formation rates and how do disturbances such as logging or fire influence long-term erosion rates?

Progress has been made in gaining a rather complete understanding of the actual mechanisms of both surface erosion and mass soil movement; however, we are still unable to predict with an acceptable degree of accuracy long-term erosion rates from forested uplands (Swanson et al. 1974). Scientists in the Coniferous Biome have attempted to devise an erosion model for the Pacific Northwest that takes into account all forms of soil movement and couples these with stream channel dynamics, to investigate the questions of interest. The proposed model, which is conceptualized in Figure 5.1, includes those subsystem models that attempt to describe the three principal classes of sediment transfer, surface processes (rainfall and nonrainfall-caused surface erosion), subsurface processes (mass soil movements), and channel dynamics (storage and transport of mineral and organic debris in stream channels).

Figure 5.1. Erosion model.

Showing essential linkages among landscape compartments and among the vertical strata (vegetation, slope surface, slope subsurface) within a compartment.



INPUT

PROCESS

- > Flow of mineral and organic matter
- - - - -> Flow of water shown only as far as necessary to drive erosion processes
-> Important information feedback

A number of interrelated field research programs are providing the necessary data for the model. Ongoing geology and geomorphology studies in the H. J. Andrews Forest are designed to correlate data on bedrock geology, geomorphology, and shallow soil mass movements during the period of land management (since the early 1950s). The coordinated program of erosion monitoring by R. L. Fredricksen, L. F. Glenn, and D. N. Swanston will yield a better understanding of the relative importance of creep, deep-seated earth flow, and stream channel storage. Similar studies are being initiated by the USDI Geological Survey and USDA Forest Service in a number of sites in California, Oregon, and Washington in order to obtain the overview necessary to apply the erosion model to the diverse geological and geomorphic terrains of the Coniferous Biome region.

The model is being developed in close cooperation with other modeling efforts in the Biome. The hydrology model of J. P. Riley and G. C. Shih will be used to generate waterflow on the surface and in the subsurface and stream channels. Vegetation models, including primary production and succession, will be used to develop estimates of organic sediment supply and to index factors of rooting strength and groundcover. The preliminary conceptualization of the stream channel submodel (Figure 5.2) is presented to stimulate interest and input from related modeling groups, particularly the stream modeling group.

5.7. Invertebrate Consumers

Two types of defoliation models have been used to test hypotheses concerning the effects of insect population on the dynamics of Douglas-fir ecosystems. Linear models have been used to test the effects of climatic factors on triggering outbreaks. These models are the first step in the development of a model for prediction of "high-risk" periods of potential epidemics and would be of great use to forest managers who must make decisions on control alternatives.

A complex relationship exists between defoliators and bark beetles. Defoliation has the effect of weakening host resistance factors to bark beetle attack. In effect much of the total observed mortality from defoliation is in reality associated with bark beetle infestations. Thus the Douglas-fir bark beetle population simulation models now under development will be able to serve as a starting point for the development of further models that can be used to generate hypotheses about defoliator-bark beetle interactions.

We have been able to perform experiments on our stand level carbon-water model to simulate the effect of defoliation on other ecosystem components. An example is shown in Table 5.2. The model indicates that removal of the current year's foliage by insects has little effect on net assimilation or increment (P. Sollins pers. commun.).

5.8. Vertebrate Consumers--Wapiti

The impact of ungulate browsing on forest regeneration has been known for some time. Studies by R. D. Taber have indicated that wapiti on the Cedar River watershed, because of their recent rapid population

Table 5.2. Simulated effect of increased selective consumption of current year foliage by insects^a.

Total Consumption	New foliage		CH ₂ O pool ^a	Buds ^{b,c}	Net assimilation (1 yr)	Increment (stems and roots-1 yr)
	Peak	^c				
0.23 (endemic level)	1.4	1.4	19.0	0.119	21.95	9.8
0.71	1.0	0.85	19.0	0.118	21.89	9.8
1.49 (yearly complete defoliation)	0.5	0.06	18.5	0.117	21.38	9.8

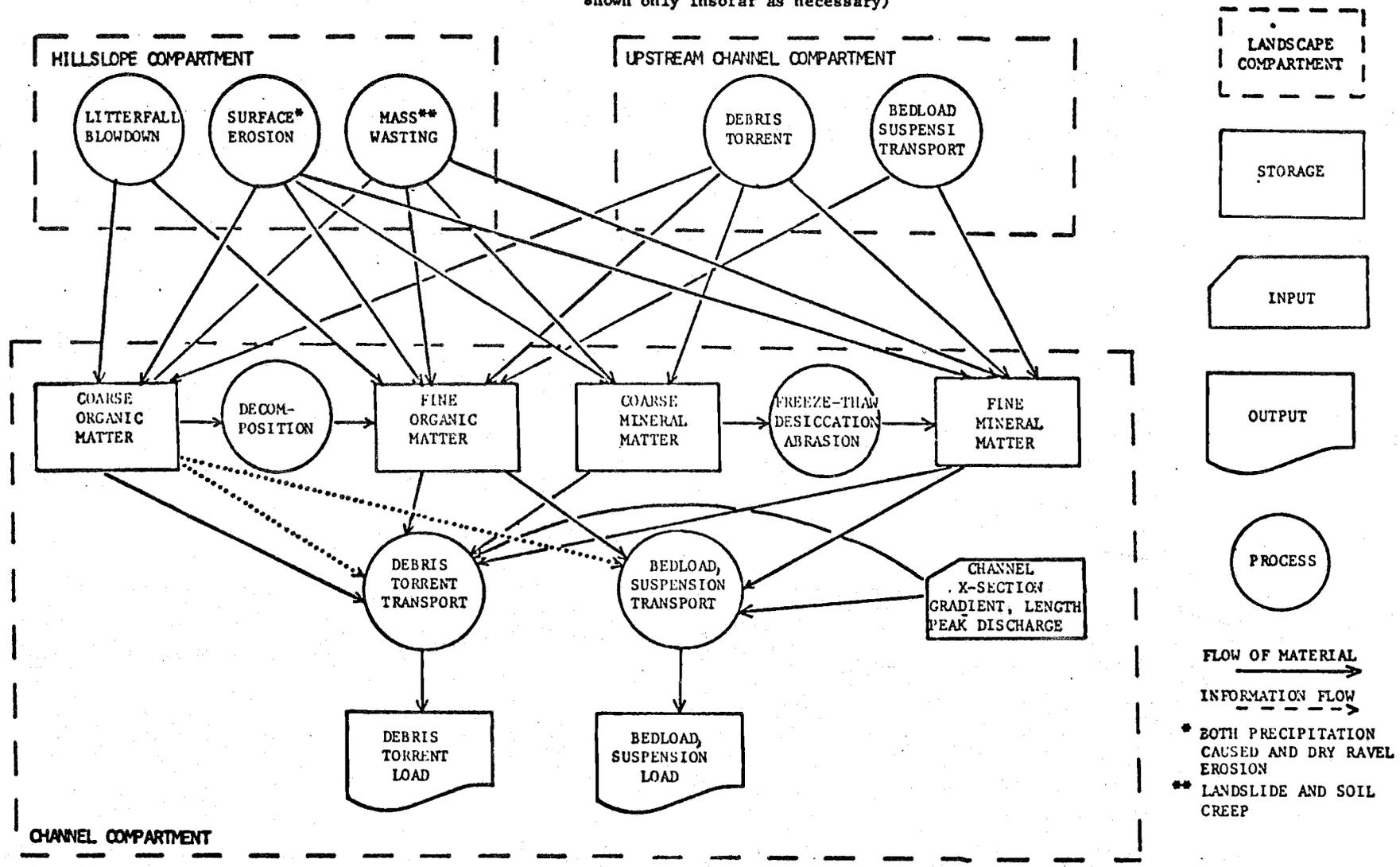
^aAll values are in metric tons carbon per hectare. Parameters, initial conditions, and driving variable values are based primarily on watershed 10, H.J. Andrews Experimental Forest, Oregon.

^bValues provide relative index of bud set, not actual biomass.

^cend of growing season.

Figure 5.2. Stream channel model.

(Detail of input landscape compartment shown only insofar as necessary)



increase, are having an unprecedented impact. Fifteen years ago wapiti were unknown in the Cedar River watershed; in 1973 the population was estimated to be 300. The overall population, however, is not as ecologically significant as the degree of seasonal concentration. It is uncommon for wapiti to concentrate. On the contrary, they are gregarious animals that ordinarily associate in groups.

With limited resources for field investigation, we concentrated first on capturing, handling, radio-marking, and following wapiti, so as to gain an appreciation of their seasonal patterns of landscape use. From such studies, which now have been carried on for about one year, we have discovered that wapiti are highly mobile and their landscape use is highly localized. There is no evidence of significant mortality or egress, and inspection of concentration areas shows heavy use of some plant species and light or no use of others; it also shows soil compaction.

Wapiti, then, are now having an impact on the plant community, and since they are apparently increasing at an as-yet unimpeded rate (approximately 20% per year), it may be expected that they will become more abundant and produce a still greater impact in years to come. (Parenthetically, one recalls the Olympic Rain Forest, where the open aspect of the forest floor is produced largely by wapiti browsing, as can readily be shown by rapid woody growth within an enclosure, and where the only redcedar reproduction occurs on sites beyond reach of wapiti.)

As soon as our initial field data were available for study in October 1973, we established a weekly workshop to develop an integrated modeling effort. This at once produced results: It helped modify the design of field research, and it established the initial mathematical constructs on correct biological bases.

Two avenues of study have resulted from work to date. Wapiti apparently respond to measureable cues in landscape use. If this hypothesis is correct, we should be able to develop a regional wapiti traffic-flow model. The second avenue concerns the ecological impact of wapiti with respect to their population densities, plant populations, and wapiti nutrition. The hypothesis we propose to test is as follows: In the absence of predation, wapiti populations are controlled by nutrient constraints, but not before significant impacts have been made on plant productivity and populations.

Such studies would provide information for the development of a managerial decision model in which wapiti density and environmental impact are integrated.

5.9. Response of Carbon-Water Model to Changes in Climate

As part of the climatic impact assessment program of the U.S. Department of Transportation, we investigated the behavior of the current version of the coupled carbon-water model to changes in mean annual temperature, total precipitation, and solar radiation. Results were compared with

measured growth response of Douglas-fir in the Oregon Coast Range and analyzed by H. J. Fritts and T. J. Blasing of the University of Arizona (pers. commun.). Fritts and Blasing found little response of Douglas-fir to changes in light and precipitation but a substantial increase in growth with a decrease in summer temperature. Increases in winter temperature, however, increased annual growth.

Simulation results in general agreed with measured responses. Changes in precipitation and light had little effect on model behavior. A decrease in temperature evenly distributed throughout the year caused a substantial increase in carbohydrate reserves, which undoubtedly would lead to increased growth if the simulations were continued for several years. Photosynthesis increased and leaf respiration decreased. Respiration decreases sharply with temperature and is, in this version of the model, unaffected by moisture relations. Photosynthesis of Douglas-fir, according to our recent cuvette field results, is relatively unaffected by either light or temperature over the range typically encountered during early and late summer, but is strongly affected by plant water status. The decrease in temperature caused a substantial decrease in transpiration and evaporation and thus increased rooting zone moisture content. This in turn decreased stomatal resistance during a critical part of the growing season, increasing photosynthesis.

We plan to examine effects of summer versus winter changes in temperature to further check model behavior against observed responses and to obtain growth data for other stands against which model behavior may be compared.

5.10. Water Pollution

Nutrient loading studies by the Coniferous Biome indicate that mesotrophic Lake Sammamish has not responded significantly in five years following diversion of about one-third of its phosphorus income. In contrast, nearby Lake Washington responded rapidly to diversion with decreases in phytoplankton biomass in proportion to decreases in phosphorus income and winter phosphorus concentrations. A supposition that may explain the slow response of Lake Sammamish is the phosphorus income change that occurred on the asymptote portion of a response curve, which allows for less lake response (change in phytoplankton biomass) for a given increase in phosphorus income that was observed in Lake Washington. The internal mechanism that possibly controls the phosphorus content available to spring algal blooms is high iron concentrations released from sediments into an anaerobic hypolimnion. The iron then complexes and removes phosphorus by sedimentation before it is available to the phytoplankton. Control of water column total phosphorus concentrations in Lake Sammamish by nutrient exchange with sediments was supported by a general model predicting phosphorus response to income change (Welch and Spyridakis 1972). If the sediment exchange rate were held constant and sedimentation were permitted to vary with phosphorus levels, then only 7% reduction in phosphorus would be predicted in 1.4 years. This change apparently is not detectable within annual differences in phosphorus income, and supports the hypothesis of nutrient control by sediments in the range of phosphorus income studied. It is hypothesized that if the

phosphorus income rate were increased, the binding capacity of high ambient iron concentrations would be overcome and an increased rate of response would occur. This level could be near the two- or threefold increase that Lake Sammamish would now be receiving if diversion had not taken place.

1

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