Integrated Research In The Coniferous Forest Biome

R. H. Waring and R. L. Edmonds

Editors

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ii

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FOREWORD

Before embarking on the third year of field research, the Coniferous
Forest Biome presented an initial synthesis of its major programs at
the national meeting of the American Institute of Biological Sciences
held on 21 June 1973 in Amherst, Massachusetts.

Integration is still incomplete, but major strides have been made. The
coupling of processes and development of a system viewpoint has emerged.
This publication is thus a contribution of all Biome participants. It
is dedicated to Dr. Jerry F. Franklin, present director of ecosystem
programs for the National Science Foundation and past deputy director
of our Biome. It was through his effort, more than that of any other
one person, that the idea of integrating ecosystem research passed from
a vision to reality.

R. H. Waring

CONTENTS

STRUCTURE AND FUNCTION OF THE
CONIFEROUS FOREST BIOME ORGANIZATION[1]

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ABSTRACT

Integrating the research effort for an analysis of ecosystems requires a
strong but flexible organization. The Coniferous Forest Biome's research
groups reflect our changing perception of the major processes operating in
both terrestrial and aquatic systems. They also reflect changing goals as
our understanding increases and wider application and longer range predic-
tions are desired. In addition, there is a geographic perspective express-
ing the concentration of effort on different processes and systems across
the Biome.

The evolution of field research and modeling are intimately linked. Directors
and research committee chairmen take leading roles in designing and coordi-
nating the research with the aid of workshops to measure progress, modify
model structure, and identify critical data needs. Often a small task force
is appointed to address particular problems that require shifting resources
and personnel to meet a critical need. A key group of integrators has
developed, consisting of people who have an ecosystem perspective and train-
ing in more than one discipline. Their contributions to the program are
essential and their experience and talents make them capable of leading the
next generation of ecosystem studies.

INTRODUCTION

The kind of science that can be accomplished by large integrated research
differs from that which can be done by individuals or small groups. The
structure of large scientific programs, although more formal than smaller
ones, need not be less efficient. Integrated research, however, requires
a special structure and a special kind of people to accomplish its task.
This paper explains how integrated research has evolved in the Coniferous
Forest Biome.

The Coniferous Forest Biome was initiated in September 1970 as one of the
five programs in the Ecosystem Analysis Studies sponsored by the National
Science Foundation as part of the U.S./International Biological Program
effort. The general research objectives are to increase the understanding
of whole ecosystems with special emphasis on land-water interactions. To
keep track of details, help organize the research, and test the validity of
certain assumptions, we make use of computers and system modeling.

Our general research philosophy is that knowledge of the internal structure
and function of ecosystems comes from understanding basic processes that
operate across a biome. Coupling these processes into subsystems and link-
ing these into terrestrial and aquatic ecosystems provide a hierarchical

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[1]This is contribution no. 59 from the Coniferous Forest Biome.

means of understanding the internal structure and function of these complex systems. With this general philosophy, the structure for conducting the research and administering the program was developed.

STRUCTURE OF THE CONIFEROUS FOREST BIOME

Geographic Structure

As illustrated in a map of the Coniferous Forest Biome (Figure 1), the eco-systems under study encompass extremes from spruce forests on permafrost in Alaska and alluvial flat redwoods in California to steppe forests of pine

and oak in Arizona. From its initiation, the Biome has had liaison with agencies and institutions conducting research in these areas. As members of the advisory committee, representatives from throughout the West have counseled and helped to shape the program. There are two major areas where intensive studies are focused, the Lake Washington--Cedar River drainage in Washington, and the H. J. Andrews Forest in Oregon. Both sites are located in the Cascade Range. At the first site studies are concentrated on terrestrial photosynthesis, energy exchange, and mineral cycling; subalpine lake and adjacent forest land where lake and forest interaction are being investigated; and four lake ecosystems. At the second site watershed and small-stream studies are the focus of research. These geographical focuses are important because they permit the scientific exchange so necessary in integrating field and laboratory research to produce an ecosystem level of understanding.
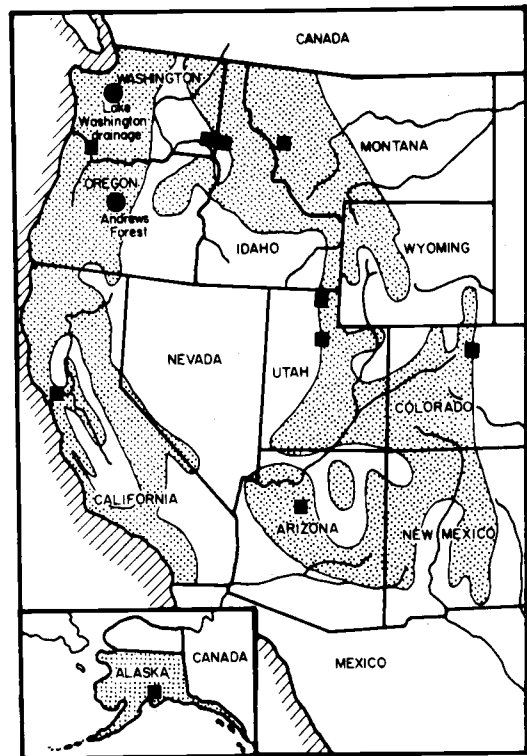
Figure 1. Geographical extent of the Coniferous Forest Biome.

Administrative Structure

The complete organizational chart, Figure 2, gives some hint as to the decisionmaking processes in the Biome. The Biome advisory board, made up of the Analysis of Ecosystems executive board and senior scientists from representative institutions, counsels the Biome director, Dr. Stanley Gessel. This advice is relayed to the executive directorate, where major policy decisions are made. The central office and technical committees provide additional support. The central office disperses funds for projects, travel, and workshops; publishes material; and serves as a clearinghouse for Biome activities announced through newsletters.

The technical committees initially coordinated efforts within the Biome so that methods were comparable. Recently, committees such as phenology and data management have turned their scope outward and now assist in intra-Biome coordination.

Figure 2. Coniferous Forest Biome organization chart.

The geographic structure of the Biome is also reflected in the listing of the site directors for Oregon, Washington, and the coordinating sites program. The scientific directorate, made up of representatives of the three divisions, terrestrial, aquatic, and ecosystem integration, reflects our perception of the major ecosystems and our desire to integrate the study of these systems. Deputy directors are responsible for activities w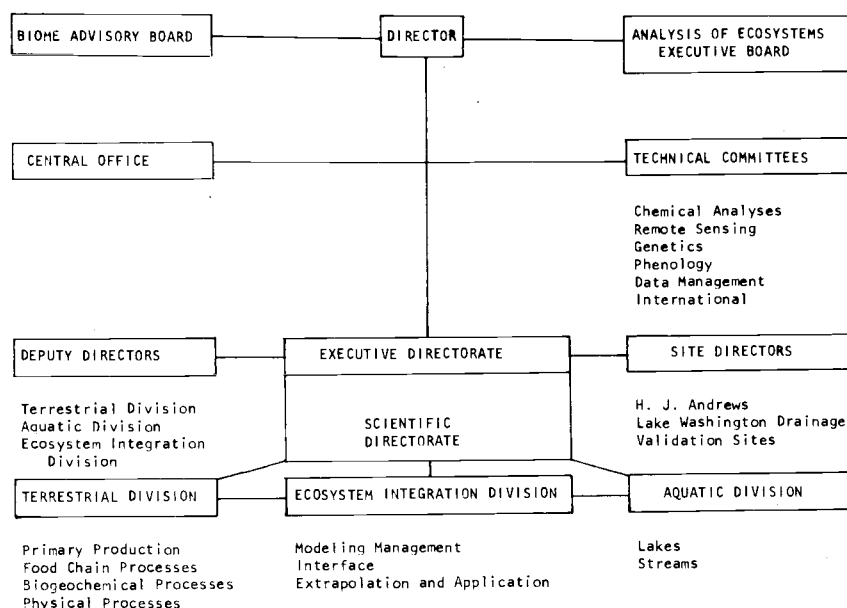ithin the three major scientific divisions. These are senior scientists who have been assigned full-time assistants to help them administer and coordinate their responsibilities. Site directors, deputy directors, and their assistants function with the Biome director as the executive directorate in making major policy and budgetary decisions.

Although some members of the executive directorate are involved directly in research, the Biome relies heavily on committee chairmen representing major subsystems within the whole program to direct and coordinate the research program.

FUNCTIONING OF THE BIOME

The Biome as a Complex System

As in any large organization, many decisions are delegated to people who have a broad perspective and the trust of the executive directorate. The development of this trust and appreciation for the total program came slowly, for the Biome is a complex system in itself. In fact, it has many properties in common with the objectives under study: it runs on energy and material purchased with money; its production, in terms of operational models or hard data, is perceived as a function of information as well as the level of funding; rewards are based on production and information furnished to other groups; the information is selective; the general needs of each group are shared; and the specific proposal for meeting these needs evolves within the subsystems.

Formulation of Specific Tasks

From counsel with the scientific directorate, a series of tasks are for-
mulated by the executive directorate and these serve as the focus for
overall synthesis and direction for a one- or two-year period. For
example, one of the eight tasks defined for 1973-1974 (Gessel 1972) was
to complete initial nutrient water and energy models for unit watersheds
and to begin their refinement with particular attention to simplifying
process models describing the behavior of large drainages and strongly
contrasting coniferous ecosystems across the Biome. Each task is scru-
tinized and responsibility for various components is assigned to appro-
priate site directors and committee and subcommittee chairmen.

Design of Specific Research Proposals

Initially, the Biome accepted proposals written by individual scientists.
These proposals were modified and assembled into categories more repre-
sentative of classical disciplines than Biome objectives. The committee
and subcommittee chairmen, at that early stage in our development, pre-
sided over the editing and coordination of these research proposals.
Those projects that were funded generally depended upon graduate students
for their implementation.

As the conceptual models for ecosystems developed, notable gaps in the
program were identified. Because of the almost full commitment to con-
tract research, there was little flexibility for correcting these defi-
ciencies until the following year. The acceptable approach for doing
research within an academic structure simply did not meet the objectives
of our integrated program.

Coordination and Synthesis through Research Committees

Two major changes have helped correct the deficiency and assure coordi-
nated field measurements and synthesis. One was a decision to entrust
committee and subcommittee chairmen with the additional responsibility
of managing and coordinating research proposals within their area of
responsibility. The second was the addition of full-time coordinator
positions with needed technical assistance to assure more complete inte-
gration and additional flexibility. In reality, this means individual
research proposals are now rare. Committee chairmen have available a
certain amount of resource to provide information for other groups and
aid in better understanding the internal operation of the particular
subsystem or area of responsibility.

Computer Simulation Workshops

Workshops are among the most valuable tools aiding assemblage of data
and identifying important assumptions. With the introduction of a
general computer processor developed by our central modeling group under
the direction of Scott Overton, we now have a system that permits us to
have an efficient and common means of studying subsystems and also to
couple these subsystems to one another at mixed resolutions of time.
This major breakthrough has increased the value of workshops even more
by permitting scientists working in the program or consultants from
other Biomes to join in explicitly questioning assumptions incorporated
in the models. As a result of these workshops we gain a better under-

standing of the subsystems, and are able to identify specific deficiencies
that can be corrected during the oncoming field season with resources
kept available for such needs.

Integration by Task Force

The process of integration requires a full commitment. Chemical analyses,
storage of data in the information bank, and modeling must all receive
attention to assure that the assembling of ecosystem models is accomplished
efficiently. Setting priorities is a function of the site director or a
modeling coordinator. The site directors, as members of the executive
directorate, have direct access to personnel throughout the Biome and,
by invitation, to specialists throughout the world. To accomplish one
of the integration tasks, such as the assemblage of a watershed ecosystem,
a site director forms his own team, usually consisting of some of the
committee and subcommittee chairmen. At each site the director has a
coordinating group representing various specialties and service groups
from the information bank and chemical laboratories. These usually meet
monthly to assess progress and resolve problems.

The task forces are usually divided into smaller groups with specific
responsibilities that can be accomplished within a time span of two or
three months. These latter groups meet at least weekly to assess their
own progress. The chairmen of these smaller task forces can change as
the synthesis proceeds. Often special reports are assembled and data
are forwarded to the information bank. At the monthly site coordinating
meetings, special workshops, or seminars, the results of this intensive
effort is shared with others. Eventually, material is assembled in
internal reports and presented to a wider audience at national and
international meetings.[2]

The Integrator

Often in this kind of large research program, time, not money, is limit-
ing. The time of dedicated, informed, and competent people is always
valuable, but in a large integrated research program using models, both
as goals and as an aid in directing the program, the contributions of
these people cannot be overstressed.

Probably the most valuable product of the International Biological Pro-
gram in the United States will not be the systems models that will aid

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[2]Following the success of the task force approach and the completion of
conceptual models in 1973, the Biome administrative structure has evolved
to recognize integrated research at the stand, watershed, land-water
interactions, aquatic, and regional levels. At each level an integrated
team was established. A full-time Biome researcher leads each team,
which includes a modeler and programer. This reorganization has eliminated
the formal role of site directors although coordination of research at
different institutions is still of concern.

6

in making decisions concerning land and water management, but the train-
ing of people able to bridge the communication gap between disciplines
and institutions. Such people chair the committees and subcommittees;
coordinate the field programs at the intensive sites; and grapple with
biology, mathematics, and personalities in serving the information banks
and central laboratories of the Biomes. All exhibit special traits,
which include competence in more than one discipline, interest in and
dedication to the synthesis of knowledge at a level higher than their
own specialties, and a willingness to sacrifice their time and talents
to such a joint effort.

Only these kinds of people, fully committed, if not fully funded by the
Biome, make the synthesis possible. It is an honor, as well as a neces-
sity, to have such talented people. The extent of their contributions
to ecosystem studies should be formally recognized.

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A SYSTEMATIC FRAMEWORK FOR MODELING AND STUDYING THE PHYSIOLOGY OF A CONIFEROUS FOREST ECOSYSTEM[1]

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ABSTRACT

A coupled set of models of carbon, water, and mineral element processes is being developed as part of the Coniferous Forest Biome terrestrial research program. In this paper we present the rationale and objectives, a summary description of the structure and method of implementation, and a statement of progress as of November 1973. Objectives of the modeling include presentation of hypotheses concerning system behavior, research coordination, identification of information voids, and study of system response to perturbations. Perturbations of interest include climatic change, defoliation, fire, thinning, fertilization, and irrigation. Responses of interest include growth of trees, runoff volume and pattern, and nutrient concentrations in the runoff.

Implementation is by means of a coupled set of nonlinear difference equations, about 80 in all. The equations are divided into six groups of processes (modules): carbon, water, cationic elements except H^+, H^+, anionic elements, and HCO_3^-. Documentation accompanies conceptualization and precedes programing. Both documentation and code use a consistent notation reflecting what we believe to be structure inherent in the natural system. The notation permits identification of state variables, and parameters. Mnemonics are not used. Extensive written description of each variable, function, and parameter is included in the documentation. Only minimal written "comments" appear in the code.

Model parameters for processes that have not been studied extensively are calculated from annual budgets of transfer and accumulation of carbon, water, and the four "nutrient" element groups. Material balance and electrical neutrality are principles assumed in calculating these budgets. Function forms for processes that are not well understood are usually postulated to be linear and donor-controlled although they often include effects of driving variables such as air or litter temperature. Ultimately we wish each process to be described by a function of comparable complexity and realism. Current information precludes this and we feel that the most important task at present is identification of processes and construction of an adequate framework for analysis of ecosystem response.

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[1]This is contribution no. 60 from the Coniferous Forest Biome.

INTRODUCTION

Early in their history each of the US/IBP Ecosystem Analysis Studies projects decided to develop some sort of overall ecosystem model. Some later abandoned the project as unrealistic, others pursued the goal with little success or created models too large and complex to be of general use. The IBP Grasslands model, for example, is difficult to comprehend or modify because of the lack of any consistent notational scheme, particularly one reflecting the structure inherent in the model and the real system.

The Coniferous Forest Biome was a latecomer to this endeavor and, although desiring an ecosystem model of coniferous forests, was determined not to produce a white elephant. In this effort we developed a series of objectives and a sequence of tasks. We agreed to model the ecosystem as a set of coupled difference equations describing flow of materials between compartments representing storages in various substrates, positions, and species groups. The methodology has been applied widely to ecological problems. It is described by Reichle et al. (1974) and Sollins et al. (1974) and is an outgrowth of earlier work by Olson (1965) and Odum (1971).

As our first task we attempted to list the important processes and their interactions. From such a table we then constructed box-and-arrow diagrams to aid communication and research design. Next we used these diagrams to display the properties of the ecosystems under study. Thus, annual budgets of accumulation and transfer among different components of the system were used to locate data voids and inconsistencies and to document our progress in data synthesis. Many unmeasured transfers were calculated by assuming material balance. From the budget data and information on factors affecting rates of processes we began to construct dynamic simulation models that would enable us both to study the ecosystems further and to solve real-life problems related to their behavior.

Profiting by the experience of the other Biomes, we recognized the need to impose constraints on the development of our ecosystem model. First, our objectives had to be realistically narrowed. We chose as outputs of primary interest the growth of primary producers, water runoff from the ecosystem, and nutrient loss in the runoff. The susceptibilities of the ecosystem to fire and to insect outbreaks were desired but not required model products.

Second, we felt that we had to define beforehand the perturbations that we wanted to study. We chose fertilization, defoliation, fire, thinning (including clearcut), and climatic changes. We recognized that the model structure would reflect the perturbations and outputs we had chosen, and that the structure might well be inappropriate for other studies. We realized that the degree of detail included in each part of the model would be a tacit statement of our estimate of the importance of that part. We agreed that we could not omit processes felt to be important simply because they were difficult to measure or model.

Third, we recognized that the model had to be operational before the Biome project ended and in a format understandable by ecologists if it

were to serve its first two objectives of increasing communication and improving research design and coordination. To accomplish the last objective of increasing our understanding of the functioning of the system, the model had to be used in a large variety of situations and, where possible, compared with the behavior of real systems.

Fourth, we recognized that our modeling approach restricted us to areas of land that could be assumed homogeneous with respect to their soils, topography, and climate, and with respect to the species composition and age of the vegetation. We expected to be able to model spatial heterogeneity by operating in parallel models of hydrologic or vegetational subunits. There were still, however, many problems that could not be studied with a whole-system compartment model and we realized that alternative modeling approaches were necessary. Detailed models of individual processes were of interest to Biome scientists and are being developed (K. L. Reed and co-workers, MS in prep., Hatheway et al. 1972, Strand 1974). Study of spatial variation within a stand and long-term processes of species succession seemed more appropriately considered in a "tree-by-tree" model in which empirical equations are used to predict establishment, growth, and mortality. Such a model is also under development (K. L. Reed et al., MS in prep.).

Finally, all of these constraints and objectives demanded that the model be kept simple, that it be constructed modularly, that the couplings between modules be defined early in the modeling, and that a consistent modeling paradigm be adopted for the duration of the project.

This report was written at the point at which we had defined the outputs, adopted a paradigm, constructed the box-and-arrow diagrams, and determined most of the budgets. We are in the process of testing or constructing the various modules. The first two objectives have been accomplished; however, we require at least another year before we can assess our ability to meet the third objective of predicting patterns of ecosystem response.

OVERALL MODEL STRUCTURE

Our ecosystem model is conceived as a hierarchical structure in which the first level consists of six modules for different substances. These are carbon, water, and four groups of other elements, namely, H^+ (hydrogen ions), other cationic elements, HCO_3^- (bicarbonate ions), and other anionic elements (Figure 1). For lack of a better term these last four will be referred to as the nutrient modules although neither H^+ nor HCO_3^- is nutritionally significant.

Material balance is maintained strictly in all except the H^+ and HCO_3^- modules (see below). Driving variables of the model consist of air temperature, precipitation, dew point, incident shortwave radiation, day length, and concentrations of the four nutrient groups in precipitation. Soil and litter moisture and temperature are state variables calculated dynamically. Transfers are calculated at intervals of one day for the water module and one week for the carbon module. Nutrient transfers are computed at daily or weekly intervals depending on whether they are calculated as part of a water or a carbon transfer, respectively.
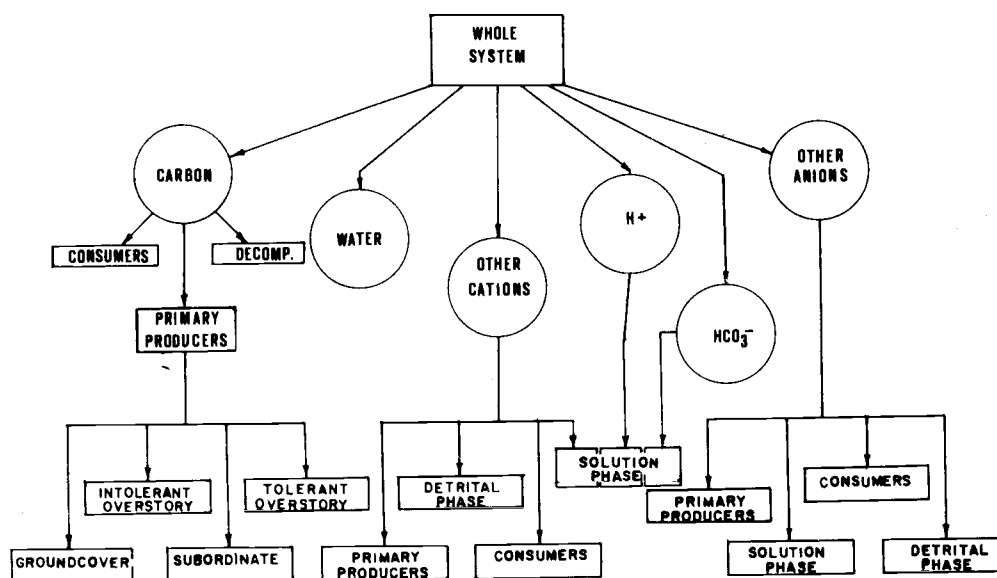
Figure 1. Hierarchical arrangement of modules composing the coupled carbon-water-nutrient model.

Although this report is not the appropriate place (nor are we ready) to present the model equations in their entirety, we do wish to indicate the range of realism encompassed in our "physiological" approach.

In cases where the process is not well studied or definitive data are lacking, linear donor control (perhaps modified by some function of a driving variable) is all we feel justified in using. For example, decomposition of dead roots is expressed as:

$$F_{62,21} = B_{38}G_{50}X_{62}$$

where $F_{62,21}$ refers to the transfer from the dead-root compartment X_{62} to the rooting zone organic matter compartment, X_{21}; B_{38} is a parameter obtained by curve-fitting; G_{50} is a function of rooting zone soil temperature and rooting zone moisture.

The expression for net daytime photosynthesis is more complex and is based on simple assumptions regarding light filtering through a canopy and the photosynthetic response of individual leaves to temperature, light, and foliage resistance (see Sollins et al. 1974). The equation has been validated by comparison with a detailed mechanistic model developed from basic gas exchange data (K. L. Reed et al., MS submitted for publ.). For net weekly daytime photosynthesis of current foliage we use:

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

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

Definitions: Z_3 is day length (fraction of the day); G_2 is the air temperature effect on photosynthesis; Z_2 is air temperature (°C); B_7 is a factor such that $G_2 = 1$ for $Z_2 = 22°C$; X_2 is new (current year) foliage biomass (t carbon ha^{-1}); X_3 is old foliage biomass; B_6 is the light extinction coefficient (ha t^{-1}); G_{26} is current foliage resistance averaged over a week (sec cm^{-1}); B_4 is the maximum rate at some temperature, day length, foliage resistance, and foliage biomass; B_5 is the light intensity at which photosynthesis is one-half the maximum rate at those conditions; and Z_4 is incident shortwave radiation (ly min^{-1}) averaged for the week.

The photosynthesis expression exemplifies the sort of function we would like to, but obviously cannot, develop for each transfer. It is, we claim, physiologically reasonable, testable in the field (at least part by part), and includes (except for the nutrient effect, which is not shown) all factors expected to be of importance. Our modeling approach permits us to substitute easily more realistic expressions (e.g., regarding the effect of foliage resistance) as they become available. We feel the more pressing problem is development of an adequate structure that includes all the processes and interactions needed to predict the selected outputs.

MODELING PARADIGM

The modeling paradigm we adopted was developed by Overton (1972) based on earlier work by Klir (1969, 1972). This essentially provided a language, called FLEX, for describing the models.

In the FLEX modeling paradigm, flow expressions are calculated from state variable and driving variable values and values of intermediate functions (sometimes called dummy variables), which in FLEX are called G functions. In order to avoid problems with the sequence of computation, flow expressions are not permitted to depend on other flow expressions. An intermediate G function instead must be created and both flows must be calculated from it.

These rules and terminology have proved extremely useful in describing the couplings between the modules. In the simplest case a G or F function in one module may contain reference to a state variable of another module.

For example, stand conductance, a G function in the water model, requires knowledge of leaf biomass, a state variable of the carbon module (Figure 2).

Another possible coupling occurs when an F or G function in one module depends on the value of a G function in another module. Consider, for example, a set of couplings between the carbon and water modules involving foliage biomass, soil moisture content, and a G function, foliage resistance (see Figure 2). (This example is a simplification of the actual model.) Photosynthesis, respiration, and transpiration all depend on foliage resistance which has been made a G function, for convenience,

Figure 2. Example of couplings between the carbon and water modules.

within the water module. Foliage resistance is a function of another G function, plant moisture stress, which is calculated from soil temperature and moisture content of the soil. Two of these processes (photosynthesis and respiration) also depend on foliage biomass through an implicit relationship between foliage biomass and surface area. Interception of precipitation is also dependent on foliage area as is light penetration through the canopy. Both of these factors affect moisture content and temperature of the soil. Study of these circular causal chains is an exciting part of ecosystem analysis. Because of them, perturbations often result in the unexpected. Much of the inherent stability of an ecological system may have its roots in such a linked chain of processes and structural units.

STRUCTURE OF THE CARBON MODULE

The carbon module divides logically into three parts (Figure 3), primary production, consumers, and decomposition. The decomposition part includes litter, dead roots, standing deadwood, soil organic matter, and the associated free-living organisms. The consumer section is at present only a single compartment but should be adequate for initial studies of effects of consumers on primary producers. We will later substitute for this one compartment a more complex food chain model (Strand 1974) in order to study effects of changes in the primary producer module on the consumers. We also are considering duplicating the primary producer compartments several times and operating the modules in parallel to study interactions among different vegetation components. For example, Sollins et al. (1974) used parallel models of shade-intolerant overstory species, shade-tolerant overstory species, understory species, and ground-cover to study competition between the species groups during and after various perturbations.

The arrangement of the compartments within the primary producer carbon model builds on lessons learned in a previous study by Sollins et al. (1974). They divided the vegetation into three parts, a photosynthetic layer, an uptake layer, and a massive but relatively inert layer of supporting and conducting tissue. Ideally each of these layers would be divided into structural and labile components. The structural would include protein, cellulose, and lignin while the labile would include sugars, starch, and amino acids. The labile pool associated with the foliage is very small and transitory, however, and, in the current version of the model, we do not allow for carbohydrate storage in it. On the other hand, because of lack of data, the labile pool associated with the fine roots has been included in the larger pool associated with stems, branches, and large roots.
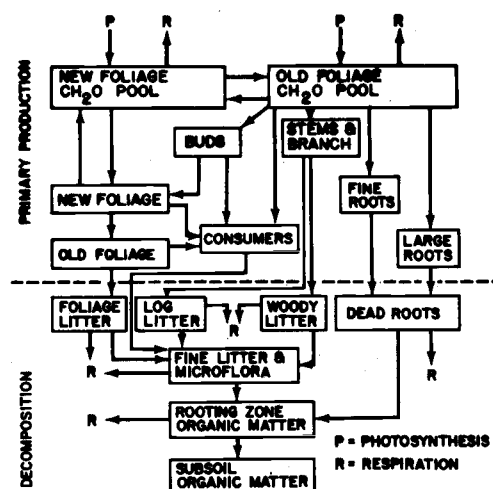

Figure 3. Storages and transfers of the carbon module. All couplings with other modules and intermediate variables have been omitted for simplicity.

Another feature of this model and its predecessor is the presence of a bud compartment that limits the possible leaf production during a growing season (see Sollins et al. 1974). In addition, fine roots include the mycorrhizae associated with them and standing deadwood is included in the woody litter compartment.

The structure of the decomposition module is routine (see, for example, Sollins et al. 1974). A perhaps novel feature is the fine litter compartment. This compartment includes most of the free-living organisms of the litter layer and includes all material that is readily decomposable. Thus frass goes directly into the fine litter compartment while logs and even leaf litter must first undergo initial processing before being available for mineralization. Immediately beneath the litter is a layer we call the "rooting zone." The rooting zone typically corresponds to the A or A1 horizon but is defined as that region of the mineral soil from which uptake occurs and in which most fine roots are found. We realize the name is misleading since we allow, even in the model, for uptake by fine roots directly from the litter solution; however, we lack a better term.

Important couplings between the carbon module and others include the dependence of photosynthesis and respiration on foliage resistance as well as foliar anion and cation content, and dependence of root death on rooting zone moisture. Rooting zone moisture is also used in calculating respiration and decomposition of rooting zone organic matter and dead roots. Litter and rooting zone temperature are used to calculate decomposition and respiration rates as well as plant moisture stress (and thus foliage resistance) and the timing of budbreak.

Variables against which the behavior of the carbon module will be compared (calibration variables) are growth of woody tissues (stems and branches) and seasonal patterns of foliage biomass, forest floor respiration, and fine root biomass.

STRUCTURE OF THE WATER MODULE

The water module (Figure 4) is based on one developed to predict water outflow from a watershed of the H. J. Andrews Experimental Forest by W. S. Overton and C. White (MS in prep.). The philosophy of this model is unusual compared with previous hydrologic models (e.g., Huff 1968, Brown et al. 1972, Goldstein and Mankin 1972) in that it attempts a more realistic representation of biological phenomena such as interception and transpiration.

We are modifying the model to include even more biology and to be more suitable for coupling with the carbon and the various nutrient modules. For example, a litter moisture compartment, omitted from Overton and White's model because of its nearly inconsequential storage capacity, is included here because of the dependence of litter decomposition on litter moisture content and because various functions in the nutrient modules

Figure 4. Storages and transfers of the water module. Couplings with other modules and intermediate variables have been omitted.

require this information (see below). In their model, Overton and White separated evaporation of intercepted water from transpiration but included evaporation from the soil and litter in the transpiration flux. Evaporation from soil and litter would be negligible in a closed stand but, following clearcut or even defoliation, it could become an important process. In our model we separate it from transpiration and evaporation from the canopy even though data are presently lacking, because we feel the model cannot possibly simulate effects of these perturbations without it. The transpiration function is a modified Penman equation (Montieth 1973) in which transpiration is an explicit function of vapor pressure deficit, canopy resistance, windspeed, net radiation, and several other variables. Canopy resistance is in turn calculated from leaf area, soil temperature, and rooting zone moisture using relations proposed by Sucoff (1972) and Running (1973).

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

Calibration variables include streamflow, soil moisture, and evapotranspiration patterns through the year. Evapotranspiration is being calcu-
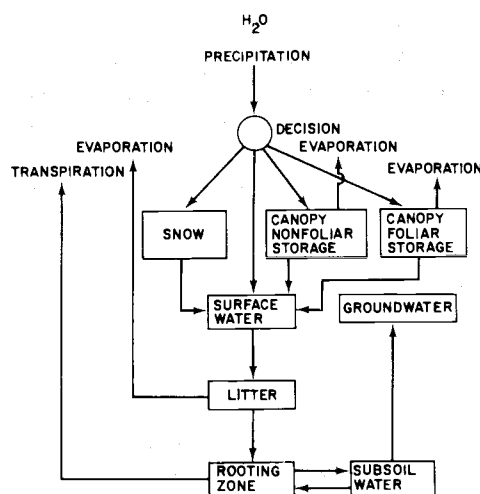
lated independently for the site on the H. J. Andrews Experimental Forest based on energy balance considerations that do not depend on measurements of dewpoint temperature. This may provide an additional check on the behavior of the water module.

In addition, the weighing lysimeter tree (Fritschen 1972) will provide data on the change in weight of a representative portion of a stand. Since CO_2 fixation is negligible any changes must be due to changes in the water content of the system, thus providing a continuous record of evapotranspiration against which to check the model.

STRUCTURE OF THE NUTRIENT MODULES

The nutrient modules (Figures 5 and 6) are based on the separation of the "nutrient" elements into four groups: H^+, other cations, HCO_3^-,
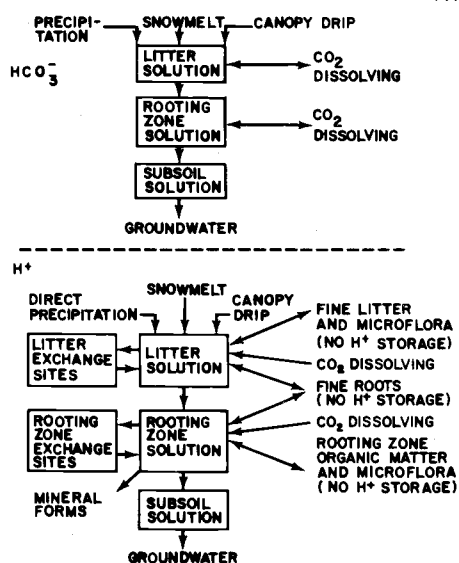
Figure 5. Storages and transfers of the H^+ and HCO_3^- modules. Couplings have been omitted.
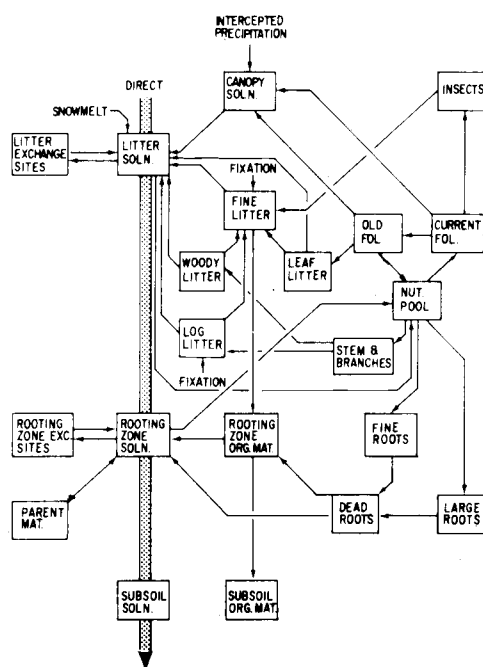
Figure 6. Storages and transfers of the cation and anion modules (other than H^+ and HCO_3^-). Couplings have been omitted.

and other anions. A major assumption, implicit in the distinction between anions and cations, is that most nutrient relations involve ionic forms and that differences in charge are more important than differences in chemical composition (see McColl and Cole 1968). This reflects the perturbations and responses that interest us. Although unpleasant to admit, we do not know enough about the physiology of trees to postulate the mechanisms through which concentrations of specific nutrients in the trees affect growth (carbon transfers) except to say that increased foliar nutrient concentrations cause an increase in photosynthetic efficiency and thus leaf area. We are thus seriously constrained in our ability to predict, for example, effects of fertilization on growth. We can, however, study the overall mineral cycle, the role of the vegetation therein, and the various mechanisms that might lead to increased nutrient loss in the groundwater. The vegetation at present is included primarily for completeness and is viewed as a pump (or perhaps a waterwheel), which draws nutrients out of the rooting zone and then allows

them to return at some later time in the form of litterfall and root death. Because we have included foliar nutrient compartments as well as an overall plant nutrient pool, however, we should be able to predict changes in these compartments under different perturbations and perhaps infer relationships between these changes and corresponding changes in carbohydrate production and wood formation. Later, as we develop hypotheses regarding nutritional control of growth, we can incorporate these easily into our model.

The transfers of the nutrient modules are for the most part of two types solution phase and solid phase (see Cole and Ballard 1968). Four solution compartments and the attendant transfers compose the solution phase modules. Each solution compartment corresponds to a compartment of the water module, and any transfer of water, which of course occurs only between, into, or out of solution compartments, also results in the transfer of dissolved nutrients. Every rule has exceptions; ours is that uptake by roots does not follow the flow of water in the transpiration stream. We assume that uptake is primarily an active process dependent on fine root biomass, nutrient concentration, temperature, and perhaps nutritional deficits in the plants. Rooting zone moisture content, however, is assumed to limit uptake as the soil dries. Many other transfers also occur as flows (that are not related to water movement) either into or out of a solution compartment. For example, uptake by microorganisms is assumed to occur only from the various solution compartments.

The second group of processes consists of solid phase transfers in which nutrients accompany the transfer of carbon. Each storage compartment in the carbon module has a corresponding storage in each of the nutrient modules. Many carbon transfers such as litterfall, foliage consumption by insects, incorporation of fine litter into rooting zone organic matter, and root death have corresponding nutrient transfers. Mostly for convenience, nutrients are assumed to be incorporated into stemwood and branchwood in proportion to the incorporation of carbon.

The HCO_3^- and H^+ modules (Figure 6) require special explanation. HCO_3^- is separated from other anions because one of the hypotheses we most wish to study is that HCO_3^- and H^+ produced by dissociation of dissolved CO_2 may play a crucial role in determing nutrient availability in the rooting zone solution (McColl and Cole 1968). (Uptake by plants and loss in groundwater are assumed to be directly related to nutrient concentrations in the rooting zone.) The primary source of this CO_2 is of course respiration of roots and rooting zone organisms, thus providing another interesting example of a circular chain of events most appropriately studied with a whole-ecosystem model. To elaborate, we hypothesize that rates of CO_2 production affect nutrient availability which affects uptake. Uptake affects growth and thus litter production and root activity which in turn affect CO_2 production.

Hydrogen ion is separated from other cations because of its importance in determining ionic exchange equilibria and thus nutrient availability. It is also an easily monitored variable that we may be able to use as a calibration variable. Another of the objectives of our nutrient cycle modeling is to examine the H^+ balance of the entire soil-root-decomposition complex. We wish to determine the relative magnitude of the various processes resulting in production and absorption of H^+ ions. Only by

considering H^+ and HCO_3^- separately from other ions can we evaluate the importance of the bicarbonate equilibrium in controlling pH. Likewise the role of cation exchange processes in the litter and soil and the importance of H^+ in precipitation can be judged.

We are not at present modeling the aluminum hydrolysis reactions:

$$Al\ (H_2O)_6^{3+} \rightleftarrows Al\ (OH)_2\ (H_2O)_4^+ + 2H^+$$
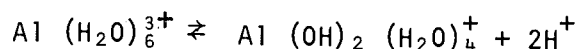
If we cannot achieve ionic balance when a yearly H^+ budget is calculated, that is, we cannot account for the majority of the H^+ production or loss, then we may be forced to consider this or other processes.

In our initial version of the model we make extensive use of the concept of balance of charge and include a set of processes (discussed below) that previously have been ignored in forest soil solution modeling. Balance of charge, like material balance, allows inferences about processes not easily measured, particularly H^+ processes. For example, concentrations of "other" (non-H^+) cations in the solution compartments typically exceed concentrations of "other" (non-HCO_3^-) anions. We expect that uptake of these cations by roots and microorganisms typically will exceed the corresponding uptake of non-HCO_3^- anions; however, charge balance must be maintained in all compartments. We assume that H^+ is released to do so and that HCO_3^- release and uptake do not occur. Preliminary calculations suggest that the release of H^+ from roots and microorganisms may be comparable to exchange processes in transferring H^+ and may exceed by several orders of magnitude the importance of waterflow in transferring H^+.

In contrast to our treatment of cations and anions, we have not maintained material balance in the H^+ and HCO_3^- modules in that we do not follow these substances through the organic matter pathways. This is because, as we stated above, we have no indication that they are nutritionally important for the vegetation and consumers. We are primarily interested in the role of these ions in the soil and litter. Uptake and return of H^+ and HCO_3^- through the vegetation is probably inconsequential compared with the production of H^+ by the dissociation of water in the litter and soil solutions (plus any input in the precipitation). Likewise, uptake and return of HCO_3^- through the vegetation are apparently inconsequential in comparison with dissociation of H_2CO_3 (plus any input in the precipitation). With respect to the carbon cycle material balance, we feel that consideration of interchanges between the carbon and the HCO_3^- cycle is not very important.

Couplings between the nutrient modules and the carbon and water modules are of course many and complex. Many transfers, as discussed above, are assumed to be directly proportional to transfers of carbon or water.

Other couplings include dependence of uptake by roots on fine root biomass, a relation between exchange capacity and organic matter content, and the effect of rooting zone CO_2 production on input of HCO_3^- to the rooting zone solution. This last process may be affected by rooting zone water content in two ways: (1) The dissociation of H_2CO_3 is modeled as an equilibrium reaction and is thus dependent on HCO_3^- concentration, which is affected by water content. (2) Rooting zone water content affects the volume of the rooting zone atmosphere and thus the partial pressure of CO_2 in the rooting zone atmosphere.

Calibration variables for the nutrient modules include pH, conductivity, and individual ion concentrations in each of the solution compartments, and annual nutrient accumulation in the vegetation. We will also calculate a ratio between optimum and simulated values of foliar nutrient concentration and compare this with observations of apparent nutrient deficiency under various conditions of perturbation. This and the relatively insensitive calibration variable of nutrient accumulation measured annually for the vegetation as a whole unfortunately will be our only vegetation calibration variables.

DISCUSSION

To our knowledge this is the first time a nutrient model has been designed as part of a hierarchical structure in which it is coupled to water and carbon models. The soil part of the cation and anion modules is similar to that constructed by Ulrich et al. (1973) in which they considered uptake and exchange (as well as physical binding of phosphorus anions), but they did not, in the published version, attempt a coupling with a working water model. Likewise the ELM model of the Grasslands Biome (G. S. Innis and co-workers, personal communication) includes various couplings between carbon, nutrients, and water, but they did not attempt systematic modeling of the complete cycles of anything other than carbon.

We are very much interested in developing efficient schemes for constructing, documenting, and testing complex models. We feel it is most efficient to study modules individually before attempting coupling. This process of uncoupling prevents changes in the module of interest from affecting variables in the other modules. We use tabulated (often average) values of the external variables and avoid rerunning modules that are not changing. Not only are computation costs decreased but the behavior of the module of interest is made easier to interpret.

As of November 1973 the primary producer and decomposition parts of the carbon module and the water module had been tested and studied individually under a variety of conditions. As is evident in this report, our conceptualization of the overall model structure is about complete (although constantly changing) and coding of the remaining parts has begun. Documentation is accompanying the conceptualization and construction. This documentation, admittedly FLEX oriented, is available upon request.

ACKNOWLEDGMENTS

This report is based to a great extent on the unpublished ideas and data of many persons within the Coniferous Forest Biome, the Eastern Deciduous Forest Biome, and the other Biome programs. To the extent that it proves correct, it is a statement of the combined knowledge of these persons with respect to the construction of a material balance, compartment-oriented model of a forested landscape. To the extent that it proves incorrect or impractical, it reflects the biases, misconceptions, and naiveté of the authors.

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NUTRIENT CYCLING IN 37- AND 450-YEAR-OLD DOUGLAS-FIR ECOSYSTEMS[1]

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ABSTRACT

Biomass and nitrogen, phosphorus, potassium, and calcium distribution, and biogeochemical and stand nitrogen, phosphorus, potassium, and calcium budgets were determined for 37- and 450-year-old *Pseudotsuga menziesii* (Mirb.) Franco stands in the U.S. Pacific Northwest. Biomass of the 450-year-old stand is greater, but annual growth is less than that of the 37-year-old stand. About 50% of the annual growth and over 50% of the nutrient uptake and return in the 450-year-old stand occurs in subordinate vegetation compared with less than 15% in the 37-year-old stand. Chemical differences in soil parent material between the two stands are reflected in both the biogeochemical and stand nutrient cycles.

INTRODUCTION

Coniferous forests of the U.S. Pacific Northwest are among the most productive forests in the world. In the Douglas-fir region, for example, stands often reach 1000 metric tons ha^{-1} of standing biomass in 100 years. Because nutrients are involved in almost all ecosystem processes, studies of nutrient movement and accumulation yield a great deal of information about factors affecting productivity of these forests. Further, studies of nutrient cycling contribute much to understanding overall behavior of coniferous forest ecosystems.

In general terms, the objectives of nutrient cycling research of the Coniferous Forest Biome are: (1) to study the role of nutrients in ecosystem function; (2) to develop conceptual and simulation models representing our understanding of nutrient cycling; and (3) to use those models both to extend our understanding of ecosystems and to evaluate the effects of various perturbations on ecosystem processes and entire ecosystems.

This paper is intended as an overview of current nutrient cycling research in the Coniferous Forest Biome. The discussion here emphasizes research directed toward meeting the first two of the above objectives with the research reported by comparing nutrient cycling between two intensive research sites. A comparison of nutrient cycling rates and processes between the 37- and 450-year-old stands on these sites should increase our understanding of some of the broader aspects of ecosystem behavior.

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[1]This is contribution no. 61 from the Coniferous Forest Biome.

RESEARCH AREAS

Thompson Research Center, Washington

The Allan E. Thompson Research Center is a research area developed for
study of nutrient cycling in second-growth Douglas-fir stands. It is
located about 64 km southeast of Seattle, Washington, at an elevation of
215 m in the foothills of the Washington Cascades. A full description
of the geology, soils, vegetation, and climate is given by Cole and Gessel
(1968).

The study site is located on a glacial outwash terrace along the Cedar
River. This outwash terrace was formed during the recessing of the Puget
lobe of the Fraser ice sheet about 12,000 years ago.

The soil underlying the research plot described in this paper is classi-
fied as a Typic Haplorthod (U.S. Department of Agriculture 1960, 1972)
and is mapped as Everett gravelly sand loam. This soil contains less
than 5% silt plus clay and normally contains gravel amounting to 50%-80%
of the soil volume. The forest floor is classified as a duff-mull
(Hoover and Lunt 1952) and ranges from 1 cm to 3 cm thick. This forest
floor represents the accumulation since 1931 when the present stand was
established following logging (around 1915) and repeated fires.

The present overstory vegetation is a planted stand of Douglas-fir
(*Pseudotsuga menziesii* [Mirb.] Franco) which was established about 1931.
Currently, the trees average about 19 m high with a crown density of
about 85%.

The principal understory species are salal (*Gaultheria shallon* Pursh.),
Oregon grape (*Berberis nervosa* [Pursh] Nutt.), red huckleberry (*Vaccinium
parvifolium* Smith), and twinflower (*Linnaea borealis* L. ssp. *americana*
[Forbes] Rehder). Various mosses are the principal understory vegetation
beneath the denser portions of the canopy.

The climate is typical of foothill conditions in the Puget Sound basin.
Temperatures have ranged from -18°C to 38°C, but these extremes are sel-
dom reached. The average temperature for July is 16.7°C and for January
is 2.8°C. The average annual precipitation is 136 cm, almost all falling
as rain. Precipitation rates are generally less than 0.25 cm hr^{-1} and
over 70% of precipitation falls between October and March.

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

Watershed 10 is a 10.24-ha watershed located in the western Cascade
Range about 70 km east of Eugene, Oregon. Elevations on the watershed
range from 430 m at the stream gaging station to about 670 m at the
highest point. Slopes on the watershed average about 45% but frequently
exceed 100%.

The study site is located in an area underlain by volcanic tuff and
breccia. Soils of the watershed are derived from these materials.
Soils of the watershed are classified as Typic Dystrochrepts (Inceptisols;
U.S. Department of Agriculture, 1960, 1972) and range from gravelly,

silty clay loam to very gravelly clay loam. The <2-mm fraction of these soils ranges from 20% to 50% clay and contains gravel amounting to 30%-50% of the soil volume. The forest floor ranges from 3 to 5 cm thick and is classified as a duff-mull (Hoover and Lunt 1952).

The present overstory vegetation is dominated by a 60- to 80-m-tall, 450-year-old stand of Douglas-fir (*Pseudotsuga menziesii*) containing small islands of younger age classes. Distribution of understory vegetation reflects topography and slope-aspect on this watershed. Dry ridgetops and south-facing slopes have an understory composed primarily of chinkapin (*Castanopsis chrysophylla*), Pacific rhododendron (*Rhododendron macrophyllum*), and salal. More mesic parts of the watershed support an understory of vine maple (*Acer circinatum*), rhododendron, and Oregon grape, with a well developed intermediate canopy of *Tsuga heterophylla*. Subordinate vegetation of the moist areas along the stream and on north-facing slopes is primarily vine maple and sword fern (*Polystichum munitum*).

The climate of watershed 10 is typical for the western Oregon Cascades. Average annual precipitation is 230 mm per year with over 75% of the precipitation falling as rain between October and March. Snow accumulations on the watershed are not uncommon, but seldom last more than two weeks. Based on two years' data, the average daytime temperature for July is 21°C and for January is 0°C. Observed extremes have ranged from a high of 41°C in August to a low of -20°C in December.

METHODS

Mapping of Watershed 10

A 25-m by 25-m grid system, corrected to horizontal distance, was established on watershed 10. All mapping used this grid system for reference. Soils were mapped on the basis of depth, stone and gravel content, and water storage in the upper 100 cm of profile. Subordinate vegetation was mapped using methods outlined by G. M. Hawk (pers. commun., 1973). Diameter, species, and location of all living and standing dead trees on the watershed greater than 15 cm dbh (diameter breast height) were mapped. These data were punched on computer cards. Trees less than 15 cm dbh were considered to be understory vegetation.

Organic Matter and Nutrient Distribution

Biomass, nutrient capital, and productivity of the overstory vegetation of the Thompson site were estimated from destructive analysis of trees from that area (Dice 1970). Overstory biomass and nutrient distribution on watershed 10 were estimated from regression equations using diameter and species data compiled for the stem map. The regression equations were based on data from destructive analysis of the major overstory species on the watershed based on a modification of the fixed-internal stratification method outlined by Monsi and Saeki (1953). The modification used consisted of dividing both the branchless stem and the canopy of each felled sample tree into three equal segments and weighing and sampling component mass in each of these segments.

Annual growth of stands on watershed 10 was estimated as follows: Average diameter increment over the past five years was determined for 10-cm-diameter classes for each species on the watershed. This increment was added to recorded tree diameters according to species and diameter class and overstory biomass was recomputed using the new diameters. Productivity was then estimated as the difference between the first and second biomass estimates. Nutrient distribution in overstory biomass and nutrients incorporated in new growth were estimated by sampling and analyzing new growth and older plant components during the sampling for biomass estimation.

Understory biomass and nutrient distribution on watershed 10 were estimated by regression methods based on destructive sampling for larger understory species, while the mass of smaller shrubs and herbs was determined by total harvest. Methods used in understory biomass estimates are described by Russel (1973). Understory biomass and nutrient capital of the Thompson site was determined by harvest of small plots.

Litter layer mass on watershed 10 was determined by sampling the litter layer in two areas representative of the entire watershed. Total and exchangeable nutrients; water storage; depth of L, F, and H layers; and litter mass were determined using methods outlined by Youngberg (1966). Litter layer mass and nutrient capital at the Thompson site were determined using methods reported by Grier and McColl (1971).

The mass of standing and down dead trees on watershed 10 was estimated from data gathered during stem mapping. Heights of standing dead trees were estimated and diameters were measured. Length and diameter of all recognizable fallen trees were measured. Similar methods were used for the Thompson site. Mass of standing and down dead was computed from the Smalian volume of logs and standing dead, assuming a density of 0.3 and a uniform taper of 2%.

Soil nutrient and organic matter content of watershed 10 were determined by sampling of soil in the areas where litter mass was determined. Total and exchangeable nutrients and organic matter were determined by methods outlined by R. B. Brown and R. B. Parsons (pers. commun., 1973). Methods used for soil analysis at the Thompson site are outlined by Grier and Cole (1972).

Epiphyte standing crop and nitrogen content in the overstory of watershed 10 were determined by methods reported by Pike et al. (1972). Epiphytes are a negligible component of the stand at the Thompson site.

Organic Matter and Nutrient Fluxes

Litterfall at both sites is collected on screens placed approximately 15 cm above the soil surface. Eight 0.21-m^2 screens are used in the plot at the Thompson site. On watershed 10, litter is collected from 75 0.26-m^2 screens located randomly within each of the 15 soil-vegetation units with approximately the same area sampled in each unit. Total area sampled is 0.41% for the Thomson site and 0.02% on watershed 10. Litter is collected monthly, dried at 70°C, and sorted into the following categories: conifer foliage, hardwood foliage, woody material, reproductive

parts, living foliage and twigs, and "other material." Nutrient content of each of these categories is determined.

Throughfall at both sites is collected in 20-cm-diameter polyethylene funnels having a neck screen of the same mesh as the litter screens. The funnels are inserted in 20-liter polyethylene bottles and the assembly is placed immediately adjacent to each litter screen. Eight collectors are used at the Thompson site and 75 are used on watershed 10. Litter is allowed to collect in the funnels so that nutrients leached from the litter are collected in throughfall. Collections are made monthly and analyses are performed on unfiltered samples. Chloroform is added to the collectors to retard microbial effects on water chemistry.

Stemflow on watershed 10 is collected on fifteen 10-m by 10-m plots in which all trees >5 cm dbh are fitted with polyurethane foam collars at breast height (Likens and Eaton 1970). On each plot, water is piped from the sampled trees to a group of opaque 125-liter polyethylene trash cans fitted with tight lids. Collections are made as necessary to avoid overflow, with a maximum interval of one month. At the Thompson site, stemflow is diverted from six representative trees into opaque 160-liter trash cans by rubber collars at breast height (130 cm).

Litter decomposition studies based on litterbags filled with specific substrates are in progress on watershed 10. Methods used are reported by Cromack (1973). Mineralization and leaching of nutrients from the litter layer are directly measured at both sites using tension lysimeters (Cole 1968).

Nutrient leaching in the soil profile at the Thompson site is measured with tension lysimeters placed at the lower boundaries of the A1 and B2 horizons and at 1 m in the C horizon to collect percolating soil water. On watershed 10, Soiltest soil solution extractors are placed at the base of the rooting zone (1 m) and at different depths in the subsoil to determine nutrient concentrations in the subsoil water.

Incorporation of nutrients into growth by overstory and understory vegetation was estimated by sampling and analysis of new growth at the end of the growing season and using nutrient concentrations and annual growth estimates to compute nutrient content of new growth.

Annual biogeochemical nutrient budgets for watershed 10 were prepared from measurements of quantity and chemistry of input and outflow water. Methods used are reported by Fredriksen (1972). Annual budgets for the Thompson site are based on data from the lysimeter installation (Cole et al. 1968). Chemical analyses of plant tissue and water were done using methods outlined by Grier and Cole (1972) and Fredriksen (1972).

RESULTS AND DISCUSSION

As would be expected, there are large differences in distribution of organic matter, nitrogen, phosphorus, potassium, and calcium between the 37-year-old stand of the Thompson site and 450-year-old stand on watershed 10 (Tables 1 and 2). These differences reflect not only the age

difference between the stands but also differences in soil and soil parent material. In terms of biomass and nutrient distribution, age differences between these two ecosystems are best illustrated by the larger accumulation of stem biomass, subordinate vegetation, and woody litter on watershed 10.

The stem mass on watershed 10 is about 3.4 times greater than that of the Thompson site. In contrast, the proportional difference in nutrients in boles on the two sites is smaller with N, 1.5; P, 0.63; K, 1.3; and Ca, 2.4 times greater on watershed 10 than on the Thompson site. These differences reflect a changed proportion of relatively high-nutrient-content sapwood between young and old stands. Sapwood normally has higher nutrient concentrations than heartwood (Kramer and Kozlowski 1960). Since sapwood basal area is directly proportional to foliage mass in Douglas-fir (Grier and Waring 1974) and the foliage mass of the two sites is about the same, the differences are due to the higher proportion of heartwood on watershed 10.

Overstory foliage mass of the two stands is essentially the same. This supports numerous observations regarding stabilization of overstory foliage mass early in stand growth (Marks and Bormann 1972) with only minor fluctuations later, largely because of mortality and breakage. On watershed 10, however, overstory foliage is concentrated on a relatively few large trees leaving numerous gaps in the canopy. These light gaps are responsible for a much greater mass of understory vegetation on watershed 10 than beneath the denser canopy of the Thompson site (Tables 1 and 2).

Table 1. Organic matter, nitrogen, phosphorus, potassium, and calcium distribution in vegetation, soil, and litter in a second-growth Douglas-fir ecosystem, watershed 10, Andrews Forest, Oregon.

System component	Organic matter (kg ha^{-1})	Nutrient content (kg ha^{-1})			
		N	P	K	Ca
Overstory					
Foliage	8,906	75	20	70	93
Branches	48,543	49	10	49	243
Bole	472,593	189	12	123	284
Understory					
Large shrubs and small trees					
Foliage	1,604	17	2	5	10
Stems	4,834	8	3	7	21
Small shrubs					
Foliage	1,991	17	2	9	11
Stems	270	1		1	1
Herb layer	65	1		1	1
Epiphytes	1,100	14	ND	ND	ND
Roots (all plants)	74,328	62	5	21	97
Total vegetation	614,234	433	54	286	761
Litter layer					
O1 + O2[a]	43,350	434	61	50	363
Logs	55,200	132	9	20	80
Soil (0-100 cm)	79,250[b]	4300	29[c]	1200[d]	5500[d]
TOTAL ECOSYSTEM	792,034	5300	153	1556	6704

[a] O1 = fresh litter; O2 = litter in various stages of decomposition.
[b] Walkley-Black carbon. [c] Exchangeable phosphorus. [d] Ammonium acetate extracted. ND = not determined.

Table 2. Organic matter, nitrogen, phosphorus, potassium, and calcium distribution in vegetation, soil, and litter in a second-growth Douglas-fir ecosystem, Thompson Research Center, Washington (from Cole et al. 1968).

System component	Organic matter (kg ha^{-1})	Nutrient content (kg ha^{-1})			
		N	P	K	Ca
Overstory					
Foliage					
Current	1,990	24	5	16	7
Older	7,107	78	24	46	66
Branches					
Current	513	4	1	3	2
Older	13,373	40	9	32	65
Dead	8,145	17	2	3	39
Wood					
Current	7,485	10	2	10	4
Older	114,202	67	7	42	43
Bark	18,728	48	10	44	70
Roots	32,986	32	6	24	37
Total tree	204,529	320	66	220	333
Understory	1,010	6	1	7	9
Litter layer					
O1 + O2	16,427	161	24	24	120
Logs	6,345	14	2	8	17
Total forest floor	22,772	175	26	32	137
Soil (0-60 cm)	111,552[a]	2,809	3,871[b]	234[c]	741[c]
TOTAL ECOSYSTEM	339,863	3,310	3,971	493	1,220

[a] Total carbon times 2. [b] Total phosphorus. [c] Ammonium acetate extracted.

The large mass of understory vegetation on watershed 10, relative to the Thompson site, implies major differences in nutrient cycling pathways between young- and old-growth stands. Calculations, based on average foliage turnover rates for understory and overstory species of the two sites, indicate that between 40% and 60% of leaf litterfall on watershed 10 is contributed by understory compared with about 15% for the Thompson site. The large litter input from understory vegetation on watershed 10 is confirmed by litterfall data indicating that from 10% to 70% of annual leaf litter input on individual litter screens is hardwood foliage (C. C. Grier, unpublished data).

Generally, nutrient return by foliage of understory vegetation should be proportionally greater than overstory foliage return because of the generally higher nutrient content of hardwood foliage. For example, hardwood litter from watershed 10 has 15%, 28%, 32%, and 55% higher respective N, K, Ca, and Mg concentrations than does conifer litter, while P concentrations in understory litterfall are 22% lower than in overstory litter (Abee and Lavender 1972).

These data indicate that in the 450-year-old stand of watershed 10, a major portion of the nutrient cycling is taking place through subordinate vegetation. In contrast, the major nutrient pathway in the young stand of the Thompson site is through the overstory.

Litter layer mass and nutrient capital also reflect the large age dif-ference between these two stands (Tables 1 and 2). Standing crop of the 01 and 02 layers of the forest floor is 2.6 times greater on watershed 10 than at the Thompson site. This difference reflects in part the large input of woody material from the decadent overstory vegetation of water-shed 10. Abee and Lavender (1972) found that 47% of litterfall in two plots on watershed 10 was woody material. This is in contrast to the approximately 30% reported by Bray and Gorham (1964) for cool-temperate forests of the world and the 33% woody material in litterfall of the Thompson site.

Mass of standing and down dead trees is substantially greater on water-shed 10 than at the Thompson site. The stand at the Thompson site has had little mortality since it was established in 1931 and forest floor logs here are remnants of the former stand. In contrast, tree mortality in the stand of watershed 10 is high, estimated at 2% per year currently. In addition, much of the mortality on watershed 10 is of larger trees.

The litter layer, including logs, of both sites constitutes a substantial pool of potentially available nutrients. About 11% N, 4.5% K, and 6.6% Ca are in the litter out of the total amounts of these elements in the watershed 10 ecosystem, in comparison with 5.2% N, 6% K, and 11% Ca in the litter layer of the Thompson site. Phosphorus values for the two sites (Tables 1 and 2) are not directly comparable because of the dif-ferent extraction procedures used for soil phosphorus.

Soil parent material differences between the two sites may be reflected in the higher total concentrations of Ca and K in the watershed 10 eco-system. Total ecosystem Ca and K (Table 1), expressed as percentages of total ecosystem organic matter, are 0.85% Ca and 0.2% K for watershed 10

and 0.36% Ca and 0.14% K for the Thompson site. On the other hand, calcium and potassium concentrations in the total vegetation component of the two systems are reversed, with the stand of the Thompson site having 0.16% Ca and 0.11% K compared with 0.12% Ca and 0.05% K for watershed 10.

Higher Ca and K concentrations in the total watershed 10 ecosystem probably reflect the relatively high concentration of these elements in the andesite and andesitic-tuff soil parent material of this ecosystem. In contrast, soil parent material at the Thompson site is primarily granitic and acid metamorphic rocks. Contributions of these different parent materials to nutrient cycles of the two ecosystems will be discussed later in this paper.

An unexpected difference between the old-growth forest of watershed 10 and the second-growth stand of the Thompson site is the difference in overstory foliar nutrient concentrations. Average nutrient concentrations in the overstory foliage mass are 1.12% N, 0.32% P, 0.68% K, and 0.80% Ca for the Thompson site, and 0.84% N, 0.22% P, 0.78% K, and 1.04% Ca for watershed 10. New foliage N concentrations for overstory Douglas-fir average <1%.

Considering the large differences in distribution of organic matter and nutrients, the large age difference and the different soil parent material in these two stands, the overall N, P, and K budgets of the sites are remarkably similar (Table 3). Similarities are especially marked when compared with nutrient budgets of stands in other regions of the United States. For example, Likens and Bormann (1972) report a nitrogen increment of 3.5 kg ha^{-1} yr^{-1} for an undisturbed hardwood forest at Hubbard Brook, New Hampshire, while W. T. Swank (pers. commun., 1972) reports an annual accumulation of 3.34 kg ha^{-1} for an undisturbed hardwood forest of the Coweeta Experimental Forest, North Carolina.

The larger input of phosphorus to watershed 10 may be because of fallout of phosphorus fertilizer dust from grass-seed fields in the Willamette Valley. Prevailing winds across watershed 10 are usually from the direction of the Willamette Valley.

Cation balances of the two study sites probably reflect differences in the chemical composition of the subsoil. As previously noted, soil and subsoil of watershed 10 are derived primarily from andesite and andesitic tuffs, while those of the Thompson site are derived from ice- and water-transported, granitic and acid metamorphic rock. Andesite has a higher proportion of hornblende, olivine, and plagioclase feldspars than granitic and acid metamorphic rocks, which are high in quartz and orthoclase feldspars (Longwell and Flint 1955). Calcium is a major cation in hornblende and plagioclase feldspars (Hurlbut

Table 3. A comparison of annual inputs, losses, and balances of nitrogen, phosphorus, potassium, and calcium at the Thompson site, Washington, and watershed 10, H. J. Andrews Experimental Forest, Oregon (kg ha^{-1}).

Location	N	P	K	Ca
Thompson site[a]				
Input (precipitation)	1.1	trace	0.8	2.8
Loss (leached beyond rooting zone)	0.6	0.02	1.0	4.5
Forest stand balance	+0.5	-0.02	-0.2	-1.7
Watershed 10[b]				
Input (precipitation)	0.90	0.27	0.11	2.33
Loss (runoff)	0.38	0.52	2.25	50.32
Unit watershed balance	+0.52	-0.25	-2.14	47.99

[a]Measured in 1964-1965 measurement year (Cole et al. 1968). [b]Measured from 1 October 1970 to 1 October 1971 (Fredriksen 1972).

1959). Weathering of these minerals in the soil and subsoil probably contributes much of the calcium and potassium lost from watershed 10. Similar calcium losses have been observed from watersheds on limestone-derived soil-subsoil. For example, W. T. Swank and J. W. Elwood (unpublished document, 1971) report an annual loss of 58.6 kg ha^{-1} from a watershed on limestone near Oak Ridge, Tennessee.

Within the overall nutrient budgets of these two stands, considerable differences in pathways of nutrient cycling can be observed. For example, the relative importance of litterfall, throughfall, and stemflow in returning nutrients to the soil surface are quite different in these two stands.

At the Thompson site, stemflow contributes about 0.9% N, 14% P, 12.5% K, and 17% Ca of the total quantity of these elements returned to the soil (Table 4). These quantities are transferred by stemflow amounting to 5%-10% of total precipitation. In contrast, stemflow in old-growth Douglas-fir is reported to be only 0.27% of total precipitation (Rothacher 1963), suggesting this to be a minor source of nutrient input on watershed 10. Rothacher's study, however, was done in a more uniform old-growth stand than watershed 10 and included only trees >28 cm dbh. Our preliminary results from the more heterogeneous stands of watershed 10 and based on trees 5 cm dbh and larger indicate that 2%-4% of total precipitation returns to the soil as stemflow. This suggests that small stems carry a disproportionate share of total stemflow in old-growth stands and further indicates that stemflow volume estimates based strictly on tree basal area may be inaccurate.

Nutrient return by throughfall is greater on watershed 10 than for the Thompson site for all elements except calcium (Table 4). Throughfall return of N, P, K, and Ca on watershed 10 is 130%, 800%, 205%, and 65%, respectively, of the return of these elements at the Thompson site.

Table 4. Annual nutrient return by litterfall, throughfall, and stemflow[a] in 43- and 450-year-old stands at the Thompson site, Washington, and watershed 10, H. J. Andrews Experimental Forest, Oregon (kg ha^{-1} yr^{-1}).

Location	N	P	K	Ca
Thompson site				
Litterfall	21.0	0.3	0.5	1.8
Throughfall	1.5	0.3	10.7	3.5
Stemflow	0.2	0.1	1.6	1.1
Total	22.7	0.7	12.8	6.4
Watershed 10				
Litterfall	27.3	4.7	8.0	67.3
Throughfall[b]	2.0	2.5	22.0	2.3
Total	29.3	7.2	20.0	29.6

[a]Stemflow at Thompson site only. [b]Average for two watershed 10 plots from Abee and Lavender 1972.

A variety of factors have been shown to contribute to the quantity of nutrients leached from plants (Tukey 1970) including: (1) plant species involved (hardwoods tend to have larger amounts leached than conifers); (2) nutrient elements (potassium is leached in greater amounts than calcium); (3) age of foliage (older foliage is leached more readily than young foliage); (4) intensity and volume of precipitation (more nutrients are leached by long, low-intensity precipitation than by short intense storms).

Most of the above factors probably contribute in some part to the differences observed between throughfall on watershed 10 and the Thompson site. Watershed 10 has a much higher proportion of hardwoods (Tables 1 and 2), and a greater proportion of older foliage. Additionally, water-

shed 10 has 170% greater precipitation, which falls at about the same rate as at the Thompson site, and greater total foliage and branch mass exposed to leaching (Tables 1 and 2).

In combination, these factors probably account for the major differences observed in leaching of N, K, and Ca. The factors responsible for the 800% greater return of P on watershed 10 cannot be satisfactorily explained at present, especially since P is usually leached from plants in relatively small amounts (Tukey 1970). Further research is proposed to examine this phenomenon.

Organic matter and nutrient transfers by litterfall also reflect the differences between the two sites. Annual litterfall in the 37-year-old stand of the Thompson site is currently about 2900 kg ha^{-1} compared with 5900 ka ha^{-1} on watershed 10. Annual foliage litterfall, however, is similar for the two sites, with 2200 kg ha^{-1} and 2800 kg ha^{-1} for the Thompson site and watershed 10, respectively. The larger amount for watershed 10 is due to the large mass of hardwoods in the understory.

Of total nutrients returned in litterfall for the two research sites (Table 4), about 90% are returned in the foliage component of the litter at the Thompson site. In contrast, 48% N, 69% P, 61% K, and 70% Ca are returned annually in foliage litter on watershed 10; the remaining nutrients are returned in woody material, reproductive parts, epiphytes, microlitter, and other minor categories.

Nutrients returned in epiphyte- and microlitter make a measurable contribution to the annual nutrient cycle on watershed 10. In this old-growth stand, epiphytes on branches alone amount to a dry weight of 800-1600 kg ha^{-1} and contain about 13.5 kg ha^{-1} N (Pike et al. 1972). Many lichens fix atmospheric N and, because of this and their possible role in adsorbing and desorbing nutrients in precipitation and through-fall, further studies of the role of epiphytes in nutrient cycling are planned. Annual nutrient by epiphyte-fall on watershed 10 is 6.7% N, 3.6% P, 5.6% K, and 0.7% Ca of total nutrients in litterfall (Abee and Lavender 1972). Epiphytes are a negligible component of litterfall at the Thompson site.

A portion of nutrient return by litterfall is in the form of fine organic matter such as insect frass, spores, pollen, and dust. This material is overlooked in many nutrient cycling studies in spite of nutrient concentrations such as 2% N in pollen and 7.8% N in some insect bodies (Stark 1973). This microlitter is a strongly seasonal input to the litter layer. Studies of microlitter input and turnover are currently in progress on watershed 10.

As previously mentioned, over 80% N, 30% P, 20% K, and 70% Ca reaching the soil surface of these two research sites do so by litterfall. Research is currently in progress at both sites to determine factors involved in making nutrients returned by litterfall available for plant uptake, including studies of the relation between climate and litter decomposition, the relation between decomposition and mineralization, and ion leaching in the soil.

Data on nutrient mineralization during decomposition are being provided for both sites from two sources, tension lysimetry (Cole 1968) and analysis of litterbags (Cromack 1973). Tension lysimetry provides integrated mineralization data for the total litter mass and data of nutrient flux in the soil, while litterbag studies provide mineralization data for specific organic substrates. Preliminary results of litterbag studies indicate that in the first six months of decomposition, weight loss of green needle litter was 17%, while potassium, magnesium, and calcium concentrations decreased by 75%, 75%, and 15% respectively, and nitrogen and phosphorus concentration showed no change (K. Cromack and R. Fogel, unpublished). Similar data are now available for a wide variety of substrates. For example, weight loss of fallen conifer needles and moss (*Isothecium stoloniferum*) is 10% in the first year (K. Cromack and R. Fogel, unpublished), while nitrogen-rich lichens lose 50% to 60% of their weight in one year (Rossman, unpublished).

Overstory vegetation of the Thompson site is currently over four times more productive than that of watershed 10 (Table 5). Over 40% of annual growth on watershed 10 is in the understory vegetation, however, so total production on watershed 10 is actually about one-half that of the Thompson site. The values given in Table 5 do not include mortality; doing so would probably reduce the overstory growth value for watershed 10 considerably. Nutrient utilization by understory of watershed 10 should nearly equal that of the overstory because of higher nutrient concentrations in new hardwood growth (Russel 1973). Onsite observations indicate mortality is high for watershed 10 and negligible for the Thompson site, but long-term data will be needed to establish mortality at both sites.

Nutrient accumulation in new growth in the overstory is low for both sites compared with stands in other parts of the world. For example, Nelson et al. (1970) report 34.3 kg/ha N, 4.7 kg ha^{-1} P, 18.9 kg ha^{-1} K, and 22.0 kg ha^{-1} Ca accumulated by 5-year-old loblolly pine (*Pinus taeda* L.) in producing 9400 kg ha^{-1} of organic matter during one year. Annual nutrient accumula-tions in new tissue of the old-growth forest are substantially below those of the 37-year-old stand of the Thompson intensive site in spite of the threefold greater biomass accumulation on watershed 10. The lower demand for nutrients by the old-growth forest may indicate a successional pattern of reduced nutrient utilization that will be continued into climax *Tsuga heterophylla* stands typical of this area.

Table 5. Net[a] annual organic matter and nutrient accumulation by vege-tation of 37- and 450-year-old Douglas-fir stands[b] on the Thompson site, Washington, and the H. J. Andrews Experimental Forest, Oregon (kg ha^{-1}).

Location	Organic matter	N	P	K	Ca
Thompson site (43 years old)					
Total all vegetation	9988	23.6	6.6	14.4	8.7
Watershed 10 (450 years old)					
overstory	2362	5.0	1.1	4.4	4.3
understory[c]	1840	d	d	d	d
Total all vegetation	4202				

[a]Mortality not deducted from above figures. [b]Does not include root pro-duction. [c]From Russel 1973. [d]Not available at time of writing.

SUMMARY

Biomass and nutrient distribution and nutrient cycling process in 37- and 450-year-old Douglas-fir stands of the Thompson site in Washington and watershed 10 in Oregon reflect both the differences in age and soil and

soil parent material. total biomass of the older stand is greater.
Overstory foliage mass of the two sites is the same. In the 450-year-old
stand, foliage is concentrated on fewer stems causing light gaps in the
canopy. The greater light penetration through the older canopy promotes
dense understory vegetation. Litter accumulation is fourfold greater
in the older stand because of larger input of slowly decomposing woody
material. Nutrient concentrations are generally lower in the less physio-
logically active 450-year-old overstory.

Input-output nutrient budgets for the two stands are relatively similar
except for calcium. The large calcium output from watershed 10 is probably
due to subsoil weathering.

Annual return of nutrients to the litter layer is greater in the 450-
year-old stand, with approximately half this annual return contributed
by understory vegetation. In contrast, less than 15% of annual return
is contributed by understory in the 37-year-old stand.

The greater nutrient return by throughfall on watershed 10 is probably
explained by the greater precipitation, larger amounts of older foliage,
greater foliage and branch mass, and the larger mass of hardwoods in this
stand. Nutrient return by stemflow is significant in the 43-year-old
stand of the Thompson site. Stemflow is less important in the older
stand but comparable data are not yet available.

Annual incorporation of nutrients in overstory growth is 4.7, 6, 3.3,
and 2 times greater for N, P, K, and Ca, respectively, in the 43-year-old
stand. Including the understory, nutrient incorporation in growth should
be at least twice the above figures, since understory production is nearly
equal that of the overstory.

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ESTIMATING EVAPOTRANSPIRATION FROM FORESTS BY METEOROLOGICAL AND LYSIMETRIC METHODS[1]

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ABSTRACT

The development of meteorological models (Bowen ratio, aerodynamic, and eddy correlation) for short-term prediction of fluxes of latent heat is discussed. Evapotranspiration of a Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) tree in a weighing lysimeter, located on the Cedar River watershed near Seattle, Washington, was determined during the summer and fall of 1972 and 1973. Details are given on the installation of the lysimeter, on methods, and on the lysimetric measurements of latent energy. Results from the lysimeter tree are compared with meteorological model results.

INTRODUCTION

Meteorological models have been developed from physical theory to predict the fluxes of momentum, sensible heat, latent heat, and carbon dioxide for short periods. These models have several advantages for determining the fluxes of momentum and matter from natural surfaces. The flux of water vapor (evapotranspiration), for example, can be determined with meteorological models. The instruments needed to sample the input variables can be constructed so that the models can be used with a great deal of transferability, and assumptions concerning the wetness of the surface or the status of soil moisture are not required.

Meteorological models also have disadvantages. The most serious of these is the assumption that the fluxes are vertical (i.e., no horizontal advection). This assumption is not always met under the conditions of interest. The second disadvantage is two of these models, the energy balance and aerodynamic models, require vertical gradients of input parameters. Vertical gradients exist in most ecosystems under forced convection conditions. In many localities, however, free convection prevails more often than forced convection. The meteorological model not requiring vertical gradients, which operates under free convection conditions, is the eddy correlation model.

Additional testing of meteorological models is needed before they can be used widely in forestry. This testing can be accomplished only by comparing the results of evaporative fluxes determined with a weighing lysimeter with meteorological model outputs. The objectives of the meteorological program were to (1) construct a weighing lysimeter; (2) test the meteorological models; and (3) evaluate the fluxes of latent and sensible heat, carbon dioxide, and momentum.

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[1]This is contribution no. 62 from the Coniferous Forest Biome.

WEIGHING LYSIMETER METHODS AND RESULTS

Details of design, construction, and use of lysimeters are described in many articles and need not be discussed here. An excellent review by Tanner (1967) lists criteria for good agricultural lysimetry. To ensure that a lysimeter is representative of the surrounding area the following criteria must be met: (1) similar water availability, (2) similar soil aeration, (3) similar thermal regime, (4) similar soil porosity and texture, and (5) similar vegetation density per unit area. In addition, (6) the lysimeter surface should be large compared with the wall area, (7) aboveground structures and paths should be minimized, (8) chemical balance should be maintained, and (9) condensation and evaporation from tanks should be avoided.

The greatest lysimetric problem in forestry is the scaling of data from a single tree to a representative unit area. Ideally, more than one tree should be installed in a lysimeter, but this is difficult to accomplish in tall forest stands. In addition, it is also very difficult to select a single tree in a naturally regenerated stand that is representative of the local forested area because of the variation in size and location of trees with respect to each other and to holes in the canopy.

Determination of the absolute volume of evapotranspiration is straight-forward with the lysimeter. Interpretation of the water balance, however, which includes interception and throughfall, becomes difficult when the tree crown extends beyond the lysimeter surface. All of the interception, but only a portion of the throughfall, is recorded as a weight increase on the lysimeter. Evaluation of these components of the water balance requires minute scrutiny of the weight records. In practice, a weighted percentage of the total rainfall can be used to minimize this problem.

The effect of wind upon the lysimeter signal is far more serious in forestry than in agriculture. When strong winds occur, only daily evapotranspiration can be resolved.

At the A. E. Thompson Research Center in the Cedar River watershed near Seattle, Washington, a codominant Douglas-fir (*Pseudotsuga menziesii*) was installed in a weighing lysimeter during the spring of 1971 (Fritschen et al. 1973). The salient features of the weighing lysimeter are: the soil container is 3.7 m in diameter, 1.2 m deep; the soil container is resting on 165.5 m of 6.4-cm butyl rubber tubing filled with water; the soil container was constructed around the root ball of a 28-m-high, 38-cm-dbh tree in a 45-year-old naturally regenerated stand; the container, soil, and tree weigh 28,900 kg; weight changes are detected by measuring the differential pressure between an active and a dummy stand-pipe. The sensitivity of the system is 6.3 g, which is equivalent to 0.06 mm of water.

Vegetation surrounding the lysimeter tree consists mostly of Douglas-fir and a few western hemlock and maple. Average tree spacing is 5.8 m (vegetation density is 472 trees per hectare), and the average diameter at breast height (dbh) is 20 cm. The soil on the site is a Barneston gravelly loamy sand originating from glacial outwash laid down at the end of the Vashon glacial period (Paulson and Miller 1952).

Evapotranspiration (ET), representing (1) differences between standpipe readings and (2) accumulated evapotranspiration for the period April through December 1972 is shown in Figure 1. In addition, daily precipi-
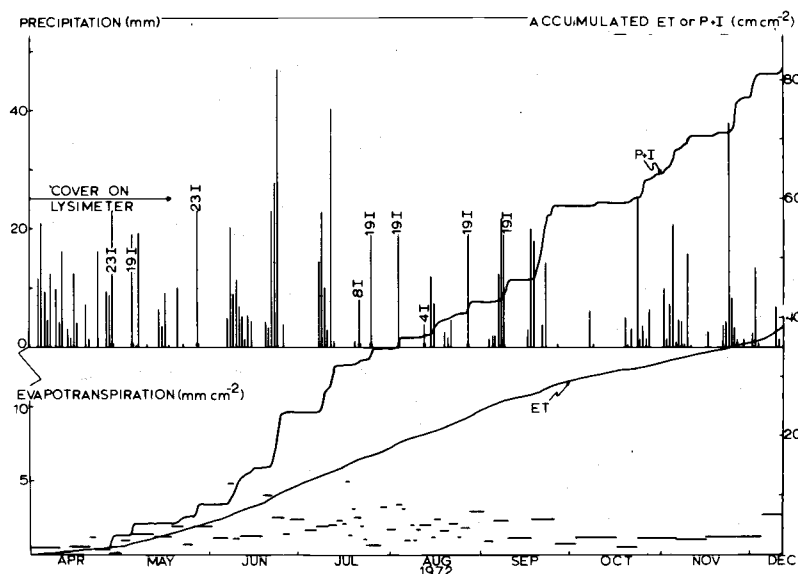

Figure 1. Evapotranspiration of Douglas-fir as averages over short periods and accumulation (ET), daily precipitation and accumulation (P + I), and irrigation (I) during 1972 on the Cedar River watershed near Seattle, Washington.

tation (P) and irrigation (I) (e.g., 8 I [mm]) and P + I are shown. During the winter months a cover was placed over the lysimeter to prevent the buildup of a water table within the lysimeter. This procedure is necessary when precipitation minus evapotranspiration is greater than the capacity of the drainage system. When the cover was in place 0.075 x P was used in the evaluation of evapotranspiration.

Evapotranspiration rates ranging from a low of about 0.2 mm day^{-1} to a high of 3 mm day^{-1} occurred during periods of clear weather in July and August. These rates are assumed to be representative of the forest. To assure representativeness, the lysimeter tree was irrigated when its moisture stress exceeded that of adjacent trees. This was necessary because the root area occupied by the lysimeter tree (10.5 m^2 was less than the area occupied by the average tree (17.5 m^2). Consequently the soil water content in the lysimeter decreased faster than that in the surrounding soil.

The average evapotranspiration during the nine-month period shown in 1972 was 1.4 mm day^{-1} (Fritschen et al. 1974b). A variety of rates is presented in Table 1 converted to an area and a volume basis. Assuming that

Table 1. Evapotranspiration rates from the lysimeter tree[a] expressed on a rate and area basis using the crown projection of 29.5 m^2 as a scaling factor, and on a volume basis. The rates represent low and high and intermediate values for 1972.

Rate (mm day^{-1})	Volume (liters day^{-1})	(gal day^{-1})	Area basis (kl ha^{-1}day^{-1})	(gal Ac^{-1}day^{-1})
1	29.5	7.8	10	1069
1.4	41.3	10.9	14	1497
1.8	53.1	14.0	18	1925
2	59.0	15.6	20	2138
3	88.5	23.4	30	3208

[a]The hydrologic balance of the lysimeter tree was determined for two clear days in May 1972 (Fritschen and Doraiswamy 1973). The results suggest dew as an addition to the hydrologic balance of 6.4 liters (1.7 gal) and 10.9 liters (2.9 gal) when the total evaporation was 42.5 liters (11.2 gal) and 55.2 liters (14.6 gal), respectively. By use of the stand density of one tree per 17.5 m^2 the above figures of dew amount to 3.7 and 6.3 liters ha^{-1} (393 and 670 gal Ac^{-1}) of dew and 24.3 and 31.6 liters ha^{-1} (2587 and 3373 gal Ac^{-1}) of evaporation. Thus 15% and 19% of the hydrologic balance were evaporation of dew.

the 1.4 mm day^{-1} rate would approach an average for the entire year, a total of 5110 kl ha^{-1} (546,405 gal Ac^{-1}) would be utilized in evapotranspiration.

METEOROLOGICAL MODEL RESULTS

Lysimetric measurements of latent energy were used to check Bowen ratio estimates at Cedar River (Fritschen et al. 1974a). The diurnal energy budget and totals (cal cm^{-2} day^{-1}) for 10 August 1972 are given in Figure 2. The latent energy (LE) term was measured directly by the lysimeter, and the water loss was considered to have originated from the 29.5-m^2 area of the projection of the crown of the lysimeter tree. The sensible heat flux was obtained as a residual in the energy balance equation.

The Bowen ratio method used to obtain latent energy estimates at the lysimeter site was based on three levels of temperature and humidity measurements at each of two towers (Gay 1972). Results for the Bowen ratio estimates and the lysimeter tree are shown in Figure 3. Tower 1 (LE$_1$) was about 20 m from the lysimeter tree; tower 2 (LE$_2$) was about 100 m away.

The trends shown in Figure 3 are in reasonable phase with each other, although the nighttime variability in LE$_2$ invites caution. Such variability is often reported during periods when the gradients are slight. Total LE's for the lysimeter tree and the Bowen ratio, however, do not agree as well as expected. The lysimeter estimate of -275 cal cm^{-2} day^{-1} (Figure 2) is only 14% greater than the mean (-240 cal cm^{-2} day^{-1}) of LE$_1$ and LE$_2$, but the two Bowen ratio estimates differ by 37% of their mean. Such a discrepancy raises doubts about the adequacy of the instrumentation and about the homogeneity of the site.
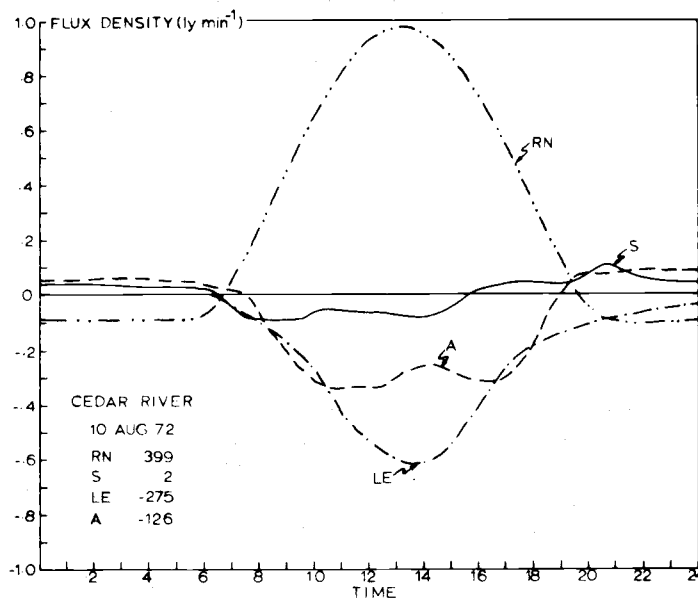
Figure 2. Diurnal course of the energy budget at Cedar River near Seattle, Washington. Latent energy flux (LE) is measured by lysimeter, and atmospheric sensible heat (A) is obtained by difference; RN = net radiation; S = soil heat flux. Totals in calories per square centimeter per day are given in the lower left corner.
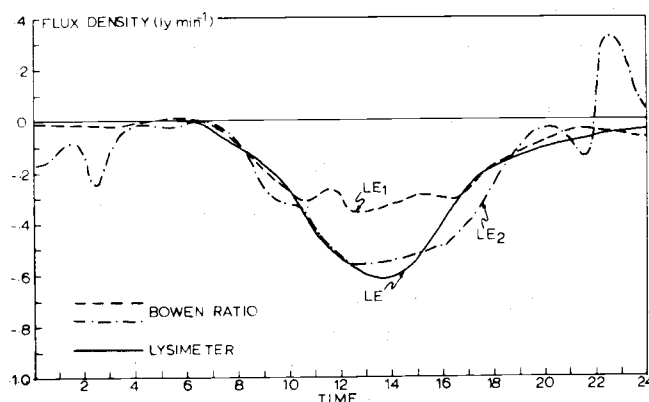
Figure 3. Latent energy flux estimates at Cedar River near Seattle, Washington, on 10 August 1972. Diurnal trends in the latent energy estimates of the lysimeter (LE), and the Bowen ratio method of mast 1 (LE$_1$) and mast 2 (LE$_2$).

This is the first report of comparative energy budgets from two techniques applied to more than one point in a forest. The comparison shown here will be extended in the future to include other days, in order to obtain a better picture of the variability to be expected. Even with just one day, variability found here indicates clearly that replication must be incorporated into future forest experiments.

Several aerodynamic model analyses also have been attempted at the lysimeter site. The results of a test using data from the two towers described above is shown in Figure 4. The results generally have not been satisfactory. The work with the aerodynamic models, even though unsatisfactory at this time, and the comparisons between the lysimetric and Bowen ratio results have stimulated us to reexamine the problems associated with forest energy budget analyses.

At the present time the most promising methods for determining evapotranspiration from small forests appear to be lysimeters, the energy balance model, and the eddy correlation technique. Lysimeters and the eddy correlation technique appear to be the most promising methods for use in more mature forests.
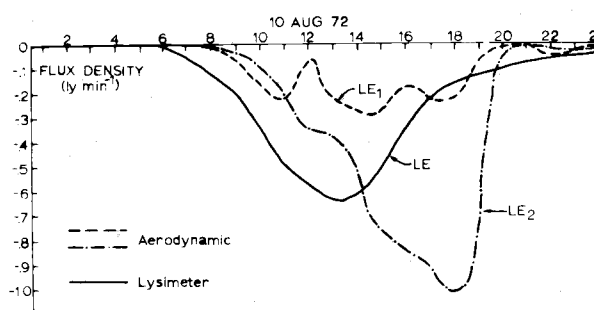

Figure 4. Latent heat flux estimates at Cedar River, Washington, on 10 August 1972. Diurnal trends in latent energy estimates of the lysimeter (LE) and the aerodynamic method on mast 1 (LE_1) and mast 2 (LE_2).

Combining measured net radiation with sensible heat flux determined with the eddy correlation method, however, may be the most practical method of obtaining estimates of evapotranspiration. Net radiation is an easily measurable quantity and it would provide reasonable limits on evapotranspiration estimates. Eddy correlation equipment of the "Fluxatron" type is fairly simple and it appears to provide reasonable estimates of sensible heat. The need for spatial sampling requires further investigation, however. Ignoring stored energy terms could result in significant errors over short periods during the day and during warming and cooling periods; the errors should not be too important over longer periods and under other conditions.

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CANOPY FOOD CHAIN
IN A CONIFEROUS FOREST WATERSHED[1]

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ABSTRACT

The internal structure and external couplings of the canopy food chain are examined to quantify the pattern of energy distribution in an old-growth Douglas-fir watershed. The food chain has been divided into nine functional groups: grazing vertebrates, grazing insects, sucking insects, seed and cone insects, predaceous birds, parasitic invertebrates, predaceous invertebrates, omnivorous birds, and nest predators. Surveys of the watershed fauna have shown that these functional groups are complex and may contain large numbers of species. For example, the five invertebrate groups may include as many as 450 species.

Modeling techniques are employed to compute total annual consumption and secondary production for two functional groups, grazing insects and omnivorous birds. The estimates are based on field density records, published data, and simplifying assumptions. The annual consumption by grazing insects on the watershed is estimated to be 42.5 kg/ha or about 1.6% of total primary production. The omnivorous bird population consumes 6.2 kg/ha while on the watershed; about 75% of their diet consists of insects. The consumption rates and mean standing crop values are similar to those reported for other forests. At current population levels, this food chain represents only a minor pathway in the total watershed energy flux.

INTRODUCTION

The canopy food chain is a subsystem within the forest ecosystem. The internal structure and external couplings of this subsystem have been examined as part of an integrated research effort to quantify the pattern of energy distribution in an old-growth Douglas-fir watershed. This watershed is designated number 10 in USDA Forest Service studies and is located at the H. J. Andrews Experimental Forest on the west side of the Cascade Range in Oregon. The distribution of biomass within the vegetation subsystems is described by Grier et al. (1974) in this volume. Other descriptions have been made by Fredriksen (1972). This paper discusses the role of the canopy food chain as a user of energy.

FOOD CHAIN STRUCTURE

In 1972 the conceptual structure of the canopy food chain was presented
(Strand and Nagel 1972). Figure 1 shows the main routes of energy trans-
fer between the functional groups in the postulated structure. Since
then, two survey projects were begun to examine the bird and invertebrate
populations. The bird surveys were coordinated by Dr. Ronald Nussbaum.
They were located in several sites, some in the intensively studied water-
shed and others in similar stands. The invertebrate survey was the
responsibility of Drs. William Nagel and Gary Daterman. Their sampling
sites were in several forest types and stand ages. The purpose of these
surveys was to identify the important animal types and to observe the
relative diversity of types. Grazing vertebrates were not sampled, but
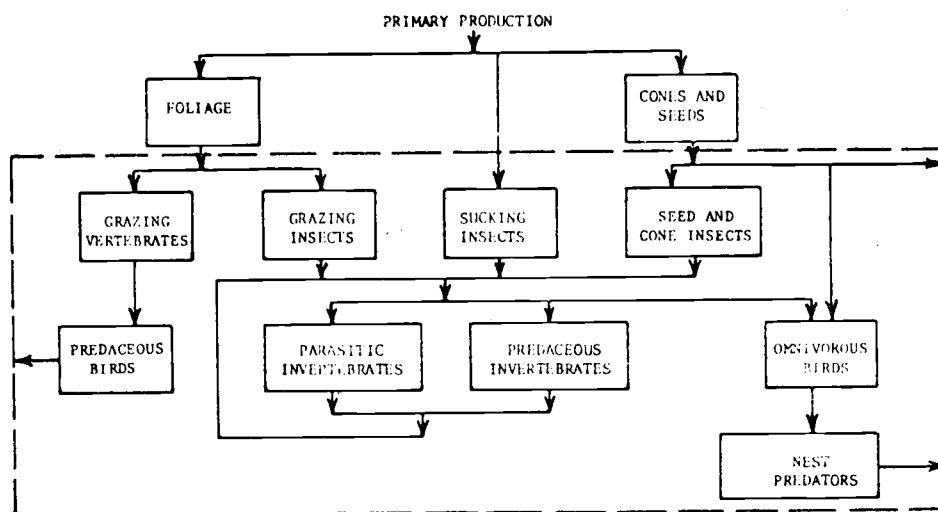they have been the subject of previous investigation (Maser 1966).

Figure 1. The major energy pathways between components of the forest canopy food chain
(from Strand and Nagel 1972).

More detailed papers on sampling techniques and results of surveys will
be presented later, but some preliminary results show the complexity of
this food chain. Table 1 shows the
distribution of taxa found in the
various functional groups of inverte-
brates. About 65% of the species cap-
tured potentially dwell in the canopy.
The sampling methods included rotary
nets; window, sticky, and pitfall
traps; and foliage beating. The bird
survey observed 23 species in 11 stand
types and as many as 15 species in one
location. At watershed 10, seven spe-
cies of omnivorous canopy birds were
found. Densities of breeding birds
and migration dates were also recorded
(Table 2). From these observations,
representative taxa were named for
each functional group (Table 3).
These representatives are listed to
illustrate both the prevalent types
and general life habits.

Table 1. Number of species of invertebrates captured in
three Douglas-fir stands (W. P. Nagel, pers. commun.).

Invertebrate	No. of species	
Herbivores feeding on:		
Any plant	166	
Herbs	6	
Trees and shrubs	63	
Lower plants	24	
		259
Predators		150
Parasites feeding on:		
Invertebrates	94	
Vertebrates	1	
		95
Saprophytes feeding on:		
Plant material	78	
Animal material and feces	14	
		92
General scavengers:		100
	Total	696

Table 2. Breeding birds observed at the intensively studied watershed in 1972 (R. A. Nussbaum, pers. commun.).

	Arrival begins	Departure complete	Breeding birds
		(month/day)	(indiv./ha)
Chestnut-backed chickadee	a		1.98
Golden-crowned kinglet	a		2.22
Hammond's flycatcher	5/7	9/22	0.68
Hermit warbler	4/28	8/15	1.60
Steller's jay	a		0.34
Western flycatcher	5/4	9/8	1.36
Western tanager	4/10	9/28	0.42

[a]Year-round residents.

Table 3. The canopy food chain.

Functional group	Principal representative
Grazing vertebrate	Red tree mouse
Grazing insects	Leaf beetles (Chrysomelidae)
Sucking insects	Adelgidae
Seed and cone insects	Douglas-fir midge
Predaceous birds	Spotted owl
Parasitic invertebrates	Wolf spiders (Lycosidae)
Omnivorous birds	Golden-crowned kinglet
Nest predators	Black raven

ENERGY USE

Birds

To determine the energy distribution among some of the food chain members, modeling techniques were employed. Because density estimates were available only for the omnivorous birds, they were the first group to be examined. They were modeled in two groups, the breeding adults and the young of the year. An equation for daily consumption per individual adult bird was derived from equations by R. A. Nussbaum (pers. commun.) and from a set of assumptions. The assumptions are as follows: (1) Assimilation balances respiration. (2) Respiration is a function of ambient temperature, body size, and bird activity. (3) Digestive efficiency is constant (0.70).

Daily consumption is calculated by:

$$C = a_1 a_2 W^{a_3} \qquad (1)$$

where C = daily consumption per individual (grams dry wt), a_1 = activity factor (a_1 is 2.0 during the breeding season, and 1.4, otherwise), a_2 = temperature factor ($a_2 = -0.008T + 0.39$), and a_3 = body weight exponent ($a_3 = 0.003T + 0.53$) where T = daily mean temperature, and W = adult weight (grams dry wt). This relationship is illustrated in Figure 2.

Equations for juvenile birds were derived by assuming that: (1) birds follow a prescribed growth curve; (2) energy derived from assimilation goes either to maintain the prescribed growth rate or to basal and activity metabolism; and (3) digestive efficiency is constant (0.70).
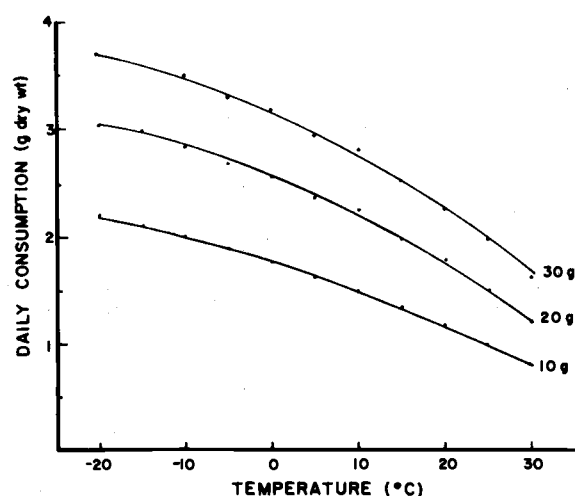

Figure 2. The modeled relationship between daily consumption and temperature for adult birds weighing 10, 20, and 30 g.

The expressions used to compute daily consumption are:

$$S_i = b_1 - b_2 \exp b_3 i, \tag{2}$$

$$G_i = S_i - S_{i-1}, \tag{3}$$

$$M_i = a_1 a_2 S_i^{a_3}, \tag{4}$$

$$C = M_i + f G_i, \tag{5}$$

where S_i = body weight of an individual on the ith day after hatching, b_1, b_2, b_3 = parameters of the growth equation that are unique for each species, G_i = weight gain on the ith day, M_i = metabolic energy require-ments, a_1, a_2, a_3 = parameters same as those in equation (1), C = daily consumption per individual (grams dry wt), and f = consumption for growth conversion factor (= 1.14). The growth and consumption curve for a juvenile western tanager is illustrated in Figure 3.

The total annual consumption while at watershed 10 was computed for the seven bird populations found there. Temperature data from the watershed, observed migration dates, bird densities, and survival rates were used in the computation. Also, the proportion of insects in the diet was estimated for each season and annual totals were computed. Insects composed 75% of the diet of the bird population; the other 25% was mostly seeds (Table 4).

Figure 3. Juvenile growth and consumption by the western tanager at constant temperature of 16°C.

Insects

Although the survey did not re-cord densities of the inverte-brates, estimates of production and consumption of grazing in-sects were made using the bird model consumption estimate. To make these predictions, the fol-lowing assumptions were made:

1. Of the insects eaten by the omnivorous birds, 35% are canopy grazers. This is the percentage
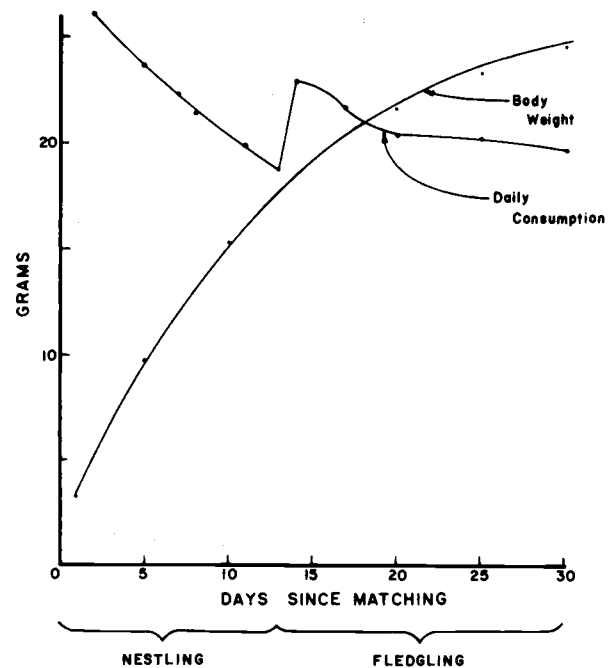
Table 4. Annual consumption by the canopy bird population while in residence at watershed 10 (R. A. Nussbaum, pers. commun.).

	Days at watershed 10 per year	Annual consumption (kg/ha) Insects	Total
Chestnut-backed chickadee	365	1.7	2.1
Golden-crowned kinglet	365	1.7	1.8
Hammond's flycatcher	112	0.2	0.2
Hermit warbler	88	0.3	0.3
Steller's jay	365	0.2	1.2
Western flycatcher	100	0.3	0.3
Western tanager	145	0.3	0.3
Total		4.8	6.2

of grazers found in all samples taken by window traps, foliage beating, and rotary net from an old-growth Douglas-fir stand (W. P. Nagel, pers. commun.

2. The birds consume 20% of the annual production o f the grazing insects. Birds consume about 1% of the spruce budworm population during epidemic periods and as much as 50% during endemic periods (Morris et al. 1958).

3. Growth efficiency of these insects is 0.20. This is the median value given by Waldbauer (1968) for a number of species of grazing insects.

The annual consumption by grazing insects is computed to be 42.5 kg/ha and annual production is 8.5 kg/ha.

ENERGY BUDGET

To illustrate the distribution of energy, a partial energy budget for the canopy food chain was constructed (Figure 4). The values used in the budget were computed in the previous section or estimated from other studies. The relationship between the mean standing crop and annual production was derived by simulation (M. A. Strand, MS in preparation). For grazing insects, the mean standing crop r epresents 15% of total production and for birds it is 125%. Nonassimilated energy was assumed to be 56% of consumption for the insects (Waldbauer 1968) and 30% for birds (R. A. Nussbaum, pers. commun.). Respiration was computed by subtraction.

The grazing insects are probably the major foliage consumers in the canopy food chain. Table 5 shows the percentage of annual production and standing crop of trees that this consumption represents. The data for the vegetation mass are from the paper by Grier et al. (1974). Although the percentage of foliage production that is consumed is very high, the other percentages compare favorably with those reported for forests by other authors (Table 6). A younger forest, for example the 40-year-old stand at the Thompson site (Grier et al. 1974), would have sustained only a 2% loss of foliage production with the same rate of consumption. The standing crop of the insects and the birds estimated in this paper are nearly the same as those reported by Ovington (1962) for other forests (Table 7).
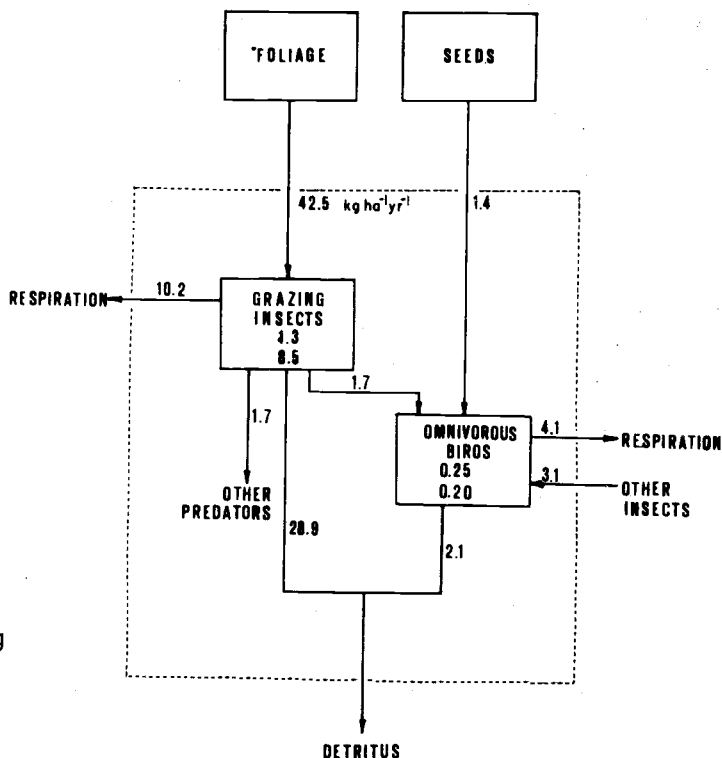

Figure 4. The energy flux through two functional groups in the canopy food chain. Under 'grazing insects' and "omnivorous birds," the first number indicates mean standing crop during spring and summer, and the second number indicates annual secondary production; both are in kilograms per hectare.

Table 5. Estimated percentage of plant stand-ing crop and production consumed annually by grazing insects.

	Standing crop (%)	Primary production (%)
Foliage	0.5	102
Aboveground	0.008	1.8
Total	0.007	1.6

Table 6. Primary consumption as a percentage of primary production in various communities.

Community type	Percentage consumed	Authority
Prunus mixed forest	2.5[a]	Bray 1964
Acer-Fagus forest	1.7[a]	Bray 1964
Fagus forest	1.5[a]	Bray 1964
Liriodendron forest (model)	2.6[b]	Reichle et al. 1973
Old field	20[c]	Odum et al. 1962
Salt marsh	7[c]	Teal 1962

[a]Net aboveground primary production. [b]Net foliage production. [c]Net primary production.

Table 7. Standing crops of animals in various forests reported by Ovington (1962) and the estimated values for watershed 10.

Animal	Standing crop (kg/ha)	Forest
Canopy insects	1.3	Douglas-fir (WS 10)
	0.1-5.0	Scotch pine
	0.01-2.0	Corsican pine
Birds	0.25	Douglas-fir (WS 10)
	0.48[a]	Spruce
	1.17[a]	Beech mixed
	1.15[a]	Oak mixed

[a]Fresh weight.

At current population levels, the canopy food chain uses a rel-atively small amount of the net energy entering the watershed. Some members, however, have the capacity for extreme population fluctuations that can make them major energy users. Keene (1952) lists 14 species of grazing and sucking insects that have been reported as economic pests in Douglas-fir forests. The complete defoliation of watershed 10 would mean a loss of leaves equivalent to 335% of one year's primary produc-tion, and the influences would go far beyond the mere loss of tissue (Rafes 1971, Grison 1971). The canopy food chain at present population levels represents a small energy pathway, but it is potentially a major factor in the distribution of energy in the forest ecosystem.

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CORRELATION OF FOREST COMMUNITIES WITH ENVIRONMENT AND PHENOLOGY ON THE H. J. ANDREWS EXPERIMENTAL FOREST, OREGON[1]

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G. M. Hawk, and C. T. Dyrness

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ABSTRACT

Air and soil temperature, leaf nutrient content, late summer plant moisture stress, and phenology were measured on 14 of the 23 forest communities recognized in the study area. The three vegetation zones identified differ considerably in a temperature index. Comparisons of an existing vegetation ordination with ordinations made using the results of this study showed that the x axis of the vegetation ordination represents a moisture axis. Although both temperature and nutrition correlate to some extent with the y axis of the ordination, it is not simply a response to any one or two factors studied. Yearday of selected phenological stages is well correlated with the temperature index used, but not with ordination axes.

The maximum predawn moisture stress and the calculated temperature index effectively separate the previously classified communities in the study area. The range of the environmental indexes measured in this area is very similar to that in the eastern Siskiyou Mountain forests.

INTRODUCTION

The Oregon intensive study site of the Coniferous Forest Biome is the H. J. Andrews Experimental Forest. A considerable diversity of forest communities is included in this 6000-ha watershed, which extends from 450 to 1600 m elevation (Dyrness et al. 1974). Available resources allow only a small part of this area to be studied, requiring results to be extrapolated to the unsampled portion of the watershed. To extrapolate results in describing the area, and in modeling the processes occurring there, some meaningful method of stratification must be employed. The plant community is being used as a primary unit of stratification, as vegetation has long been considered to represent an integration of the total environment (Billings 1952).

For a stratification system to serve the needs of workers in several fields, more information about the stratification units than simply their species composition is necessary. To increase the usefulness of the community stratification, several environmental variables and plant phenology were measured on stands representing the more common and contrasting plant communities. These measurements were intended to provide data for use by other investigators, as well as being of interest in examining vegetation-environment relationships.

[1]This is contribution no. 64 from the Coniferous Forest Biome.

The forest vegetation of the H. J. Andrews area has been described and classified into 23 communities shown in Figure 1. These communities occur in three vegetation zones: The *Tsuga heterophylla* zone of lower elevations, the *Abies amabilis* zone of the higher elevations, and a transition zone in which both *T. heterophylla* and *A. amabilis* apparently will be dominants in climax vegetation (Dyrness et al. 1974). The relationship between these communities within zones has been further clarified by a two-dimensional ordination technique. Dyrness et al. (1974) suggest that the zones differ significantly in temperature, whereas intrazonal variation in vegetation results primarily from differences in plant moisture stress. This paper reports environmental indexes derived from the measurements of environment made, and the relationship of these indexes to community composition and phenology.
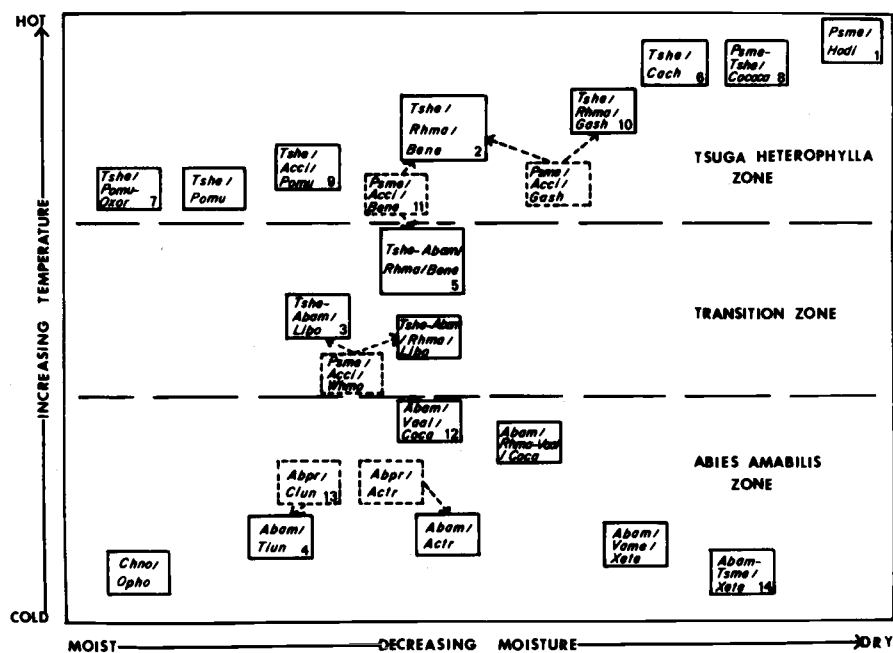

Figure 1. Hypothesized relationships between forest communities and environment on the H. J. Andrews Experimental Forest (after Dyrness et al. 1974). This figure is based on a vegetation ordination, somewhat modified by the intuition of the investigators. Communities enclosed with dashed borders are considered to be seral; the others, to be climax. Communities sampled in this study are identified by the reference stand number in the box. Abbreviations for communities are identified in Table 1.

STUDY AREAS

The more common and contrasting plant communities were chosen for study. In each community a reference stand (RS) was established. Each RS was chosen to exemplify the modal conditions of vegetation in the community it represented. Nineteen RS were established, but only 14 with the most complete data are used in this report (Table 1).

METHODS

Measurements made on the reference stands included predawn plant moisture stress, air and soil temperature, and foliar nutrient content. The phenology of selected species was observed.

Table 1. Forest community, elevation, slope, aspect and date of installation of each reference stand (RS).

RS	Forest community	Abbrev.	Elev. (m)	Aspect	Slope (deg)	Date
1	*Pseudotsuga menziesii/Holodiscus discolor*	Psme/Hodi	490	S40W	30	Apr 70
2	*Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa*	Tshe/Rhma/ Bene	490	N70W	21	May 70
3	*Tsuga heterophylla--Abies amabilis/ Linnaea borealis*	Tshe/Abam/ Libo	945	S85W	5	Apr 70
4	*Abies amabilis/Tiarella unifoliata*	Abam/Tiun	1310	N54W	20	Jun 70
5	*Tsuga heterophylla--Abies amabilis/ Rhododendron macrophyllum/Berberis nervosa*	Tshe-Abam/ Rhma/Bene	880		level	May 71
6	*Tsuga heterophylla/Castanopsis chrysophylla*	Tshe/Cach	610	S25W	30	Apr 71
7	*Tsuga heterophylla/Polystichum munitum-- Oxalis oregana*	Tshe/Pomu/ Oxor	460	N30W	29	May 71
8	*Pseudotsuga menziesii--Tsuga heterophylla/ Corylus cornuta var. californica*	Psme-Tshe/ Cococa	490	S85W	39	Apr 71
9	*Tsuga heterophylla/Acer circinatum/ Polystichum munitum*	Tshe/Acci/ Pomu	460	N50W	41	Apr.71
10	*Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon*	Tshe/Rhma/ Gash	610		level	Apr 71
11	*Pseudotsuga menziesii/Acer circinatum/ Berberis nervosa*	Psme/Acci/ Bene	1010	S20W	11	May 71
12	*Abies amabilis/Vaccinium alaskaense/ Cornus canadensie*	Abam/Vaal/ Coca	1010	S40W	8	Jul 71
13	*Abies procera/Clintonia uniflora*	Abpr/Clun	1310	S20W	23	Aug 71
14	*Abies amabilis--Tsuga mertensiana/ Xerophyllum tenax*	Abam-Tsme/ Xete	1430	N33W	27	Aug 71

Plant moisture stress was measured on saplings under the stand in late summer of 1970-1972, using a pressure chamber (Scholander et al. 1965). At least four saplings, representing the major reproducing conifers, were sampled at each site on each date of measurement. Data presented here are the readings of the pressure chamber ("plant moisture stress" of Waring and Cleary 1967). This value represents the negative of the pressure potential of the xylem sap. For each year, the value used is the greatest average stress recorded on a single date at each site.

A thermograph was installed in each RS to continuously monitor air and soil temperature. Air temperature was measured at 1 m above the forest floor under an insulated A-frame shield. The soil temperature probe was buried 20 cm deep nearby. Averages were computed after the recorder charts were digitized. The mean daytime air and soil temperatures were used to compute a temperature-growth index (TGI). This index weights the temperatures by their relative effects upon growth of *Pseudotsuga menziesii* seedlings in a controlled environment and is summed over the "growing season" each year (Cleary and Waring 1969). This is intended to provide a representation of temperature that is more closely related to plant growth than are arithmetic averages alone. It is used as a uniform index to compare all the communities we studied; however its use over this wide range of conditions does not imply that other species, or even all populations of Douglas-fir, respond to temperature in a similar manner.

Foliage from several conifer saplings on selected RS was collected for chemical analysis in 1971 shortly after expansion of the current year's

twigs. At this time of year nutritional stress in the plant should be at a maximum (Waring and Youngberg 1972). Samples were also collected in the fall. Nitrogen concentrations, presented here, were determined by a micro-Kjeldahl procedure by the Oregon State University Forestry Research Laboratory.

Both vegetative and regenerative phenological stages were observed in 1971 and 1972 for a variety of common and widespread species at all RS.

The community ordination based on vegetation alone (Dyrness et al. 1974) was compared with ordinations of the communities (as represented by RS) determined by plant moisture stress, temperature, foliar nutrient content, and phenology. Rank correlation methods were used to compare dates of phenological stage occurrence with x and y coordinates of the communities, and regression data of phenological stage on stand TGI also were computed.

RESULTS

Vegetation Zones and Temperature-Growth Index

The vegetation zones, as represented by the RS, had markedly different TGI. For the *Tsuga heterophylla* zone, all RS had TGI >73 in 1971 and >78 in 1972; the transition zone RS were 56 and 60 in 1971, and 67 and 70 in 1972, whereas the *Abies amabilis* zone RS had TGI <40 in 1971 and <49 in 1972.

Intrazonal Variation in Ordination Axes

Vegetation within the two warmer zones was used in a single two-dimensional ordination. Dyrness et al. (1974) had considered the x axis to represent variation in response to moisture stress, and the y axis to represent variation due to temperature.

To check these interpretations, and axis positions of a given community in the *Tsuga heterophylla* and transition zones were compared with the moisture stress or TGI for the RS that represent it. Data from the *Abies amabilis* zone were insufficient to make such a comparison.

The x-axis coordinate of the communities measured correlates well with the late summer predawn moisture stress as measured on the conifer saplings (Figure 2). The single major exception was RS 3, with less stress than predicted in 1970
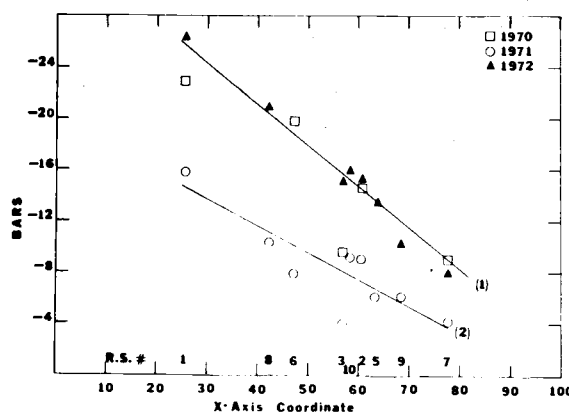

Figure 2. Relationship of maximum yearly predawn moisture stress to position of the community on the x-axis of the vegetation ordination of Dyrness et al. (1974). The community represented by each reference stand is listed in Table 1. Linear regressions: (1) 1970 + 1972: $y = -33.96 + 0.319x$, $r^2 = 0.95$; (2) 1971: $y = -20.00 + 0.207x$, $r^2 = 0.83$. (Data from RS 3 were excluded from the regression equations.)

and 1971. In 1972 RS 3 fit the regression, but only after a nearby selective cut increased the exposure of the stand to the west.

The y axis of the communities shows a rough relationship to TGI, but it breaks down at low y coordinates (Figure 3). Part of the stand variation in y-axis position could be related to nutritional status as well as to temperature. Reference stands 6 and 10 both have lower y-axis coordinates than would be expected from their TGI (Figure 3), but both are also lower in spring foliar nitrogen than the other stands (Figure 4). Reference stand 6 also has the lowest foliar nitrogen in fall sampling. Both *Tsuga heterophylla* and *Pseudotsuga menziesii* were sampled only at RS 6, where their foliar nitrogen contents were very similar. These stands also have lower nitrogen content in the upper soil horizons than other RS (R. B. Brown and R. B. Parsons pers. commun.). Unlike the x axis of the ordination, the y axis does not seem to be closely correlated with any single factor or combination of factors studied. This is not surprising. The y axis probably represents the effects of many environmental factors. Especially since the x axis is closely related to moisture stress, many environmental factors influencing plant distribution differently than moisture stress would be included in the y axis. The y axis probably includes, in addition, such variables as stand age and history.
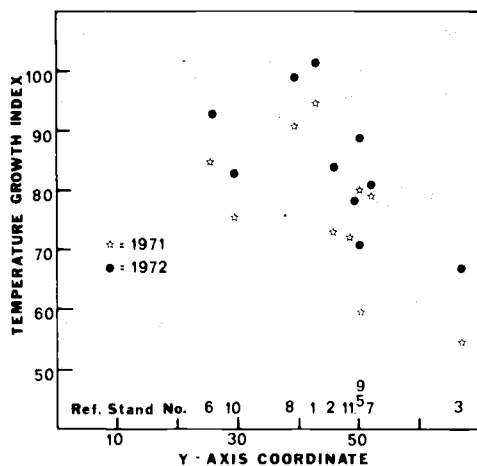

Figure 3. The relationship of TGI of a reference stand and the y-axis coordinate, in a vegetation ordination, of the community the stand represents.
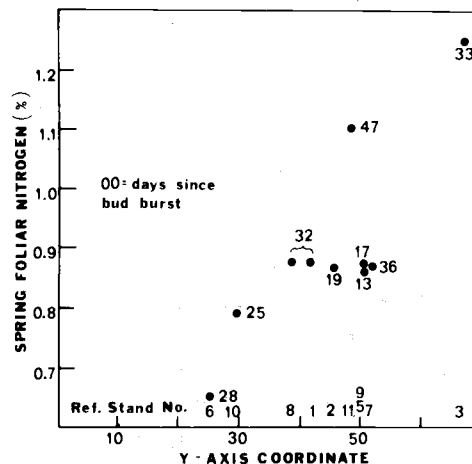
Figure 4. The relationship of foliar nitrogen content of year-old needles after budbreak in the spring (1971) to the y-axis coordinate of the community represented by each reference stand. Time since budbreak is listed with each point (days).

Phenology, Community Composition, and Environment

Although analyses of phenological data are not complete, those available do indicate that phenology may provide a useful alternative method of ordering communities. Dates of occurrence of selected phenological stages were observed for a number of species and their relationships to community ordination axes were examined. Ordering stands by different phenological stages gave similar results for several phenological stages of widespread species, except for *Tsuga heterophylla*. Budbreak of western hemlock

occurred earlier in RS 6 and 10 than in RS 2 and 9, contrary to the other phenological stages studied. The ordination by phenological stages does not compare well with the vegetation ordination axes. Rank correlations of relative time of occurrence of a phenological stage at a particular RS with the position of the RS in the community ordination gave no good relationships with the x axis and only two with the y axis for the six phenological stages examined. Correlation of phenological stage occurrence with TGI at the various RS, however, was considered better than with the y-axis position of the communities. Phenological stages of common species showing a strong correlation of yearday of occurrence with TGI are listed in Table 2. All this indicates that phenology may provide an alternate means of determining temperature relationships of unstudied communities within the area, without actual measurements. Some phenological stages showed much poorer relationships with TGI, however, making calibration of each phenological stage necessary.

Table 2. Regression of yearday of phenophase (y) on TGI for the site for the given year (x).

Species	Phase[a]	Year	n	r^2	b
Tsuga heterophylla	01	1971	8	0.75	-0.80
		1972	9	0.95	-0.66
Abies amabilis	01	1972	5	0.86	-0.82
Linnaea borealis	01	1971	9	0.75	-1.29
		1972	13	0.88	-1.56
Chimaphila umbellata	01	1971	8	0.76	-0.94
		1972	11	0.91	-0.94
Viola sempervirens	12	1972	8	0.82	-1.35
Trillium ovatum	12	1972	8	0.91	-1.60

[a] Phase 01 = vegetative budbreak, phase 12 = occurrence of first flower; n = number of sites compared, b = regression coefficient, r^2 = coefficient of determination.
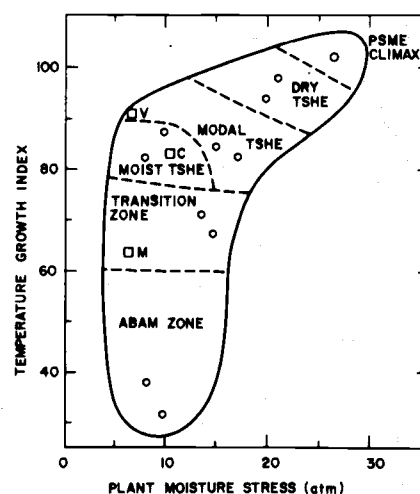

Figure 5. The position of reference stands in a two-dimensional environmental field. Temperature is represented by "temperature-growth index" computed by the method of Cleary and Waring (1969). Moisture is assessed as the late-summer predawn moisture stress on conifer saplings. Most data are for 1972. Psme = *Pseudotsuga menziesii*, Tshe = *Tsuga heterophylla*, Abam = *Abies amabilis*; "L" is discussed in the text.

The smaller negative regression coefficients for budbreak of the trees than of herbaceous species (Table 2) reflect greater uniformity in budbreak date with changing temperature conditions than for the smaller life forms examined. These herbaceous species thus should be more sensitive indicators of TGI than the trees studied.

Environmental Space Occupied by Communities

The variety of temperature and moisture conditions occupied by major forest communities of the H. J. Andrews area is represented in Figure 5. The moisture-temperature combinations present occupy only a part of the combinations possible, given the ranges of the two variables encountered. Reference stands 11, 12, and 13 have TGI for 1972 of 78, 49, and 37, respectively, but conclusive moisture stress data are lacking; RS 12 apparently is in the gap between RS 4 and 14 and RS 5 and 3, and RS 13 is very close to RS 4. Very warm stands with low moisture stress and moderate to cold stands with high moisture stress were not found. One site ("L" in Figure 5) on a rocky south slope on the Andrews Forest was measured with TGI = 63 and plant moisture stress = 26 (Zobel 1974).

This area had vegetation of a type not included in the classification of Dyrness et al. (1974), being a mixed stand of young *Pseudotsuga menziesii* and *Abies grandis*.

The relationship of the RS to the environmental indexes (Figure 5) is very similar to the hypothetical relationships shown in Figure 1. (Figure 1 was constructed before any of the environmental data reported here were available.) The only major exception is that there is not as much variation in moisture stress within the *Abies amabilis* zone as Dyrness et al. (1974) anticipated. The temperature-growth index separates the zones well, and the variation within the *Tsuga heterophylla* zone is mostly in response to moisture stress, as they predicted. That RS 2 and 10 are more different in vegetation (Figure 1) than in TGI and moisture stress (Figure 5) may be because of the apparently limited nitrogen availability on RS 10 (Figure 4).

Interestingly, the portion of the two-dimensional "environmental field" occupied by the RS in this study is very similar to that found for the eastern Siskiyou Mountains (Waring 1969), even allowing for differences caused by use of different years and definitions of "growing season" for TGI summation (Figure 6).
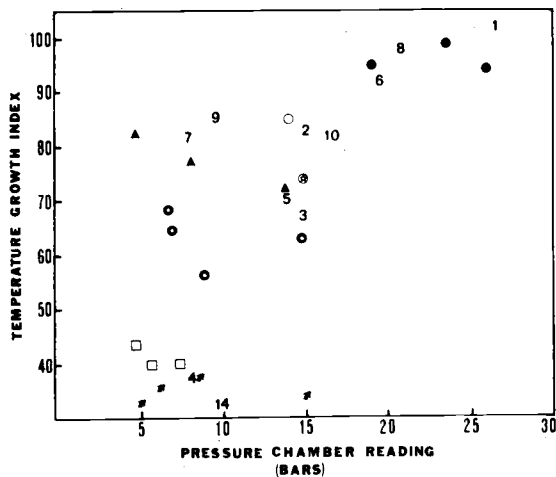

Figure 6. Comparison of temperature growth index and late season predawn plant moisture stress for forest communities in the central western Cascades and in the eastern Siskiyous (from Waring 1969). Numbers represent H. J. Andrews reference stands. Symbols represent eastern Siskiyou types: solid circles, black oak; open circle, yew; open circle and star, ponderosa pine; triangles, mixed conifers; solid circles and stars, white fir; open squares, Shasta fir; and arrows, mountain hemlock.
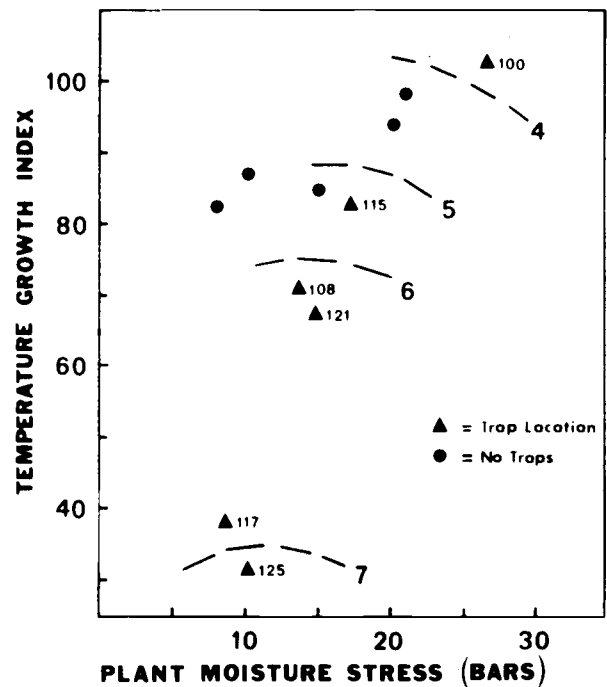

Figure 7. Numbers of individuals (small figures) and species (large figures) of shrews, voles, and mice on selected reference stands. A total of seven species were trapped. Data are total catch for five days, and are courtesy of R. A. Nussbaum.

Use of Reference Stand Data

Within the program of the Coniferous Forest Biome, the reference stands and the environmental and phenological data gathered there have been and will be used in many ways. Several types of studies have been done on or immediately adjacent to the reference stands: litterfall (Abee and Lavender 1972); litter decomposition, animal distribution and population density (Figure 7); soil properties (R. B. Brown and R. B. Parsons pers. commun.), vegetation composition; and understory biomass. Data on phenology are necessary inputs to

modeling consumer and decomposition processes. Temperature is important for these models, as well as for hydrologic modeling. Primary production models depend on both temperature and phenology, as well as plant moisture stress (Sollins et al. 1974). The H. J. Andrews reference stand data will also be used as a part of the Biome environmental grid, which will attempt to determine Biomewide vegetation-environment relationships, as outlined by Waring et al. (1972).

ACKNOWLEDGMENTS

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SOURCES AND FATES OF ORGANIC INPUTS IN CONIFEROUS FOREST STREAMS[1]

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ABSTRACT

A study of the quality and magnitude of particulate organic inputs was undertaken in two streams in the Oregon Cascades. Objectives included estimation of litterfall and lateral movement of organic debris into a stream, estimation of litter breakdown rates, and construction of a first-approximation organic material budget.

In this study, approximately 65% of the litterfall input consisted of Douglas-fir and hemlock needles, which fall throughout the year. Deciduous inputs occurred primarily mid-October through November and consisted principally of vine maple and bigleaf maple. Preliminary lateral movement data indicated that organic material entering watershed 10 from the bank was 1.5 times the litterfall. The total estimate of litter input is approximately 2.5 g m^{-2} day^{-1}. Both streams have the capacity to process all types of leaf litter within a year. Needles, the most refractory leaf litter, are processed by microbes and, once conditioned, are consumed readily by invertebrate shredders. Thus the large amounts of needle litter that enter the stream in late summer and fall constitute a food source usable by stream detritivores after deciduous litter has decomposed.

Leaf-pack experiments have revealed the danger of extrapolation of biological information from smaller to larger streams. Faster processing times for larger streams have been suggested by information on weight loss, invertebrate biomass, and leaf quality. Changes in litter quality were determined by increases in the percentage of lignin content. Increases in lignin composition were compared with decreases in non-cell-wall constituents to obtain an estimate of microbial activity.

Information on litterfall and lateral movement, in conjunction with previously collected data, led to a first-approximation particulate organic matter budget for watershed 10. When compared with a similar budget from a very different stream system, processing capabilities of the two streams were remarkably similar. In both streams almost 99% of the particulate organic material entered from terrestrial systems. About two-thirds of the organic inputs entering each stream were processed within the system, indicating the processing role of small forest streams.

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[1]This is contribution no. 65 from the Coniferous Forest Biome.

INTRODUCTION

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

Part of the work under way in Oregon under the Coniferous Biome program is designed to study the interrelations between the terrestrial and aquatic components of small watersheds. Under investigation in the stream ecosystem are the rates of production of aquatic plants, insects, and fish, along with the input of particulate organic material and the processing of it by microorganisms and invertebrates. The work reported in this paper represents a part of that research, with emphasis on the fate of the particulate organic material.

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

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

Study Area

The study was conducted in the H. J. Andrews Experimental Forest, a 6000-ha watershed in the western Cascades of Oregon. The drainage is characterized by steep topography, with about one-fifth of the study area consisting of more gentle slopes or benches. Elevation varies from 457 m to more than 1523 m. Mean forest air temperature varies from 2°C in January to 18°C during the summer months. Annual precipitation ranges from 225 cm at lower elevations to 350 cm at the highest ridges. Highest elevations are characterized by extensive snowpack during the winter, while rain predominates at lower elevations (Berntsen and Rothacher 1959). Mack Creek and the stream draining watershed 10 were the two streams in the drainage basin that were studied intensively.

Watershed 10 (WS 10) covers 10.1 ha and rises from 430 m at the outlet stream gaging station to 670 m at the highest point. The overall slope of the stream channel is 45%. Side slopes and headwall, however, range up to 90% because of the deep incision of the basin into the main ridge.

Stream discharge varies from around 0.23 liter/sec in the summer to about 140 liters/sec during winter freshets. The uppermost forks are intermittent during the summer months. Mean width of the stream channel ranges from 0.25 m in the upper reaches to 0.75-1.0 m at the base of the watershed.

Streambed morphology is best described as a "stairstep" series of small pools connected by free-fall zones or riffles running on bedrock. Pools are formed mainly by accumulations of organic debris. The substrate consists of loose rocks and gravel from weathered tuff and breccia material and bedrock of unweathered tuff and breccia.

Mack Creek is one of the three major streams that drain the entire Andrews Experimental Forest. The area being studied is between 700 m and 900 m in elevation and drains approximately 650 ha. The watershed slope in this area is 44%. Stream discharge at the study area is estimated between 100-140 liters/sec in late summer and 1500-1800 liters/sec during winter freshets. The stream morphology is a stairstep of gouged pools, free-fall zones, and fast water around large boulders. The substrate ranges from large boulders to fine silt. Unlike WS 10, Mack Creek has a well-developed armor layer on the bottom, which prevents all but the largest winter storms from moving large particles of sediment. Watershed 10 has no such layer and only the organic debris dams act as protection from stream-bed erosion during winter storms. In WS 10 even small winter storms cause extensive substrate movement in the pools.

Both streams have comparable water chemistry and temperature regimes ranging from 0°C to 15°C, with a mean of approximately 8°C. Water chemistry has been extensively investigated on WS 10 and preliminary results were reported by Fredriksen (1972). The streams are low in dissolved materials, carrying an average concentration of total dissolved solids of 40 mg/liter (Fredriksen 1971).

MATERIALS AND METHODS

Particulate organic material input and export was studied intensively on WS 10 only. The investigation to determine rates of litter breakdown was conducted on both WS 10 and Mack Creek. Litterfall input to the WS 10 stream system was sampled with eleven 1.0-m^2 litter traps placed randomly over the stream. The traps stand on angle iron legs about 0.5 m above the water. Traps are 15 cm deep and each has a removable muslin insert with a mesh opening of 500-800 μm. Litterfall was sampled monthly from March 1972 to March 1973. Litter was sorted into eight categories: cones, leaves, needles, twigs, wood, frass, bark, and fruit; it was dried at 50°C and weighed.

Since WS 10 is at the bottom of a deeply incised basin, organic material also enters by sliding down the bank slope and into the stream. This lateral movement across the forest floor is being sampled by 30 randomly placed, rectangular boxes (0.1 m high by 0.3 deep by 0.5 m wide) with aluminum tray inserts. Traps are placed on the forest floor adjacent to the streambed with the open end (0.5 m) oriented parallel to the stream and facing upslope. Lateral movement is collected monthly. Litter is sorted into categories as above, dried, and weighed.

To determine the rate of litter breakdown and the effect of streamflow on the rate of litter disappearance, a leaf-pack experiment was undertaken on two streams of different size. Four types of leaf litter, representing the predominant streamside vegetation and a range of decomposition rates, were used: conifer needles (*Pseudotsuga menziesii* and *Tsuga heterophylla*), vine maple (*Acer circinatum*), bigleaf maple (*Acer macrophyllum*), and red alder (*Alnus rubra*). In addition, mixed leaf packs consisting of alternating leaves of bigleaf maple and red alder were placed in Mack Creek. Leaves or needles of each litter type were collected at abscission, air dried, and strung on monofilament line to produce a 5- to 15-g leaf pack. Leaf packs were oven-dried (50°C), weighed, tied to bricks, then placed in the stream. Packs were oriented upstream with the current holding the pack against the leading face of brick. Incubation in this manner allowed leaf packs to remain unconfined and completely accessible to all types of invertebrates. As a result, there was a great variation in weight loss due to physical abrasion, decomposition, and shredding by the insects. Nonetheless, this method was preferred over litterbags, since it more closely simulated natural leaf accumulations.

Three leaf packs of each type were collected monthly from each stream and returned to the laboratory for processing. Leaf packs were washed and insects and ancillary debris were removed by hand. Packs were then dried and reweighed to obtain weight loss information. Loss rates were estimated by fitting data to the exponential model $Y_t = Y_o e^{-kt}$. Leaf packs were combined by leaf type and ground through a 40 mesh on a Wiley mill for chemical analysis. Kjeldahl nitrogen content was determined monthly for each leaf type. Phosphorus was determined monthly by digestion in nitric and perchloric acid and reduction with ammonium molybdate and sodium bisulfate for spectrophotometric analysis. Detritus quality was determined by the acid-detergent, lignin-cellulose method of Van Soest (1963).
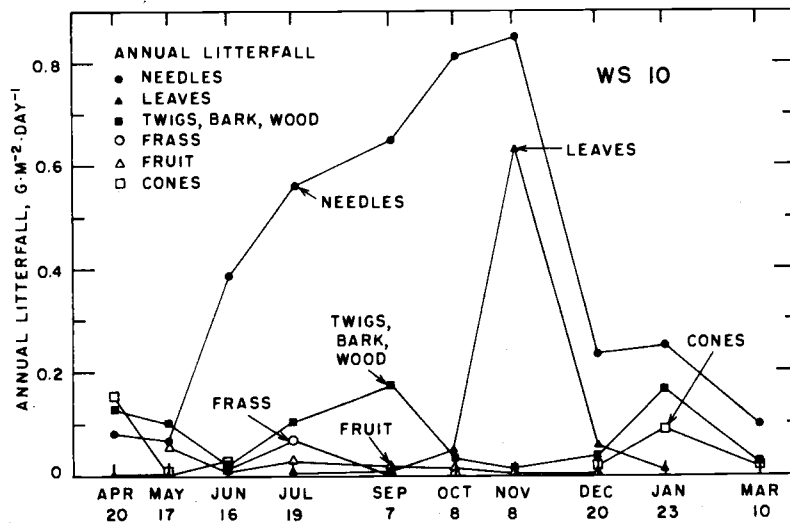

Figure 1. Annual litterfall into watershed 10 by litter type.

RESULTS AND DISCUSSION

Litter Input

Monthly collection of litterfall for a full year indicated a dominance
by coniferous needles (Figure 1). Approximately 65% by weight con-
sisted of litter from Douglas-fir and hemlock. Needle fall occurred to
some extent throughout the year, but was particularly heavy from the
conclusion of the rainy season in June until the return of autumn rains
in November. As expected, major inputs of deciduous leaf material occurred
from mid-October through November. Deciduous inputs consisted primarily
of vine maple and bigleaf maple. Insect frass falling through the canopy
during dry summer months constituted a significant energy input whose role
remains to be clarified. Highly refractory material (twigs, bark, and
wood) constituted 10% of the energy input. On a yearly basis, WS 10
averaged a daily input of 1 g m^{-2}. This value is low c ompared with the
finding of Abee and Lavender (1972), who estimated 1.5 g m^{-2} day^{-1} for
homogeneous reference stands of the same forest.

The first three months of lateral movement sampling (March-May) indicate
that the amount of organic material entering the stream from the bank is
approximately 1.5 times the litterfall. Thus approximately 2.5 g m^{-2} day^{-1}
entered WS 10 in the form of litter. This value is in the low middle
range of a series of values for input of large particulate detritus
(>1 mm) from several eastern streams reported by C ummins et al. (1973).

Litter Breakdown

There were significant differences between streams and among species in
the rate of disappearance of leaf material from the packs (Figure 2).
All species broke down more rapidly in Mack Creek than in WS 10. In the
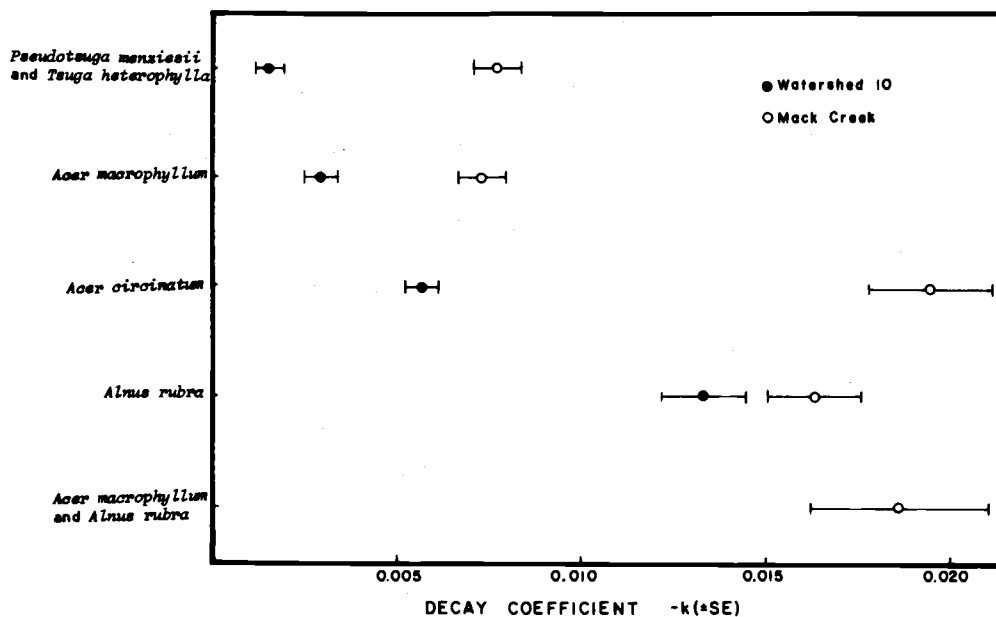single-species packs, coniferous needles disappeared most slowly and alder

Figure 2. Decay coefficients (-k) and one standard error for five leaf-pack types in two Cascade streams.

and vine maple most rapidly. Mixed packs of leaf species that decomposed at different rates, fast for alder and slow for bigleaf maple, resulted in a decay coefficient higher than that of either species individually. This suggests that naturally occurring mixtures of leaves may decompose faster than monospecies leaf packs.

Linear trends of the data on weight loss of vine maple and conifer packs (Figure 3) indicated that regression analysis would be a valid technique for comparing weight losses from the leaf packs for both streams. All regression lines were highly significant ($P < 0.01$). Vine maple packs in Mack Creek lost 50% of their initial weight in 36 days as compared with 123 days in WS 10. Conifer packs in Mack Creek required 89 days to lose 50% of their weight as compared with an estimated 465 days in WS 10.

The differences in disappearance rates for the same leaf species between the two streams might be explained in part by the difference in the num-
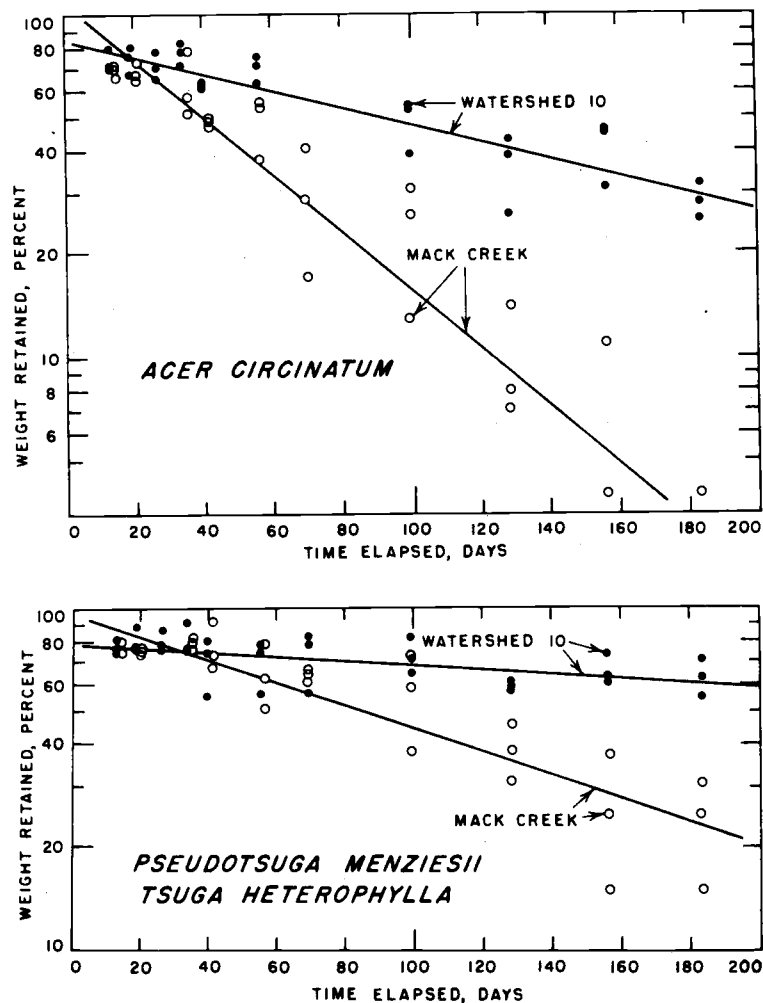

Figure 3. Disappearance rates by weight loss of vine maple (*Acer circinatum*) leaf packs, and Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) needle packs in Mack Creek and the watershed 10 stream.

ber of shredding invertebrates found in the two streams. There were greater numbers and biomass of invertebrates in Mack Creek compared with WS 10. The ratio of invertebrate biomass to leaf-pack biomass was also significantly greater in Mack Creek than in WS 10 (Figure 4). A large percentage of the invertebrate biomass on the conifer packs in WS 10 was composed of small snails. The two WS 10 ratios that rise above the Mack Creek ratios were due to large numbers of snails that appeared in the packs after 90 days' incubation.

The range of rates among leaf species is not surprising in that different leaf species become conditioned by microbial activity at different rates and, thus, more readily acceptable as food for shredding invertebrates (Triska 1970, Boling et al. 1974). Needle litter, generally considered highly refractory, was expected to be exported from the watershed prior to decomposition and to provide only a minor source of food energy for
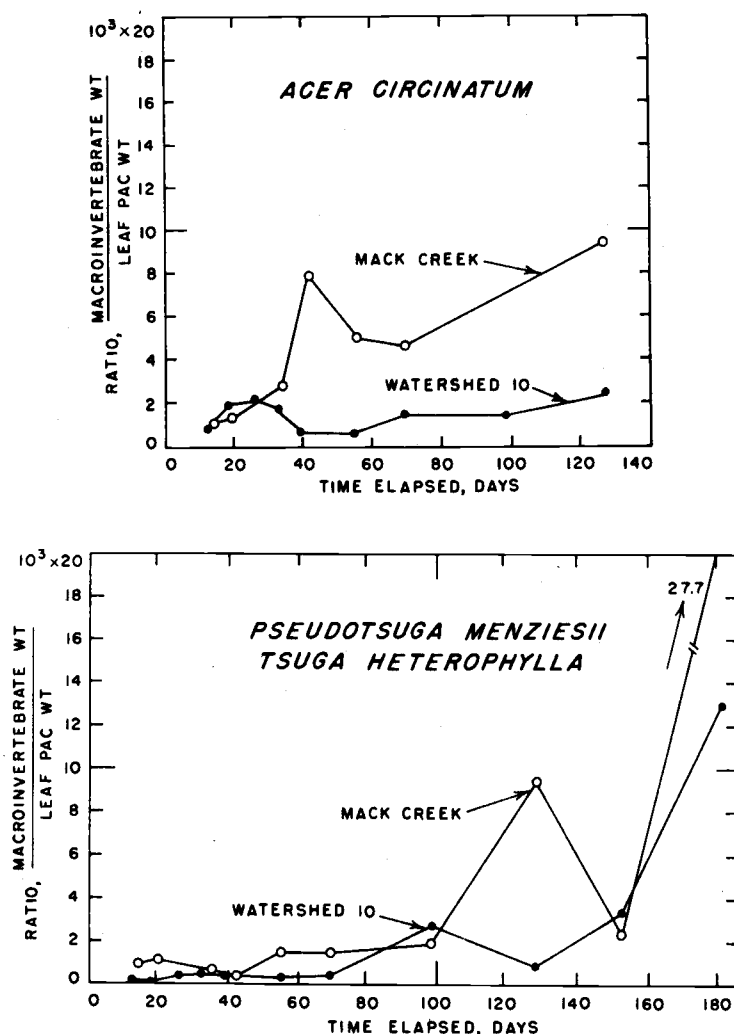
Figure 4. Ratio of macroinvertebrate biomass to mean leaf-pack weight for vine maple (*Acer circinatum*) leaf packs, and Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) needle packs in Mack Creek and the watershed 10 stream.

invertebrates. Conifer packs incubated in Mack Creek indicate, however, that after 140-180 days in the stream needle litter became palatable to shredding insects. After this conditioning, needle packs were heavily grazed by *Lepidostoma* sp. until they were entirely consumed. Prior to conditioning, needles were grazed minimally by insect detritivores.

A comparison of the decay coefficients in this study with other values reported in the literature shows that decay rates in Mack Creek for vine maple, alder, and the mixed pack are much higher than the fastest rates ($k = 0.22$) reported by investigators in Michigan (Boling et al. 1974). The slow decay rates of conifer and bigleaf maple from Mack Creek are in the middle range of their values. The decay rates of conifer needles and bigleaf maple in WS 10 are lower than in the lowest Michigan values. Approximate decay rates calculated for red maple, tulip poplar, and white oak in Tennessee (Thomas 1970) fall within the range of decay coefficients from Mack Creek.

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

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

Since weight loss is a measure of leaf disappearance rather than decomposition, the biochemical parameter of lignin composition was used to obtain an additional index of microbial activity to help separate biotic from abiotic processes. Lignin was chosen since it is the leaf constituent most resistant to decomposition, and therefore increases in percentage of total composition as decomposition proceeds. Changes in lignin were compared with decreases in the most labile fraction, the non-cell-wall constituents. Alexander (1961), Peevy and Norman (1948), and Pinck et al. (1950) have indicated that changes in lignin composition may provide a good relative prediction of litter decomposition rates. In addition Cromack (1973), working in a wet hardwood forest and a white pine plantation, found that the rate of change of lignin content may be the best single criterion predicting leaf litter decay rates.
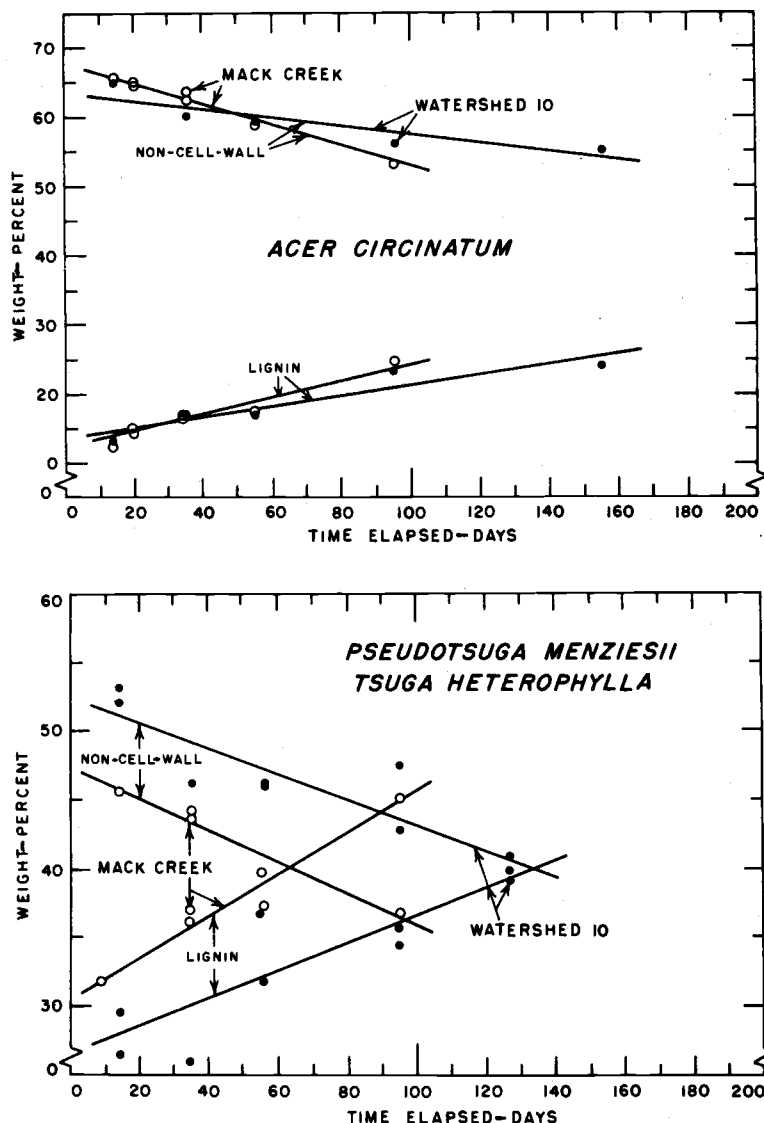
Figure 5. Percent changes of non-cell-wall constituents and lignin composition for vine maple (*Acer circinatum*) leaf packs, and Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) needle packs in Mack Creek and the watershed 10 stream.

In our study, increase in percentage of lignin and decrease in percentage of non-cell-wall constituents (NCWC) were consistent with the weight-loss data for conifer and vine maple packs (Figure 5). The NCWC consists of soluble carbohydrates, soluble protein, organic acids, nonprotein nitrogen, hemicellulose, and additional soluble organic material. The slower increase in percentage of lignin and the slower loss of NCWC in WS 10 than in Mack Creek indicated that decomposition was occurring at a slower rate in the smaller stream. Preliminary data on respiration rates of litter from the two streams also confirm greater microbial activity in Mack Creek.

Changes in litter quality may have proceeded at a slower rate in WS 10 because of fluctuating water levels that occasionally left leaf packs

exposed to air. Although leaf packs remained wet continually, inter-
mittent exposure to air could have altered bacterial and fungal communi-
ties. In Mack Creek all leaf packs were continually submerged.

The differences in processing rates of leaf litter material were also
reflected in the chemical constituents of the litter. Throughout the
experiment percentages of nitrogen and phosphorus for all leaf substrates
were higher in Mack Creek than in WS 10.

Particulate Organic Budget for WS 10

The data gained from the lateral movement and decomposition study provided
an opportunity to construct a first-approximation particulate organic
matter budget (Figure 6). All values were measured independently rather
than by difference; however, the results must be interpreted with caution
because many of the estimates have been based on short-term sampling.

The stream bottom area was esti-
mated at 300 m^2. Measurements
of input were litterfall, lat-
eral movement, throughfall,
algal production, and moss pro-
duction. Throughfall was esti-
mated by G. C. Carroll (pers.
commun.) at 0.1 g m^{-2} day^{-1}
based on a three-day sample.
Algal biomass was estimated at
0.33 g m^{-2} by chlorophyll extrac-
tion; turnover time was assumed
to be 40 days. Moss production
was estimated at 2.1 g m^{-2} yr^{-1}
from Fisher (1970). Standing
crop of detritus was calculated
from 20 core samples, 15 cm in
diameter. Macroinvertebrate
biomass was based on an averag-
ing of two different methods.
The first was a single standing

Figure 6. Annual flux of particulate material biomass (in kilograms
per stream per year) in watershed 10 (1972-1973). The percentage
value associated with each vector indicates the proportion of total
input or output represented.

crop estimate (ten 15-cm cores), with production estimated at 3.5 times
standing crop (Waters 1969). Standing crop was calculated by this method
to be 1.3 g m^{-2}, with an annual production of 4.55 g m^{-2}. The second
method used was year-round emergence data from WS 10 and indicated a
standing crop of 2 g m^{-2}. This value was obtained by assuming emergence
was one-fourth of the average standing crop. Annual production was cal-
culated to be 7 g m^{-2}, using Waters' 3.5 turnover ratio. Respiration of
detritus was based on 100 measurements of five size classes of detritus
at 10°C. Caloric content was assumed at 16.7 x 10^3 J/g (4000 cal/g).

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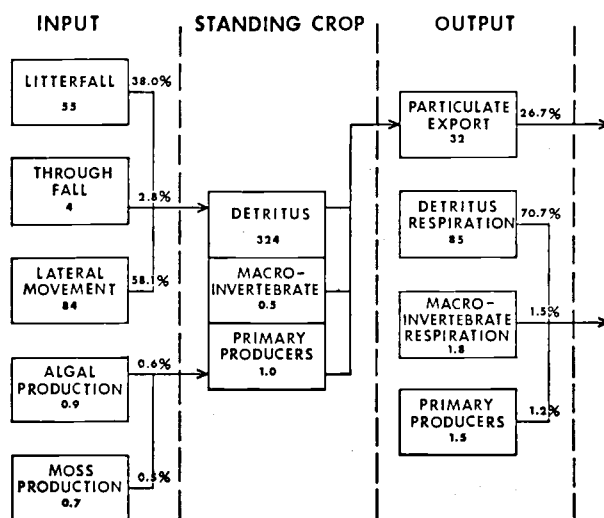need for more accurate assessment of this process.

The same general approach has previously been used by Fisher and Likens (1972) to construct an organic budget for a stream in New Hampshire. This stream has a relatively low gradient (14% streambed slope), receives the bulk of its litter input in the autumn, and has a fairly evenly distributed precipitation pattern of about 123 cm/yr. The Fisher and Likens organic budget assumed the stream was in steady state; that is, the inputs equaled the outputs. In addition, their largest component of the particulate organic output (microbial respiration) was obtained by difference. Watershed 10, as previously mentioned, is a high-gradient stream (45% slope), receives the bulk of its litter input over the summer and fall, and receives precipitation of 240 cm/yr, 90% of which falls in a six-month period between October and March. Nonetheless, for both systems, 99% percent of the particulate organic input is detritus or litter, and 1% or less is contributed by the primary producers. For both streams, about two-thirds of the detrital inputs were processed by organisms in the stream. Only about one-third of the detrital input was exported out of these small streams (Figure 7). Such data indicate small woodland streams are indeed significant biological processing units.

Reichle (1974) has compared some computed metabolic parameters of several different terrestrial ecosystems. The object of his comparison was to demonstrate consistent patterns that could be extrapolated between systems. One such ratio discussed by Reichle is ecosystem maintenance efficiency. This ratio represents the cost of production in an ecosystem and is defined as the ratio of autotrophic respiration to gross primary production. For purposes of comparison, one could assume that detrital input to a stream system is analogous to gross primary production in a terrestrial system. Both represent nearly all the gross energy input to their respective systems. Likewise, detrital respiration in streams could be substituted for autotrophic respiration in calculating an analogous ratio for stream ecosystems.
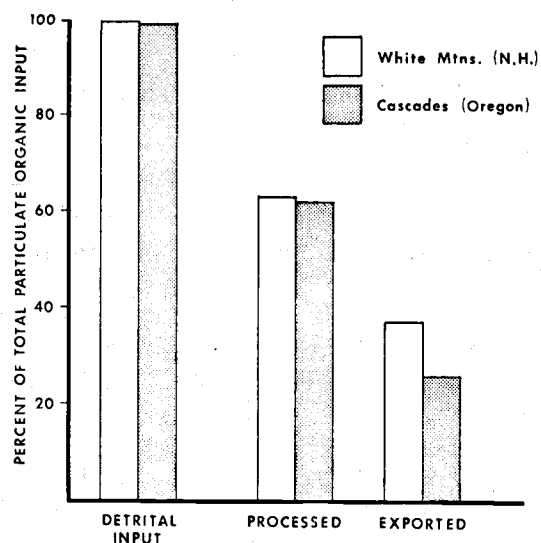
Figure 7. Comparison of particulate organic material input, processing, and export for two small mountain streams, Bear Brook in the White Mountains of New Hampshire, and watershed 10 in the Oregon Cascades.

For three terrestrial systems (coniferous forest, deciduous forest, and grassland) the maintenance efficiencies ranges from 0.53 to 0.62 (Reichle 1974). The corresponding values for the Oregon and New Hampshire streams were 0.59 and 0.63, respectively. These values suggest an unsuspected similarity between terrestrial and aquatic systems.

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cellulose analysis; Nancy Triska for leaf-pack processing; Dick Aho, Ken Brophy, and Ed Grafius for field sampling and sorting; and Ellen Sedell and Bonnie Hall for the line drawings.

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ANALYSIS OF LAKE ECOSYSTEMS: LAKE WASHINGTON DRAINAGE BASIN[1]

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ABSTRACT

Research on four lake ecosystems of the Lake Washington drainage basin is discussed using a hierarchical design depicting the system components nested in four levels: drainage basin, lakes, limnetic and littoral zones, and process models. Comparisons are made of these lakes of different trophic states using parameters inherent to process models. Dynamic processes of the fourth level include phytoplankton, zooplankton, benthos, and fish. Related research activities and information on the Cedar River and Fern and Castle Lakes are discussed.

INTRODUCTION

Analysis of lake ecosystems in the Coniferous Forest Biome encompasses research programs on four lakes of varying trophic states in the Lake Washington drainage basin near Seattle, Washington. This paper presents a systems organization for the lakes within the drainage basin and a summary of research activities for 1972 and 1973. The hierarchical classification incorporates influences of developed and undeveloped watersheds, the trophic conditions of lakes, and detailed process models for food chains and nutrient cycles within each lake.

The principal question addressed by the Coniferous Biome lake program is: If research and theory are combined with mathematical modeling, can a better understanding of the acute and chronic behavior of ecosystems be obtained by studying lakes of different environments and biological communities? Our approach follows the concept that productivity and maintenance of biological structure within lakes is at least partly dependent upon the form, quantity, and flux of organic matter and nutrients from different terrestrial sources and upon internal variations of carbon and nutrient cycles for each lake type. Some of the studies include the assessment of interrelationships between plankton production and nutrient cycles, the effect of organic matter supply on benthic metabolism, and responses of fish populations to the composition and magnitude of food resources. Research and modeling programs are intended to simulate responses of lakes to natural and cultural effects. Such simulations are useful in studying changes in lakes due to thermal discharges, dam construction, dredging, alteration of organic and nutrient loading by industrial and urban development, agricultural practices, navigational management, and logging activities.

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[1]This is contribution no. 66 from the Coniferous Forest Biome and contribution no. 393 from the College of Fisheries, Univ. Washington. See methods section for list of contributors.

STUDY AREA

The Lake Washington drainage basin has two distinct subdrainages, Lake
Sammamish and the Cedar River Valley, which includes Chester Morse and
Findley Lakes.   These subdrainages exhibit contrasting patterns of land
use and morphometric features with differing water, carbon, and nutrient
budgets.   The principal flow of the Sammamish system originates at a low
elevation and drains through Lake Sammamish into Lake Washington.   Lake
Sammamish (12 m elevation, 19.8 km^2, 31 m deep) is a mesotrophic lake
affected by urbanization and some agricultural pollution.   The Cedar
River system originates at higher elevations in the Cascade Mountains,
with nutrient inputs mainly from forested ecosystems.   The upper water-
shed of the Cedar River includes two oligotrophic lakes, Findley Lake
(1131 m elevation, 0.11 km^2, 27 m deep) and Chester Morse Lake (473 m
elevation, 6.54 km^2, 38 m deep), both of which are part of the controlled-

Table 1. Research contributors, determinations, and references for lake studies by the
University of Washington.

Contributors	Determinations	References
Department of Oceanography		
Devol, A. H.	Respiratory ETS	Packard (1971)
Packard, T. T.	do	do
Pamatmat, M. M.	Benthic respiration	Pamatmat and Bhagwat (1973)
Department of Microbiology		
Staley, J. T.	Nitrogen transformations	Mague and Barris (1973)
Department of Civil Engineering		
Barnes, R. S.	Sediments	Birch (1974)
Birch, P. B.		do
Monahan, F. C.		Monahan (1974)
Spyridakis, D. E.		Welch and Spyridakis (1972)
Hendrey, G. R.	Plankton	Hendrey (1973)
Litt, A. H.		do
Pederson, G. L.		Pederson (1974)
Rock, C. A.		Emery (1972)
Stoll, R. K.		Stoll (1973)
Welch, E. B.		Welch et al. (1974)
College of Forest Resources		
Gara, R. I.	Detritus	
Jensen, A.	Logistics	
Olson, P. R.	do	
Rau, G.	Detritus	
College of Fisheries, Fisheries Research Institute		
Berggren, T. J.	Fish	Berggren (1974)
Bissonnette, P. A.	Benthos	Bissonnette (1974)
Burgner, R. L.	Fish	
Casne, S. R.	do	
Chapman, D. G.	do	
Costa, H. H.	do	Noble (1972)
Dawson, J. J.	do	Dawson (1972)
Delacy, A. C.	do	
Doble, D. D.	do	Doble (1974)
Kittle, L. J.	Limnology	
Male, L. M.	Modeling	Male (1973)
Malick, J. G.	Benthos	
Matches, J. R.	Bacteria	Harrison et al. (1971)
Nishimoto, M.	Fish	Nishimoto (1973)
Olney, F.	do	
Richey, J. E.	Modeling	Richey (1974a)
Stober, Q. J.	Benthos	
Taub, F. B.	Benthos	
Thorne, R. E.	Fish	Thorne et al. (1974)
Traynor, J. J.	do	Traynor (1973)
Wekell, M. M.	Bacteria	Harrison et al. (1971)
Whitney, R. R.	Fish	
Wydoski, R. S.	do	
Wyman, K. H.	do	
Hansen, R. G.	do	Hansen (1974)
Departments of Zoology and Botany		
Adams, D.		Adams (1973)
Edmondson, W. T.		Edmondson (1972)
Del Moral, R.		
Tsukada, M.		
Paulson, D. R.		

access municipal water supply area of the City of Seattle. The Cedar
River enters the southern end of Lake Washington and Lake Sammamish
drains into the northern end. Lake Washington (8.6 m elevation, 87.6 km^2,
64 m deep), which is currently recovering from eutrophication (Edmondson
1972), empties through the Hiram Chittenden Locks into Puget Sound. The
contemporary trophic conditions of the lakes have been discussed by Taub
et al. (1972) and Welch and Spyridakis (1972).

METHODS

Research contributors, determinations, and references are presented in
Table 1.

SYSTEM DESIGN

The systems approach for the study of the Lake Washington drainage basin
follows the hierarchical concepts of Overton (1972) and Clymer (1972).
The design depicts system components nested in the following four levels:
level one, drainage basin with inputs, outputs, and budgets for carbon,
nutrients, and water (Figure 1); level two, lakes with different sources
and degrees of organic matter production and nutrient loads (Figure 1);
level three, limnetic and littoral zones of water column and benthic
communities of a lake (Figure 2); level four, process models within com-
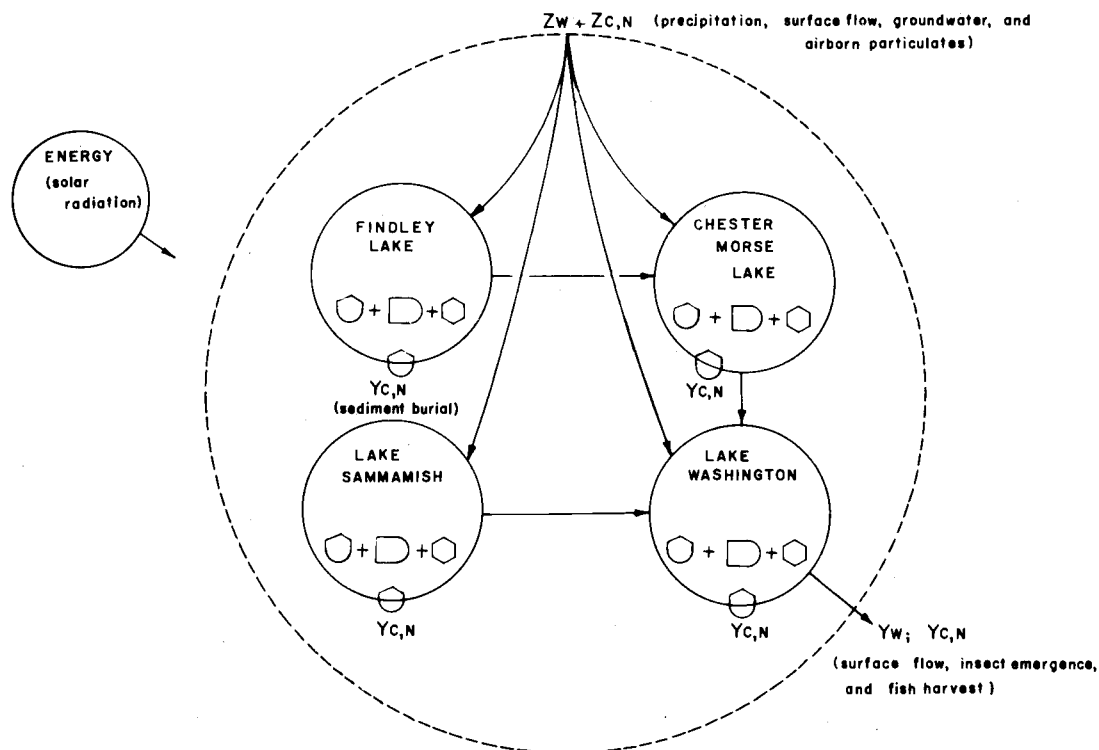munities (Figures 3 and 4).

Figure 1. Inputs and outputs of water, carbon, and energy sources of the Lake Washington drainage basin and lakes.
Z = inputs, Y = outputs, C = carbon, W = water, N = nutrients, ◯ = pools, ▢ = producers, ◯ = consumers.

This organization considers ecosystems as having two dimensions: holistic, according to their overall behavior, and mechanistic, according to how internal parts of the ecosystem are coupled. Holistically, inputs (Z) and outputs (Y) of carbon, nutrients, and water for the drainage and lakes are used for development and discussion of the system (Figure 1).

The mechanistic community couplings (J) and transfers (T) for process models are presented in Figures 2, 3, and 4. The couplings and transfers indicate losses from some levels and gains to others. The hierarchical approach uses a minimum of couplings among such levels as lakes and communities, while most of the transfers are related to detailed internal models. The identification and maintenance of the integrity of couplings is intended to allow different lake submodels to be uncoupled and developed independently of other system levels.

SYSTEM LEVELS

The first level depicts the carbon and nutrient budgets for the Lake Washington drainage (Figure 1). Water acts as the coupling agent and
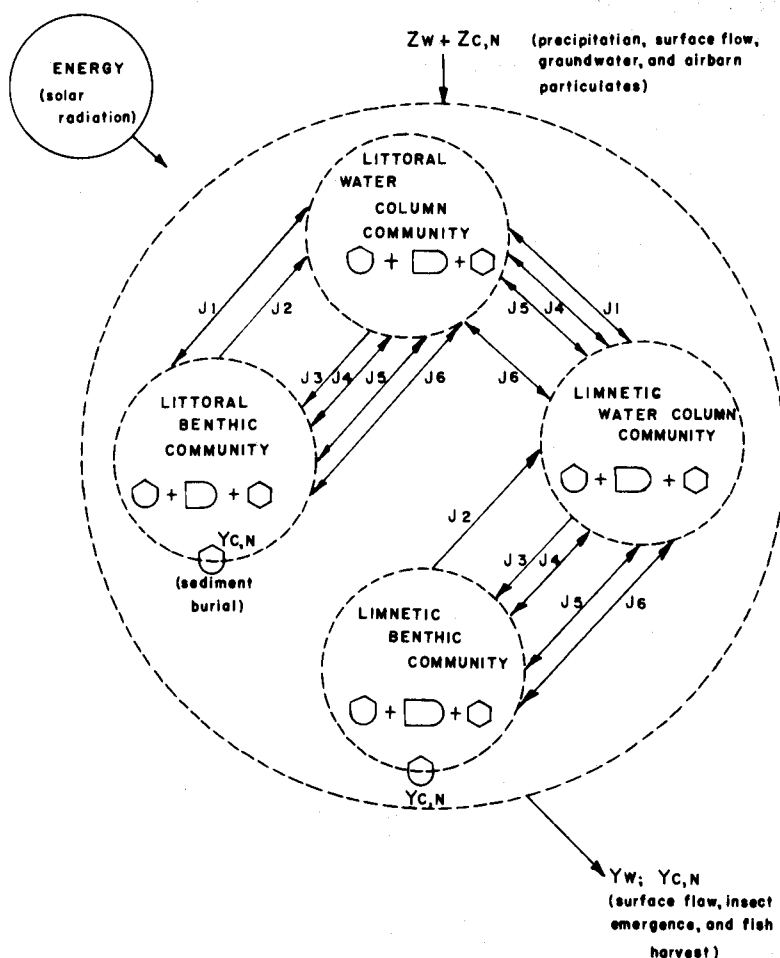
Figure 2. Conceptual lake ecosystem with limnetic and littoral zones of water column and benthic communities. Z = inputs, Y = outputs, C = carbon, W = water, N = nutrients, $\bigcirc$ = pools, $\square$ = producers, $\bigcirc$ = consumers, J = couplings ($J1$ = algal carbon fixation, nutrient uptake and release; $J2$ = fish predation; $J3$ = sedimentation; $J4$ = mineralization, nutrient uptake and release; $J5$ = wind mixing; $J6$ = fish, zooplankton, and insect movement).

74

carrier of carbon and nutrients within the system. Water budgets for some of the lakes are being estimated by measurements of surface inflow-outflow, lake level changes, evaporation, precipitation, and groundwater. Additional information is available from hydrologic and nutrient models of the Cedar River--Lake Washington drainage as developed by the Municipality of Metropolitan Seattle (METRO). Carbon and nutrient inputs include dissolved and atmospheric carbon dioxide exchange, terrestrial litterfall, snowpack release, and point sources for pollution. Energy influences upon the drainage basin include solar radiation and wind stress derived from regional meterological data. Drainage basin outputs include carbon and nutrients lost through substrate burial by sedimentation, water outflows, insect emergence, and fish harvest.

Lakes represent the next level and are described by their nutrient availability, autochthonous and allochthonous sources of organic matter, and resultant biological production and structure (Figure 1). Nutrients and organic matter are transported to lakes mainly by water, which links directly to the edaphic, vegetative, and climatic conditions of a drainage. Additional factors influencing lake productivity include size, slope, and water retention time of a drainage; lake flushing time; currents; surface area; and bottom morphometry. For example, subalpine Findley Lake's productivity is basically dependent upon allochthonous inputs from a forested watershed, and on a short summer growing season

Figure 3. Water column communities of the limnetic and littoral zones. Z = inputs, Y = outputs, C = carbon, W = water, N = nutrients, $\bigcirc$ = pools, $\square$ = producers, $\bigcirc$ = consumers, J = couplings ($J1$ = algal carbon fixation, nutrient uptake and release; $J2$ = fish predation; $J3$ = sedimentation; $J4$ = mineralization, nutrient uptake and release; $J5$ = wind mixing; $J6$ = fish, zooplankton, and insect movement). Compartments: (1) = bacteria, (2) = dissolved and particulate carbon and nutrients, (3) = zooplankton, (4) = algae (phytoplankton), (5) = fish. Transfers: $T4,2$, $T1,2$ = carbon and nutrient uptake; $T3,4$, $T3,1$ = zooplankton feeding; $T3,2$, $T5,2$, $T2,4$, $T2,1$ = carbon and nutrient release; $T5,3$ = fish feeding.

for periphyton and phytoplankton, while productivities of the other lakes are dependent upon land use practices, cultural inputs, and long growing seasons for phytoplankton.

Within each lake are limnetic and littoral zones that constitute the third level (Figure 2). Each zone is further subdivided into water column and benthic communities for nesting more detailed process models of the fourth level. This approach retains nearly all lake inputs and outputs (Z_W; $Z_{C,N}$; Y_W; $Y_{C,N}$). The only difference in transfers for limnetic and littoral benthic communities is carbon fixation by algal periphyton in the littoral community. Similarities between benthic communities include sedimentation; mineralization; nutrient uptake and release; fish predation; fish, zooplankton, and insect movement; mixing; and substrate burial. Allochthonous inputs of dissolved and particulate carbon and nutrients derived from cultural influences are included in transfers of sedimentation and wind mixing. Little if any allochthonous transport is assumed to occur between the boundaries of the limnetic and littoral benthic communities, except for possible lateral movement during
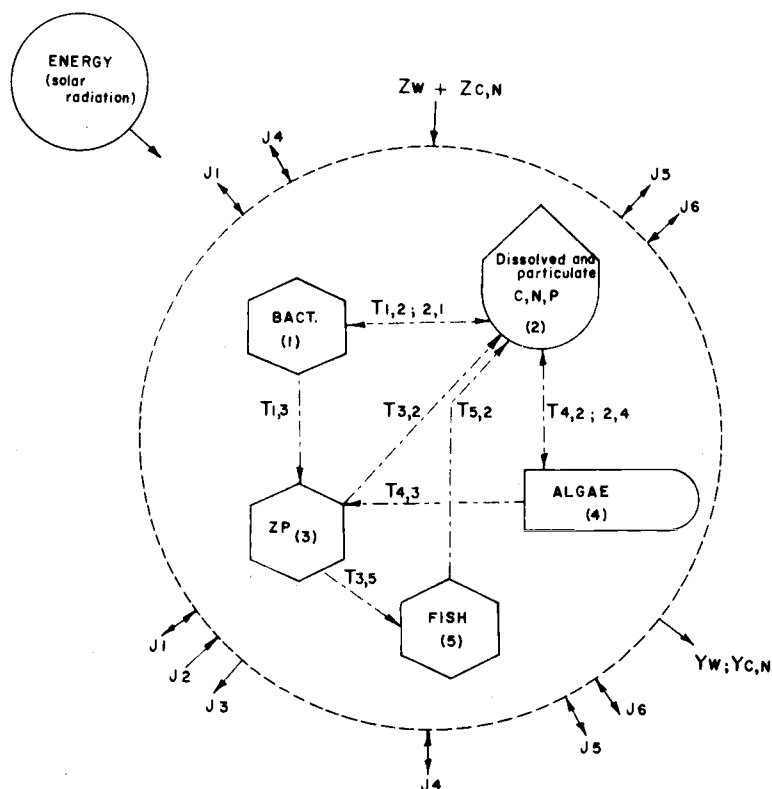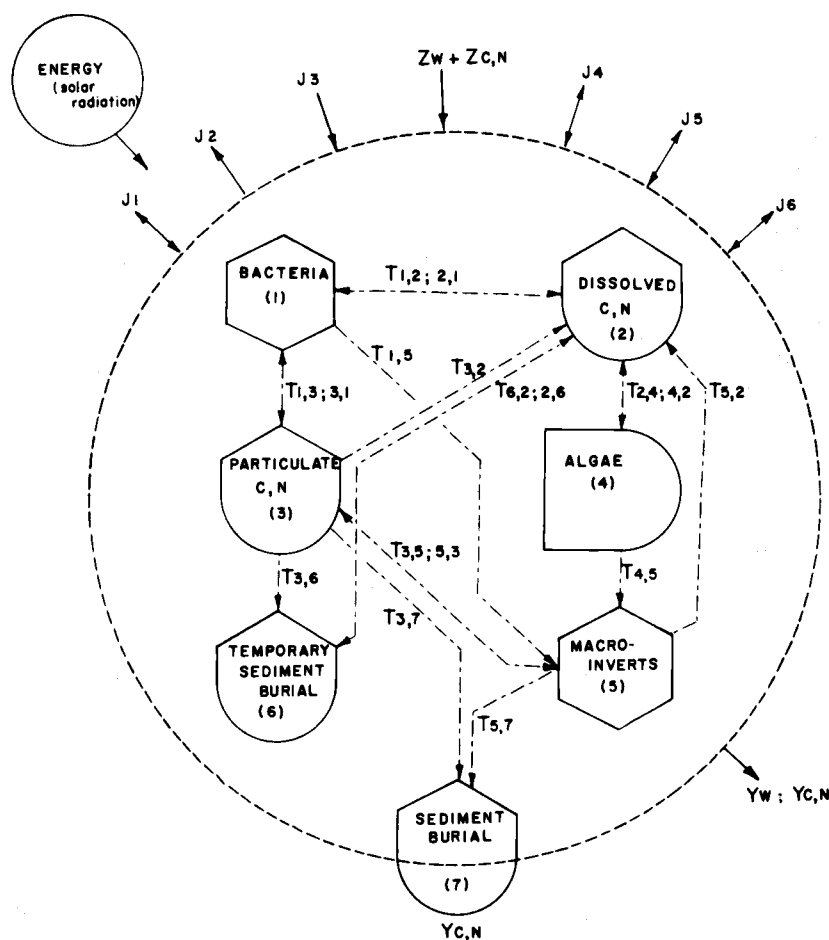

Figure 4. Benthic community of the limnetic and littoral zone. Z = inputs, Y = outputs, C = carbon, W = water, N = nutrients, $\bigcirc$ = pools, $\square$ = producers, $\bigcirc$ = consumers, J = couplings ($J1$ = algal carbon fixation, nutrient uptake and release; $J2$ = fish predation; $J3$ = sedimentation; $J4$ = mineralization, nutrient uptake and release; $J5$ = wind mixing; $J6$ = fish, zooplankton, and insect movement). Compartments: (1) = bacteria, (2) = dissolved carbon and nutrients, (3) = particulate carbon and nutrients, (4) = algae (periphyton), (5) = macroinvertebrates, (6) = temporary sediment burial, (7) = permanent sediment burial. Transfers: $T2,1$, $T2,4$, $T3,1$, $T3,5$ = carbon and nutrient uptake; $T3,2$, $T5,2$, $T1,2$, $T1,3$, $T6,2$, $T5,3$, $T4,2$ = carbon and nutrient release; $T5,7$, $T3,6$, $T3,7$, $T2,6$ = sediment burial; $T4,5$, $T1,5$, $T3,5$ = macroinvertebrate feeding.

sedimentation. Limnetic and littoral communities exist in all lakes
except Findley Lake, where the littoral community predominates throughout
the growing season (July to October).

Process research and models constitute the fourth level and involve the
transfer of carbon and nutrients between pools, processes, and consumers
(Figures 3 and 4). Fourth-level processes include simulation of growth
and feeding for limnetic fish, distribution of benthic-littoral fish and
plankton production, benthic metabolism, and nutrient interactions. The
plankton and nutrient modeling is scheduled to be expanded by an approach
developed by Richey (1974a). Model expansion for limnetic fish includes
optimal foraging, schooling behavior, and distribution in the water column.
Benthic-littoral fish models are currently being constructed for growth,
feeding, and competition. Benthic modeling is conceptual and awaits
further analysis of data sets.

PROCESS MODELING

Primary production by phytoplankton is the principal source of organic
matter formation in many lakes. The amount of carbon fixed or the re-
sponse of algal photosynthesis to natural and cultural inputs of nutrients
and carbon provides a means for initial and long-term assessment of the
effects of eutrophication and consequent management of water quality.
Modeling activities during 1971 to 1973 attempted to simulate quantitative
relationship between nutrient concentrations and differences in phytoplankton
utilization rates, as well as phytoplankton biomass changes, nutrient
supply, and nutrient cycling dynamics of various lakes. The primary
production nutrient cycling submodel (Male 1973) incorporates in situ
and in vitro nutrient experiments, field data, and a system of partial
differential equations for evaluating both the temporal and spatial
dynamics of phytoplankton production.

Process models are constructed such that transfer coefficients can be
formulated from field and laboratory data. For example, a normalized
productivity index (production per biomass per insolation, $[P/B]/I$)
can be obtained by dividing productivity by an estimate of the carbon
biomass and by daily insolation. The $(P/B)/I$ values tend to increase
over time following an actual production peak, so that a $(P/B)/I$ peak
usually occurred later in the growing season. The effect of light
intensity and nutrient availability on the production/biomass quotient
can be examined by the function

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

where μ is P/B, μ_m is maximum P/B, S is inorganic phosphate concentration,
k_t is S at $1/2\ \mu_m$, R is lux, and R_o is optimum lux, was found to describe
experimental results at the 0.05 level of significance, with a high
degree of correlation. It was initially hypothesized that the k_t values
of natural phytoplankton populations were related to the productivity
of the ambient waters in such a fashion that as productivity increases
so does k_t. The half-saturation constant k_t reflects the relative

ability of phytoplankton to use low levels of nutrients. The k_t values obtained were 0.17, 0.36, 0.42, and 2.84 µg P/liter for Findley, Chester Morse, Sammamish, and Washington, respectively. By comparing these k_t values for the four lakes, the direct correlation between the trophic status and k_t confirms this hypothesis for natural phytoplankton communities in lacustrine environments (Hendrey 1973).

Zooplankton models are still at the conceptual stage; however active laboratory and field research is being conducted (see Research Activities).

At present, the limnetic fish model consists of a feeding dynamics and energy budget model for sockeye salmon in Lake Washington. Other major limnetic fish such as stickleback and smelt will be included after completion of successful simulations for sockeye. Emphasis is placed on sockeye because of its unique feeding behavior, "entirely" on zooplankton. This model provides a useful structure for analysis of growth in sockeye salmon and relates to other sockeye salmon producing systems with widely differing zooplankton population characteristics.

Earlier biological studies (Woodey 1972, Dryfoos 1966) have contributed information regarding feeding behavior (food selectivity, vertical migration, feeding period) for sockeye salmon, and to a limited extent for longfin smelt, in Lake Washington. Woodey (1972), Traynor (1973), and Dawson (1972) have provided information on population density, production, biomass, and patterns of horizontal movement for all three major limnetic fish species (sockeye salmon, longfin smelt, and three-spine stickleback) in Lake Washington. Berggren (1974) has provided similar but less complete information regarding Lake Sammamish sockeye. D. M. Eggers has constructed a process-oriented model for the limnetic growth of sockeye salmon, consistent with behavioral patterns observed in the above studies. The effects of the external variables such as light and water temperature are provided in the model. These allow us to study energetic implications of the observed feeding behavior of salmon, which include diel vertical migration and the limitation of feeding to hours of dusk and dawn. The model is tied to the wider ecosystem structure through two major couplings. These are species-specific grazing rates on zooplankton and release of carbon, nitrogen, and phosphorus through excretion of metabolic wastes (Figure 3). The present limnetic growth model utilizes the Holling (1966) concept of predation extended to a multiple-prey situation. Optimal foraging theory combined with specific rates of prey size encounter and prey species capture success allows one to predict that component of the total zooplankton population encountered which is utilized by the predator. The predator's strategy of prey utilization changes seasonally. The above model gives us the potential ability to study successional changes exerted on the zooplankton population by limnetic fish predators, which will be realized only when the model is coupled with the model of the zooplankton population dynamics incorporating selecting predation.

The present model incorporates a single predator, with five species of zooplankton prey. The zooplankton population density and size distribution by species are inputs, together with the environmental variables of light intensity and temperature. There exist three components of the model: predator-prey interactions, other predator behavioral processes, and growth of the predator. They are discussed below.

The predator-prey interaction model component relates quantity of prey consumed by the predator and is an extension of earlier work by Charnov (1973) and Werner (1972). The general form of the model is:

$$C_T = \frac{\sum\limits_{i \in A} \int_{L_i}^{U_i} \lambda_i(\xi)N_i(\xi)[S_i(\xi)C_i(\xi) - E_i(\xi)] \, d\xi}{1 + \sum\limits_{i \in A} \int_{L_i}^{U_i} \lambda_i(\xi)N_i(\xi)H_i(\xi) \, d\xi} \tag{2}$$

where C_T is net carbon consumed, (L_i, U_i) is size interval of prey species i that are pursued when encountered by the predator, A is a set of prey species available to the predator, $\lambda_i(\xi)$ is a function that yields encounter rate for a given size ξ of the ith prey species, $S_i(\xi)$ is function that yields the proportion of prey successfully captured when pursued for a given size ξ of the ith prey species, $H_i(\xi)$, is a function that yields the total time needed to pursue, capture, and eat an individual size ξ of the ith prey species, $C_i(\xi)$ is carbon content of an individual of size i of the ith prey species, $E_i(\xi)$ is expected carbon expended by the predator per pursuit of an individual of size ξ of the ith species, and $N_i(\xi)$ is density of prey size ξ of the ith prey species.

The feeding behavior model simulates sockeye salmon encountering a number of prey species, consisting of individuals of varying size. Because encounter rate increases with size of the prey, larger individuals of a given species are encountered more frequently than smaller individuals of the same population density. Hence they occur more frequently in the diet. Even if the predator is taking all prey as encountered, there is a difference between the size distribution of the prey in the stomachs and prey in the water column.

To illustrate this point, the model was used in simulating the results of an experiment conducted by Brooks (1968). Here, 65 *Alosa pseudoharengus* were put in a 250-liter aquarium. At the outset of the experiment the aquarium contained a known density of five size classes of *Diaptomus minutus*, together with incidental *Epischura nordenskiöldi* and *Daphnia catawba*. These large prey disappeared quickly and are ignored in application of the model. The effect of the predation by *Alosa* was measured by following the density of the five size classes over the course of the experiment. The density of the larger size classes declined much faster than the density of the smaller size classes.

In the application of the model, the predator exploited five prey types of constant size. Encounter is a Poisson process, where the expected number of encounters is simply the product of volume searched in a unit of time and the prey density. The volume searched depends upon a constant parameter that is a property of the predator. The parameter is the minimum angle of visual perception. Hence prey of different sizes are perceived at varying distances, with larger individuals seen at greater distances than smaller individuals. Handling time was assumed to be constant for each of the given size classes. A minimum angle of vision of 0.02088 radian with the predator searching at one length per sec, and with 1.84 sec to pursue, capture, and eat a prey once that prey is encountered, generated and predicted densities presented in Figure 5.

In this case the predator is pursuing all prey as they are encountered, and the predator is not being selective in the sense of actively avoiding encountered prey.

The total carbon ingested depends on which prey are pursued when encountered. D. M. Eggers has shown that there exists a unique optimal set of prey organisms for which C_T in equation (2) is maximized when only prey contained in that set are pursued when encountered. That is because it takes time for the predator to pursue, capture, and eat its prey regardless of prey size. Hence the predator can more efficiently use its time by pursuing only the larger prey, provided that large prey are sufficiently abundant

Figure 5. Results of simulating an experiment by Brooks (1968). Time course of predatory mortality of size classes of *Diaptomus minutus* when fed upon by *Alosa pseudoharengus*. X = adults, O = copepodid III+, △ = copepodid II, + = copepodid 11, □ = nauplii. Results were generated by differential rates of encounter due to prey sizes.

and can be easily captured. Given suitable information on prey density, size distribution, and parameters that related the predator's ability to encounter and capture the prey, the optimal set can be computed numerically.

The seasonal pattern of prey utilization by juvenile sockeye salmon in Lake Washington can be generated assuming the predator is feeding optimally. This pattern results from the seasonal change in the prey population and increasing efficiency of capture of large prey with the growth of the salmon.

In the spring as the salmon first enter the limnetic area of the lake, they exploit medium-sized *Diaptomus* and the large *Epischura*, ignoring the abundant but smaller *Cyclops*. As the season progresses, *Epischura* increases in abundance and the large cladoceran *Diaphanosoma* begins to appear in the water column. At this time the sockeye cease utilizing the now very abundant *Diaptomus* and take only the *Epischura* and *Diaphanosoma*, which are much rarer. In the late autumn *Diaphanosoma* and *Epischura* are virtually the only organisms consumed by the sockeye. In some years *Epischura* become very sparse during the winter. During the winter in these years *Diaptomus* as well as *Epischura* are taken by the sockeye. There is evidence to suggest that when the salmon are small they are less effective in capturing large zooplankton, and learn to capture them more effectively as they grow. There is a lag between the times the *Diaphanosoma* appear in the water column and the times they appear in the sockeye stomachs in proportion to their density. Since the *Diaphanosoma* are very mobile, the salmon may require a period of time to learn to capture these organisms.

Additional processes monitor whether the predator is feeding or non-feeding, location of feeding in the water column, and schooling. (1) The time that the sockeye are actively feeding depends on light intensity and level of hunger in the predator. This feeding time has definite seasonal trends and reflects temperature influences on digestion rate and inability of
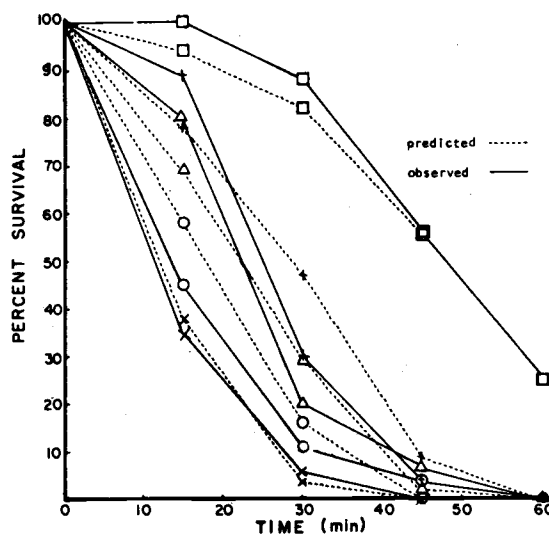
large predators to fill their guts during fall and winter. A very high
level of hunger appears to be necessary to initiate feeding, which con-
tinues until satiation or darkness. Once feeding ceases it is not
reinitiated until the hunger threshold is reached. (2) Vertical migra-
tion and location of feeding in the water column depend upon light
intensity and temperature. There exist maximum light and temperature
levels that the salmon can tolerate. (3) Schooling occurs when light
is above threshold levels. Schooling, an antipredator device, serves
to reduce foraging success. Visual fields overlap among members,
resulting in competition for available food.

Growth in the limnetic feeding model is realized through a system of
differential equations that depend upon size of the fish and temperature.
These equations partition ingested carbon into the various metabolic
pathways of standard metabolism, specific dynamic action, activity level,
and growth. In addition to growth, outputs from the model include waste
material supplied to nutrient pools in the water column (see Figure 3).

The level of food in the stomach reflects hunger, which cues the initia-
tion of feeding. The lag between the time food is ingested and when it
becomes metabolizable energy is incorporated in the system of differen-
tial equations.

The second major fish group in Lake Washington is composed of benthic
and littoral fishes. These fishes, numbering 28 species in Lake Wash-
ington, represent a major proportion of the standing crop and production
in the lake. Of these 28 species extensive data sets are being developed
for the three most important species (yellow perch, squawfish, and pea-
mouth) for implementing the benthic and littoral fish model.

The benthic and littoral fish model is organized to be operated as both
an independent predictive fish model and as a predictive model integrated
to the complete aquatic modeling program. The model is to predict
standing crop and production by regions or strata in Lake Washington.
To do this, three basic submodels are employed. The first, a migration
or distribution model, is used to predict movements of the fish species
as a function of water temperature and temperature differences between
strata. The second submodel is a conventional year class population
dynamics model that predicts numbers, reproduction, growth, standing
crop, losses, and production of each age group of a particular species.
The third submodel is a growth and feeding model that predicts changes
in growth rates and feeding rates, based on population information from
the population dynamics model and information from other major aquatic
models on the size of the food base and its availability. A fourth model,
an information-integrating slave model, is used to link separate species
together. This competition model uses information from the three major
submodels of each species and predicts necessary changes in food base
available to each species as a result of the existing population conditions
for each species. Its outputs go to the growth and feeding model.

The first submodel, the distribution model, is founded on Coniferous Forest
Biome data and results given by Bartoo (1972). Bartoo mapped the distribu-
tion of the three major benthic and littoral fish species of Lake Washington
(peamouth, yellow perch, and northern squawfish) by strata for each

season of the year. He further correlated the distribution of the fish to a preferred temperature regime within the lake. Using these results, a simple deterministic model was constructed that predicts biomass flow of each species between strata, based on temperature differences between the strata. Flow rates are controlled by a simple exponential using a time constant. Figure 6 shows the observed data (derived from Bartoo 1972) and the results predicted by the model. The fit is good, with few discrepancies in the present model and results shown in Figure 6.

The second submodel, the population dynamics model, is based on life history studies by Nishimoto (1973), F. Olney, R. S. Wydoski, and R. Whitney (pers. communs.), as well as catch statistics supplied by N. Bartoo, F. Olney, J. Traynor, and M. Nishimoto of the College of Fisheries, University of Washington. Each of the life history studies

Figure 6. Predicted (---) and observed (●) peamouth biomass distribution in Lake Washington.

supplies, for a major species, data and functions expressing growth, basic food habits, reproductive capabilities, and other relationships. Estimates of natural mortalities and equilibrium population estimates were made by N. Bartoo as part of the model construction. Portions of this submodel have been validated. Incorporated in the model is a finite-difference Malthus-type representation of population survival as a result of natural mortality. This portion has been validated. Production is the product of growth rate x biomass (Ricker 1971), and allows for changes in natural mortality rates as well as growth rates. Fecundity rates and egg deposition are calculated using life history data. The only unmeasurable rate for which literature approximations are needed is the survival rate from egg deposition to recruitment àt age 0. Other necessary rates are supplied for equilibrium conditions and are adjustable by the submodels for competition and for growth and feeding. Model results are available for most of the submodels and functions of the population dynamics submodel.

The third submodel is a growth-regulating feeding model. This submodel will assess the demands of the population using consumption rates, food habits, and feeding strategies. The demands will be expressed in terms of required biomass of a specific food base. Few data other than for benthic invertebrates (Bissonnette 1974) have been taken that are applicable to this stage of the modeling effort. The future plans call for an assessment of the abundance and distribution of the principal food base and the feeding rates and strategies of the three major benthic and littoral fish species.
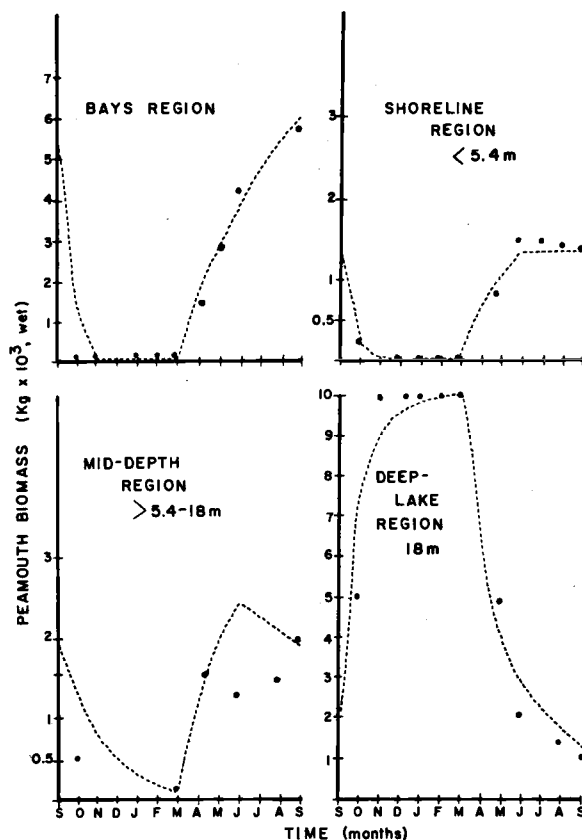
The fish feeding studies will function as the basis for linkages between the three principal fish species. The competition model, as formulated, takes the projected required food base needs for each species, computes the total demand for a given food base, and compares the total demand for the available biomass. In case of marked competition, the demand for the available food base may exceed 100% of the base. Based on observed feeding strategies and expected success in the face of increased competition, each species will be allotted less of the food base than required for continued maximum growth, thus the growth and survival rates will be modified. In order that the several benthic and littoral fish populations can be linked together and to allow for competition and changes in population parameters, the necessary feeding data are being estimated.

The benthic and littoral fish model, in addition to acting as a submodel of the general aquatic model, will be independently able to address the following principal types of questions: (1) What relationships exist between production and nutrient pools and the recycling of nutrients to the other aquatic processes? (2) What is the relative importance of the spatial distribution of benthic and littoral fishes relative to their effects on distribution of food organisms and nutrient recycling into different strata? (3) How much energy is transferred to and from the benthic and littoral fish populations? (4) How do the benthic and littoral fish populations behave with changes in competition from other species? (5) How do the benthic and littoral fish populations and their distributions respond to perturbations of the aquatic system such as changes in water temperatures caused by localized water heating, fish harvests, selective fish eradications, changes in food bases, and introduction of competing fish species?

RESEARCH ACTIVITIES

Plankton-nutrient cycling research on the four lakes includes seasonal patterns of phytoplankton productivity, biomass, respiration, growth kinetics, cell size, composition, light conditions, and nutrient supply; and zooplankton populations and grazing rates; and uses modeling to simulate and evaluate the temporal-spatial dynamics of plankton production. A comparison of several trophic status indicators in these four lakes is presented in Table 2.

Experiments have shown that the phytoplankton, from oligotrophic to mesotrophic lakes and under varying light conditions, were all stimulated

Table 2. Comparison of trophic status of four lakes in the Lake Washington drainage basin (average yearly values).

Lake	Total P (µg/ℓ)	PO_4-P (µg/ℓ)	NO_3-N (µg/ℓ)	Chloro-phyll a (µg/ℓ)	Productivity (mg C m^{-2} day^{-1})	Secchi (m)	ETS (mg O_2 m^{-2} hr^{-1})	$k_t(PO_4)$	N fixation
Findley	11.4	3.1	5.41	0.6	220	16.4	9	0.17	insig
Chester Morse	6.9	2.1	9.36	1.1	262	8.3	13	0.36	insig
Sammamish	48.0	7.0	86.0	7.11	499	3.5	2	0.42	sig
Washington	18.7	1.1	56.5	9.5	1070	2.3	55	2.84	sig

by phosphorus concentrations as low as 1 µg P/liter. The light treatments had less effect than was anticipated; the greatest response to light intensity was found at the lowest nutrient concentrations. It appears that cells grown at higher nutrient concentrations achieve their maximum growth response regardless of light intensity because of light adaptation, while cells at lower nutrient concentrations, being relatively nutrient starved, are unable to make physiological adaptations to varying light regimes.

Concurrent investigations included the relative contributions of three size classes of the phytoplankton to lake productivity in four lakes of contrasting trophic state. Some of the routine in situ carbon-14 productivity samples were fractioned by selective filtration into net, nanno-, and ultraplankton by passing the carbon-14-labeled sample through a stacked series of three filters of 50, 5, and 0.45 µm nominal porosity. The results for the ultraplankton were not entirely successful because of filtering characteristics of the 5-µm filter (E. B. Welch and G. R. Hendrey, pers. communs.). Except in Findley Lake, the contribution of the net plankton to that of the total community increased in a nearly linear fashion with lake productivity. The discrepancies in Findley may result from a lack of disruptive circulation, allowing the inclusion in the net plankton of cells that in the other lakes would have passed into the nannoplankton. In all four lakes the relative contributions of the net plankton to productivity were at a maximum early in the growing season in response to increased temperature during a period of relatively high nutrient concentration (Hendrey and Welch 1974). The hypothesis that the relative contributions of the various size classes of the phytoplankton communities are related to the overall productivity of the lake is supported by observations both in nature and experimental research (Hendrey 1973).

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

Plankton research has included estimates of the seasonal distribution of the respiratory electron transport (ETS) activity and nitrogen fixation in the four lakes (Table 2). Respiration and nutrient regeneration rates for net plankton in the euphotic zone have been calculated from ETS activities (A. Devol, pers. commun.; Packard et al. 1974, Conover and Corner 1968, Beers 1964). Nitrogen fixation rates were determined periodically by the acetylene reduction technique at three depths in each of the lakes. Fixation began in June in Lakes Washington and Sammamish and peaked during July and August. Chester Morse and Findley Lakes did not exhibit acetylene reduction activity until August and the rates encountered were much lower than in the other two lakes.

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

Grazing rates of zooplankton (in situ) were partitioned for three phytoplankton size classes (same sizes as previously described) to assess the effect of feeding on particle size and to relate to concurrent studies on fractioned phytoplankton productivity and nutrient responses. Zooplankton grazing appeared to account for a considerable proportion of the loss of nannoplankton in all lakes except for more eutrophic Lake Sammamish, where blue-greens and net plankton are more frequent and detritus feeders are favored. Grazing of phytoplankton by zooplankton stimulated photosynthetic carbon uptake in the light in excess of 200% over ungrazed populations. Phytoplankton loss rates from grazing ranged from 0.002 to 0.268 µg chlorophyll *a* per animal per day. Feeding was found to be maximum at low concentrations of algae. These rates account for from 2% to 247% of the average growing season productivity in the lakes. Net plankton (>50 µm) were seldom grazed and, since that size fraction and algal mass in general increased with mean productivity and nutrient content in the lakes, such decreasing efficiency in food transfer is seen as a major effect of eutrophication (Stoll 1973).

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

Investigations of the limnetic fish populations of Lake Washington were continued through 1973. Population estimates were established through the acoustical procedures developed under the Sea Grant program and were used in conjunction with biological information obtained from midwater net sampling to obtain point estimates of abundance and biomass. From these, growth rates and production of the different species were deter-

mined. Seasonal patterns in population parameters and changes in the horizontal and vertical distributions of the major pelagic species and year classes in the lake were analyzed also. A high correlation was found between the distribution of densities of the 1971 year classes of sockeye salmon and longfin smelt, and was hypothesized to be due to physical factors acting simultaneously on the two species. A comparison of the vertical distributions of the major pelagic species provided a highly significant multiple correlation coefficient, perhaps indicating that the same factors controlled the vertical distribution of each species.

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

Estimates of the abundance of presmolt sockeye salmon in the lake were used in conjunction with estimates of adult escapement for further definition of the spawner-recruit relationship for the Lake Washington sockeye salmon run. A major goal in the continuing work on the spawner-recruit model is to develop the capability to predict escapement accurately from acoustic estimates of smolts prior to outmigration (Traynor 1973).

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

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

The amount of food consumed, size of fish, and time of year were noted. Estimates of the rate of gastric evacuation were made by length group of fish from nighttime samples. Inherent in the procedure was the assumption that no feeding occurs at night and that the volume of stomach contents decreases with time. The results indicated a decrease in a rate of gastric evacuation with increasing size of fish and with advancing time of year, the latter probably as a result of decreasing night temperature of residence. The daily ration was computed by length group of fish from samples collected throughout the 24-hr sampling period. The

procedures assumed that on the average the rate of food consumption equals the absolute value of the rate of gastric evacuation. The amount of food consumed increased with increasing size of fish; however, expresse as a percentage of body weight, it decreased. Food consumption reached a peak in autumn. Comparisons of stomach contents with the simultaneously collected plankton samples indicated selection of the larger prey species. Some differences in diet with respect to size of fish were noted in summer (Doble 1974).

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

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

The Chester Morse Lake study is designed to determine the population sizes, age and growths, length-weight relationships, fecundity, sex ratios, mortality rates, and feeding habits of rainbow trout (*Salmo gairdneri*) and Dolly Varden (*Salvelinus malma*). Biomass and production of the two species are being estimated from this information. Peterson estimates from the August data result in population estimates of 4650 $\leq$8138 $\leq$15,752 rainbows and 1684 $\leq$3015 $\leq$6147 (α = 0.05) Dolly Varden. A Schnabel estimate over the eight-month sample period results in population estimates of 9830 rainbows and 1305 Dolly Varden. Age determinations are being completed to calculate age distributions of sampled populations. The feeding habits of pygmy whitefish, *Prosopium coulteri*, and the age, growth, and fecundity are being incorporated in the discussion of this significant food item of Dolly Varden. Rainbow data will be used in the basic population dynamics model.

Development of studies on benthic processes is based on distinct transfers with the plankton community and between internal compartments of benthic communities. The benthic community of a lake is being considered as dependent upon transfers of energy, carbon, and nutrients from sedimented organic and inorganic matter into paths of substrate burial, chemical oxidation, microbial-macroinvertebrate metabolism, fish predation, and insect emergence. Sedimentation; exchange of carbon, nitrogen, and

phosphorus; and carbon fixed by periphyton are linked to the available carbon, nitrogen, phosphorus, and microflora-mesofauna components of the benthic community. Sedimentation measurements include inputs of major cations, heavy metals, and dissolved and particulate carbon, nitrogen, and phosphorus from endogenous organic matter production, and organics and inorganics from exogenous sources. Exchange of carbon, nitrogen, phosphorus, and oxygen by the benthic community occurs during chemical oxidation, oxygen consumption, microbial mineralization, and macro-invertebrate respiration (Figure 4).

Sedimentation patterns were measured in the four lakes of the Lake Washington drainage basin. More extensive treatment of sediment fluxes were made in Findley Lake and sediment nutrient regeneration from in situ Lake Sammamish experiments. Sediment aliquots were analyzed for total carbon (99% organic carbon), phosphorus, nitrogen, and iron and a number of trace metals. Basic differences in the lakes have been assessed by elemental fluxes, percent contents, and ratios of carbon: nitrogen, nitrogen:phosphorus, and carbon:phosphorus. The sediment trap data indicate that a major input to Findley Lake is allochthonous organic while in Chester Morse Lake inorganic inputs from either bottom sediment resuspension or from allochthonous sources are predominating. The sedimentation data from Lake Sammamish indicate the relative importance of inputs, especially of phosphorus and iron, from sediments brought about by the reduction of Fe^{3+} and dissolution of phosphorus in the oxygen-depleted sediment-water interface. Seasonal plankton sedimentation data rank the lakes in the same order relative to productivity as measured by carbon-14 assimilation: Lake Washington > Lake Sammamish > Chester Morse > Findley Lake (D. Spyridakis pers. commun., Birch 1974). Physical and chemical characteristics of the lake sediments have been measured by Bauer (1971) and Horton (1972).

Research on the contribution of allochthonous inputs to the particulate carbon and nutrient pools of the benthic community are being conducted at Findley Lake. Particulate carbon enters the lake by litterfall, surface runoff, and snowmelt, and is composed mainly of needles of western hemlock (*Tsuga heterophylla*) and silver fir (*Abies amabilis*). Litterbags of conifer needles are being used in decomposition studies by measuring weight loss and changes in nutrient content (G. Rau pers. commun.).

Pollen, diatom, and sedimentary chlorophyll analysis of Findley Lake indicates distinct relationships between the aquatic and terrestrial environments. Any severe disturbance of the terrestrial environment caused shifts in the aquatic ecosystem. These changes often involved a sequence of changes in the dominant diatom present. Further, the pattern of changes in the aquatic ecosystem tended to be related to the type of disturbance in the surrounding watershed, for example, forest fires. Sedimentary chlorophyll either did not change significantly or varied in relation to changes in the number of conifer needles in the sediment (Adams 1973).

The sediment nutrient regeneration studies in Lake Sammamish involved the incubation of six sediment-water columns in enclosed cylinders. Starting in the fall of 1972, water samples were removed from the columns and analyzed for total phosphorous and total soluble phosphorus, total

and soluble iron, dissolved oxygen, and alkalinity. Specific conductance, pH, temperature, total nitrogen, total soluble nitrogen, NO_3-plus-NO_2-N and NH_4-N were also monitored. This experiment was repeated in the spring of 1973 employing the same methods. Differences in the rates of phosphorus and iron release as well as oxygen depletion are easily attributable to the distinct temperature regimes observed in the lake water during the winter and spring incubations. The loss of oxygen was accompanied by increases in phosphorus, iron, and nitrogen contents. Conductivity and alkalinity increased while pH decreased to 6.8 in most cases.

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

With respect to nitrogen, NO_3-plus-NO_2-N generally decreased in the columns but did not disappear. In most cases NH_4^+-N was initially increased to between 150 and 180 µg/liter before decreasing to values less than 100 µg/liter. In general it was found that total inorganic nitrogen increased 20%-25% above the initial levels followed by a marked decrease in the later stages of incubation. This decrease represented a 40%-50% loss of the initial inorganic nitrogen contents. It appeared that as the anoxic conditions became more pronounced there was a loss of nitrogen from the system by biological or chemical denitrification, or both.

The maximum rates of phosphorus release were from 4 to 6 mg m^{-2} day^{-1} at temperatures between 6° and 10°C and increased to 11-15 mg m^{-2} day^{-1} at temperatures between 10° and 18°C. The maximum amount released was not a function of temperature. The release of phosphorus in the columns increased to a maximum between 550 and 600 mg/m^2 for total phosphorus and 350 and 400 mg/m^2 for total soluble phosphorus. These values compared well with those obtained for the lake but were 50%-60% lower than those in a laboratory experiment conducted at 25°C under completely mixed and anaerobic conditions. Comparison of the maximum amounts of phosphorus in the in situ column and in 30-m-deep lake water column with the surface (10-cm-deep) sediment phosphorus contents revealed that as much as 19%-20% of the sediment phosphorus was released in both cases. The corresponding maximum iron values in the water columns represented 4%-5% of the amount of iron in the surface sediments.

It can be concluded that sediment phosphorus release is a primary input factor in the dynamics of phosphorus in the lake. The release of phosphorus from the sediments could supply enough phosphorus to support summer production in Lake Sammamish provided that a lake mixing mechanism

were available to supply hypolimnetic phosphorus to the photic zone. About 75% of the total phosphorus released into the hypolimnion of the lake is supplied by the sediments, on the basis of the in situ column study results. The lack of response in the trophic status of Lake Sammamish following sewage diversion in 1968 could very well be attributed to this demonstrated ability of lake sediments to supply large amounts of nutrients to the lake water column. It will be difficult to anticipate any changes in the nutrient status of the lake within a time period comparable to that observed in Lake Washington case, as long as hypolimnetic oxygen deficits continue during stratified periods (D. Spyridakis pers. commun., Monahan 1974).

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

Mineralization of organic compounds in the benthic community by bacteria has been assessed by [14C]glucose uptake. Sediment samples have been collected and analyzed from the four lakes. The rate of glucose mineralization by the bacteria was measured by incubating sediment and uniformly labeled [14C]glucose at the in situ temperature. In each lake sampled, the bacteria associated with the shore sediment were more numerous and exhibited a higher rate of glucose mineralization than those found in the sediment of deepwater stations. In all lakes the glucose mineralization rate was greater in summer, decreased in fall, and attained a minimum value in winter and early spring. Sediment samples collected in winter were incubated at the in situ temperatures prevailing at other seasons of the year. The rate of glucose utilization or turnover time fell very close to the rates obtained at the different seasons. Samples collected during the summer and tested under conditions prevailing during colder periods also gave excellent results. These data indicate that the temperature in the environment has a great influence on the activity of the bacteria responsible for mineralization.

Aerobic and anaerobic bacterial plate counts were run on the sediments collected. Counts obtained with anaerobic incubation, which enumerates anaerobes and facultative anaerobes, were one order of magnitude lower than aerobic counts. Sediment samples collected from deep water were also about one order of magnitude lower than those obtained from shallow or shore stations. In addition, the numbers of organisms capable of digesting chitin or cellulose were estimated by adding reprecipitated chitin (0.6%) or reprecipitated cellulose (0.1%) to the medium. Chitinoclastic or cellulolytic bacteria were easily detected on the medium by a clear zone or plaque that appeared around the colonies hydrolyzing

the complex molecules. The highest bacterial counts were obtained with aerobic incubation. Bacteria capable of digesting chitin were found in all stations sampled in the four lakes. All but one chitinoclast tested were obligate aerobes. As with total bacterial counts, the total chitinoclast biomass and the percentage of total aerobic chitinoclasts counted were higher for shallow or shore samples than for the deeper stations. There appeared to be an increase in numbers of chitinoclasts in the winter months over the summer months. Studies on the four lakes showed that the highest numbers of chitinoclasts were found in the shore stations of Chester Morse and Findley Lakes; however those organisms isolated from Lakes Washington and Sammamish were more rapid in hydrolyzing chitin.

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

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

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

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

A length-weight relationship has been established for chironomids and similar relationships for *P. affinis*, oligochaetes, and sphaerids are

being explored. Preliminary estimates of chironomid larval mortality
and growth rates show predation pressure in the spring and fall coinci-
dent with their primary growth periods. Stratification over the summer
limits predation and growth because of lack of oxygen on the bottom.
Temperature drops over the winter reduce metabolic activity of both
predator and prey, with mortality and growth leveling off. Emergence
occurs in the spring, and very high mortality in the pupal stage is due
to increased visibility during migrations to the surface.

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

The productivity of benthic organisms has been shown to depend heavily
on primary production, allochthonous input, lake sedimentation rates,
fish feeding, and several physical properties (temperature, mixing,
depth, oxygen concentration, etc.; Johnson and Brinkhurst 1971). Cor-
relations with these parameters are planned when the data become
available.

The production of macroinvertebrates and fish in the Cedar River is
under investigation as part of the studies of streams in the Coniferous
Forest Biome. The Cedar River system is unique by virtue of its multiple
use. The free-flowing river is divided into three rather discrete
reaches. The upper reach, immediately above Chester Morse Reservoir,
is relatively unaffected by man's activities except for well-controlled
logging. The middle reach, immediately below the dam, is directly
influenced by the reservoir and fluctuating discharge due to hydro-
electric generation. The lower reach, extending to Lake Washington, is
delineated by the City of Seattle water supply diversion at Landsburg.
This diversion limits the upstream extent of migration of anadromous
fish, of which sockeye salmon are the most numerous. The watershed
above the diversion is a source of municipal and industrial water supply
for metropolitan Seattle, and has unexploited resident fish populations.

Initially, quantitative macroinvertebrate and water quality samples
were collected from the three river reaches over a 17-month period.
This is being followed by a quantitative study of the fish populations
through electrofishing methods. Preliminary estimates of the fish popu-
lations indicate a general increase in biomass downstream and a pre-
dominance of rainbow trout or rainbow-steelhead trout (*Salmo gairdneri*)
at each station during the summer sampling period. Significant numbers
of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon were
also found below the Landsburg diversion. Water quality analysis was
also conducted, and an increase was found in total alkalinity, pH, con-
ductivity, hardness, and temperature from upstream to downstream. The
contribution of plankton from Chester Morse Reservoir to the river insect
community is reflected in increased abundance of Hydropsyche and Simuliidae.
The production of Simuliidae was estimated to increase by about two
orders of magnitude immediately below the reservoir. Further work is
being devoted to production estimates of Plecoptera (with the assistance

of Dr. Arden Gaufin, University of Utah), Ephemeroptera, Trichoptera, and Diptera, as well as the input of allochthonous material in the stream system (J. Malick pers. commun.).

FUTURE RESEARCH AND MODEL VERIFICATION

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

LAKE RESEARCH AT FERN AND CASTLE LAKES

Lake research outside the Lake Washington drainage basin but supported by the Coniferous Forest Biome has been completed (Olsen and Chapman 1972). Results of the Fern Lake research by the College of Fisheries were synthesized into an ecosystem model during 1973 (Fowler 1973). Submodels for hydrology, nutrients, phytoplankton, and zooplankton were combined into a simulation model that uses temperature and climatological data as driving variables to predict the levels of various other components of the ecosystem. Predictions from all portions of the model have been compared with those observed in data collected at Fern Lake, Washington.

Modeling and research on the phosphorus dynamics (Richey 1974b) and heat budgets in Castle Lake, California, were completed in 1973. This study identified important phosphorus parameters and developed a methodology to measure them in the lake. Expected rates of phosphorus fluxes were estimated by the use of isotope measurements, and phosphorus pool sizes were assessed through chemical determinations and from calculations of phytoplankton, bacteria, and zooplankton carbon masses and transfers. The heat budget of Castle Lake was considered as an accounting system for energy flux and a physical framework that governs a majority of biological processes. The heat budget encompasses the important abiotic phenomena of lake stratification, absorption of net radiation, heat storage and loss, net advection of energy into and out of a lake, turbulence, and light regimes (J. E. Richey pers. commun.).

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