CONIFEROUS FOREST BIOME

Progress Report

July 1974 - August 1975

Edited by

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Coniferous Forest Biome
College of Forest Resources
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1. INTRODUCTION

This summary of Coniferous Forest Biome research results for the period July 1974 to August 1975 is organized around a new framework which was adopted in August 1974 as a result of a program review by the National Science Foundation.

The Coniferous Forest Biome Program was fully funded as a segment of the U.S./International Biological Program (US/IBP) in 1972. Although the IBP was terminated on 30 June 1974, the Coniferous Forest Biome will continue to operate until 31 December 1977. Parts of the program are being considered for separate funding after that date so that the ecosystem analysis approach developed by the Biome can be continued.

The Biome central office remains located at the College of Forest Resources, University of Washington, Seattle, and a second office is located at the Forest Research Laboratory, Oregon State University, Corvallis. Initially scientists from many universities and government laboratories in nine states were involved but as the program nears termination, the number of people and institutions associated with the program has dropped.

2. OBJECTIVES OF CONIFEROUS FOREST BIOME RESEARCH

The specific objectives of the program are: (1) To understand the relative behavior of terrestrial and aquatic ecosystems in various environments in the biome. (2) To develop conceptual and computer simulation models that describe nutrient, carbon, and waterflows on a short-term basis (fewer than ten years) and which integrate research results and increase our understanding of coniferous forests and associated aquatic ecosystems. These models are being developed at the process, forest stand or water column, and watershed levels. (3) To develop conceptual and computer simulation models that describe the long-term behavior of coniferous forest ecosystems involving succession and erosion. (4) To understand the linkages between terrestrial and aquatic ecosystems. (5) To determine the effect of manipulations, such as clearcutting, fertilization, and defoliation on terrestrial and aquatic ecosystems.

3. HIGHLIGHTS OF RESEARCH PROGRAM ACCOMPLISHMENTS JULY 1974-AUGUST 1975

3.1 Research Sites

Ecosystem research efforts continued to be concentrated on two intensive sites; the Cedar River-Lake Washington drainage basin in Washington and the H. J. Andrews Experimental Forest in Oregon. Both sites are located in the Cascade Mountains. Data were also gathered from other sites in Washington, Oregon, Alaska, Montana, Idaho, Colorado, California, Arizona, and Utah. Studies at these sites involved key processes, such as photosynthesis and decomposition, and they enabled us to increase the time and space dimensions of our data base.

The H. J. Andrews Forest, administered by the USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, is a 6080 ha drainage, ranging in elevation from 460 to 1615 m, located near Blue River, Oregon, east of Eugene. Work on the Andrews Forest has focused on hydrologic and nutrient cycles in unit watersheds and has been concerned with the mature old-growth Douglas-fir-western hemlock stands that dominate the Forest. The eight gaged watersheds on the Forest range in size from 10 to 100 ha and provide excellent areas on which to carry out manipulation studies. Considerable effort has been focused on watershed no. 10 which was clearcut in summer 1975. Extensive data on climate, soils, geology, flora, plant communities, mammals, gound-feeding birds, hydrology, and stream biology are available from past and current studies. Considerable attention has been focused on the interface between stream and land ecosystems.

The Cedar River-Lake Washington drainage basin located just east of Seattle, Washington, is composed of two distinct subdrainages: the Sammamish valley which includes Lake Sammamish, and the Cedar River valley which includes Findley Lake at 1070 m elevation and a large reservoir system (Chester Morse Lake) at 475 m. Both valleys drain into Lake Washington. All of the Cedar River watershed above 185 m is part of the municipal water supply for the City of Seattle which is carefully protected and has limited access.

Detailed studies of terrestrial processes including transfers of carbon, nutrients and water between compartments of the forest ecosystem have been conducted at the A. E. Thompson Research Center which is within the extensive areas of young second-growth Douglas-fir forests that occupy the lower elevations of the watershed. Findley Lake is the primary site for interface research on the transfer of carbon, nutrients, and water from the land to the lake. These studies are complemented by sedimentation and decomposition measurements in the lake.

Aquatic studies have focused on the processes controlling succession in lakes of varying nutrient status. Washington, Sammamish, and Findley Lakes are the principal lakes being studied.

3.2 Research Highlights

Coniferous Forest Biome research is organized for the 1975-1977 period around three major themes: (a) Analysis of Individual Terrestrial Ecosystems, (b) Analysis of Watersheds, and (c) Analysis of Aquatic Ecosystems as shown in Figure 1. Each theme is further divided into major research areas and the linkages between themes and major research areas are also shown in Figure 1. Particular note should be made of the linkages between terrestrial and aquatic themes.

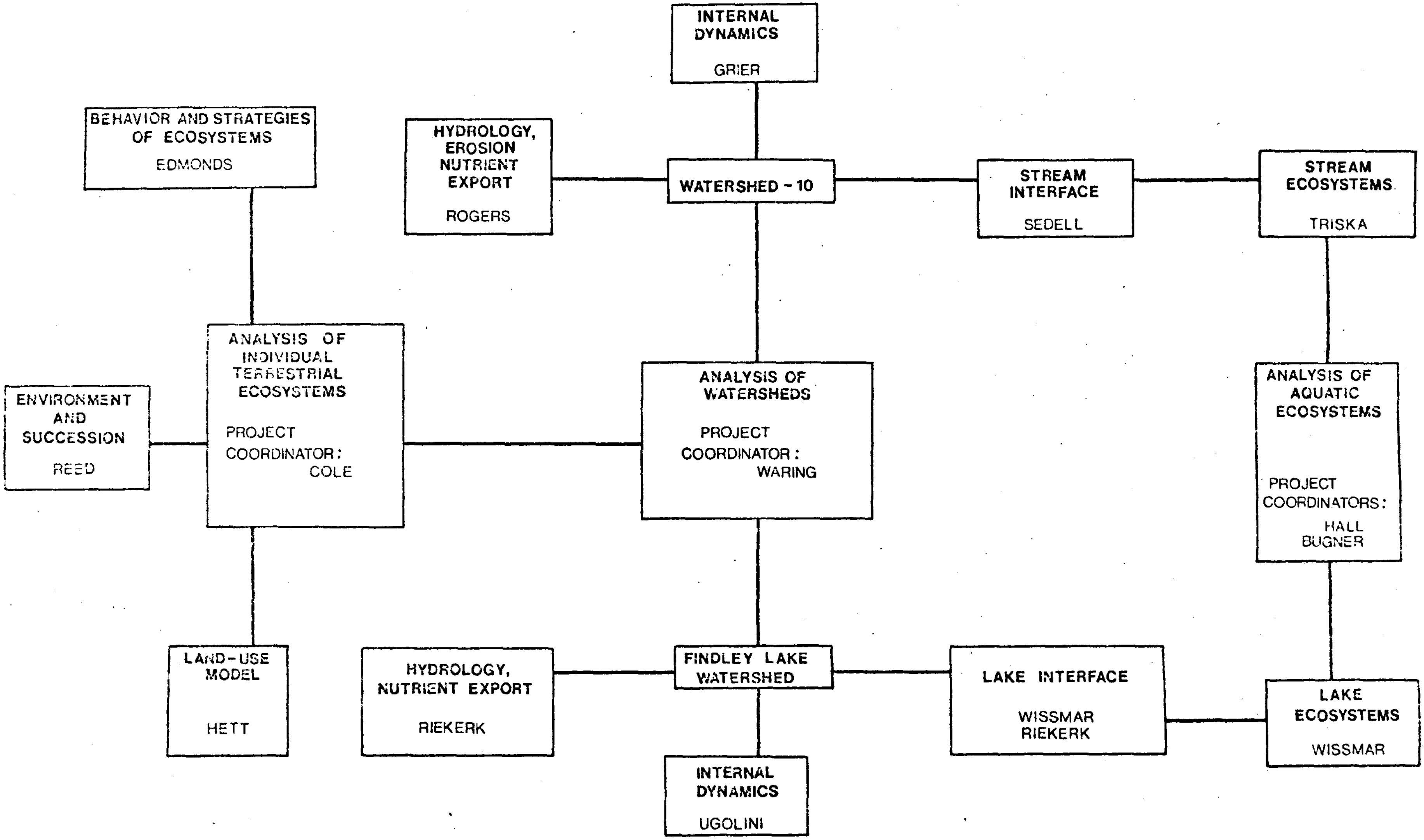

Figure 1. Coniferous Forest Biome organization 1975-77.

Publications resulting from each research area in the period July 1974 to August 1975 are presented in the Appendices.

3.2.1 Analysis of Individual Terrestrial Ecosystems

This theme which is coordinated by Dale Cole is divided into three major research areas: (a) behavior and strategies of individual ecosystems, (b) succession and, (c) the land use model. Figure 2 shows the individual projects on this component, principal investigators, and research coordinators.

3.2.1.1 Behavior and strategies of ecosystems.

This research area which is coordinated by Robert Edmonds has the following objectives:

(1) To examine the behavior of old-growth and young-growth Douglas-fir ecosystems through the use of the carbon, water, and nutrient cycling model.

(2) To fill in research gaps needed for the model.

(3) To examine the strategies of individual ecosystems particularly with respect to carbon and nutrient cycling as a function of succession and changing environment.

Progress reports for individual projects in Figure 2 follow. Publications resulting from this research are presented in Appendix I.

Decomposition. Decomposition studies involving litter bags were set up in a series of stands in Oregon by Kermit Cromack and in Washington by Robert Edmonds in order to examine decomposition and nutrient availability as functions of changing environment and succession. Decomposition of needles, leaves, twigs, cones, and large woody material is being studied.

A significant environmental trend in rate of Douglas-fir needle decomposition has been established for the following site series in Oregon: Cascade Head (coastal site), Bull Run, H. J. Andrews, Coyote Creek (north to south, mesic to dry stands in the western Cascades), and Pringle Butte (dry site east of Cascades). Highest decomposition rates were obtained at Cascade Head and Bull Run, both mesic sites, while lowest decomposition rate was at the driest and coldest site, Pringle Butte (Table 1). Percent decomposition (weight loss) ranged from 39.2 to 22.6 after 300 days. One critical factor for microbial decomposition is the presence or absence of summer moisture during the time of year when temperature is optimal for decomposition. Generally, it is the combination of temperature and moisture rather than total precipitation that relates more meaningfully to decomposition.

Comparative stand level sclerophyll indices based upon foliage N, P, and structural C constituents have been completed. The vegetation in the Coniferous Forest region is generally sclerophyllous in nature in the majority of overstory and understory species. An interesting new finding

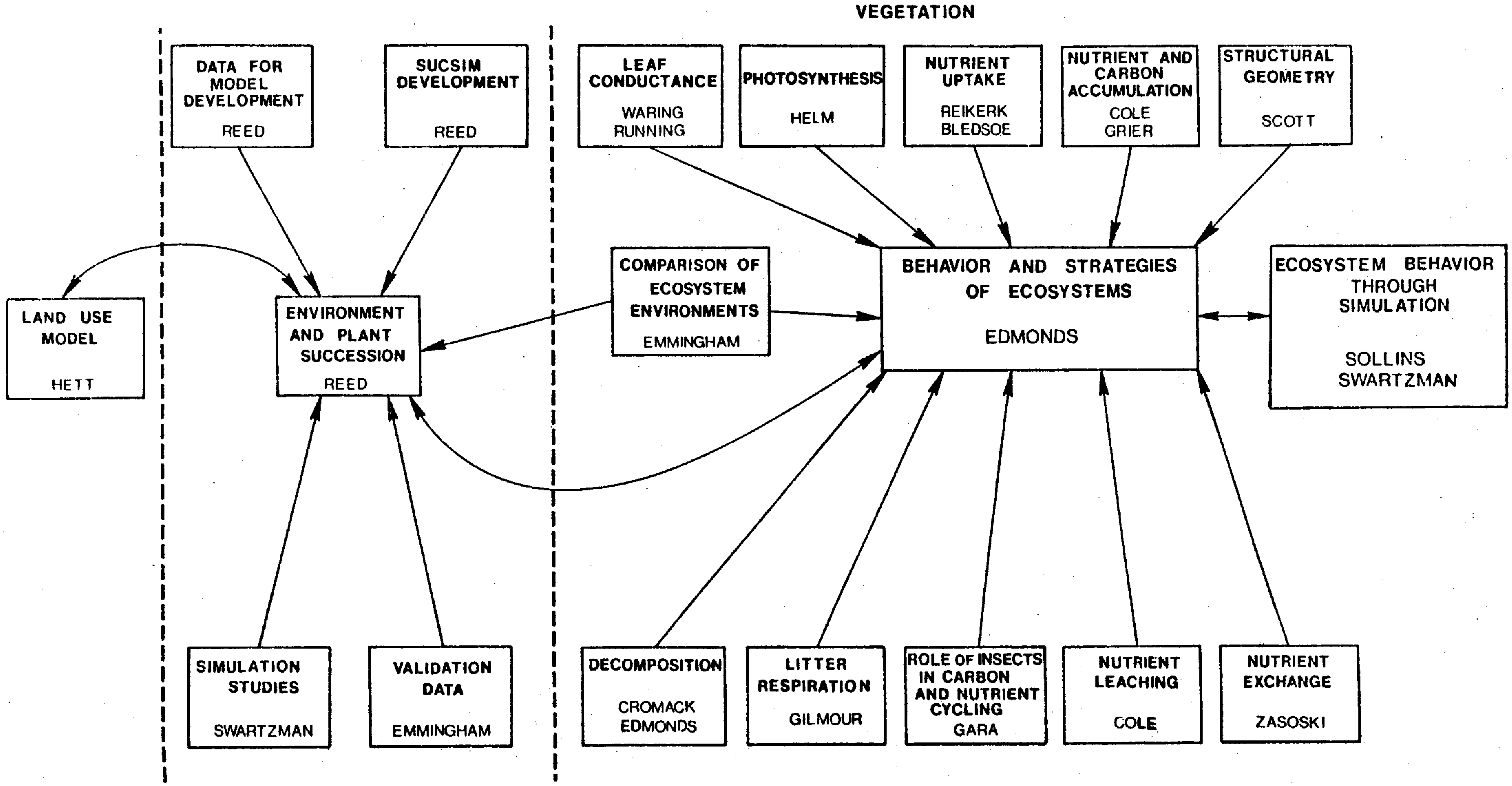

Figure 2. Research organization and projects in the analysis of individual ecosystem component.

Table 1. Douglas-fir needle decomposition: Oregon climatic grid.

Location	Annual rainfall (cm)	January temp. (°C)	Summer litter moisture	Percent decomposition--weight loss (300 days)
Coastal site - Cascade head	149	6	moist	39.2
Northern Cascades Bull Run	304	2	moist	33.9
Mid-Cascades H. J. Andrews - high elevation	250	0 (snowpack)	dry	30.0
Southern Cascades - Coyote Creek	79	2	dry	28.4
Eastern plateau - Pringle Butte	31	-0.5 (cold, dry)	dry	22.6

is that nitrogen fixing species such as red alder, Ceanothus, Lotus, and bitterbrush do not fit the typical sclerophyll model. Nitrogen fixation studies in wood are in progress in combination with the stream ecology group.

In 1976 comparative stand decomposition studies on an environmental grid basis will be completed. Information will be compiled to enable examination of the hypotheses that (1) foliage litter of late successional stages is less decomposable, and (2) nitrogen-fixation is a significant long-term process in biodegradation of wood residues. Table 2 shows some preliminary results for foliage decomposition of representative species on the Oregon environmental grid. Alder decomposed at the fastest rate, 59.6% weight loss after 300 days and Ponderosa pine had the slowest, 15.0%.

In Washington decomposition studies have been initiated in the Cedar River watershed in a 43-year-old alder, in a 70-year-old western hemlock, and a 175-year-old Pacific silver fir ecosystem and in a successional series of Douglas-fir stands which are 9, 22, 35, 43, 73, and 95 years old. Litter moisture and air temperature are being monitored in each of these stands in order to relate decomposition rates to these environmental variables. A greater rate of decomposition after 220 days was found in the alder ecosystem (42% weight loss) with a slower rate in the Douglas-fir ecosystem (33%). Slowest rates were found in the western hemlock ecosystem (28%). Decomposition under snow in the Pacific silver fir ecosystem was considerably faster than expected (31% weight loss after 280 days) and was equivalent to that in Douglas-fir ecosystems at lower altitudes. Presence of a winter snowpack can compensate for low air temperatures, and may be an important factor for nutrient cycling and productivity at high altitude sites.

Decomposition in the age sequence of Douglas-fir stands reached a maximum in the 22-year-old stand (28% weight loss after 180 days) and tended to fall off a little in the older stands (24% in the 95-year-old stand). This was further supported by CO_2 evolution data from the forest floor. Age 22-30 would appear to be an important point in time for these Douglas-fir stands for at this stage the trees start to internally recycle more nitrogen and require less from the forest floor and soil. Also canopy closure occurs at this time.

It is proposed to investigate in 1976 the role of fungi in nutrient release in the forest floor as a function of succession and changing chemical and physical environments.

Litter respiration. Litter respiration studies have been carried out by Chet Youngberg using a respirometer containing forest floor (O1 and O2) material on the following sites in the H. J. Andrews Forest; a wet (*Polystichum munitum*) site, a moist (*Rhododendron macrophyllum*/*Berberis nervosa*) site, and a dry ridge (*Castanopsis chrysophyllum*) site. Seasonal CO_2 evolution on a dry weight basis indicates very little difference in litter respiration between wet and moist sites. Generally the dry ridge site had less CO_2 evolution in fall, winter, and spring, but interestingly CO_2 evolution was greater on the dry site than either the moist or wet sites in the summer months. These results need further examination with

Table 2. Foliage decomposition of representative species on Oregon environmental grid.

Location	Species	Summer litter moisture	Percent decomposition--weight loss (300 days)
Coastal site - Cascade head	Red alder	moist	59.1
Willamette Valley - Pigeon Butte	Oregon oak	dry	22.2
Wildcat Mt. -- high elevation	Silver fir	dry	25.2
H. J. Andrews - high elevation	Douglas-fir	dry	29.6
Eastern plateau Pringle Butte	Ponderosa pine	dry	15.0

respect to the hypothesis that decomposition in summer months is limited by moisture conditions of the forest floor.

Nutrient leaching. Nutrient leaching processes have been examined through tension lysimetry and soil solution chemistry in a tropical ecosystem (Costa Rica), a temperate Douglas-fir ecosystem (Thompson site), a high altitude Pacific-silver fir ecosystem (Findley Lake), and a high latitude western hemlock/Sitka spruce ecosystem (Petersburg, Alaska) by Dale Johnson.

The role of carbonic acid as a leaching agent was evaluated in these ecosystems. It was hypothesized that high temperature and heavy rainfall in the tropical systems would cause high soil CO_2 levels and intensive leaching relative to temperate systems. It was also proposed that, because of similarities in climate, forested soils in alpine and northern sites would be analogous with respect to carbonic acid leaching. It was hypothesized that organic acids would be produced in soils in colder climates and that these acids would tend to lower solution pH and bicarbonate levels.

These basic hypotheses were confirmed: soil CO_2 pressures and soil solution bicarbonate salt concentrations were higher in the tropical than in the temperate system (Tables 3 and 4). The alpine and northern systems were analogous in that organic acids lowered pH and bicarbonate concentrations within the rooting zone (Tables 5 and 6). Most available literature shows that the presence of organic acids lowers pH and reduces the dissociation of carbonic acid, thus lowering the level of mobile inorganic anions in the rooting zone.

The intensity of carbonic acid leaching within each of these soils corresponds to the mineral cycling rates at the given site. At the colder sites, the suppression of carbonic acid leaching probably prevents massive losses of cation nutrients during snowmelt periods. This is because CO_2 can build up to high levels beneath the snowpack, creating a high potential for carbonic acid leaching. The intensive carbonic acid leaching at the tropical site apparently coincides with rapid mineral turnover rates described by others.

The roles of atmospheric sulfate and chloride deposition in solution cation transfer were evaluated for each system. The proximity of SO_2 (volcanic or industrial) sources and salt water apparently determined the magnitude of sulfate and chloride deposition, respectively, but the concentration of these ions in solution was mediated by interactions with the vegetation and soil. With the exception of the northern system, where the proximity of salt water resulted in high chloride concentrations, carbonic or organic acids dominated the leaching processes in the soils at all sites.

As part of the nutrient leaching studies, the potential effects of acid rainfall and sulfate deposition were also examined by Dale Johnson. Acid rainfall from industrial sources of SO_2 and NO_x has caused concern in recent years because of its potential effects on both terrestrial and aquatic ecosystems. With respect to forest nutrition, it is feared that

Table 3. Weighted average concentrations of anions and total cations in solutions from La Selva, Costa Rica, for July, 1973 (meq/l).

Sample station	pH	Cond. (µmho/ cm)	HCO_3^-	SO_4^{2-}	NO_3^-	Total[a] Cations	Total Anions	Calculated CO_2 Pressure (atm)
<u>Area 1:</u>	<u>La Selva Series</u>							
Precip.	4.52	13.4	0.000	0.020	Tr.	0.030	0.020	-
Through-fall	5.70	13.0	0.080	0.048	0.010	0.130	0.120	0.009
All Hor. (15 cm)	5.72	23.1	0.263	0.015	0.011	0.231	0.289	0 035
Al2 Hor. (45 cm)	6.01	31.9	0.285	0.018	0.011	0.319	0.314	0.018
Al2 Hor. (60 cm)	5.68	18.2	0.140	0.015	0.009	0.182	0.164	0.019

[a] Ca^{24}, Mg^{24}, K^+, and Na^+ are major constituents.

Table 4. Weighted average anion and total cation concentrations of solutions from the Allen E. Thompson site (meq/l)

Sample station	pH	HCO_3^-	SO_4^{2-}	Cl^-	NO_3^-	Total cations	Total anions	PCO_2 (atm)
Intensive Monitoring Plot (Feb. 1973-1974)								
Precipitation	4.92	0.041	0.015	0.028	0.004	0.095	0.088	-
Throughfall	5.16	0.056	0.024	0.050	Trace	0.100	0.130	-
Forest floor	5.85	0.131	0.144	0.126	Trace	0.429	0.401	-
A horizon	6.14	0.114	0.047	0.067	Trace	0.252	0.228	0.0045
B horizon (50 cm)	6.12	0.117	0.043	0.074	Trace	0.239	0.234	0.0048

Table 5. Weighted average anion and total cation concentrations of solutions from the Findley Lake site (meq/l)

Sampling station	pH	HCO_3	SO_4^{2-}	Cl^-	Total cations	Total anions
Precipitation	5.55	0.066	0.035	Trace	0.106	0.101
Throughfall	4.35	0	0.064	Trace	0.116	0.064
Plot 6						
Forest floor	4.60	0.021	0.058	0.035	0.205	0.114
A2 horizon	4.41	0.009	0.049	0.022	0.170	0.080
IIIB2hir horizon	4.90	0.044	0.043	0.021	0.123	0.108
IIIB3 horizon	5.80	0.238	0.048	0.035	0.406	0.321

Table 6. Weighted average anion and total cation concentrations for the sites near Petersburg, Alaska (meq/l)

Sampling station	pH	HCO_3^-	SO_4^{2-}	Cl^-	Total cations	Total anions
Plot 1: Well-drained, Kupreanoff soil (September-December, 1974)						
Precipitation	5.64	0.048	Trace	0.030	0.058	0.078
Throughfall	5.25	0.084	0.038	0.140	0.287	0.262
Forest floor	4.59	0.027	0.051	0.303	0.513	0.381
A2 horizon	5.25	0.093	0.035	0.213	0.390	0.341
B2hir horizon	5.70	0.098	0.029	0.197	0.308	0.324
C horizon	6.02	0.155	0.023	0.221	0.324	0.399

NOTE: (Calculated PCO_2 in the C horizon is 0.0081 atm.)

sulfuric or nitric acid precipitation will take a toll on cation nutrient reserves over and above that occurring in natural systems (e.g., by carbonic acid leaching). The Thompson Research Center has been subject to acid rainfall for at least the last ten years (when records of rainfall pH were begun). More recent analysis show that sulfuric acid is most common, though inputs of nitric acid occasionally occur. The source is presumably the copper smelter in Tacoma. At present levels, however, acid rainfall and sulfate deposition account for only about 20% of the total cation removal from the rooting zone (Table 7). Since the ecosystem is nitrogen-limited, this loss is not considered critical.

The sulfur cycle is being evaluated at present, and like the cycles of other nutrients, the transfers of sulfur internal to the ecosystem are far greater in magnitude than the input and output figures. Should the system be subject to increased sulfuric acid loading as the use of high-sulfur coal increases, the situation may change.

It has been shown that the Everett soil at the Thompson site has a sulfur adsorption capacity and that this soil property buffers out temporary high acid inputs. The mobility of sulfur in both the biological and physical systems over long periods is not known, however. It is an open question as to whether the biological and physical systems will be able to absorb constantly higher acid input levels with little or no ill-nutritional effects. It should be recalled, however, that sulfate is an essential nutrient, and elimination of the sources of its input may have deleterious effects. Sulfur deficiencies have been noted in soils of the midwest since the advent of low sulfur fuels there, for instance.

Simulation of soil CO_2 entrapment by an incoming wetting front with a finite elements model clearly demonstrated the inappropriateness of steady-state solutions for soil CO_2 diffusion. Simulated short-term variations in pH and total ionic concentration during soil CO_2 entrapment showed much less variation than experimental data. Assumptions inherent in the model are probably responsible for these discrepancies, particularly the assumption of soil-soil solution equilibrium.

A soil leaching model was developed and tested against data from field experiments involving acid and urea application. The model successfully simulated the behavior of actual soil solutions following acid and urea applications, but failed to provide accurate quantitative data. The model thus demonstrated that the proposed mechanisms of soil leaching are feasible, but that certain other assumptions (such as soil--soil solution equilibrium) are questionable.

Nutrient exchange. This study was initiated by Robert Zasoski to investigate the behavior of Findley Lake, A. E. Thompson site, and H. J. Andrews Forest soils with respect to cation exchange behavior and prediction of soil solution concentrations over a range of soil moisture conditions. Soils from Findley Lake and the Thompson site have been collected and characterized. Soils from the Andrews Forest were collected in September. Because of the delays in acquiring soil samples, it is more appropriate to discuss the analysis which will be completed during 1975.

Table 7. Total leaching of bicarbonate, sulfate, and total cations for one year at the Thompson site, February 1973 - February 1974 (Cole and Johnson, 1974).

Sampling station	HCO_3^- eq/ha	HCO_3^- %	SO_4^{2-} eq/ha	SO_4^{2-} %	$HCO_3^- + SO_4^{2-}$[a] eq/ha	$HCO_3^- + SO_4^{2-}$[a] %	Total cations (eq/ha)
Precipitation	780	61	200	16	980	77	1280
Throughfall	820	60	360	26	1180	86	1380
Forest floor	1110	33	700	21	1810	54	3400
A-horizon	1430	53	620	23	1940	76	2700
B-horizon	1070	60	360	20	1420	80	1780

[a] Analysis of noncontaminated samples for chloride indicates that it accounts for most of the remaining anion balance except in forest floor solutions.

Soils will be characterized by measuring cation exchange capacity (CEC) at several pH's to determine the pH dependence of soil CEC. In addition, the selectivity coefficients for Cedar River soils are being determined, and the selectivity coefficients for the soil horizons from Findley Lake and Andrews Forest will also be determined. The quantity-intensity relationships for these soils will also be determined to give a measure of the soil solution cation buffering capacity. These relationships will allow for the prediction of soil solution concentrations based on exchangeable cations and profile characteristics. Soil solutions collected by displacement techniques will be used to verify the predicted soil solution concentrations for each horizon.

In 1976, it will be determined if the equations developed to explain the exchange process are applicable to modifications of the system such as a high pH from fertilization and burning. Questions which will be investigated are:

1. How will a high pH from either burning or fertilization influence cation exchange equilibria?

2. Will high levels of NH_+^4 from fertilization affect the solution buffering for potassium levels?

3. How do nonbuffered reagents such as NH_4Cl and $CaCl_2$ compare to NH_4OAl as predictors of CEC in these soils?

4. What other extractants might be useful as indicators of soil cation supplies?

Nutrient uptake. Douglas-fir nutrient uptake has been examined by Caroline Bledsoe and Hans Riekerk by use of greenhouse seedling studies in nutrient solution and moist soil plugs.

During the summer of 1974, the greenhouse experiments (Rains and Bledsoe) on cation nutrient uptake by Douglas-fir seedlings in solution culture were completed. The results were reported at the annual Plant Physiology meetings in Ithaca, New York, in June. In the fall of 1974, these data were further analyzed. The variation among plants was high, so the experiments were repeated in 1975, with certain modifications. The linkage between soil (nutrient uptake) and plant (growth) processes has been studied in 1975.

Twenty-eight Douglas-fir seedlings were grown in a growth chamber in solution culture, and all essential nutrients were supplied. The N was supplied as NO_3^- to half the seedlings, and as NH_4^+ to the other half. Over a period of nine weeks, several growth variables of these plants were measured; uptake of N (as NO_3^- or NH_4^+), Ca^{++}, K^+, and Mg^{++}, increase in fresh weight, photosynthetic rates, dark respiratory rates, transpiration rates, and xylem sap exudate concentrations. Figure 3 illustrates the uptake data for 1 week, showing sustained uptake of the cations by

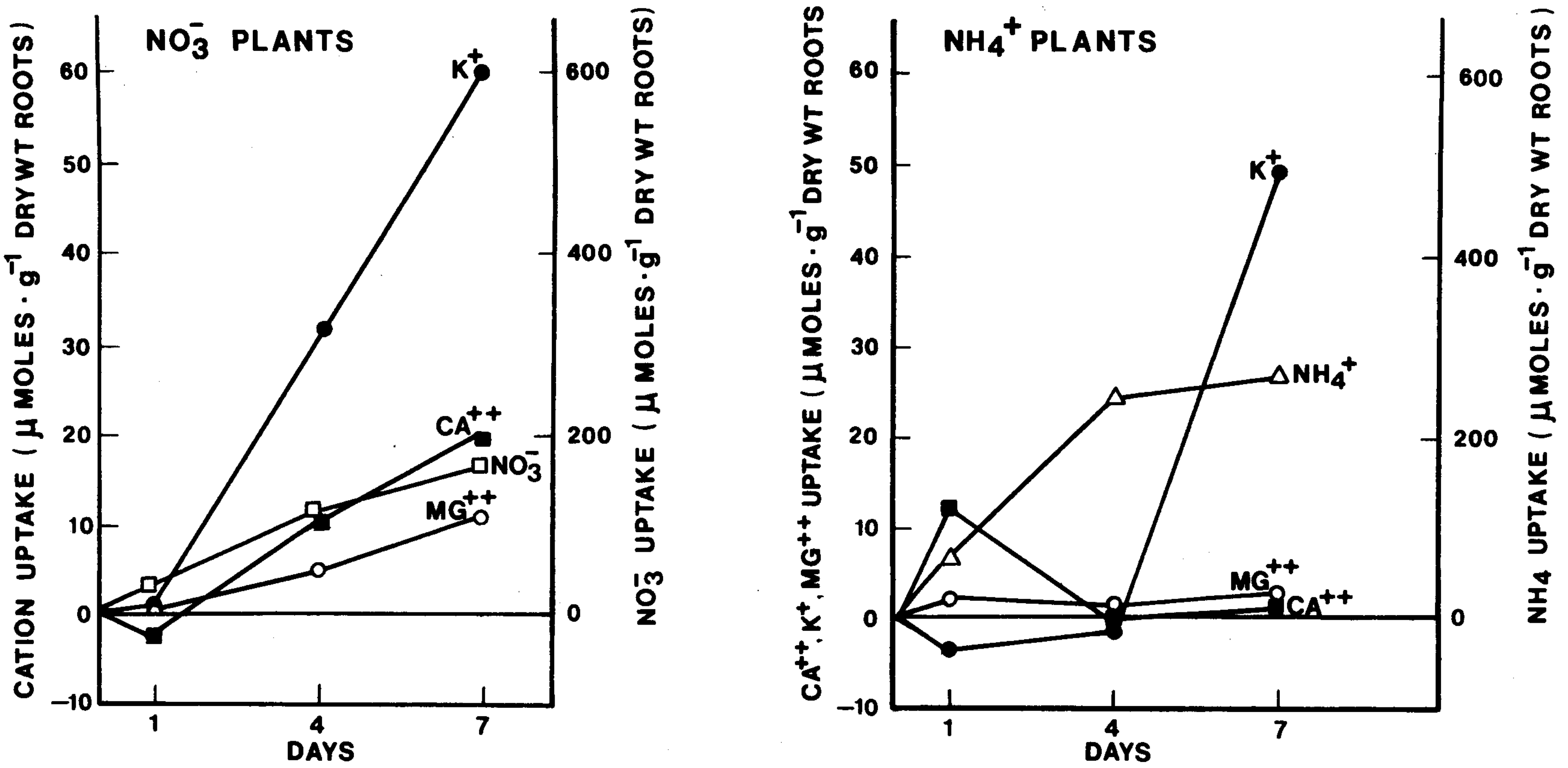

Figure 3. Uptake of ammonium, nitrate, calcium, magnesium and potassium for Douglas-fir seedlings grown in nitrate and ammonium solutions. Values are averages of 10 plants.

nitrate-grown plants, while ammonium-grown plants appear to take up NH_4^+ in preference to K^+ and Mg^{++}.

These data were collected by several researchers working as a team (Amundson, Bledsoe, Farnum, and Riekerk) during April, May, and June. The data are now being processed. Relationships between (1) nutritional status of the plants and relative photosynthetic rates, (2) nutrient uptake rates and transpiration rates, (3) nutrient concentrations in the xylem sap and nutrient concentrations in the foliage and (4) cation uptake, cation competition, and overall charge-balance will be examined. These data will be used to model the cation-anion transfers into the plant, at least on a "micro" basis.

Questions to be investigated in 1976 are:

1. Can the results of the seedling-nutrient uptake experiment be expanded to a model of larger trees?

2. Can root biomass be successfully used as an estimator of root surface area?

3. Can uptake rates be measured on attached roots of trees in the forest?

4. Can nutrient uptake rates be measured in Douglas-fir seedlings grown in an inert "simulated-soil" system, inoculated with the appropriate mycorrhizal fungi?

5. How do Douglas-fir trees maintain charge neutrality in a situation where cation uptake exceeds anion uptake?

The objective of the study by Hans Riekerk is to estimate nutrient uptake rates of a Douglas-fir forest growing on poor gravelly soil by (1) an evaluation of potential uptake rates (mg nutrient per g root per hr) under different soil moisture and temperature regimes and (2) a correlation between fine root biomass and stem sapwood cross-sectional area at breast height (over bark).

The first attempt was made with greenhouse seedlings, growing in moist peat-vermiculite soil plugs, which were decapitated for xylem sap extraction in a pressure bomb (5 atm) at 20°C. Exudation rates were very low (<0.1 ml/hr) and the nutrient concentrations of sap and soil solutions showed 80-100% error variation. The sap/solution accumulation ratios were around unity mainly due to the rather vigorous soil solution extraction (centrifuged at 2000 rpm for 30 min).

The second attempt was made with greenhouse seedlings growing in 1% Johnson's culture solution with either NH_4^+-N or NO_3^-, and extracted for 3-4 hours at the rate of 0.2 ml/hr. This rate corresponded with transpiration rates measured by Farnum. The error variation was slightly less and xylem sap nutrient concentrations similar to those of the plug seedlings. The NH_4^+ vs. NO_3^- treatment indicated quick reduction of NO_3^- to NH_4^+ in the root system. The sap/solution accumulation ratios were significantly larger than unity.

At present, solution culture experiments with oxygen deprivation, low temperature, high nutrient concentration, and different extraction pressure treatments are being conducted to further explore functional relationships in conjunction with studies by Bledsoe, Farnum, and Amundson. Also, analysis techniques for microvolume sap samples are being explored and tested.

In a separate effort four suppressed and intermediate young Douglas-fir trees growing on gravelly soil at Pack Forest were carefully excavated and fine root (<2mm) biomass measured. With only a few data points, no correlation with sapwood cross-section area has been established to date. More excavations (of larger trees) are planned.

A note describing the pressure-bomb technique for sap-exudate analysis with some preliminary data has been submitted to Forest Science.

In 1976 the following questions will be investigated.

1. What are the rates of uptake (mg nutrient per g root per hr) by soil-grown seedlings under different degrees of moisture status and temperature, with other factors controlled and constant. This is in conjunction with the "simulated-soil" work proposed by Bledsoe.

2. Are the rates of uptake by larger seedlings (5-10 yrs old) growing in fluctuating field conditions of moisture and temperature comparable to those of greenhouse conditions?

3. Does the weighted product of estimated uptake rate and total root biomass of a Douglas-fir forest stand account for annual uptake rates estimated by nutrient budget analyses?

Nutrient and carbon accumulation. Studies have been conducted in the Cedar River watershed in Washington by Dale Cole, John Turner, and Jim Long and by Charles Grier in sites in Oregon ranging from the seacoast to 1524 m elevation.

The phase of work by John Turner and Dale Cole on examination of nutrient cycling and carbon accumulation patterns has focused on (a) an age sequence of Douglas-fir ecosystems ranging from 9-95 years and (b) 34-year-old red alder and 175-year-old Pacific silver fir ecosystems.

(a) Changes of nutrient cycling dynamics with stand development in Douglas-fir ecosystems. During the initial phases of stand development, the stand draws upon soil nutrient pools and begins to build up a reserve within the biological component (Figure 4). Also, during this initial phase prior to canopy closure, understory biomass is at its highest (Figure 5) and the understory plays an important role in the total mineral cycling of the system (Figure 6). With the advent of canopy closure, foliar biomass reaches a steady-state condition (Figure 7). The age at which canopy closure occurs is dependent upon stand density.

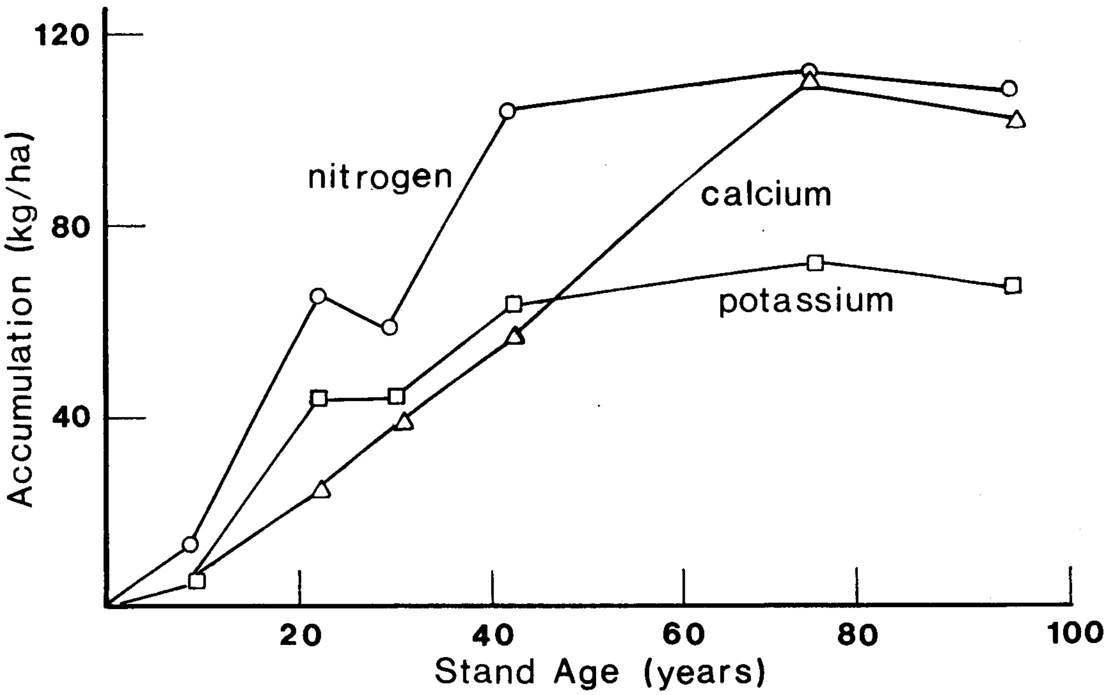

Figure 4. Accumulation of nitrogen, potassium, and calcium in the foliage of various aged stands of Douglas-fir (Cole, D. W., J. Turner, and S. P. Gessel. 1975. Elemental cycling in forest ecosystems of the Pacific Northwest. Paper presented at 12th International Botanical Congress, Leningrad, July 1975).

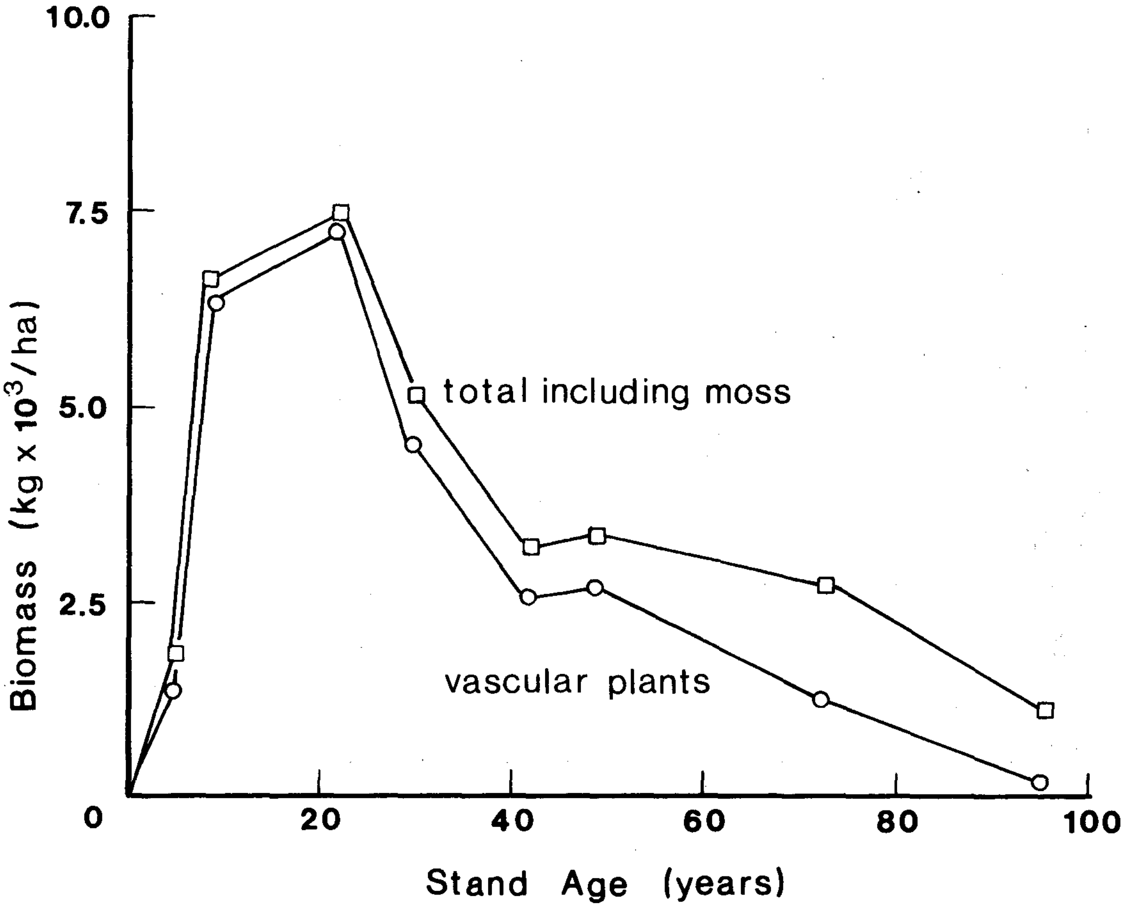

Figure 5. Accumulation of biomass in the understory vegetation of various aged stands of Douglas-fir (Cole et al. 1975).

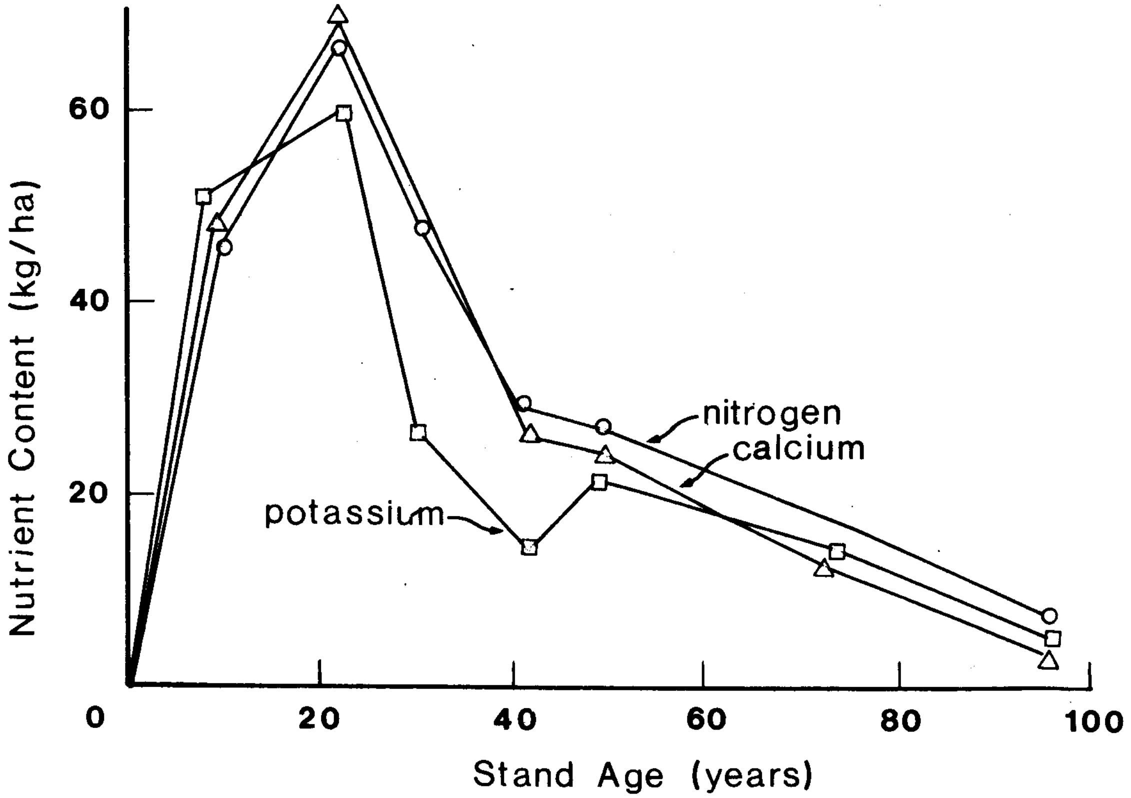

Figure 6. Accumulation of nitrogen, potassium, and calcium in the understory vegetation of various aged stands of Douglas-fir (Cole et al. 1975).

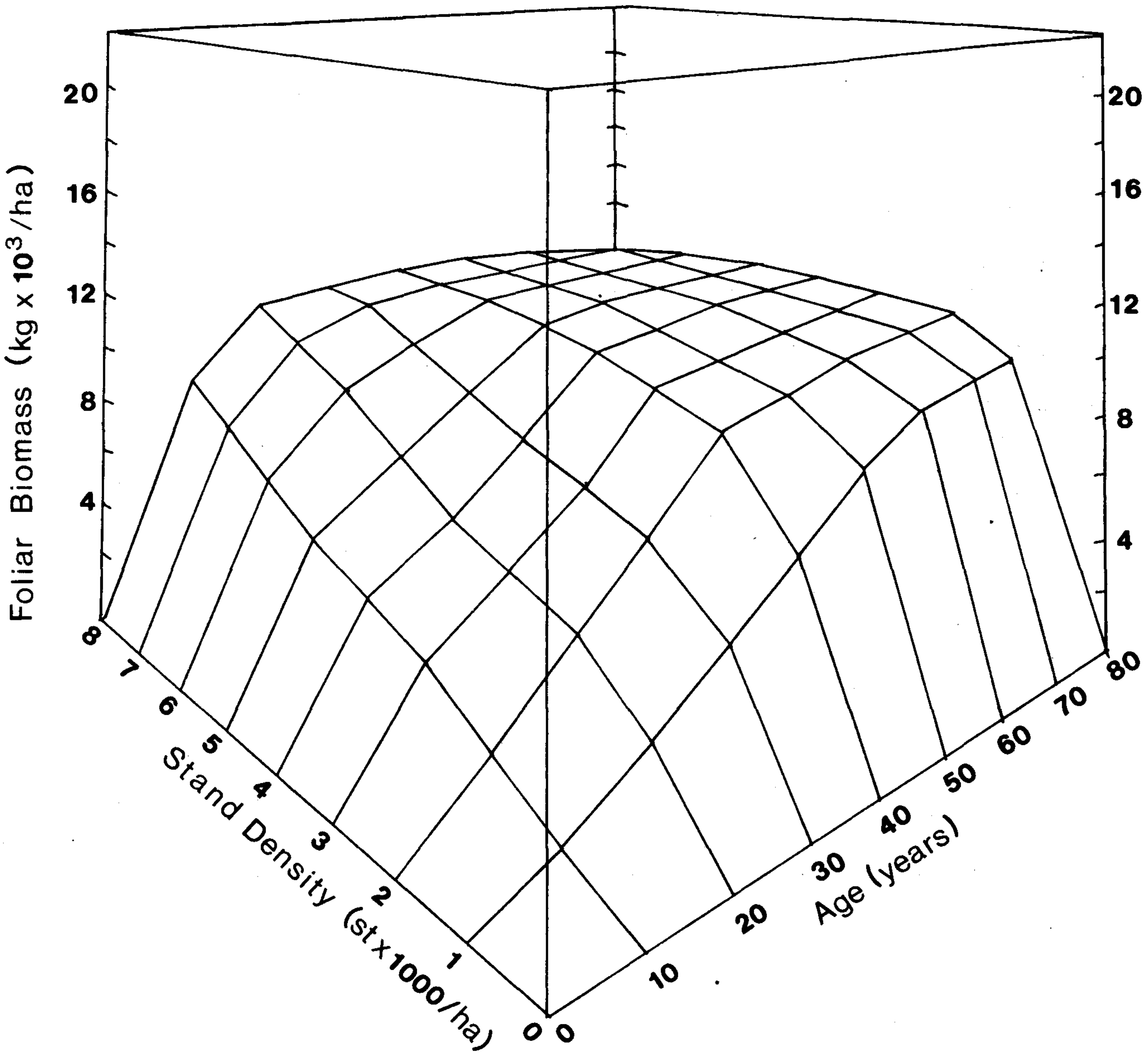

Figure 7. Relationship between foliar biomass, stand age, and stand density (stems per hectare) for Douglas-fir stands of low productivity (site quality IV) (Cole et al. 1975).

The accumulation of nitrogen and potassium, which are relatively mobile within the biological system (i.e., not tightly bound in organic forms, but relatively available for retranslocation and foliar leaching) reaches a steady-state condition along with foliar biomass (Figure 4). Calcium, being relatively immobile in the biological system, continues to accumulate, especially in older foliage. The forest floor weight increases throughout the first 90 years of stand development (Figure 8) contradicting the long-standing assumption that the forest floor reaches a steady-state in mature forest ecosystems. The humus component increased in a linear fashion, whereas the total weight increased drastically after approximately age 40. The latter can be attributed to the increased branches and smaller trees.

The nitrogen and calcium content of the forest floor parallels the total forest floor biomass during this time span, since these nutrients are not mobile in dead tissue (Figure 9). As will be shown later, nitrogen is relatively mobile in live tissue by virtue of retranslocation with the tree. Nitrogen is accumulating in the forest floor where it is much less availble to the tree, however, suggesting increasing nitrogen deficiency during stand development.

The mobility of potassium is related to the physical process of leaching; potassium remains in ionic form in tissues, and it is therefore readily leached. Thus potassium accumulation in the forest floor is markedly lower than it is for nitrogen or calcium (Figure 9).

After canopy closure, the uptake of nitrogen declines and the trees become increasingly dependent upon internal recycling from older tissues to meet their nitrogen demands. The nitrogen demands are ameliorated somewhat by longer needle retention times in older trees as well in that this allows constant foliar density with less needle replacement.

Potassium and calcium uptake stabilize at 25-30 years and neither nutrient is retranslocated within the tree. The reasons for the lack of retranslocation are evident. Potassium is readily leached from foliage before retranslocation occurs, whereas calcium is tightly bound as a cell wall constituent or a precipitate such as calcium oxalate and accumulates in older folaige. Thus as the stand matures and needle retention time increases, calcium consumption by older foliage increases.

It appears that the stand derives an increasing proportion of its nitrogen and calcium uptake requirements from the forest floor as the stand matures (Table 8). (Potassium is apparently taken from the soil throughout this period, however, since the forest floor accumulates less of it.) Thus rather than draining nutrients from the living system, the forest floor appears to provide a storage pool that further tightens the system's control over the cycle of some critical nutrients.

(b) Cycling in other forest ecosystems. Nutrient cycles in red alder (Alnus rubra) have been regarded with interest in that alder enhances the soil properties and nitrogen status of sites denuded by logging and fire. Since logging began in the Douglas-fir region, alder stands have

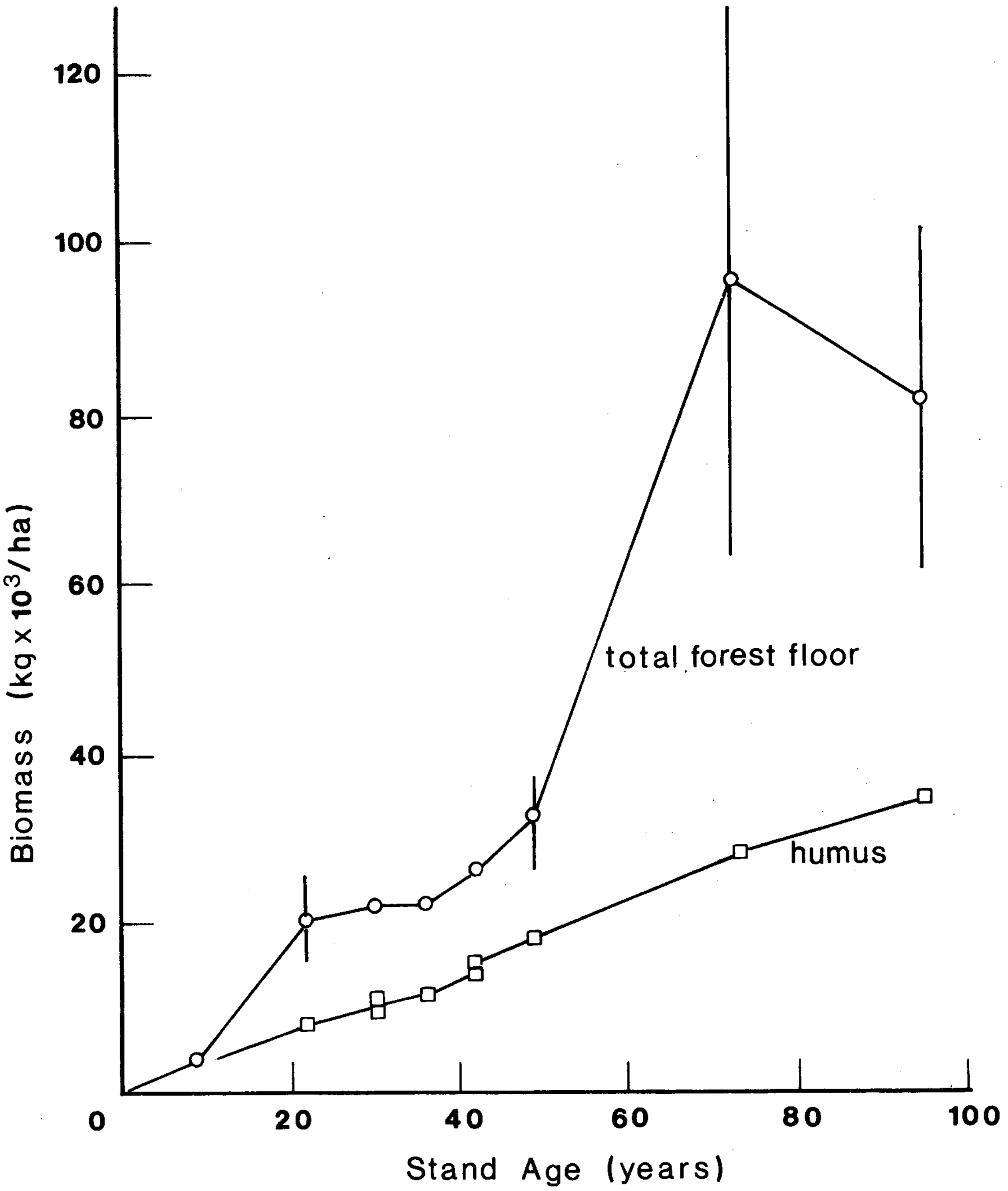

Figure 8. Accumulation of forest floor biomass under various aged stands of Douglas-fir (Cole et al. 1975).

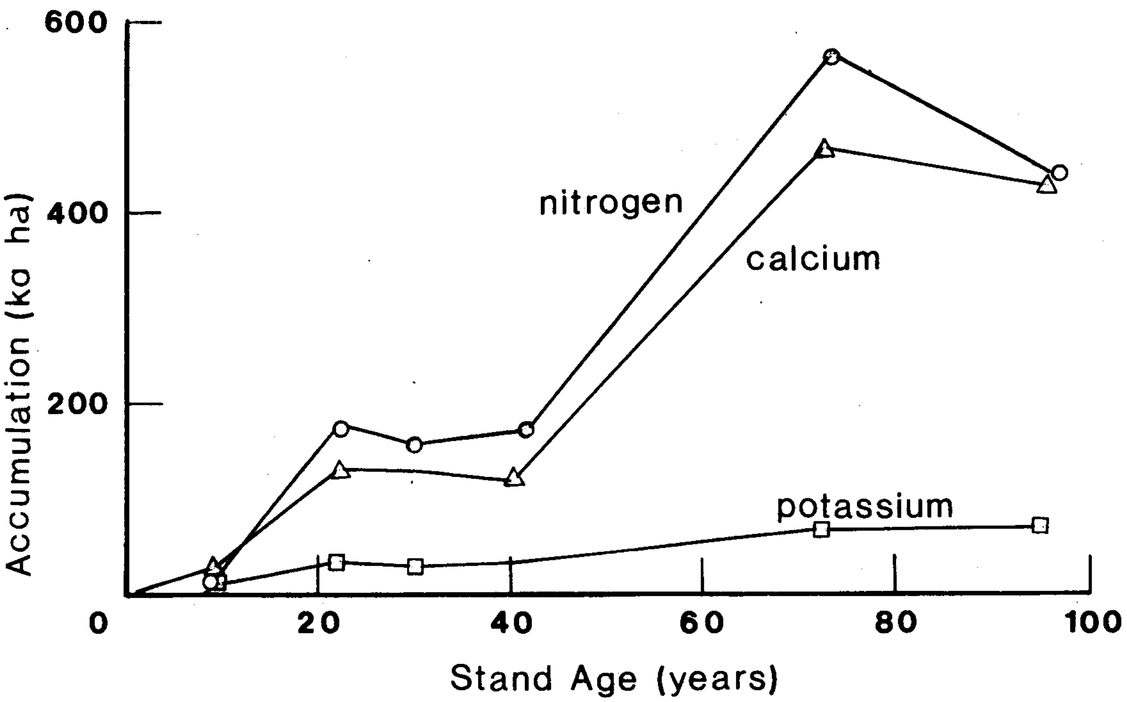

Figure 9. Accumulation of nitrogen, calcium, and potassium in the forest floor of various aged stands of Douglas-fir (Cole et al. 1975).

Table 8. Nutrient removed from the forest floor by the total vegetation (% of total uptake) (Cole et al. 1975).

Age class	N	K	Ca
0-20	55	15	25
20-60	65	-5	35
60-90	100	0	55
Average	70	5	40

become increasingly extensive. Recently alder has attained some commercial value.

Nutrient cycling patterns during stand development in alder are similar to those of Douglas-fir (Turner et al., submitted).* The major difference is that alder is short-lived relative to Douglas-fir. Thus at age 34 the alder stand studied by Turner et al. is in a stage of decline comparable to that of a 450-year-old Douglas-fir stand; the understory becomes an increasingly important component of the total biomass and nutrient content within each system as the stand declines.

Nitrogen content in a 34-year-old alder stand is high relative to a 36-year-old Douglas-fir stand, presumably because of alder's nitrogen fixing capabilities (Table 9). Magnesium content is high in the alder stand as well. The nutrient content of the understory (mainly sword fern, _Polystichum munitum_) in the alder stand is striking, particularly with respect to potassium. As stated previously, the understory is increasing in importance as the alder stand declines. The understory in the Douglas-fir forest contains only a small fraction of the total nutrient pool, since the canopy is closed and the stand is still developing.

The mineral cycle in a subalpine Pacific silver fir (_Abies amabilis_) ecosystem contrasts to the alder and Douglas-fir ecosystems (Turner and Singer, in press).** Foliar growth is slow, but foliar biomass is high because of long needle retention time (up to 14 years). Since foliar biomass is high, the foliar nutrient pools are high (Table 10). Since decomposition and mineral release are slow, this is an advantage in terms of an accessible nutrient supply in the subalpine ecosystem.

In conjunction with Turner's work, a study of forest community types in the Cedar River watershed is being conducted by Jim Long. This work was initiated because of the importance of understanding how all plant components, including the understory, contribute to nutrient cycling and carbon accumulation patterns.

A class description of the forest community types occurring both on the upper and lower portions of the Cedar River watershed has been completed (Del Moral and Long, manuscript in preparation). A total of 10 community types have been delineated, and a key has been prepared to aid in their identification. This classification was accomplished utilizing computerized clustering techniques which will ultimately be used in mapping the vegetation of the Cedar River drainage.

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*Turner, J., D. W. Cole, and S. P. Gessel. Nutrient accumulation and cycling in a red alder (_Alnus rubra_ Bong.) ecosystem. Submitted to Ecology.

**Turner, J. and M. J. Singer. Nutrient cycling and distribution in a sub-alpine forest ecosystem. J. Appl. Ecol. (in press).

Table 9. Comparison of organic matter and nutrient distribution in a 34-year-old alder and a 36-year-old Douglas-fir stand in kilograms per hectare. (Turner et al., submitted to Ecology).

	Organic matter	N	P	K	Ca	Mg	Mn
Red alder							
Total tree	209,800	589	37	99	299	111	24
Understory	9,530	103	7	132	95	16	1
Forest floor	66,350	877	34	91	391	57	14
TOTAL	285,680	1569	78	322	785	184	39
Douglas-fir							
Total tree	204,529	320	66	220	333	50	34
Understory	1,010	7	1	7	9	2	1
Forest floor	22,772	175	26	32	137	41	15
TOTAL	228,311	402	93	259	479	93	50

Table 10. Biomass and nutrient content (in kg/ha) of the live tree component Pacific Silver-fir (*Abies amabilis*) at Findley Lake (Turner and Singer, in press).

	Biomass	N	P	K	Mn
Component					
Foliage	15,698	172.7	18.06	168.9	23.0
Branch	17,711	17.7	9.39	119.7	19.5
Bark	38,713	116.1	8.17	22.5	3.3
Wood	265,011	13.3	13.35	81.9	66.3
Total aboveground	337,133	319.8	48.97	393.0	112.1

Ordination of the vegetation occurring on the upper watershed has resulted in the identification of those factors of the physical environment most important in accounting for the distribution of this vegetation. The identity of these gradients and their correlation with gradients in plant species distributions has been established utilizing pre-dawn moisture stress and winter snow depth measurements.

An investigation of the dynamics of community development in _Abies amabilis_ zone forests has been initiated. A chronosequence has been established utilizing eight different-aged stands. These stands which are all between 750 and 900 m in elevation, range in age from one to about 600 years.

Data collected from 15 x 20 m plots established within each stand includes the age and size of each tree and estimates of aboveground biomass for each understory plant species. These data are to be used in the study of the dynamics of age structure and biomass accumulation within the chronosequence.

Additional work completed during the period of this report includes the publication of results obtained in the investigation of a series of different aged Douglas-fir stands occurring in the vicinity of the Thompson Research site (Long and Turner 1975).* A second report on this series of stands, specifically detailing changes in aboveground productivity and the accumulation of aboveground biomass, has been accepted for publication.

Primary production and nutrient cycling comparisons by Charles Grier have been made along environmental gradients in Oregon. Biomass, net production, nutrient distribution, and nutrient cycling have been quantified for: (1) a 130-year-old _Tsuga heterophylla/Picea sitchensis_ stand near sea level; (2) a 100-year-old _Pseudotsuga menziesii_ stand at 365 m elevation; (3) a 130-year-old _Pseudotsuga menziesii_ stand at 915 m elevation; and (4) a 130-year-old _Tsuga mertensiana/Abies amabilis_ stand at 1524 m elevation. All stands are of above average productivity for their respective climatic zones and are roughly comparable in terms of soil parent material.

A manuscript describing biomass and productivity in stands 1, 2, and 4 has been prepared and submitted to the Japanese Journal of Forestry. A manuscript (1) describing biomass, productivity and nutrient cycling, (2) showing environmental constraints on production in Northwest coastal forests, and (3) suggesting a relation between nutrition of coastal forests and the biology and chemistry of the adjacent ocean has been prepared and submitted to Ocecologia.

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*Long, J. and J. Turner. 1975. Aboveground biomass of understory and overstory in an age sequence of Douglas-fir stands. J. Appl. Ecol. 12:179-188.

Further progress has been made in showing the effect of snow and wind damage on stand production and nutrient cycling. Additional studies should confirm the apparently large effect of wind and snow pruning of photosynthetically active foliage.

The following hypothesis will be tested in 1976. Snow and wind pruning of foliage provides a serious limitation on primary production in coastal and high elevation forests. Species competitive in these environments have evolved morphological and physiological adaptations to ameliorate environmental effects.

Stand structural geometry. Ecosystem studies on nutrient cycling and carbon accumulation generally do not take into account the three-dimensional stand structure. Data are being gathered by Alan Jensen and David Scott at the A. E. Thompson site on a Douglas-fir tree as an initial description of three-dimensional stand structure.

The project consists of a high resolution dissection of a co-dominant Douglas-fir. The following measurements were taken on every branch: (1) branch height (m); (2) branch orientation (compass bearing); (3) a horizontal photograph; and (4) a vertical photograph.

On every third branch up one quadrant of the tree the following measurements were taken at each internode:

(1) branching order;
(2) foliage age;
(3) location of the internode;
(4) internode length;
(5) angle to the horizontal;
(6) angle to the internode it is attached to;
(7) distribution of foliage around the internode;
(8) diameter of the foliage cylinder;
(9) internode weight;
(10) diameter of the internode;
(11) weight of the needles;
(12) surface area of the needles; and
(13) number of needles

The data are currently being analyzed and a three-dimensional model of a single tree will result.

Comparison of physiological capacity of different species in particular environments--net photosynthesis, respiration, and transpiration. Questions of land use often require information on the relative capacity of plants to function in particular environments. In forest management, stand treatments cause specific changes in microclimate and one needs the capacity to predict the likely response of forest vegetation to these changes. To address these kinds of questions, field studies of tree physiology in California by John Helms and Mark Rutter (University of California, Berkeley) are currently aimed at determining the relative capacity of several species to produce carbohydrate and to maintain satisfactory water relations in natural environments.

The research approach is to develop for each species a wide response surface quantifying the relation between net photosynthesis, respiration, and transpiration, and controlling factors such as leaf resistance, light intensity, temperature, and vapor pressure deficit.

Currently, three species are being studied which grow in a natural mixture. These are ponderosa pine (Pinus ponderosa), Douglas-fir (Pseudotsuga menziesii), and incense cedar (Libocedrus decurrens), which represent a wide range in relative tolerance.

Equipment used includes a Siemens assimilation chamber and a computer-controlled data acquisition system. The equipment is mounted in a mobile trailer and can be taken to any desired field location. The use of the Siemens system permits the development of a wide response surface by firstly monitoring physiological behavior in relation to ambient conditions. Then, the foliar sample can be subjected to controlled levels of temperature and vapor pressure.

In this initial phase of the study, complexities of within-tree variation in processes were avoided by restricting sampling to the same relative location in the crowns of each tree. Preliminary data, obtained during the summer and fall, are now available which permit a comparison of species performance (Figure 10).

Temperature optima for net photosynthesis appear to be unexpectedly low for species growing naturally in a hot, dry summer area. This may be partially due to the combined effects of increased foliar water stress, vapor pressure deficits, and leaf resistance as leaf temperatures increase above 15-20°C. Douglas-fir, which is the most shade tolerant of the three species, produced maximum rates of net photosynthesis of about 3 mg CO_2 per g per hr at the low temperature of 8-12°C. The more intolerant pine exhibits maximal rates of 4 mg CO_2 per g per hr in the field at about 18°C and sustains higher rates of photosynthesis at higher temperatures than does Douglas-fir. Incense cedar, which has an unusually wide range of relative tolerance, exhibits photosynthetic rates intermediate between the other two species. It is interesting to note that the limited amount of data obtained on Douglas-fir photosynthesis in late fall shows that rates of photosynthesis at low temperature are much higher than during the summer, reaching average rates of about 4.5 mg CO_2 per g per hr. This higher performance is probably associated with favorable water relations and low leaf resistance.

All species appear to become saturated at light intensities of about 1.25 ly. The more intolerant pine produced more photosynthate at any given light level than did either incense cedar or Douglas-fir. The late fall Douglas-fir data indicate very rapid responses of photosynthesis to increases in light intensity. In fact, at any given level of light intensity, rates of net photosynthesis in late fall and early winter were more than twice those obtained for this species in summer. In late fall and early winter, a given level of light intensity is associated with lower temperature and lower vapor pressure deficits than the same light level in summer.

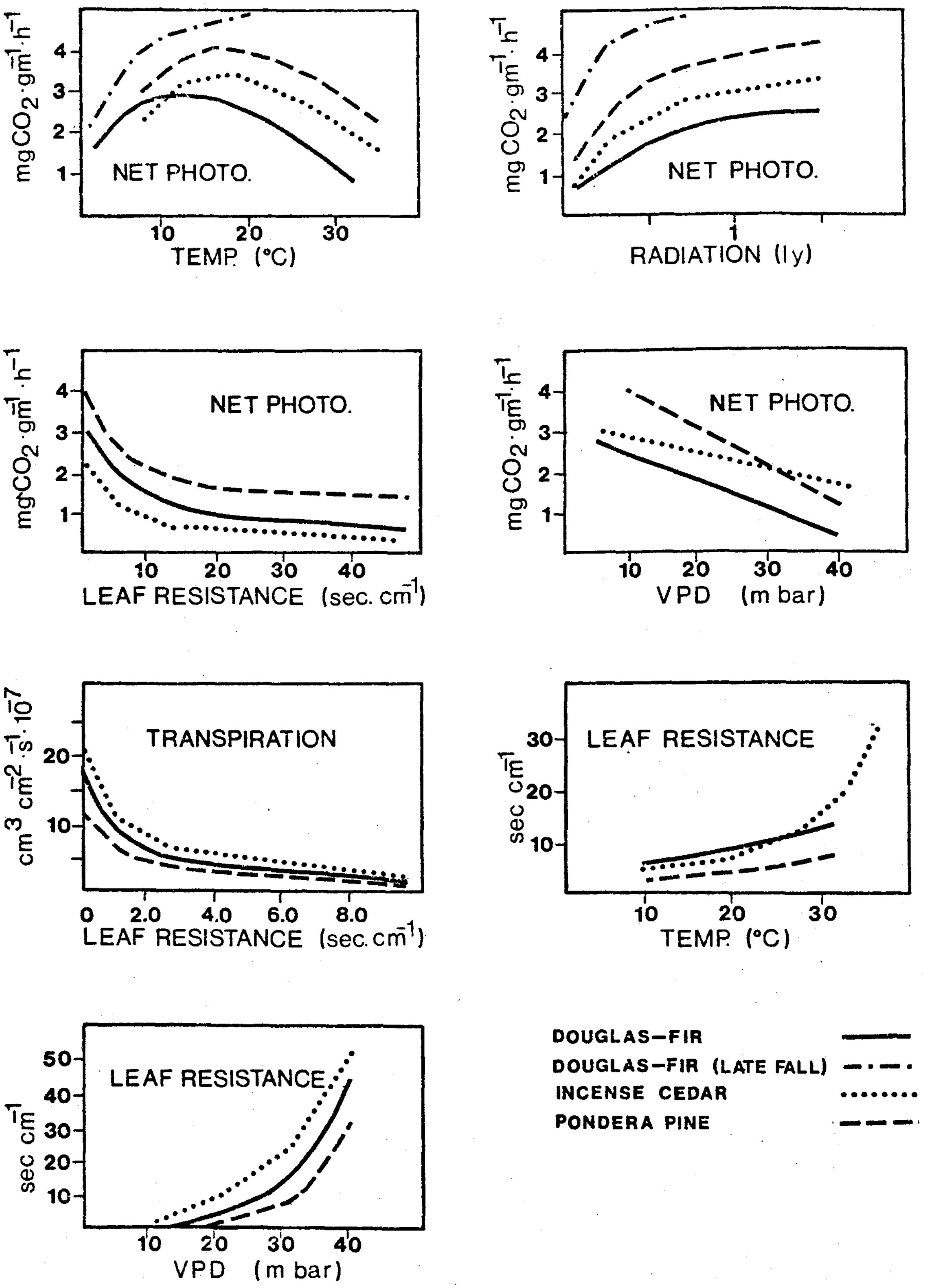

Figure 10. Net photosynthesis as a function of temperature, radiation, leaf resistance and vapor pressure deficit (V.P.D.) transpiration as a function of leaf resistance and leaf resistance as a function of V.P.D. for three conifer species in California.

As leaf resistance increases, rates of net photosynthesis decrease with the greatest reduction occurring between a leaf resistance of 0-20 sec/cm. The more intolerant pine maintains higher rates of net photosynthesis at any given leaf resistance than does either Douglas-fir or incense cedar. A similar relationship is shown for each species with increases in vapor pressure deficit. Again, pine maintains higher rates of net photosynthesis at any given vapor pressure deficit than does incense cedar and Douglas-fir.

Rates of transpiration decline rapidly with increase in leaf resistance. At resistances of 10 sec/cm, transpiration of all species dropped to about 2×10^{-7} per cm^3 per cm^2 per sec. Maximum rates of transpiration of about 20×10^{-7} per cm^3 per cm^2 per sec were measured at levels of leaf resistance approaching zero. At any given leaf resistance, ponderosa pine exhibited lower rates of transpiration than either Douglas-fir or incense cedar.

Leaf resistance of all species was not markedly influenced by changes in leaf temperature from 10°C to 25°C. Within this temperature range leaf resistance increased from about 4 to 9 sec/cm. With further increases in leaf temperature above 30°C, leaf resistance appeared to increase exponentially. Intolerant ponderosa pine was shown to have lower leaf resistance at any given temperature compared with the other two species. The relationship between leaf resistance and vapor pressure deficit was similarly exponential. At deficits of 10-20 mbar leaf resistance of all species was essentially zero, but at deficits of about 38 mbar, leaf resistance of ponderosa pine, Douglas-fir, and incense cedar was approximately 30, 45, and 50 sec/cm, respectively. Again, the more intolerant pine exhibited the lowest leaf resistance at any given level of vapor pressure deficit.

These preliminary findings illustrate different physiological behavior of trees of different relative tolerance growing side-by-side in the same field environment. The data indicate that the more intolerant ponderosa pine has the greatest physiological capacity to exploit the hot, dry environmental conditions during summer. Douglas-fir and incense cedar appear to be at a physiological disadvantage and this is borne out by general observations on survival and relative growth rate on exposed sites.

Currently, these data are being analyzed to quantitatively describe the relationships between processes, productivity, and environment. Similar response surfaces will be developed describing physiological performance in each season of the year and for other representative regions in the tree's crown. With this information simulations can be constructed which predict the likely response of vegetation to natural or induced changes in field environment.

Leaf conductance and water relations of Northwest conifers. Leaf conductance and water relations have been studied in a number of stands in Oregon by Steven Running and Richard Waring. Following initial studies of a variety of conifers we have concentrated this year on filling gaps in our knowledge. We now conclude that root temperatures above 1°C have little effect upon leaf conductance in Douglas-fir. Freezing air temperatures the preceding night, however, may result in a 2- to 3-fold decrease in leaf conductance during the day.

Where root activity is high or seepage water is available, mid-afternoon stomatal closure under high evaporative demand may not occur. From additional sampling of sapwood, we find water withdrawal during periods when the soil water is adequate but evaporative demand is consistently high. Data are expressed as a percent on a saturated volume. The pines, both sugar and ponderosa, appear to have more sapwood water storage than Douglas-fir.

In interpreting responses of seedlings or saplings exposed to different thinning regimes, we find it is important to determine rooting volume, sapwood volume, and ratio of leaf area to cross section area of sapwood.

<u>Role of insects in carbon and nutrient cycling</u>. Two research projects are being attempted in this area: (a) examination of the species, numbers and role of insects in dead Douglas-fir trees (by Mark Deyrup and Robert Gara), and (b) examination of differences in populations of epidemic and endemic Douglas-fir bark beetles with respect to host selection behavior by Andy Eglitis and Robert Gara.

(a) <u>Insects associated with dead and downed Douglas-fir</u>. A surprisingly large number of species of insects are involved in colonizing dead and downed Douglas-fir trees. Generally the bark beetles are the first colonizers and these are followed by the wood boring type insects. In all, several hundred species are involved. Suppressed trees were found to have different insect colonization patterns than healthy fallen trees. The orientation of the woody material is also important since material in the vertical orientation has different colonization pattern than horizontally placed material. Descriptions, habitats and roles of the Hymenoptera and Coleoptera associated with dead Douglas-fir trees are being compiled and will appear in two Biome Bulletins.

Examination of insects colonizing Douglas-fir in areas other than the Thompson site in the Cedar River watershed and outside the watershed revealed considerable geographic variation in patterns. It is proposed to examine further the role of certain key insects in carbon and nutrient cycling.

(b) <u>Population differences in Douglas-fir bark beetles</u>. Results of experiments conducted during 1974 suggested that population differences indeed exist in the Douglas-fir beetle (<u>Dendroctonus pseudotsugae</u>) both at the inter- and intra-population level. In comparing endemic (Cedar River, Washington) and epidemic (Idaho) populations, different response patterns emerged in the two areas. Epidemic beetles responded in greater proportions to secondary attraction (pheromones) than did endemic beetles, and displayed a strong perference for vertically positioned host material. Endemic beetles from the local Cedar River population responded more readily to host or "primary" attractants while preferring host material of a horizontal configuration. Furthermore, seasonal monitoring of flight and attack behavior in Cedar River had revealed a clear heterogeneity within the endemic population.

Research in 1975 was directed at a local comparison of individuals from both populations to further refine interpopulational differences by removing the geographical factor. In addition, other experiments were replicated in both areas testing each local population where it naturally occurs.

In one test conducted in the Cedar River watershed beetles were marked as they emerged for flight. The beetles bearing fluorescent powder were then retrieved from traps placed in concentric circles around the release point. Although few of the marked beetles (8 Cedar River; 9 Idaho) responded to attractants within the trapping circles, a differential response pattern between populations was observed. Once again, the endemic (Cedar River) beetles were found to be more responsive to horizontal than to vertical configurations, had a greater proportion of individuals landing on primary atractants (8 Cedar River; 3 Idaho) and flew further than epidemic beetles prior to responding to attractants.

Other experiments indicated that the secondary attractant (pheromone) produced by Cedar River (endemic) females is "preferred" by both local popoulations over that produced by Idaho (epidemic) females feeding in host material. Additionally, it was found that one repellent pheromone (trans-verbenol) may have differential activity between epidemic and endemic populations.

The proportion of each population responding to secondary attraction was tested, but results were inconclusive due most likely to artifacts of experimental design.

Intrapopulation studies with endemic beetles were directed primarily at the separation of individuals into "pioneer" and "follower" beetles. These differences remain unresolved, but continually appear throughout all experiments conducted over the course of the flight season of *D. pseudotsugae*. "Pioneers," or those beetles responding exclusively to host odors were more prevalent early in the 1975 season and were considerably less frequent as the season progressed. Behavior studies on these two "groups" failed to qualify these differences, requiring further elaboration of experimental techniques.

The role of nutrition as it relates to pheromone production was touched upon and gave interesting leads to be followed up next season. Beetles having developed in thin phloem seemed to either (1) produce greater amounts of attractant when feeding as adults or (2) feed for greater periods of time in test bolts, since they were more attractive than females reared in thick phloem portions of the tree.

Although results of the 1975 field season are still incomplete, a few study areas are immediately apparent and shall be pursued during 1976.

1. Isolation of "pioneer" and "follower" beetles from within an endemic population, defining the role of each, as each relates to population level and attack patterns.

2. Investigation of the nutritional basis to population differences within the endemic situation.

3. Further studies on the attack patterns in low and high level populations.

4. Comparative study of roles of the 10 active compounds in the pheromone attraction complex of _D_. _pseudotsugae_ for both epidemic and endemic populations.

5. Continuation of genetic studies of gene frequencies from an array of Douglas-fir beetle populations.

6. Host factor considerations as they relate to behavior differences in beetles.

7. Further work on identification and field testing of primary attractants.

In addition, a cooperative study will be laid out to examine litterfall and decomposition rates in stands with epidemic and endemic populations and control stands in order to examine the possible role of bark beetles in carbon and nutrient cycling.

Comparison of ecosystem environments. William Emmingham (Oregon) has monitored in conjunction with Ted Daniels (Utah), Fred Johnson (Idaho), and Ken Reed (Washington) environments in series of stands along environmental gradients. Stand temperature and plant moisture were the major variables measured and data have been incorporated into photosynthesis and transpiration simulators.

Twenty-two reference stands are being monitored in the H. J. Andrews Forest and maximum pre-dawn moisture stresses for selected stands for 1970-1974 are presented in Table 11. Vegetation descriptions and climatic data are nearly complete for the following extensive sites, Idaho (5), Alaska (2), Colorado (2), Utah (3), Arizona (1), Washington (5).

Some interesting data have emerged from monitoring of plant moisture stress. Small Douglas-fir and true fir trees in clearcuts are generally under less moisture stress than those under a well-developed forest canopy of the same forest type. This was especially true of the more droughty Douglas-fir/ocean spray type. Reduction of the leaf area probably leads to less total water loss through evapotranspiration even though evaporative demand in the open increased. This contradicts the commonly held belief that trees die in clearcuts because of lack of water. The water may be there, but roots of young plants apparently cannot reach the available water.

In contrast to the above observation, small residual western hemlocks were generally under more stress than similar hemlock in undisturbed

Table 11. Maximum pre-dawn plant moisture stress on H. J. Andrews reference stands from 1970 through 1974 (atm).

Reference stand no.	3 Sep 1970	20 Aug 1971	31 Aug 1972	23 Sep 1973	23 Oct 1974
1	23.0	16.0	26.6	18.4	25.7
2	8.3	6.0	15.4	9.7	8.4
3	9.8	3.7	15.0	6.4	7.6
4	8.3	3.6	8.8	6.1	8.1
5	--	8.1	13.8	7.9	8.2
6	--	4.4	14.4*	11.1	12.6
9	--	6.3	9.6*	8.1	8.0
10	--	9.4	13.0*	11.2	11.4
14	--	--	--	9.2	13.4

*6 September 1972.

forests. Studies by Steven Running indicate that hemlock may be unable to control water loss through its stomata.

Integration of results and examination of ecosystem behavior through simulation modeling.

(a) Carbon, water, and nutrient cycling modeling. Much of the data collected by Coniferous Forest Biome researchers has been integrated into the carbon, water, and nutrient cycling model of Phillip Sollins and Gordon Swartzman. The model which was initially developed with H. J. Andrews Forest data has undergone considerable development in the past year. Figures 11, 12, and 13 show the conceptual framework of the three modules.

The carbon-water modules of the model have been termed CONIFER and Gordon Swartzman has been largely responsible for development of this part of the overall model while Phillip Sollins has concentrated largely on development of the nutrient module. CONIFER has been expanded and improved by: (1) including energy balance for snowpack dynamics as well as for evapotranpiration, (2) running it for two years of weather data, (3) refining the litter moisture dynamics, and (4) including (and assembling) more process and annual total information.

Two manuscripts have been prepared for publication, (1) a manuscript describing model structure and assumptions, (2) a manuscript outlining modeling philosophy and methodology for model building and evaluation.

A complete documentation of CONIFER is being prepared as a biome bulletin, and a methodology for running a canonical data set having realistic correlation properties between major environmental factors (e.g., solar radiation, precipitation, dew point temperature, air temperature) has been developed and tested on H. J. Andrews Forest data. The model has been used as an experimental tool to examine effects of defoliation to thinning as well as abiotic perturbations.

CONIFER is currently being calibrated for a young-growth Douglas-fir stand using Thompson site data. In addition, the nutrient module will be expanded to incorporate nutrient effects on growth.

(b) Simulation of growth and nitrogen dynamics in a second-growth Douglas-fir forest. A mathematical model is being developed by Philip Riggan that combines information about the nitrogen dynamics and growth of a second-growth Douglas-fir stand with hypotheses concerning the influence of nitrogen nutrition upon growth. The model will be used to test the plausibility of the incorporated hypotheses and given their validity, evaluate the sensitivity of the system to component processes, and generate hypotheses concerning the behavior of the system under various perturbations and levels of nutrition.

The model solves a set of differential equations numerically for the values of 15 state variables with time. The model structure is shown in Figure 14. It describes the growth and death rates of foliage, wood,

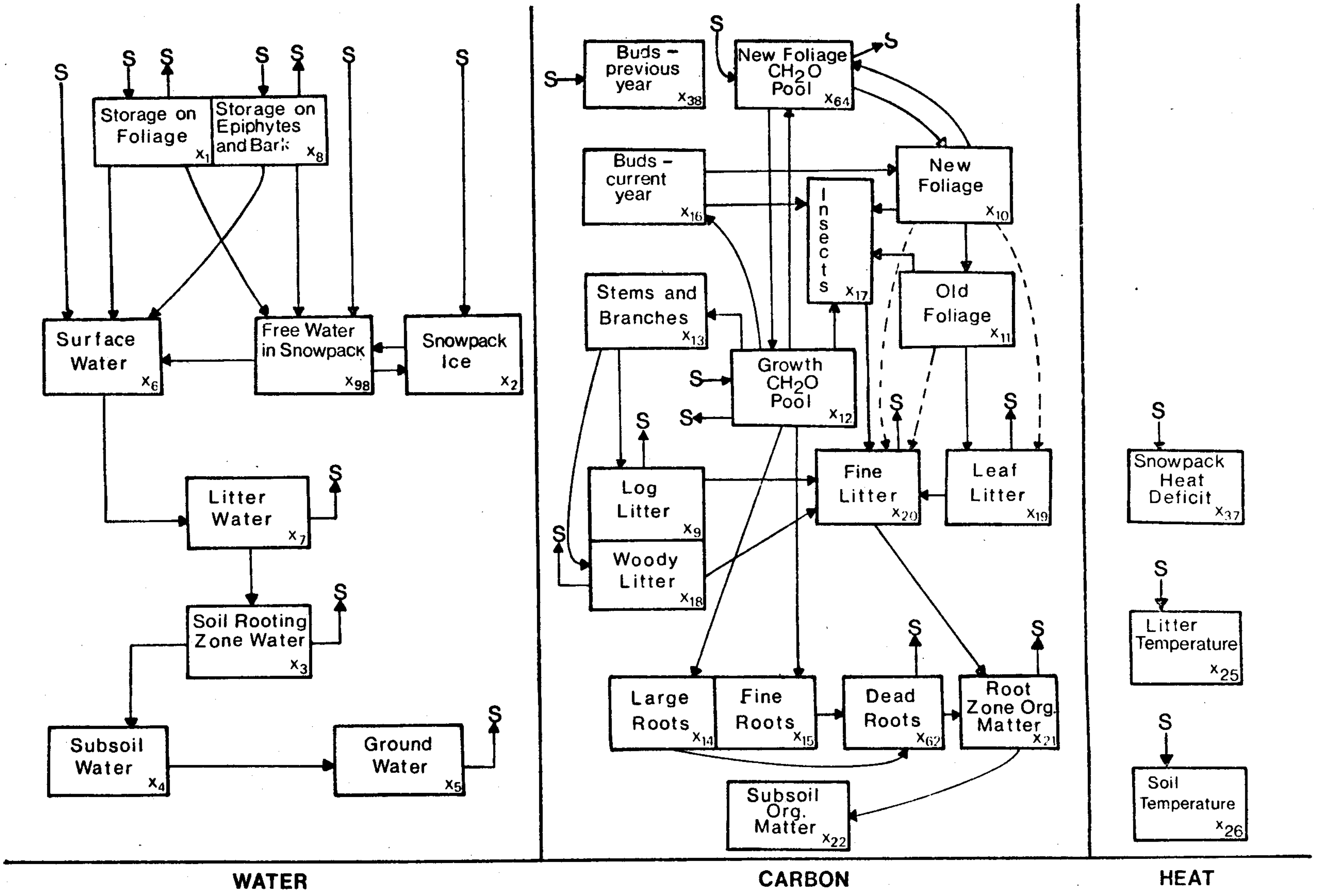

Figure 11. Conceptualization of carbon, water, and energy compartments and flows.

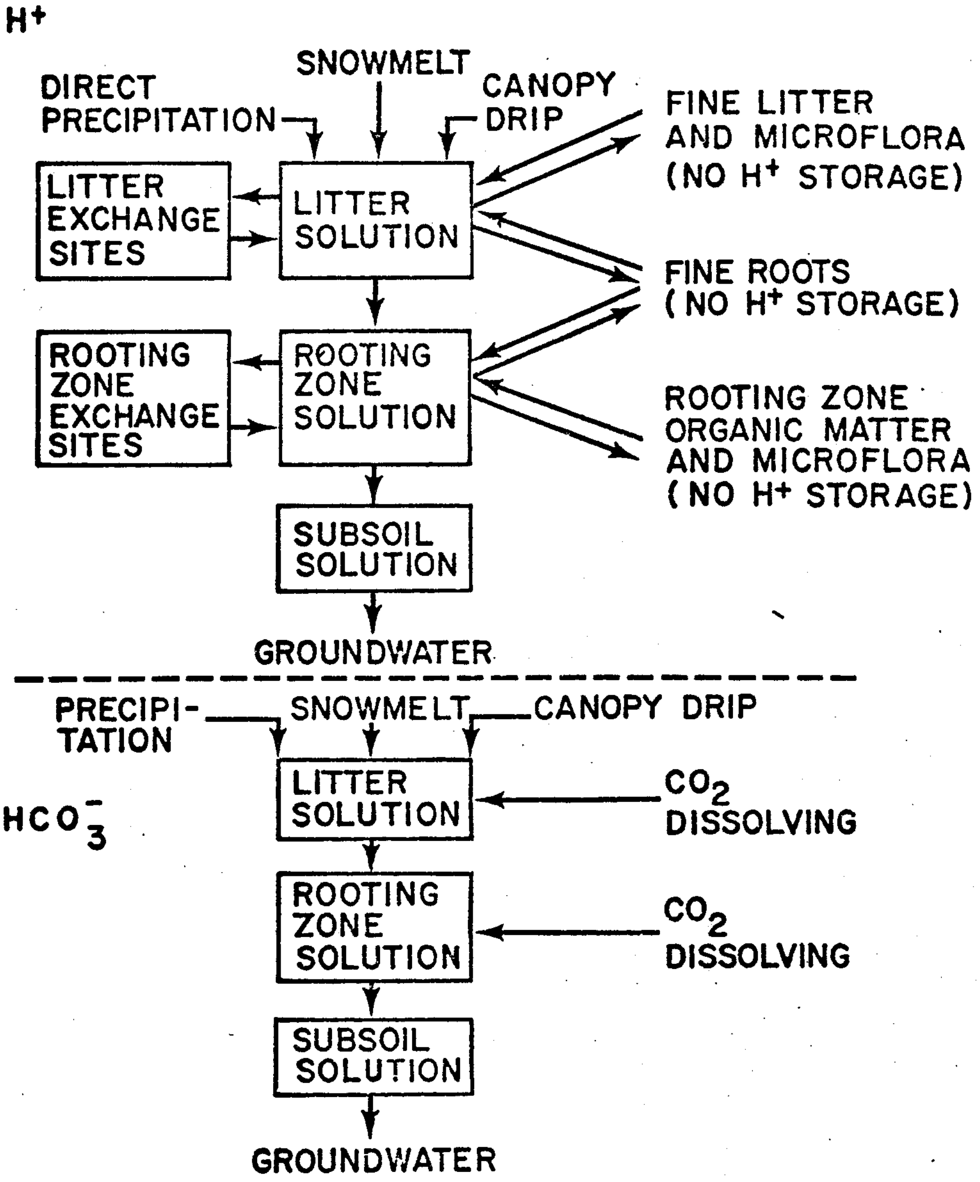

Figure 12. Conceptualization of the H^+ and HCO_3^- compartments and flows.

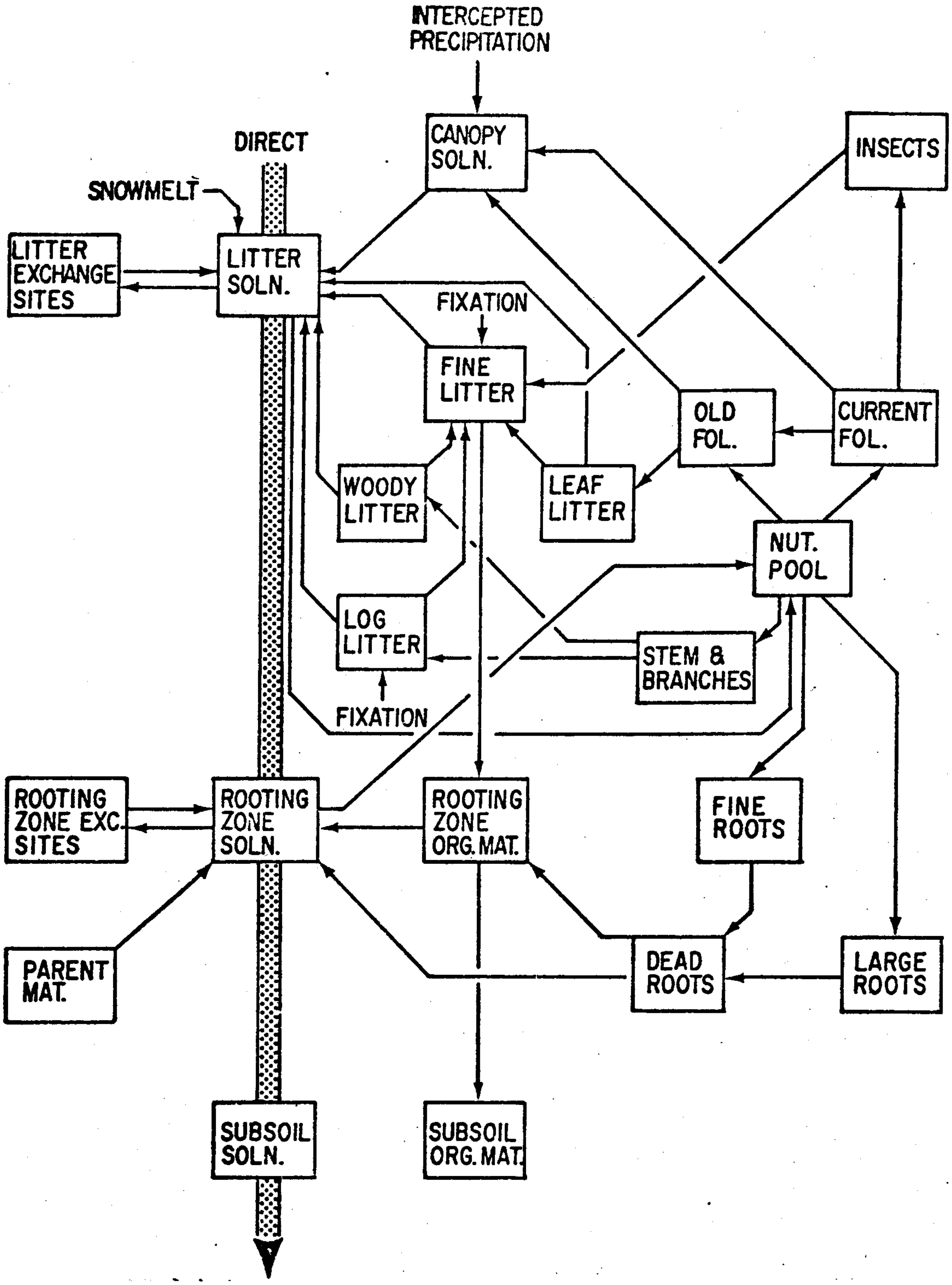

Figure 13. Conceptualization of the cation and anion compartments and flows.

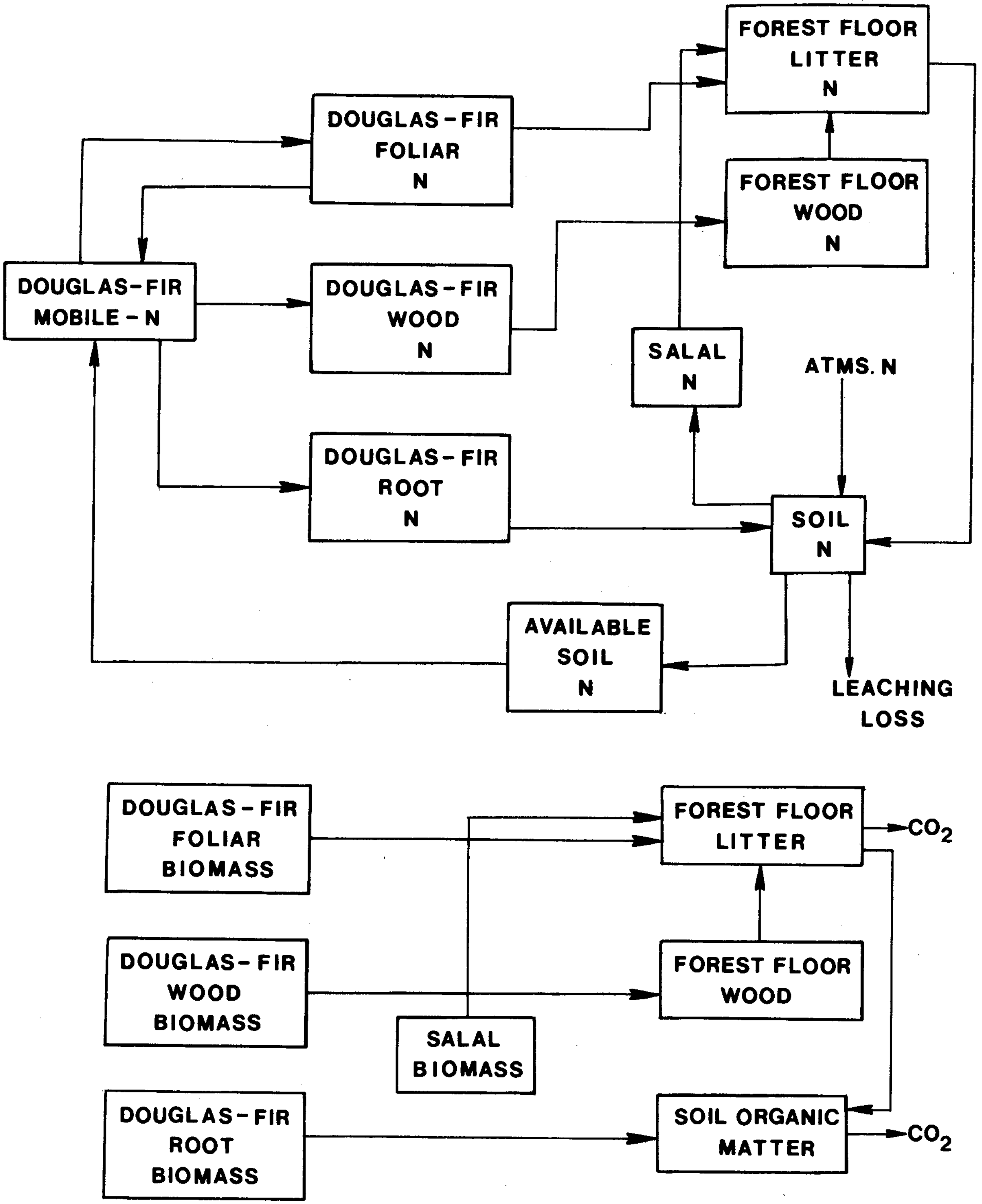

Figure 14. Structure of nitrogen model.

and roots of the Douglas-fir overstory and salal understory; forest floor accumulation and decay; and nitrogen transfers between vegetation, forest floor, and soil, and within the tree overstory. Nitrogen within the trees is partitioned between a free form including free amino acids and amides, and a fixed form which includes structural and enzymatic protein.

Biomass dynamics in the trees are governed by changes in the nutritional state of the stand. Growth of foliage, wood, and roots is described as a function of the fixed nitrogen concentration in foliage, which assumes the levels of protein are affecting metabolism associated with growth. The rate of transfer between the free and fixed forms in foliage is functionally related to the free nitrogen concentration. Thus, the rate of incorporation of nitrogen into new foliage and the senescence of protein and/or redistribution of amino acids from older tissue are assumed to be controlled by amino acid concentration.

Death of foliage is also described as a function of fixed nitrogen concentration. Thus, low levels of nutrition lead to increased senescence and litterfall. Death of whole trees is described as an empirical relation between number of trees per hectare and the average diameter at breast height (d.b.h.).

Uptake rates are computed from total soil nitrogen values, assuming a constant relation between total and available soil nitrogen. Forest floor decomposition is currently described as a constant rate.

The functional relationships for nitrogen and biomass dynamics are based on annual transfer and accumulation data from John Turner. This data includes an age sequence of 42-95 years and a nitrogen manipulation experiment conducted on a 42-year-old stand. Data for tree geometry and root biomass and whole tree death are from past workers at the A. E. Thompson site. The functional relations used in the model are shown graphically in Figure 15.

Although this model is designed primarily to analyze the effect of nitrogen nutrition upon growth, other environmental factors such as light are included empirically. Thus, suppression and death of whole trees, which may be due to low light levels, is included as a function of change in d.b.h. Also, increased self-shading and litterfall as a result of fertilization and changing growth and death rates was included in litterfall estimates. This points out that environmental factors are often interrelated. Therefore, the model describes the response of the stand to the overall environment with different nutritional levels, and not just the component of the response directly attributable to nitrogen.

A preliminary model run of 50 years' duration is shown in Figure 16. The model is quite stable and shows accumulation of biomass in foliage and wood, increase in forest floor weight and nitrogen content, and slowly increasing soil nitrogen content.

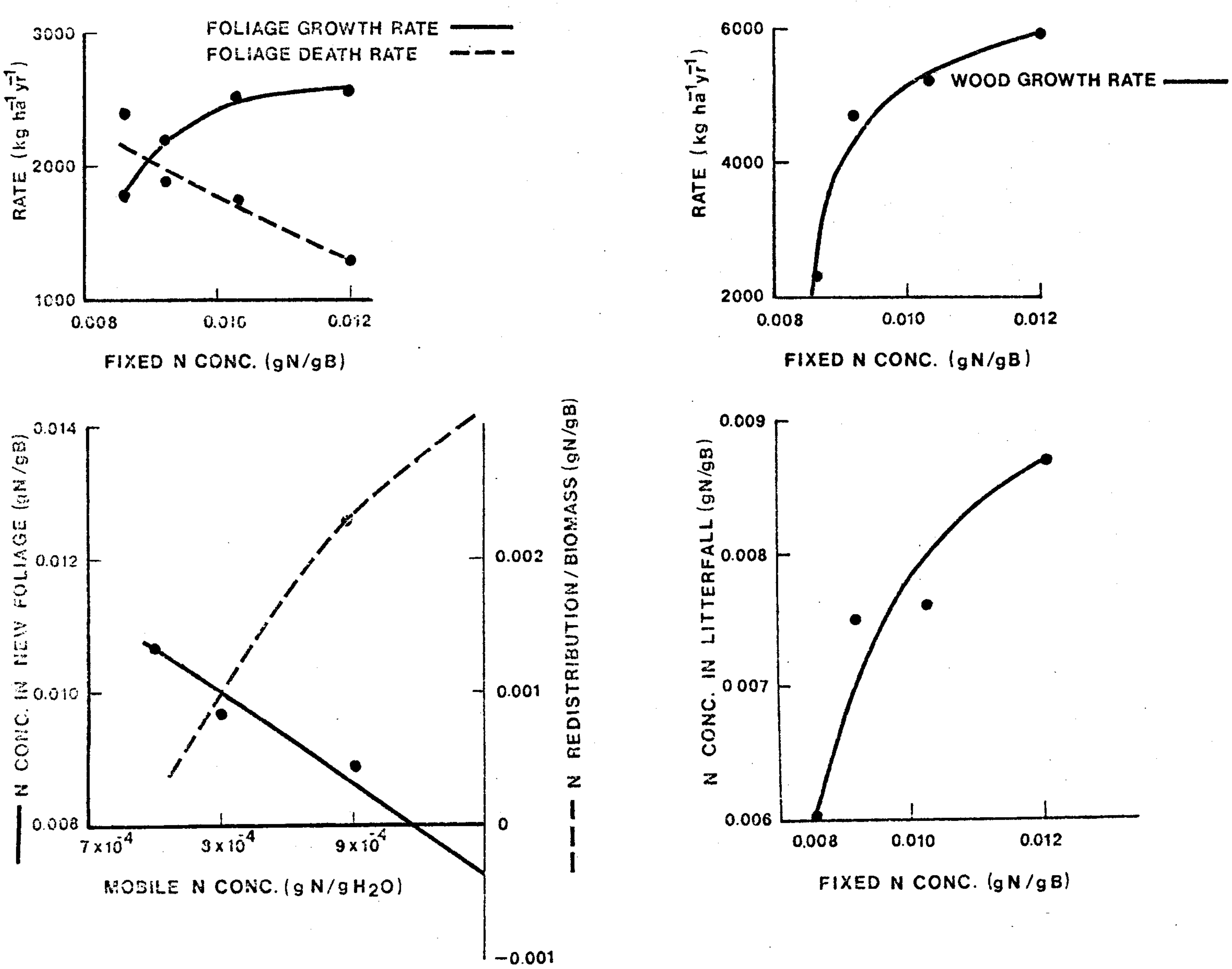

Figure 15. Functional relationships used in the model;
B = biomass, N = total nitrogen.

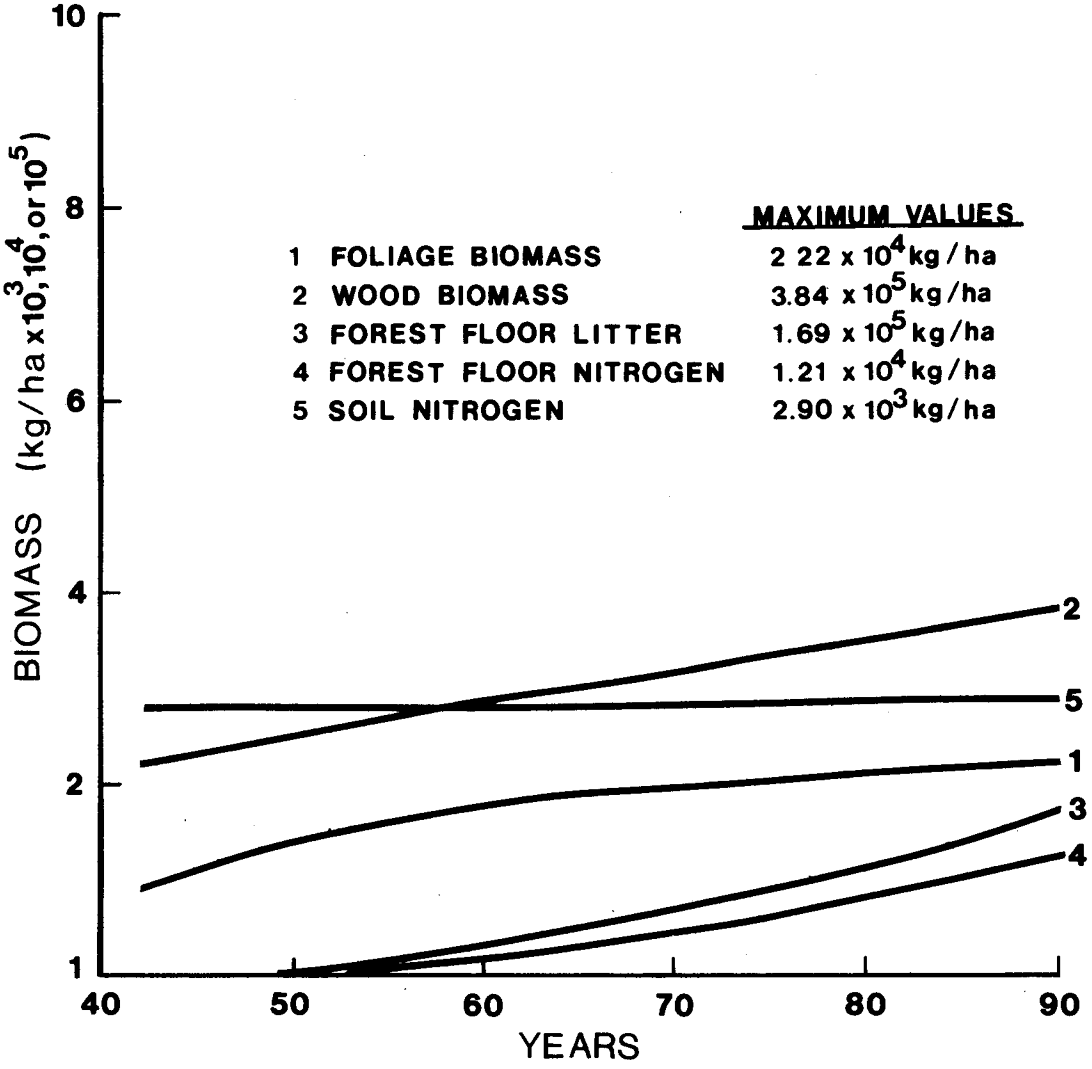

Figure 16. Preliminary model output.

Strategies of individual terrestrial ecosystems.

(a) Biological mechanisms controlling nutrient uptake--Kermit Cromack, Phillip Sollins. As a byproduct of research on litter decomposition, soil and litter solution chemistry, and modeling of ion transport and uptake, we have formulated, and to a large extent experimentally established, a theory of the functioning of mycorrhizae, and the role of organic acids in nutrient solubilization and uptake. Oxalate salts, particularly calcium oxalate, and HCO_3^- play key roles in these mechanisms thus reinforcing our desire to model aqueous HCO_3^- and organic acid transfers in forest ecosystems.

A complete description of our hypothesis is being prepared including supporting work from published reports, some dating back to 1887, and recent experiments of our own. Thus we will only outline the theory and briefly discuss its significance.

First, we believe that a substantial part of the energy source of mycorrhizal fungi is organic acids produced by roots. On the basis of published data by Smith at Yale, we feel that malic, acetic, and oxalic acids play particularly important roles. Uptake of organic anions by fungi is accompanied by release of HCO_3^- which is taken up by the roots. We believe that because a significant energy source for mycorrhizal fungi is organic acid anions, considerable quantities of anions are released by fungi in exchange. These include HCO_3^- and essential nutrient species such as NO_3^- and $HPO_4^=$, or perhaps low energy organic anions containing N and P.

Second, we believe that fungi (both mycorrhizal and free-living saprophytic decomposer species) release large amounts of oxalate, often accompanied by K^+ rather than H^+. The oxalate is a low energy product (60 cal) compared to glucose (683 cal) and therefore does not encourage the growth of potentially competing flora. The oxalate combines with Ca and any free Al or Fe, to produce essentially insoluble compounds. By removing Ca, Al, and Fe, this precipitation reaction increases the rate at which $HPO_4^=$ is solubilized from $Ca_3(PO_4)_2$, $Al(OH)_2H_2PO_4$ and $Fe(OH)_2H_2PO_4$, resulting eventually in replacement of insoluble phosphate compounds with the corresponding oxalates. Even such insoluble organic forms of phosphorus as calcium phytate (calcium inositol hexaphosphate) may be decomposed with oxalate. We found that treatment with L-malic acid followed by addition of oxalic acid resulted in nearly complete release of phosphorus from phytin.

If oxalate is released into soil solution with K as the accompanying cation, then the replacement of Ca with K as the Ca is precipitated will lead to an increase in pH. This provides a mechanism whereby fungi can increase the pH of their surroundings by releasing K^+ and oxalate anion. That calcium oxalate accumulates in litter, particularly on the surfaces of fungi was first established in 1887 by De Bary. That this also occurs in forest litter is clearly shown by current results from electron probe microanalysis of fungi and by gas chromatographic analysis of decomposing wood for oxalic acid.

Third, the fate of these large amounts of calcium oxalate, and the smaller amounts of iron and aluminum oxalates, interests us. Bacteria and streptomycetes have been reported in the literature, and we have isolated from Douglas-fir ecosystems species of both types of microorganisms, which can decompose calcium oxalate. Fungi apparently depend upon other microorganisms for the decomposition of insoluble oxalates, possibly due to the low solubility of most divalent cation complexes with oxalic acid. We have isolated these bacteria from Douglas-fir roots, heartrot columns of white fir, and gut systems of soil arthropods. From an analysis of the stoichiometry of this reaction we hypothesize that metabolism of the insoluble metallic salts of oxalic acid should raise the pH of the medium. This may explain the increase in pH that occurs as litter substrates pass through the guts of various soil arthropods, and may provide a biochemical basis for operations of the calcareous gland in earthworms.

Fourth, we think that fungi utilize advantageously the variations in pH within the litter and soil to colonize more acid substrates and that this relates to the exchange of HCO_3^- and organic anions between mycorrhizal fungi and roots discussed above. Our idea is that in regions of lower pH fungi release K^+ rather than H^+ to balance cation uptake and release oxalate anion rather than HCO_3^- as their metabolic waste product. As discussed above, this both solubilizes P and raises the pH in the vicinity of the fungi. In more alkaline regions, fungal hyphae can release H^+ and absorb excess potassium. The region surrounding fine roots is more acid due to the large amounts of organic acids produced. Mycorrhizal fungi may respond by releasing K in this region also. We do not think oxalate is released here in large quantities because as mentioned above we believe release of HCO_3^- and subsequent uptake by the roots triggers the organic acid release. In other words, oxalic acid is not a significant anion released by mycorrhizal fungi to roots, while oxalic acid release from hyphae distal to roots in the soil is a significant process essential to uptake of phosphate and ionized nitrogen species.

In current experimental work with Jim Trappe and his students, we have successfully grown fungi on organic acid media and shown accumulation of calcium oxalate. We proposed to study the solubilization of P from $Al(OH)_2H_2PO_4$ or $Fe(OH)_2H_2PO_4$ by fungi and to test for the accumulation of iron and aluminum oxalates. The role of HCO_3^- in soil transport processes, successfully investigated by Dale Cole and students at the University of Washington, has been extended to include a major role for this anion's nutrient solubilization and subsequent uptake by fungi. Bicarbonate labeling by ^{14}C of mycorrhizal fungi has been documented from published work by Harley and Reid, and for both saprophytic and mycorrhizal fungi in current work by Ausmus at Oak Ridge National Laboratory. We anticipate in future work an interaction and probable collaboration with a number of people, including Beverly Ausmus at Oak Ridge, Robert Todd at the University of Georgia, Dale Cole and Robert Edmonds at the University of Washington, Jim Trappe and his students at OSU, and Vern Cole at Colorado State University.

(b) Maritime influences on forest ecosystems--Charles Grier and **Robert Logan**. Studies of forests growing in the zone of strong maritime influence along the northwest coast suggest that several links may exist between these forests and the adjacent nutrient-rich upwelling ocean ecosystems. Large quantities of nitrogen, phosphorus, and nutrient cations as well as large amounts of sodium and chloride ions are annually introduced to these ecosystems by sea spray. Large nutrient inputs in combination with high forest productivity and flocculation of soil organic colloids by sodium ions has resulted in large accumulations of organic matter and nitrogen in the soil of these ecosystems. For example, a 130-year-old hemlock-spruce stand on the central Oregon coast has a total biomass of 1854 t/ha and nitrogen accumulation of 36 t/ha. Of these amounts, 776 t/ha of organic matter and 35 t/ha of nitrogen are in the soil.

The maritime influence also appears to limit productivity of the forests of this zone. The coastal environment supports large leaf areas and rapid growth. For example, net primary production of 36 t per ha per yr has been observed in a 26-year-old forest in this area. However, when these forests reach a height where strong Pacific storms can penetrate the canopy, large amounts of foliage, up to a third of annual foliage production, are lost by wind damage. This in combination with unusually high loss of individual trees by windthrow causes a reduction in stand growth rates.

(c) Response of Douglas-fir ecosystems to urea fertilization--Dale Johnson. The application of urea-N to the forest affect the nature of both the biological cycling of nitrogen and the soil leaching processes. Given luxury amounts of nitrogen, the trees rely less upon internal redistribution to meet their nitrogen requirements for growth (Turner 1975).* Less nitrogen is retranslocated from older to newer foliage, and foliage retention time is increased resulting in a buildup in the foliar nitrogen pool. Conversely, when nitrogen is stressed (by the addition of carbohydrate to the soil, widening the C/N ratio), the trees respond by increasing the amount of nitrogen retranslocation to meet growth needs. The ability to retranslocate nitrogen gives the trees the flexibility to survive nitrogen deficient conditions and to capitalize on nitrogen-rich conditions.

Urea fertilization has profound effects on the amount of cation transfer in upper soil horizons as well. This has been found to be true at the A. E. Thompson site (Crane 1972)** and at the Findley Lake site (D. Johnson pers. comm.). Urea is a highly soluble nonionic polar organic compound, and it is therefore readily leached if applied during rainy

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*Turner, J. 1975. Nutrient cycling in a Douglas-fir ecosystem with respect to age and nutrient status. Ph.D. Thesis, University of Washington, Seattle. 191 p.

**Crane, W. J. B. 1972. Urea-nitrogen transformations, soil reactions, and elemental movement via leaching and volatilization in a coniferous forest ecosystem following fertilization. Ph.D. Thesis, University of Washington, Seattle. 285 p.

periods. However, urea hydrolyzes to ammonia and carbon dioxide through an enzymatic reaction involving urease. (Urease is commonly present in forest soils). NH_3 then consumes hydrogen ions to form NH_4^+ and CO_2 hydrolyzes to form carbonic acid which in turn dissociates into H^+ and HCO_3^-, dependent upon pH. Since carbonic acid is a weakly dissociated acid and there are two NH_3 molecules produced for each CO_2, the net result is a sharp rise in solution pH. In most cases HCO_3^- remains the dominant carbonate form (pH remains near or below 8.3), so that an ammonium bicarbonate solution results. (This must result in the initial transfer of NH_4^+ to exchange sites in order to maintain mass balance). As the ammonium bicarbonate solution moves through the soil profile, NH_4^+ displaces native cations such as K^+, Ca^{++}, Mg^{++}, and H^+ from the exchange sites by mass action. Thus, urea fertilization makes many cation nutrients available for uptake in addition to NH_4^+. Displaced H^+ combines with HCO_3^- to form H_2CO_3, so that bicarbonate concentrations as well as ammonium concentrations decrease as solutions pass deeper into the soil. The result is that NH_4^+ is largely retained in the upper 15 cm of the soil. Should the initial hydrolysis of urea be delayed or blocked, far greater leaching losses of N would occur. In most cases the hydrolysis is rapid enough so that little N loss occurs, however.

For reasons unknown, nitrification did not occur following urea fertilization. This is fortunate in terms of N retention, in that NO_3^- is a relatively mobile anion in the soil and would readily leach out.

In total, then, it appears that both the biological and physical mechanisms regulating nitrogen transfers retain nitrogen in useful and available forms in the system following urea fertilization.

3.2.1.2 Environment and succession.

Succession modeling on an ecosystem basis: Ken Reed has the major responsibility for development of this research area which is focused on a succession model (SUCSIM) which is based on relationships between how plants respond to their environment and the successional patterns resulting from response. The model is planned to relate tree growth and succession to temperature, light, and moisture regimes as well as to mortality, tree recruitment, and soil nutrient status.

The model currently incorporates effects of temperature, moisture, and light on growth. By the end of 1975 preliminary models of mortality, growth, and recruitment will be running. Growth of understory species will also be incorporated.

The development of a data base for parameter estimation and model development has been an important accomplishment in 1975. Much time has been spent digitizing data and writing programs to process the data. To date digitizing and merging of the 1974 M-3 weather data and thermograph charts have been completed. Further processing is necessary for computation of the environmental ordinates of our research plots.

In addition, Gordon Swartzman has developed a documentation scheme for the SUCSIM which reflects computer code. He has used the CONIFER model to evaluate realism of growth curves as affected by environmental variables and adjusted the light attenuation and tree growth model to reflect more realistic output.

Additional to the Mt. Adams (Washington) field sites which have been in operation for some time, five soil and air temperature thermographs were set up in the Cedar River watershed. Plant moisture stresses are currently being collected from these sites plus 16 other sites in the Cedar River in coordination with Jim Long.

3.2.1.3 Land use model.

Land use modeling is the major responsibility of Joan Hett. There have been three major modeling developments, (a) the Cedar River land use model, (b) the Mount Adams land use model; and (c) cooperative modeling with SUCSIM.

Cedar River land use model: A preliminary simulation model of secondary succession for the upper Cedar River drainage has been parameterized using a vegetation map provided by Richard Taber and his wildlife students, and past forestry research conducted in the drainage. The vegetation map was prepared from information derived from ERTS photographs and forest management records provided by METRO. Information included on the map includes land use type by broad categories, canopy closure and dominant tree species where appropriate, and year of stand origin if available from management records. Although there is no community information at a finer resolution, Jim Long has provided additional information on community types based on elevation and aspect allowing us to expand the ecological information on the map. This map has been digitized by 10-acre cells and stored on the CDC 6400 in a data set which can be retrieved using SVENESE (a data retrieval program developed by the RANN sponsored SVEN project). Also stored with the vegetation information are physical characteristics of each cell including slope, aspect, elevation, and distance from water and roads. Initial conditions for the Cedar River model are obtained from this data set.

The Cedar River watershed has been an area of many graduate research studies and a survey of these has provided growth data on many of the dominant species. What is missing is ecological, growth, and successional information on the lowland red alder (*Alnus rubra*) communities. A survey of these communities will be completed during 1975 and results included in the model.

Following a modeling review in April 1975, objectives of the Cedar River model were modified at the suggestion of the reviewers. Now, we are designing a model to examine elk/vegetation interactions which will include effect of elk on the naturally expected succession sequence. Because the elk have their greatest impact on the vegetaion in the lowland alder communities, we must collect information discussed above before the model is finalized. We plan to finalize and document the model in time to present it at a MAB/SCOPE workshop in January 1976.

Mount Adams land use model: Prior to the 1975 field season, a preliminary vegetation map of the southeastern region of Mount Adams was prepared from aerial photographs and a data set provided by the State of Washington Department of Natural Resources (DNR) from their GRIDS program. GRIDS (Gridded Resource Investory Data System) is a one-acre sample of each of ten acres of land managed by the DNR throughout the state of Washington. Stored data can be retrieved in map form, showing land use and/or forest type by township.

The preliminary vegetation map was field checked this summer and increment borings of trees in each size class in each forest type were taken. These cores will allow us to age each size class and calculate both species replacement rates and species sequences as well as allowing calculations of growth rates for each species.

The preliminary Mt. Adams model showing undisturbed successional sequences will be finalized by January 1976. At that time forest management and biological factors affecting succession as well as forest economics will be included.

Cooperative program with SUCSIM: Cooperation with the SUCSIM project has taken the form of data analysis and data collection. The Cedar River environmental transect has been instrumented and plant moisture stress data were collected on a three-week schedule. These data will contribute to succession research being done by Jim Long and to the Cedar River land use model by providing environmental gradient constraints for transfer rates.

There has been a concentration of effort on digitizing the meteorological data collected by Ken Reed and the SUCSIM project. 1974 data are now completed and ready for use and a recent purchase of an optical scanner for the NOVA computer at the University of Washington will streamline the entire digitizing process allowing us to keep up to date as data comes in from the field.

The major thrust for 1976 will be to continue development and testing of Mount Adams regional land use model. This will include the following:

1. Forest management, fire, and pest impacts on the successional model defined in 1976.
2. Conceptualization and incorporation* of economic constraints on the model.
3. Definition and development of couplings needed to use SUCSIM for parameter estimates and possible driving functions.

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*Dependent upon support from DNR.

3.2.2. Analysis of Watersheds

This theme is being investigated at two research sites; watershed 10 in the H. J. Andrews Forest in Oregon, which is also the site of land-stream interface studies, and the Findley Lake watershed which is the site of land-lake interface studies. Richard Waring is coordinating the studies.

Three major research areas are being investigated at each site, as shown in Figure 17; (a) hydrology and nutrient export (which also includes erosion in watershed 10); (b) watershed internal dynamics; and (c) the terrestrial-aquatic interface component. Research projects and principal investigators are also shown in Figure 17. Publications resulting from this research are presented in Appendix II.

3.2.2.1. Watershed 10.

Considerable monitoring of watershed 10 has been carried out over the past years. One of the objectives of the Biome program was to investigate effects of clearcutting. Thus during the summer of 1975, watershed 10 was logged. Plots will be re-established in the fall to monitor vegetation, residue accumulation, root decay, soil, litter and seep chemistry, erosion, and total export of water, sediment, and nutrients. In addition, stream interface work will continue to compare the biological processing of energy and nutrients received directly or through export from the terrestrial system and upstream areas.

Many of the research results presented below are testing hypotheses based on our understanding of basic processes controlling the accumulation and transfer of energy and matter through coniferous forest and stream ecosystems.

Watershed internal dynamics. Research by the watershed internal dynamics group, which is coordinated by Charles Grier, is concerned with examining biological and related physical and chemical processes operating within coniferous forest watersheds. The overall objective of these studies is to study movement, accumulation, and processing of carbon, water, and nutrients in ecosystems comprising defined watersheds.

Figure 18 shows the organizational framework for studies being conducted by this group of scientists. Not indicated in the diagram are our efforts to describe simultaneous movement of carbon, water, and nutrients. This largely successful research, based primarily on data and concepts from this group, is described in detail in the section on modeling.

The watershed internal dynamics group has made substantial progress in research synthesis over the past year in studies on watershed 10, the principal research site, and on comparative study areas across western Oregon. The following describes some of the highlights of the past year's work.

Biomass, net production, and nutrient cycling. This project conducted by Charles Grier and Robert Logan is examining the old-growth forests on

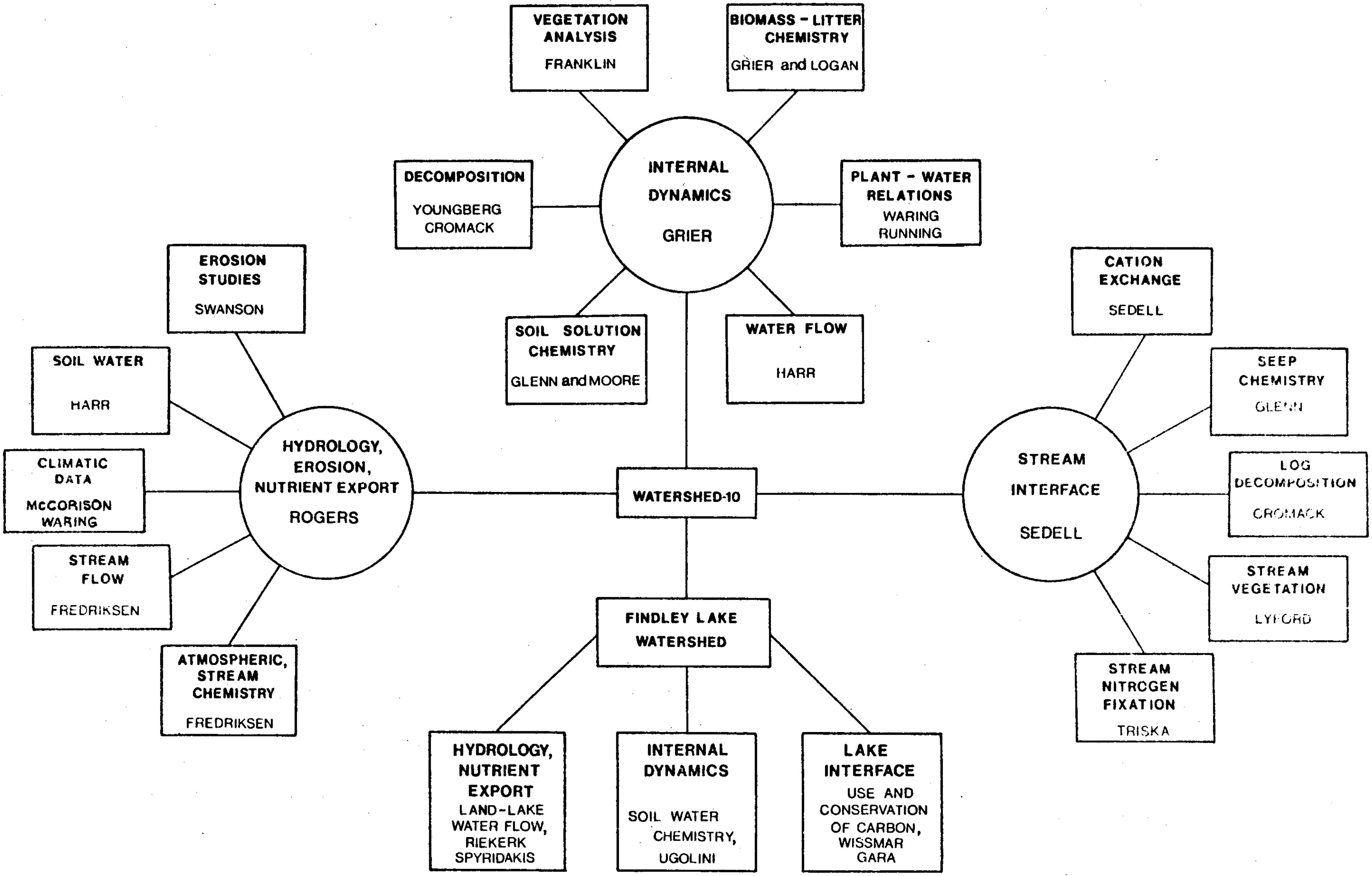


Figure 17. Research organization in the analysis of watersheds component.

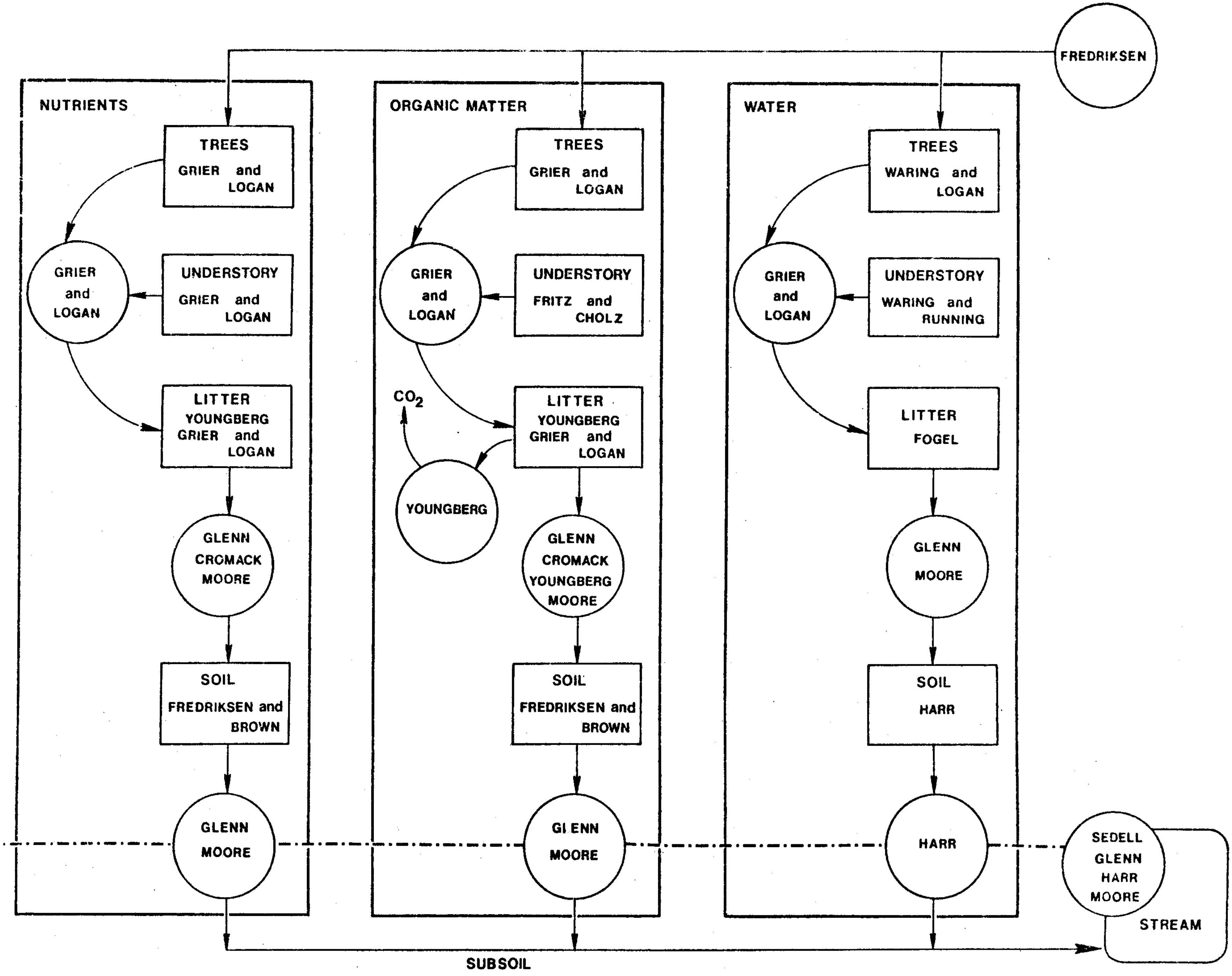


Figure 18. Conceptual framework for studies of Watershed 10 internal processes. Boxes = accumulations of carbon, water or nutrients; Circles = transfers or utilization processes; Names = scientists responsible.

this watershed which are in an early climax successional stage. At present, net primary productivity of the overstory tree layer of the watershed averages about 2 t/ha, while productivity of the herb, shrub, and small tree layer averages 1.8 t/ha. Because of the higher nutrient concentrations in understory species and their higher rate of foliage turnover, larger quantities of nutrients are being cycled through the understory of several community types on this watershed than through the overstory. Turnover of forest floor organic matter averages about 10 years through a forest floow averaging 60-65 t/ha.

Foliar nitrogen concentrations in old-growth trees on watershed 10 are 15%-20% lower than those in adjacent younger stands. In contrast, foliar phosphorus concentrations average 30%-100% greater than in younger stands. Moreover, concentrations of N, P, K, Ca, and Mg are generally higher in older foliage than in current year's foliage. These observations indicate that redistribution of nutrients from older to current foliage which apparently occurs in young-growth stands at the Thompson site is apparently not occurring in this stand. Changes in N and P concentrations in old-growth trees relative to younger trees on comparable sites suggest that physiological changes occurring in older trees are manifested even in new growth. The high foliage P concentrations are reflected in much higher annual P return in throughfall, stemflow, and litterfall. For example, movement of P to the soil by throughfall is 1-2 kg per ha per yr on watershed 10 compared with 0.3 kg per ha per yr in a 37-year-old stand. Phosphorus concentrations in needle litterfall are equal to P levels in green foliage of comparable younger stands.

All field measurements and sampling on watershed 10 were terminated as of 1 June 75, prior to scheduled harvest. Current activities are focused on data processing and chemical analysis of remaining samples.

The following hypothesis will be investigated in 1976. Barring disturbance, a gradual shift in relative proportions of net production and nutrient utilization by overstory and understory vegetation occurs as a stand ages. In some cases production and nutrient utilization by understory and young climax vegetation can exceed that of overstory trees.

<u>Watershed studies on terrestrial litter decomposition</u>. (a) <u>Decomposition studies based upon habitat stratification of watershed 10</u>: Two years' weight loss decomposition data have been obtained by Kermit Cromack for Douglas-fir needle litter and woody litter categories consisting of Douglas-fir bark, cones, and twigs on four major habitat types corresponding to subdivisions of these habitats upon watershed 10. Major initial finding is a definite trend in needle decomposition with habitat types, which validates for the decomposition process at least, the approach taken in stratifying a Douglas-fir watershed ecosystem such as watershed 10. The habitat decomposition studies will continue for an additional year.

(b) <u>Environmental measurements</u>: Regressions have been developed relating air and litter temperatures such that extensive use can be made of air temperature data from other locations. Litter moisture measured gravimetrically is being converted to litter water potential by use of a moisture characteristic curve being determined at the present time.

(c) Nutrient release and cation exchange capacity of decomposing litter: Nutrient status of needle and woody litter is in progress for the two-year decomposition series and includes N, P, K, Ca, Mg, Mn, Fe, Cu, B, and Zn. The carbon/nitrogen ratio has decreased significantly in the needle, cone, and twig litter, but not in the bark litter, corresponding generally to decomposition trends in these litter components. Cation exchange capacity determinations have been made comparing initial conditions of litter components with decomposition time series. Cation exchange capacity has tripled in two years of Douglas-fir needle decomposition and doubled in woody litter components except bark.

(d) Carbon substrate analyses: Carbon substrate analyses have been used to develop a regression relating litter quality to decomposition rate for foliage litter of Douglas-fir, red alder, chinkapin, rhododendron, swordfern, and woody litter components including Douglas-fir needles, cones, and bark. Part of these data have been incorporated into a forthcoming publication in 1975 in the AEC Symposium Proceedings: Mineral Cycling in Southeastern Ecosystems.

The following areas will be examined in 1976: Environmental modification of watershed 10 following clearcutting will be examined utilizing Douglas-fir litter components plus foliage litter of secondary succession species on the watershed. The role of nitrogen fixation in woody litter remaining from clearcutting also will be assessed. Changes in foliar sclerophyll indices following clearcutting will be assessed; preliminary data suggest significant changes in nutrient capital and leaf morphology under clearcut conditions. The role of litter and soil fungi in the production of organic acids, particularly oxalic acid, and their role in cycling of calcium and other nutrients will be tested in secondary succession on watershed 10 following clearcutting. Root decomposition and nutrient loss will be tested on the clearcut.

Decomposition and energy flow in litter on clearcuts. Initial decomposition studies by Chet Youngberg, Mike Phillips, and Susan Warner in three habitat types on watershed 10 and on burned and unburned clearcuts have shown substantial differences in seasonal trends in CO_2 evolution from forest floors, varying with both temperature and moisture regimes. Current field work on this project is to be completed by 8/15/75 with a master's thesis completed by 1/1/76 by Mike Phillips.

Studies are being done on litter cation exchange capacity in forest floors of the same habitat types as done by Mike Phillips for CO_2 evolution. These studies by Susan Warner will also compare stream litter cation exchange capacity.

The main hypothesis to be tested in 1976 is that substantial increases occur in cation exchange capacity of terrestrial and aquatic litter components concomitant with increases in litter base saturation and pH. Preliminary data substantiates this hypothesis. These changes are important in retention of nutrients by litter, and proceed at a significantly faster rate in stream habitats than on land for both foliage and woody litter components.

Soil solution chemistry. Soil solution chemistry studies have been conducted by Fred Glenn, Fred McCorison, and Duane Moore. Six watershed compartments have been designated for evaluating movement of precipitation and nutrients through watershed 10, H. J. Andrews Experimental Forest. Rates of transfer between each of the following compartments have been monitored for over a year preceding clearcutting: (1) throughfall, (2) litter leachate, (3) 30 cm rooting zone, (4) 100 cm leaving rooting zone, (5) 200 cm subsoil, and (6) ground water (seepage) entering the stream. Results are currently being evaluated with respect to slope, aspect, vegetation, soil depth, and profile characteristics.

Leaching of nutrients from forest floor layers into the soil is distinctly different in different plant communities on the watershed. These differences reflect (1) the different decomposition environments (e.g., hot-dry versus cool-moist sites), and (2) differences in litter quality (e.g., crude fiber-protein ratios) in species characterizing various environments.

Available nutrients in the soil as determined by extraction from soil cores indicate that highest seasonal levels of available N, P, Ca, Mg, and K occur in late summer and early autumn. Available nutrients are lowest in spring, during the period of plant growth. Nitrate levels in soils of the watershed are low during fall and winter when gravitational water movement is taking place (Figure 19), and high in summer when they may equal ammonium levels. Soil ammonium levels are generally higher and reach a maximum in fall and winter (Figure 20). Ammonification is apparently the dominant nitrogen transformation mechanism in these soils. Low nitrate levels thus enter the stream channel throughout the year. Total concentrations in water entering the stream channel are related to soil depth in the water source area of seeps feeding the stream. Concentration of Ca, Mg, and K in seep water are also related to soil depth but not in such a direct way as are N and P.

A manuscript detailing the results of throughfall, litter leachate, and soil core sampling is in draft form. Seasonal trends in both total mass and transfer rate of all observed minerals are quite evident. Soil core extraction data displays a change with depth for only potassium, magnesium, and sodium. Only K, Mg, and pH showed a significant difference between ecological units. Ammonium concentration was strongly correlated with soil moisture and was highest in the fall and winter.

The following hypothesis will be evaluated in 1976. Nutrient conservation by the watershed 10 ecosystem will be only briefly influenced by clearcutting. Rapid site occupancy of shrubs and small trees will result in increased competition for mineral nutrients. A large part of increased nutrient loss will be due to temporarily increased water yield from watershed.

Soil water flow. Tensiometers were used by Dennis Harr to evaluate the timing and pathway of subsurface water on a steep slope during the between winter storms. Unsaturated flow predominated in the top 150 cm of the soil mantle on the middle to upper portions of the slope. The vertical location of transient saturated subsoil conditions predicted

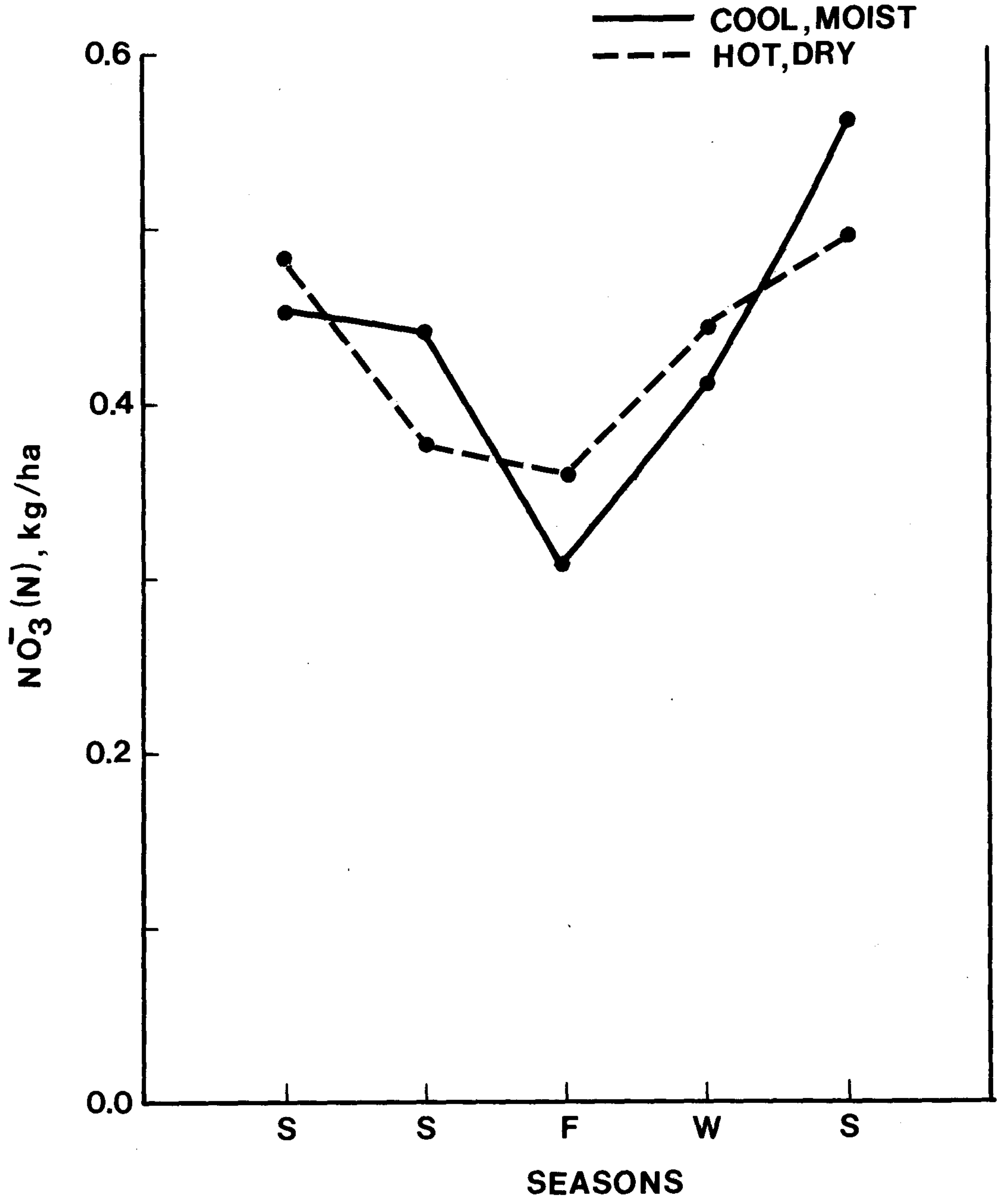


Figure 19. Average seasonal nitrate concentrations in the surface 1 m of mineral soil for a hot dry site and a cool moist site.

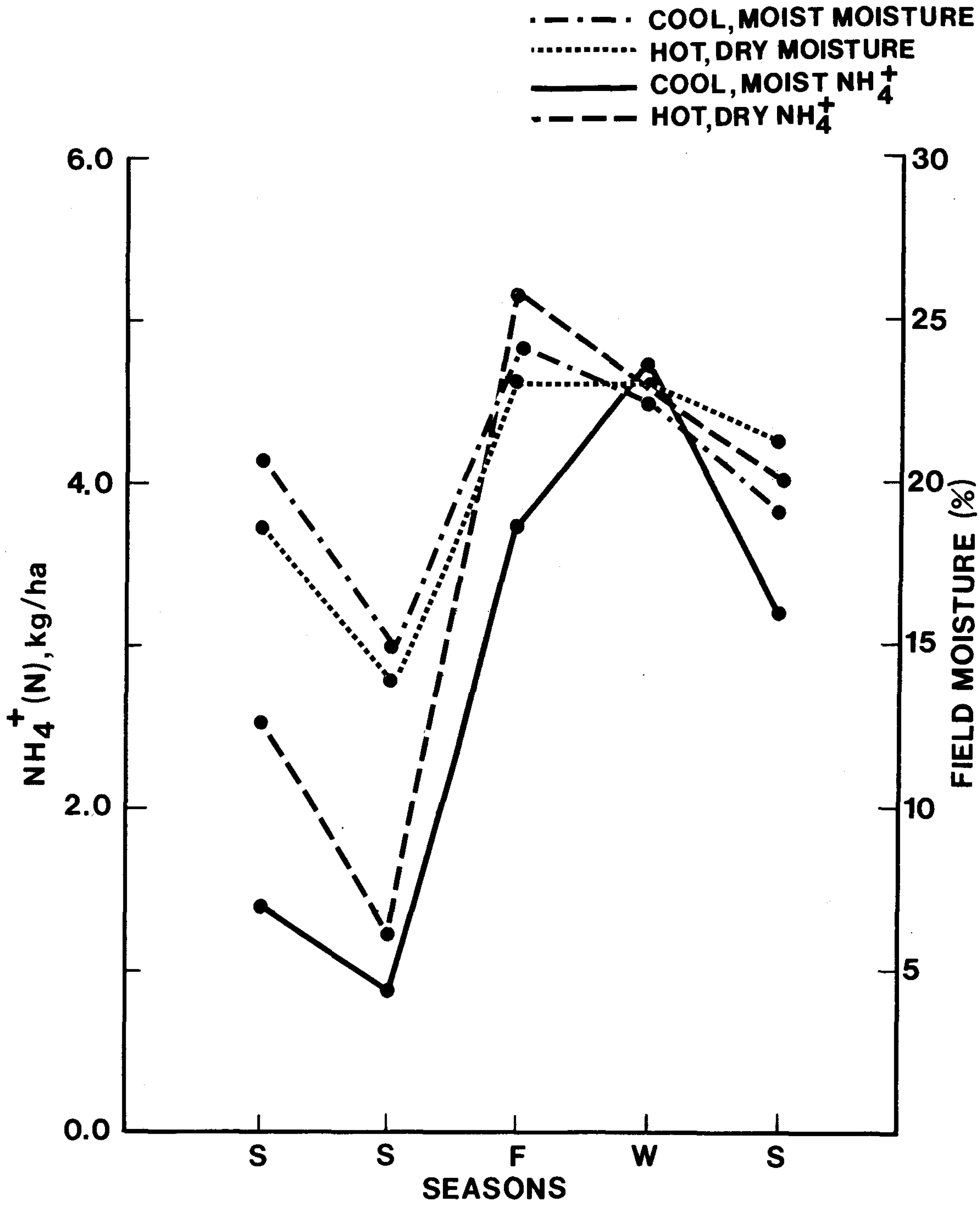


Figure 20. Average seasonal ammonium concentrations in the surface 1 m of mineral soil for a hot dry site and a cool moist site. Soil moisture is also indicated.

from soil data was verified by tensiometry. Nonuniform saturation of subsoil occurred after at least 30 mm of rain fell in a period of 12 hours or less. Saturation persisted less than 24 hours. Maximum soil water flux in the top meter of soil was 4.5 mm/hr. Maximum fluxes below 110 cm were generally slightly less than the minimum fluxes in the top meter of soil. The latter appears to be by far the most active zone of downslope movement of water.

Plant water relations. Water relation studies by Steven Running and Richard Waring illustrate that the understory vegetation in old-growth forests utilizes very little water, in part because the microclimate is less severe, but more importantly because stomata on leaves remain essentially closed until direct sunlight falls upon the foliage. On clearcuts no such restrictions exist and because deciduous plants and recently established evergreens have leaves with high conductances, leaf area well below that of the original forest can transpire equal amounts of water if it is available. More accurate estimates of shrub leaf areas were needed and have been achieved through a linear correlation with cross-sectional areas of conducting tissue.

Vegetation analysis on watershed 10 following logging. Basic sampling techniques to estimate leaf area of understory species were developed by Henry Gholz and Franklin Fitz. Rhododendron, selected to test the general reliability of techniques, is being studied under a variety of environments and stand histories. Leaf area to leaf weight ratios are being assessed in relation to light, and the internal distribution of nutrients from older to newer foliage is being monitored at weekly intervals under a range of stand conditions. Leaf area determinations of overstory and understory components have been summarized for six stands and the results submitted for publication. It was found that the maximum projected leaf area was above 20 for mid-elevation Douglas-fir/western hemlock stands. A hypothesis is offered that this could be a result of a relatively low mean annual temperature about 5°C and absence of moisture stress. These conditions could contribute to high foliage production and low maintenance respiration. Stands grown under such conditions show good growth at greater than 100 years and massive biomass accumulations.

Summary of major findings by Internal Dynamics Group. In summary, watershed 10 is in a growth stage where net production is low compared to younger stands. As a consequence, competition for nutrients is relatively low. Water use is mainly by the overstory, but the understory turns over considerable nutrients. Large quantities of organic matter and nutrients have accumulated in standing vegetation, standing and fallen dead material, and in the forest floor. Nutrient input to the forest floor and nutrient leaching into the soil are apparently both greater than in younger Douglas-fir stands. In spite of this, conservation of nitrogen and phosphorus by the ecosystem as evidenced by the watershed nutrient budget, is about the same as for younger more nutrient stressed sites. Losses of K, Ca, and Mg are greater than observed in younger stands, but this is most likely a result of weathering of primary minerals in the subsoil.

Hydrology, erosion and nutrient export of whole watersheds. This research area is coordinated by James Rogers and Fred Swanson. Following advancements in our understanding of water relations, snowmelt, and subsoil water movements, Rogers has improved the general hydrologic model and completed simulation runs under a variety of climatic and state conditions representative of the watershed in Oregon where much of the biome's research is concentrated. Figure 21 shows the stratification of watershed 10 which is currently being used.

During a year with 158 cm of precipitation, the predicted distribution into soil storage, stream flow, evaporation or transpiration is presented in Table 12. In most cases predicted values agree well with measured state variables. In the same table, the effects of complete and partial defoliation are predicted. The partial defoliation of the upper slope has a greater influence than expected from studies in North Carolina on Coweeta watershed. Since Rogers is comparing Coweeta responses using the same model, it is possible to explain these differences. In Oregon the long summer drought depletes the soil water in the upper regions of the watershed, while lower slope positions are maintained nearer maximum storage capacity through seepage. Defoliation of the upper slope results in reduced water use (confirmed by defoliation experiment on watershed 10) and subsequent rapid stream response to the first major fall storms following summer drought. In North Carolina, frequent summer storms prevent soils from being greatly depleted so defoliation has much less effect upon soil storage.

The hydrologic simulations are now sufficiently tested to serve as a component for evaluating sediment and nutrient movement through the watershed and will serve this function in the coming year.

Erosion, stream flow, and nutrient export. Erosion studies have continued by Fred Swanson to examine the full range of processes that transfer organic and inorganic particulate material in forest watersheds. These studies are designed to: (1) document rates of particulate matter transfer from hill slopes to stream channels by surface erosion, creep, slow earthflow, and debris slides and avalanches, and through stream channels by bedload transport and debris torrents; (2) determine variation in rates of erosion response to wildfire, management activity, and successional changes in vegetation; and (3) delineate the distribution of sites of active erosion within watersheds.

Certain processes (creep, various surface erosion processes, stream channel storage, and sediment routing) are profitably studied on the scale of small watershed manipulation experiments. Budgets of organic and inorganic matter inputs to the stream channel, storage within the channel, and transport through the channel have been compiled for watersheds 9 and 10 (Glenn, McCorison, Fredriksen, Sedell, and Froehlich). A striking feature of the particulate matter budget for watershed 10 (Figure 22) is the large volume of material stored in the channel relative to input, output, and through-channel transfer rates. Massive logs, limbs, and root wads have fallen and slid into the channel over the past century, setting up obstructions, slowing sediment transfer, and increasing

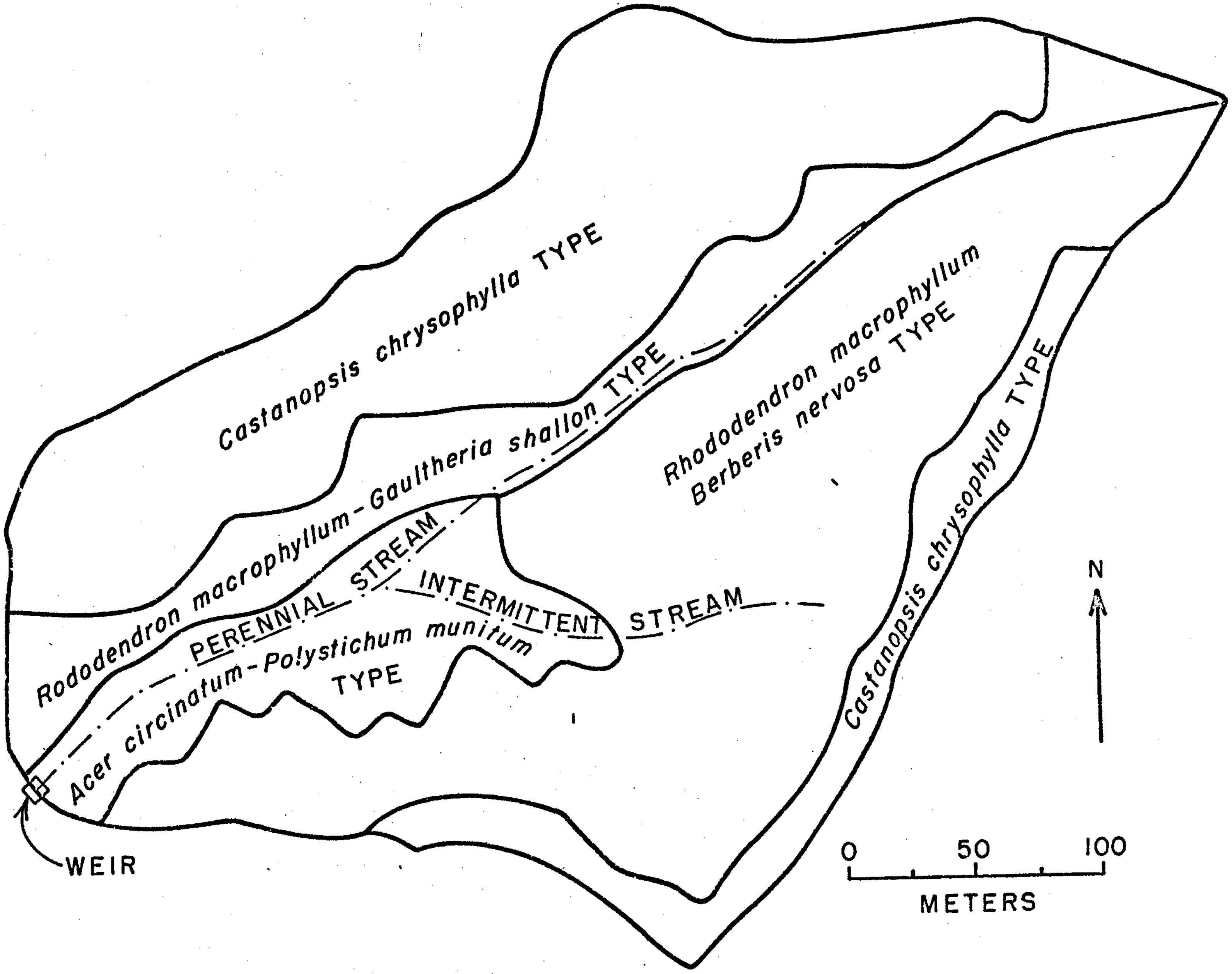
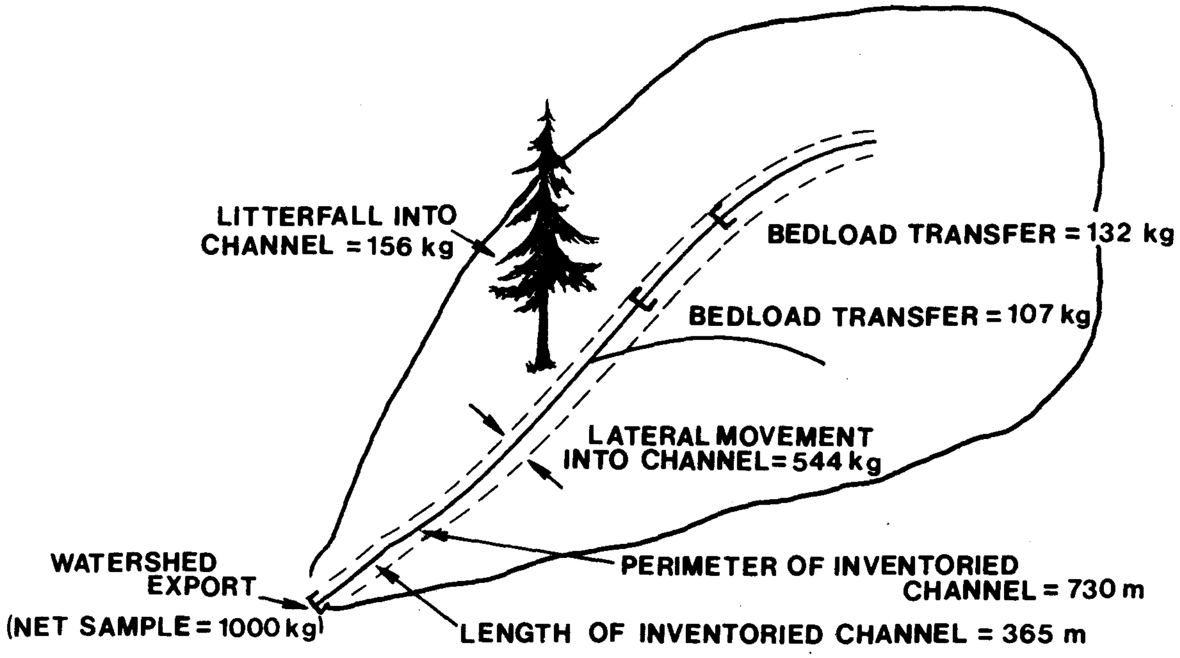


Figure 21. Stratification of Watershed 10.

Table 12. Annual hydrologic budget for watershed 10. Precipitation = 158 cm, soil storage = 42 cm, sapwood storage = 6 cm (Rogers).

	CASE I Complete forest cover	CASE II Upper third defoliated	CASE III Total defoliation
Canopy evaporation	12.5	9.2	2.8
Litter evaporation	0.6	4.0	11.0
Snow evaporation	- 1.8	- 1.3	- 0.5
Transpiration	34.0	15.3	0.2
Evapotranspiration	45.3	27.2	13.5
Flow to stream (routed by root zone subsoil and springs)	88.0	97.3	107.0
Change in soil storage	24.7	35.0	37.5



STORAGE IN INVENTORIED CHANNEL:

INORGANIC + BURIED ORGANIC = 301,000 kg
FINE ORGANIC (<10 cm) = 4,700 kg
COARSE ORGANIC (>10 cm) = 29,800 kg

Figure 22. Particulate budget for Watershed 10 in ecological units reflecting vegetation and physiographic position.

channel storage. Stream cleaning following logging will eliminate many of these obstructions, thereby releasing much of the sediment stored in the channel. We anticipate that the pulse of sediment following logging of watershed 10 not only will be a result of accelerated soil erosion from hill slopes but also will reflect release of sediment transported into the stream channel before logging. Postlogging research will identify and quantify management impacts on sediment sources, transfers, and storage within the watershed. Although this type of sediment routing study is critical to the interpretation of erosion processes in small forested watersheds and erosional impacts of management activities, this is the first systematic effort known.

Fredriksen has recently analyzed the significance of erosion in terms of nutrient export from five small watersheds, including watersheds 9 and 10 in the Andrews Forest. In four of the watersheds, which are erosionally stable and heavily forested, N and P content of exported detritus was low relative to estimated inputs to the watersheds. Indeed, for watershed 10 during 1971 dust deposition alone was 84% of suspended sediment outflow in solution together with that in suspended sediment. These trends can be dramatically reversed, however, when erosion rates are accelerated which commonly follows stand disturbance.

Major differences exist in potential erosion depending upon bedrock geology. Small watershed experiments are conducted on a scale inappropriate for the study of earthflows and debris slides, avalanches, and torrents. Because erosion by these processes is scattered both in time and space, they are best studied over areas of tens of square kilometers and at time periods of at least several decades. We have compiled a 25-year history of shallow-soil mass movements in the Andrews Forest. These data have been used to stratify landscape stability and to quantify the impacts of clearcutting and road construction on rates of slide erosion (Table 13). If it is assumed that slide erosion in forested areas represents a natural or background level of erosion by slides, then clearcutting in the unstable half of the forest increased slide erosion by 2.8 times (on the basis of volume of eroded soil/km^2) and roads accelerated slide erosion by 30 times in the area of road right-of-way. Because of contrasting soil and hydrologic factors, the stable half of the forest experienced only two small road related failures during the same period that 139 slides occurred in the unstable zone.

Ongoing studies of the mechanisms, histories, and relationships with forest vegetation of surface and mass wasting erosion processes are providing valuable input to our efforts to develop conceptual models of erosion on the time scales of individual storm events and over the course of primary and secondary vegetation succession.

Meteorological data collection and evapotranspiration. Meteorological data have continued to be recorded and analyzed since May 1972 by Richard Waring and Steven Running. Summaries include total daily radiation, dew point, air temperature extremes, and averages for daylight and nocturnal hours. Also included is wind speed. From this information, potential evapotranspiration is calculated for watershed 10. Listings of summarized

Table 13. Summary of data on slides that have occurred in the H. J. Andrews Experimental Forest, 1950–1974.

Land status	Area (%)	Area (km^2)	No. of events	No./km^2	Volume material moved (m^3)	Volume material moved (m^3/km^2)	Slide erosion relative to forested area
UNSTABLE ZONE (30.8 km^2)							
Forest	69.4	21.4	32	1.5	46600	2180	X 1.0
Clearcut	25.6	7.9	36	4.6	48400	6130	X 2.8
Road right-of-way	5.0	1.5	71	47.3	98200	65470	X 30.0
STABLE ZONE (33.4 km^2)							
Forest	85.9	28.7	0	0	0	0	
Clearcut	12.3	4.1	0	0	0	0	
Road right-of-way	1.8	0.6	2	3.3	420	700	

meteorological data are available from the OSU Biome Data Bank for the period from May 1972 through January 1975.

The second part of the project characterizes leaf conductance patterns of various understory shrubs which are expected to be a major vegetative cover following logging. Estimates of leaf area are available through techniques developed by Gholz and Fitz. So far we have found that even when water is not limiting, stomata of understory vegetation may be essentially closed unless light is falling almost directly upon the foliage. Resistances greater than 40 sec/cm are common. Where light is adequate, a variety of understory plants have resistances between 5 to 10 sec/cm. Where soil drought occurs, resistances increase dramatically. Differences among plant species appear to reflect rooting depth.

Leaf conductances of shrub species growing both in the forest understory and on clearcuts are being compared throughout the summer. This information together with leaf area estimates will permit us to predict evapotranspiration following clearcutting on watershed 10.

Stream interface studies. Stream interface studies conducted by Jim Lyford, Jim Sedell, Fred McCorison, Kermit Cromack, and Frank Triska are coordinated by Jim Sedell. Stream outflow chemistry classically has been used to interpret terrestrial processes within unit watersheds. Generally, the outflow chemistry is assumed to be a function of terrestrial processes, while the capacity for streams to alter and process the various kinds and forms of chemicals has not been considered. We have found, however, that the stream outflow may be controlled by at least four different processes: (1) direct organic inputs from litter; (2) surface runoff during snowmelt and the first fall rains; (3) subsoil exchange characeristics of the watershed; and (4) biological and physical activity in the stream itself. During the late summer and fall, litter leaf leachate and subsurface drainage may dominate in influencing stream chemistry. Where heavy rains saturate the soils during the winters, as at lower elevations in Oregon, the subsoil chemistry becomes important. In the spring at higher elevations, snowmelt predominates and saturates the soils in a similar manner. During times of low flow, characteristic of summer conditions in the Pacific Northwest, both subsoil and stream processes become equally important.

The hypothesis we are presently posing is that stream chemistry is modified significantly at times by both physical and biological processes in the stream. From this hypothesis, the questions can be asked as to how and when small streams affect output chemistry. If the aquatic ecosystem does significantly modify stream chemistry, the classical ways of interpreting terrestrial processes by stream-water chemistry are in doubt since two different ecosystesm have processed the input to a degree and altered the output. In addition, cations may behave quite differently than nitrogen in these small streams. Nutrient retention of cations may be dependent on the exchange capacity of detrital pools and uptake by mosses, whereas nitrogen cycling and retention may be primarily a microbial process.

The above hypothesis that endogenous, not exogenous, processes control stream chemistry arises from three different kinds of data sets; soil solution and streamwater chemistry, production or accumulation of moss and organic debris within the stream, and the decomposition of leaf tissues.

Progress in testing the hypothesis has been quite good in the last year. Seven seeps are identified in watershed 10 and have been sampled for water chemistry for the past year (Figure 23). Location of tension lysimeters and litterfall traps are also shown. For each seep studied a profile over the seep and above it was determined (Figure 24). These profile of inclination of side slope and soil depth served as an aid in identifying watershed parameters which may control the seepage chemistry. For example, aspect and its riparian vegetation zone may greatly influence the seep chemistry. The soil profile affects the hydrologic properties of the seep. The deeper the soils the longer the equilibration time of the water and the slower and more prolonged is the response to storms. Seeps RS and US are on steep, shallow soil slopes. They wet up and illute the soil rapidly in the winter and the peak seep discharge corresponds with the peak on the stream hydrograph. There is little storage capacity and the area is flushed very quickly. These two seeps are intermittent, being dry in the late spring, summer, and early fall.

Seep LT is another intermittent seep which is a hybrid, in that it has deep soils but a small drainage and shows a quick response to storms. With a larger drainage area the response to storms would probably be more prolonged. LS has a continuous flow fall, winter, and spring, and shallow soils near the stream, but it has very deep soils above it. The other three, LF, TB, and RF are perennial.

A problem which we have not yet solved is what does the water coming from each of the seeps represent? We don't know for certain if each seep represents the total flow from the area above it, only a small part, or whether it has just been channeled into a seep. We have assumed that each seep is an adequate representation for a given soil profile and have partitioned the watershed into seven areas each represented by a seep (Figure 25). Thus, we feel we can make useful approximations as to how concentrated the water entering the stream is in comparison with the stream chemistry at the flume. Such a value was arrived at by multiplying the concentration of each seep by the proportion of the watershed it represented. By summing up the seven products (seven seeps) a predicted or weighted value is arrived at.

If the ground water concentration is the same as that at the flume, a plot of predicted values versus observed values will fall on a perfect fit line. Figure 26 shows predicted versus observed values for sodium, orthophosphate, total nitrogen, and magnesium.

Most of the dissolved materials exhibit a 1:1 relationship, indicating the predictions made from weighting the areas each seep represents, accurately predicts the values observed in the stream at the bottom of the watershed.

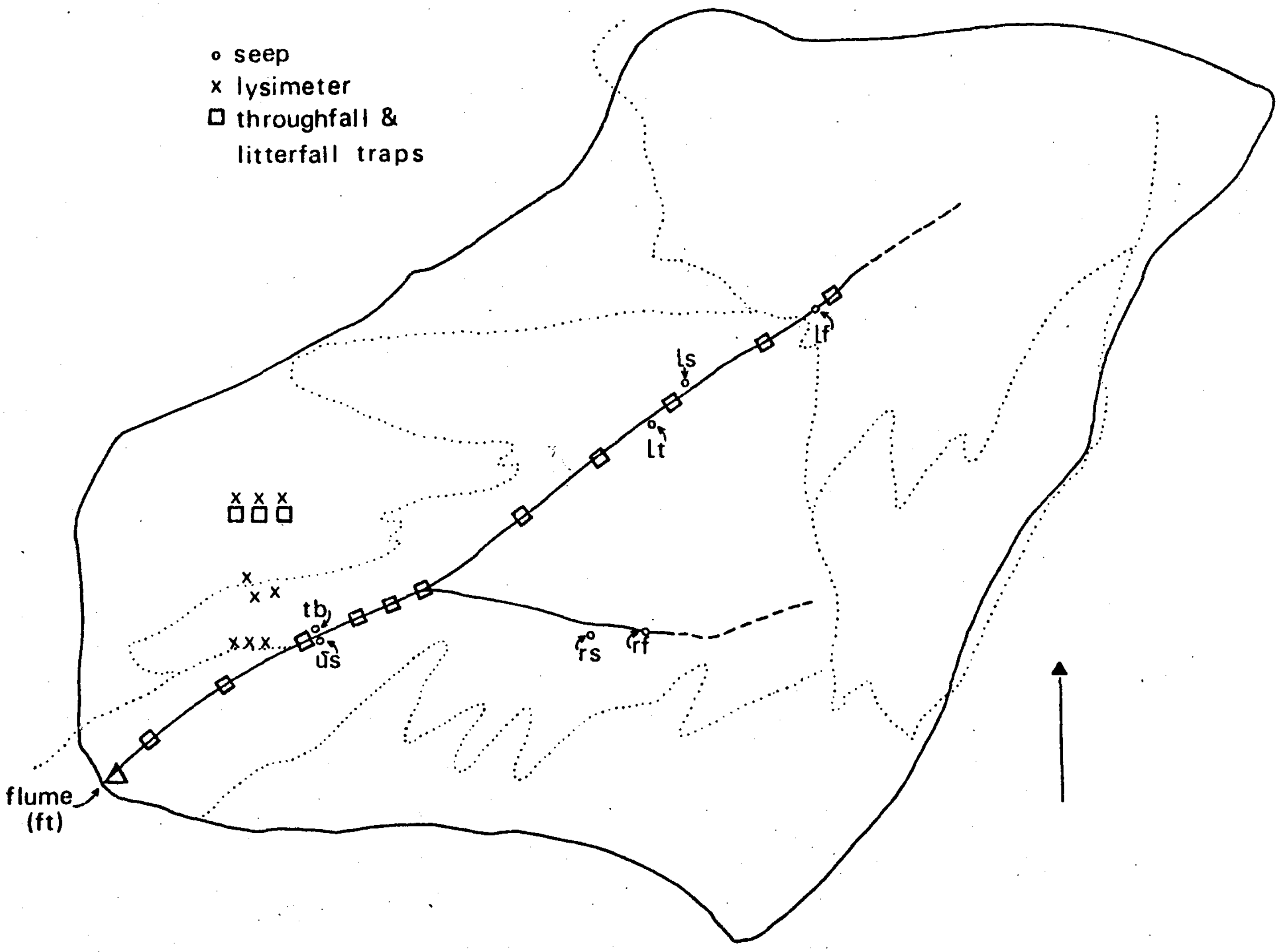


Figure 23. Location of seeps, throughfall, and litterfall collectors and tension lysimeters on Watershed 10; f = fork, L = left, r = right, s = seep, t = trail, u = opposite, tb = tipping bucket.

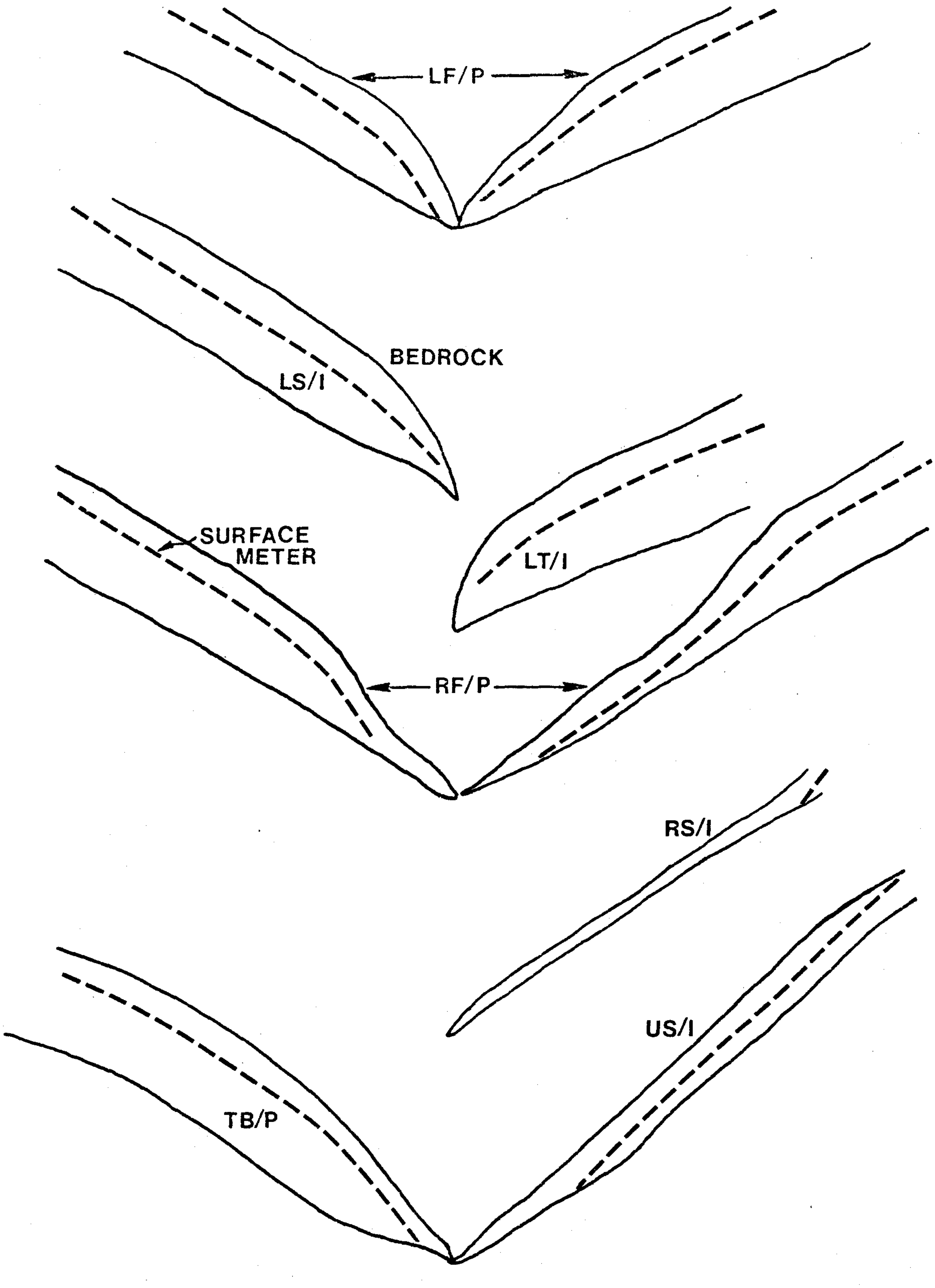


Figure 24. Cross section of seeps on Watershed 10. See Figure 25 for codes to abbreviations. P = perennial, I = intermittent.

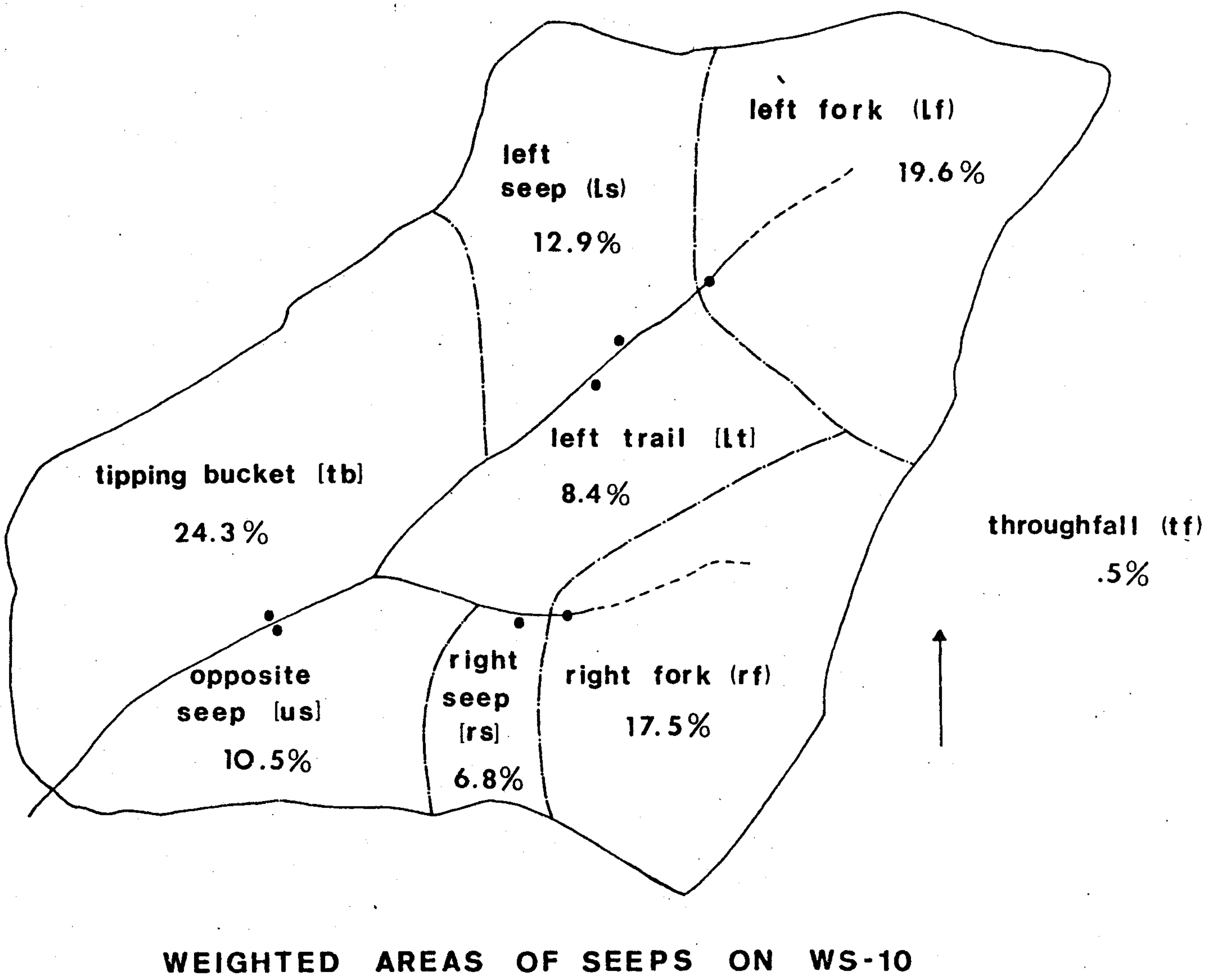


Figure 25. Weighted area of seeps on Watershed 10.

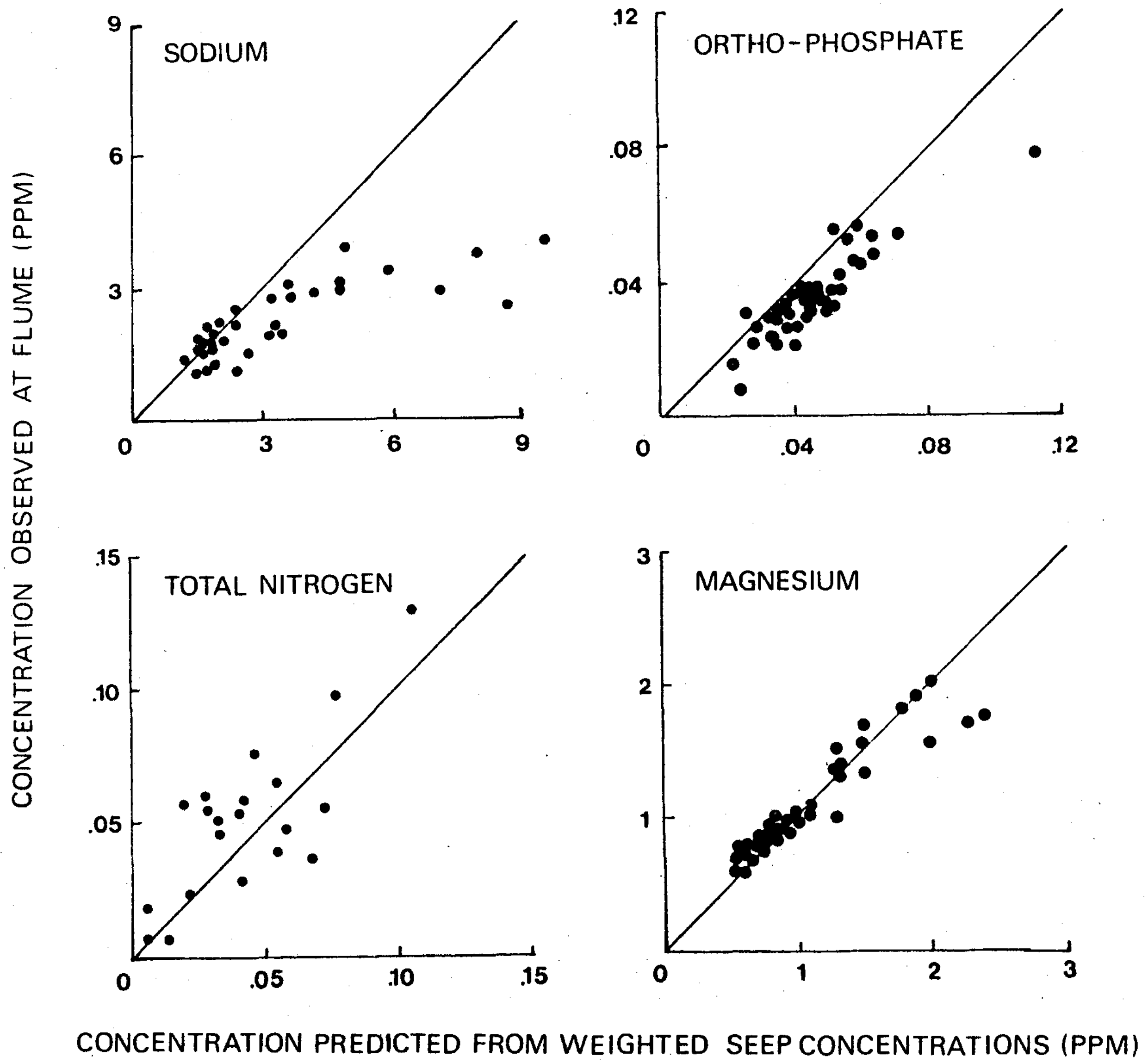


Figure 26. Observed nutrient concentrations at the flume in Watershed 10 versus observed concentrations predicted from weighted seep concentrations.

However, some materials, ortho-phosphorus, sodium, and total nitrogen do not behave in the same manner. Ortho-phosphorus and sodium are accumulated by the stream. More comes into the stream from the seeps than goes out at the bottom. Total nitrogen is the reverse, more goes out of the watershed than enters through the seeps. One explanation which could account for this is the high nitrogen content of the precipitation and throughfall (Richard Fredriksen and George Carroll personal communication).

Such plots work very well in the winter season after the soil mantle is wet and the entire watershed is contributing to the stream. In the summer, with no precipitation and only about 25% of the watershed contributing, the three permanent seeps have been reweighted. The deviation of the predicted concentration from the perfect fit line occur during the spring and summer (Figure 27).

When one compares the weighted seep chemistry to that of the stream where it leaves the watershed (Figure 27), the potential for the stream and its immediately adjacent riparian vegetation to process biologically dissolved materials on a seasonal basis can be seen.

Four things can be seen from Figure 27: (1) all the concentrations increase from fall to summer with the exception of potassium and total nitrogen during the rainy quarter; (2) the predicted values are greater than the observed values; (3) sodium is unexpectedly processed in and around the stream in significant amounts; and (4) the greatest difference between observed and predicted values comes in the summertime. The high biological activity in the summer reflects both high temperatures and stable substrates. There is an abundance of leached, refractory, and comparatively nutrient poor particulate organic materials in the stream. The higher dissolved material concentrations and longer retention time of water in the watershed allow microbes, mosses, and hydrovascular plants to take up these materials in significant quantities.

Another factor affecting the chemical properties of streams is the large volume of organic material in the stream (15 kg/m^2). Last year's research sought to determine if litterfall debris in streams acts as a short-term nutrient sink. In effect, we estimated the capacity of leaf material to capture and exchange cations.

The cation exchange study was undertaken on the basis of the hypothesis that leaf species with the lowest percentage base saturation tend to accumulate cations such as magnesium and calcium at sometime during decomposition. This hypothesis was verified by our studies. Douglas-fir needles started out with both a lower cation exchange capacity and a lower percentage base saturation than vine maple leaves. In both streams, Douglas-fir needles accumulated a higher base saturation and calcium, magnesium, and potassium cation. On the other hand, vine maple leaves which started with a high base saturation, lower lignin content, and which also decomposed faster did not show an increase in base saturation, or cation exchange capacity. The stream in which decomposition proceeded most rapidly (watershed 10) also demonstrated a more rapid rise in cation exchange capacity (Figure 28).

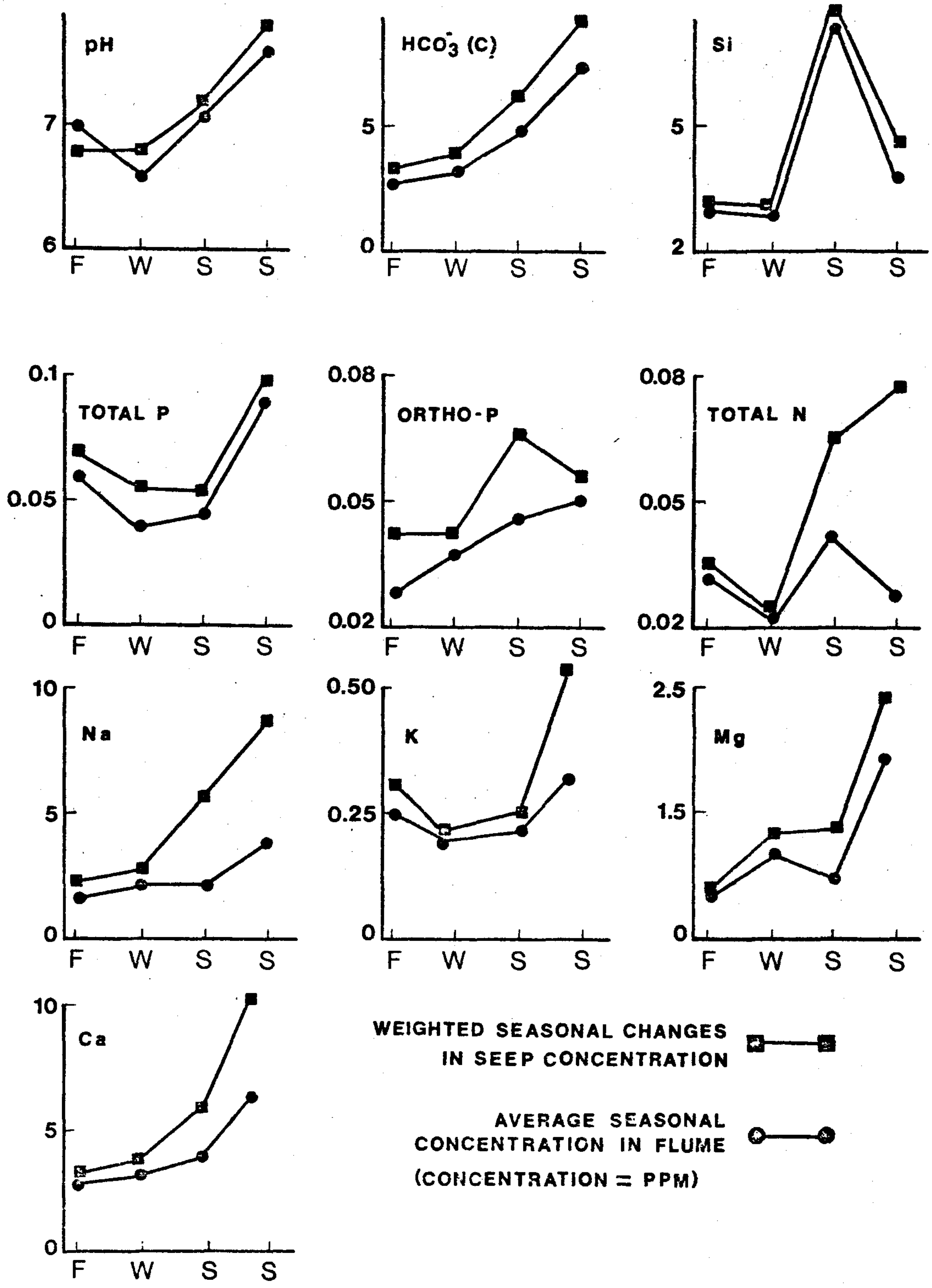


Figure 27. Weighted and average seasonal nutrient, pH and bicarbonate concentrations in the seeps and the flume in Watershed 10.

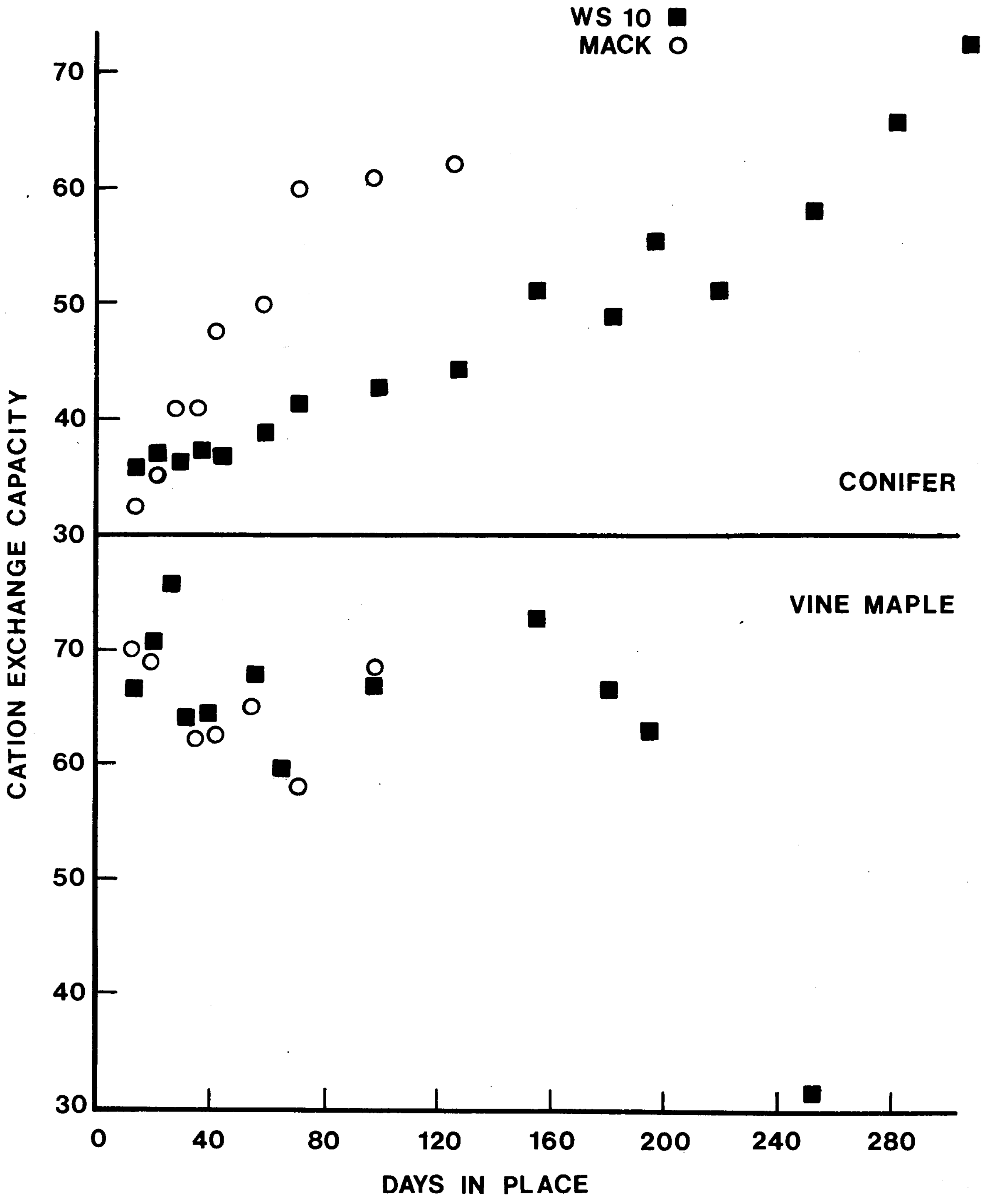


Figure 28. Change in cation exchange capacity (meq/100 g) for litter of conifer and vine maple in the Watershed 10 stream and Mack Creek.

Trace metals (e.g., zinc) did not accumulate during the decomposition process suggesting that cation exchange mechanisms do not seem to be important in accumulating trace metals.

In coniferous forest streams where the vast amount (>90%) of the organic materials that reach the stream are considered refractory (having a high lignin content), this cation exchange mechanism may be extremely important as a biological sink and in the preparation of these refractory residues for decomposition. The mechanism will be studied more thoroughly for wood and bark during the coming year.

3.2.2.2. Findley lake watershed--Internal dynamics, hydrology, nutrient export, and lake interface studies.

This research is coordinated by Hans Riekerk and Robert Wissmar.

Watershed hydrology and stream chemistry. Hydrologic measurements have been continued during the past year with refinements in the calibration of streamflow measurements. Estimates of annual evapotransportation (8% of precipitation), inflows from creeks and springs (20-30% of outlet flow), inflows from groundwater seepage (50-70% of outlet flow), and direct precipitation on the lake (4-10% of outlet flow) have been determined. Table 14 is a summary of climatic and hydrologic data for 1973 and 1974.

The chemistry of these waterflows has been measured at monthly intervals resulting in estimates of a geochemical budget of the lake system and total watershed. Cation losses from the total watershed appear to be low as compared to watershed 10 and other watershed studies.

Internal dynamics--biogeochemical studies. The chemistry of ground water solutions has been measured by Hans Riekerk and considerable attention has been placed on soil solution (biogeochemical) studies by Fiorenzo Ugolini and Ralph Minden.

Tension lysimeters were used to continuously extract soil solutions from the O2, A2, IIB2hir, and IIIB31 of Spodosols at three sites at Findley Lake. Seasonal snow packs ranging in depth from 2 to 7 m precluded sampling at one of these three sites. The first soil solutions were obtained in April 1973 and the collection and the chemical analyses has continued since. The results obtained so far have confirmed *in situ* processes of podzolization and corroborated the information previously obtained from the conventional approach to soil studies.

Concentration of the major ions percolating through the soil shows a definite trend and points out clearly the existence of two compartments; one starting from the top of the canopy of the Pacific silver fir (*Abies amabilis*) and ending in the lower boundaries of the IIB2hir horizon and another compartment starting below the IIB2hir and including the thickness of the parent material where solutions are able to circulate. The upper compartment is the biopedological compartment; the lower, the geochemical compartment. Lysimeter data from two sites (6 and 7) (Table 15) show that electrical conductivity, summation of cations, total N, total P, total and soluble Fe, soluble Al, and to some extent

Table 14. Summary of climatic and hydrologic data for Findley Lake in 1973 and 1974.*

Date	Precip. (cm)	Air temp. (°C)	Soil temp. (°C, 20 cm depth)	Soil water tension (atm)	Outflow (m^3 x 1000)	Channel inflow (m^3 x 1000)	Groundwater inflow (m^3 x 1000)	Direct ppt inflow (m^3 x 1000)
Jan	32.9				16.6	18.1	114.6	32.8
Feb	13.8				49.6	1.0	33.1	15.5
Mar	17.1	-4.5	1.0		78.6	3.7	57.9	17.0
Apr	13.3	2.0	1.5		136.1	16.4	106.5	13.3
May	11.8	3.2	1.2		546.2	208.3	327.3	11.8
June	22.4	5.8	6.0		398.1	117.9	257.9	22.4
July	1.4	7.3	7.0	<0.1	72.9	5.0	65.5	1.3
Aug	2.2	11.2	9.1	0.14	16.1	0	13.9	2.2
Sept	13.2	8.0	6.8	0.17	19.9	0	8.4	12.6
Oct	22.2	5.1	3.6	0.13	98.2	1.1	67.5	22.1
Nov	30.2	(4.4)	3.0	0.14	198.0	32.9	135.0	30.1
Dec	21.9	(-0.4)	1.0	<0.1	264.4	58.4	184.2	21.9
Annual	202.4				2043.6	462.7	1371.7	203.0
% of total	100				100	23	67	10
Jan	60.8				197.0	22.6	113.6	60.8
Feb	41.9				150.0	13.1	95.0	41.9
Mar	38.6				137.3	11.7	87.0	38.6
Apr	27.4				240.9	50.6	162.8	27.4
May	17.7				562.8	220.1	325.0	17.7
June	18.9				1796.8	1041.6	736.3	18.9
July	5.4				1351.0	713.9	631.8	5.4
Aug	3.1				386.6	137.7	245.8	3.1
Sept	6.2				67.1	4.0	57.2	6.2
Oct	6.6				30.7	0	24.0	6.6
Nov	28.6				333.1	97.6	207.0	28.6
Dec	1.3				586.4	246.1	339.0	1.3
Annual								
% of total					5839.8	2559.0	3024.3	256.5
					100	44	52	4

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*Data from Olson, Larsen, Ugolini/Singer (Report no. 73). Riekerk/Noetzelman and data bank. Calculated annual evapotranspiration is 8% of total precipitation.

Table 15.

			Mean standard deviation range	pH	Cond. (µmhos/cm^2)	Total cations (meq/l)	Total (ppm)			Soluble (ppm)		
							N	P	Fe	Fe	Si	Al
Precipitation				5.84	14.4	0.032	0.605	0.013	<0.01	<0.01	0.09	0.03
				0.44	5.9		0.510	0.010			0.11	0.03
				4.61-6.40	6.4-24.6		0.035-1.653	0.004-0.040			0.05-0.45	0.01-0.12
Throughfall			$\bar{x}$	5.05	15.9	0.100	0.406	0.055	0.02	0.02	0.09	0.06
			s	0.55	8.3		0.333	0.048	0.01	0.02	0.10	0.07
			Range	3.89-6.30			0.111-1.536	0.007-0.171	0.02-0.06	0.01-0.04	0.00-0.35	0.01-0.25
Site	Depth (m)	Horizon										
6	0.00	02	$\bar{x}$	4.75	22.0	0.140	0.536	0.038	0.11	0.04	4.92	0.27
			s	0.55	10.3		0.483	0.025	0.09	0.02	6.82	0.16
			Range	3.50-6.30	9.0-38.0		0.020-1.875	0.005-0.116	0.02-0.31	0.02-0.07	0.15-26.50	0.08-0.53
6	0.15	A2	$\bar{x}$	4.66	17.7	0.124	0.340	0.028	0.09	0.04	4.31	0.33
			s	0.35	6.7		0.257	0.016	0.06	0.03	5.03	0.21
			Range	3.80-5.24	6.2-36.5		0.045-1.230	0.005-0.068	0.02-0.14	0.02-0.10	0.30-20.37	0.03-0.72
6	0.30	IIB2hir	$\bar{x}$	5.07	11.1	0.078	0.194	0.020	0.05	0.01	3.61	0.19
			s	0.29	3.5		0.123	0.019	0.04	0.01	3.00	0.09
			Range	4.72-5.92	6.0-22.5		0.008-0.435	0.005-0.083	0.01-0.15	0.00-0.01	0.10-8.54	0.10-0.35
6	0.60	IIIB31	$\bar{x}$	5.60	19.3	0.248	0.352	0.034	0.05	0.02	2.80	0.20
			s	0.56	11.7		0.307	0.033	0.03	0.02	2.22	0.18
			Range	3.94-7.05	7.6-47.5		0.045-1.506	0.006-0.115	0.01-0.11	0.00-0.04	0.40-7.35	0.03-0.62
7	0.00	02	$\bar{x}$	4.52	24.4	0.174	0.619	0.219	0.08	0.04	3.33	0.59
			s	0.39	13.0		0.308	0.168	0.05	0.01	3.13	0.43
			Range	3.32-5.56	7.5-64.4		0.202-1.287	0.022-0.590	0.04-0.16	0.02-0.06	0.18-12.40	0.04-0.95
7	0.15	A2	$\bar{x}$	4.59	23.6	0.175	0.454	0.026	0.06	0.02	5.17	0.31
			s	0.49	9.1		0.198	0.014	0.07	0.02	3.52	0.16
			Range	3.67-5.88	10.5-41.8		0.195-0.645	0.010-0.058	0.02-0.16	0.01-0.05	0.32-12.00	0.06-0.45
7	0.30	IIB2hir	$\bar{x}$	4.92	16.4	0.122	0.277	0.019	0.01	0.01	3.57	0.17
			s	0.28	5.7		0.155	0.011	0.01	0.01	2.03	0.04
			Range	4.48-5.60	8.6-28.8		0.133-0.645	0.004-0.042	0.01-0.03	0.00-0.02	1.06-9.35	0.11-0.25
7	0.60	IIIB31	$\bar{x}$	5.35	25.7	0.194	0.449	0.099	0.04	0.02	4.12	0.29
			s	0.41	22.3		0.275	0.086	0.02	0.01	2.14	0.15
			Range	4.39-6.00	8.9-121.0		0.106-1.059	0 020-0.322	0.02-0.08	0.00-0.02	0.15-7.05	0.05-0.54
Lake Inflow			$\bar{x}$	6.17	20.3	0.26	0.142	0.010	<0.01	0.01	4.29	0.02
			s	0.54	6.0		0.087	0.005		0.01	1.49	0.02
			Range	5.00-6.75	7.8-31.0		0.020-0.328	0.002-0.028		0.00-0.05	1.10-7.59	0.00-0.05
Lake Outflow			$\bar{x}$	6.23	18.6	0.20	0.218	0.009	<0.01	0.01	3.67	0.01
			s	0.54	6.1		0.182	0.007		0.01	0.99	0.00
			Range	5.00-7.12	7.0-43.0		0.006-0.858	0.002-0.28		0.00-0.05	1.90-5.50	0.00-0.01

soluble Si achive a minimum concentration in the IIB2hir horizon. In the IIIB3 and ground water below, virtually all the elements and parameters measured, including pH, increase again (Table 15). The existence of these compartments is extremely important for the function and stability of the ecosystem. Of significance is the role of the IIB2hir as an illuvial horizon. The IIB2hir plays the role of maintaining the stability of the biopedological compartment. The logical question to ask is how stable is the IIB2hir with respect to induced and natural perturbations? Is the pedological inertia of these illuvial horizons sufficient to retain the properties after a windstorm, clearcutting, or fertilization operation? Another important result of this study is the finding that the chemical composition of the leachate below the soil-solum of the springs, ground water, and streams does not reflect either the composition of the solutions or the processes occurring in the soil-solum. Therefore, in areas subjected to podzolization, the assumption that stream water can reflect the chemistry of the soil-solum solution may not be valid. Consequently, loss ascribed to the soil-solum or rooting zone may instead have originated in the C horizon, in the lithological substratum below the spodic horizon, or at the surface via erosion.

Lake interface studies. Transport of organic matter and associated nutrients has been determined with litterfall and snowlitter transects, and with periodic collections of floating creek debris (Robert Gara/Greg Rau, Hans Riekerk). Litterfall and creek debris appear to account for 60% of the total carbon inputs into the lake. Presently, these measurements of forest litter inputs are being continued. Relationships with shore forest stand characteristics and with creek channel boundaries are being explored this year.

Presently, controlled-flow sections of inlet creek A and the outlet creek are being built for better calibration of associated stage recorders. Direct groundwater flow measurements will be attempted this summer with more piezometer pipes, soundings through colluvial debris to bedrock, and hydraulic conductivity measurements. A small area (50 x 20 m^2) draining into the lower pond will be treated with urea to assess effects on groundwater chemistry.

The following questions will be investigated in 1976.

1. What is the effect of nutrient mobilization by urea-fertilization on transfer pathways and rates into the lake system?

2. What are the effects after a timber harvest on the carbon and nutrient transfer pathways and rates into a similar lake system of the Green River watershed?

3. Can litter production and dispersal into the lake be predicted from forest stand characteristics along the lake shoreline and creek channel boundary conditions?

3.2.3. Analysis of aquatic ecosystems

This theme is coordinated by Robert Burgner and Jim Hall. Figure 29 illustrates the projects and principal investigators associated with this theme which is focused on two major research areas (1) stream ecosystems and (2) lake ecosystems.

Publications resulting from aquatic ecosystem research are presented in Appendix III.

3.2.3.1. Stream ecosystems.

Overall emphasis of the stream research program which is coordinated by Frank Triska during the past three years has been to elucidate linkages between the stream and its adjacent forest community in the H. J. Andrews Forest in Oregon. These linkages have proven to be more than simple transport functions. Our interaction and cooperation with terrestrial ecologists has provided a mutual realization of the scope of these interactions, whose complexity we are beginning to realize and understand.

Initial stream studies focused on carbon inputs and utilization. Last year we hypothesized: *The productivity of natural stream systems is more directly related to streamside vegetation than water chemistry or geology*. Crucial to this question is the amount and rate of carbon flux through the hetrotrophic (shredder/collector/decomposer) pathway resulting in secondary production. Also crucial is the flux of carbon through the periphyton/grazer/collector pathway based on autotrophic primary production. This latter question is currently being studied in detail using dual tracer techniques with ^{14}C and ^{51}Cr. These experiments when completed at the end of 1975 will provide essential information for assessing the contribution of autotrophy to secondary production, and will also provide data necessary for final refinements of the stream model.

Leaf pack experiments in previous years led to the hypothesis that the *microbial conditioning of litter inputs is a necessary prerequisite for conversion of such debris to a food resource for invertebrate detritivores*. Experiments using shredder insect larvae and needle litter conditioned for various time periods were presented at the SIL Congress in Winnipeg last year and will be published by the end of this year. Additional laboratory studies on conditioning, food density, and temperature on consumption rate, fecal production, and growth are continuing and will be completed by the end of 1976. Two earlier studies on leaf pack decomposition have been completed on watershed 10, and will also be published by the end of this year in *Vert. Int. Ver. Limnol.* Leaf pack studies on three replicate streams with different nitrate input, and large autotrophic production which were proposed last year have been completed. The results of these studies, undertaken in cooperation with scientific personnel from the Weyerhaeuser Corporation have been submitted to *Ecology*. Preclearcut studies on watershed 10, including litterfall, lateral movement of debris, standing crop, and respiration are currently being analyzed.

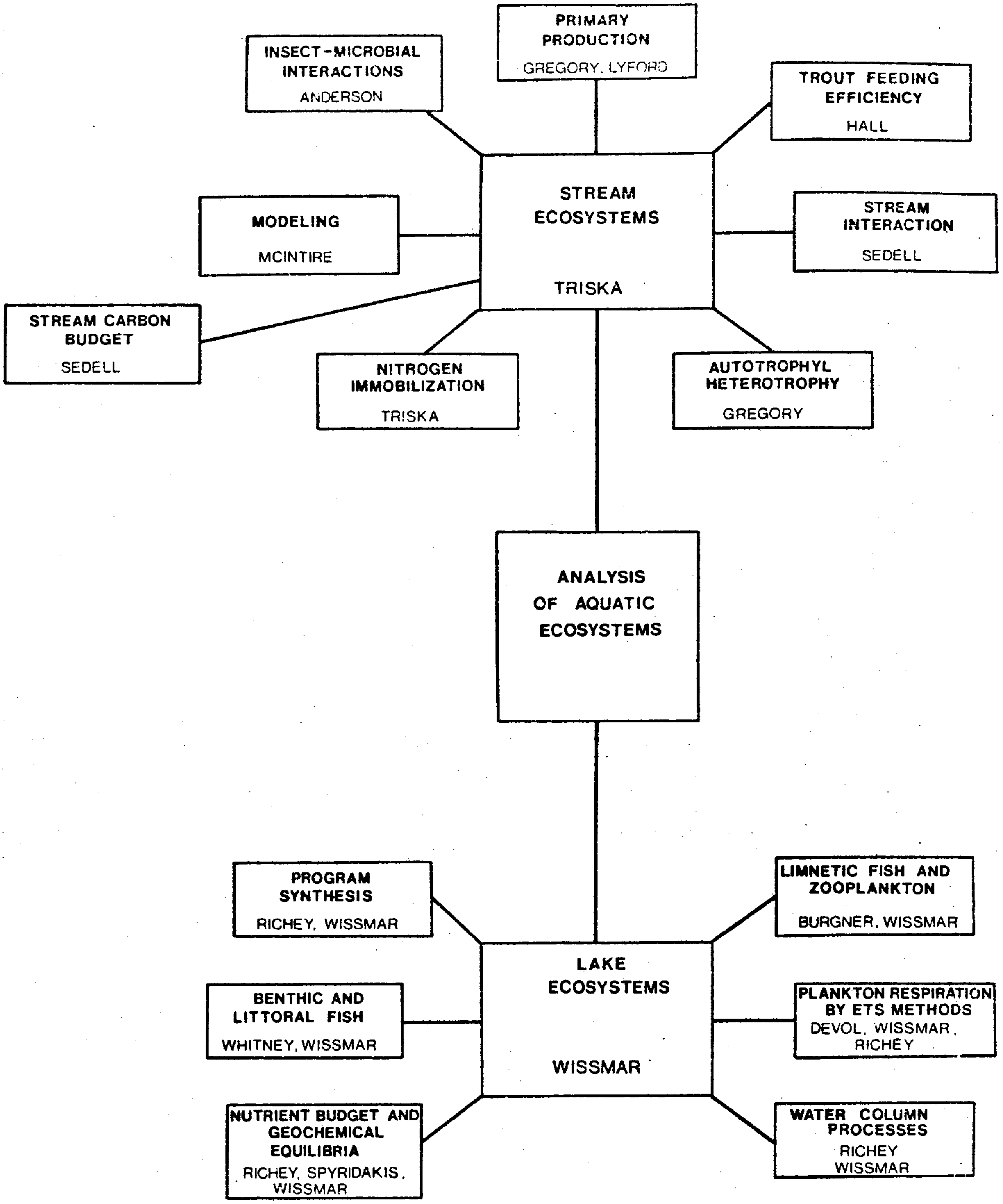

Figure 29. Research projects in the Analysis of Aquatic Ecosystems component.

Aspects on the biotic cycling of nutrients were also addressed in last year's proposal. We hypothesized: *Organic matter decomposing in small streams forms an important nutrient pool cycled by microbial processing and insect feeding*. Measurements needed to complete a nitrogen budget were completed prior to the clearcutting of watershed 10 and are currently being analyzed. We also propose that the *nitrogen content of allochthonous detritus is conserved in a nutritionally dilute flowing water system by microbial immobilization and by microbial nitrogen fixation*. To this end a study on long-term decomposition was begun on watershed 2 using the refractory substrates, bark, wood, and twigs of Douglas-fir, on both land (Reference Stand 2) and in water (watershed 2). Within three months twigs have confirmed nitrogen fixing ability in pure culture. Identification of these cultures is currently being undertaken.

Autotrophic aspects of stream production are controlled by the interrelationships between light nutrients and temperature. Last year we hypothesized: *Light is the major limiting factor of primary production in coniferous forest streams*. To test this hypothesis, a section of heavily shaded stream was artifically illuminated. A control station of natural light and nutrients was compared with three treatment stations: (1) a station of natural light + 100 ppb nitrate, (2) a station of light addition and no nutrient enhancement, and (3) a station of both light addition and 100 ppb nitrate enhancement. This experiment confirmed the role of light as the major limiting factor in small stream primary production. This paper is currently in manuscript form and will be submitted to *Ecology*. Other studies of primary production comparing clearcut and forested sections of Mack Creek will continue through 1976. A past experiment using 32_P to measure primary production is in manuscript form and will be submitted for publication by September. Previous experiments on algal standing crop and community structure submitted last August are in press and will be published later this year in *Vert. Int. Ver. Limnol.*

Quantitative benthic insect sampling and fish production led to a finding of greater insect biomass, and greater biomass and trout production in the open clearcut section than in the closed forest section of Mack Creek. These results led to two hypotheses concerning trout production:

1. *Increased light and a reduction of small drifting debris in open areas increase trout feeding efficiency*.

2. *Competition of trout with salamanders in heavily forested stream reaches may result in decreased fish production*.

The former hypothesis was tested in laboratory streams. The dilution effect of debris when mixed with drift did provide some interference with trout feeding. The amount of interference, however, did not seem sufficient to account for the differences between trout production of the clearcut and forested sections. As a result, this hypothesis was rejected and the project discontinued.

The latter hypothesis has not been thoroughly tested but, at this time, appears credible. In the autumn of 1974 an intensive effort was made to assess salamander biomass in the clearcut and forested sections of Mack Creek. Results indicated both greater numbers and biomass of salamanders in the forested section. Further investigation of salamander growth rate, biomass, and food preference to properly test this hypothesis will continue during autumn of 1975.

A major emphasis of last year's proposal concerned the application of ideas and methods to other streams in the Coniferous Forest Biome. These proposed activities, to begin in 1976 and continue to 1977, will involve a wide perspective and low detail approach, with a seasonal rather than monthly time resolution. Streams will be chosen on an environmental grid to represent four different coniferous forest environments: Coast Range, Willamette Valley, east slope of the Cascade Range and the west slope of the Cascade Range.

A final major research effort will be the post-clearcut examination of watershed 10. Standing crop, processing and export of debris will be analyzed. Changes in P/R ratio will be compared with those prior to clearcutting, to assess the change from heterotrophy to autotrophy due to increased light intensity and elimination of litterfall inputs. Shifts in major insect functional groups and changes in overall insect productivity will be determined by insect emergence. The efficiency of carbon utilization will also be continued by reconstructing a post-clearcut carbon budget.

Modeling of autotrophic-heterotrophic processes is largely completed. The activities we proposed in 1975 included: (1) model conversion from FLEX to REFLEX, (2) documentation of the existing model, (3) addition of a predator component. These have already been completed. Experiments with periphyton grazing to strengthen the modeling of carbon flux through the autotrophic pathway will be completed this autumn. Major biological modeling effort to July 1976 will be a revision and incorporation of our results from previous studies into the model. Final refinements will include utilization of data obtained from the Weyerhaeuser Corporation as part of the coordinating sites program for model validation studies in streams with high autotrophic production. The major area of potential expansion, the role of abiotic parameters (incorporation of the hydrologic model and nutrient cycling) will be evaluated in July 1976.

Work in the final two years of this program will be divided into two efforts, a research effort and a data analysis and publication effort. The research effort will consist of a major commitment to past clearcut aspects of watershed 10, and to the validation of our ideas by comparative stream studies. Analysis of data collected prior to 30 May 1975 is still underway and will continue for at least another year. As a result, the program outlined last year remains basically unchanged and no new research other than that presented in the original proposal will be undertaken during the next year.

3.2.3.2. Lake ecosystems.

Lake ecosystem studies are coordinated by Robert Wissmar and have concentrated on Lakes Washington, Findley, Chester Morse, and Sammamish. A summary of research accomplishments for each project follows.

Phytoplankton respiration. Phytoplankton night respiration may be more important in controlling primary productivity than previously thought. In Lake Washington during the summer stratification period (July through September), the microplankton, primarily phytoplankton, respire at night at an average of 35% of the carbon fixed during the daylight hours. This figure is about three times higher than previously thought and should reduce considerably the high specific loss rate invoked by some workers to rationalize ^{14}C-productivity with observed changes in phytoplankton biomass. Using ^{14}C-productivity measurements that have not been corrected for night respiration, Jassby and Goldman (Limnol. and Oceanogr., Vol. 19, 1974) have shown that in Castle Lake a specific loss rate of 0.6/day is often necessary to balance ^{14}C-productivity against observed changes in phytoplankton standing stock. A similar analysis of Lake Washington reveals that specific loss rates of only 0.3/day are necessary when night respiration is taken into account.

Nutrients. A combination of tracer-kinetics and modeling approach to the study of phosphorus dynamics has revealed some interesting findings. At other than peak plankton bloom times, much of the energy for phosphorus uptake comes through plankton respiration, rather than photosynthesis, with bacteria competing with phytoplankton for phosphate. Uptake of phosphate is usually greater than metabolic needs which results in the excretion of inorganic phosphate by these cells. The implications of these findings are currently being related to overall lake metabolism. These and similar experiments will provide a much increased understanding of the role of phosphate in lakes.

Nutrients and phytoplankton. The interaction of N and P on the growth rate of phytoplankton was determined in Lakes Washington and Sammamish during summer 1974. Growth rate was found to be dependent upon PO_4-P only with no influence from N. Other experiments have indicated that increased NO_3-N would stimulate the uptake of PO_4-P. Such a mechanism in these lakes cannot be inferred insofar as growth rate as a function of carbon uptake is concerned.

The lack of N effect across a PO_4-P gradient of approximately 1 to 11 μg/l was not because NO_3-N was above limiting levels, since the NO_3-N gradient in Lake Washington was 7.5 to 108 μg/l. Thus, the treatment of PO_4-P as the principal nutrient ontroller represents the best approach for modeling the phytoplankton biomass, at least in Lakes Sammamish and Washington. The sensitivity in the Findley Lake results was not adequate to determine if interaction occurred.

The growth rate parameters μ_{max} and K_t (maximum growth rate and half saturation constants) have been found to vary greatly within one lake--so much so that it is not safe to attribute a great deal of significance to the gradient previously observed in the constants from the most oligotrophic to the most eutrophic lake. Surely the constants vary with lake richness, but with only three experiments per lake, as has been done on this project, the differences among the lakes are not discernible. The mean μ_{max} for the four lakes determined in culture was 0.27, 0.25, 0.34, and 0.90 for Lakes Findley, Chester Morse, Sammamish, and Washington. The mean K_t was 0.34, 0.40, 0.60, and 1.46 μg/l PO_4-P for the four lakes, respectively. The range for these means was ± 53%, thus emphasing the variability of these parameters. Confidence intervals of 50 to 75% of the mean for K_s values are the rule in the literature.

Biomass was measured in replicate in Lakes Washington and Sammamish by several indicators on seven different occasions. The mean coefficient of variation for the five indicators was as follows: Chl a, 11%; ATP, 24%; ash free dry weight, 17%; POC, 24%; and algal volume, 22%. The ratios of these indicators, one to the other, varied on the order of ± 50%, but ATP/algal C in Lake Washington varied only ± 19%. The algal C/Chl a ratio for Lake Washington biomass was 51 ± 49% and ATP/Chl a for both lakes was 0.35 ± 43%.

In culture, the algal C/Chl a ratio, determined indirectly by two methods of measuring growth rate by C^{14} uptake, was 77/1. That was very close to the directly measured value in culture of 82/1; thus in all past culture growth rate results it seems fair to use 77/1 as a reasonable C/Chl a ratio and probably remain with the 50/1 for *in situ* work, based on the Lake Washington observations.

Zooplankton grazing. Results from grazing experiments conducted during 1972 through 1974 showed a rather predictable response pattern to algal density. Of the 12 experiments in the four lakes, in only two was net plankton significantly grazed. Thus, zooplankton feeding was usually on the nanoplankton size class less than 50 μ. If fitted to a Michaelis-Menton expression, the maximum grazing rate on algae (G_a) was 2.7/day with a half saturation constant (K_a) of 1 μg/l Chl a or using a C/Chl a ratio of 77/1, 77 μg/l C. Interestingly enough, at a Chl a concentration of 8 μg/l, 90% of the maximum G_a would be attained, which is precisely what Winter, et al. (personal communication) report in their modeling paper for Puget Sound phytoplankton.

Grazing on detritus is also thought to be important, particularly in Findley Lake. To determine the total C uptake rate by zooplankton (G_t) and to separate algal (G_a) from bacterial and detrital grazing (G_{b+d}), the "a" fraction has been tagged by inorganic C^{14}, as usual, and separated from the "b+d" fraction. The latter was tagged by acetate C^{14}. Filtering rates and subsequently grazing rates can then be estimated for the two fractions. Three such experiments were completed on Findley Lake and two on Lake Washington during summer 1975.

Food chain efficiency. A significant finding in the primary-secondary production work has been strong support for the hypothesis that food chain efficiency decreases with eutrophication. The ratio of secondary productivity to primary productivity during 1972-73 decreased from 13% in Findley Lake to 4% in Chester Morse Lake to 1% in Lake Sammamish. One reason for this could be the progressively larger fraction of net plankton that contributes the primary productivity as enrichment increases in these four lakes and the fact that zooplankton usually did not graze the net plankton. The high Findley Lake efficiency may be due to the large contribution of detritus C to that system from the forest.

Findings in the Eastern Deciduous Biome suggest that as enrichment increases and larger-celled algae become prevalent in the zooplankton production shifts from largely copepods, which are selective on nanoplankton, to cladocerans, which are "generalists." This was not found in at least three of these lakes because cladocerans contributed as much as one half of the production even in the highly oligotrophic lakes. The soundness of this hypothesis and further comparison with the Deciduous Biome results will be further tested as more data are analyzed. This could be particularly rewarding with the zooplankton productin data from Lake Washington in recent years and in comparison with past data during conditions of heavy enrichment.

Detritus. A synthesis of ecosystem research (1971-1973) on subalpine Findley Lake examined the effects of inputs of terrestrial organic carbon from a coniferous forested watershed upon carbon and nutrient cycling in the lake. Our results indicate that the amount of terrestrial carbon received by Findley Lake constitutes a more important source of carbon than phytoplankton photosynthesis for consumer trophic levels. Of the annual income of particulate organic carbon (14.2 g/C m^2) for Findley Lake, terrestrial inputs supplied twice the carbon fixed by phytoplankton, 66% and 34%, respectively.

A model of the rate of change of phytoplankton carbon has proved valuable in partitioning carbon fluxes into assimilation and losses due to advective processes, zooplankton grazing, sinking, and death. Such calculations show that of the carbon fixed by phytoplankton, 36% goes to gross production which can be respired or lost to grazing by zooplankton, with the remaining 64% lost by excretion, death (autolysis and mineralization, and sinking). In contrast, to the terrestrial carbon inputs, only 2% goes to gross production in the water column, with approximately 82% settling to the sediments for use by insects. Loss in the outflow is 16%. Nutrient levels associated with these carbon fluxes provide evidence of nutrient immobilization by microbiota attached to terrestrial detritus and suggest an important nutrient conservation or loss mechanism in the ecosystem.

Transfers of carbon in the consumer communities of zooplankton and insects reflect a low maintenance respiration for the lake ecosystem owing to subsidies of terrestrial carbon high in cellulose and lignin. The influence of terrestrial detritus is also apparent in the insect production being nearly four times the zooplankton production, which is converse to the predominately plankton food chains in most lakes. Such results illustrate the probable dependence of many lakes in coniferous forests upon watershed detrital inputs and their sensitivity to land-based perturbations. Research for 1974 and in 1975 on watershed inputs and lake responses involving fine particulate organic carbon, dissolved organic carbon, nutrient cycles, and spatial-temporal change for plankton processes using such techniques as ATP, ETS enzyme assays and tracers are confirming these findings.

Fish feeding behavior. From past studies dealing with the trophic role of planktivorous fish in the biome lakes, we have found the impact of a population of planktivorous fish on the lake ecosystem to be a complex interplay of fish behavior and environmental conditions. With the aid of modeling and experimental data, we have constructed in detail the mechanisms of food selection and have been successful in describing the potential rate of food intake by juvenile sockeye salmon. Juvenile sockeye salmon represent approximately 60% of the biomass of limnetic fish in Lake Washington. Ongoing research is expanding this data base to include longfin smelt and threespine stickleback, the other principal limnetic fish in Lake Washington. Intimately tied with feeding mechanisms in planktivorous fish are the adoption of anti-predator and wintertime behavior patterns which occur at the expense of food obtainment. These findings suggest that any increase in the secondary production of a lake will not necessarily result in increased fish production. One must consider such changes as food particle size, species composition, and distribution, in addition to the actual magnitude of change in secondary production.

Modeling. A major problem with the use of most lake computer models that were developed for management purposes has been the lack of model sophistication. The model being built by the lakes group of the Coniferous Forest Biome is constructed from detailed process experiments and is designed for application to management problems. Dialogue with the City of Seattle's Metro Agency identified this inadequacy in Metro lake models and there is an attempt to familiarize them with lake research and modeling in the Biome.

Problem solving exercises. A relatively simple multiparametric phosphorus cycling model was developed using rate contants determined for Lake Sammamish. The model couples a mixing model with a compartmental phosphorus cycling model, which predicts mixing depth given weather data input, and thus considers the effect of mixing depth on light availability and nutrient supply to the lighted zone. The model output simulates reasonably well the years with early (April) diatom outbursts as well as those with later, more modest blooms (May-June) of mixed algal populations. While our original hypothesis was that the early bloom is possible because of earlier water column stability allowing more light, the model now suggests earlier column stability actually prevents the early outburst by restricting phosphorus supply to the lighted zone. The model has also shown the large dependence of algal growth upon regenerated nutrients in the lighted zone and the relative unimportance of phosphorus entrained from the hypolimnion or from inflow streams in midsummer.

APPENDIX I

Analysis of Individual Terrestrial Ecosystems Publications
June 1974 - August 1975

Billings, R. F., and R. I. Gara. Rhythmic emergence of *Dendroctonus ponderosa* (Coleoptera: Scolytidae) from two host species. Submitted to Annals of Entomological Society of America.

Cole, D. W., and D. W. Johnson. Atmospheric sulfate additions and cation leaching in a Douglas-fir ecosystem. Submitted to Water Resources Research.

Cromack, K., Jr., and C. D. Monk. Litter production, decomposition and nutrient cycling in a mixed hardwood watershed and a white pine watershed at Coweeta Hydrologic Station, North Carolina. AEC Symposium: Mineral cycling in southeastern ecosystems, held at Augusta, Georgia, 2-4 May 1974 (in press).

Cromack, K., Jr., D. M. Sharpe, B. S. Ausmus, C. D. Monk, R. Fogel, and W. C. Johnson. A regional approach to forest decomposition processes. Submitted to Ecol. Monogr.

Cromack, K., Jr., P. Sollins, R. L. Todd, and R. Fogel. The role of organic acids in elemental cycling by fungi, roots, and bacteria. To be submitted to New Phytologist.

del Moral, R., and J. N. Long. Classification of forest community types in the Cedar River drainage. Submitted to J. Appl. Ecology.

Edmonds, R. L. Effect of cold and warm extracts of nondecayed and decayed western hemlock heartwood on the growth of *Fomes annosus*. Submitted to Can. J. For. Res.

Emmingham, W. Comparison of seasonal cambial and leader growth for various *Pseudotsuga menziesii* sources in different environments. Submitted to Can. J. For. Res.

Fogel, R. 1975. The genus *Leucogaster* (Basidiomycetes, Leucogastraceae). Ph.D. thesis, Oregon State Univ., Corvallis. 115 p.

Fogel, R. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas-fir stand. Submitted to Can. J. Bot.

Fogel, R. Insect mycophagy: A preliminary bibliography. Pacific Northwest Forest and Range Expt. Stn. Bull. USDA Forest Service (in press).

Fogel, R., and S. B. Peck. Ecological studies of hypogeous fungi. I. Coleoptera associated with sporocarps. Mycologia (in press).

Fogel, R., and J. M. Trappe. Small mammal mycophagy: A review. Submitted to J. Anim. Ecol.

Fujimori, T., S. Kawanabe, H. Saito, C. C. Grier, and T. Shidei. Biomass and net primary production of three coniferous forest types of the U.S. Pacific Northwest. Submitted to Japanese J. For.

Gessel, S. P., and J. Turner. Litter production in western Washington Douglas-fir stands. Submitted to Forestry.

Grier, C. C. Short-term effects of fire on nutrient cycling processes in a ponderosa pine-Douglas-fir forest in north-central Washington. Submitted to Can. J. For. Res.

Grier, C. C. Biomass, productivity and nutrient distribution and cycling in a mature hemlock-spruce forest on the Oregon coast. Submitted to Oecologia.

Grier, C. C., and D. W. Cole. The role of fire in nutrient mineralization and transfer processes in coniferous forest ecosystems. Submitted to Ecol. Monogr.

Hagen, A., S. Kjelvik, K. Liestol, E. Ostbye, H. J. Skar, and G. Swartzman. 1974. A simple ecosystem model with emphasis on small rodents. Rapp. Hoyfjellsokol Forsk. Sta Finse, Norway.

Hett, Joan. 1974. Age-structural dynamics of some forest trees. Symp. on Plant Population Dynamics, AIBS Meeting, August 1974, Tempe, Arizona (Abst: Can. Bot. Assoc. Bull. 7(4):9).

Johnson, D. W. 1975. Processes of elemental transfer in some tropical, temperate, alpine and northern forest soils: Factors influencing the availability and mobility of major leaching agents. Ph.D. thesis, Univ. Washington, Seattle. 169 p.

Johnson, D. W., and D. W. Cole. Sulfate mobility in an outwash soil in western Washington. First International Symposium on Acid Precipitation and the Forest Ecosystem (in press).

Johnson, D. W., D. W. Cole, and S. P. Gessel. 1975. Processes of nutrient transfer in a tropical rain forest. Biotropica 7(3):208-215.

Johnson, D. W., M. J. Singer, R. V. Minden, and D. W. Cole. Soil leaching processes in a subalpine ecosystem. To be submitted to J. Appl. Ecol.

Long, J. N., and J. Turner. 1975. Aboveground biomass of understory and overstory in age sequence of four Douglas-fir stands. J. Appl. Ecol. 12:179-188.

Pike, L. H., W. C. Denison, D. M. Tracy, M. A. Sherwood, and F. M. Rhoades. Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. Submitted to Z. Bryologist.

Reed, K. L., E. Hamerly, B. E. Dinger, and P. G. Jarvis. An analytical model for field studies of photosynthesis. J. Appl. Ecol. (in press).

Running. S. W. Environmental control of leaf conductance in Northwest conifers. Can. J. For. Res. (in press).

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Salo, D. J. 1974. Factors affecting photosynthesis in Douglas-fir. Ph.D. thesis, Univ. Washington, Seattle. 150 p.

Scott, D. W., and R. I. Gara. Antennal sensory organs of two Melanophila species (Coleoptera: Buprestidae). Submitted to Annals of the Entomological Society of America.

Singer, M., and F. C. Ugolini. In situ study of spodosol development in mixed parent materials. Submitted to Soil Sci. Soc. Am. Proc.

Strand, R. H., B. S. Ausmus, and K. Cromack, Jr. litter decomposition analysis: A time series approach. Submitted to Ecol. Monogr.

Swartzman, G. L. 1975. An intrinsic environmental framework for adoptation. In Ecosystem analysis and prediction. Proceedings of a conference on ecosystems. Alta, Utah. SIAM. Philadelphia, Pennsylvania.

Swartzman, G., and J. S. Singh. 1974. A dynamic programming approach to optimal grazing strategies using a succession model for a tropical grassland. J. Appl. Ecol. 11:537-548.

Turner, J. 1975. Nutrient cycling in a Douglas-fir ecosystem with respect to age and nutrient status. Ph.D. thesis, Univ. Washington, Seattle. 191 p.

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Turner, J., and S. P. Gessel. 1974. Litter production by red alder in western Washington. For. Sci. 4:325-330.

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APPENDIX II

Analysis of Watersheds Publications
June 1974 - August 1975

Internal dynamics group

Avery, C. C., F. R. Larsen, and G. H. Schubert. Fifty-year records of virgin stand development in southwestern ponderosa pine. USDA Forest Service General Tech. Rep. USDA Forest Service (in press).

Cromack, K., Jr., R. L. Todd, and C. D. Monk. Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. Soil Biol. Biochem. 7 (in press).

Edwards, N. T., K. Cromack, Jr., J. M. Kelly, D. E. Reichle, and W. F. Wittingham. Forest litter decomposition and mineralization. Submitted to Ecol. Monogr.

Emmingham, W. H. Genetics comparison of seasonal growth and growth patterns in Douglas-fir. Submitted to Can. J. Bot.

Gholz, Henry L., and Franklin K. Fitz. Foliage relations of six old-growth forest communities in the western Oregon Cascades. Submitted to Can. J. For. Res.

Grier, C. C. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. Can. J. For. Res. (in press).

Grier, C. C., and R. S. Logan. Biomass distribution and net primary production in old-growth Douglas-fir communities of a small watershed. Submitted to Ecol. Monogr.

Harr, R. D., and C. C. Grier. A moderately sensitive, inexpensive manometer for tensionmeters. Submitted to SSSAP.

Hermann, R. K. Growth and production of tree roots: A review. In J. K. Marshall [ed.], The belowground ecosystem: A synthesis of plant-related processes. Dowden, Hutchinson, and Ross, Stroudsburg, Pa. (in press).

Nussbaum, R. A., and C. Tait. Reproductive biology of the Olympic salamander Rhyacotritou olympicus. Copeia (in press).

Santantonio, D., R. K. Hermann, and W. S. Overton. Root biomass studies in forest ecosystems. Submitted to Pedo. Bio.

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Waring, R. H., W. H. Emmingham, and S. W. Running. The environmental limits of an endemic spruce (Picea breweriana Wats.). Can. J. Bot. (in press).

Webb, W. L. Dynamics of photo-assimilated carbon in Douglas-fir seedlings. Plant Physiology (in press).

Whittaker, J. O., Jr., and C. Maser. Food habits of five western Oregon shrews. Northwest Sci. (in press).

Zobel, D. B., W. A. McKee, C. M. Hawk, and C. T. Dyrness. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Submitted to Ecology.

Hydrology, erosion, and nutrient export group

Fredriksen, R. L. 1970. Erosion and sedimentation following road construction and timber harvest on unstable soils in three small western Oregon watersheds. USDA For. Serv. Res. Pap. PNW-104. 15 p.

Fredriksen, R. L. 1975. Nitrogen, phosphorus, and particulate matter budgets of five coniferous forest ecosystems in the western Cascades Range, Oregon. Unpub. Ph.D. thesis, Oregon State Univ., Corvallis. 127 p.

Harr, R. D. Water flux in soil and subsoil on a steep, forested slope. Submitted to J. Hydrology.

Holbo, H. R., and R. D. Harr. An electronic water level recorder for small diameter piezometers. J. Hydrol. (in press).

Swanson, F. J., and C. T. Dyrness. 1975. Impact of clearcutting and road construction on soil erosion by landslides in the western Cascade Range, Oregon. Geology 3(7):393-396.

Swanson, F. J., and M. E. James. 1975a. Geomorphic history of the lower Blue River Lookout Creek area, western Cascades, Oregon. Northwest Sci. 49(1):1-11.

Swanson, F. J., and M. E. James. 1975b. Geology and Geomorphology of the H. J. Andrews Experimental Forest, western Cascades, Oregon. USDA For. Serv. Res. Pap. PNW-188.

APPENDIX III

Analysis of Aquatic Ecosystems and Interface Research Publications
June 1974 - August 1975

*Manuscript in preparation

<u>Stream ecosystems</u>

Aho, R., and J. D. Hall. Biomass and growth rates of cutthroat in forested and adjacent clearcut sections of a Cascade stream.*

Anderson, N. H. Carnivory by an aquatic detritivore, <u>Clistoronia magnifica</u> (Trichoptera: Limnephilidae). Submitted to Ecology.

Anderson, N. H., and E. Grafius. Utilization and processing of allochthonous materials by stream Trichoptera. Proceedings of the 19th International Congress of Limnology (Verh. Int. Ver. Theor. Angew. Limnol.) (in press).

Gregory, S. V. Effect of light and nutrient addition on colonization rate and primary production in a small Cascade stream. Submitted to Ecology.

Gregory, S. V. Investigation of a ^{32}P material balance method for measuring net periphyton production and grazing rates on periphyton in streams. Submitted to Limnol. Oceanogr.

Hall, J. D., and R. Aho. Population estimation by the removal method: A cautionary note.*

Lyford, L. H., Jr., and S. V. Gregory. The dynamics and structure of periphyton communities in three Cascade mountain streams. Proceedings of the 19th International Congress of Limnology (Verh. Int. Ver. Theor. Angew. Limnol.) (in press).

McIntire, C. D., J. A. Colby, and J. D. Hall. Dynamics of small lotic ecosystems: A modelling approach. Proceedings of the 19th International Congress of Limnology (Verh. Int. Ver. Theor. Angew. Limnol.) (in press).

Sedell, J. R., F. J. Triska, J. D. Hall, N. H. Anderson, and J. H. Lyford, Jr. A two-year energy budget for a small coniferous forest stream.*

Sedell, J. R., F. J. Triska, and N. S. Triska. The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. Proceedings of the 19th International Congress of Limnology (Verh. Int. Ver. Theor. Angew. Limnol.) (in press).

Triska, F. J., Cromack, K., and J. R. Sedell. Nitrogen budget for a small mountain stream. (In conjunction with watershed interface.)*

Triska, F. J., J. R. Sedell, and B. Buckley. The processing of conifer and hardwood leaves in two coniferous forest streams: II. Biochemical and nutrient changes. Proceedings of the 19th Internaional Congress of Limnology (Verh. Int. Ver. Theor. Angew. Limnol.) (in press).

Lake ecosystems

Bartoo, N., and R. I. Balfour. A simple predictive model for estimating remaining concentrations in continuous dilution situations.*

Bartoo, N., and R. Hansen. Gill net selectivity.*

Bartoo, N., and N. Rickard. Sled trawl selectivity.*

Birch, P., R. Barnes, and D. Spyridakis. Sedimentation rates in lakes of the lake Washington drainage basin.*

Devol, A. The seasonal cycle of ETS activity in lakes of the Lake Washington drainage basin.*

Devol, A. The importance of zooplankton nutrient recycling in two lakes of contrasting trophic status.*

Devol, A., and R. Wissmar. ETS activity, ATP, POC, and chlorophyll in size fractions of plankton at different depths in Lake Washington.*

Doble, B. Diel feeding periodicity, instantaneous rate of gastric evacuation and daily zooplankton ratio of juvenile sockeye salmon in Lake Washington.*

Eggers, D. On the nature of food selection by planktivorous fish. Submitted to Ecology.

Eggers, D. The effect of schooling on food acquisition by planktivorous fish.*

Eggers, D. The effects of behavior on food acquisition by juvenile sockeye salmon in the limnetic environment of Lake Washington.*

Eggers, D. A synthesis of feeding behavior and growth of juvenile sockeye salmon in the limnetic environment of Lake Washington.*

Hendrey, G. R., and E. B. Welch. 1974. Phytoplankton productivity in Findley Lake. Hydrobiologia 45(1):45-63.

Hendrey, G. R., E. B. Welch, and P. Sturdevant. Growth rate kinetics of natural phytoplankton assemblages in four Washington lakes. Submitted to Limnol. Oceanogr.

Palmer, F. E., R. Methot, and J. T. Staley. Patchiness in the distribution of planktonic heterotrophic bacteria in lakes. Submitted to Appl. Microbiol.

Pederson, G. L., and A. H. Litt. A classic example of congeneric occurrence of two Diaptomus species.*

Pederson, G. L., E. B. Welch, and A. H. Litt. Plankton secondary productivity and biomass: Their relation to lake trophic state. Hydrobiologia (in press).

Perkins, M. A., and J. E. Richey. Intracellular portioning of phosphate.*

Perkins, M. A., P. Sturdevant, and E. B. Welch. Comparison of phytoplankton biomass measurements in situ and in vitro.*

Rau, G. Plant litter dispersal into a subalpine lake. Oikos (in press).

Richey, J. E. Phosphorus cycling in lakes of the coniferous forest.*

Richey, J., A. Devol, and M. Perkins. Diel phosphate flux in Lake Washington. Verh. Int. Ver. Theor. Angew. Limnol. (in press).

Richey, J., M. Perkins, and C. Goldman. Effects of salmon decomposition on the ecology of a subalpine stream. J. Fish. Res. Board Can. (in press).

Richey, J., R. Wissmar, A. Devol, M. Perkins. Diel nutrient and production dynamics in Lake Washington.*

Tison, L. D., F. E. Palmer, and J. T. Staley. Nitrogen fixation in four Washington lakes.*

Wekell, M. The mineralization of glucose by lake sediment bacteria in four lakes in the Lake Washington drainage basin.*

Wekell, M. The effect of temperature on glucose mineralization rates by sediment bacteria in four lakes of the Lake Washington drainage basin.*

Wekell, M. The hydrolysis of chitin by lake sediment bacteria.*

Welch, E. B., R. Burgner, and D. Spyridakis. 1975. Comparisons of nutrient status, remineralization and production in an altitudinal gradient of lakes. Presented at AAAS Meeting, 28 January 1975, New York.

Welch, E. B., M. E. Harper, and C. A. Rock. Phosphorus income and trophic state of Lake Sammamish: History and future predictions.*

Welch, E. B., G. R. Hendrey, and R. K. Stoll. 1975. Nutrient supply and the production and biomass of algae in four Washington lakes. Oikos 28:1-8.

Welch, E. B., P. Sturdevant, M. A. Perkins, and T. W. Trepanier. Dominance of phosphorus over nitrogen as the limiter to phytoplankton growth rate. Submitted to Limnol. Oceanogr.

Welch, E. B., T. Wiederholm, D. E. Spyridakis, and C. A. Rock. 1975. Nutrient loading and trophic state of Lake Sammamish, Washington. O.E.C.D., North Am. Proj. 21 p.

Wissmar, R., J. Richey, and D. Spyridakis. Detritus and carbon-nutrient fluxes in Findley Lake, Washington. Submitted to Limnol. Oceanogr.