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

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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.

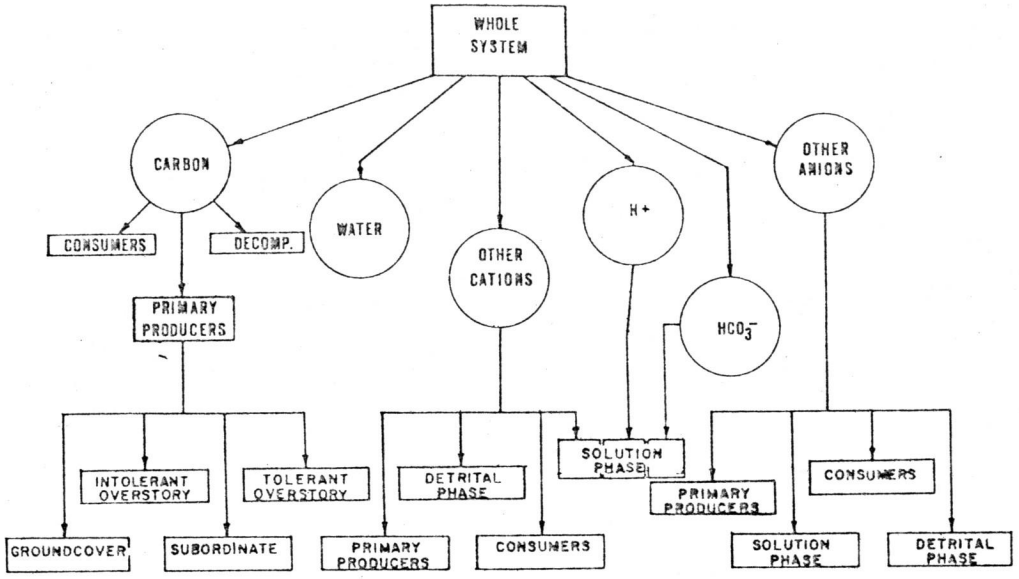

Figure 1. Hierarchical arrangement of modules composing the coupled carbon-water-nutrient model.

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

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

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).

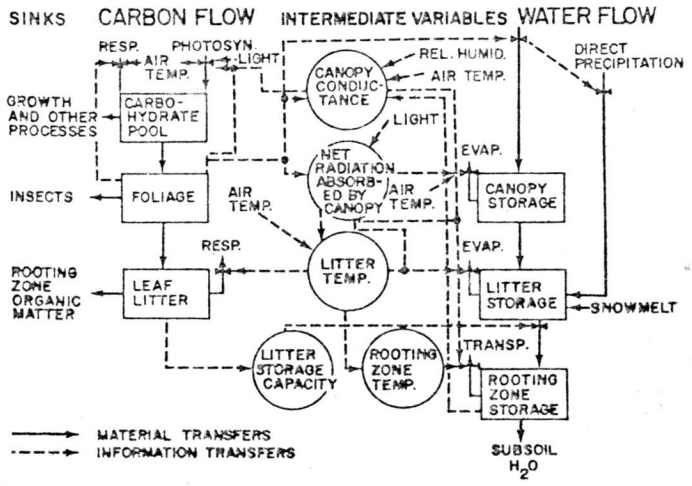

Figure 2. Example of couplings between the carbon and water modules.

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 as been made a G function, for convenience, 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 groundcover 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.

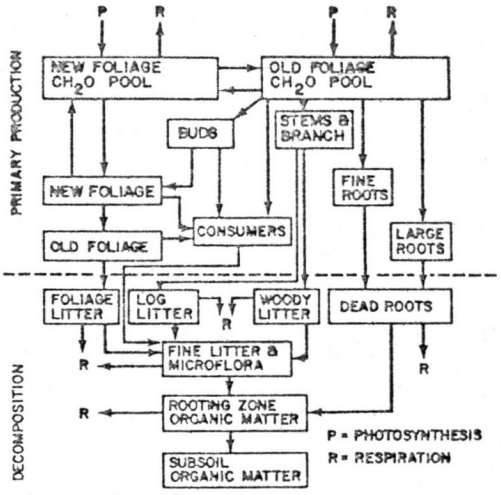

Figure 3. Storages and transfers of the carbon module. All couplings with other modules and intermediate variables have been omitted for simplicity.

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.

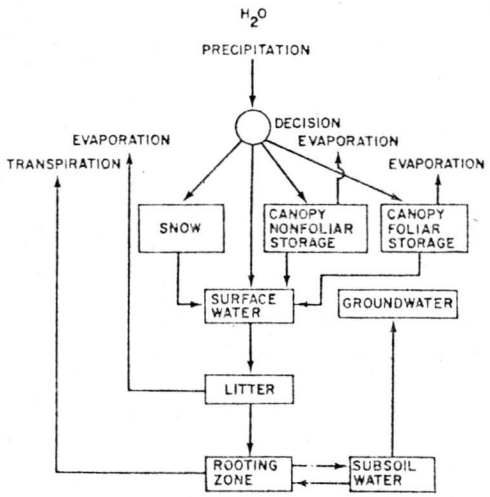

Figure 4. Storages and transfers of the water module. Couplings with other modules and intermediate variables have been omitted.

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 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^-, 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

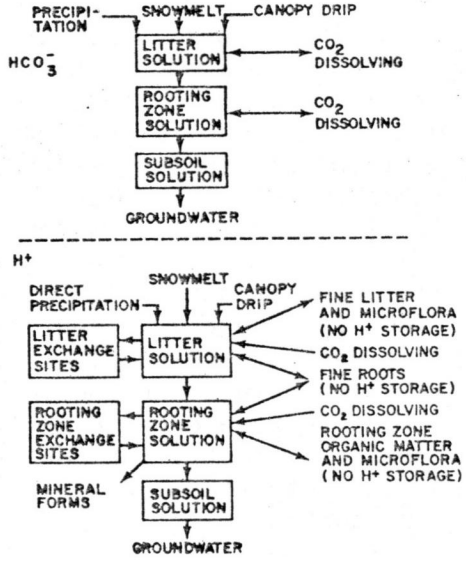

Figure 5. Storages and transfers of the H^+ and HCO_3^- modules. Couplings have been omitted.

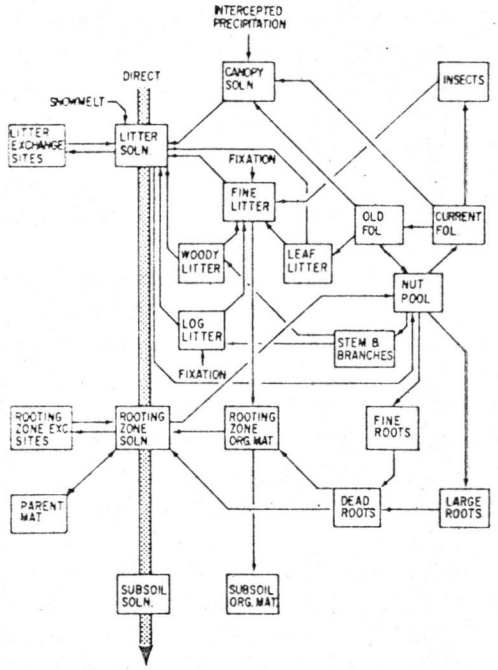

Figure 6. Storages and transfers of the cation and anion modules (other than H^+ and HCO_3^-). Couplings have been omitted.

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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