

CONIFEROUS FOREST BIOME
Summary of Research and Synthesis
Activities July 1975 - August 1976

Edited by
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1. INTRODUCTION

Research activities in the post-IBP phase of the Biome program prior to July 1975 were reported in Internal Report 162. Summaries of research and synthesis activities from July 1975 to August 1976 are presented here.

The reports are arranged in the following order: Analysis of Individual Terrestrial Ecosystems, which has three components (Behavior and Strategies of Individual Ecosystems, Environment and Plant Succession and the Land-Use Model); Analysis of Watersheds, which has two components (Watershed 10 and Findley Lake); and Analysis of aquatic ecosystems, which is divided into two components (Lakes and Streams). A total list of Biome publications is included in the Appendix. A more specific list of open literature publications is available from the Biome Office. Progress of the synthesis activities is discussed in Section 5.

2. ANALYSIS OF INDIVIDUAL TERRESTRIAL ECOSYSTEMS

2.1. Behavior and Strategies of Individual Ecosystems

2.1.1. Leaf conductance in different forest stands - R. H. Waring and S. W. Running, Oregon State University.

A manuscript was completed describing how stomata of subordinate hardwood species respond to light, evaporative stress, and soil water availability. We found that except when light directly impinged upon the leaves of understory shrubs, their stomata remained closed. As shallow-rooted species depleted their water supply stomata also closed. Species adapted to clear-cuts, whether deciduous or evergreen, had higher leaf conductance rates than more shade tolerant plants (1).

We have continued to develop more accurate means of estimating stand leaf area (2). We find that the highest leaf areas ($40-55 \text{ m}^2/\text{m}^2$ for all surfaces) occur in environments where soil water is always in good supply and the temperatures are cool (3). Where the evaporative demand is high internal resistance to water flow appears to reduce leaf area proportionally. Only in a few cases does nutritional stress appear to constrain foliage development (3).

In research comparing individual species, we have extended earlier hypotheses concerning a linear relation between cross-sectional area of conducting tissue and leaf area from conifers to Rhododendron, Castanopsis, and Acer macrophyllum. The shrub Acer circinatum was found to have non-linear relationships which means it is particularly adapted to responding to changes in the overstory (4).

Preliminary work on the sapwood of large conifers indicates that the entire reservoir may be utilized in less than 10 days during periods of high transpiration. Refilling of the reservoir appears to be a function of both supply and demand. Rapid recharge follows summer storms that wet the soil to a depth where roots are active. Fall storms are associated with reduced evaporative demand so that deficits are refilled by diffusion, requiring up to 4 months. Sapwood water flux may serve as an index to evaporative demand and root uptake under specified conditions (5,6).

References

1. Running, S. W., and R. H. Waring. Interpreting stomatal behavior of subordinate hardwoods in northwest coniferous forests (Submitted to Forest Science).
2. Gholz, H. L., F. K. Fitz and R. H. Waring. 1976. Leaf area differences associated with old-growth forest communities in the western Oregon Cascades. *Can. J. For. Res.* 6:49-57.
3. Waring, R. H., W. H. Emmingham, H. L. Gholz, and C. C. Grier. Environmental controls on the accumulation of leaf area by coniferous forests in Oregon. (Submitted to Ecology).
4. Waring, R. H., H. L. Gholz, C. C. Grier and M. L. Plummer. Evaluating sapwood cross-sectional area as an estimate of leaf area in some western hardwoods. (Submitted to Forest Science).
5. Kline, J. R., K. L. Reed, R. H. Waring and M. L. Stewart. 1976. Field measurement of transpiration in Douglas-fir. *J. Appl. Ecol.* 13:273-283.
6. Waring, R. H. 1976. Sapwood water flux as a function of evaporative demand and root uptake. *Bull. Ecol. Soc.* 57:15.

2.1.2. Nutrient uptake and translocation by young Douglas-fir trees - H. Riekerk and C. S. Bledsoe, University of Washington.

The overall objective of this study is to determine the major processes of nutrient uptake by young Douglas-fir trees in a forest. The research strategy is, first, to study seedlings growing in culture solutions in the greenhouse, then to study young trees growing in soil in the greenhouse and in the field, and finally to study trees growing in a natural forest.

A. Nutrient uptake studies--The past year has been spent on analyses of the nitrate/ammonium experiment, involving both chemical analyses of the seedlings and statistical analyses of all the data collected. This experiment was designed to look at three aspects of Douglas-fir seedling growth: (1) effects of N supply (as NO_3^- or NH_4^+) on uptake and distribution of nitrogen and the major cations; (2) rates of uptake of NO_3^- , NH_4^+ , K^+ , Ca^{++} , Mg^{++} ; and (3) correlate growth and mineral nutrition.

All the laboratory work has been completed. Data analyses concerning aspect 1 have been completed. Data analyses involving aspects 2 and 3 will be completed by early fall 1976.

The form of nitrogen supplied to Douglas-fir seedlings has a significant effect on distribution of mineral nutrients. Figure 1 illustrates the concentrations of N, P, Ca, K, and Mg in plant parts of harvested seedlings. Although seedlings grown in ammonium-N accumulate considerably more N than do those grown in nitrate-N, the accumulation of cations is much less. This may be due to the "charge-balance" problem which seedlings have in taking up N as a cation (NH_4^+) and therefore limiting their uptake

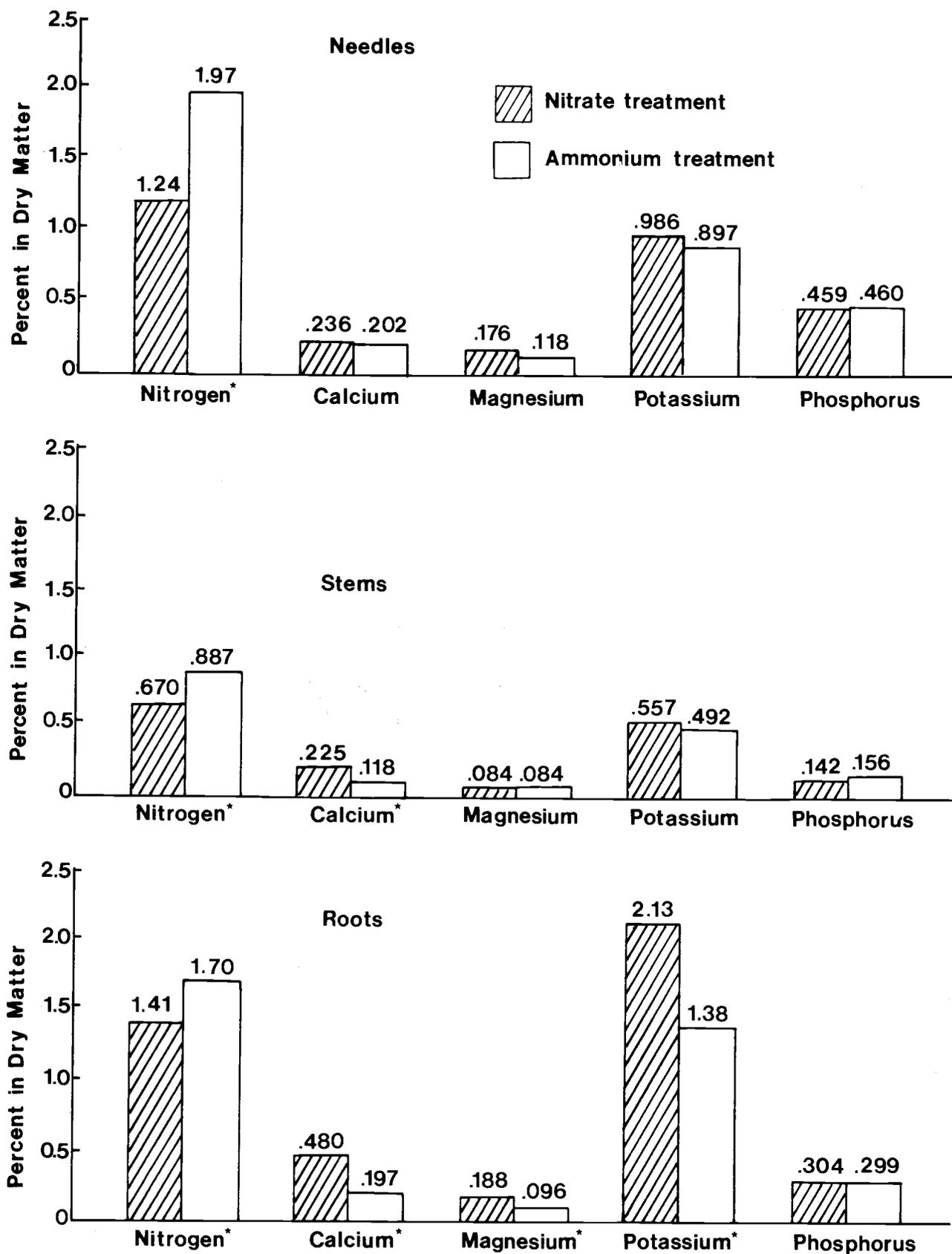


Figure 1. Distribution of nutrients in Douglas-fir seedlings.

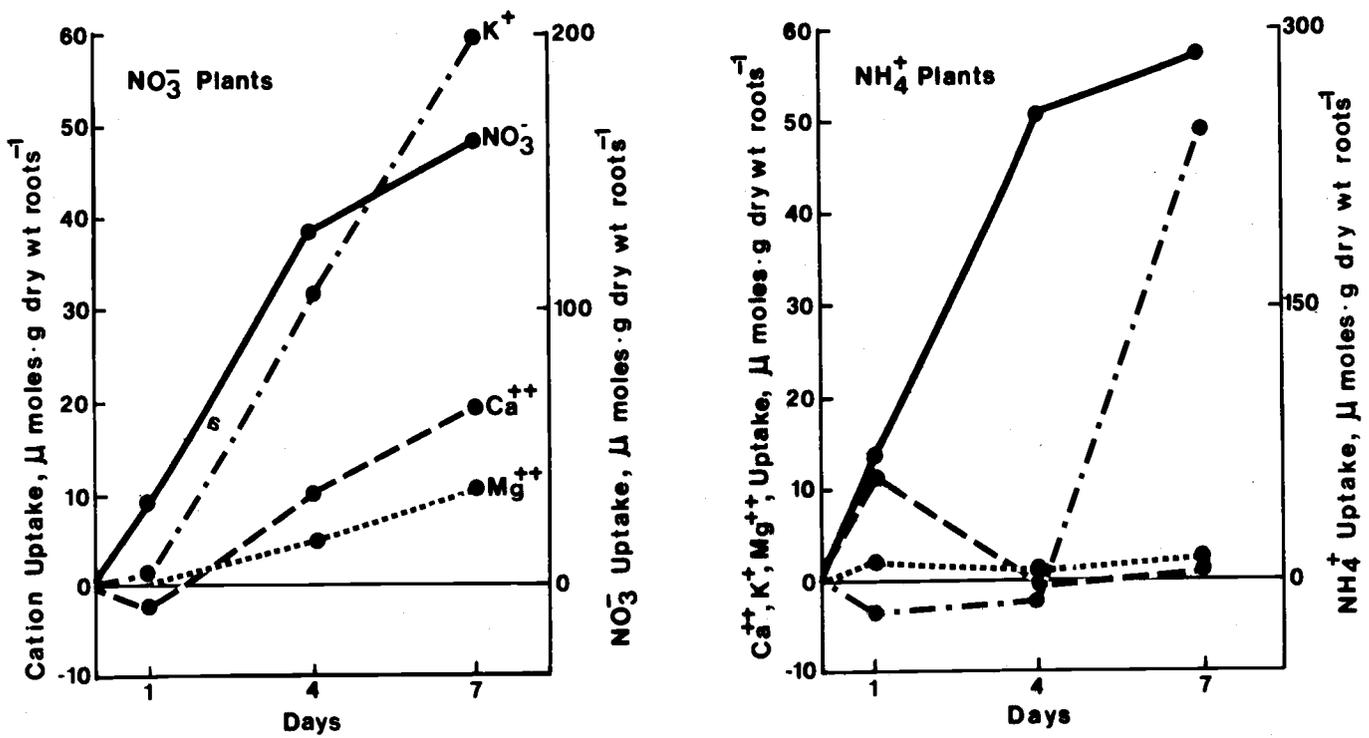


Figure 2. Nutrient uptake by Douglas fir seedlings grown in nutrient culture. Values are averages of ten seedlings.

of K^+ , Ca^{++} , and Mg^{++} . This cation concentration difference between nitrate-N and ammonium-N plants is significant in the stems for Ca^{++} and in the roots for Ca^{++} , K^+ , and Mg^{++} . Differences in N concentrations were significant in all three plant parts.

Not only does the form of N supplied have an effect on distribution (as discussed above), but the form also affects the uptake rates (see Figure 2). Note that the rate of ammonium uptake is almost double the nitrate rate. Figure 2 also illustrates the considerable differences in rates of cation uptake, where nitrate-grown plants take up K^+ most rapidly, Ca^{++} less rapidly, and Mg^{++} least rapidly. The ammonium-grown plants do not take up potassium until the supply of ammonium ions is exhausted. Figure 2 demonstrates how little the uptake rates decrease, even as the ion concentrations decrease markedly. The results of this experiment, which were reported at the AIBS annual meetings in June 1976, are being written for publication in a joint paper with D. W. Rains.

Although considerable time has been spent in looking for correlations between growth and ion uptake, the volume of data has made this task exceedingly laborious. Thus in collaboration with G. Swartzman, the data have been computerized on the CDC computer, and numerous computations are being carried out. After the statistical and graphical output has been completed and evaluated, the data will be further used in a small process model--linking growth and nutrition. It is hoped that this modeling approach may suggest links between growth and nutrition which have not been obvious previously.

B. Translocation studies--The objective is to estimate seasonal nutrient translocation rates of a young Douglas-fir forest by combining correlations of (a) plant-sap nutrient transport (milligrams of nutrient per gram per root per hour vs. soil solution concentrations (and/or soil moisture content) utilizing Douglas-fir seedlings and (b) fine-root biomass (<2 mm diameter) vs. sapwood cross-sectional area at DBH of forest-grown trees.

The work during 1976 was mainly focused on obtaining initial data to: (a) test the pressure-bomb technique of sap extraction, and (b) begin a fine-root biomass vs. sapwood area correlation. Greenhouse studies of nutrient translocation by Douglas-fir seedlings growing in solution cultures have been summarized in a short communication (Plant and Soil, 1976, Vol. 45).

The concentration of nutrients was greater in the xylem sap of nitrate-grown plants, than in ammonium-grown plants, suggesting more nutrient translocation by nitrate-grown plants. Nitrate reduction in the root tissues was demonstrated (Table 1). The translocation rate of potassium (K^+) in xylem sap may be more rapid than the rate of K^+ uptake (see previous section), suggesting release of K^+ stored in root tissues. Furthermore, the concentration of potassium in the xylem sap was much greater than any of the other nutrients (5-40 times greater for NO_3^- - grown plants; 10-450 times greater for NH_4^+ - grown plants).

Table 1. Nutrient concentrations of Douglas-fir xylem sap and external solution.

Treatment	NH ₄ -N	NO ₃ -N	PO ₄ -P	K	Ca	Mg
<i>Xylem sap solution (ppm)</i>						
NO ₃ -N culture	9.9 ± 8.8	1.5 ± 1.2	3.9 ± 2.3	69.2 ± 15.0	15.1 ± 8.1	3.0 ± 1.1
NH ₄ -N culture	3.9 ± 4.4	0.1 ± 0.1	1.9 ± 1.4	67.2 ± 22.2	6.5 ± 1.5	2.3 ± 0.8
Soil				55.5 ± 35.2	10.0 ± 8.3	5.9 ± 3.6
<i>External solution (ppm)</i>						
NO ₃ -N culture	0.5 ± 0.2	1.1 ± 0.5	0.2 ± 0.1	1.6 ± 0.8	0.7 ± 0.2	0.2 ± 0.1
NH ₄ -N culture	0.7 ± 0.1	trace	1.2 ± 0.9	2.2 ± 0.2	1.2 ± 0.1	0.3 ± 0.0
Soil				48.6 ± 42.9	11.7 ± 8.4	6.1 ± 4.5
<i>Uptake ratio</i>						
NO ₃ -N culture		7.2*	36.6	55.8	21.2	16.0
NO ₄ -N culture		5.9*	1.5	30.8	5.2	7.7
Soil				1.7	0.9	1.2
<i>Uptake rate (µg per g OD root per h)</i>						
NO ₃ -N culture	5.0 ± 5.7	0.8 ± 0.7	2.2 ± 1.5	35.3 ± 9.0	7.0 ± 1.5	1.4 ± 0.2
NH ₄ -N culture	3.6 ± 4.2	0.1 ± 0.1	1.1 ± 0.6	45.4 ± 21.9	4.3 ± 2.6	1.6 ± 1.0

*Ratio for total nitrogen.

NOTE: Error is one standard deviation derived from four replicates in solution cultures and eight replicates in soil.

Further information on two-year-old seedlings of Douglas-fir and western hemlock is being collected. Some larger plants can yield sufficient volumes of sap so that a time-series study can evaluate effects of the process of severing root and shoot by decapitation. Decapitation may cause potassium release from storage by the root cells.

A new set of Douglas-fir seedlings will be used for studies on: (a) the effects of temperature and oxygen on nutrient uptake and translocation, and (b) the origins of potassium in xylem sap utilizing ^{42}K in culture solutions.

In the field, excavations of some 50-year-old Douglas-fir trees resulted in a tentative correlation of fine-root biomass vs. sapwood area (see Table 2). Better statistical definition with more sample trees is required before use in conjunction with nutrient-uptake studies is warranted.

2.1.3. Growth and Nitrogen Dynamics in Douglas-fir - D. W. Cole and P. Riggan

Current research is examining the influence of N nutrition upon the timing, amount, and distribution of growth in young (~ 9 years old) site quality II Douglas-fir. For the experimental design, three blocks of five treatments each, including control and 100, 200, 400 and 600 kg N/ha fertilizations [as $(\text{NH}_4)_2 \text{SO}_4$] were established in early May, 1976.

As the growing season progresses, measurements are being made of soil exchangeable NH_4^+ , growth in foliage and cambium, and foliar N concentrations. From these measurements, estimates will be made of the rates of change in foliage and wood biomass and N content, tree N uptake, and foliage senescence and N redistribution.

Foliage growth is being estimated by the following technique: (1) the lengths of new shoots are remeasured at two-week intervals, with samples from different whorls, branches and positions on branches, (2) along with the length measurements, other shoots are collected (by whorl and branch position) and destructively sampled for needle dry weight and shoot length, (3) regressions are calculated for needle dry weight vs. shoot length from this sample, (4) the regressions are used to estimate the needle weight growth curves for the non-destructive sample, (5) at the end of the growing season, the tree will be destructively sampled for biomass and the calculated growth curves will be used to estimate new foliage biomass by whorl and position through time.

Cambial growth is estimated by injuring the cambium with a needle at successive time intervals, dissecting the tree at the end of the growing season, and measuring the radial distance between injuries.

Foliage samples are also being collected to determine the effect of changes in N supply upon N metabolism in the tree. New foliage from the 1974 whorl is being collected at weekly to biweekly intervals, frozen in the field with liquid nitrogen, and stored at -20 C. After collections are completed, they will be analyzed for individual free amino acids and total protein.

Results of these studies will be used in the development of a simulation model describing growth and N movement in young Douglas-fir stands. Initial model development is described in Internal Report 162.

Table 2. Summarizing total DBH, height, sapwood, total root weight, live root weight and needle weight and their logarithmic value.

	<u>TREE #1, 51 years</u>		<u>TREE #2, 45 years</u>		<u>TREE #3, 52 years</u>	
	Metric	Log 10 ^x	Metric	Log 10 ^x	Metric	Log 10 ^x
DBH	13.66 cm		11.5 cm		18.92	
Height	15.27 m		14.33 m		21.55 m	
Sapwood	72.73 cm ²	3.8617	35.19cm ²	3.5464	162.77cm ²	4.2115
Total root	12,150 g	4.0845	5055 g	3.7037	21,602 g	4.3349
Fine root	206 g	2.3138	136 g	2.1335	701 g	2.8457
Needles	3,089 g	3.4898	862 g	2.9355	9,768 g	3.9898
Fine root/sapwood	2.83	0.60	3.86	0.60	4.31	0.67

2.1.4. Primary production and nutrient cycling in different forest environments - C. C. Grier, Oregon State University.

Aside from occasional visits to field sites to collect supplementary data, all field work on this project has been terminated. Work over the past year has focused on data processing and preparation of reports.

This is a comparative study examining changes in stand structure, production and nutrient cycling along an environmental gradient from the Oregon coast to the interior "high desert." Biomass, productivity and nutrient distribution data are complete for most study sites along the transect. Nutrient cycling data are complete for three of the westernmost plots; the remainder are currently being summarized.

The following reports have resulted from this study.

Grier, C. C. and S. W. Running. Leaf area of mature northwestern coniferous forests: Relation to site water balance. Submitted to Science.

Grier, C. C. A Tsuga-Picea ecosystem of coastal Oregon: Biomass distribution and production relations. Submitted to Ecology.

Grier, C. C. A Tsuga-Picea ecosystem of coastal Oregon: Nutrient distribution and nutrient cycling. Submitted to Ecology.

Grier, C. C. Productions and nutrient cycling in some upper-slope conifer forests of the western Oregon Cascades. Can. J. For. Res.

2.1.5. Comparative stand level nutrient availability from terrestrial litter decomposition - K. Cromack and R. Fogel, Oregon State University.

Decomposition and nutrient cycling of decomposer organisms - 1. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon--Linear regression models were developed for Douglas-fir needle, female cone, branch and bark decomposition on seven sites representing four habitat types in western Oregon. Annual weight loss (k) of needles ranged from 0.22 to 0.31, from 0.047 to 0.083 for cones, from 0.089 to 0.059 for branches and from 0.040 to 0.005 for bark. Annual needle weight loss had a negative linear correlation, significant at the 1% level with maximum plant moisture stress and temperature growth index of the seven stands. In comparing substrate quality of needle and woody litter components, annual weight loss had a better correlation with lignin content than with C/N ratio.

Four habitat types were chosen on the H. J. Andrews forest to represent an environmental gradient from dry to wet sites. The driest site, a Tshe/Hodi association, is a climax Douglas-fir association with a south facing slope and shallow soils. The Tshe/Cach type is a slightly more mesic site existing on south facing slopes with deeper soils than the Tshe/Hodi site. The Tshe/Rhma/Bene site represents about 40% of the low elevation stands on the H. J. Andrews and is a mesic habitat. The Tshe/Pomu site is the wettest type habitat, existing on north facing slopes and on first order streams.

Significant associations were obtained between annual weight loss constant (k) and the following stand variables: cover of mature trees, maximum plant moisture stress, minimum soil moisture and minimum litter moisture (Table 1). A multiple regression relationship was obtained between annual weight loss constant (k) and temperature growth index plus maximum plant moisture stress.

Substrate quality and nitrogen content data were obtained on four litter components prior to decomposition studies in the four habitat types on H. J. Andrews (Table 2). This information was used to test which of the substrate quality indices, C/N ratio or % lignin would correlate best with observed annual decomposition constant (k). Percentage lignin was the best predictor of decomposition rate among all four litter substrates, and was statistically significant for all four habitat types (Table 3). The relationship between carbon substrate quality (or % lignin) and annual decomposition constant (k) for the four habitats and the four substrates is presented graphically in Figure 1. Also illustrated in the figure is environmental array of decomposition rate for Douglas-fir green needles from the driest site (#1) to the wettest site (#7). Site #1 is a Tshe/Hodi site and site #7 is a Tshe/Pomu site. Decomposition rate of the Douglas-fir needles was most rapid on the wettest site.

The role of oxalic acid and bicarbonate in calcium cycling by fungi and bacteria: Some possible implications for soil animals. K. Cromack, P. Sollins, R. L. Todd, R. Fogel, A. W. Todd, W. M. Fender, M. Crossley, and D. A. Crowley--Fungi can accumulate Ca in excess of their apparent physiological needs by release of oxalic acid to form the sparingly soluble Ca oxalate. Fungal release of oxalic acid may also form stable complexes with other metallic cations, which would influence both soil weathering processes and release of P from Fe and Al hydroxyphosphates. Both saprophytic and mycorrhizal fungi may be utilizing similar functional nutrient cycling mechanisms with respect to Ca accumulation. Bacteria and Streptomyces sp. can decompose Ca oxalate, which recycles the cation and permits formation of calcium bicarbonates or carbonates. Oxalate decomposing bacteria and actinomycetes were isolated from the digestive systems of oribatid mites, earthworms, a springtail and two immature aquatic detritivores, a mayfly and a stonefly. Earthworms and oribatid mites are among soil animals known to utilize or cycle substantial amounts of Ca. A proposed Ca cycle operative in fungi and soil animals, is presented in Figure 2. In this representation Ca may exist in several chemical forms: As Ca on an exchange site in soil or litter; Ca carbonate or bicarbonate; Ca oxalate; or as Ca^{++} in solution. It is important to emphasize that low energy products of the carbon cycle such as oxalate and bicarbonate may profoundly influence cycling of elements such as Ca and P.

References

- Fogel, R. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas-fir stand. *Can. J. Bot.* 54: 1152-1162.
- Fogel, R. 1976. Notes on distribution and spore ornamentation of Mycolevis siccigleba (Basidiomycetes, Hymenogastreae). (Accepted for publication in the July-August 1976 issue of *Mycologia*).

Table 1. Needle decomposition. Correlation of annual weight loss (k) with stand variables. C = % cover of mature trees, PMS = maximum plant moisture stress, TGI = temperature growth index, SM = minimum soil moisture (0-5 cm deep), LM = minimum litter moisture.

Stand Variable	Regression equation	r	S.E. slope $\times 10^4$	n
C	$k=0.1778+9.25 \times 10^{-4}(C)$	0.87*	2.1	6
PMS	$k=0.3102-5.30 \times 10^{-3}(PMS)$	-0.92**	11.7	6
TGI	$k=0.4350-1.99 \times 10^{-3}(TGI)$	-0.33	28.6	6
SM	$k=0.2045+2.80 \times 10^{-3}(SM)$	0.91*	6.3	6
LM	$k=0.2087+2.30 \times 10^{-3}(LM)$	0.89*	5.7	6
PMS+TGI	$k=0.0599-7.1981 \times 10^{-3}(PMS)$ $+0.003(TGI)$	0.987**	8.6=B 8.5=C	6

*Significant at the 5% level.

**Significant at the 1% level.

Table 2. Substrate quality and nutrient content of Douglas-fir needles, cones, branches and bark.

	%C	%N	C/N RATIO	% LIGNIN*
Needles	50.8	0.82	62	21.8
Cones	49.3	0.24	205	44.2
Bark	56.4	0.19	297	58.6
Branches (1 cm diam.)	49.3	0.15	329	43.4

*Determined by Van Soest's (1963) method.

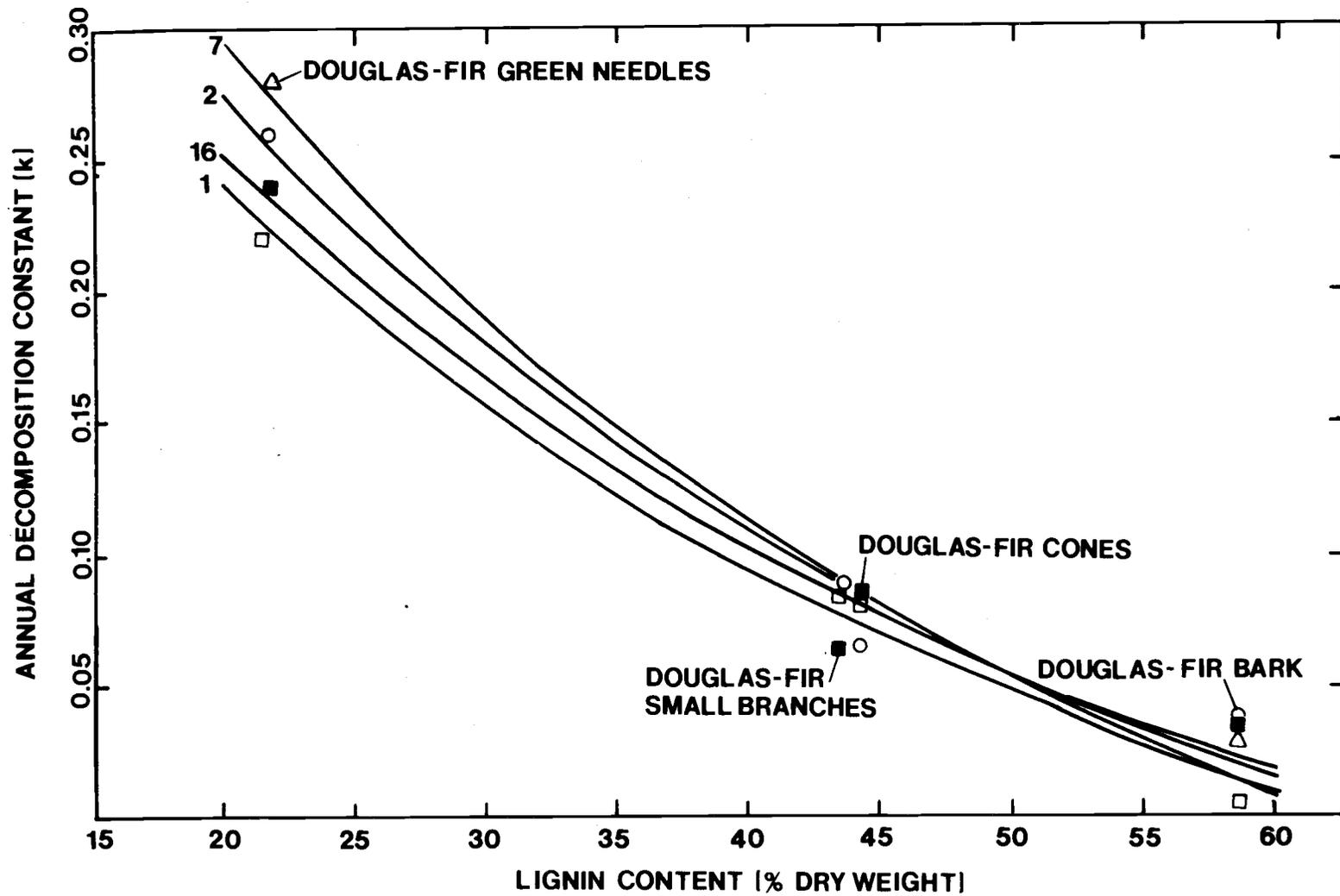


Figure 1. Lignin content as a predictor of annual decomposition rate on four habitat types, H. J. Andrews Experimental Forest, Oregon. Untransformed data line shown on graph.

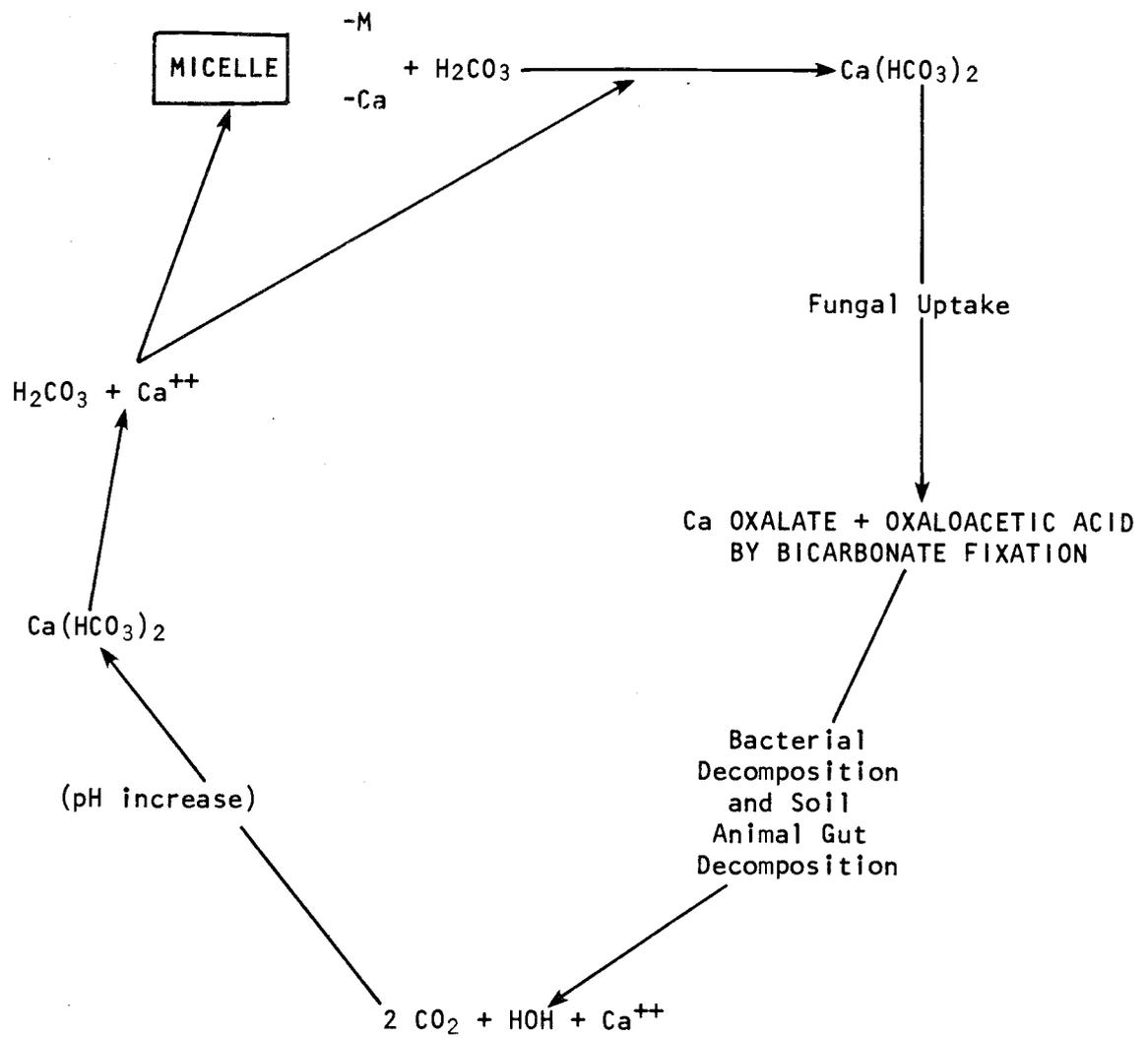


Figure 2. Proposed Calcium Cycle in Fungi and Soil Animals.

Table 2. Needle decomposition. Correlation of annual weight loss (k) with stand variables. C = % cover of mature trees, PMS = maximum plant moisture stress, TGI = temperature growth index, SM = minimum soil moisture (0-5 cm deep). LM = minimum litter moisture.

Stand Variable	Regression equation	r	S.E. slope $\times 10^{-4}$	n
C	$k=0.1778+9.25 \times 10^{-4} (C)$	0.87*	2.1	6
PMS	$k=0.3102-5.30 \times 10^{-3} (PMS)$	-0.92**	11.7	6
TGI	$k=0.4350-1.99 \times 10^{-3} (TGI)$	-0.33	28.6	6
SM	$k=0.2045+2.80 \times 10^{-3} (SM)$	0.91*	6.3	6
LM	$k=0.2087+2.30 \times 10^{-3} (LM)$	0.89*	5.7	6
PMS+TGI	$k=0.0599-7.1981 \times 10^{-3} (PMS)$ $+0.003 (TGI)$	0.987**	8.6=B 8.5=C	6

* significant at the 5% level

** significant at the 1% level

Table 3. Substrate quality and nutrient content of Douglas-fir needles, cones, branches and bark.

	%C	%N	C/N Ratio	%lignin
Needles	50.8	0.82	62	21.8
Cones	49.3	0.24	205	44.2
Bark	56.4	0.19	297	58.6
Branches	49.3	0.15	329	43.4

*Determined by Van Soest's (1963) method

Table 3. % lignin (LN) as a predictor of annual decay constant (k).

Site	Association	Regression equation	r^2	S. E. Slope $\times 10^{-2}$	N	r
7	Tshe/Pomu	$k=1.0832-0.26303(LN)$	0.974	3.02	4	0.987*
2	Tshe/Rhma/Bene	$k=0.98354-0.23676(LN)$	0.979	2.48	4	0.989*
16	Tshe/Cach	$k=0.90232-0.21678(LN)$	0.975	2.47	4	0.987**
1	Tshe/Hodi	$k=0.87764-0.21218(LN)$	0.993	1.28	4	0.996**

*Significant at the 5% level.

**Significant at the 1% level.

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2.1.6. Decomposition Cedar River - R. L. Edmonds, K. Vogt, D. Vogt, and G. Antos, University of Washington.

The major objective of the decomposition studies in the Cedar River watershed is to compare rates of decomposition and mineralization and microorganism populations in (1) four ecosystems and (2) as a function of stand age and development in Douglas-fir ecosystems.

Decomposition studies have been carried out in the Cedar River watershed, at the Thompson site and at Findley Lake since November 1974. Decomposition rates of needles, leaves, twigs, cones, and wood sections have been determined for a one-year period for Abies amabilis (Pacific silver fir) at Findley Lake, Pseudotsuga menziesii (Douglas-fir), Tsuga heterophylla (western hemlock) and Alnus rubra (red alder) at the Thompson site. In addition a study of decomposition of Douglas-fir needles as a function of stand development (stand age) was also initiated. Weight loss, nutrient content, lignin/cellulose content, CO₂ evolution from the forest floor during the early afternoon, and temperature and moisture of the forest floor have been monitored. Nutrient content and lignin/cellulose data are not yet complete but weight loss, some CO₂ evolution, and moisture and temperature data are available.

Table 1 indicates that decomposition is proceeding faster at the lowland Thompson site than at Findley Lake. Decomposition is fastest in the red alder ecosystem where weight loss of leaves was 55.1% after one year. Douglas-fir needles decomposed at a slightly lower rate (46.5% loss) and western hemlock needles decomposed at the slowest rate (37.4% loss). CO₂ evolution was also generally greater in the red alder stand than in the Douglas-fir or western hemlock ecosystems (Table 1). CO₂ evolution was similar in the Douglas-fir system to that in the western hemlock system, with the western hemlock system having slightly higher rates. Decomposition, however, was higher in the Douglas-fir ecosystem.

Interestingly, decomposition of needles appears to be proceeding relatively rapidly in the Pacific silver fir ecosystem at Findley Lake and is similar to that in the western hemlock system at the Thompson site (Table 2). This is despite the fact the forest floor is snow covered at Findley Lake ten months of the year. Decomposition of cones, twigs, and woody material is much slower at the western hemlock site than the Douglas-fir site (Table 2).

The rate of decomposition of this material is similar in the western hemlock and Pacific silver fir ecosystems. CO₂ evolution measured a single time in August 1975 at Findley gave a value a little lower than August values at the Thompson site.

Temperature and moisture data presented in Table 3 would indicate that the red alder system forest floor is moister than the Douglas-fir or hemlock. Temperatures are similar in all Thompson site ecosystems. The temperature at Findley Lake is considerably colder.

The forest floor moisture conditions would thus appear to be more closely related to the decomposition rates than forest floor temperatures at the Thompson site. The lower temperatures at Findley Lake, however, probably inhibit decomposition.

Weight loss of Douglas-fir needles as a function of stand development from ages 9 to 95 is shown in Table 4 along with CO₂ evolution data. Decomposition is slowest in the 9-year-old stand (38.3% weight loss), increases to a maximum in the 22-year-old stand (50% weight loss), and then decreases to an equilibrium status just over 40% weight loss. The smaller loss in the 30-year-old stand is probably due to the dryness of this site. This equilibrium status is similar to that observed for several other features of this stand including foliar biomass which also reaches equilibrium after canopy closure. The decomposition rates do not appear to be closely related to either forest floor temperature or moisture, except for the 30-year-old stand (Table 5). Analysis of the more definitive weekly data will elucidate this relationship. Nutrient analyses and lignin/cellulose data will be available soon and it is planned to terminate these studies after a two-year duration.

Edmonds, Vogt, Vogt & Antos

Table 1. Percent weight loss of needles and leaves after 365 days and CO₂ evolution in four ecosystems in the Cedar River valley.

Ecosystem	Percent Weight loss after 365 days	(CO ₂ evolution (mg CO ₂ ·hr ⁻¹ ·m ⁻²))					
		Dates					
		2/19	7/23	8/20	8/28	9/26	10/20
<u>Thompson Site</u>							
Western hemlock	37.4	61.0	48.7	-	136.4	125.9	402.8
Douglas-fir	46.5	51.7	35.9	-	106.1	119.4	405.3
Alder	55.1	71.8	25.1	-	270.0	141.4	354.7
<u>Findley Lake</u>							
Pacific Silver Fir	37.7*	-	-	55.8	-	-	-

*After 420 days.

Table 2. Percent weight loss of needles, leaves, twigs, cones and woody substrates after 365 days in ecosystems at the Thompson site and Findley Lake.

Ecosystem	Percent Weight Loss			
	Substrate			
	Needles or Leaves	Twigs	Cones	Wood
<u>Thompson Site</u>				
Western hemlock	37.4	19.9	11.6	12.0
Douglas-fir	46.5	22.6	24.3	5.7
Alder	55.1	-	-	12.9
<u>Findley Lake</u>				
Pacific silver fir	37.7*	11.0**	10.3*	

*After 420 days.

**After 310 days.

Table 3. Forest floor temperature and moisture data during times when CO₂ evolution was determined in four ecosystem types.

Ecosystem	<u>2/19</u>		<u>7/23</u>		<u>8/20</u>		<u>8/28</u>		<u>9/24</u>		<u>10/20</u>	
	<i>T</i>	<i>M</i>	<i>T</i>	<i>M</i>								
<u>Thompson Site</u>												
Western hemlock	2.2	373.5	12.2	105.2	-	-	13.9	171.7	12.8	97.0	10.0	270.0
Douglas-fir	2.2	427.0	12.2	98.1	-	-	14.4	231.3	12.8	85.0	11.1	241
Alder	1.7	445.8	11.1	247.8	-	-	15.0	205.0	12.2	185.7	11.7	244.0
<u>Findley Lake</u>												
Pacific silver			-	-								
fir	-	-	-	-	6.1	154.1	1	1	1	-	-	-

Temperature = °C

Moisture = percent based on dry weight.

Table 4. Percent weight loss after 365 days of Douglas-fir needles and CO₂ evolution from the forest floor in a series of stands ranging from age 9 to 95.

Stand Age	Percent wt. Loss After 365 days	CO ₂ evolution (mg CO ₂ · hr ⁻¹ · m ⁻²)			
		Date			
		7/23	8/28	9/24	11/7
9	38.3	24.3	148.8	132.7	103.3
22	50.0	86.7	237.8	154.2	73.2
30	38.0	59.0	229.7	115.7	19.2
42	43.6	95.4	290.7	141.9	63.7
73	41.1	42.6	203.8	127.9	49.9
95	42.7	53.3	179.4	120.2	84.9

Table 5. Forest floor temperature and moisture data during times when CO₂ evolution was determined for the age sequence of Douglas-fir stands.

Stand Age	7/23		8/28		9/24		11/7	
	T	M	T	M	T	M	T	M
	9	12.8	42.3	14.4	220.0	12.2	122.0	8.9
22	12.8	71.6	14.4	165.1	13.3	59.9	8.9	285.0
30	13.9	43.8	14.4	160.6	13.9	53.5	8.9	252.0
42	14.4	71.3	15.0	210.4	13.3	60.0	8.9	422.0
73	14.4	82.2	15.0	243.7	13.9	82.2	9.4	450
95	15.6	74.5	13.3	143.0	13.3	85.8	10.0	339

Temperature = °C.

Moisture = percent based on dry weight.

Soil microorganism populations are being determined on a monthly basis in the four comparative ecosystems along with CO₂ evolution. In addition isolations have been made from woody material in 1/10-acre plots in these ecosystems and pure cultures obtained. It is proposed to examine differences in these cultures with respect to their abilities to decompose various substrates at differing temperatures.

Fungus fruiting bodies have also been collected from these plots and their location mapped. Considerably more fruiting bodies occur on the western hemlock and Douglas-fir plots than the red alder plot. No fruiting bodies have been collected as yet from the Pacific silver fir plot. These fruiting bodies will be analyzed for their nutrient content.

Table 6 shows a list of the basidiomycete species obtained from both the litter and wood throughout the year on the alder, Douglas-fir, and western hemlock plots. There appears to be slightly more species diversity on the western hemlock plot than the Douglas-fir plot with least diversity on the alder plot. Only one species was recorded on litter from the alder plot.

The increased numbers and diversity of basidiomycetes from red alder to Douglas-fir to western hemlock is apparently inversely related to the rate of substrate decomposition occurring in these ecosystems. Since many of the species recorded are mycorrhizae in nature it can be hypothesized that as decomposition proceeds more slowly the mycorrhizal fungi begin assuming more and more importance in the nutrient cycling process.

The rates of decomposition in these ecosystems are being examined with respect to moisture and temperature regimes substrate quality, particularly the presence of phenolic compounds in the substrate which are known to inhibit certain fungi.

An additional study was also commenced in 1976 involving nitrogen dynamics in the forest floor and A horizon. Plots have been set up in an age sequence of Douglas-fir stands and a sequence of site qualities varying from high to low. Nitrate and ammonia levels are being monitored on a seasonal basis. The basic objective of this study is to determine factors which may be inhibiting or enhancing nitrification in this matrix of Douglas-fir stands.

Laboratory leaching experiments have also been conducted using forest floor from the four comparative ecosystems. Initial experiments simulating winter conditions were conducted at 3°C in plexiglass tubing (14 cm diameter) with a lysimeter plate attached at one end. KOH in vials was placed on a grid above the forest floor within the tubing to trap the CO₂ evolved. The KOH was analyzed titrimetrically with HCl. A simulated rainfall of 5.1 cm was applied to each forest floor; the leachates collected and analyzed were Ca, K, Mg, Mn, Fe, NH₄⁺, NO₃⁻, and reduced sugars. At the termination of the experiment, part of the forest floors were divided into the L and H layers. The total forest floor and the L and H layers and moss were analyzed for total N, C, Ca, K, Mg, Mn, Zn, and Fe.

Table 6. Basidiomycete fruiting bodies and their nutrient content in red alder, Douglas-fir, and western hemlock ecosystems at the Thompson Site.

Ecosystem	Species	Substrate
Red alder	<i>Corticium</i> sp.	wood
	<i>Mycena plumbia</i>	litter
	<i>Panellus serotinus</i>	wood
	<i>Xeromphalina campanella</i>	wood
Douglas-fir	<i>Cantherellus</i> sp.	litter
	<i>Collybia acervata</i>	litter
	<i>Cortinarius</i> sp.	litter
	<i>Cortinarius semisanguineus</i>	litter
	<i>Galerina subdecurrens</i>	litter
	<i>Gomphidius smighii</i>	litter
	<i>Hydnellum</i> sp.	wood
	<i>Hygrophorus pusillus</i>	litter
	<i>Inocybe subdestricta</i>	litter
	<i>Lactarius deliciosus</i>	litter
	<i>Mycena Aurantii</i>	litter/wood
	<i>Naematoloma capnoibes</i>	wood
	<i>Naematoloma dispersum</i>	litter
	<i>Polyporus abietinus</i>	wood
Western hemlock	<i>Cantherellus</i> sp.	litter
	<i>Chroogomphus tomentosus</i>	litter
	<i>Cortinarius amphractus</i>	litter
	<i>Cortinarius elatior</i>	litter
	<i>Cortinarius semisanguineus</i>	litter
	<i>Cortinarius subfudtoetidus</i>	litter
	<i>Cortinarius vibratilis</i>	litter
	<i>Cortinarius</i> sp.	litter
	* <i>Fomes annosus</i>	wood
	<i>Gymnopilus edinaliosporus</i>	wood
	<i>Gymhopsus macropholius</i>	litter
	<i>Hygrophus</i> sp.	litter
	<i>Mycena aurantiidisca</i>	litter
	<i>Naematoloma dispersum</i>	wood/litter
	<i>Nolaneae</i> sp.	litter
	<i>Pholiata scamba</i>	litter
	<i>Polyporus elegans</i>	litter
	* <i>Poria subscida</i>	wood
	<i>Russula occidentalis</i>	litter
	<i>Xeromphalina campanella</i>	wood

*Woody fruiting body.

No reduced sugars, NO_3^- , or NH_4^+ were measurable in the leachates analyzed. A range of 1-2 ppm of Mg, Mn, Fe, 3-5 ppm of K, and 10-20 ppm of Ca were leached from the four different forest floors. No leachate data were available from the Pacific silver fir floor since it was frozen. Even though the forest floor was frozen, 0.14 $\mu\text{g ATP}/1 \text{ g litter}$ was measured indicating possible microbial activity.

When comparing (Table 7) the nutrient content of the moss prevalent in the Douglas-fir and western hemlock stands to the total litter layer, the hemlock moss had a significantly higher concentration of Mg and the Douglas-fir moss had a significantly higher concentration of Zn. The moss in the Douglas-fir site had a significantly lower concentration of Mn and Fe in comparison to the total forest floor.

When comparing the L and H layers of the forest floors, there was a lower concentration of Mn in the H versus the L layer in the Douglas-fir, hemlock, and Pacific silver fir. There was a higher concentration of Fe in the H versus the L layer in the Pacific silver fir, hemlock and alder stands. In the Douglas-fir stand, there was a significantly higher concentration of Ca in the L versus the H layer, and in the Pacific silver fir a higher concentration of Na in the H versus the L layer.

The hemlock forest floor evolved 3762, the Douglas-fir₂ 2180, the alder 2207, and the Pacific silver fir 1793 mg CO_2 per 24 hr per m^2 . This experiment will be continued on a monthly basis throughout the year incubating forest floors at similar temperatures to those occurring in the field.

Publications

Edmonds, R. L. 1976. Effects of cold- and warm-water extractives from decayed and nondecayed western hemlock heartwood on the growth of Fomes annosus. Can. J. For. Res. 6:1-5.

2.1.7. Response of forest ecosystems to fertilizer - S. P. Gessel, University of Washington.

This research was designed to utilize a large amount of previous work in examining the overall response of forest ecosystems to changes in nutrient supply and in developing models of nitrogen use. The two principal sources of data are: (1) a series of plots established from 1950 to 1968 in various parts of western Washington which had received different forms and amounts of nitrogen, and (2) approximately 1000 plots from Regional Fertilizer Study initiated in 1968 through cooperative financing of many land owners in Washington and Oregon. The principal objective of research has been to test application of 200 and 400 kg/ha of N as urea in a variety of forest environments. Four-year growth response data are now available for all of these plots.

Research accomplished to date in 1976 includes: (a) remeasurement of all plots in item 1, above; (b) analysis of growth data resulting from these remeasurements; (c) analysis of data on litter production in some of these stands and publication of results; (d) some work on current nitrogen status of soils, especially nitrate and ammonia; (e) chemical analysis of soils from regional study; and (f) regional study funding has provided analysis of growth data from the 1000 plots.

Table 7. The mean value for total N, C, and cations for the Pacific silver fir, hemlock, Douglas-fir, and alder forest floors, and hemlock and Douglas-fir moss.

	Pacific silver fir				Hemlock			Douglas-fir			Alder			Moss	
	Total	L	H	A2	Total	L	H	Total	L	H	Total	L	H	Heml.	D-fir
Total N%	1.08	1.03	0.89	0.0	0.90	0.78	0.96	0.69	1.11	0.64	1.57	1.56	1.20	0.83	1.12
Total C%	41.4	39.2	34.7	3.0	39.5	40.8	37.2	30.8	39.3	25.4	25.5	32.4	20.1	47.6	40.0
C:N ratio	38:1	38:1	39:1	-	43:1	52:1	39:1	45:1	35:1	40:1	16:1	21:1	17:1	-	-
Ca ppm	3756	3633	3267	1933	5033	6433	6167	7733	9500	7167	9467	7567	6467	7300	10,000
K ppm	2078	2181	1745	1667	967	1033	833	1033	1033	1100	1167	967	833	1100	1,100
Mg ppm	496	480	536	273	400	550	667	600	800	733	733	867	850	750	800
Na ppm	1473	1438	1744	2171	1467	1233	1233	1800	1033	1233	1433	1033	967	1400	1,700
Zn ppm	14	12	20	2	22	20	26	37	29	25	17	19	18	19	55
Mn ppm	61	65	28	17	283	337	54	1233	1133	267	130	270	243	270	560
Fe ppm	608	537	870	343	1367	1233	2233	5400	2400	4167	3233	3767	6133	1300	1,200

Principal results from both sources of information can be summarized as follows: (a) Douglas-fir forests show a pronounced growth response to nitrogen with optimum treatment between 150-200 kg/ha. Overall volume growth increase is 25 percent. Considerable variation exists in response ranging from zero to over 100 percent. Cause of the variation has not yet been determined and this is under further study through soil and foliar analysis techniques. (b) Response of western hemlock is much more variable with some evidence suggesting that coastal area hemlock constitutes a different population from Cascade Mountain area hemlock. (c) Duration of response to one treatment is at least 7-8 years. (d) Growth response seems to be inverse to forest site and not related to stand age up to 60-70 years. (e) Total nitrogen in the forest soils systems ranges from 3000 to 15,000 kg/ha with no clear relationship to response. Available nitrogen and therefore rate of annual turnover must be an important factor in adequate nitrogen nutrition of these coniferous forests.

These results, while still preliminary in nature, do suggest that nitrogen plays a dominant role in growth and production in northwest coniferous forests. Therefore factors which determine total amount of nitrogen in the system and the distribution and available supply to the forest need to be thoroughly understood to achieve scientific management of the forests for any purpose. A good nitrogen model for a coniferous forest is also obviously needed.

Results so far show little effect of other elements and this leads to the conclusion that these other essential elements must be in adequate supply for forest growth. However, as forest lands are more intensively managed, total forest nutrition must be under continued scrutiny.

2.1.8. Stand Structural Geometry - D. R. M. Scott and E. Jensen, University of Washington.

Sampling was performed on one vertical quadrant of a standing, 45-year-old, codominant Douglas-fir at the Thompson site. Branches were individually removed from the tree and lowered to the ground, where their exact positions in the tree were duplicated. A series of measurements taken on each individual branch internode allowed the complete and accurate reconstruction of each branch by the computer. In addition to these location parameters, a complete description of each internode was obtained and further categorized on the basis of age and branching hierarchy (order). Twigs were characterized by length, diameter, and dry weight--foliage by dry weight, and the size and shape of the foliage cylinder surrounding each twig. Additional variables such as mean weight per needle, needle number per twig, and needle surface areas were calculated. A descriptive model of the crown of Douglas-fir is nearing completion. Predictive equations concerning the distribution of biomass in the crown have been formulated and shall be tested in the upcoming field season.

The most significant findings of this study are summarized below:

- (1) The structure of a large Douglas-fir crown is complex. Approximately 100,000 branch internodes hold a total of approximately 10,000,000 needles. Each year internodes and needles are added to and subtracted from this total in a somewhat regular manner. An attempt has been made to describe this process and to understand some of its implications.

- (2) Parameters dealing with gross crown morphology (e.g., yearly crown extension in the horizontal plane, the age and order structures of branches, the foliar biomass per branch, the number of internodes per branch, etc.) are generally predictable. Parameters dealing with the size and shape of individual internodes are generally not predictable, other than to say that size normally decreases with increasing age and order.
- (3) Branch development is limited. In the study tree no more than four orders were found. Primary branch elongation decreased logarithmically with increasing age.
- (4) Branch development undergoes fairly regular changes with age. As a branch ages its ability to put on growth, both terminal and lateral, decreases. In short the outer half of a 10-year-old branch is not at all like a 5-year-old branch, either in size or complexity of development.
- (5) Internodal twigs (those not occurring at the nodes of branches) comprise 50% of the foliar weight of branches but only 10% of the twig weight. Internodals are also the first branches to be shed under stress or through aging, suggesting a useful strategy of maximizing photosynthetic surface area while minimizing the energy tied up in supportive tissue. Prior to this study, internodal twigs had been totally neglected.
- (6) When non-functionality occurred in this crown, as indicated by the loss of a branch ring, crown break-up occurred immediately. The branches in the non-functional crown contained few foliated internodes and were apparently excising branchlets at a high rate.
- (7) A distinct difference in upper crown development existed between the south and north sides of the study tree. Branches on the south side generally had more internodes and the basal internode had a larger diameter than corresponding branches on the north side. This may help explain the slant in zones of photosynthetic efficiency for Douglas-fir found in studies at the University of Washington. Comparisons below whorl seven were not made.

In the coming field season an attempt will be made to validate these observations and extend them to other social positions and site classes.

2.1.9. Nutrient exchange - R. J. Zasoski and S. Colton, University of Washington.

During 1975-1976, soil samples from Findley Lake and Andrews Forest were collected in addition to those collected earlier from the Thompson site. These soils have been analyzed and characterized during the past year.

Of particular interest was the cation exchange capacity and exchangeable cation content. A procedure using unbuffered ammonium chloride rather than buffered ammonium acetate was used to measure exchangeable cations and cation exchange capacity. Exchangeable cations make up a small fraction of the total C.E.C. and the soils are high in exchangeable aluminum or hydrogen. The readily available base supply is low in all of these soils.

The ability of the soils to supply and buffer potassium was determined using the Quantity-Intensity approach of Beckett (1964a, b). Soils from Findley Lake, Andrews, and the Thompson site were faced with 0.01 M CaCl_2 solutions containing varying amounts of potassium. Figure 1 shows the results for the Everett Soil (Thompson site). The amount of K gained or lost by the soil (ΔK) is plotted on the ordinate axis and the abscissa level. If added K is low or zero, there will be a release to solution and ΔK will be positive (+). As K additions increase, potassium will be adsorbed and ΔK will be negative.

The surface horizon (A3) and the organic horizon (O2) were able to furnish K to solution while the A3, B and C horizons did not. Results from the mineral horizons at the Findley Lake site acted like the lower horizons at the Thompson site. The Andrews Forest soils also were able to furnish K to solution, and showed a greater capacity to adsorb K^+ . These results further emphasize the important role of the forest floor in short-term potassium supply especially in the more acid soils. Other assessments of potassium supply will be obtained during the remainder of the year.

Since the exchangeable potassium levels cover a limited range in the soils tested, it was possible to find, as might be expected, a highly significant relationship between solution K and exchangeable K. ($R^2 = 0.98$ and $R^2 = 0.97$, $n = 12$) for soil to solution ratios of 1:25 and 1:50. Thus, the amount of K replaced by Ca is linearly related to the exchangeable K content of the soil. This relationship was found for all horizons sampled in the three soils.

Preliminary data has been obtained for exchange constants in the A3 and A1 horizons of the Everett soil. While this data will be refined and expanded upon during the remainder of the funding year, it appears that Ca is preferred over Mg in the A1 horizon while in the A3 horizon Mg is preferred over Ca by the exchange materials.

References

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2.1.10. Nutrient Leaching - D. W. Cole and D. W. Johnson, University of Washington.

Processes of elemental transfer in some tropical, temperate, alpine and northern forest soils: Factors influencing the availability and mobility of major leaching agents. The role of carbonic acid as a leaching agent was evaluated in a tropical, temperate, alpine and a northern forest soil. 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. The alpine and northern systems were analogous in that

EVERETT SOIL
(THOMPSON SITE)

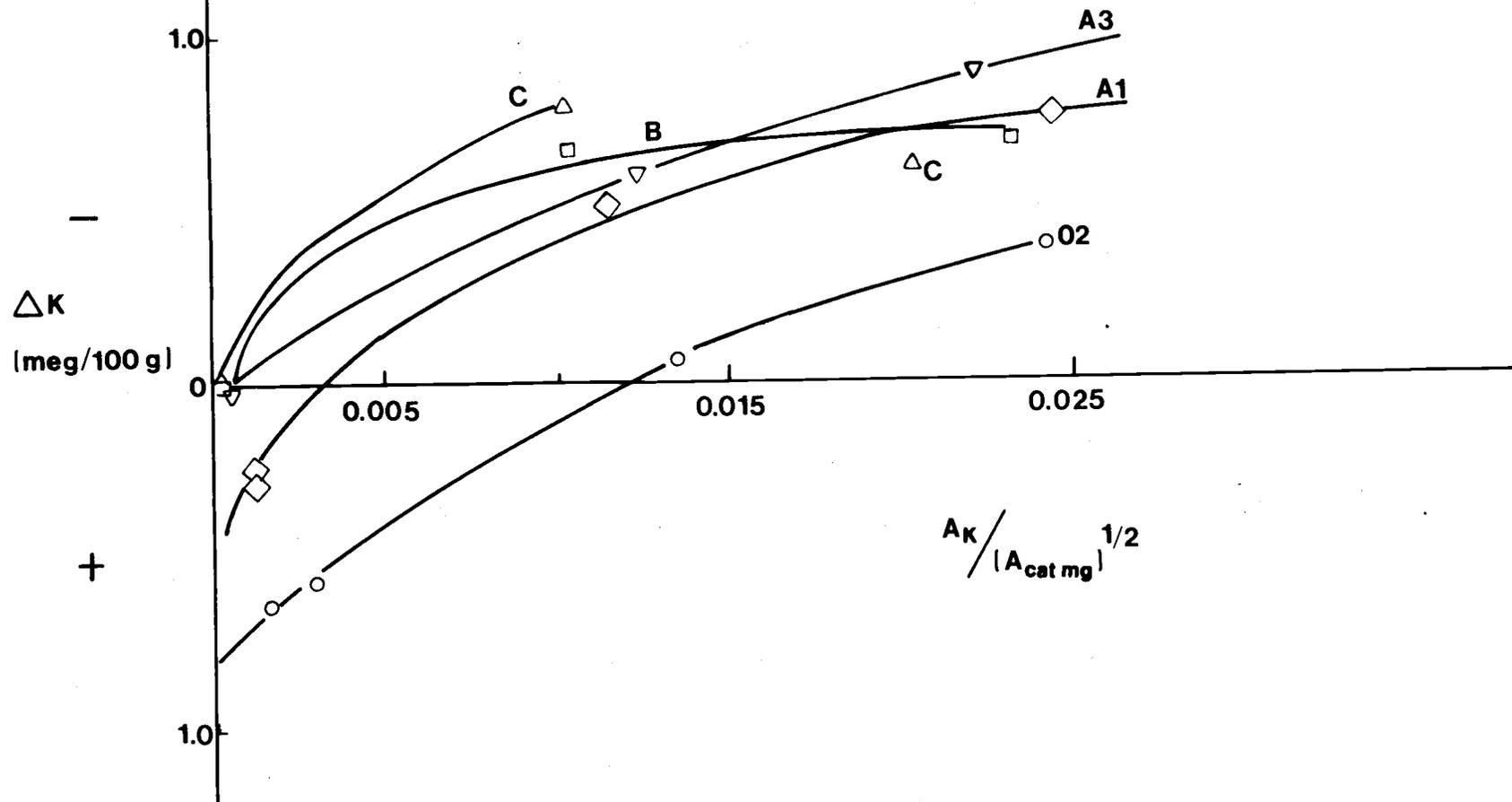


Figure 1. Quantity-Intensity relationships for the various horizons of the Everett soil (Thompson site).

organic acids lowered pH and bicarbonate concentrations within the rooting zone. 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.

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.

Soil available N study--In February 1976 two small (2 x 2 m) plots were established on Everett and Alderwood soils at the Thompson site and fertilized with 200 kg/ha urea. Following that, the soil has been sampled monthly for NH_4^+ and NO_3^- to estimate the immobilization rate of soil available N following fertilization. Control samples are also taken.

This work was initiated as a followup to former lysimeter investigations on urea-N movement in the soil. Crane found $\approx 90\%$ retention of urea-N within the top 15 cm of soil regardless of fertilization or irrigation rate, but he did not sample soils for the form of N. It is hypothesized in a larger sense that fertilizer response is related to the soil NH_4^+ level within the region, thus the changes in the NH_4^+ levels with time in both control and fertilized situations is relevant.

To date, it has been shown that over 50% of the initial post-fertilization NH_4^+ in the soil disappeared after 90 days. Resampling of plots fertilized two years earlier showed only slightly ($\approx 10\text{-}20\%$) higher soil NH_4^+ levels than control.

Seasonal trends in control NH_4^+ levels are apparent; a statistically significant increase from 1 to 3 ppm occurred between February and June.

At present, the study is planned to continue until January 1977 at which time a final sample will be taken and extracted for amino-N. Overrein found most urea-N in this fraction using isotope techniques in forest soils.

Publications

Johnson, D. W. Theoretical and actual interactions of sulfate and bicarbonate in soils following sulfuric acid application. Submitted to Soil Sc. Soc. Am. J.

2.1.11. Role of Douglas-fir bark beetles in carbon and nutrient cycling - R. Gara and A. Eglitis, University of Washington.

Field research for the 1976 flight season of Douglas-fir bark beetle (DFB) was conducted in three general areas of investigation: (a) examining inter-population differences in attractant response and attack behavior between endemic and epidemic populations, (b) studying intrapopulation behavior differences within an endemic coastal population, and (c) determining the role of DFB in forest decomposition.

Four separate field studies were used for comparing the behavior of individuals from low versus high-level populations. A marking-release-recapture experiment was conducted for the second consecutive year, this time producing far better results than in 1975. Recapture of marked beetles increased from 1% in 1975 to over 30% for most 1976 test groups. The refined trapping design provided for the recovery of large enough numbers to allow for more valid comparisons to be made of response preferences for endemic versus epidemic populations. A consistent trend evident in this experiment was that interior (Idaho) epidemic beetles were much more readily recaptured than local (Cedar River) endemic ones which retained their dispersal tendencies, responding in significantly lower numbers. A second experiment examined the quality of aggregating attractant produced by females from each population. In Idaho local beetles showed very strong preferences to attractants produced by females from their own geographical area while no preference could be established in Washington. The interaction of host material configuration combined with attractant concentration was believed to be very important in distinguishing behavior of low and high-level populations and was tested in both areas. Although statistical tests have not as yet been done on the data, there is evidence that clearly suggests different response patterns between the two populations. Epidemic beetles appear to be far less discriminatory in response behavior and attack behavior than endemic, more "fit" beetles from low-level populations. A fourth study utilizing different trap designs also suggested that this trend exists for the two populations.

Intrapopulation response trends once again showed the importance of ethyl alcohol as a primary attractant early in the season, becoming less important as a means of host recognition later. Both study localities showed a decrease in beetle response to ethanol as the season progressed--a result not expected in the epidemic area where primary attractants should have had little effect in the first place. We proposed a difference in physiological state of beetles responding to primary vs. secondary attractants and tested the theory in flight tendency experiments. Once again, the data have not yet been analyzed, but a

trend seems evident and supports the hypothesis. Laboratory studies will be conducted using extracts from insect tissues to correlate fat content with behavior observed in field tests.

An experiment was set up at the Thompson site to investigate the role of DFB in tree decomposition. Initial observations on four felled trees showed that the logs sustained heavy attacks on their unscreened sections. Rate of weight loss will be compared for screened (unattacked) vs. unscreened (attacked) log sections to determine if attack by the DFB predisposes the material to other early decomposers which are excluded by exclusion of the bark beetles. A somewhat different floral and faunal succession is suspected for the attack/exclusion situations thus altering the decomposition rate of the material. Litter production by the bark beetles is also being monitored.

2.1.12. Forest vegetation dynamics within the *Abies amabilis* zone of a western Cascades watershed - J. N. Long, University of Washington.

The *Abies amabilis* (Dougl.) Forbes zone on the Cedar River drainage of western Washington extends from 700 to 1300 meters in elevation. Within this relatively restricted geographic area the forest of the *A. amabilis* zone forms a complex vegetation pattern. Description of the vegetation and elucidation of reasons for the patterns of distribution were the purposes of this study.

A two-dimensional ordination resulted in the construction of two artificial floristic gradients. The first of these gradients is strongly correlated with elevation. It was hypothesized that changes in the vegetation represented by this gradient are associated with and controlled by a gradient in the depth and duration of the winter snowpack. This hypothesized relationship between the floristic gradient and the winter snowpack was verified using measurements of epiphytic lichens which were shown to be sensitive indicators of maximum snow depth.

It was hypothesized that the second floristic gradient is associated with a gradient in summer moisture stress. This relationship was verified using pre-dawn moisture stress measurements taken with a pressure chamber.

The distributions of individual species were examined in the context of the snowpack and moisture stress gradients. Many species were found to have an apparent response to one or both of the environmental gradients and various autecological characteristics were suggested which may be responsible for these distribution patterns. For example, *A. amabilis* and *Tsuga heterophylla* (Raf.) Sarg. occupy opposite ends of the snowpack gradient as community dominants. An autecological rationalization of this contrasting behavior is developed based on the different responses of these species to various environmental factors associated with the snowpack. Similarly, it is suggested that the relatively limited importance of *Pseudotsuga menziesii* (Mirbel) Franco in areas of deep snow accumulation may be in large part due to the susceptibility of saplings to snow breakage.

On most sites within the lower portions of the A. amabilis zone T. heterophylla is the major community dominant following removal of the overstory canopy by fire or logging. During the initial stages of community development T. heterophylla is a superior competitor to both P. menziesii and A. amabilis. T. heterophylla regularly produces abundant seed crops and the establishment of its seedlings is generally much greater than either P. Menziesii or A. amabilis. The rate of height growth for open grown T. heterophylla seedlings and saplings is greater than for those of A. amabilis. While yearly height growth for P. menziesii saplings may compare favorably with that of T. heterophylla, net growth is often limited by successive breakage of the stems by snow. Thus, the period of stand recruitment, which may last for 15-25 years, usually results in a closed canopy dominated primarily by T. heterophylla and a few P. menziesii.

It is suggested that the ability of A. amabilis seedlings to become established on the forest floor beneath mature stands is in large part a function of its seedling morphology. The relatively large seeded A. amabilis produces large, deep rooted seedlings. In contrast to those of T. heterophylla, the seedlings of A. amabilis have the ability to penetrate the typically thick layer of unincorporated litter before it dries. Rotten logs and stumps, on the other hand, provide a more suitable seedbed for the initially smaller, shallow-rooted T. heterophylla seedlings. The litter layer on the tops of logs and stumps is generally less thick than on the adjacent forest floor. In addition, the rotten wood provides a superficially moist substrate for the shallow rooting T. heterophylla seedlings. Growth rates and survival as well as response to release of understory grown seedlings of both species were also examined.

The trends associated with community development for stands in the lower A. amabilis zone involve changes in both structure and species composition. The accumulation of total aboveground biomass continues to increase throughout the range of ages sampled. This increase in aboveground biomass is primarily a function of the continued growth of individual overstory trees. The trends of biomass accumulation for other aboveground components of the community, however, are not monotonic. Overstory foliar biomass, for example, may reach an upper limit at some stage of stand development following canopy closure. Understory aboveground biomass appears to increase approximately linearly with time up to overstory canopy closure. Following closure of the canopy, biomass in the understory decreases to a relatively stable value between 500 and 1000 kg/ha. These changes are associated with major shifts in the relative importance of various understory taxa. Tall, primarily ericaceous, shrubs contribute most of the understory biomass during the stages of stand development preceding canopy closure. Subsequent to canopy closure various moss species contribute the bulk of the understory aboveground biomass.

The changes in understory species diversity associated with stand development exhibit a pattern more or less typical of many developing communities. Diversity increases to a maximum within a few years of stand initiation. This maximum is followed by a sharp decline in diversity, associated with the increase in dominance by a few shrub species, to a minimum in the stage

of stand development just preceding overstory canopy closure. Following canopy closure and the decrease in relative importance of the shrubs, species diversity again increases rapidly to a relatively high level which remains fairly constant throughout the remaining stages of stand development.

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2.2 Environment and Plant Succession

2.2.1. Succession simulation - K. L. Reed, Department of Natural Resources, Olympia, Washington.

The Coniferous Forest Biome of the US/IBP has supported the development of a forest stand growth model called SUCSIM, for SUCcession SIMulator. This report details some of the progress made this year in SUCSIM development.

At this writing, SUCSIM is a preliminary forest stand succession model. Most of the functions used in SUCSIM are to a greater or lesser extent hypothetical and reflect our attempt to develop a deterministic, mechanistic model of forest growth and community development. SUCSIM is at present a data poor model; much fieldwork is now in progress to provide data to support or replace existing models.

SUCSIM is based on the idea that tree growth is a definable function of intrinsic habitat variables, which are in turn functions of extrinsic physical environmental variables such as moisture status, temperature and light. The methodology of development of the environmental ordinates are discussed in Cleary and Waring (1969), Waring and Cleary (1967), Waring (1969), Waring, Reed and Emmingham (1972) and Reed and Waring (1974). A detailed discussion of the underlying niche theory concepts used by SUCSIM is given in my own manuscript, and a recent application of some of these concepts to community ecology appears in Zobel et al. (1976).

SUCSIM "grows" trees over a one-year time step on a variable size "plot." At present, the plot size is 20 x 20 meters (0.04 ha) representing a sample plot in a forest stand. Individual tree diameter and diameter growth, height and height growth, species, age, leaf biomass, new leaf production, litterfall and crown diameter are tracked by the model. Because of the computer core required for these arrays, we have a 100 tree limit per plot. This corresponds to 2500 trees per hectare (ca 1000 trees per acre).

Leaf biomass is assumed to be uniformly distributed in a cylinder around each tree, light is attenuated through the stand, which is stratified into R layers. Prior to crown closure, only the fraction of light passing through leaves is attenuated, the remainder strikes the ground unattenuated.

We realize that the light model is perhaps oversimplified, certainly our leaf distribution model is simplistic. However, our attempts to use more realistic leaf biomass distribution models were disappointing. Because of the complexity of dynamic leaf distribution models, our run time was tremendous and we found that the several models we tried were unstable in that leaf biomass would tend to be concentrated in a very narrow stratum. The present model gives reasonable growth and total leaf biomass values so we postponed further work until the dynamics of crown development are better understood.

Another model in SUCSIM that is hypothetical is the litterfall model. We tried several versions, including a retention period model where we kept track of each cohort of leaves, dropping the cohort older than the retention period. Other versions dropped constant or varying percentages of the total leaf biomass. None of these models were successful, primarily because as a tree ages (in the model) new leaf production declines along with diameter growth. When this happens, older cohorts are larger than new ones and the tree becomes denuded.

Field observation indicates that there are two primary controllers of litterfall: light and nutrient status. When a given batch of needles receive too little for productivity, they are dropped. Low productivity in older needles can be tolerated in sites with adequate nutrients, as mobile N can be stored in older needles, but in nitrogen poor stands that N is extracted earlier and the needles are dropped. At present, we express litterfall as a function of light and are working on a model to incorporate nutrient effects on litterfall.

SUCSIM writes individual tree data on a binary dump file. The output vector includes height, height growth, diameter, diameter growth, leaf biomass, species, age of each tree, average light seen by each tree and other variables. This dump file is read by a post processor named SUCCOT that plots several variables against time, including Scribner 6 volume (board feet per hectare) and CVTS volume (cubic meters per hectare).

SUCSIM is in a state of stasis until the quantities of field data collected in the region are analyzed. We are developing some new models but we feel that further model development is best postponed until some of the existing models are tested or until further data are available. Complete documentation will be available as a biome bulletin.

We instigated a small experiment in the greenhouse designed to test the hypothesis that the driving variable functions used in SUCSIM are multiplicative. SUCSIM assumes that the effects of the environmental variables are orthogonal and multiplicative, as opposed to a limiting factor viewpoint. In the latter, if one of the environmental variables were limiting, there would be no response to change in another. SUCSIM assumes that even in a limiting case, a change in another variable will change the growth rates.

To test this idea, we set up a sand culture experiment in the University of Washington Botany Greenhouse with four levels of N and three levels of light. SUCSIM would predict that even under limiting light levels we would observe a growth response to N and vice versa. Preliminary data analysis supports the SUCSIM formulations. Field experiments are now in progress to further test the interrelations of the environmental variables as expressed in SUCSIM.

I have prepared a manuscript for submission to Canadian Journal of Forest Research entitled "Prediction of tree growth response surfaces in a N-dimensional habitat coordinate system." The paper will be submitted by August, 1976.

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- Zobel, D. B., A. McKee, G. M. Hawk, and C. T. Dyrness. 1976. Relationships of environment to composition, structure and diversity of forest communities of the Central Western Cascades of Oregon. *Ecol. Mono.* 46:135-156.

2.2.2. Validation Data - W. H. Emmingham, Oregon State University

During 1975-1976 one paper was published, two were accepted, two were drafted and data for two major papers was analyzed (see attached list). The two papers; one comparing forest sites in western Oregon for the synthesis volume and a second comparing coniferous forest sites across the western U.S. are in the process of being drafted. Two papers were presented at scientific meetings and a third was co-authored. Major effort was required in digitizing, editing and analyzing climatic data from the H. J. Andrews reference stands and extensive sites from Alaska to Arizona. Fortunately data analysis is nearly complete so that most future efforts can be directed toward publishing (see attached list). Spring term was almost entirely devoted to developing and teaching an introductory course in Forest Ecology in which many Biome concepts were introduced.

References

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Papers Accepted

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2.3. Land Use Simulation - J. Hett, University of Washington

During the past year, effects of land use management on regional succession patterns have been investigated for two areas in western Washington. One simulation, Upper Cedar River watershed, is now complete. Comments by participants at the MAB/SCOPE Workshop on Dynamic Change in Terrestrial Ecosystems in January 1976 have been incorporated and the final manuscript is now being submitted for publication. The second simulation, Mount Adams in southwestern Washington, is now in the parameterization stage. Data necessary for calculating transfer rates, initial conditions, and successional trends were collected during the summer of 1975 and are now being analyzed.

Upper Cedar River watershed simulator-- The objective of the Upper Cedar River watershed simulation was to examine effects of forest management practices in the summer range on the resident elk population. Data from two Ph.D. research programs provided the needed information for the simulation. James Long (1976) calculated species replacement rates and provided the expected successional sequence. John Schoen (unpublished) and Dr. Richard Taber provided elk behavioral information, forest disturbance history, a digitized vegetation map for calculating initial conditions and a list of summer range ecosystems important to the elk population.

Figure 1 shows the successional sequence and the feedbacks used to mimic possible clearcutting policies. One simulation clearcut 8% of the mature timber each year while the second removed all mature timber in the first 10 years and then no harvesting was done for the next 90 years. The response of the vegetation to these management schemes can be seen in Figure 2 and, starting with a population of 250 elk (the estimated 1975 population level), Figure 3 shows the simulated elk response to these manipulations of the vegetation.

Mount Adams simulator-- The Mount Adams simulator was originally designed to complement research being conducted by Ken Reed in the same area for a stand succession simulator. However, the regional project is being phased out of the Biome program this year so the objective now is to complete the data analyses and generate a simulator based on these data albeit not sufficient to examine long-term responses to forest management policies. We have prepared a vegetation map of the region using aerial photographs, topographic maps and field data collected by the Department of Natural Resources, State of Washington. In each mapped forest type, stand structural and age data were collected as well as species composition and physical attributes of the stand including slope, aspect, elevation, etc.

A preliminary analysis of age and diameter at breast height (dbh) indicate a sigmoid curve may describe this relationship for three of the more important tree species in the area (Figure 4). Further growth analyses now underway should add to the interpretation of this relationship.

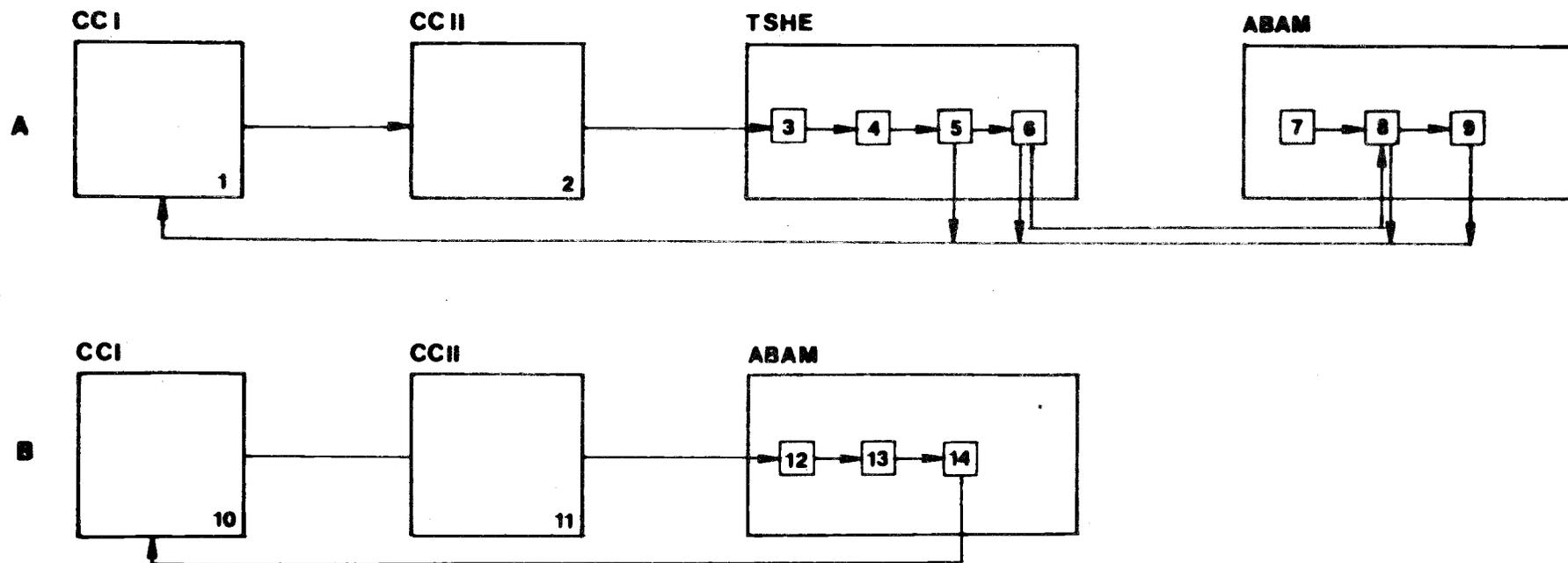


Figure 1. Successional sequence expected in the *Abies amabilis* zone in the Cedar River Watershed. A sequence is expected at elevations below 1100m and B sequence is expected at higher elevations. CCI represents clearcuts less than 6 years old while CCII represents those clearcuts 6 years and older that do not have a closed tree canopy. *Tshe* + *Tsuga heterophylla*, *Abam* = *Abies amabilis* and each ecosystem has several size or age classes. Other ecosystems included but not shown here are riparian, meadow, non-vegetated, etc. types.

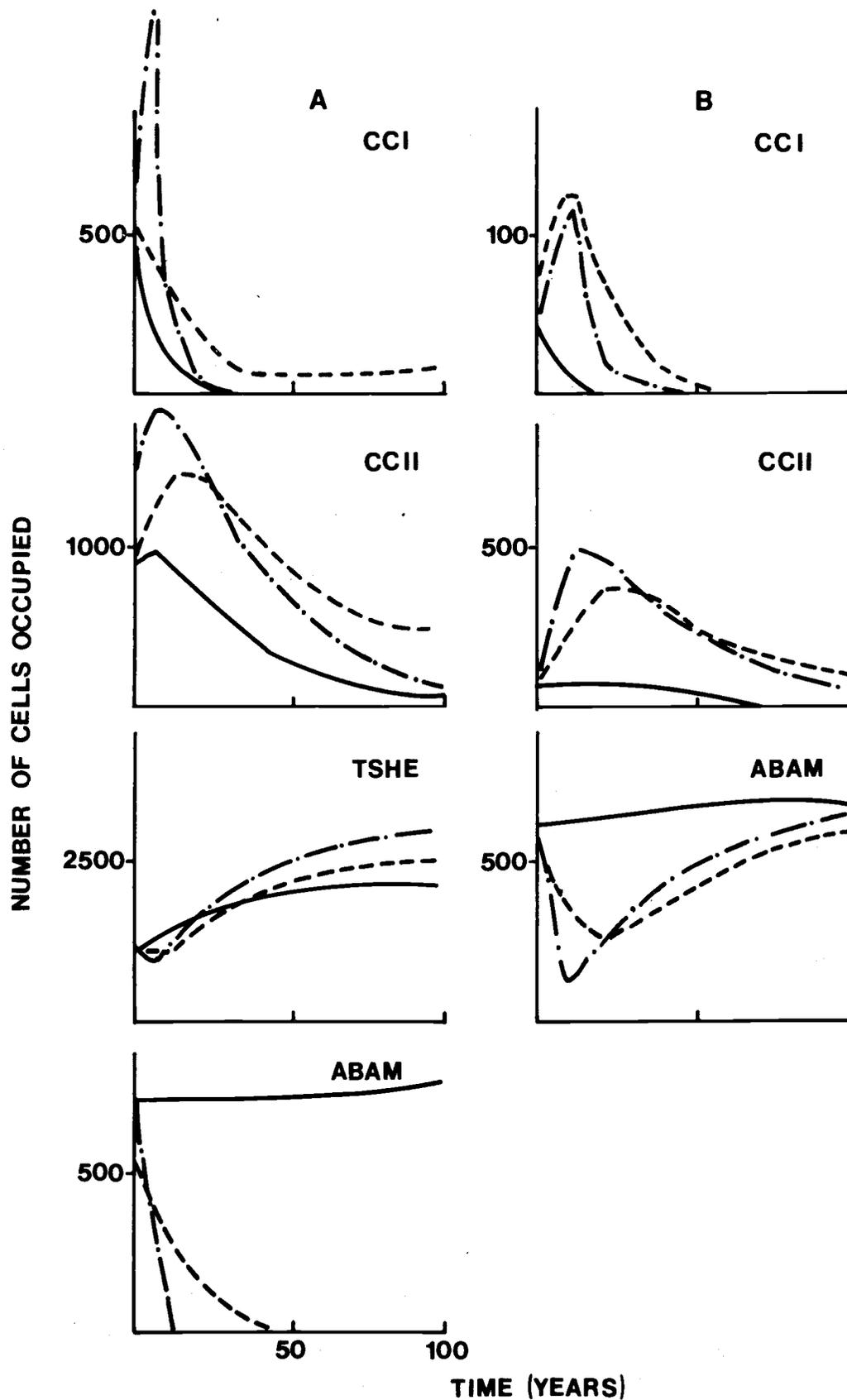


Figure 2. Vegetation response to simulated forest management policies. (—) no disturbance, (---) 8% of the mature timber harvested each year, and (-.-) all mature timber harvested in 10 years and then no disturbance for 90 years.

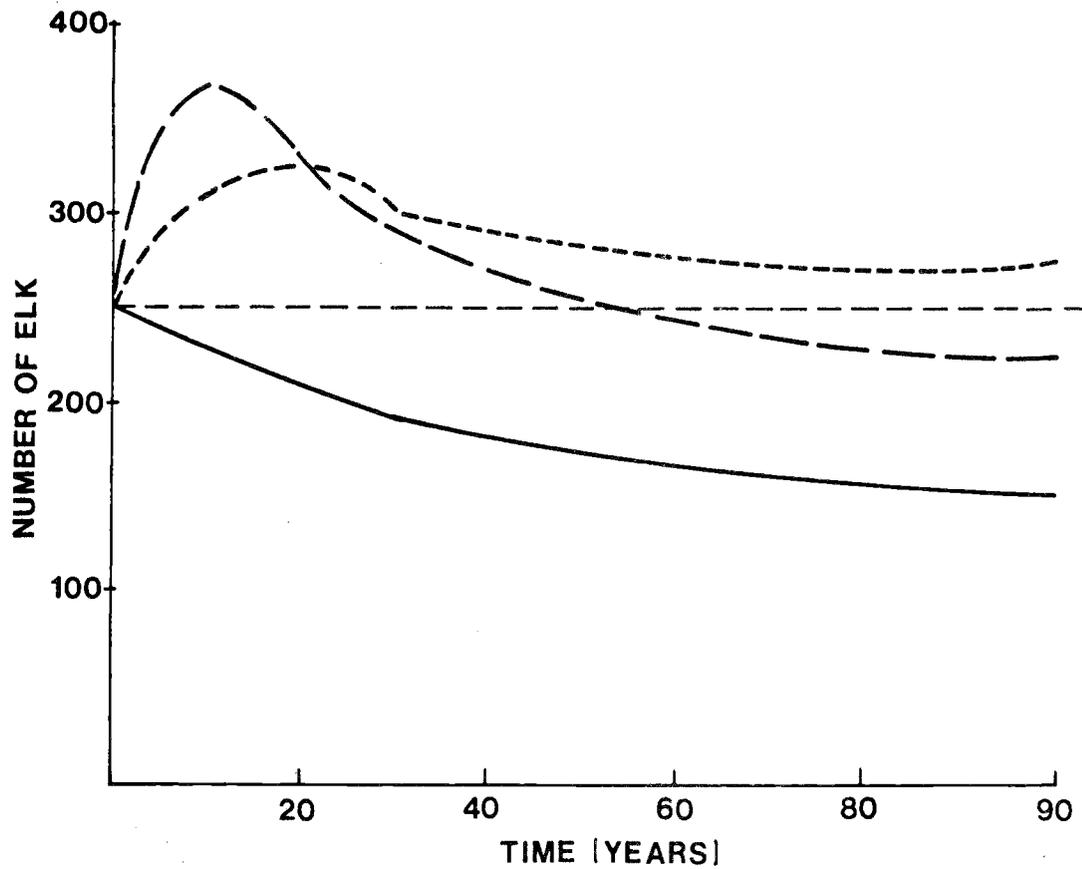


Figure 3. Elk population response to forest management policies. (—) no harvesting, (---) 8% of the mature timber harvested each year, and (— —) all mature timber harvested in 10 years and then no harvesting for 90 years.

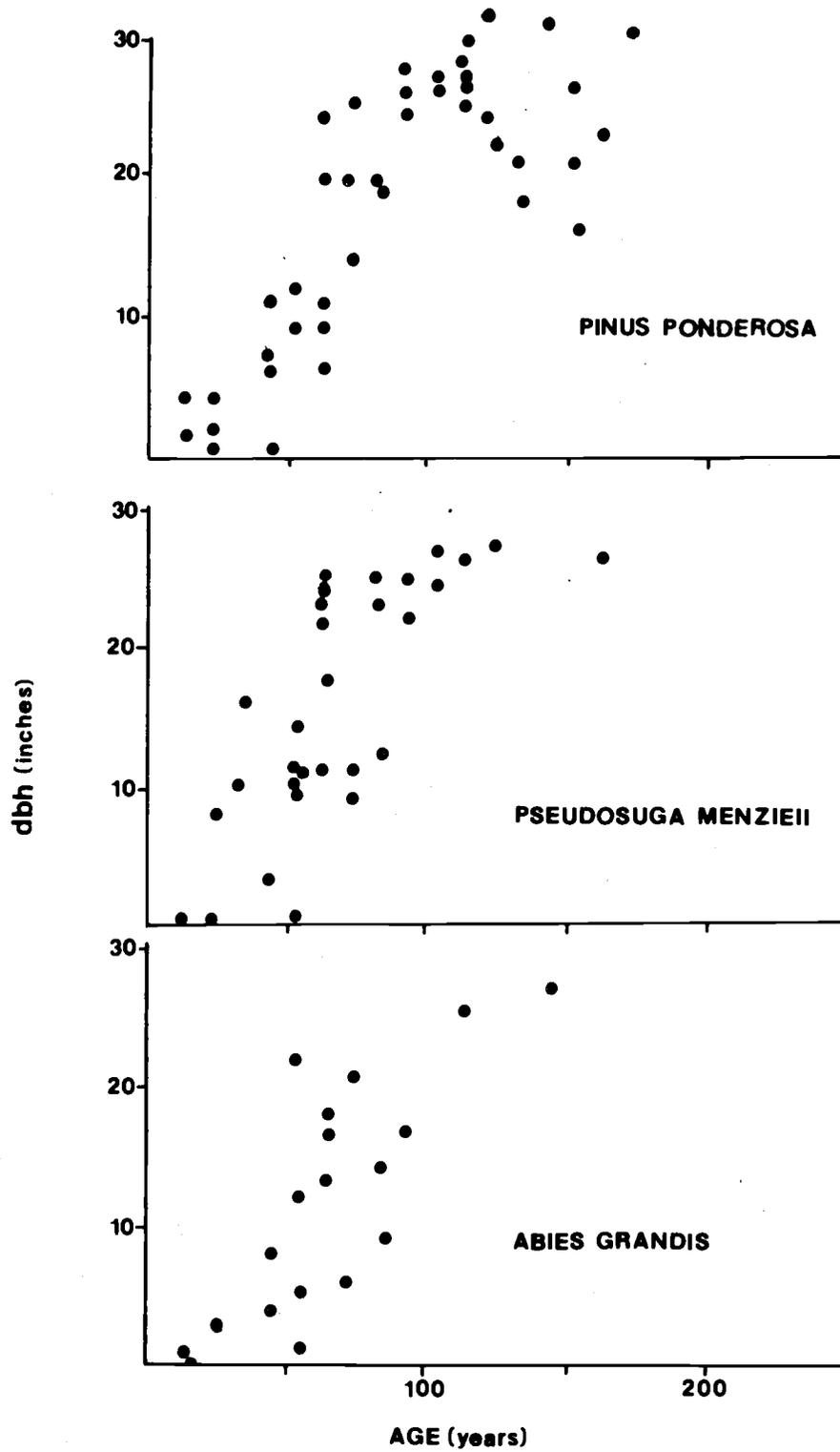


Figure 4. Age - diameter at breast height (dbh) relationship of three important tree species in the Mount Adams region.

In this region, Pinus ponderosa and Pseudotsuga menziesii are considered species capable of invading disturbed sites early in the successional sequence and as "pioneer" species, usually are considered even-aged species. Abies grandis, on the other hand, can invade under the canopy of these species and should therefore often show an uneven age distribution. Our preliminary analyses of age distributions in the region do not support these concepts. Age distributions for two forest types can be seen in Figure 5. Stand (a) has Pinus ponderosa in all three size strata, while (b) is a mixed stand with Pseudotsuga menziesii dominant in the upper two strata and Abies grandis dominant in the seedling stratum.

Further analyses will include ring width analysis, disturbance, indicators and further comparisons of age and size by stand rather than forest type. These data should allow a first cut simulation of forest succession in the Mount Adams region.

3. ANALYSIS OF WATERSHEDS

3.1. Watershed 10, H. J. Andrews Experimental Forest

3.1.1. Litter decomposition - Comparative rates of CO₂ production from the forest floor in the Douglas-fir ecosystem. - C. T. Youngberg and M. J. Phillips, Oregon State University.

To obtain data on the decomposition of the forest floor, a battery-operated electrolytic respirometer was developed making it possible to measure CO₂ evolution from field moist forest floor samples in situ independent of root respiration. Banks of four respirometers powered by two 12-volt batteries were installed in three old-growth Douglas-fir/western hemlock stands, two clearcuts, and one clearcut that had been broadcast burned. All sites were located on or immediately adjacent to the H. J. Andrews Experimental Forest located in the western Cascades near Blue River, Oregon.

Seasonal and yearly totals of mineralized carbon were similar for the three habitat types. First year totals for the Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa association (RS 2), the Tsuga heterophylla/Castanopsis chrysophylla association (RS 6), and the Tsuga heterophylla/Polystichum munitum-Oxalis oregana association (RS 7) were 77.36, 75.67, and 78.86 mg C/g litter. Spring and fall mineralization accounted for approximately 62% of this total on all three reference stands. The lowest rates occurred during the winter months. Carbon mineralization rates for the second fall of the study were similar to those of the first year. However, carbon mineralization during the second winter of the study increased unexpectedly by 88%, 123%, and 142% for reference stands 2, 6, and 7, respectively. Presumably, this was due to warmer temperatures during the second winter.

Clearcutting enhanced the rate of carbon mineralization, the magnitude of the effect being greater on the older clearcut. On the 4-year-old clearcuts (plots 29 and 36), yearly totals averaged 102.97 mg C/g litter. On the 3-year-old clearcut (Reference Stand 33 [RS 33]), total carbon mineralization was 89.49 mg C/g litter. Part of the variation was probably related to elevational effects on temperature, RS 33 being located 330 m higher

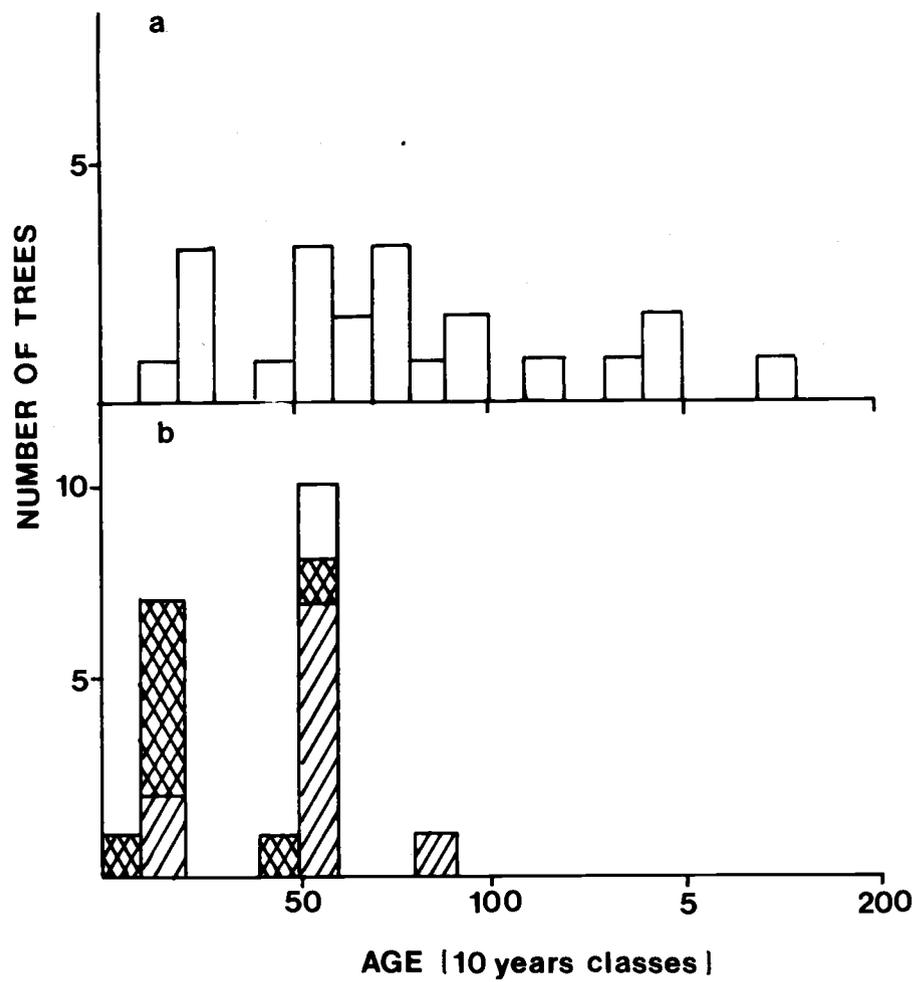


Figure 5. Age distribution in two representative forest types. *Pinus ponderosa*, *Pseudotsuga menziesii* and *Abies grandis*.

than the other clearcut. But it is also possible that the greater re-establishment of vegetation on the older clearcut could have contributed a higher proportion of fresh litter to the residual forest floor.

Clearcutting followed by broadcast burning decreased the rate of carbon mineralization. Plots were established on the site one month following a light burn. The yearly totals for carbon mineralization averaged 64.62 mg C/g litter, or 59% less than on the older clearcut (29 and 36). Nitrogen levels remained relatively high, and there appeared to be an increase in the lignin fraction of the litter.

Decomposition was significantly correlated with litter moisture content or litter temperature on a seasonal basis. In general, litter moisture content was the dominant factor during the summer and fall months. Litter temperature was the dominant factor in the winter and spring months when statistically significant correlations could be obtained. Inadequate means of estimating litter temperature under snowpack may be the reason for fewer significant correlations during these periods.

3.1.2. Vascular Plant Communities - J. F. Franklin, G. Hawk, J. Means, and A. Campbell, U. S. Forest Service and Oregon State University.

During the last year this project has focused upon three aspects of community structure and development: (1) Age structure of the original old-growth forest in watershed #10, i.e., an analysis of its history; (2) establishment and initial measurements of post-logging successional plots on watershed #10; and (3) analysis of the riparian vascular plant communities on watersheds #10 and 2 and on Mack Creek.

Age structure-- The age structure analysis of watershed #10 is based upon stump ring counts of trees 15 cm dbh (mapped and tagged prior to logging) and pre-cutting sampling of 300 trees 15 cm dbh. Thus far, approximately 500 larger trees have been counted and the data computerized and analyzed.

We have been extremely surprised by the results. Dominant, old-growth Douglas-firs ranged approximately 100 years in age (from 40 to 500 years). The mixing of the various ages of old-growth over the watershed and various habitat types gives no suggestion of a patchy distribution, i.e., the oldest specimens are not concentrated in any one locale. Our hypothesis is that re-establishment of a Douglas-fir forest on this area following a major catastrophe about 500 years ago was very slow rather than rapid as conventional wisdom suggests. There is also evidence that most of the western hemlock and chinkapin date from a low intensity fire that burned through the area in the late 1800's.

Data on sapwood cross-sectional area are being collected during the ring counting to allow an independent estimate and check on Grier's estimates of leaf biomass. The age analyses are also a part of a larger data set on fire history and its relation to forest development and erosional episodes being developed for the whole H. J. Andrews and adjacent areas in cooperation with Swanson.

Successional plots--Thirty-six 15 x 25 m permanent plots were established for detailed study of forest composition and structure on watershed #10 prior to logging. These have been re-established and will be used to provide nondestructive measurements of vegetation development. These measurements will be used with allometric equations developed by Gholz to provide the data on the vegetative component of nutrient and carbon uptake and storage.

Riparian vegetation--We have lacked information on the functional role of vascular riparian vegetation, a serious handicap in the stream and interface studies. This year, in cooperation with Sedell and Lyford, we are mapping the riparian vascular plant communities, analyzing their structure and composition, and, particularly, determining standing crops of carbon and nutrients which become stream inputs when they die in the form (mainly) of leaf fall.

Other--We are remeasuring the reference stands after five years primarily to provide an estimate of mortality and input of coarse debris for the decomposer group. We will also provide assistance to Gholz during his destructive sampling of lower plants on or near watershed #10, an activity essential to adjustment of the allometric equations for post-logging conditions. Finally, we are tallying all remaining live trees 15 cm dbh on watershed #10, independently of the successional plot work.

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- Zobel, D. B., et al. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecol. Monogr. 46:135-136.
- 3.1.3. Watershed 10 - Biomass, Productivity, and Nutrient Cycling - C. C. Grier, Oregon State University.

Field work on this project was essentially terminated when watershed 10 was clearcut in July 1975. Some tissue sampling is still in progress in areas adjacent watershed 10 to examine nutrient dynamics in vegetation.

Work during the past year has focused on data processing and writing of reports. Chemical analysis of various tissue samples is not yet completed. This should be done by mid-August 1976.

Data of biomass and production relations are completed and in review. Data of nutrient cycling are complete except for final years' litterfall analysis. Manuscript on nutrient cycling is currently in preparation.

References

The following report has resulted from this study and additional papers will be submitted in 1977 (see section 3).

- Grier, C. C. and R. S. Logan. Old-growth Douglas-fir communities of a western Oregon watershed: Biomass distribution and production budgets. Ecological Monographs (in press).

3.1.4. Soil solution and groundwater chemistry - K. Cromack, P. Sollins, and M. McCorison, Oregon State University.

The network of surface tension lysimeters was expanded on the watershed immediately following logging to better relate nutrient flux rates with the ongoing decomposition studies. Collection of soil solution from the pretreatment slope transect lysimeter installations is being continued. In an effort to establish the source of the nitrate observed in the lower cup lysimeters (Fig. 1), six new lysimeters have been installed at bedrock. Nitrate nitrogen is one of the key nutrients that finds its way to some impervious layer and then moves down slope to become part of the stream nutrient water supply after passing through the riparian rooting zone. To better understand the dynamics of the nutrient fluxes from the litter to the stream, continued measurement of the flow rate of a portion of the seep draining the slope lysimeter study is being planned. Data from the other five re-established seeps have shown increases in nitrate nitrogen content from only one of them (LF seep) during the first fall following clearcutting (Fig. 2). It is expected that with this fall's rains, however, that increase will become not only more apparent but general throughout the watershed. Other stream and seep relationships being developed are discussed under the interface portion of this report. Initial values for sulfur and organic/inorganic carbon were established for the winter and spring seasons. Analytical determination of short-chain organic acids in soil solution is being started.

A more adequate method for separating the fine organic matter from sediment collected in the catchment basins is being finalized. The chemical nature of the organic portion of this material is now being obtained. This should allow for a more complete analysis of the nutrient losses following clearcutting.

References

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- McCorison, F. M., D. G. Moore, and L. F. Glenn. Nutrient retention, mobilization and loss in an undisturbed Douglas-fir ecosystem. II. Seasonal changes in extractable soil nutrients of the rooting zone. (To be submitted to Soil Sci. Soc. Am. J.).
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- McCorison, F. M. Comments on tension lysimeters on sloping soils. (To be submitted fall 1976).
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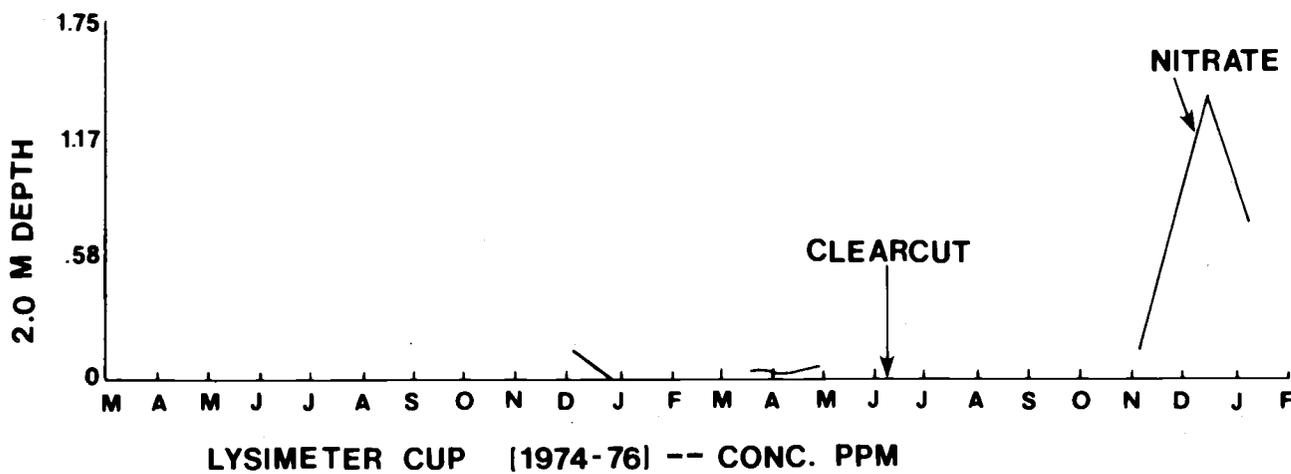
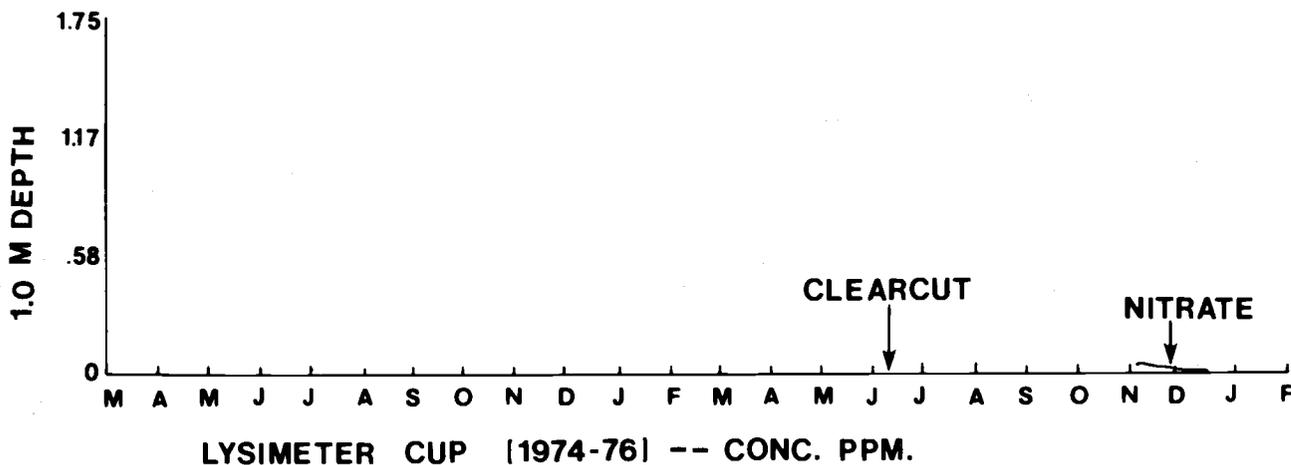
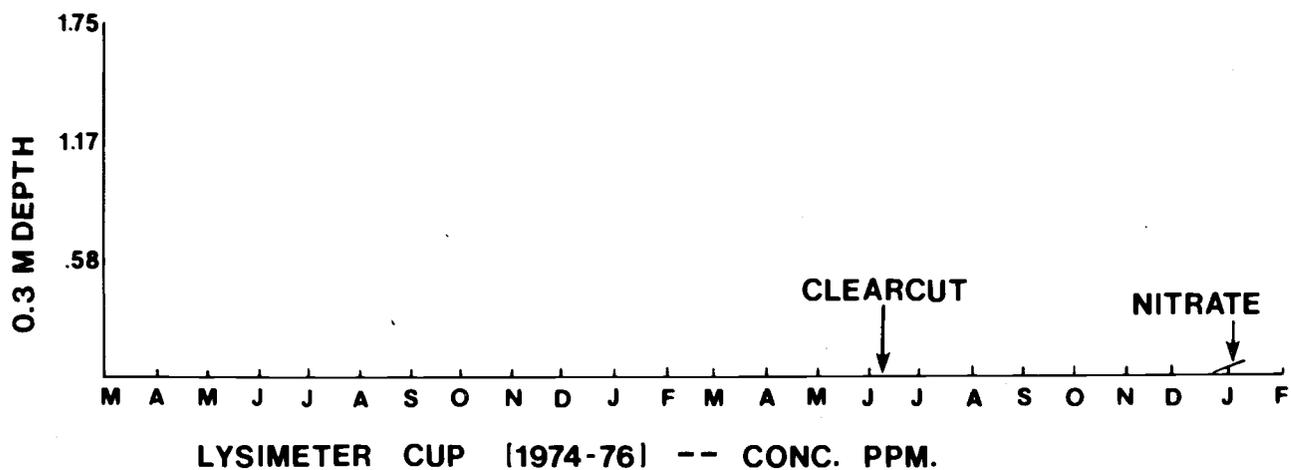


Figure 1. Nitrate nitrogen detected from three soil profiles. Periods of non-tracing. NO_3^- at or below detection limits.

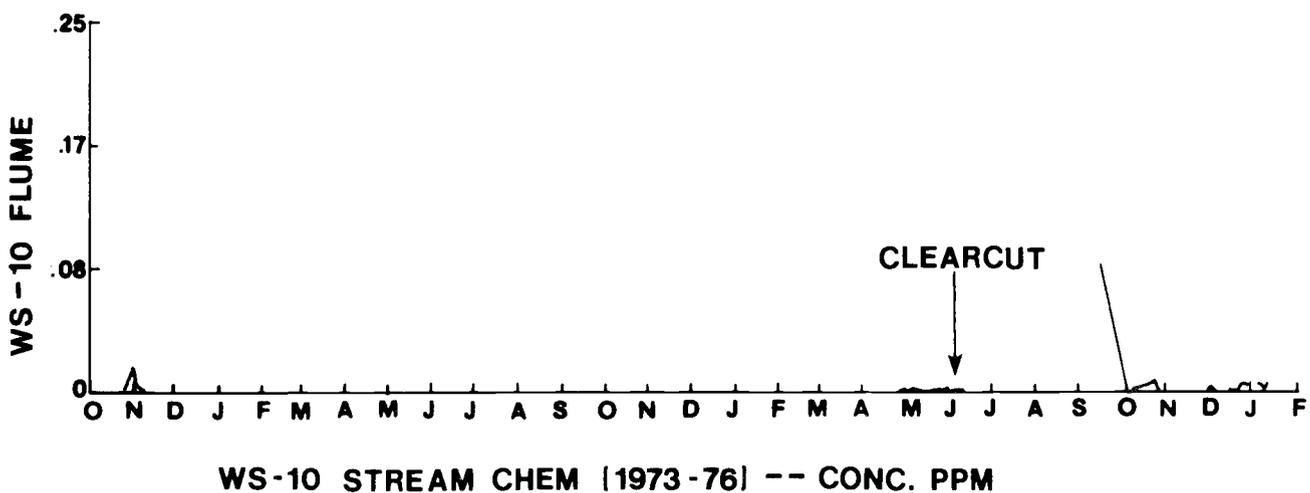
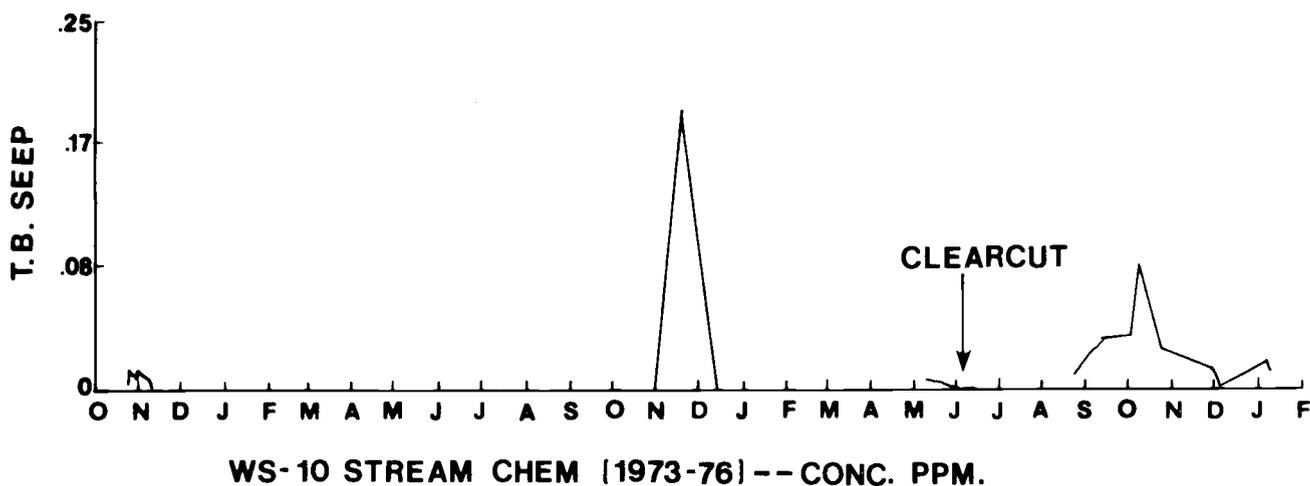
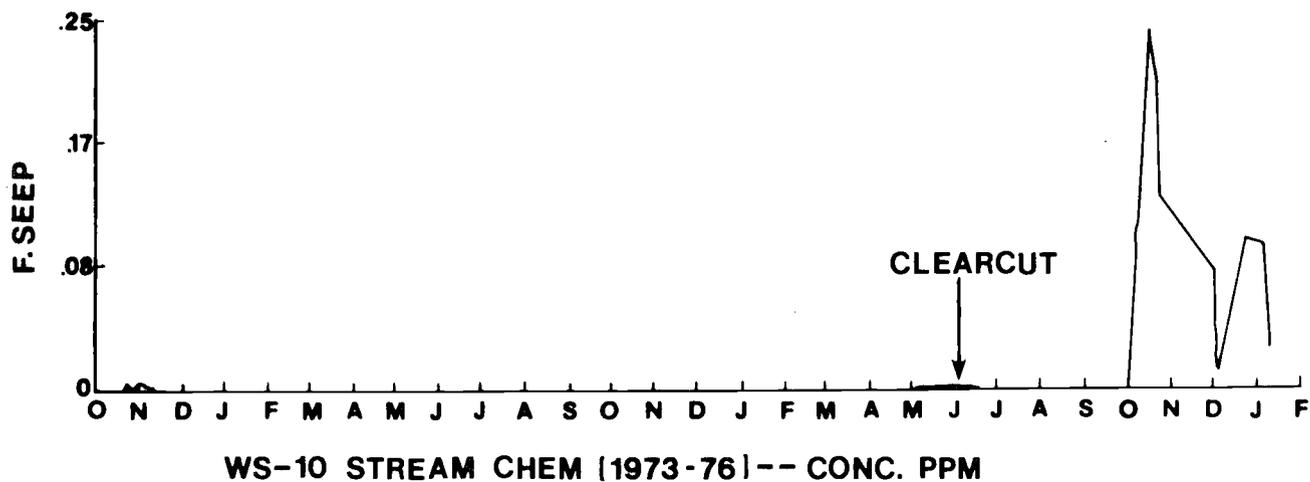


Figure 2. Comparison of seep versus stream $\text{NO}_3\text{-N}$ concentrations for WS 10 before and immediately following the clearcutting during the summer of 1975. Periods without trace indicate NO_3 at or below limits of detection.

3.1.5. Plant water relations, hydrology and meteorology - R. H. Waring and S. W. Running, Oregon State University.

In conjunction with J. J. Rogers and W. T. Swank, a mechanistic watershed level hydrology model was completed that incorporates seasonal changes in leaf area and leaf conductance (Waring et al., in press; Rogers et al., submitted).

Climatic data which has been collected over the last three years has been summarized on a daily basis and published with complete description of instruments, analyses, and data processing (Waring et al., in review). These data drive the hydrologic model described by Waring et al. (in press) and Rogers et al. (submitted).

References

Waring R. H., J. J. Rogers, and W. T. Swank. Water relations and hydrologic cycles. In D. E. Reichle (ed.), Contribution to woodland synthesis, Vol. 3, IBP (in press).

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Waring, R. H., H. R. Holbo, and R. P. Bueb. Meteorological data report from the Coniferous Forest Biome primary station on the H. J. Andrews Experimental Forest in Oregon, May 11, 1972 - December 31, 1975. Pacific Northwest Forest and Range Exp. Sta. (in review).

Waring, R. H. Reforestation in the Pacific Northwest (submitted to Land Planning).

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3.1.6. Erosion processes - F. J. Swanson, Oregon State University.

We have continued to monitor the rates of all significant erosion processes operating under forested conditions in the Andrews Forest. A manuscript has been prepared to summarize information on erosion rates of 11 different hillslope and stream channel processes. This work also examines relationships among erosion processes, the influence of vegetation on each erosion process and long-term variation in erosion rates due to wildfire, logging and climate change.

Accelerated mass erosion following logging has been reviewed in a paper (Swanston and Swanson, in press) and examined in detail in watershed 10.

We have continued work on stream processes with particular emphasis on the history and consequences of large organic debris in streams. This work has had important management implications (Swanson et al., submitted), and it has added greatly to our understanding of the coupling between aquatic and terrestrial components of coniferous forest ecosystems.

The history of major perturbations of forest vegetation is being investigated by fire history mapping and analysis of pollen and charcoal horizons in a 7000-year record contained in a core from a marsh. This history of premanagement stand disturbances is essential to the interpretation of long-term management impacts on soil erosion and the stream environment. Essentially, we are attempting to answer the question, "How did nature manage the forest?"

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- Swanson, F. J., G. W. Lienkaemper, and J. R. Sedell. History, physical effects and management implications of large organic debris in western Oregon streams. U. S. Forest Service General Technical Report (submitted).
- Swanston, D. N., and F. J. Swanson. Timber harvesting mass erosion, and steep-land forest geomorphology in the Pacific Northwest. In Geomorphology and Engineering. Publications in Geomorphology. Binghamton, New York (in press).
- Swanston, D. N., and F. J. Swanson. Complex mass movement terrains in the western Cascade Range, Oregon. In Landslides. Engineering Geology Reviews. Geol. Soc. Am. (submitted).
- 3.1.7. Carbon, water, and nutrient cycling modeling in old-growth ecosystems - P. Sollins, Oregon State University.

With Stan Clark and several work-study students, we totally reorganized the carbon-water model introducing a systematic coding scheme which a year later still seems adequate. The documentation was revised, graphs and figures prepared, and submitted to the Biome office for publication in December 1975 (Sollins and Swartzman, in press).

Following critical review of the manuscript describing the carbon-water (C-W) model by a variety of people, I rewrote the assumptions and structure part. The behavior part is still in preparation as discussed below.

In 1976 Al Brown and I implemented the C-W model of the CYBER at OSU and began comparing simulated with observed data from watershed 10. As of July 1 we had processed and graphed measured data on snowpack depth, litter moisture, and soil moisture. In the process we discovered several errors and inadequacies in the model which we have fixed. We still must process streamflow, and soil and litter temperature data (none of these had been worked up previously by the data bank). Also we have been comparing certain functions with those in Jim Rogers' model and trying to use some of his better ideas when appropriate. At the University of Washington we performed sensitivity analyses and I have reviewed the results and written up this part of the manuscript.

I completed the first-cut analysis of the preclearcut elemental cycling data and submitted a manuscript to Ecol. Monogr. in February 1976. (No abstract). Subsequently, McCorison and I reanalyzed the litter leachate, and throughfall data and eliminated the discrepancy between output from litter in solution and known inputs.

In June 1976 I began reformulating the old elemental cycling model to consider first only N (assuming it to be un-ionized). I have also tried to take into account the preliminary results of Cromack's litter bag studies which show certain substrates acting as sinks for N while others act as sources.

As a Biome representative to the interbiome decomposition and mineral cycling specialist committees, I organized and chaired a conference on "Mechanisms of elemental cycling in terrestrial ecosystems." Though one month of salary was provided through an NSF conference grant, I would estimate that this project has occupied a total of two months of my time. The conference was highly successful resulting in several new ideas and schemes for testing existing hypotheses. One proposal involving Biome personnel and resulting from the conference has already been funded.

With Kermit Cromack, I spent considerable time reading the literature on mycorrhizal and saprophytic fungal physiology. We developed several hypotheses regarding roles of short-chain organic acids in elemental cycling by these organisms. We presented papers on these ideas at AIBS Meetings (summer 1975), Northwest Science, at the Soil Zoology Congress in Uppsala (to be published) and in informal seminars at Oak Ridge National Laboratory, University of California, Davis, and the University of Calgary.

We submitted a paper to Soil Biology and Biochemistry which we are currently revising. Many of these ideas have directly affected the development of our elemental cycling model as well as our schemes for postclearcut sampling on watershed 10.

As my contribution to the International Woodlands Synthesis Volume I organized a set of simulation studies of response to defoliation. Swartzman and I performed and wrote up the simulations with CONIFER. I also collated the results from the Oak Ridge and Savannah River groups and prepared a first draft of the entire chapter.

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Sollins, P., and G. L. Swartzman. CONIFER: A model of carbon and water flow through a coniferous forest--documentation. Coniferous Forest Biome Bulletin no. 8, Univ. Washington, Seattle (in press).

3.1.8. Hydrology and erosion modeling and computer - J. J. Rogers, Oregon State University.

Last year's major work included: (1) testing and refinement of the water model and (2) incorporation of erosion and sediment routing algorithms.

The water model was tested and refined. Tests were made at Coweeta, North Carolina; H. J. Andrews, Oregon; and Beaver Creek, Arizona with excellent results (Figure 1; Table 1). A manuscript describing the model and test results has been completed and submitted (Waring et al., in press). A second manuscript has been submitted for editing (Rogers et al., submitted). A draft of model documentation is nearly complete (ECOWAT reference).

The water routing algorithms developed by R. M. Li and D. B. Simons of Colorado State University have recently been incorporated into the model. Initial testing of these routines is underway. The erosion and sediment routing algorithms developed by CSU have also been incorporated. We will test the combined water-sediment model on a number of diverse sites across the country during the coming year.

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Waring, R. H., J. J. Rogers, and W. T. Swank. Water relations and hydrologic cycles. In D. E. Reichle (ed.), Contribution to woodland synthesis. Vol. 3, IBP (in press).

Rogers, J. J., R. H. Waring, and W. T. Swank. Synthesis and modeling of the hydrology and water relation of forest ecosystems.

ECOWAT: Documentation of a model of the hydrology and water relations of managed forest ecosystems.

3.1.9. Stream linkages and comparisons - J. Lyford, J. Sedell, F. Triska, K. Cromack, and M. McCorison, Oregon State University.

Studies of seep chemistry and subsequent stream chemistry for watershed (WS) 10 before clearcutting were presented in the 1974-1975 Internal Report No. 162. Analysis of these data, both with respect to adjacent soil depth and longitudinal stream profiles, is being completed and will be submitted for publication in fall 1976. Monitoring of seep and stream chemistry is being continued following clearcutting. Preliminary data indicates that groundwater concentrations of biologically-active nutrients has increased significantly. However, the stream biota has adjusted to the increase and stream chemistry at the bottom of the watershed does not reflect this increase. Such alterations of stream chemistry are extremely critical from both a stream and watershed point-of-view. Therefore, we will be examining the relative amount of alteration of stream chemistry by the stream biota in both the WS-10 clearcut and stands of different age. This research will necessitate continual assessment of seep contribution into the final year of the Biome.

Also reported last year was the impact of wood as a potential nutrient source and sink. In addition to potential alterations of nutrient chemistry in small first order watersheds, wood also serves numerous other important functions. Wood as an organic input also serves as a carbon source for invertebrates and a source of nutrients by eventual mineralization. Wood also serves to alter stream morphology, retain sediment and create aquatic habitat. During 1975-1976, extensive sections of WS-2, Mack Creek, and

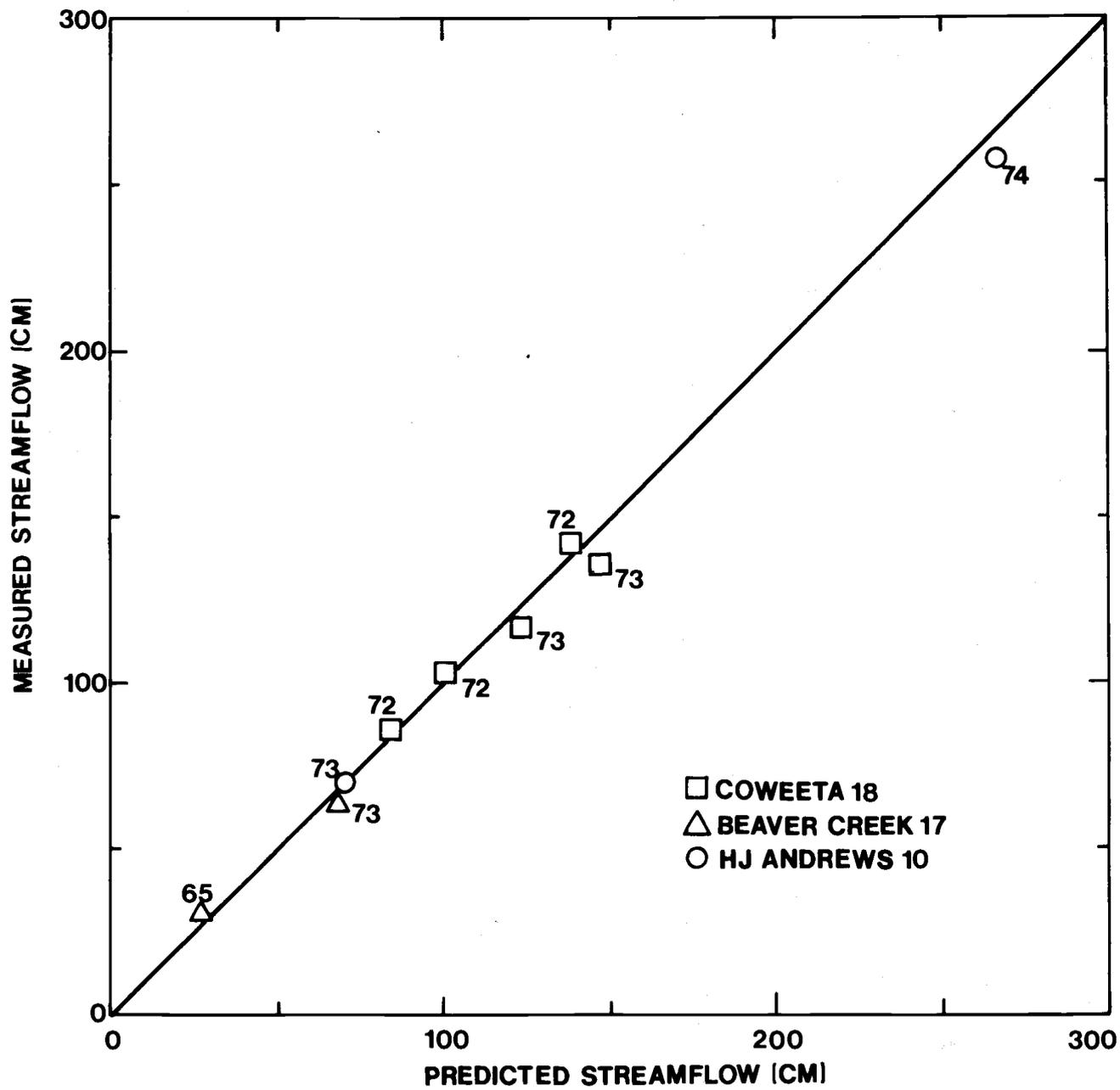


Figure 1.

TABLE 1. SUMMARY OF THE RESULTS OF SIMULATION RUNS UNDER DIFFERENT CONDITIONS.

UNITS = cm																	
Watershed	No. and Condition	Water Year	Precipitation		Evaporation				Infiltration	Transpiration				Total evapotranspiration	Streamflow		
			Rain	Snow	Canopy	Litter	Snow	Total		A	B	C	D		Total	Pred.	Actual
Beaver Creek	a. Original	1965	48	50	10.6	1.2	2.5	14.3	69.7	33.7	8.8	8.3	6.4	57.2	71.5	26.0	33.1
	b.	1973	45	74	13.7	1.5	3.9	19.1	70.3	28.6	7.8	8.3	4.9	49.5	68.6	56.3	55.4 ^{2/}
Coweeta	c. Thinned	1973	45	74	10.6	1.6	3.0	15.2	67.8	23.3	5.8	6.4	1.4	36.9	52.1	67.6	64.3 ^{2/}
	d. Shrubs	1973	45	74	9.7	1.6	3.6	14.9	67.5	18.8	5.8	6.0	.4	31.0	45.9	71.7	70.1 ^{2/}
	e. Hardwood	1972	192	3	24.4	1.4	0.0	25.8	168.0	53.7	4.4	4.3	-	62.4	88.2	103.0	104.3
	f.	1973	235	5	24.2	1.3	0.0	25.3	205.0	51.0	6.6	0.4	-	58.0	83.3	147.0	136.0
	3/g. Hardwood	1972	199	0	4/	4/	4/	24.5	4/	4/	4/	4/	-	66.6	91.1	103.6	104.3
	3/h.	1973	234	0	4/	4/	4/	22.8	4/	4/	4/	4/	-	66.0	88.8	138.0	136.0 ^{1/}
	i. Clearcut	1973	192	3	8.6	2.4	0.0	11.0	182.0	41.9	0.0	0.0	-	41.9	52.9	139.0	142.5 ^{1/}
	j.	1973	235	5	8.5	2.2	0.0	10.7	218.0	34.3	0.0	0.0	-	34.3	45.0	185.0	2/
	3/k. Clearcut	1972	199	0	4/	4/	4/	4/	4/	4/	4/	4/	-	4/	4/	140.1	142.5 ^{1/}
	3/l.	1973	234	0	4/	4/	4/	4/	4/	4/	4/	4/	-	4/	4/	180.2	2/
	m. Pine	1972	192	3	30.9	1.4	0.0	32.3	163.0	73.4	4.2	0.0	-	77.6	109.9	84.4	84.1 ^{1/}
n.	1973	235	5	30.4	1.3	0.0	31.7	200.0	65.3	6.3	1.8	-	74.2	105.9	122.0	117.7 ^{1/}	
3/o. Pine	1972	199	0	4/	4/	4/	34.2	4/	4/	4/	4/	-	82.2	116.4	83.4	84.1 ^{1/}	
3/p.	1973	234	0	4/	4/	4/	31.9	4/	4/	4/	4/	-	76.5	108.4	121.1	117.7 ^{1/}	
H. J. Andrews	q. Original	1973	119	48	32.9	0.6	-1.5	32.0	134.0	30.0	7.5	5.0	-	42.5	74.5	82.7	80.1
	r.	1974	206	98	22.3	0.7	-2.2	20.8	269.0	19.0	7.5	7.1	-	33.6	54.4	267.0	258.5
	s. Clearcut	1973	119	48	2.3	3.3	-2.4	3.2	163.0	18.8	0.1	-	-	18.9	22.1	130.0	2/
	t. Upper 37% cut	1973	119	48	21.0	1.7	-1.7	21.0	145.0	25.9	5.0	2.7	-	33.5	54.5	98.0	2/
	u. Lower 10% Cut	1973	119	48	29.9	0.8	-1.7	29.0	137.0	28.9	6.6	4.5	-	40.1	69.1	87.9	2/

1/ Estimates based on results from other watersheds at Coweeta as presented in Swift, Swank *et al.* (1975).

2/ No estimate available.

3/ Results of simulations with PROSPER as given in Swift, Swank *et al.* (1975).

4/ Not available.

5/ Estimates based on results from other watersheds at Beaver Creek (Brown *et al.* 1974).

Lookout Creek, have been mapped at a scale of 1" = 10' to obtain some impact of debris on streams of various order. Figure 1 is an example of a map showing debris distribution and some of its history of accumulation.

Using previous work as a basis, we propose: (1) to revisit the mapped stream segments to see how stream debris and general channel configuration responded to this winter's storms, and (2) to characterize channel geometry and aquatic habitats in selected segments of previous mapped streams. This work, when completed, will aid significantly in our understanding of coupling between land and water within a geomorphological framework.

References

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The physical and biological influence of wood in a river system.
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3.2. Findley Lake, Cedar River Watershed

3.2.1. Use and conservation of carbon - R. Gara, R. Wissmar, and G. Rau, University of Washington.

During the past year several research projects conducted at Findley Lake were completed. These include a writeup of a conifer needle decomposition experiment, publication of a litter income study, and a preliminary investigation of the aquatic insect community. Conifer needles exposed to the littoral environment of Findley Lake were processed at a rate (80-90% dry weight loss in the first year) comparable to that reported in forest streams (Sedell et al. 1975). In a decomposer exclusion study, needle weight loss was significantly inhibited in the absence of large invertebrates (<8 mm) indicating the importance of this community in the natural breakdown of the material. On land, needles enclosed in 8-mm mesh bags lost approximately 50% of their initial weight after a two-year exposure while needles in a similar treatment in the lake lost little or no weight other than leaching. An earlier study (Rau 1976) estimated that some 350 kg (dry weight) of conifer needles entered Findley Lake during a one-year period. This is a carbon input representing about one-fourth of the net phytoplankton production in the lake. As verified by the decomposition experiments, this terrestrial plant material can be readily utilized by the lake's heterotrophic community.

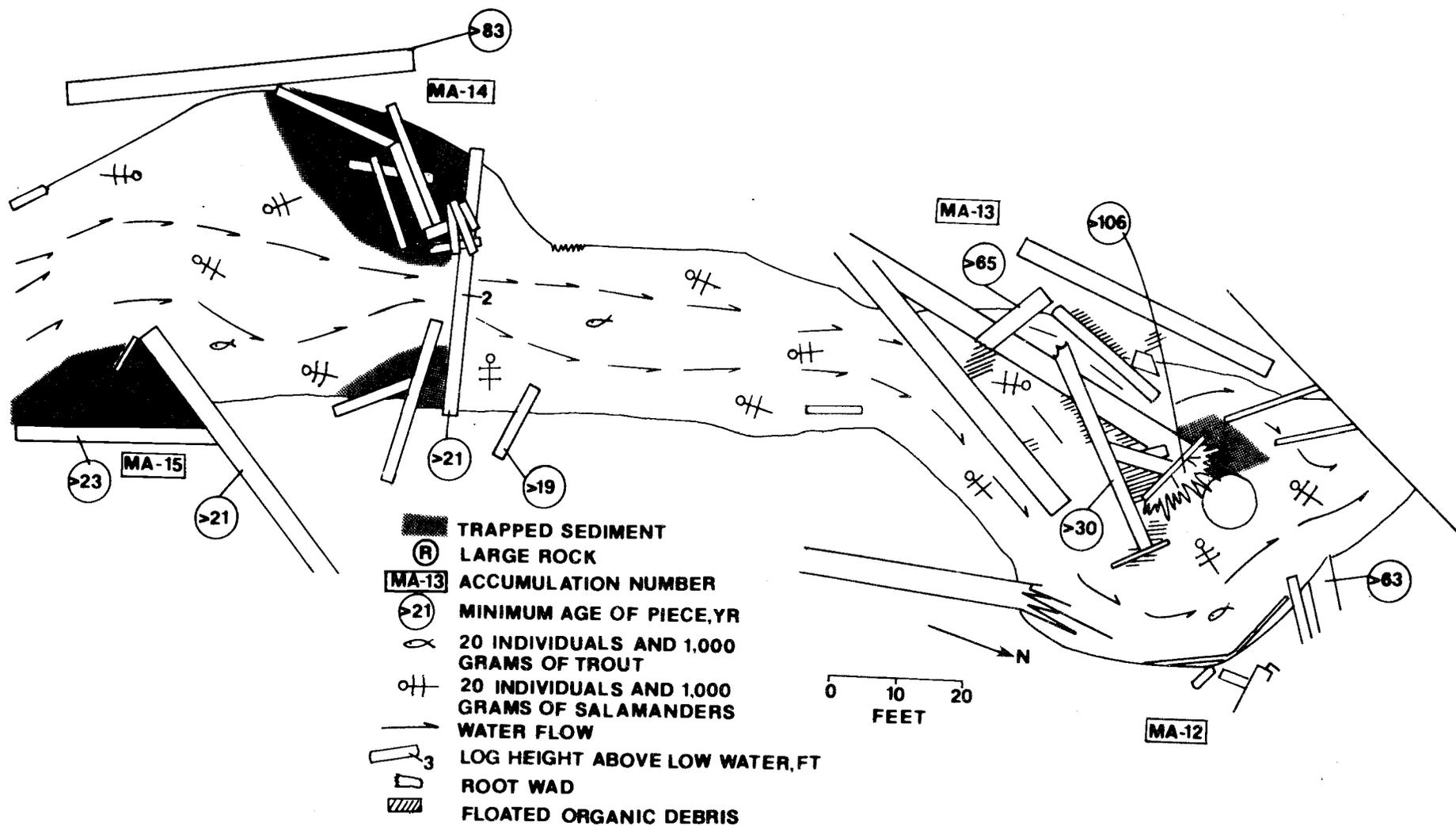


Figure 1. Map of 200 ft. forested section of Mack Creek. Fish and salamanders represent the numbers and biomass of each inhabiting this area. Note abundance of logs.

Additional evidence of the importance of allochthonous carbon in Findley Lake currently is being explored by analyzing the production of immature and adult aquatic insects. The size, distribution, and species composition of benthic insects sampled thus far indicate that carbon fixation in the water column can provide only a small amount of that community's carbon requirement. The standing crop of deep water chironomids in Findley Lake is equal to or greater than the biomass found in lakes where primary production is many times that of Findley. Further, we find that the maximum adult and larval biomass occurs in shallow water (2-5 m deep) where phytoplankton production is thought to be inhibited by U.V. light (Hendrey and Welch 1975). The emergence of adult insects from the lake represents a carbon flux of $0.36 \text{ g C}\cdot\text{m}^{-2} \cdot \text{yr}^{-1}$ (four-year average) or about 60% of the planktonic primary production annually reaching the sediments estimated by Birch (1974). A known shredder of terrestrial litter (Halesochila taylori, Trichoptera: Limnephilidae) comprises most of the emerging adult biomass.

References

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3.2.2. Litterfall and water inputs - H. Riekerk, University of Washington.

The objective of this subproject of the Findley Lake program is to identify and measure quantitatively the major pathways of carbon and nutrients from the forested land to the lake. Elucidation of the controlling mechanisms is in conjunction with studies by Ugolini, Johnson, and Wissmar et al.

Work during the past year has focused on a better definition of groundwater and litterfall inputs. In addition, an attempt has been made to measure groundwater chemistry from an urea-treated micro-watershed (0.3 acre), to extend the work done by Johnson and Cole.

The hydrology of the watershed remains a difficult problem with missing data sets especially during the winter months. D. Lettenmaier was hired temporarily to process the information and estimate missing data. Estimation was performed by constructing a multivariate autoregressive model for five daily time series. Findley outflow stage, Stampede Pass maximum and minimum temperatures and precipitation square roots and Seatack airport solar radiation. Each of these time series was first residualized by removing the annual cycle. Missing data were then synthesized by a forward-backward extrapolation technique.

The data of Table 1 summarize the average annual water and N, P flows into the aquatic component. From this information, it is apparent that water transport represents the major pathway, with creek inflows being dominant followed by direct precipitation. About half of the transport occurs during the month-long snowmelt period of early summer.

The concentration data of Table 2 are three-year averages of the monthly water samples collected from one sample point only. The soil solution and groundwater samples are from three replicate locations, and the creek samples from four of the seven inlets.

The sequence of average chemical concentrations from the soil surface to open waters shows a reduction of nitrogen and phosphorus below the B3 horizon of the podzol soil. This is coincident with changes in acidity and alkalinity suggesting changes in the mechanism of nutrient transport from the organic-acid dominated soil to the bicarbonate dominated rocky substrate (Johnson 1975). This information substantiates the hypothesis that the interface between the biochemical forest and soil solutions and the geochemical ground and stream waters is located under the slightly indurated B3 horizon (Ugolini et al., in preparation).

The data of Table 3 summarize the annual transfer rates but expressed in percent of the donor-compartment content (Turner and Singer 1976). From this it is apparent that especially phosphorus is rather mobile in the surface organic soil layers, but becomes sharply limited in the mineral soil.

The annual average concentration values of solutions from precipitation through the watershed into the Cedar River have been plotted in Figure 1. Most of these patterns behave as expected but for the exception of calcium. The reasons for deviant behavior are presently being explored.

The soil solution data from Johnson's urea experiments combined with preliminary data from the micro-watershed treated, fall 1976, have been plotted in Figure 2. This information supports the relative mobility of nutrient elements in the biologically dominated surface soil in contrast to the geochemically dominated subsoil.

This nutrient behavior combined with our tentative observations of a restriction of water flow through the indurated B3 horizon suggests the presence of two differentiated pathways of dissolved nutrients within the "groundwater" component, interflow, and deep seepage.

The data of Table 4 summarize the watershed input-output balance of nutrient elements expressed in kilograms per hectare per year. The net export in general is similar to values reported for watershed studies elsewhere in the nation, except for calcium and sodium. The calcium loss is of similar magnitude as that from a limestone dominated watershed (Walker Branch, Tennessee) raising questions as to the fixation/loss mechanisms of this element in the Findley Lake watershed conditions.

Table 1. Average annual nutrient transfers into Findley Lake.

	kg N	kg P	m ³ x 10 ³ H ₂ O
Precipitation	238	15	299
Creek inflows	321	27	3061
Groundwater	149	12	1423
Creek outflow	526	33	4749
Litterfall	7.2	1.2	-
Creek debris	?	?	-

Table 2. Average nutrient concentrations of the Findley ecosystem waters.*

	pH	Conductivity (μ mhos/cm ²)	Alkalinity (meq/l)	TOT N (ppm)	TOT P (ppm)	NO N (ppm)
Precipitation ^{1,3}	5.8	14.4	0.097	0.60	0.013	0.470
Forest floor ^{1,2}	4.6	23.2	0.010	0.57	0.128	-
A2 horizon ^{1,2}	4.6	20.6	0.014	0.40	0.027	-
B2 horizon ^{1,2}	5.0	13.8	0.044	0.24	0.020	-
B3 horizon ^{1,2}	5.5	22.5	0.197	0.40	0.066	0.023
Groundwater ³	5.1	23.8	0.055	0.26	0.010	0.012
Inlet creeks ^{1,3}	6.6	19.8	0.177	0.17	0.010	0.015
Lake ⁴	?	?	?	0.08?	0.002?	-
Outlet creek ^{1,3}	6.8	20.6	0.196	0.16	0.008	0.011

*Data sets from: ¹Ugolini-Minden, ²Johnson-Singer, ³Rieker, ⁴Wissmar-Richey.

Riekerk

Table 3. Transfer coefficients of N and P moving in the Findley ecosystem waters.*

	Compartment (kg/ha)		Output (kg/ha/yr)		Transfer coefficient (% per year)	
	N	P	N	P	N	P
Forest floor	650	44	14.8	4.6	2.28	10.45
A2 Horizon	1,125	231	14.4	0.7	1.28	0.30
B2 Horizon	2,430	923	6.2	0.5	0.26	0.03
B3 Horizon	12,300	1958	14.4	1.7	0.12	0.08
Rocky substrate	-	-	5.6	0.3	-	-
Lake	?	?	66.6	3.3	?	?

*Calculations based on data of Table 2, hydrology (Riekerk) and compartment contents (Turner-Singer). Outputs calculated from concentration Table 2 times the total inflows into lake ($=30.608 \text{ m}^3 \times 10^5$) and lake outflow ($47.486 \text{ m}^3 \times 10^5$).

Table 4. Findley Lake watershed nutrient budget.

	N	P	K	Ca	Mg	Na
Input	12.9	0.4	3.1	6.3	1.0	15.0
Output	4.4	0.3	6.0	100.8	10.9	53.1
Loss/gain	+8.5	+0.1	-2.9	-94.5	-9.9	-38.1

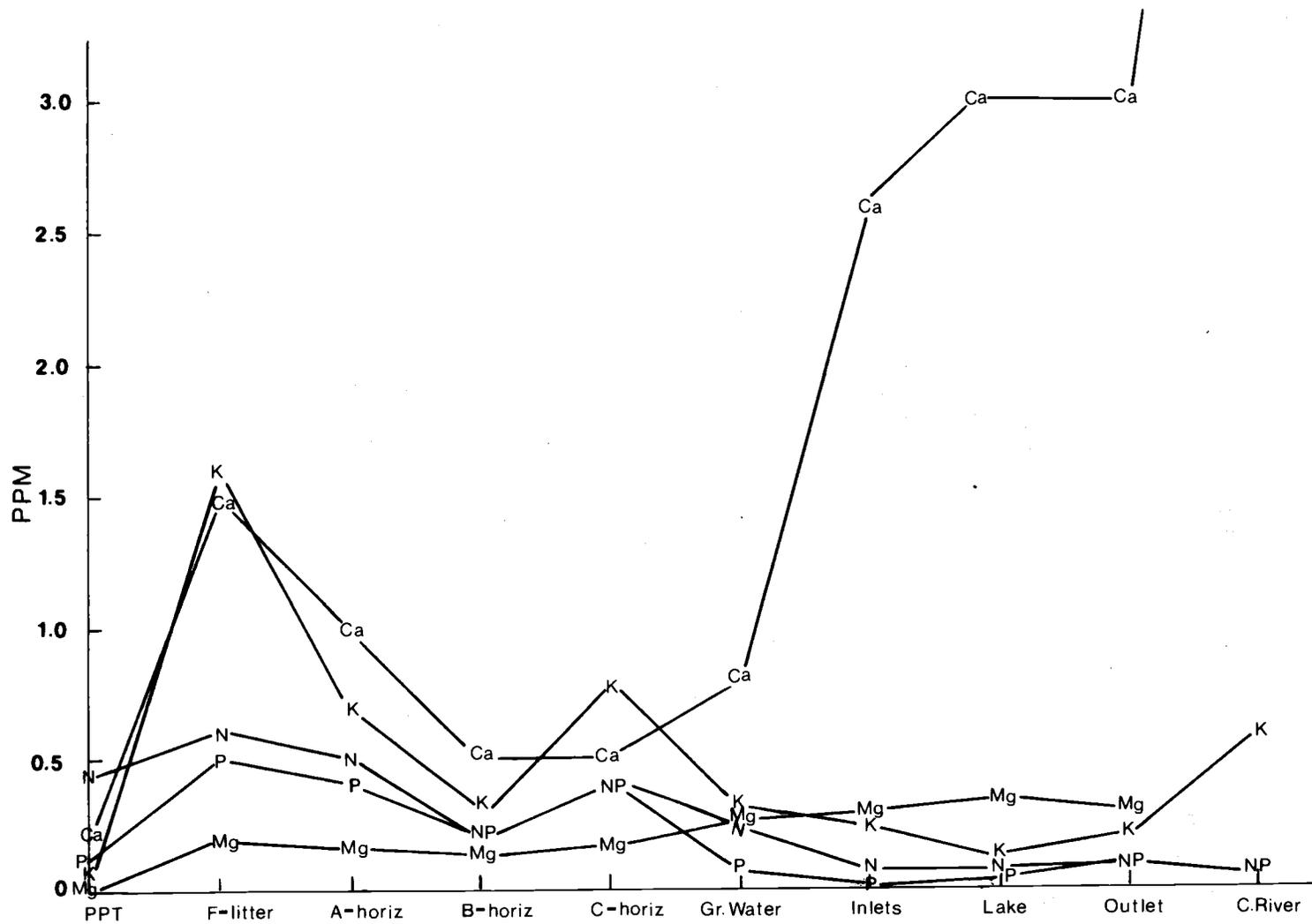


Figure 1. Annual average concentration values of K, N, Ca, P, and Mg in the precipitation, soil solution, groundwater, lake outlets and Cedar River.

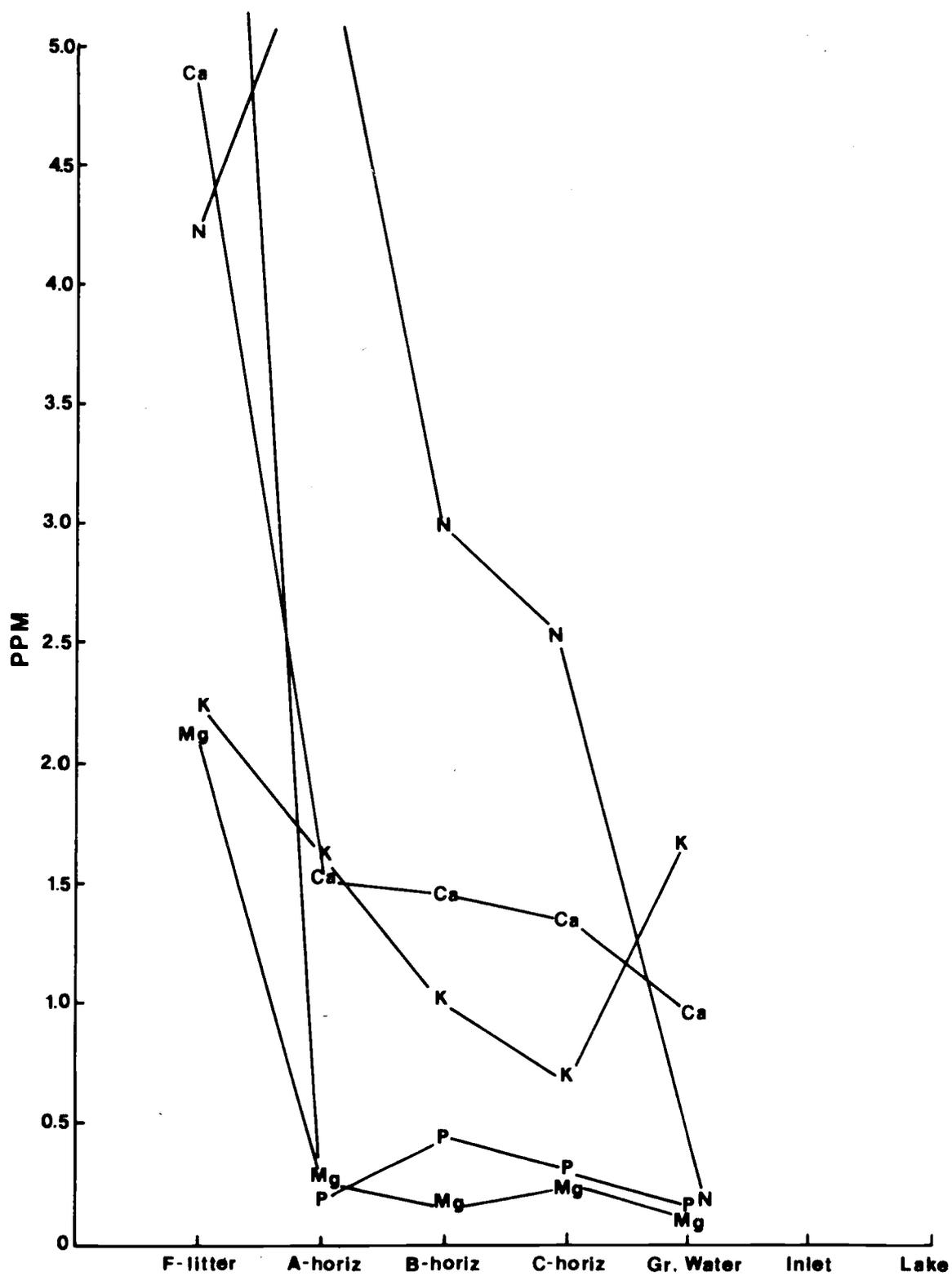


Figure 2. Soil solution data from urea-treated plots at Findley Lake.

The litterfall and creek-debris studies have been continued on a routine basis. The curves of Figure 3 show dispersal patterns similar to those reported by Rau, but of a higher magnitude. This discrepancy may be related to the use of larger-size litterfall traps.

The data of Table 1 show the litterfall component to be of minor significance in the total lake input. However, the coarse debris plays a dominant role in the detritivorous food chain of the littoral zone.

At present, litterfall production and dispersal mechanisms are being evaluated by R. Kurtz, but the study will be terminated by the end of this year. Our work has shown the higher importance of the fine debris fraction (<2 mm) for which there is only limited information. Future work should focus on this aspect.

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3.2.3. Terrestrial studies of soil water chemistry - F. C. Ugolini, R. Minden, J. Zachara, and H. Dawson, University of Washington.

The purpose of this project is to study the soil-forming processes in the Findley Lake basin as they relate to the chemistry of the streams, the lake, and the forest. Monitoring and analyses of the precipitation, throughfall, inlet and outlet in addition to the soil solutions from the O2, A2, 11B2hir, and 111B3 horizons of Podzols (Cryandeps) at two sites at Findley Lake was continued during 1975-1976. Previously, based on the chemistry of the soil solutions, two compartments were detected - One starting at the top of the canopy and ending at the lower boundary of the B2hir horizon and another one below the B2hir, including the groundwater and the streams. The data from this year confirmed this trend. Analysis of variance, to establish if the difference between the two compartments was significant, has shown that there is a significant difference at the 95 percent level of confidence between the 11B2hir and the 111B3 for pH, electrical conductivity, total nitrogen, total phosphorus, soluble iron (site 6), and soluble aluminum; at the 70% and 86%, respectively, for sites 6 and 7 for total iron and at the 78% for soluble silica. Removal of the forest floor at one site (site 6) has resulted in a temporary increase of one pH unit throughout the soil profile. This change lasted only one month. Total nitrogen total phosphorus concentrations have decreased in the area devoid of the forest floor; potassium values were also lowered, whereas calcium did not show any definite trend. A new aspect of this project--the study of the mobile organic fraction has shown that there is a decrease in either size or acidity of the "fulvic acid-like" soluble fraction with increasing depth in the

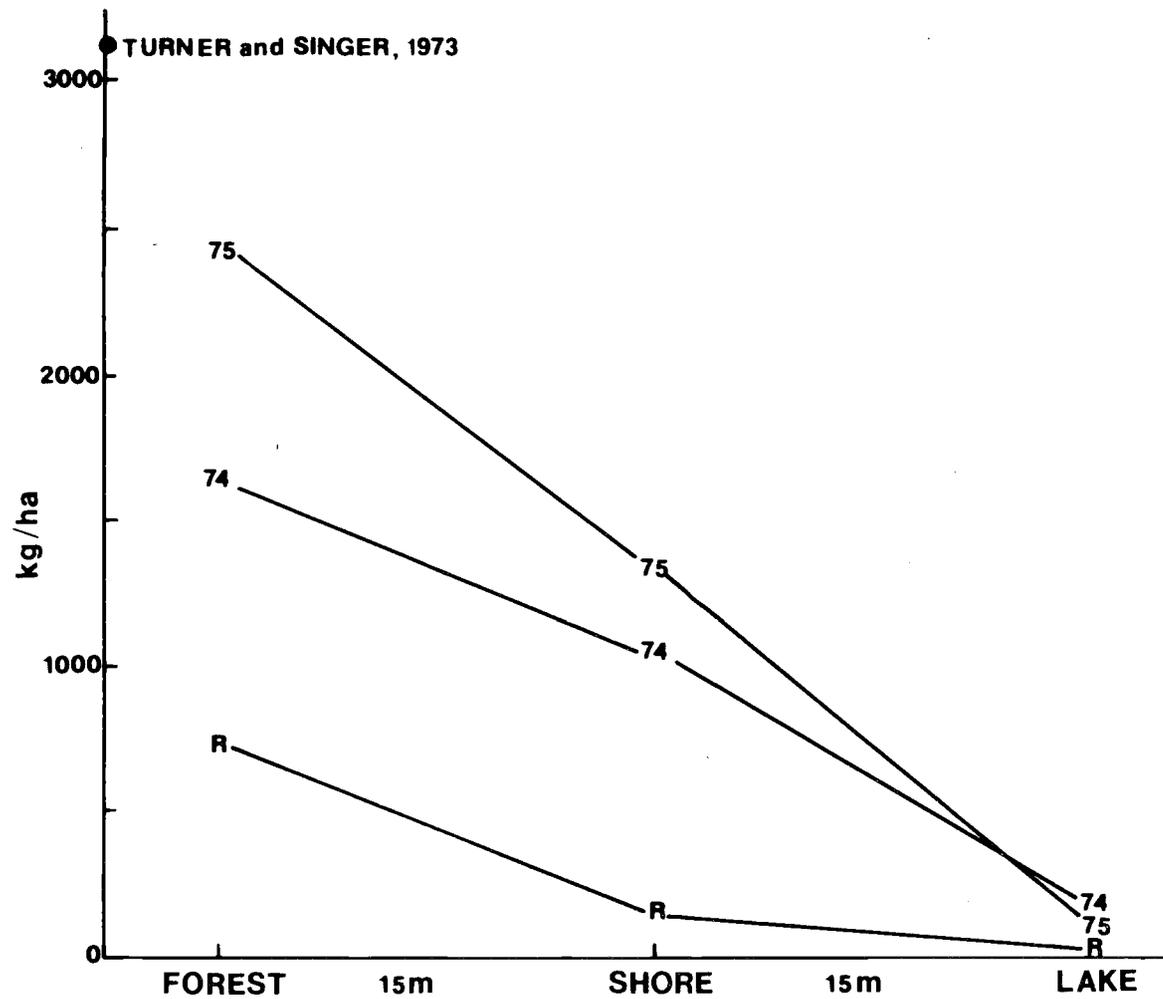


Figure 3. Annual litterfall (kg/ha) in the forest at the shoreline and in the lake. R = Rau's data, 74 = 1974, and 75 = 1975 (Riekerk).

profile. Also, it has shown that the stem flow seems to be the major source of soluble organics. The source of the "humic acid-like" is in the forest floor, throughfall, and stem flow. This fraction is retained in the A2 but reappears again in the 11B2hir and 111B3.

Implacement of lysimeters has been initiated in a clearcut area to compare the impact of the removal of the vegetation on soil solution. Among other hypotheses to be tested is to observe the stability of the 11B2hir and the retention of the two compartments after a clearcutting.

4. ANALYSIS OF AQUATIC ECOSYSTEMS

4.1. Stream Ecosystems - N. Anderson, J. Hall, J. Lyford, D. McIntire J. Sedell, F. Triska, Oregon State University

Experiments during previous years, using leaf packs to obtain litter mineralization data, resulted in the hypothesis: Microbial conditioning of litter inputs is a necessary prerequisite for conversion of litter debris to a food resource for insect detritivores. Field assessments using shredder insect larvae and needle litter conditioned for various time periods have been completed. In addition, laboratory studies on conditioning time and temperature effects on consumption growth and egestion, indicating microbial conditioning, is an important factor in rendering leaf litter palatable to aquatic invertebrates. Lepidostoma quercina (Lepidostomatidae), Lepidostoma unicolor, Clistronia magnifica (Limnephilidae), and Lepidostoma cascadenis were used in laboratory experiments.

Consumption rates (in milligrams per milligram per day) increased both with temperature and length of conditioning time of the food. Alder leaves which were conditioned most readily, were preferred over bigleaf maple leaves or Douglas-fir needles, the more refractory litter species. Consumption rate decreased with increasing size of the larvae.

Although they occupy the same areas of the stream and emerge and lay eggs at the same time, L. cascadenis and L. unicolor larvae showed very different patterns of growth. L. cascadenis larvae grew steadily from September and October through May, L. unicolor larvae gained more than 90% of their mature weight in May, June and July. Most L. unicolor larvae were still in the third instar when most L. cascadenis larvae had reached the final (fifth) instar in early April. To what extent this resource partitioning is based on detrital particle size, conditioning, or temperature remains to be investigated.

A computer simulation model was used to test laboratory data for L. quercina by comparing predicted growth rates with field growth rates. Predicted values were found to exceed actual growth rates in the late summer and early fall months. When the supply of preferred food was restricted in the first few months as occurred in the field, however, and simulated larvae were required to feed on a less palatable (conditioned) food, simulated values agreed closely with the measured growth rate.

In addition to providing evidence of conditioning, the combination field and laboratory studies provided measurements of biomass, instantaneous growth rate, consumption, fecal production, and respiration which are necessary

to assess the ecological role of invertebrate activity on litter mineralization. Experimental results on Clistoronia magnifica have been accepted for publication by Ecology. Results on the other shredder species will be included in a Ph.D. thesis by the end of this year.

Ideas generated in conditioning experiments of leaf litter have been extended to preliminary studies on wood debris. Wood debris constituted the major particulate organic input to watersheds 10 prior to clearcutting (Table 1.). In addition, wood constitutes a reservoir of refractory carbon slowly utilized both as food and habitat (substrate for oviposition, shelter, emergence, etc.).

Characteristic species that reduce the particle size of woody material are the elmid beetle, Lara avara, and the caddisfly, Heteroplectron californicum. Studies have been conducted to compare life history strategies and egestion rates of wood feeders with those of typical shredders of deciduous leaves and conifer needles. We have found that the particle size, lignin:cellulose ratio, and seasonal production of egested material differs between the two groups. The net result is a continuous supply of fine particulate organic material suitable for further microbial degradation and available to the collector functional feeding group. Results of these preliminary studies will be presented in three papers at XV International Congress of Entomology in Washington, D. C., August 1976, two of which will be published in the Proceedings.

In 1974 we hypothesized: Light is the major limiting action of primary production in coniferous forests. To test this hypothesis an experiment in a heavily shaded stream was conducted to compare light and nutrient effects on primary production. The experiment confirmed the role of light as a major limiting factor to primary production in heavily shaded streams. As a result we proposed further studies of primary production to compare a clearcut and forested section of Mack Creek through 1975-1976.

During that year, gross primary production, net community primary production and community respiration were measured monthly. Gross primary production and community respiration were 2.3 times greater in the clearcut than the forest (Figures 1 and 2). Winter production rates were approximately half the summer rates. The changes in respiration lagged behind changes in primary production, both for fall decrease and spring increase. This result was due to respiration of senescent algae and the associated bacteria in the fall and the typically low respiratory demand of juvenile communities during spring.

Insect emergence was four times greater in the clearcut than in the forest although insect standing crop was only slightly greater. The higher emergence to standing crop ratio in the clearcut indicates a greater influence of multivoltine insects in the clearcut. Such insects with short life cycles, such as midges and mayflies, are types expected to benefit most from increased algal production. Increase in insect emergence could result in higher trout production in the clearcut section. Indeed, cutthroat trout production in the clearcut section was also significantly higher than in the forest section. Studies of trout food selection by gut analysis indicated greater percentages of mayflies and midges in trout in the clearcut than in the forest section during summer months (Murphy, personal commun.). Thus, the opening of the canopy not only increased the production of algae but may also lead to increased insect and fish production and a shift in algal and insect community structure.

Table 1. Litter inputs ($\text{g}/\text{m}^2/\text{day}$) to the small watershed stream of a 450-year-old Douglas-fir forest.

Method of Measurement	Leaf Litter Deciduous	Leaf Litter Coniferous	Fine Wood Debris	Coarse Wood Debris
Litterfall	.070	.346	.244	-
Lateral Movement	.096	.143	.728	-
Scaling	-	-	-	.548
Totals	.166	.489	.972	.548
% Composition	7.6	22.5	44.7	25.2

Wood Debris 69.9%

GROSS PRIMARY PRODUCTION

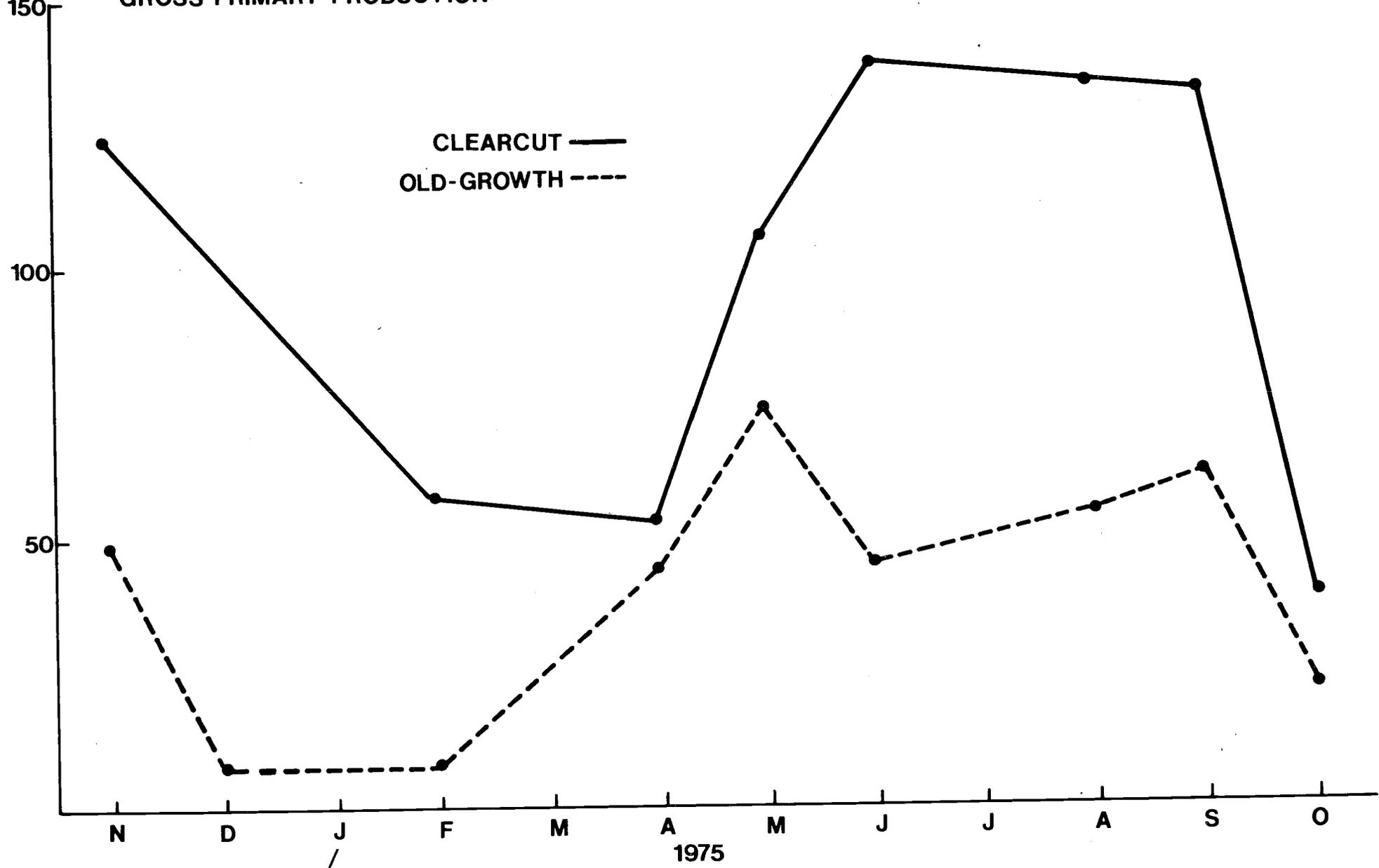


Figure 1. Gross primary production in Mack Creek, a stream flowing through a 10-year-old clearcut, and an old growth Douglas-fir forest.

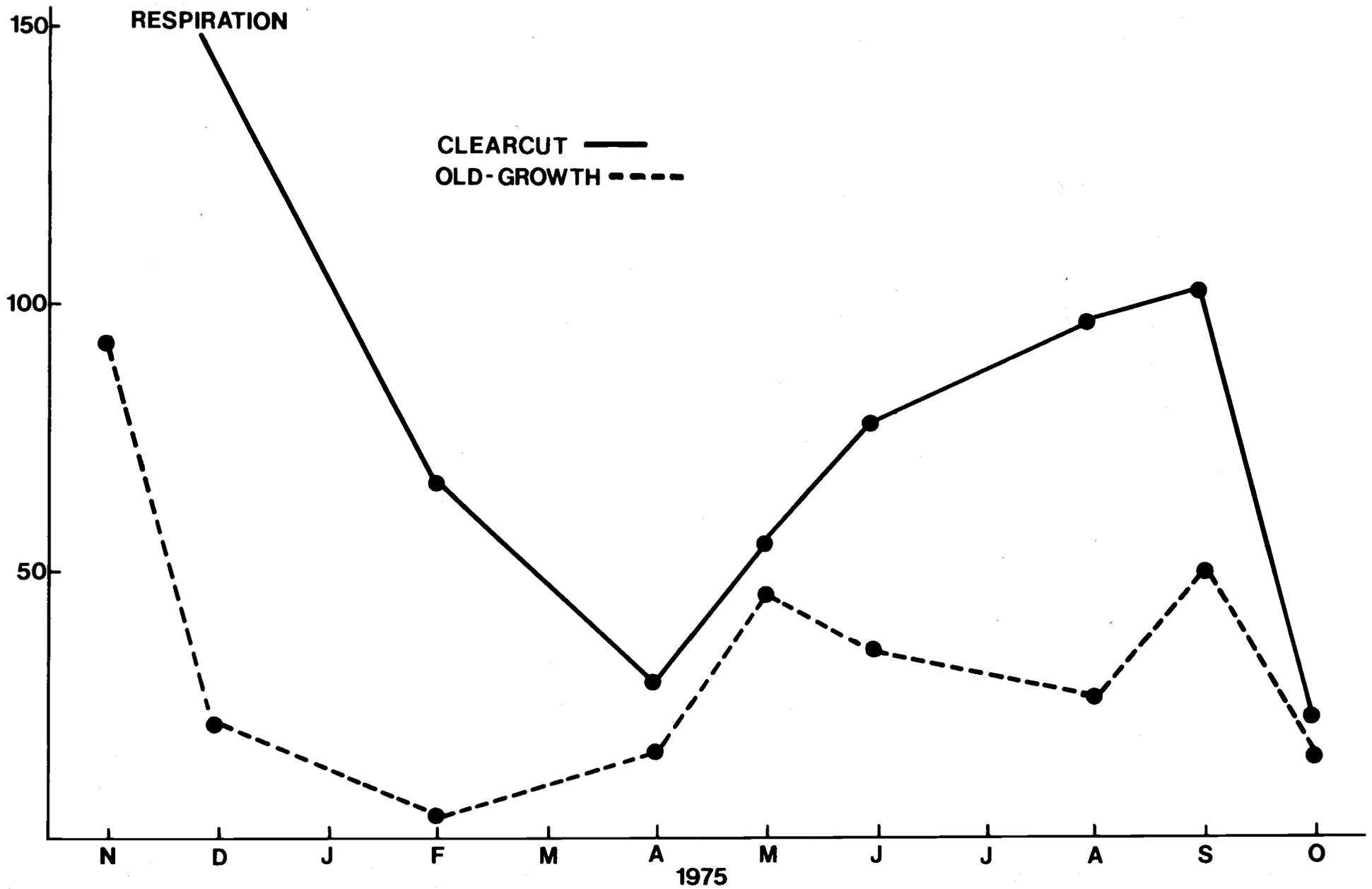


Figure 2. Gross primary production of the periphyton community from Mack Creek, a stream flowing through a clearcut and old-growth.

The above study is now completed and was presented at the AIBS Meetings in June 1976. It will also be included in a Ph.D. thesis being written at this time; a manuscript will be submitted for publication during 1977.

The above Mack Creek studies raised the question of the grazer effects on primary production and led to the hypothesis that cropping of the periphyton community stimulates even greater primary production. Several literature studies in lakes or aquaria had suggested this might be the case. To test this hypothesis we set up five laboratory stream channels with densities of: 0, 90, 180, 540, and 1080 snails/m². Algal standing crop was measured with chlorophyll a every five days, primary production and respiration at 0, 15, and 40 days, and grazing rates of snails at 30 days. Algal standing crops were the same for both the control and the lower two densities of snails. The standing crop of algae in the stream with 540 snails/m² was reduced by half and algae in the high density stream was five times lower than the control. The highest density of snails (1080 snails/m²) most rapidly decreased algal standing crop, while the channel with 540 snails/m² showed a much more gradual decrease. Snail grazing was much more variable at high algal standing crops, indicating that snails at high densities must graze more continuously to satisfy their ingestion needs. Thus, evidence from this laboratory study indicates that the algal communities can withstand standing crop or primary production. Only at grazer levels of 690 and 1040 snails/m² did significant loss of the periphyton community occur due to grazing pressure. Although not all the data has been analyzed at this time, we hope to have a manuscript submitted for publication by the end of 1976.

Measurements necessary to complete a nitrogen budget have been taken with the exception of some inputs from nitrogen fixations. Preliminary estimates of nitrogen fixation on wood by free-living bacteria indicate that fixation may be significant ecologically both in terms of annual input, and as a factor in long-term wood mineralization. To adequately investigate these processes will take a longer time than the final year remaining in the Coniferous Biome. As a result we will seek additional, separate funding to continue this work. Measurements of nitrogen fixation in the final year will be confined to moss (colonized by either free-living, nitrogen-fixing bacteria or blue-green algae) and Nostoc, both of which are important components of the streams we have been studying. Results of our preliminary experiments were presented at the American Society for Microbiology Meeting May 1976, and will be submitted for publication during 1977.

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4.2. Lake Ecosystems

4.2.1. Carbon, nutrient and elemental cycling. During this year the field work was completed for the comprehensive study of sedimentation and nutrient cycling in Lakes Findley, Chester, Morse, Sammamish, and Washington. The results have been analyzed and form the basis of the Doctoral Dissertation "The Relationship of Sedimentation and Nutrient Cycling to the Trophic States of Four Lakes in the the Lake Washington Drainage Basin" by P. B. Birch (1976), 200 pp. The most significant findings in this work were:

- a) There is a linear relationship between sedimentation of C, N, and P and primary production in the four study lakes.
- b) Nutrient cycling in the trophogenic zone of the four lakes is very efficient during the growing season. This was further supported in an in-depth study in Lake Sammamish. In early spring in Lake Sammamish, however, recycling of N and P was relatively inefficient due to the rapid sinking rate and slow decomposition rate of diatoms which dominate the phytoplankton at this time. This resulted in a depletion of the dissolved pools of N and P in the very early growing season.
- c) A paleolimnological study which involved dating (^{210}Pb method) and C, N, and P analysis of sediment cores revealed that there have been marked increases (2 - 10x) in the rate of sedimentation in Lakes Chester Morse, Sammamish, and Washington, in the last 80 years. These increases were thought due to increases in erosion induced by logging activities (lumber removal and associated road construction) in the watershed. Using the

relationship defined between sedimentation and primary production it was estimated that logging activities resulted in increases in primary production in the three lakes. The estimated increase in Chester Morse Lake was modest and the lake remains oligotrophic, but in Lakes Sammamish and Washington, larger estimated increases in primary production suggested that Lake Sammamish changed from oligotrophic/mesotrophic to mesotrophic and that Lake Washington changed from oligotrophic to mesotrophic around the turn of the century.

Experiments have been completed on phosphorus and carbon cycle coupling in Lake Washington. The hypothesis was investigated that the plankton community responds to the addition of phosphate by varying inorganic carbon uptake and organic carbon release in proportion to internal carbon-phosphate coupling. Two experiments from Lake Washington on 28-29 May, 1975 (just after peak bloom) and 14-15 August, 1975, (summer steady state) are reported here in which ^{32}P tracer kinetics, PO_4 addition and depletion and ^{14}C bioassay techniques were used to test the hypothesis. Response to PO_4 addition differed markedly. On 28-29 May, a k_s of $3.86 \mu\text{gl}^{-1}$ was observed, phosphate flux in response to PO_4 flux was $0.03 \mu\text{gl}^{-1}$. On 14-15 August, an initial k_s of $10.9-12.8 \mu\text{gl}^{-1}$ was measured, yet after 2 days, turnover rates dropped in proportion to the PO_4 added. There was no significant difference of either ^{14}C uptake or ECR from controls. Expected PO_4 flux was $0.05 \mu\text{gl}^{-1} \text{hr}^{-1}$ and observed was $4.23 \mu\text{gl}^{-1}$. These results support the hypothesis and suggest that (1) PO_4 was a primary factor limiting the bloom in May, yet the lack of clear response in August implies a variety of factors were limiting, and (2) the carbon-phosphorus cycles were coupled more closely in May than in August.

Information has been obtained on the dominance of phosphorus over nitrogen as the limiting factor to phytoplankton growth. Laboratory experiments with natural phytoplankton assemblages from three lakes (two mesotrophic and one oligotrophic) showed that added PO_4 predictably affected growth rate (μ ; P:B) while NO_3 had little effect even when the N:P ratio approached one. The response to PO_4 followed the typical Monod-type function. The lack of effect of NO_3 on μ at such low N:P ratios is in striking contrast to the added effect of NO_3 plus PO_4 on maximum biomass produced versus only PO_4 alone.

PO_4 was shown to have slightly more effect than NO_3 in the oligotrophic lake when used in a Monod-type model to predict P:B (observed in situ). However, light intensity was shown to be more critical than either nutrient if a good fit between calculated and observed μ was obtained. A poorer fit at 10 than 20 m may be a result of unpredicted UV radiation, which is thought to cause severe inhibition and maximum photosynthesis to occur at 15 m.

Experiments were conducted in situ in Findley Lake and Lake Washington to determine the rates of feeding by zooplankton on the bacterial/detritus and algal components of the plankton. The method used was that of tagging the bacterial/detritus component in the dark and the algal component in the light with $^{14}\text{CO}_2$. The bacterial/detrital component was large in both lakes during each of two experiments (several thousand cpm). The phytoplankton component was rather small in Findley (a few hundred cpm).

The filtering rate was determined by noting the amount of tagged biomass removed after intervals up to six hours. The filtering rate per animal or annual weight is then multiplied by a measure of algal biomass to obtain the grazing or feeding rate. There is a problem with this method which apparently stems from the recycling of labeled organic carbon excreted by zooplankton and taken up by bacteria or held in detritus. A probable increase in that fraction in the presence of zooplankton resulted in more apparent tagged biomass than in the control without zooplankton. This led to negative rates in many instances. Where positive changes in tagged biomass existed, and could be transformed into a filtering and grazing rate, the rates are most likely underestimates.

In Findley Lake the filtering rates for algae, including all size fractions (net, nanno, ultra and total), ranged from 4.4 to 71 ml animal⁻¹ hr⁻¹ with a mean for the three significant values for total of 6.7 ml animal⁻¹ hr⁻¹. The corresponding mean grazing rate was 8.2×10^{-1} µg chl a animal⁻¹ hr⁻¹ or 8.1 µg chl a µg animal⁻¹ hr⁻¹. The results were from experiments on July 24 and August 6, 1975. These values were statistically significant.

No grazing was measurable in Lake Washington on September 3, but on September 25, the rate was about the same after 3 hours and 6 hours - 3.8 and 3.5 ml animal⁻¹ hr⁻¹. Grazing was 20×10^{-1} µg chl a animal⁻¹ hr⁻¹ and between 6 and 7 x 10⁻¹ µg chl a µg animal⁻¹ hr⁻¹. These values were for the total and were statistically significant.

Filtering rates were practically nondetectable for the large bacterial/detrital component. The amount of tagged material was high and rather stable and thus should have provided a measure of zooplankton utilization, if in fact such utilization existed.

A careful literature review into techniques for measuring grazing rates by phytoplankton indicate that the greatest accuracy is probably attainable by directly counting the activity in the zooplankton themselves rather than the changes in activity in the algal biomass. While we and others have had difficulty with the method used here, it has been used successfully.

Carbon size fractions of plankton were defined for Lake Washington. Chlorophyll, respiratory electron transport system (ETS) activity, particulate organic carbon (POC), and ¹⁴C-uptake were measured seasonally in six size fractions and four depth intervals from April, 1974 to August 1975. Phytoplankton carbon (φC) was estimated from chlorophyll a, primary production (PPR) from ¹⁴C-uptake, and respiration from ETS activity. During the winter when the water column was chemically homogeneous, about 55% of the POC, ¹⁴C, and ETS activity were found in the upper 10 m. As stratification developed, the percent in upper 10 m increased with maximum values found during maximum stratification in August: POC (81%), ¹⁴C (75%), and ETS (92%). Virtually all the PPR occurred in the upper 10 m in all seasons. The data indicate that much of the carbon produced during the spring bloom is transferred to deeper waters. During high nutrient concentration in the winter, the <53µ fraction contained 85%, 96%, 65%, and 84% of the POC, ¹⁴C, PPR, and ETS, respectively, and was dominated by Cryptomonas caudata. During the spring bloom, the <53µ fraction decreased in importance accounting for only 52%, 43%, 13%, of the POC, ¹⁴C, and ETS, respectively while PPR was unchanged. The <53µ fraction was dominated by C. caudata, Cyclotella sp., Melosira italica, Asterionella formosa. The decrease in POC and ETS activity was due primarily to an increase in zooplankton in the <53µ fraction. During the summer period of nutrient depletion, the <53µ fraction was again dominant in terms of all variables measured. Of the large zooplankton present

- c) P may be rather mobile in surface organic soil layers, but becomes more limited in the mineral soil.
- d) Loss of nutrients to the lake may be regulated through HCO_3^- induced leaching below the B2hr soil horizon.
- e) Allochthonous particulate inputs to the lake are either washed out or sedimented, where they support an insect population.
- f) Patterns of ice-cover melt and insolation regulate the timing of the plankton bloom, but the size of the bloom is regulated by input of PO_4 .
- g) Microbial communities on allochthonous litter may immobilize lake N.

A preliminary examination was made of carbon budgets of lakes in different trophic states. A comparison of carbon budgets indicates that the inputs, exports, and respiratory estimates for each lake differ because of morphometric, hydrologic and vegetative characteristics of their drainage basins. Carbon budgets include allochthonous and autochthonous carbon subdivided into dissolved organic carbon (DOC) and particulate organic carbon (POC). Carbon sources for Lake Wingra (Gasith, 1974) and Lawrence Lake (Wetzel, et al., 1972) are predominantly from phytoplankton and macrophytes. Mirror Lake (Jordan and Likens, 1975) receives most of its carbon from phytoplankton while Findley Lake has high inputs from allochthonous DOC and POC. Respiratory losses suggest the refractory nature of carbon in Findley Lake.

Research on hydrology was conducted in three principal areas: Time series analysis, input-output methods, and data filling techniques. Work in the first two areas was concentrated primarily on analysis of techniques which are new or previously unapplied in ecosystem analysis. Time series analysis is intended for use on the relatively long limnological records from Lake Washington. The principal tool being used is spectral analysis. Input-output analysis, "borrowed" primarily from the economics field, is being applied to annual nutrient budgets (phosphorus, nitrogen and carbon) from Findley Lake for calendar years 1974 and 1975. Data filling techniques were applied to missing Findley Lake hydrologic data for calendar years 1973-1975.

A primary concern in the spectral analysis of Lake Washington biological and chemical data has been that the data were not collected at equal intervals in time. The basis for spectral theory is that sampling interval is uniform; little work has been published on the analysis of unequally sampled data. An analytic technique which will accommodate unequal spacing has been reviewed and programmed (Jones, 1971). Analysis of Lake Washington data should be completed in 1977. Spectral analysis of the Lake Washington data is expected to yield two important results: first, for each individual record of nutrients and biomass indicators, an estimate will be made of the Nyquist frequency, which in turn will define the minimum sampling frequencies required in future data collection programs; second, for multiple records, an estimate will be made of the coherence function, essentially an indicator of the correlation between two records as a function of frequency, and the phase relationships between record pairs.

Input-output analysis has been assessed for use in ecosystem modeling and found to be quite applicable to the compartment-flow style models most commonly used in ecosystem modeling. The method has been applied to synthetic data and found to be useful in estimating the effects of second and higher order interactions. The best application of these models ultimately appears to be in the management area, where they have particular utility because they are entirely data-based.

throughout the study, Diaptomus ashlandi, Cyclops bicuspidatus, and Neomysis awatchensis, only N. awatchensis was found to migrate vertically.

The measurements of respiratory electron transport (ETS activity) of the microplankton ($<76 \mu\text{M}$) and net plankton ($<75 \mu\text{M}$) have continued. Respiration rates of the phytoplankton community have been estimated from ETS activity and the ratio of primary productivity to respiration (P/R) calculated. Although this ratio has been investigated previously, in both the field and laboratory, for the most part these earlier studies only dealt with the P/R ratio under a limited set of conditions (laboratory studies) or over a short period of the annual cycle (field studies). A review of previous studies indicates that the P/R ratio ranges between about 2 and 50 (mgC produced mgC respired) with the large range attributable to differing growth conditions, variations in methodologies, and differences in the definition of the P/R ratio. Ratios calculated for both lakes Findley and Washington fall within the range of those previously reported, with high ratios occurring during the early bloom and low ratios found during the warmer, nutrient depleted periods. It is proposed that, for the most part, this shift in P/R ratios is due to uncoupled responses of the respiratory and photosynthetic systems to environmental temperature changes and nutrient stress. This results in a 12-hr dark loss of photosynthetically fixed carbon that varies from a low of only 7% early in the spring bloom to over 100% during periods of high temperature and severe nutrient depletion.

If the phytoplankton and zooplankton respiration figures are combined along with an estimated sinking rate, it is possible to construct a simple carbon budget for the euphotic zone of Lake Washington. The results of such a calculation indicate that on a yearly basis all but about 5% of the photosynthetically fixed carbon is accountable. This is in sharp contrast with other studies in which the unaccountable carbon constitutes nearly 50% of the budget. It is felt that one of the main differences between the two budgets is the lack of estimates of phytoplankton dark respiration losses in the latter.

4.2.2. Land-Lake Interactions.

Watershed ecosystems are complex and varied assemblages of aquatic and terrestrial vegetation, substrates, and associated fauna. Ecosystem responses differ according to basin morphology, climate, geology, drainage area, and species composition. Characterizing carbon and nutrient distribution and transfer along the interface between the land and the lake or stream is an important step in determining the dynamics of a watershed.

We are examining the allocation and movement of carbon, nitrogen, and phosphorus in the Findley Lake watershed. The objectives are (1) to establish the major pools in the system and the pathways of flow of dissolved and particulate matter into the lake; (2) to assess the mechanisms controlling the major interface flows; and (3) to identify the mechanisms of utilization and storage of both allochthonous and autochthonous matter in the lake.

Results indicate that:

- a) The forest has a relatively slow rate of turnover and low production.
- b) The forest strongly retains nutrients through internal redistribution and large, tightly bound soil nutrient reservoirs, with input = output and soil leach = uptake/

This feature is especially useful in a management context since projected effects of altered nutrient supply rates, etc., may be estimated directly from the data rather than by calibrating a cumbersome dynamic water quality model and projecting on an "alternative futures" basis. The availability of nutrient budget data from Findley Lake for 1974-1975 will allow analysis of the stability of the models for predictive purposes; i.e., 1974 data will be used to project 1975 production.

Estimation of missing Findley Lake outflow data (daily) for 1973-1975 has been completed. Estimation was performed by constructing a multivariate autoregressive model for five time series. Each time series was first re-sidualized by removing the annual cycle. Missing data were then synthesized using a technique proposed by Gilroy (1971). This model should prove helpful in the estimation of other missing time series data.

A model was developed to simulate the phosphorus cycle in Lake Sammamish. The model is composed of two parts: (1) a mixing model which computes daily mixing depths by determining the point in the water column where the kinetic energy from wind and the convective mixing energy equals the potential energy in the thermal gradient, and (2) a phosphorus model that computes the quantity in the state variables phytoplankton, ortho-phosphorus, zooplankton and detritus on a daily basis. Of 12 constants used to define the various subprocesses, 7 were obtained from experiments on Lake Sammamish itself and the remaining 5 were approximated from literature research.

Although relatively simple in its ecological structure, the sensitivity analyses with the model have provided some insight into significant questions about phosphorus dynamics in the lake. For example, the variation in the timing of the spring diatom outburst from year to year and its comparison with mixing depth computations suggests that prolonged mixing may favor larger diatom masses in some years by supplying more phosphorus to the lighted zone. While earlier stratification would provide more light there is not enough phosphorus available during those years to build as much biomass as is the case if mixing is prolonged. Previously we had thought that early stratification was most important for early blooms.

Further, insufficient phosphorus was available in some years to allow the biomass to attain the level of observed values. This meant that another source had to be imposed during those periods. The most likely source now seems to be increased stream runoff just prior to the spring growth period, which is another possibility that would not have been considered plausible.

Also, the optimum light intensity was changed to a relative value - 50% of the incident value - from an absolute intensity. That change resulted in a more realistic growth pattern.

Lastly the Michaelis-Menten function was altered to the extent that biomass of phytoplankton replaced the half saturation constant. This has resulted in a better fit with observed data but also has led to many discussions about the effect of changing biomass on the instantaneous uptake of phosphorus by phytoplankton.

The nutrient load supplied to urban lakes through runoff from paved surfaces and its effects in nearshore areas was studied in Lake Sammamish. Three west-side inputs, from the "developed" side of the lake were compared with two inputs from the relatively undeveloped eastside. The content of phosphorus in the inflow streams were found to vary widely in the developed area streams while the levels in the eastside streams were very constant, although very high in one- on the order of 500 g/l total P. That source was determined to be affected by septic tank seepage.

Periphyton growth on artificial substrates located in the lake 2 m below the surface and several meters from the end of the inflow pipe or stream was not affected by the nutrients in the urban inflows. However, in November when the lake turned over and phosphorus content increased dramatically throughout the lake, periphyton biomass also made its most marked increase. This occurred in spite of reduced light at that time of the year. Periphyton mass on substrates in the nearshore areas is still believed to be responding to the unevenly distributed inputs of phosphorus from impervious urban areas, but placement of the artificial substrates was not precise enough to detect that effect.

4.2.3. Higher consumers "Lake Washington Fish"

The Lake Washington fish studies are a unique holistic consideration of the fish community of a highly perturbed large mesotrophic lake. We are evaluating the role of consumers in the lake ecosystem as a successional force on the prey community and in nutrient cycling. We are also concerned with the effect of perturbations (eutrophication, fishery exploitation, spawning habitat deterioration, introduction of exotic species, and enhancement of economically important species). Work to date has concentrated on modeling and process development as well as population and community assessment with respect to both limnetic and benthic-littoral fish species.

Limnetic fish--A. Modeling and process development. This work has focused on determining the dynamics of energy flow between zooplankton and the planktivorous fish community. It is clear that the rate of prey consumption is not a strict function of prey and predator abundance but rather depends on the behavioral mode of the predator. In any realistic model we must consider cueing mechanisms for alternative behaviors as well as how the rate of prey consumption is modified under alternative behavior. Specific components of the model are:

- 1) Absolute limits on rate of prey consumption, prey as predator abundance, prey sighting distance, capture success, handling times, and predator swimming speed.
- 2) Behavioral considerations: (a) Diel feeding and non-feeding, (b) schooling, (c) adoption of winter feeding behavior (fasting and a generally low rate of feeding intensity), (d) vertical migration, (e) hunger, and (f) nature of prey selectivity; prepatterns of prey selection due to optimal foraging, physical limitations of the predator, prey availability and ability to avoid capture, or some combination of these effects.
- 3) Bioenergetics and growth. These considerations allow simulation of fish growth and rates of nutrient regenerations.

B. Community and population assessment. This work is aimed at constructions, long-term trends in abundance species composition, and growth of the limnetic fish community. Any response of the limnetic fish community to trophic changes in Lake Washington will provide insight to the importance of various processes identified in the modeling activities.

Considerable modeling and process development for juvenile sockeye has been completed (Eggers, 1975, 1976, 1977). During the past year extensive field sampling, to provide the information base for extension to other limnetic fish species, has been completed.

The laboratory processing of those samples is now 80% complete. Preliminary analyses of a small component of this important information has produced significant results regarding optimal foraging by planktivorous fish (Eggers and Doble 1976).

Other research on the limnetic fish community of Lake Washington is very important to those management agencies involved with the run of anadromous sockeye salmon to Lake Washington. In view of the declining primary productivity of Lake Washington, recent decline in the size of the run of sockeye to Lake Washington and urgent need (because of Indian fishing rights) for salmon enhancement activity throughout the state, it is necessary to establish whether the level of secondary production in Lake Washington is limiting the abundance of limnetic fish.

At this time there is conflicting evidence. Evidence which supports the hypothesis that food is not limiting to sockeye salmon is:

- 1) Lake Washington sockeye smolts are among the largest produced in the world.
- 2) Behavior observed in Lake Washington juvenile sockeye reflect that adequate rations can be achieved easily because (a) sockeye select the larger prey available, and exploit only a small component of the prey population; (b) sockeye feed briefly, and (c) sockeye fast during the early winter and resume active feeding during the late winter when conditions are less favorable for growth. This suggests that reduced growth rates observed during the winter reflect the effect of behavior which is only partly influenced by the level of available food.
- 3) Zooplankton cropping rates (day^{-1}) are 3-4 orders of magnitude less than the standing crop, even for the rare large forms that are heavily selected by sockeye.
- 4) The ratio of spawning escapement to resultant smolts is highly negatively correlated to flood discharge during incubation. Although this statistic confounded the effects of the lake, spawning and egg incubation environment, it suggests the importance of the Cedar River environment. It is noteworthy that midwinter floods were more frequent during 1968-1975 (five floods) than during 1960-1967 (one flood). Flow conditions in the Cedar River may have been an effect to the rapid change in the trophic state of Lake Washington following sewage diversion.
- 5) In the lake sampling from 1967 to present, there is no consistent trend in growth of juvenile sockeye.

There also exists evidence which supports the hypothesis that food is limiting.

The total lacustrine growth of sockeye can be estimated from adult scales, based upon conversion from the width of the lacustrine growth zone to body length. These data, based in part on the work of Isakkson (1970) show that there has been a significant decline in lacustrine growth since the 1950 brood year.

We need to re-evaluate Isakkson's thesis work. The sample sizes from the early brood years need to be increased. Also, the "false check" common in the lacustrine growth pattern on scales of sockeye in the 1960-1966 brood years must be reconciled with the timing of fry entry into the lake and actual growth trajectories. In particular, what is the ecological significance of the disappearance of the false check after the 1967 brood year? Samples collected by Dryfoos in the early 1960's are important because they were collected when the false check pattern on scales was common and will aid in determining its ecological significance.

The completion of this work will tell us if there has been a change in freshwater growth of sockeye resulting from trophic changes in Lake Washington. If these changes have occurred, the data on intraseasonal growth will provide clues to the interpretation of these changes. Most of the year-to-year variation in size of migrating smolts is due to variation in the time of entry of emergent fry to the lake, variation in the time when the decline of growth rates begins during the late fall and early winter, and variation in the time when the spring "plus growth" begins. In determining the component of environment that is responsible for the change in growth, one must consider the length of growing season as well as instantaneous rate.

Benthic and littoral fishes. For the benthic and littoral energy flow model, a detailed description of the parameters associated with the three species are under study (yellow perch, peamouth, and northern squawfish). The parameters are natural mortality rates, population structures, historical recruitments, individual growth, food consumption, and food utilization. During the past year all these areas were investigated using data previously collected, current data, and literature data and results. Following the development of analytical techniques for removing the selectivity of the sampling gear used, the gill net data yielded some interesting results.

As expected, the natural instantaneous mortality rates (\hat{z}) varied with the maximum age of each species. Table 1 shows the mortality rates, maximum ages, and population estimates of age 2 fish.

Table 1. Partial results of population analysis of benthic and littoral fish species from Lake Washington.

Species	Total Mortality	Maximum age (yrs.)	Population est. (age 2 and up)
Peamouth	1.4489	8	147,206
Yellow perch	0.2472	7	133,221
Northern squawfish	0.2711	21+	55,701

The population numbers were arrived at using the relative cohort strengths, natural mortality rates, a single cohort population estimate, and the corrected relative abundance ratio for age 2+ fish of 1.0: 0.496: 0.905 for peamouth, yellow perch, northern squawfish, respectively.

Both the peamouth and yellow perch cohorts are well represented by a geometric mortality function indicating fairly constant recruitment over time. The northern squawfish shows a 5-or 6-year cycle of recruitment peaks with a gradual build and decline for each peak. Further, the northern squawfish recruitment appears to be dropping from approximately 1.2 million in 1952 to a constant 20 or 30 thousand per year for the 1967 to 1971 period.

In April of 1974 research was begun on the life history and daily food ration of the yellow perch, Perca flavescens, in Lake Washington as part of the benthic and littoral fish modeling program of the Coniferous Forest Biome. The basic goal of the research is to provide estimates of the parameters necessary to describe the population dynamics and yearly production of the yellow perch population in Lake Washington. The study consists of four major areas:

- a) Age and growth
- b) Reproductive cycle and fecundity.
- c) Food habits and daily feeding patterns
- d) Estimation of the daily food ration of yellow perch

The description of the age and growth of the yellow perch can be subdivided into two areas: (1) estimation of growth in length at each age, and (2) description of seasonal and yearly individual growth patterns in length and weight. The growth in total length for each age was estimated from the back-calculation of length obtained from fish aged from scale readings. It was found that female fish obtain a significantly greater total length at each age. The information from the back-calculated lengths is being used in conjunction with estimates of monthly growth increments in length and weight and with weight-length relationships to describe the individual seasonal growth patterns of yellow perch.

Information from fecundity estimates of female yellow perch and a description of the reproductive cycle of both male and female yellow perch will be used to estimate the yearly recruitment to the yellow perch population. A calculated gonadal index and the calculated condition factor are being used to describe the reproductive cycles of male and female fish. Fecundity estimates of female yellow perch show that this species is a very fecund fish. Individual estimates ranged from a minimum of 16,000 eggs/fish to a maximum of 140,000 eggs/fish.

The major organisms which appear in the diet of the yellow perch are Neomysis awatchensis, fish (comprised mainly of the prickly sculpin and the threespine sticklebacks) and larvae and pupae from the family Chironomidae. Neomysis is the major food organism in terms of frequency of occurrence in all seasons except winter. Fish, on the other hand, are the major food organisms in terms of volume consumed in all seasons except spring.

The life history parameters of the yellow perch will be more than adequately described in the thesis now in preparation. The estimate of daily food ration will supply adequate information for the benthic and littoral fish model as now planned, but there is room for more work in this area. Ideally, the daily ration portion of the study could be expanded to include a study of the bio-energetic budgets of the major fish species covered by the modeling program. This would greatly increase the ability of the program to describe the major interactions between the species of fish concerned and their impact upon the other organisms in Lake Washington.

Research on the prickly sculpin in Lake Washington was begun in January, 1974. The major goals of the project included a description of: a) reproduction and fecundity, b) age and growth, c) food habits, d) distribution and e) population and biomass estimates.

Intensive sampling began in December, 1974, and continued through December 1975. A description of the reproductive cycle of the prickly sculpin includes sex ratio by month and depth category, gonadal index by sex, month and depth category, condition factor by sex and month, and fecundity estimates for female sculpins. Spawning has been found to take place between late April and early June in shallow water and slightly later in deeper regions of the lake. Fecundity estimates have ranged from 850 ova in an 87 mm female to 9,575 ova in a 190 mm female.

Calculations of age and growth are based on back-calculations of length at annulus formation from otolith readings and length-weight relationships. It was found that no significant difference exists between the growth of males and females.

Food habit analysis included frequency of occurrence, counts of number of organisms per stomach and total wet weight of all organisms in each category per stomach. Chironomids, fish and miscellaneous items are consistently important throughout the year. Mysids, Amphipods, Graulus and Trichopterans show seasonal trends of importance.

Prickly sculpins are found at all depths and in all major bottom habitats in Lake Washington. They are not uniformly distributed, however, but are found in aggregations of varying size and dimension. Pronounced distributional shifts have been observed, and example being a profound offshore migration of sculpins in July presumably associated with an elevated inshore bottom temperature.

The population estimate of prickly sculpins in Lake Washington was achieved through the integration of several sources of data. The age frequency catch curve supplied the instantaneous mortality rate and indices of relative abundance. A series of experiments were conducted to calculate the average area each trap fishes. Catch-per-unit-effort data was used in conjunction with the average area each trap fishes to yield the average density of sculpins that were fully selected by the gear. Utilizing the exponential model $N_t = N_0 e^{-zt}$ a preliminary mean population of prickly sculpins in Lake Washington was calculated to be 1.04×10^9 for all age classes combined. This estimate will be further subdivided by season and major bottom habitat.

Fish community structure. From the past information base of Lake Washington fish studies (largely supported by WCFB) we are determining the total fish community structure of Lake Washington. Included in this is information on abundance, growth, biomass, annual production, age structure, timing of spawning

and spawning habitat preference, seasonal and life history patterns of prey selection and feeding habitat preference, seasonal patterns of horizontal and vertical migration for the major fish species in Lake Washington (juvenile sockeye, threespine stickleback, longfin smelt, peamouth, yellow perch, squawfish, and prickly sculpin). Yellow bullheads, largemouth bass and black crappie are also common but occur in restricted habitats (weedy bogs and undeveloped shorelines) and their production is small compared to the production of the major fish species.

Preliminary results are:

- 1) The production of all other species is small compared to that of prickly sculpin. There are problems with the method used to estimate cottid abundance, but these are currently being worked out. Nevertheless, even the minimum estimate of cottid abundance is very large.
- 2) Populations that feed solely on benthos (peamouth and age 2 - age 3 squawfish) show long-term changes in growth that are sensitive to trophic changes in Lake Washington.
- 3) Threespine sticklebacks were only occasionally caught in limnetic sampling prior to 1969. Now they are as abundant as sockeye and smelt. This change most likely results from changes in littoral areas of the lake resulting from sewage diversion.
- 4) Size selective predation is common in all fish species.

This work has provided a very different perspective of the lake ecosystem, emphasizing the importance of the dynamics of benthos and littoral production to the lake fish community.

One must consider the fate of uncropped water column primary and secondary production, as well as the contribution of littoral vegetation and detritus. These sources may contribute more to fish production than water column secondary production that is cropped directly by fish.

These insights from holistic consideration of the fish community raises some intriguing questions. Why is planktonic secondary production not utilized more heavily by the fish community? If abundance of planktivores can be greatly increased through enhancement, what are the consequences to the total fish community? If enhancement policy is adopted, a large portion of secondary production should be shunted directly to planktivores, and will not be available to the benthos.

Papers published, accepted and submitted in 1976

Bartoo, N. G. Proportions of fish populations surfacing following rotenone treatments. Submitted to Progressive Fish Culturist.

Birch, P. B., D. E. Spyridakis, and R. S. Barnes. Sedimentation and its relationship to the trophic status of four lakes in the Lake Washington drainage. Submitted to Limnol. Oceanogr.

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5. SYNTHESIS ACTIVITIES JULY 1975 - AUGUST 1976

5.1. Publications

5.1.1. The Biome synthesis volume. Work commenced on the Biome synthesis volume in late 1974. Several draft outlines have been compiled and an outline was approved in 1975 by the IBP editorial committee chaired by Dr. W. Frank Blair. Since then, some activity has gone into compilation of a first draft. Dr. Dale

Johnson has taken over the major responsibility for the terrestrial productivity/nutrient cycling aspects, and Dr. Jim Long has been compiling material on plant distribution and succession in response to environmental gradients. Dr. Frieda Taub, working in conjunction with Drs. Richey and Wissmar, has compiled a first draft of the lake program synthesis and Dr. Frank Triska is working on the stream component. Watershed (terrestrial/aquatic interface) synthesis is moving along with Drs. Richey, Wissmar, and Riekerk compiling the material for Findley Lake. The Watershed 10 synthesis is being written by Drs. Sedell, Waring, and Cromack. A complete first draft of this volume will hopefully be completed by January 1977.

5.1.2. Other synthesis publications. A list of publications completed in the reporting period appears after each progress report in this section. In addition, a total list of Biome publications is presented in the Appendix.

5.2. Presentations at Meetings

Much of our initial synthesis effort has been directed toward presentations at meetings. Presentations were made at the Northwest Scientific Association meeting 15-17 March 1976 by Biome scientists. The AIBS meetings in New Orleans in June provided an opportunity for much of the synthesized material on terrestrial/aquatic interfaces to be presented. Richey, Wissmar, and Riekerk presented the initial synthesis for Findley Lake.

Many individuals presented papers at the AIBS meetings including a strong representation from the stream and lake programs. Other meetings at which Biome scientists presented papers were: IV International Congress of Entomology, Washington, D. C. August; Entomological Society of America, June 1976, Ventura, Calif.; American Society for Microbiology, May 1976, Atlantic City, New Jersey; Oregon Academy Sciences; Geological Society of America, Cordillerean Section; Western Forest Genetics Meeting, IUFRO Meeting, Oslo, Norway.

5.3. Use of Biome Material in Teaching and Management

As more and more Biome data are synthesized it is being incorporated into teaching programs. Much of the information on nutrient cycling is being incorporated into courses at the University of Washington. The soils curriculum has been particularly fortified by inclusion of courses on forest soil microbiology (Edmonds) and a specific course on nutrient cycling processes including interaction of terrestrial and aquatic ecosystems (Riekerk). The fisheries program at the University of Washington is also beginning to incorporate Biome data into courses.

Courses at Oregon State University have also been strengthened by Biome information and approaches. Dick Waring, Bill Emmingham, and Charles Grier have spearheaded these efforts. The short course program at OSU has also benefited from Biome input.

REPORTS OF BIOME INVESTIGATIONS

Biome Contributions *

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