To the Graduate Council:

I am submitting herewith a dissertation written by David A. Weinstein entitled "The Long-Term Nutrient Retention Properties of Forest Ecosystems: A Simulation Investigation." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

H. H. Shugart, Jr., Major Professor

We have read this dissertation
and recommend its acceptance:

Edward E. C. Clebsch

J. Frank McCormick

Darrell C. West

Accepted for the Council:

L. Evans Roth
Vice Chancellor
Graduate Studies and Research

THE LONG-TERM NUTRIENT RETENTION PROPERTIES OF FOREST ECOSYSTEMS: A SIMULATION INVESTIGATION

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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David A. Weinstein

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ABSTRACT

A computer simulation model of the interplay between successional dynamics and long-term nutrient retention was constructed for the purpose of comparing the retention characteristics of two southern Appalachian forest stands. Descriptions of mechanisms of competition for light, water, and nutrients included in the model were tested by comparing the 12 year average diameter increment of trees in four stands from different slope positions in the Walker Branch Watershed (WBW) with model predictions. With only competition for light controlling growth in the model, predictions of diameter increment for lower-slope tulip poplar, mid-slope chestnut oak, upper-slope oak-hickory, and ridge-top pine stands were 0.36, 0.35, 0.33, and 0.39 $cm \cdot yr^{-1}$, respectively. Including water limitation, predicted rates decreased to 0.32, 0.27, 0.27, and 0.26 $cm \cdot yr^{-1}$. Addition of nutrient limitations caused rates to decrease to 0.29, 0.20, 0.22, and 0.20, respectively, which compare favorably to field measurements of 0.27, 0.19, 0.23, and 0.18 $cm \cdot yr^{-1}$. In an assessment of long-term nutrient retention characteristics in the dry mid-slope forest of the WBW, in the Ridge and Valley Province of eastern Tennessee, losses of calcium from the soil pool during 500 years of simulation were large. In contrast, simulation of the dry mid-slope forest of the Hannah Branch Watershed (HBW), in the Great Smoky Mountains National Park, showed large losses of nitrogen and an increase of soil calcium. The differences in species dominance or community structure which developed during the succession of each forest were insufficient

to produce the differences between the two forests. The greater cycling rate of the more productive HBW stand did not account for the differences. The differences were the result of the accumulated effects of short term imbalances between uptake and mineralization rates rather than the result of a chronic characteristic of the nutrient cycles. The balance of mineralization and uptake is dependent on site-specific characters varying through time. When tree uptake is similar to mineralization release, nutrients will be tightly held in the system. Losses are the result of releases from the litter layer in excess of quantities taken up by trees. Losses increase when tree uptake is limited by environmental conditions. The large calcium losses on the simulated WBW could have been caused by low nitrogen supplies limiting growth and uptake, while the HBW nitrogen losses could have been caused by calcium limitation. Many mechanisms, such as translocation alteration, tissue concentration alteration, and nitrogen fixation relationships, were shown to be capable of enhancing the adjustment of tree uptake to efficiently capture available nutrients and reduce nutrient loss. This study demonstrated the importance of spatial variability from plot to plot as well as the importance of temporal dynamics in assessing the causes of nutrient losses from an entire landscape. Although a general condition of calcium limitation might exist in the HBW, in any given year nitrogen might be the element limiting growth. Such transient conditions were likely due to the differential response of microbial mineralization processes and the tree uptake processes to climate and weather.

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CHAPTER I

INTRODUCTION

Among the essential commodities required by trees for growth, the one which is available in smallest supply compared to an individual tree's requirement will determine the amount of growth of that tree (Liebig, 1840). In the broadest sense, the availability of moisture and appropriate temperature regimes has long been recognized to produce a geographical response in plant communities (Kuchler, 1964). It is clear from a comparison of the quantity of nutrients entering a forest, the quantity available in the soil, and the quantity required for production of new plant tissue, that nutrient recycling is necessary for the long-term forest production. It follows that the ability of the forested system to maintain a given level of tree growth can be assessed by monitoring all of the processes by which nutrients become available.

Data detailing the sites of nutrient storage in forest systems and the rates of flow of nutrients among these sites typically involve measurements of the nutrient pools at a point in time and measurements of the nutrient flows over a single year. However, nutrient pools and flows are not in equilibrium; rather, they change through time. These changes are due in large part to the changing nature of the vegetation as the forested system undergoes succession in plant dominance. Due to these changes our ability to utilize the traditional data sets on nutrient pools and flows as keys to ecosystem sensitivity and stability

can be questioned. The cost and effort of monitoring pools and flows over periods long enough to identify trends and natural variation is prohibitive. Typically, investigators have extrapolated annual pool and flow budgets to longer time periods using computer simulation techniques. In these simulations the interactions between storage pools are assumed to be linear. The rate of loss of a nutrient from a pool is assumed to be dependent only upon the size of the pool. Such a representation does not explicitly incorporate the effect of plant succession. Since structural and compositional change in the forest over time can be significant, the forest nutrient cycling dynamics simulated in this study were developed by equipping a model of vegetation succession in the southern Appalachians with information on the associated cycling of nutrients. With this tool, annual nutrient budget information from two sites could be extrapolated through time without invoking assumptions of linearity. The resulting simulations were used to assess the long-term dynamics of nutrient cycles as influenced by succession.

The questions asked were:

1. What are the patterns of dynamics in pool sizes and flow rates of cycling nutrients?

2. What are the long-term nutrient retention properties associated with these patterns?

3. Can critical functions be identified which are responsible for the cycling and retention patterns?

CHAPTER II

STUDIES OF NUTRIENT RETENTION

Watershed Input-Output Analysis

A method for analysis of forest ecosystem nutrient cycling commonly applied is the watershed method. The watershed is a logical unit for study because the nutrient cycles are easily defined as part of the hydrologic flow (Bormann et al., 1968). An assumption in this method is that the more easily measurable inputs such as precipitation and dryfall, and outputs such as stream runoff, are far more important to the balance within the watershed than inputs such as nitrogen fixation and bedrock weathering, and outputs such as denitrification, permeation of the bedrock, wind aided seed dispersal, and animal migration. This balance is used as an indicator of the efficiency with which the plant/soil system within the watershed retains nutrients. Dynamics in the output are related to dynamics in the input to identify factors controlling output.

These studies have revealed a pattern of net loss of calcium, magnesium, and potassium in most watershed studies, with net accumulations of phosphorus and nitrogen (Armson, 1977; Likens et al., 1977; Henderson et al., 1978). However, results from a wide range of watersheds have led to the conclusion that solubility of bedrock plays a more important role than the quantity of input in determining losses. Walker Branch watershed in Tennessee, underlain by a sedimentary dolomitic bedrock, showed a much greater loss of cations than did the H. J. Andrews forest

in Oregon, underlain by less soluble andesite bedrock (Henderson et al., 1978). The Andrews watershed had, in turn, greater losses than did the Coweeta watershed in North Carolina, with an even less soluble bedrock of granitic metamorphic rock (Henderson et al., 1978). Further, the ratios of cations in the outflow from each of these systems were in proportion to the ratios of their concentrations in the respective bedrocks, an additional indication that minerals in outflow streams were primarily derived from bedrock weathering. Estimates of weathering from Brookhaven watershed in New York indicate that primary mineral decay in the soil releases nutrient quantities in excess of the amount lost in leaching out of the rooted zone of the soil (Armson, 1977). This result strongly suggests the influence of bedrock weathering on outflow quantities. The great variation in quantities of elements lost from forested ecosystems (Likens et al., 1977) further reduces the likelihood of finding a significant relationship between input and output of ecosystems.

This is not to say that inputs and outputs are not important to system functioning. The import of dissolved nutrients can be significant additions to the cycle, particularly in industrialized regions in which these additions have been accelerated due to increased atmospheric pollution (Likens et al., 1977; Swank and Henderson, 1976; Cole et al., 1967). Nitrogen fixation can add an amount of the same order of magnitude as precipitation (Likens et al., 1977; Mitchell et al., 1975; Henderson and Harris, 1975). Although inputs are small compared to the amounts of nutrients stored in the system and cycled annually, these

inputs become significant to ecosystem functioning due to accumulation over long time periods. In the case of calcium, magnesium, and potassium, these inputs are large in comparison to the annual accumulation in harvestable boles (Ovington and Madgwick, 1959; Ovington, 1959; Ovington and Madgwick, 1958). In fact, since significant proportions of the total soil pool of calcium and magnesium are required to be released each year to meet plant requirements, augmentation of this release by atmospheric input is vital to the system. Further, the weathering of soil minerals is a crucial input to the forest ecosystem, particularly in the renewal of exchange capacity and the replacement of cation exchange sites lost to hydrogen ions. Outputs also are important, particularly for calcium and magnesium, which may be lost in greater quantities than phosphorus, nitrogen, and potassium (Armson, 1977). Though volatilization losses are generally considered to be small, they can become sizeable under manipulations such as fertilization (Overrein, 1969). Net calcium dust export due to road networks can be as high as 6 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Tamm and Troedsson, 1955). Outputs are, however, small compared to total quantities of nutrients within forests, and bear little consistent relationship to input.

Several additional problems are inherent in the watershed approach. First, the importance of those transfers which are more difficult to measure and which were deemed insignificant may be more consequential than first assumed. Losses through deep ground water channels in the bedrock have proved to be a problem in several studies. Much of the release of nutrient from mineral weathering may occur below the

rooting zone in the soil, making the nutrients unavailable for retention by the vegetation. Since the majority of the rooting occurs in the upper 10 to 30 cm. of the soil (McGinity, 1976; Henderson and Harris, 1975), it is possible for the vegetation to have greatly depleted nutrient supplies in the section of the soil available for root mining while the system continues to experience large quantities of outflow. Consequently, only elements such as nitrogen, which do not become released in large quantities through mineral weathering would be expected to show much relationship to input or to internal ecosystem properties. Even in the case of these elements, there is debate over whether successional processes would cause the outflow to increase over time (Vitousek and Reiners, 1975) or decrease (Odum, 1969) due to changes in the tightness of the nutrient cycles.

Soil properties, weathering rates, and cation exchange selectivities in anion leaching processes are the real controlling factors of output of cations. Cation leaching is determined by the concentrations of major anions in soil solution, since the solution must maintain electrochemical neutrality (Nye and Greenland, 1960). Therefore a cation cannot remain in solution unless a complementary anion is present. Cations must, of course, be in solution to be leached. The major anions in soil solutions are bicarbonate, nitrate, chloride, sulfate, phosphate, and organic acids (Johnson and Cole, 1980). The predominant anion varies with soil properties such as adsorption and pH. Bicarbonate ion transformations generally regulate leaching of cations in undisturbed temperate (McCole and Cole, 1968; Johnson, 1975) and tropical (Johnson, 1975)

forests. Organic acids dominate the leaching systems in undisturbed cold region soils (Johnson and Cole, 1980). Adsorption and precipitation of anions restrict the presence of phosphate and sulfate in solution, reducing their contribution to leaching as well as their ability to be lost from the system (Cole and Johnson, 1977). The presence of chloride in solution is governed by weathering rates (Johnson et al., 1977), while that of nitrate is controlled by plant and microbial activities (Vitousek et al., 1979). Due to the absence of soil chemical reactions, nitrate can show rapid fluctuation, depending upon the amount of plant uptake. However, nitrate represents such a small percentage of the total anion concentration in solution that changes would be unlikely to cause large changes in the amount of cation leaching. Consequently, the anions present in largest quantity, and thus most likely to control cation outflow, are those regulated by physical properties rather than biological manipulation. Thus, the net accumulation or loss of cations from watersheds tells little about the ability of the system to maintain fertility and productivity. Even an absence of cations in stream outflow might indicate only that cations were being redistributed in the soil profile, leaching from the rooted zone only to precipitate in the lower soil horizons.

The observed accumulation of phosphorus in the forest watershed studied is likely to be a physically moderated process. Phosphate is readily removed from soil solution by adsorption reactions of ortho-phosphates with aluminum and iron present at the surfaces of layer aluminum-silicate minerals or in hydroxide phases in the soil (Reed, 1972).

Phosphorus will accumulate in the upper-most segment of the soil profile. While phosphate leaching has been reported from sandy soils, more heavily textured soils show little indication of leaching to lower soil horizons (Black, 1970), even after long term application of phosphorus (Sopper and Kardos, 1973). While large applications of sewage effluents have produced localized movement of phosphorus (Weinstein, 1976), possibly due to solubilization of weakly bonded phosphorus under reducing conditions (Etherington, 1975), such conditions are not expected in unmanipulated forest environments. Strong indications have been given that plant requirements of phosphorus are met through the release of phosphorus by root exudates (Richards, 1974), either through pH changes or enhancement of rhizosphere microorganism communities and their subsequent action (Cosgrove, 1975). Such elaborate biological mechanisms are adjustments to the low mobility of phosphorus and to the frequent depletion of soluble phosphorus from the sphere of influence of individual roots (Nye, 1968). Regardless of these mechanisms, the physical nature of the system would tend to cause phosphorus to accumulate in watersheds.

Nitrogen is also reported to be accumulated in watersheds (Henderson et al., 1978; Likens et al., 1977). Since it is the least subject to physical soil processes, nitrogen outflow could reflect the importance of input and vegetational uptake processes in nutrient retention. If gaseous inputs and outputs are also considered, however, the picture is not as clear, because these fluxes are difficult to measure and because they have not been satisfactorily quantified in many

systems. Fixation and denitrification may involve total gains and losses in excess of those involved in the hydrologic cycle (Todd et al., 1975). The importance of these microbially mediated processes, the heterotrophic control of decomposition immobilization (O'Neill, 1976; Vitousek et al., 1979), along with the lack of significant geological inputs of nitrogen have suggested that nitrogen losses are biologically controlled (Henderson et al., 1978). Nitrogen is much more dependent on the mineralization cycle of soil microorganisms. Nitrogen is prevented from leaching by many mechanisms, but chief among them may be uptake by plants whose ability to respond to nitrogen availability by increasing uptake or by adjusting fall translocation is marked (Cole and Rapp, 1981).

A large number of studies have attempted to look at nitrogen as an indicator of the level of disruption of the system following the report of large losses in the Hubbard Brook cutting-herbicide disturbance experiment (Bormann and Likens, 1967). However, nitrogen outflow may be simply an accurate barometer of the state of resources available to and limiting the soil heterotrophic population. When the disturbance has produced an abundance of available nitrogen (by reducing plant uptake), if climatic conditions restrict the rate at which heterotrophs can utilize this nitrogen, large losses of nitrate will result. However, when heterotrophic populations are unlimited, usually in the presence of an abundant carbon source, losses of nitrate are minimal. Vitousek et al., (1979) found that trenching (eliminating plant uptake) increased nitrate outflow in forest stands with carbon limited heterotrophs, but not in

stands with abundant carbon resources. Clearcutting with herbicide additions at Hubbard Brook (eliminating plant uptake) led to increased nitrate loss because soil temperatures were raised, favoring nitrifiers, but readily available carbon was not raised significantly. A West Virginia clearcut produced much lower nitrate outflow increases, probably due to a greater responsiveness in the heterotroph populations (Aubertin and Patric, 1974). Girdling (Johnson and Edwards, 1979) increased nitrate loss by eliminating uptake in the presence of a carbon restricted heterotroph population. In addition, when carbon was applied in this experiment the heterotroph population increased and nitrate loss decreased. Consequently, nitrogen outflow may be an accurate measure of the state of the heterotrophic control of nutrient release in a watershed, but it cannot be considered to be a good barometer of all aspects of system functioning. Variability of heterotrophic response within a watershed may cause nitrate outflow to be unreflective of significant perturbations in the watershed.

Thus, the net accumulation or loss from watersheds tells much more about the soil, bedrock, and heterotrophic populations in the watershed than it does of the ability of the system to efficiently recycle nutrients and maintain fertility and productivity. Another approach is to quantify the sizes of nutrient storage pools within systems and the magnitude and rate of flow between those pools on small plots with arbitrary boundaries. The size of pools and flows could then be related to nutrient cycling efficiency and nutrient retention capability.

Using the Magnitude of Internal Pools and Transfers as Indicators of Nutrient Retention

Another method of assessing the processes controlling nutrient retention is to consider the watershed to be subdivided into a series of independent plots. Each of these plots has surface and subsurface flow input, but for the purposes of this analysis they are considered to be negligible. The input from trees outside each plot (litterfall, reproduction, and treefall) is considered to be balanced by the export of these quantities from trees within the plot. Measuring output of such plots was pioneered by Cole et al., (1967) using tension plate lysimeters in his study of cycling in douglas fir forests. Input-output balance is of less importance in this type of study because the reduction in scale allows the evaluation of cycling efficiency and also considers microsite diversity. These studies are often combined with input-output analysis to attempt to compare internal fluxes of nutrients with losses to separate the influences of biological and geological mechanisms on nutrient cycles (Henderson et al., 1978). Typically in nutrient cycling analysis, the amount of each element in the larger components of the system is determined. Each of these components (or pools) has associated with it quantities of nutrients entering the pool from other components and quantities being transfered to other components. These transfers may occur largely at one time of the year, but the timing of transfers is assumed to be unimportant at the annual scales used.

Information has been accumulated on the size of storage pools in different forest ecosystems, but little relationship between storage

pool size and nutrient retention ability has been detected. These static measures contribute to our comprehension of the total quantity of usable reserve within the system, but changes in any or all of these measures are more likely to indicate that a change in retention has already occurred than that such a change is about to occur.

The exchanges of nutrients between storage pools are more likely to be sensitive predictors of impending change. These flows involve the uptake of mineral elements by vegetation, the storage of mineral elements in plant parts, the partial elemental return to the forest floor (through leaching, leaf senescence, or wood tissue shedding), and the immobilization and remineralization of mineral elements by microbial decomposers.

Nutrient uptake is typically the largest flux in the forest system. Nutrients are required for the building of tissue, the replacement of damaged or shed parts, the construction of a new canopy, and the replacement of loss through leaching from leaf tissue. Sometimes the quantities reported as uptake are actually the difference in nutrient content of the aboveground vegetation between successive years, or biomass increment. Various authors also include litterfall and canopy leaching (Henderson et al., 1978), and root litter and root exudates (Likens et al., 1977). Consequently, uptake values are difficult to compare between studies. The rate of cycling appears to be related to ecosystem functioning. High productivity is associated with large quantities of nutrients cycling annually (Cole and Rapp, 1981). This implies that during the periods of highest productivity in the course

of stand development the forest is very susceptible to disruption in nutrient cycling. The annual uptake, which is the yearly nutrient demand placed by the vegetation on the system, is related to biomass increment (Curlin, 1970) and is maximum when net primary productivity is greatest. The pattern of maximum uptake will vary from nutrient to nutrient, as stand development proceeds from a stage early in succession when a nitrogen-rich canopy is formed to a stage later in succession when large amounts of calcium-rich woody tissue is produced (Switzer et al., 1978). Though the absolute uptake demand can also vary with soil type (Duvigneaud and Denayer-DeSmet, 1970), vegetation type (Duvigneaud and Denayer-Desmet, 1975; Ulrich and Mayer, 1972; Ovington, 1968), and canopy closure (Turner et al., 1976), the amount of demand which is met by the system recycling processes is a significant measure of ecosystem health.

Other transfers are of interest as they relate to this ability to supply nutrient demand. Most nutrients return to the forest floor by litterfall (Rodin and Bazilevich, 1967; Henderson et al., 1978). Significant quantities are also returned in root sloughing (Harris et al., 1973; Ralston, 1978). Litterfall quantity is generally related to productivity, as is the quantity of nutrient retained in permanent growth within the vegetation (Rodin and Bazilevich, 1967). However, while the maximum rate of nutrient retention peaks at twenty to forty years following the beginning of stand development, litterfall remains at its maximum.

An exception to the dominance of the litterfall pathway exists for potassium, which, due to high mobility, is leached in large quantities

from leaf tissue. It is leached from senescing tissue in particular. Leaching is also a significant transfer for calcium and magnesium, but is much less important for phosphorus and nitrogen. Nitrogen leaching losses from leaf tissue are reduced as a result of active translocation within the plant (Kramer and Kozlowski, 1960). In contrast, translocation of calcium does not occur (Kramer and Kozlowski, 1960). Calcium concentrations in leaf tissue build as the growing season continues (Day, 1974). The retention of nutrients within the system is greatly enhanced through the retention of nutrients within the plant after leaffall. The annual retention of nutrients is small with respect to litterfall (40% for nitrogen, 50 to 60% for potassium and calcium). Retention may be more nearly equivalent to litterfall in slowly-growing forests (Duvigneaud and Denaeyer-Desmet, 1970).

In forests there is a critical gap between the quantity of nutrients coming available each year and the annual requirement of the vegetation (Ralston, 1978). The size of this gap can be decreased by an increase in external inputs to the system, by a decrease in productivity, by a decrease in the plant tissue concentrations, or by an increase in the nutrient utilization efficiency within the plant. Decreases in productivity are related to decreases in vegetation nutrient requirement only in the case of the nitrogen requirement in temperate deciduous stands and in the case of nitrogen and potassium requirement in temperate coniferous stands. In both cases this relationship is strong and linear only when productivity is already low (Cole and Rapp, 1981). However, forest ecosystems show other

adaptations to the problem of meeting biological nutrient requirements. For example, deciduous stands, which utilize twice the amount of nutrients in yearly growth as do coniferous stands, meet this increased demand by greater internal translocation (Cole and Rapp, 1981). Productivity in coniferous stands appears to be much more closely related to uptake of elements than in deciduous stands, suggesting more dependence on external availability than internal recirculation. In another example, more northerly stands require less nitrogen per unit productivity than do southerly stands (Cole and Rapp, 1981). This suggests that more northerly stands have adaptations to deal with the low availabilities associated with nutrient immobilization in the large litter layers which tend to form under cool conditions. In a third example, efficiency of nutrient utilization in production in coniferous stands was observed to decrease as more nitrogen was input from precipitation (Cole and Rapp, 1981). Efficiency decreased as supply became more plentiful, and vice versa. Due to these adaptations there is no clear reason to suspect that flow sizes, cycling rates, or nutrient use efficiencies calculated for a single year would be good indicators of the ecosystem nutrient retention capability.

A New Technique for the Assessment of Nutrient Retention

The problem in both watershed and plot studies is that pools and flows must be quantified over limited periods of time. Due to the difficulty of sampling and intensity of effort involved, pool size and dynamics are measured over periods rarely longer than a few weeks to one

growing season. These time spans are brief compared to stand development. Forests are rarely in a state of dynamic equilibrium with respect to the characteristics of the vegetation. Since many aspects of nutrient cycles of these forests are dependent upon the stage of stand development (Switzer et al., 1968; Rodin and Bazilevich, 1967), it is likely that the long term cycling dynamics of any one forest stand are not predictable from short term studies. Recently, researchers have attempted to assess the pattern of changes in these cycling dynamics by quantifying pools in a successional chronosequence of stands (Covington, 1981). However, it is not clear to what degree these dynamics are dependent on individual stand history, or more precisely, whether enough variability was included in these experiments to eliminate the potential consequences of stand history. Consequently, for this study a computer model of forest succession was used to permit the simulation of forest nutrient cycling through time.

A computer model is a dynamic metaphor for a forest system. It is created by aggregating compartments, processes, and mechanisms into functionally equivalent units. The problem is to know whether the functional dynamics in the model are equivalent to the real system. The mathematical descriptions of behavior of system components often have been created in isolation from the rest of the system. When the component is treated as part of a larger system it can be difficult to determine to what degree the observed behavior is altered by interaction with other components. Simple environment-organism relationships, such as those amenable to traditional controlled experimentation, are often

insufficient to explain the response to a perturbation. Instead, a complex web of biological, physical, and chemical interactions must be considered to explain system responses. Such systems of relationships can be so large as to preclude controlled hypothesis testing under a wide variety of conditions. Further, response parameters of forest systems are often too slow or are too delayed for the lifespan of the scientific study. Evaluation using computer models in an attempt to circumvent these problems was developed. In this type of analysis, the basic relationships known from studies concentrating on component behavior in isolation are allowed to interact within a web of interrelationships.

A model of a forest ecosystem can be thought of as an ecosystem itself. It has a defined set of functional components, such as decomposer organisms or rapidly growing trees. This set is developed from the set found in the real forest ecosystem. It may or may not include all of the functional components that exist in the real forest. The model behavior will track the behavior of the real forest only if all functional components important to producing that behavior have been included in the model. While it is difficult to assess the precision with which the model tracks the forest behavior due to the long time periods involved, the model can be used to clarify the amount of influence that each functional process in the model contributes to producing the overall behavior. In this way we will attempt to understand the relative importance of these components in the real system.

An additional problem with the classical nutrient cycling studies has been the inaccuracy of estimating average stand level nutrient

cycling properties from average pool sizes and average flow rates. Nutrient cycling is very variable among localized landscape units, depending upon the particular size and species characteristics of the trees dominating the site. Although the discussion will be of stand dynamics it must be understood that stand level dynamics are considered to be the statistical summary of the response of individual sites located within a stochastic environment. In this way the variance among sites in the forest is explicitly considered.

CHAPTER III

METHODS

Description of FORNUT

A mixed-age, mixed-species stand model was used to simulate long term nutrient retention in the two forest systems. In this type of model, also called gap replacement model type, tree establishment, growth, and mortality simulations are based on general silvicultural information. This information includes: (1) site requirements for germination, (2) palatibility of seedlings for browsers, (3) sprouting potential, (4) shade tolerance, (5) germination and growth temperature requirements, (6) inherent growth potential, (7) longevity, and (8) sensitivity to crowing stress. Since the information is consistent over entire species' ranges, the model is capable of simulating the response of these tree species over large regions, assuming that other limiting factors do not become important.

In gap replacement models, the maximum growth of each tree on a plot is computed from the inherent radial increment potential and the longevity of the tree species. This maximum growth is modified by the response of the tree to environmental conditions such as light availability (determined from the leaf area of overtopping trees), annual temperature and growing degree days, spatial crowding, and root competition. The size of the simulation plot is one-twelfth hectare. All environmental factors and nutrient cycling characteristics are assumed to be homogeneously distributed over the plot. The size of

the plot chosen is appropriate for the examination of nutrient cycling properties since a single large tree can come to dominate this size plot, and a single tree is capable of integrating all of the nutrient cycling processes of the plot into a single behavioral response.

The establishment of seeds and sprouts is based on the availability of light, proper temperatures, substrate requirements for germination, and sprouting capabilities of dying trees. Mortality is a function of the growth and expected maximum age of the tree. Each growth response to environmental conditions is described as a probability distribution. The model is stochastic, and the average outcome of many simulations of a given set of initial conditions is used as the predicted response of the system. In this way the wide variation in the response of any individual tree is considered. Further, provided that the mean and the variance of the biological response of an individual tree to a natural disturbance or management technique is known, the model can simulate the subsequent effect on the tree community.

The nonlinear stochastic simulation model FORET, developed by Shugart and West (1977) and described in general above, was modified to allow analysis of nutrient cycles along gradients of altitude, moisture availability, and soil properties in the Hannah Branch watershed in Great Smoky Mountains National Park and in the Walker Branch watershed in Oak Ridge, Tennessee. The FORET model simulates the annual change of a forest stand by allocating annual growth increment for each tree within the stand (Subroutine Grow), by the addition of new seedlings to the stand (Subroutine Birth), the addition of resprouted saplings

(Subroutine Sprout), and by tabulating the death of trees (Subroutine Kill). The model assumes that tree volume increment is:

$$\frac{d(D^2H)}{dt} = r \times LA \times \left(1 - \frac{D \times H}{D_{max} \times H_{max}}\right) \quad (1)$$

where:

r = a growth rate parameter;

LA = leaf area of the tree;

D = diameter at breast height;

H = height of the tree;

D_{max} = maximum recorded diameter for the species;

H_{max} = maximum recorded height for the species; and

D^2H = index of volume.

Thus, growth is proportional to the leaf area, although the amount of growth capable with a given leaf area decreases as the tree ages. This equation calculates optimal growth, which is then reduced based on the amount of shading and exposure to less than optimal site conditions of climate. To calculate shading, the leaf area of all trees taller in height than the one in question is summed using the relationship of Sollins et al., (1973):

$$(LA)_i = 0.1193 \times D_i^{2.393} \quad (2)$$

$$L = \sum_{i=1}^{N} (LA)_i \quad (3)$$

where:

$(LA)_i$ = the leaf area of a tree i of diameter D_i;

L = total leaf area of overshadowing trees; and

N = total number of overshadowing trees.

The light available (AL) to the tree given the amount of shading caused by the overstory leaf area L is given by:

$$AL = \exp(-.25L) \quad . \tag{4}$$

Two equations are used to calculate growth reduction as a function of available light:

$$R_1 = 1 - \exp(-4.64(AL-0.05)) \tag{5}$$

for shade tolerant species, and

$$R_2 = 2.24 \times (1 - \exp(-1.136\ (AL-0.08)) \tag{6}$$

for shade intolerant species, based on measured photosynthesis curves (Kramer and Kozlowski, 1960). Other growth reducing calculations are discussed later for responses to temperature, moisture, and nutrient levels.

Since the original model was designed to simulate average conditions on wetter slopes in east Tennessee, the construction of the modified version involved considerable alteration of the environmental modifiers of growth. The information tabulated for each tree in the model was expanded from a list including specie's age, diameter, and biomass to include information on the existing pools of nutrients (calcium, magnesium, potassium, phosphorus, and nitrogen) in six tree

components (leaves, branches, boles, and three sizes of roots). The dynamics of nutrient pools and the dynamics of the fluxes between pools were added. These changes fell into two categories as detailed below: (1) modifications to the basic functions in FORET, and (2) additions of nutrient cycling functions to FORET. The altered version of FORET with these modifications and additions was named FORNUT.

Modifications to the Subroutine Kill

Several functions required modification since they were effective in simulating the growth of species appropriate only for the area modeled in the original Shugart and West (1977) studies.

The original model randomly simulated the death of trees according to a probability function that assumes 1% of all seedlings of a species will live to reach the maximum age possible for that species. This probability of surviving is decreased to only one chance in 100 that the tree will live ten years if the growth rate of the tree in question falls below an acceptable minimum of 0.1 $cm \cdot yr^{-1}$. However, some species, specifically hemlock (Tsuga canadensis), beech (Fagus grandifolia), white oak (Quercus alba), and red oak (Quercus rubra), that are compositionally important in the Smokies, have an enhanced ability to reduce growth to low levels without physiological impairment (Fowells, 1965). These species were given twice the probability of surviving slow growth periods as the other species, or an 82% chance of surviving a year of slow growth versus a 63% chance for most species. Two additional species, rhododendron (Rhododendron maximum) and mountain laurel

(Kalmia latifolia), also known for slow growth were given a 95% chance of surviving a slow growth year.

Modifications to Subroutine Sprout

The original FORET model assumed that conditions would be favorable for the sprouting of only one of the species for which an individual had died in a given year. The number of sprouts was a function of characteristic number of sprouts per stump of a species, but not related to the total number of individuals dying. Under the reconstructed sprouting subroutine each dying individual could sprout a clump of 0.1 cm diameter saplings if the diameter of the tree before death was within the range of the prime sprouting age for that species. The exact number of sprouts per tree was a stochastic function of the characteristic number of sprouts for that species. The probability of a given tree sprouting was determined by the minimum and maximum diameter for sprouting and by the function:

$$P = 1.8 - (D \times 0.018) \text{ , when } P \leq 0.9 \text{ ;} \qquad (7)$$

$P = 0.9$, when P from the above equation exceeds 0.9 .

These equations were formulated by Harmon (1980) for trees in the Hannah Branch watershed.

Modifications to Subroutine Grow

The basic growth equation, calculating yearly tree growth under ideal conditions, assumes that the tree trunk is a cylinder and that the

volumetric increment is a function of the leaf area of the tree, the maximum diameter of the species, and the tree age. Tree growth is limited by reduced light availability in proportion to the sum of the leaf area of all trees taller than the one in question. Tree growth is further reduced in the original model by a parabolic function of growing degree days. However, many species in the southern Appalachians grow to large dimensions under regimes of temperature vary close to their supposed required minimum. Tulip poplar (Lirodendron tulipifera), for example, reaches record size in an area with an average growing degree day value of 2600 when it is thought to require at least 2100 growing degree days. Under a climatic regime of 2600 growing degree days, a tulip poplar tree would be capable of growing at only 40% of its maximum rate according to the original model function. Consequently, the growth-reducing temperature effect was assumed to occur only when the annual degree day value was very close to the minimum required by the species. The function used was:

$$DDG = \frac{((DEGD - DMIN) / DEGD)}{((DEGD - DMIN) / (DEGD + 0.05))} \quad (8)$$

where:

DDG = the growth reduction due to degree days;

DEGD = the growing degree days available;

DMIN = the minimum required degree days.

Using this function a growth reduction of 50% would be experienced by the tree when the available growing degree days were 5% greater than the minimum requirement. Further, since the southern extremes of the

ranges of species are more likely limited by moisture stress than heat stress, a maximum degree day limitation was eliminated.

Soil moisture availability can further reduce growth, based on a linear relationship between growth potential and the number of days during the growing season with soil moisture below the wilting point. A soil moisture limitation on growth was necessary as an addition to the model, since within a watershed the variety of soils, evapotranspiration stresses, and precipitation inputs can affect the variability in plant communities. Further, as Whittaker (1956) suggested, species distributions throughout a watershed in the southern Appalachians can be related to a general moisture index variable. The number of days with sufficient water required by a particular species is based on the geographical relationship between the most westerly extension of a species range and the number of days with available water common at that location.

Nutrient Cycling Process Additions to the FORET Model

The original FORET model reduced growth of all trees on the plot uniformly as a function of the ratio of the biomass of the stand to the potential maximum biomass achievable in the region, as observed in old growth stands. This function prevented stands from exceeding this observed value as an analog for the combined effects of crowding and root competition. A more detailed response of the individual plant to its environment is possible when it is assumed that nutrient resource

limitation is the real factor controlling biomass accumulation (given abundant moisture and light) and that crowding and root competition are manifestations of this effect. Net production of biomass will not cease until nutrient resources become limiting.

A definitive relationship between plant productivity and soil nutrient status has not yet been determined in the literature. Armson (1977) reports increasing concentrations in tissue with increases in available quantities of limiting nutrients, an idea which has been used for nutrient deficiency diagnosis (Morrison, 1974). Changing concentrations do not necessarily mean increased productivity. However, plants growing on low fertility soils show low growth rates, less tissue production, and less uptake of nutrients (Armson, 1977). A particular problem in relating these changes to any measure of soil nutrient status is that trees collect nutrients which are released gradually over long time periods from the decomposer community. Therefore, the level of exchangeable nutrients in the soil at any one time would not be expected to correlate with tissue concnetrations or productivity.

Nevertheless, foliar analysis has occasionally proved useful in evaluating the response of trees to the soil nutrient status. Tamm (1964) listed concentration ranges for detecting deficiencies in several species. Safford and Young (1968) were able to show a relationship between red spruce foliage and soil phosphorus and potassium levels, and Bard (1945) and Scott (1955) related calcium, potassium, and phosphorus concentrations in foliage of a number of

northeastern tree species with soil nutrient levels. Metz et al., (1966) and Ovington (1968) found little relationship, however. Crocker (1959) found a relationship only when soil nutrient levels were extremely low.

Mitchell and Chandler (1939) were able to show that, for red oak (Quercus rubra), the relative nutrient supplying capability of different forest plots could be compared through changes in leaf nitrogen concentrations following various amounts of fertilization. Such methods do not answer the questions of evaluating the actual quantities of nitrogen available and of what percentages of the added fertilizer are actually being utilized. However, Mitchell and Chandler did show that red oak trees generally increased their annual growth rate with additions of nitrogen. The relationship was such that, at very low levels of background soil nutrient supply, additions of nutrients produced the largest growth response. As more nutrients became available to the plant, the amount of increased growth diminished. Finally, addition of fertilizer showed no increase in tree growth rate. Addition of fertilizer in excess of optimum levels can produce toxic effects and growth reduction, due to metabolic poisoning or antagonism between ions, with the ion in excess reducing the availability of other ions.

Mitchell and Chandler used a polynomial function to designate the response of trees to fertilization. They defined three classes of responses, describable by three separate equations: (1) a class of nutrient-tolerant species, characterized by slow responses to increasing nutrient availability and less growth impairment by low nutrient levels;

(2) a class of nutrient-intolerants, which show marked response to increased availability, but low growth rates at low levels of nutrient availability; and (3) an intermediate growth class. Aber et al. (1978) used the Mitchell and Chandler (1939) equations in their simulation of nitrogen flow in a northern hardwood forest, relating foliar concentrations from the Hubbard Brook watershed plots to concentrations reported in the Mitchell and Chandler study plots to estimate background nitrogen availability in the 1939 study. However, the potential error in such an estimate is large. Consequently, for the present study the Mitchell and Chandler equations were not used, although the general shape of the response function and the concept of nutrient-tolerance classes of species was used. Three generic equations were used (Figure 1), relating the ratio of available nutrient to the optimal level of available nutrient to the reduction in growth caused by this suboptimal level. Thus, instead of attempting to predict the actual tree growth based on relative available nutrients, these equations are used to calculate a growth multiplier, similar to the ones used to reduce ideal growth in response to light or moisture limitations. The use of a multiplier instead of the actual growth rates found by Mitchell and Chandler is necessary, since the growth response to changing fertility can be altered by the density of the stand, the shading, and the water availability. Since Mitchell and Chandler's analysis did not include all of the species which must be considered in a southern Appalachian model, some extrapolation of expected nutrient response classification had to be made, based on similarities between

Figure 1. The relationships used in the FORNUT model for reducing growth as a function of nutrient availability. (Both axes are dimensionless.)

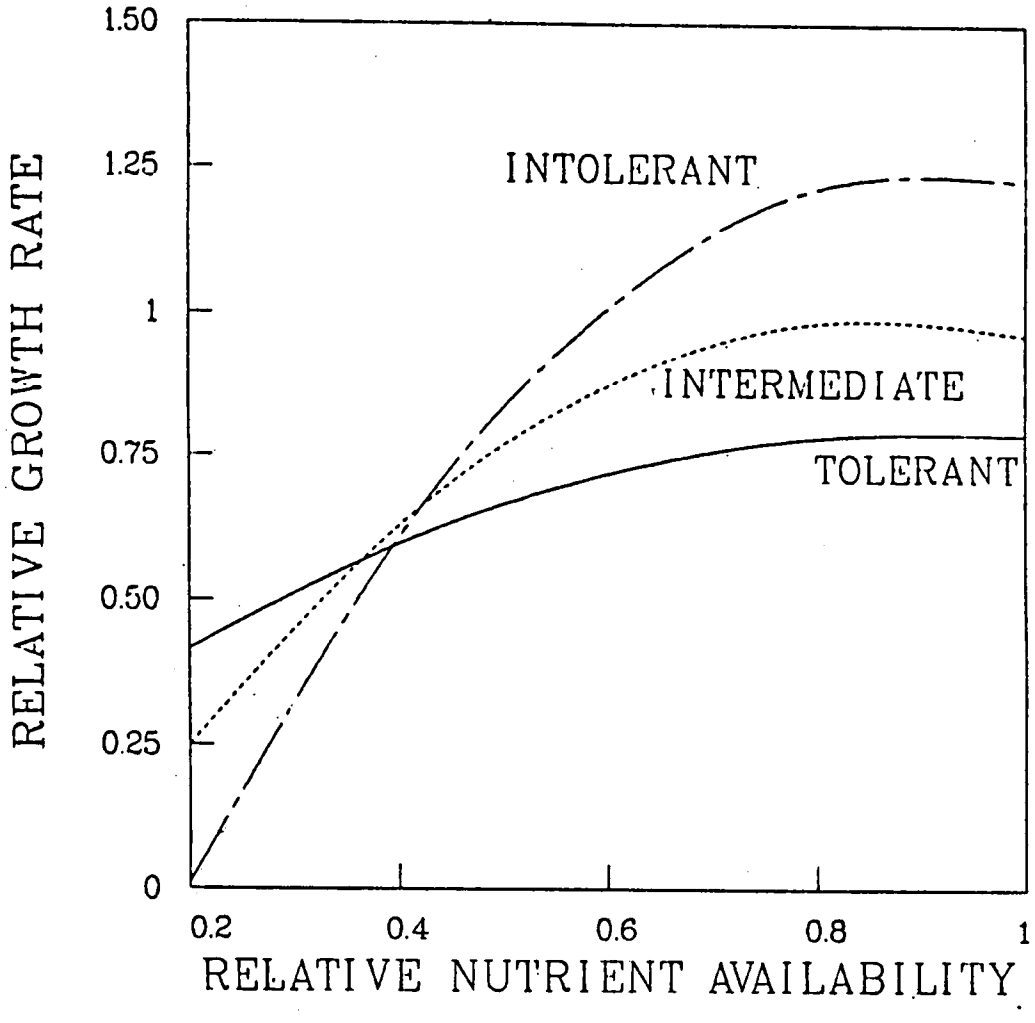

1.50
1.25
1
0.75
0.50
0.25
0
RELATIVE GROWTH RATE
INTOLERANT
INTERMEDIATE
TOLERANT
0.2
0.4
0.6
0.8
1
RELATIVE NUTRIENT AVAILABILITY

Figure 1

general growth characteristics and strategies among species. Table 1 shows the classification scheme used in this study.

In reality, growth is limited by the amount of a nutrient available for uptake when needed by the plant. Since a model such as FORNUT operates on a yearly time step, any variation in requirement or availability during the course of the season is not considered. Trees are assumed to be capable of timing their uptake to the timing of the entry of nutrients into the available pool. The tree is capable of meeting its requirement by integrating over the growing season, with delayed uptake in spring compensated with greater summer uptake. Unfortunately, total availability for most elements is difficult to calculate. The amount of exchangeable nutrients can be measured at any one time period, but the rate at which this source becomes exhausted and is replenished by weathering cannot easily be estimated. The soil exchangeable pool may not be even an estimate of the total supplying power of the soil, since inputs and outputs may be large.

Consequently, some general assumptions were made. First, it was assumed that only one element could be limiting in any one year. Second, annual element limitation was caused by two interrelated factors, the total size of the exchangeable pool (or in the case of phosphorus and nitrogen, the soil extractable pool), and the total amount of the nutrient stored in the weatherable soil material. This material included the soil organic matter, which is especially important for nitrogen availability. Thirdly, the exchangeable pool was considered to diminish in size proportionately as the weatherable pool diminished, assuming that the weathering slowed as less was available to be weathered.

Table 1. Nutrient response classification scheme (Refs. Mitchell and Chandler, 1939; Aber and Melillo, 1979). Intolerant class are trees which show strong growth response to nutrient availability. Intermediates show less response, tolerants show small response.

Intolerant		Intermediate	
(Aesculus octandra)	Yellow buckeye	(Acer saccharum)	Sugar maple
(Acer pensylvanicum)	Moose maple	(Amelanchier laevis)	Downy serviceberry
(Fraxinus americana)	White ash	(Betula alleghenesis)	Yellow birch
(Juglans nigra)	Black walnut	(Betula lenta)	Black birch
(Liriodendron tulipifera)	Yellow poplar	(Carpinus caroliniana)	American hornbeam
(Magnolia acuminata)	Cucumber magnolia	(Carya cordiformis)	Bitternut hickory
(Prunus serotina)	Black cherry	(Carya glabra)	Pignut hickory
(Robinia pseudoacacia)	Black locust	(Carya ovata)	Shagbark hickory
(Tilia heterophyla)	White basswood	(Carya tomentosa)	Mockernut hickory
		(Cornus florida)	Florida dogwood
		(Cercis canadensis)	Eastern redbud
		(Diospyros virginiana)	Common persimmon
		(Fagus grandifolia)	American beech
		(Halesia caroliniana)	Carolina silverbell
		(Liquidambar styraciflua)	Sweetgum
		(Nyssa sylvatica)	Blackgum tupelo
		(Morus rubra)	Red mulberry
		(Oxydendron arboreum)	Sourwood
		(Pinus taeda)	Loblolly pine
		(Ulmus americana)	American elm

Table 1 (continued)

Tolerant	
(Acer rubrum)	Red maple
(Ilex montana)	Mountain holly
(Juniperus virginiana)	Red cedar
(Kalmia latifolia)	Mountain laurel
(Pinus echinata)	Shortleaf pine
(Pinus rigida)	Pitch pine
(Pinus strobus)	White pine
(Pinus virginiana)	Virginia pine
(Quercus alba)	White oak
(Quercus coccinea)	Scarlett oak
(Quercus falcata)	Southern red oak
(Quercus marilandica)	Blackjack oak
(Quercus prinus)	Chestnut oak
(Quercus rubra)	Red oak
(Quercus stellata)	Post oak
(Quercus velutina)	Black oak
(Rhododendron maximum)	Rosebay rhododendron
(Sassafras albidum)	Sassafras
(Tsuga canadensis)	Eastern hemlock

Thus, the following function was used to limit growth in response to nutrient availability:

$$GMF = A + (B \times RNA) + (C \times RNA^2) \quad ; \qquad (9)$$

where:

GMF = growth modification factor, ($0.0 \leq GMF \leq 1.2$) ;

A, B, and C = coefficients of the equations fitted to the nutrient-tolerance curves in Figure 1; and

RNA = relative nutrient availability.

The relative nutrient availability in this equation is a variable with a value of from 0.0 to 1.0, representing the proportion which the exchangeable pool would be reduced if the trees were allowed to grow without nutrient limitation. RNA has a value of 1.0 (no reduction in available pool size) if the amount of the limiting element released through mineralization and weathering is larger than the amount the vegetation would require for uptake without nutrient limitation. If the uptake requirement exceeds the amount released, the fraction by which the available pool would have to be reduced to meet this excess uptake requirement becomes the relative nutrient availability. This reduced availability would then yield a nutrient growth modifier of value less than 1.0, except possibly for an intolerant species at low requirement excesses. This reduction in growth would in turn reduce the actual uptake of the vegetation. Consequently, the available pool serves as the ultimate reservoir for meeting yearly uptake requirements once the mineralization releases from decomposition and the weathering releases

from the soil are fully utilized. The processes which replenish the available pool (including the exchangeable pool) from the fixed soil pool after each year's uptake are considered to be independent of the weathering processes. However, the soil fixed pool is reduced by both weathering and by replenishing the soil exchangeable pool. In other words, the model considers two types of weathering. Both weathering releases are assumed to decrease as the total soil fixed pool decreases. Thus, the growth limiting function causes limitation from both the long-term depletion of the soil nutrient pool and the corresponding delays in the replenishment of elements by weathering.

The releases from weathering are difficult to determine. Theoretically, in a watershed the difference between the inputs to the soil pool (precipitation, decomposition, mineralization, and throughfall) and the outputs (streamflow and plant uptake) represents the amount taken up by the plants which had to come from weathering. However, mineralization in the rooting zone consists of release of nutrients through decomposition of leaf tissue, woody tissue, and roots, as well as the releases of temporarily immobilized quantities from throughfall and precipitation. An assessment of the actual mineralized quantity differs from merely noting the change in contents of the litter layer from year to year. Consequently, weathering was calculated in this study to be the difference between the input of elements to the litter layer (litterfall, precipitation, and throughfall) and outputs (rooting zone leaching and plant uptake). With the assumption that the litter layer was not changing perceptibly in the course of one year, this calculation

represented the total of available nutrients not supplied by release from microbially-mediated processes. The sum of weathering input, microbial release, and the exchangeable pool then represented a maximum quantity of nutrients which a tree stand could possibly draw upon without large changes in the exchangeable pool. The weathering rate and the exchangeable pool size would be expected to shrink as nutrients were lost from the system.

Subroutine Weight

The Weight subroutine, a new subroutine in the FORNUT model, is used to calculate the biomass and contents of each of the five elements in each tree. It is also used to calculate the quantity of biomass and nutrients added to the standing crop each year, as well as litter production removed during the year. This subroutine can be used to calculate standing crops, to add the dead trees to the various litter compartments, to zero all stand information at the beginning of a simulation, and to calculate the projected uptake requirement for use in the nutrient limitation growth multiplier calculation. The biomass and nutrient pools for each of the tree components are calculated based on regression equations of the form:

$$\text{Pool mass} = A + (B \times \ln(D)) \qquad (10)$$

where:

A and B = coefficients based on the tree species, the tree component, and the element; and

D = the diameter of the tree at breast height, in cm.

In this way the pools of each tree are reconstructed from three aboveground equations for each element, and three belowground equations. The aboveground equations were established for the southern Appalachians (and the Great Smoky Mountains in particular) by Shanks and Clebsch (1962). The three belowground components are calculated by dividing the total root mass for the tree into three sections, based on the proportions found by Harris et al. (1973):

Fine roots (< 0.5cm in diameter) = 36% ; (11)

Medium roots (0.5 to 2.5 cm) = 12% ; and (12)

Large roots (> 2.5 cm) = 52% . (13)

The equation for total root mass is:

$$\text{Root mass} = 1.056 \times e^{(-2.392 + (1.845 \times \ln(D)) \times 1.21)} . \quad (14)$$

The concentrations in the corresponding aboveground component were used for root concentrations (leaf for fine root, branch for medium root, bole for large root).

The pre-spring pools of each element in a tree were assumed to be equal to the previous summer pool. The pools are adjusted for the loss of litter, throughfall, reproduction, consumed parts, and the addition in overwintering storage of nutrients translocated from leaves and fine roots. The adjustments, with the exception of litter, were a fixed percentage of leaf tissue contents.

The amount of uptake, therefore, includes the regrowth of tissues shed the previous year, the growth of new tissue according to the

yearly growth increment, the reabsorption of elements lost in throughfall, the material needed for reproductive tissue, and the reconstruction of tissue lost to consumers. The uptake is reduced by the amount of nutrients which has been translocated before leaf fall. This translocation from leaf and root tissues prior to senescence was calculated as the difference in tissue concentration measured in July, at the height of the growing season, and in October, just before leaf fall.

Subroutine Decomposition

The Decomposition subroutine is designed to calculate the amount of nutrients being added to the soil solution each year. Litter is added to the primary decomposition layer. This litter is separated into six components based on material type (leaf litter, branch, bole, fine root, mid-sized root, and large root). Consequently, the primary decomposition layer does not represent a process occuring at one physical location in the forest floor, but rather a functional process with components defined by the similarity of material decomposition. Within each component the rate of release of each element differs based on site-specific information.

Rates vary from year to year, based on the lignin content of the material, the exposure of the site to light (the inversely proportional to the leaf area index), and the available moisture. The decomposition rate of organic matter is based on the Meentenmeyer (1978) equation which calculates this rate from lignin content and actual evapotranspiration:

$$y = (-3.4462 + (0.10015 \times AET)) - ((0.01341 + (0.00147 \times AET)) \times LIG) \quad (15)$$

where:

Y = percent decomposition per year;

AET = actual evapotranspiration; and

LIG = percent lignin in the leaf tissue.

For leaf decomposition the lignin concentration used is the average in the litterfall, weighted by species contribution and species' lignin concentration. The ratio between this rate and the site specific rates in the initializing data set is used to adjust the rates of nutrient release from leaves uniformly in response to species compositional shifts. The decomposition of roots and of woody material is assumed to depend more on abiotic factors than on species characteristics. Consequently, these rates remain constant throughout the simulation.

Decomposition of material is dependent upon the moisture available in a given year. The function used to describe this relationship increases the decomposition rate by a maximum of 35% in wet years and decreases the rate by a maximum of 35% in dry years:

$$MF = 1 + (0.5 \times \text{Log } (ADD/TDD)), \quad ADD/TDD \leq 5.0 ;$$
$$MF = 1.35 \qquad\qquad ADD/TDD > 5.0 ; \quad (16)$$

where:

MF = moisture factor growth multiplier;

ADD = average number of dry days; and

TDD = dry days of present year.

The amount of available moisture could in turn be modified by the influence of direct sunlight, since the litter layer is very susceptible to drying. It is assumed that the smaller the canopy leaf area, the more exposure to drying of the litter, and the less available moisture would be present for decomposition. The reduction in decomposition rate could occur to a maximum of 40%.

Once new and old litter have undergone decomposition, the released nutrients enter the secondary decomposition zone for possible nutrient immobilization. The undecomposed primary material remains in that layer as old litter, while 70% of the decomposed carbon is released to the atmosphere as CO_2 (Edwards and Harris, 1977). The decomposed litter, along with the precipitation, throughfall, and fire-released input is then subjected to immobilization by the soil microbial organisms. The immobilization is based upon the amount of carbon available to these organisms. The rate of disappearance of carbon is modelled as a function of the lignin to nitrogen ratio (Swift et al., 1978):

$$\text{RATE} = e^{-(0.075 \times \text{RATIO})}, \text{ for RATIO} > 17 ;$$

$$\text{RATE} = e^{-(0.030 \times \text{RATIO} + 0.79)}, \text{ for RATIO} \leq 17 ; \qquad (17)$$

where:

RATE = the disappearance rate for carbon; and

$$\text{RATIO} = \frac{\text{the secondary layer lignin content}}{\text{the secondary layer nitrogen content}} .$$

Nutrient concentrations in this layer are determined by the tendency of the microbes to utilize the carbon and nutrients in a fixed ratio according to biological requirements. When the input of carbon or nutrients to this layer causes the carbon-to-nutrient ratio to increase above this ideal ratio, the tendency will be for the nutrient concentrations to increase until one nutrient becomes limiting to microbial processes. The tendency is for the concentrations to be changed in the direction of the ideal carbon-to-nutrient ratio. Nutrients will then be immobilized in this layer according to the concentrations. Nutrients which are not immobilized will be released. It is from this pool of nutrients, those released through mineralization from the secondary decomposition layer, that the trees draw to meet their uptake requirements.

Carbon which is not respired to the atmosphere during microbial processing goes into the soil as organic matter. Ninety percent of carbon available to microbes is respired. The remainder, now in the soil pool, disappears at the average rate of 1% per year, depending on the carbon-to-nitrogen ratio in the soil each year. Lignin entering the secondary decomposition layer is assumed to be utilized in proportion to the rate of accumulation of lignin in this layer. Consequently, lignin content tends to reach a steady-state level. Nutrients that are released, but not utilized in uptake, are adsorbed within the soil according to a fixed retention percent. The amounts not adsorbed and added to the fixed soil pool are assumed to be leached from the rooting zone. Since weathering rates are relatively difficult

to determine, it is assumed that nutrients are released (or weathered) from the nonexchangeable soil pool as they are needed to replace nutrients removed from exchange sites to meet plant uptake requirements. Thus, the size of the exchangeable pool is assumed to decrease in proportion to decreases in the size of the nonexchangeable pool. Since weathering rates appear to exceed the cation exchange site replacement rate, and since the rate of change of exchangeable pools is low, these assumptions represent a conservative estimate of the rate of decrease of the nutrients stored in the nonexchangeable pool of the forest. No exogenous disturbances, such as high winds, fires, or floods are assumed to occur in the simulations.

CHAPTER IV

THE SITES

Information from three experimental watersheds was used in this study. The Walker Branch watershed, located on the Oak Ridge reservation in the Ridge and Valley section of Tennessee, is a 97 hectare area of forest underlain by Knox dolomite. Soils are deep, well-drained, typic paleudults of the Fullerton and Bodine series (Peters et al., 1970). The overstory is predominantly oak-hickory, with smaller sections of pine and mesic hardwoods (Grigal and Goldstein, 1971). The forest is second growth, the land having been abandoned from subsistence farming 60 to 80 years ago. A system of detailed hydrologic and mineral flow monitoring was established during the IBP program in the late 1960's. Vegetation is inventoried by 298 permanent nested circular plots, established in 1967 (Grigal and Goldstein, 1971). For each of the four major forest types (pine, dominated by Pinus virginiana and P. echinata; yellow poplar, dominated by Liriodendron tulipifera; oak-hickory, dominated by a mixture of upland oaks and hickories; and chestnut oak, dominated by Quercus prinus), six plots representative of the range of conditions in each forest type were sampled intensively to determine processes affecting element cycling (Harris et al., 1973; Henderson and Harris, 1975; Henderson et al., 1978; Edwards and Harris, 1977). The elevation in the watershed ranges from 265m to 365m.

The Hannah Branch watershed parameters were constructed from two data sets. Vegetation and disturbance information came from the Hannah

Branch watershed, collected by M. E. Harmon (1980). The watershed is approximately 1000 hectares and is located at the extreme western end of Great Smoky Mountains National Park. The watershed is underlain by sandstone and shale of Precambian age (King, 1968). Soils are of the Ramsey series, lithosols with poor horizon development, strong acidity, and low fertility (Elder, 1959). Elevation ranges between 260m and 940m. Precipitation at low elevations is 155 cm per year, but increases with elevation to 200 cm per year (Shanks, 1954; Smallshaw, 1953). Although never extensively logged, the area has been subjected to periodic disturbances of fire (Harmon, 1980), chestnut blight, and infestations of the pine bark beetle. Vegetation was sampled in 1977-78 in rectangular 0.1 hectare plots, revealing nine canopy cover types which can be loosely grouped into four categories based on elevation and site moisture considerations: mesic coves (cove hardwoods, hemlock), submesic midslope (mixed hardwoods, mixed oaks, white pine), mid-slope oaks (chestnut oak, scarlett oak), and xeric ridge top pines (yellow pines) (Harmon, 1980). The mid-slope oaks were used in the simulations presented later.

Nutrient cycling parameters were adapted from the Coweeta watershed in the Nantahala Mountains of southwestern North Carolina (Day and Monk, 1975). The information was appropriate for use in these simulations in part because of the proximity of the two areas, the similarities in precipitation, and the similarities in vegetational composition. Nutrient cycling data for this watershed and for the Walker Branch watershed used in the model are given in Tables 2-6.

Table 2. Organic matter parameters used in the FORNUT model.

	Walker Branch Watershed	Hannah Branch Watershed
Primary decomposition rate ($\%$ lost$\cdot$year^{-1}) (refs. 1,2,3,4,5,6,7):		
Leaves	52.6	46.8
Branches	23.2	32.0
Boles	13.6	5.0
Small roots	90.0	50.0
Medium roots	42.0	32.0
Large roots	5.0	5.0
Weight of soil organic matter (kg$\cdot$ha$^{-1}\cdot$12^{-1}) (refs. 8,9):	6000.0	6380.0
Weight of reproductive tissues ($\%$ of leaf weight) (refs. 1,10):	20.0	20.0
Weight of primary decomposition layer (kg$\cdot$ha$^{-1}\cdot$12^{-1}) (refs. 1,2 3,4,5,6,7,8):		
Leaves	725.0	480.0
Branches	150.0	137.0
Boles	312.0	61.0
Small roots	367.0	367.0
Medium roots	75.0	75.0
Large roots	146.0	146.0
Weight of secondary decomposition layer (kg$\cdot$ha$^{-1}\cdot$12^{-1}) (refs. 1,2, 8,11,12):	1400.0	1400.0

Table 2 (continued)

	Walker Branch Watershed	Hannah Branch Watershed
Lignin concentration (%) (refs. 13):		
Leaves	17.0	17.0
Branches	22.0	22.0
Boles	26.0	26.0
Small roots	17.0	17.0
Medium roots	22.0	22.0
Large roots	26.0	26.0
Respiration loss during decomposition (%) (refs. 5,7):		
Leaves	30.0	30.0
Branches	59.0	59.0
Boles	88.0	88.0
Small roots	30.0	30.0
Medium roots	60.0	60.0
Large roots	80.0	80.0
Fraction of live tree components lost to litterfall (% • $year^{-1}$) (refs. 3,10,14, 15):		
Leaves	100.0	100.0
Branches	5.0	5.0
Boles (bark)	10.0	10.0
Small roots	70.0	90.0
Medium roots	10.0	5.0
Large roots	0.5	0.5

Refs. and Notes

1. Cromack (1973)
2. Cromack and Monk (1975)
3. McGinty (1976)
4. Kelly (1973)
5. Edwards and Harris (1977)

Table 2 (continued)

6. Harris and Todd (in prep)
7. Environmental Sciences Division, ORNL, Annual Report (1972)
8. Henderson et al., (1978)
9. Sollins et al., (1973)
10. Grizzard (1975)
11. Eastern Deciduous Forest Biome Annual Report (1978)
12. Environmental Sciences Division, ORNL, Annual Report (1971)
13. Swift et al., (1978)
14. Day (1974)
15. Harris et al., (1972)

Table 3. Element parameters used in the simulation of the Walker Branch watershed.

	Calcium	Magnesium	Potassium	Phosphorus	Nitrogen
Primary decomposition layer size ($kg \cdot ha^{-1} \cdot 12^{-1}$) (refs. 1,2,3,4)					
Leaves	9.4	0.5	0.42	0.42	8.2
Branches	0.83	0.08	0.08	0.08	1.0
Boles	0.81	0.04	0.02	0.02	0.23
Small roots	4.7	0.25	0.20	0.20	4.10
Medium roots	1.2	0.04	0.04	0.04	0.50
Large roots	0.40	0.02	0.01	0.01	0.09
Secondary decomposition layer size ($kg \cdot ha^{-1} \cdot 12^{-1}$) (refs. 1,2,3,4)	27.0	1.6	1.6	1.2	16.5
Soil exchangeable pool size ($kg \cdot ha^{-1} \cdot 12^{-1}$) (refs. 3,5)	59.2	7.1	14.1	0.75	6.25
Soil total pool size ($kg \cdot ha^{-1} \cdot 12^{-1}$) (refs. 3,5)	450.0	1480.0	5120.0	150.0	470.0
Atmospheric input ($kg \cdot ha^{-1} \cdot 12^{-1} \cdot yr^{-1}$) (ref. 6)	1.0	0.2	0.25	0.04	1.08
Weathering rate ($kg \cdot ha^{-1} \cdot 12^{-1} \cdot yr^{-1}$) (ref. 7)	3.03	0.62	1.37	0.152	0.383

Refs. and Notes

1. Harris and Todd (in prep)
2. Environmental Sciences Division, ORNL, Annual Report (1972)
3. Henderson et al., (1978)

Table 3 (continued)

4. Harris et al., (1972)
5. Peters et al., (1970)
6. Henderson et al., (1977)
7. Calculated as the difference between the input to the forest floor (litterfall, throughfall, precipitation, and root mortality) and outputs (uptake and outflow), assuming that litter layer and soil pool sizes do not change appreciably.

Table 4. Miscellaneous element parameters used in the simulation of the Walker Branch watershed.

	Calcium	Magnesium	Potassium	Phosphorus	Nitrogen
Average concentration in leaves (%) (ref. 1)	1.03	0.10	0.22	0.08	1.20
Concentration in primary decomposition layer (%) (refs. 2,3,4)	0.68	0.03	0.03	0.02	0.49
Concentration in secondary decomposition layer (%) (refs. 2,3,4)	1.82	0.11	0.10	0.08	1.11
Concentration in reproductive tissue (% of leaf content) (ref. 1)	12.0	16.0	19.0	12.0	11.0
Throughfall content (% of fall leaf content) (ref. 5)	18.0	11.4	37.0	5.0	5.0
Withdrawal from leaves during growing season (leaf fall weight/ leaf summer weight) (ref. 1)	2.6	1.1	1.1	0.75	0.70
Withdrawal from roots during growing season (root fall weight/root summer weight) (ref. 2)	1.0	0.82	0.59	0.70	0.50
Concentration in bark tissue (%) (ref. 1)	0.63	0.03	0.13	0.01	0.20

Table 4 (continued)

	Calcium	Magnesium	Potassium	Phosphorus	Nitrogen
Soil retention (% of input) (ref. 3)	75.0	75.0	25.0	99.0	5.0
Microbial carbon: nutrient ratio (carbon content/ element content) (ref. 6)	11.0	346.0	136.0	94.0	26.0
Primary decomposition rate (% lost·yr^{-1}) (refs. 2,3,4,7,8,9, 10,11)					
Leaves	29.0	19.9	73.0	39.0	31.0
Branches	30.0	10.6	58.6	30.0	30.8
Boles	5.6	0.8	10.0	4.8	5.7
Small roots	33.0	57.0	80.0	45.0	50.0
Medium roots	30.0	10.6	58,6	30.0	30.8
Large roots	5.6	0.8	10.0	4.8	5.7

Refs. and Notes

1. Grizzard (1975)
2. Environmental Sciences Division, ORNL, Annual Report (1972)
3. Henderson et al., (1978)
4. Environmental Sciences Division, ORNL, Annual Report (1971)
5. Henderson et al., (1977)
6. Swift et al., (1978)
7. Kelly (1973)
8. Peters et al., (1970)
9. Ausmus (1973)
10. Henderson and Harris (1975)
11. Harris et al., (1975)

Table 5. Element parameters used in the simulation of the Hannah Branch Watershed.

	Calcium	Magnesium	Potassium	Phosphorus	Nitrogen
Primary decomposition layer size ($kg \cdot ha^{-1} \cdot 12^{-1}$) (refs. 1,2,3,4,5)					
Leaves	6.6	0.9	1.5	0.-6	6.8
Branches	1.2	0.1	0.05	0.12	0.82
Boles	0.3	0.02	0.02	0.05	0.23
Small roots	4.7	0.25	0.20	0.20	4.10
Medium roots	1.2	0.04	0.04	0.04	0.50
Large roots	0.4	0.02	0.01	0.01	0.09
Secondary decomposition layer size ($kg \cdot ha^{-1} \cdot 12^{-1}$) (refs. 1,2,4,5)	20.4	3.0	4.6	1.9	17.7
Soil exchangeable pool size ($kg \cdot ha^{-1} \cdot 12^{-1}$) (refs. 6,7,8,9, 10)	78.3	5.0	42.5	2.2	9.7
Soil total pool size ($kg \cdot ha^{-1} \cdot 12^{-1}$) (refs. 6,7,8,9, 10)	208.3	683.3	10333.0	100.0	566.7
Atmospheric input ($kg\ ha^{-1}\ 12^{-1}\ yr^{-1}$) (refs. 6,11)	0.4	0.105	0.175	0.009	0.730
Weathering rate ($kg\ ha^{-1}\ 12^{-1}\ yr^{-1}$) (ref. 12)	3.57	1.01	1.0	0.49	0.558

Table 5 (continued)

Refs. and Notes

1. Cromack (1973)
2. Cromack and Monk (1975)
3. McGinty (1976)
4. Best and Monk (1975)
5. Mitchell et al., (1975)
6. Henderson et al., (1978)
7. Eastern Deciduous Forest Biome Annual Report (1978)
8. Golden (1976)
9. Wolfe (1965)
10. Swank and Waide (1980)
11. Johnson and Swank (1973)
12. Calculated as the difference between the input to the forest floor (litterfall, throughfall, precipitation, and root mortality) and outputs (uptake and outflow), assuming that litter layer and soil pool sizes do not change appreciably.

Table 6. Miscellaneous element parameters used in the simulation of the Hannah Branch watershed.

	Calcium	Magnesium	Potassium	Phosphorus	Nitrogen
Average concentration in leaves (%) (ref. 1)	2.0	0.6	1.0	0.2	2.0
Concentration in primary decomposition layer (%) (refs. 2,3, 4)	1.05	0.24	0.32	0.10	0.76
Concentration in secondary decomposition layer (%) (refs. 2,3)	1.36	0.20	0.27	0.13	1.18
Concentration in reproductive tissue (% of leaf content) (ref. 1)	10.0	5.0	33.0	20.0	20.0
Throughfall content (% of fall leaf content) (ref. 3)	19.0	47.0	170.0	11.0	12.0
Withdrawal from leaves during growing season (leaf fall weight/ leaf summer weight) (ref. 1)	-2.7	0.04	0.45	0.26	0.55
Withdrawal from roots during growing season (root fall weight/ root summer weight) (ref. 5)	1.0	0.18	0.41	0.70	0.50

Table 6 (continued)

	Calcium	Magnesium	Potassium	Phosphorus	Nitrogen
Concentration in bark tissue (%) (ref. 1)	1.1	0.03	0.13	0.01	0.20
Soil retention (% of input)	75.0	75.0	25.0	99.0	5.0
Microbial carbon: nutrient ratio (element content/ carbon content) (ref. 6)	11.0	346.0	136.0	94.0	26.0
Primary decomposition rate (% lost·yr^{-1}) (refs. 1,2,4,5,7)					
Leaves	54.1	56.1	43.8	18.8	32.3
Branches	36.0	12.0	61.8	25.0	35.0
Boles	3.5	1.0	20.0	14.3	7.5
Small roots	80.0	80.0	80.0	80.0	80.0
Medium roots	7.0	14.0	82.0	42.0	42.0
Large roots	5.6	0.8	10.0	4.8	4.7

Refs. and Notes

1. Day (1974)
2. Cromack and Monk (1975)
3. Best and Monk (1975)
4. Mitchell et al., (1975)
5. McGinty (1976)
6. Swift et al., (1978)
7. Cromack (1973)

CHAPTER V

RESULTS

Validating the Model

On the Walker Branch watershed twelve years of tree growth on forty-four field plots in four different vegetation types and slope positions have been recorded and could be compared to model predictions of growth behavior. In the model, water, light, and nutrient availability are integrated into the calculation of the yearly diameter increment of each tree. The availability of each of these resources in turn integrates a wide variety of processes simulated in the model. Therefore, it was reasoned that analyzing the ability of the model to correctly estimate average annual growth at different locations in the watershed would provide a test of the accuracy of the representations of these processes included in the model. Each plot was initialized with the actual data of the 1967 tree size and species and the appropriate soil condition (Table 7) and nutrient cycling information (Tables 2-6, pages 46-58) for the location within the watershed. Each of the 44 plots was simulated separately for twelve years of simulation time. Monthly weather data from 1967 to 1979 was used.

Figure 2 gives the average growth increment by vegetation type for three different types of simulations and from the field data. The average growth increment from the twelve year remeasurement of the field plots (from left to right, a moist ravine bottom slope tulip poplar stand, a midslope chestnut oak stand, an upper-slope oak-hickory stand, and a

Table 7. Site characteristics used in FORNUT.[1,2,3,4]

	Walker Branch Watershed	Hannah Branch Watershed
Elevation (m)	330.0	750.0
Soil depth (cm)	60.0	30.0
Percent rock in soil (%)	20.0	40.0
Water holding capacity (%)	10.0	7.0
Field capacity (%)	25.0	25.0
Field capacity (cm)	27.0	4.5
Actual evapotranspiration (cm)	797.0	775.0
Average annual growing degree days (days)	3150.0	2900.0
Average annual dry days (days)	75.0	50.0

Refs.

1. Golden (1975)
2. Broadfoot and Burke (1958)
3. Shanks (1954)
4. Peters et al., (1970)

Figure 2. The comparison of the growth rates in the field with simulated growth rates for four stands on the Walker Branch Watershed, using 90 cm rooting depths.

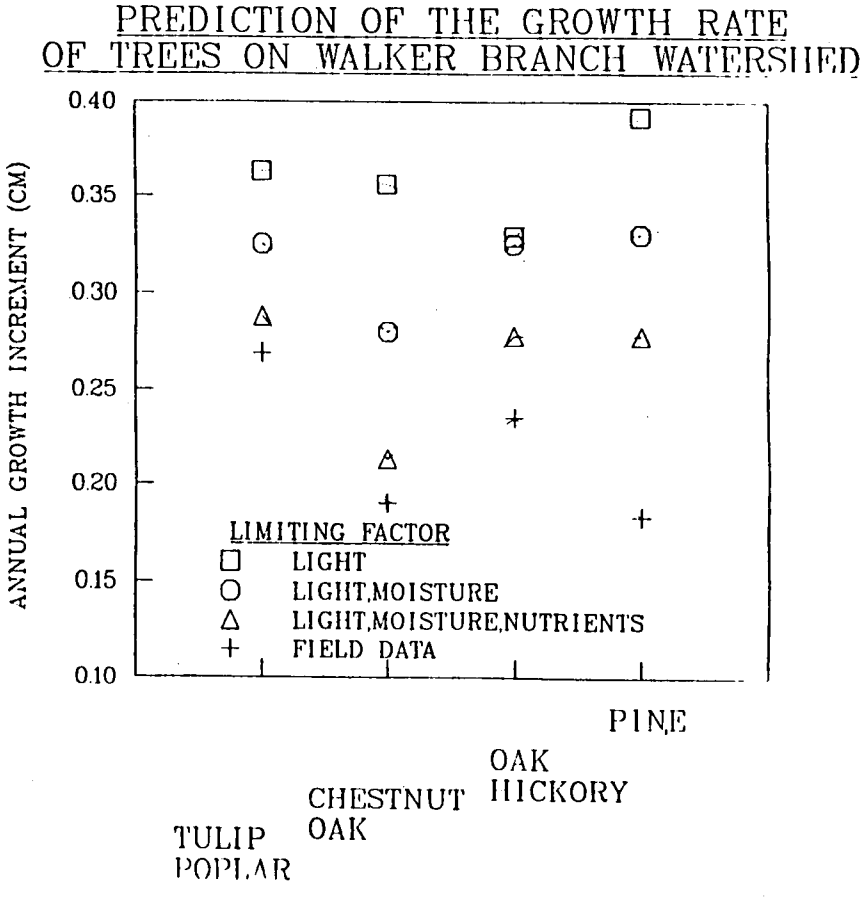

PREDICTION OF THE GROWTH RATE
OF TREES ON WALKER BRANCH WATERSHED
ANNUAL GROWTH INCREMENT (CM)
0.40
0.35
0.30
0.25
0.20
0.15
0.10
LIMITING FACTOR
LIGHT
LIGHT,MOISTURE
LIGHT,MOISTURE,NUTRIENTS
FIELD DATA
PINE
OAK
HICKORY
CHESTNUT
OAK
TULIP
POPLAR

Figure 2

ridgetop pine stand) are indicated on this figure as the field data. The values of yearly increment from the field data were lower than any of the simulations. The highest increment values were obtained during a twelve year simulation of these plots with light being the only limiting factor on growth (Figure 2). In this simulation the growth restrictions due to insufficient moisture and nutrients were not allowed to affect growth. The growth increments from this simulation not only fell considerably above the actual field data, but did not follow the same community type to community type pattern. The pine stand had the highest increment in this simulation, nearly 0.40 $cm \cdot yr^{-1}$, while the actual data for pine showed the lowest rate, 0.17 $cm \cdot yr^{-1}$. The increment of the chestnut stand was similar to the tulip poplar stand in the simulation, while it was only 60% of the tulip poplar stand growth in the actual data. The oak-hickory stand showed the lowest growth in the simulation, but the second highest in the field data.

In a second set of simulations moisture limitation processes were permitted to affect growth along with the light limitations. These conditions resulted in reducing the increment of the simulations (Figure 2) in three of the four stand types, having very significant effects in the chestnut oak and pine stands, but no effect on the oak-hickory. The soil was assumed to be a full meter in depth in the simulation of the oak-hickory stand. However, the effective rooting depth from which water can be drawn by the trees may be shallower. When a 60 cm rooting depth was used in the simulation in place of the 90 cm depth, the stand simulations produced behavior which was very similar to the field data (Figure 3).

Figure 3. The comparison of the growth rates in the field with simulated growth rates for four stands on the Walker Branch watershed, using 60 cm rooting depths.

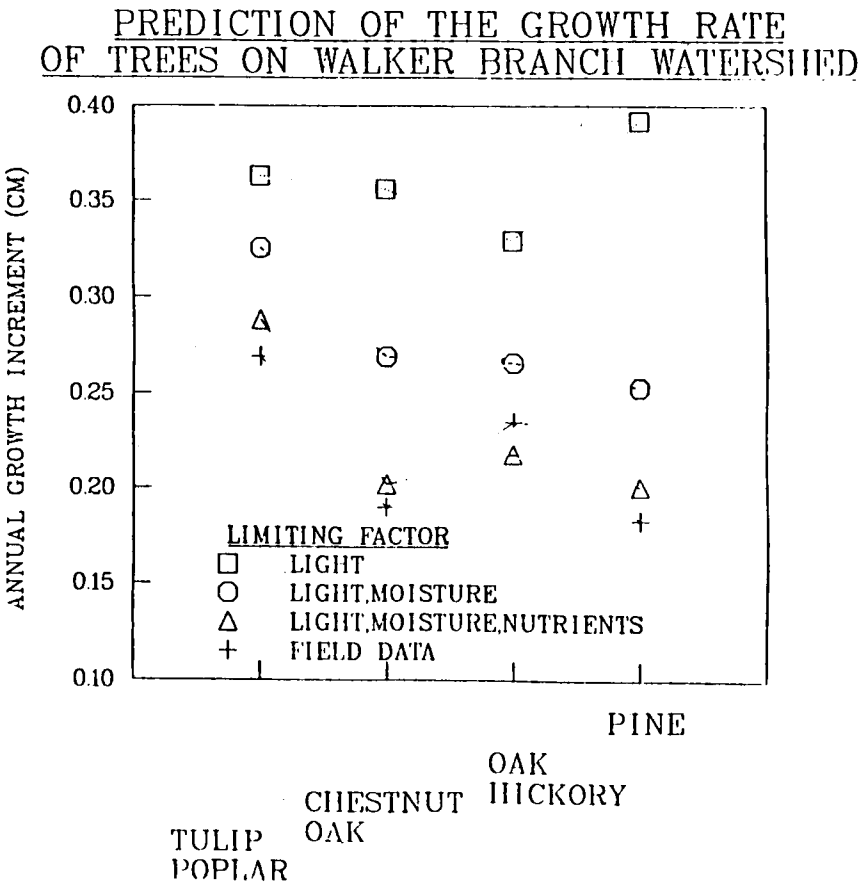

PREDICTION OF THE GROWTH RATE
OF TREES ON WALKER BRANCH WATERSHED
ANNUAL GROWTH INCREMENT (CM)
0.40
0.35
0.30
0.25
0.20
0.15
0.10
LIMITING FACTOR
LIGHT
LIGHT,MOISTURE
LIGHT,MOISTURE,NUTRIENTS
FIELD DATA
PINE
OAK
HICKORY
CHESTNUT
OAK
TULIP
POPLAR

Figure 3

In the last set of validating simulations, the nutrient limitations were added to light and water limitations. These simulations produced growth rates very similar to observed field data, particularly in the mid-slope and lower-slope stands (Figure 2, page 61), and in all stands in the shallower soils (Figure 3). In all stands, nutrient limitations on growth produced significant reductions in increment. The slowing of growth in the chestnut oak stand was somewhat greater than in the others.

In summary, moisture and nutrient response additions to the model explain much of the difference between model predictions based on light limitations alone and independent field data. It can be concluded that the moisture limitation mechanisms and the nutrient cycling mechanisms included in the model produce the correct growth response in trees. Further, these mechanisms were sufficiently flexible to produce the desired responses to changes in the nutrient cycles over time in compositionally diverse stands.

Patterns of Successional Dynamics

Figure 4 shows the average percent contribution of each species to the biomass of the Walker Branch Watershed (WBW) during the 500 year simulation. At the start of the simulation pignut hickory contributed over 30% of the total biomass of the stand, with white oak and chestnut oak contributing 10 and 15%, respectively. By year 300, pignut hickory had decreased to a 20% contribution while white oak had increased to over 30% and chestnut oak's contribution had become insignificant. Some species, such as red maple, pignut hickory, and chestnut oak, were reduced in importance during the simulation. The presence of some

Figure 4. Average percent contribution of species to the total biomass on the WBW during the simulation.

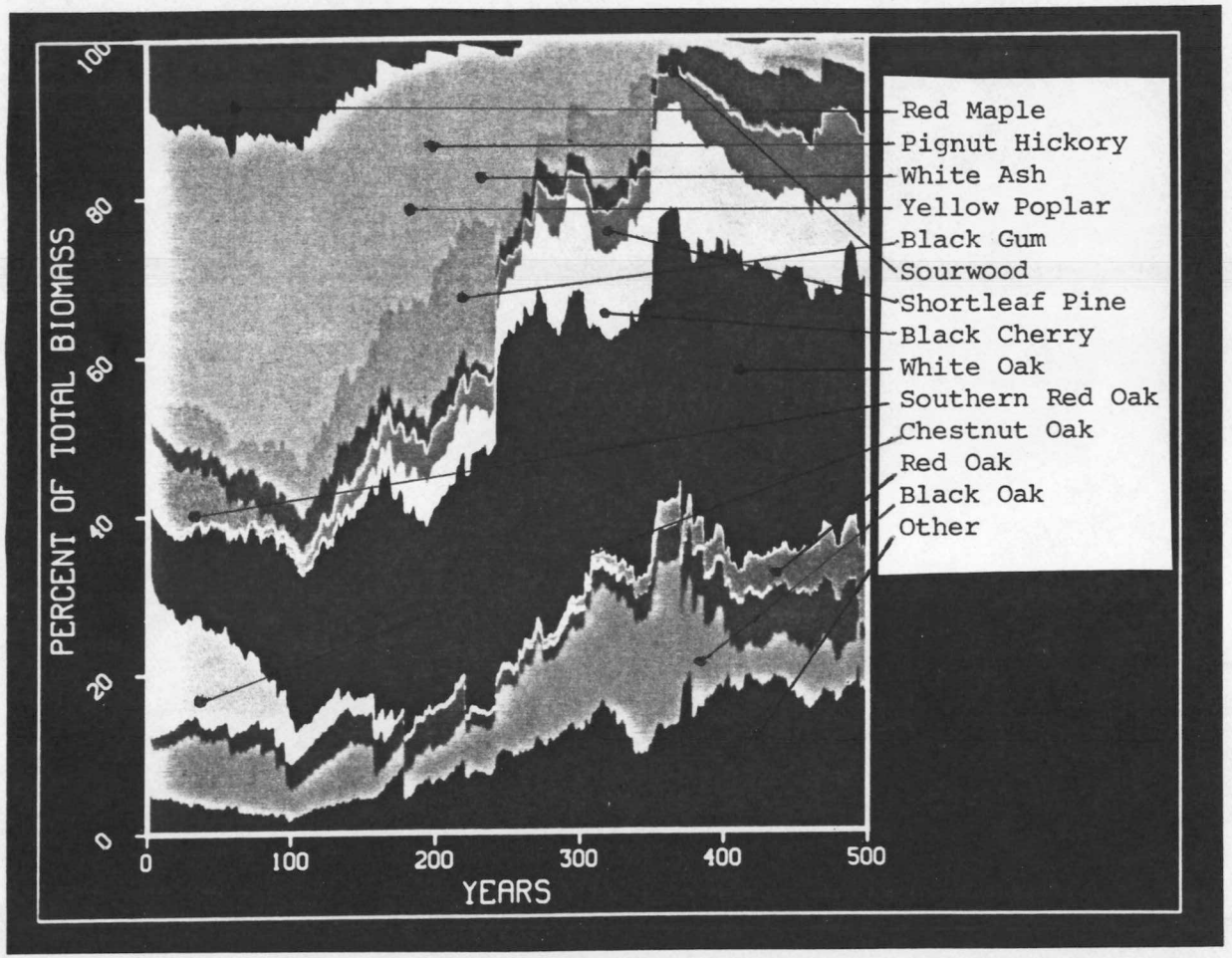

PERCENT OF TOTAL BIOMASS
0
20
40
60
80
100
0
100
200
300
400
500
YEARS
Red Maple
Pignut Hickory
White Ash
Yellow Poplar
Black Gum
Sourwood
Shortleaf Pine
Black Cherry
White Oak
Southern Red Oak
Chestnut Oak
Red Oak
Black Oak
Other

Figure 4

species was enhanced in mid-simulation and then became insignificant once again during late simulation. Yellow poplar and red oak, species with two very different life history characteristics, are both examples of this pattern. A third group of species grew in importance as the simulation progressed. Examples of this behavior could be found with shortleaf pine, black cherry, and white oak. The representatives of this class are a seemingly incompatible mixture of intolerants (such as shortleaf pine and black cherry) which depend upon the creation of gaps in the canopy, and light tolerant species (such as white oak) which capitalize on the lack of large scale disturbance to maintain position in the canopy over long time periods.

Unlike the simulated pattern of the WBW, the pattern for the Hannah Branch Watershed (HBW) (Figure 5) showed much more consistency in the species dominating the stand over time during the simulation. The percent contributed to total biomass of the stand by chestnut oak remained high throughout the simulation. White pine also contributed significantly throughout the simulation, although this species was particularly important during the period from years 200 to 300. Sugar maple and silverbell also became important during this period, at the expense of black oak. Red maple, white oak, and assorted other species maintained a consistent presence throughout the simulation.

Patterns of Nutrient Cycling Dynamics on the Walker Branch Watershed

Twenty-five dry mid-slope oak-hickory dominated plots one-twelfth hectare in area from the Walker Branch watershed (WBW) were simulated

Figure 5. Average percent contribution of species to the total biomass on the HBW during the simulation.

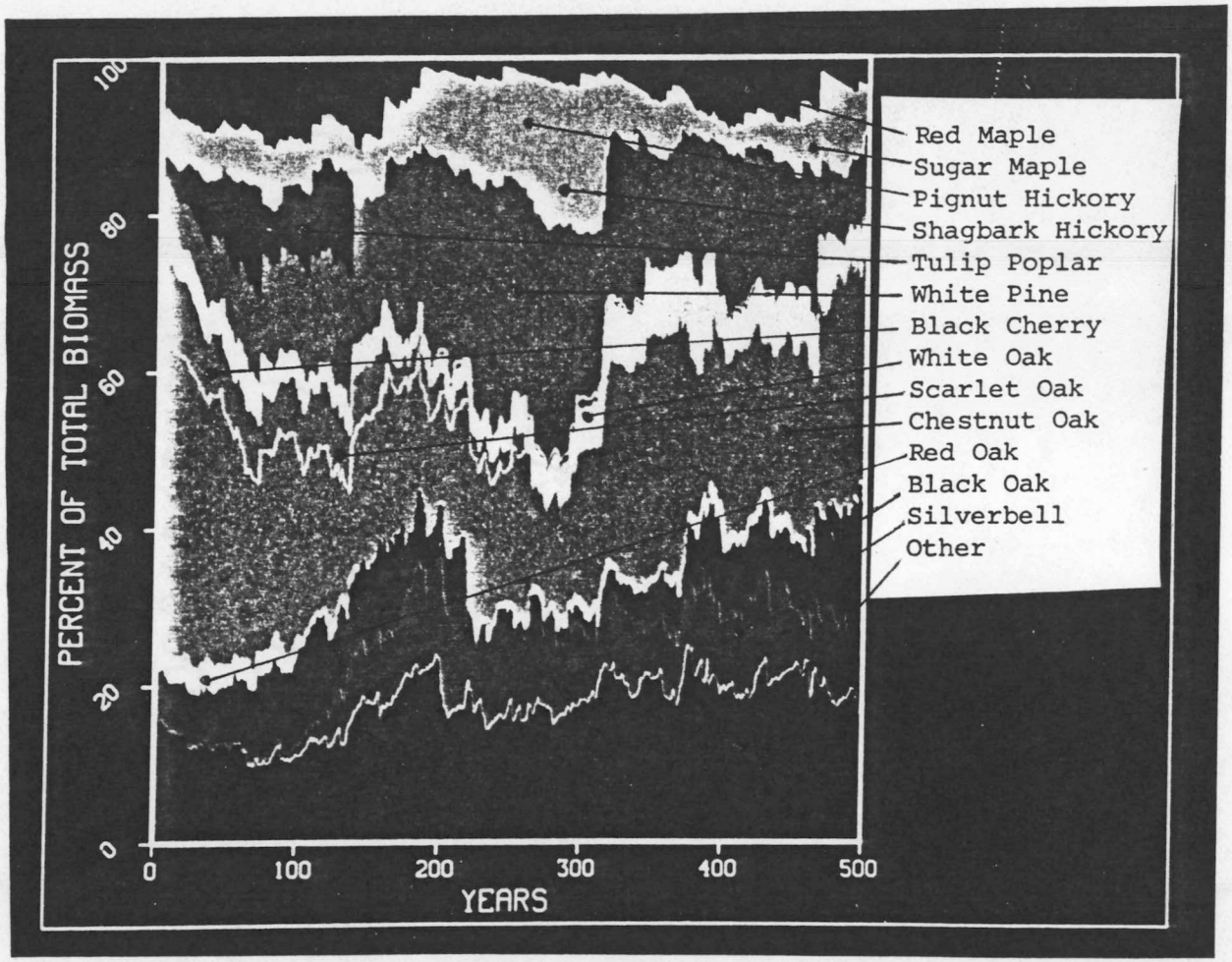

PERCENT OF TOTAL BIOMASS
0
20
40
60
80
100
0
100
200
300
400
500
YEARS
Red Maple
Sugar Maple
Pignut Hickory
Shagbark Hickory
Tulip Poplar
White Pine
Black Cherry
White Oak
Scarlet Oak
Chestnut Oak
Red Oak
Black Oak
Silverbell
Other

Figure 5

for 500 years. Figure 6 shows the magnitude of average annual flows of organic matter in these plots beginning in 1979 and extrapolating 500 years into the future. The top curve represents the annual net biomass increment before leaf fall. The WBW stand is growing on farmland which was abandoned 60 to 80 years ago. The simulated stand showed a high rate of biomass accumulation, common for a stand of this age, to continue for the next 50 years. As these plots became occupied by older, less vigorously growing trees in the simulation the biomass accumulation rate dropped rapidly. During the period from year 100 to year 200 many of the dominant individual trees approaching 200 years of age experienced death. This process led to the succession to dominance of more vigorous subcanopy trees. As a consequence the character of the twenty-five plots shifted during this period from a relatively uniformly aged stand, in the midst of successional recovery from farmland abandonment to a more all-aged structure. The lack of large increases or decreases in the biomass accumulation during the remaining years of the simulation was evidence of the continued all-aged character of the simulated forest under an environment free of exogenous disturbance.

Figure 6 also shows the amount of annual organic matter contributed by litterfall. This curve generally follows the pattern of biomass accumulation. High carbon fixation during a growing season is followed by high organic matter releases in the fall. The litterfall value on the graph does not include the additions contributed by the boles of trees that have died during the year since a single tree fall represents too large an amount to be expressed on the same scale as the other flows.

Figure 6. Simulated changes in the quantity of organic matter transferred annually in the WBW.

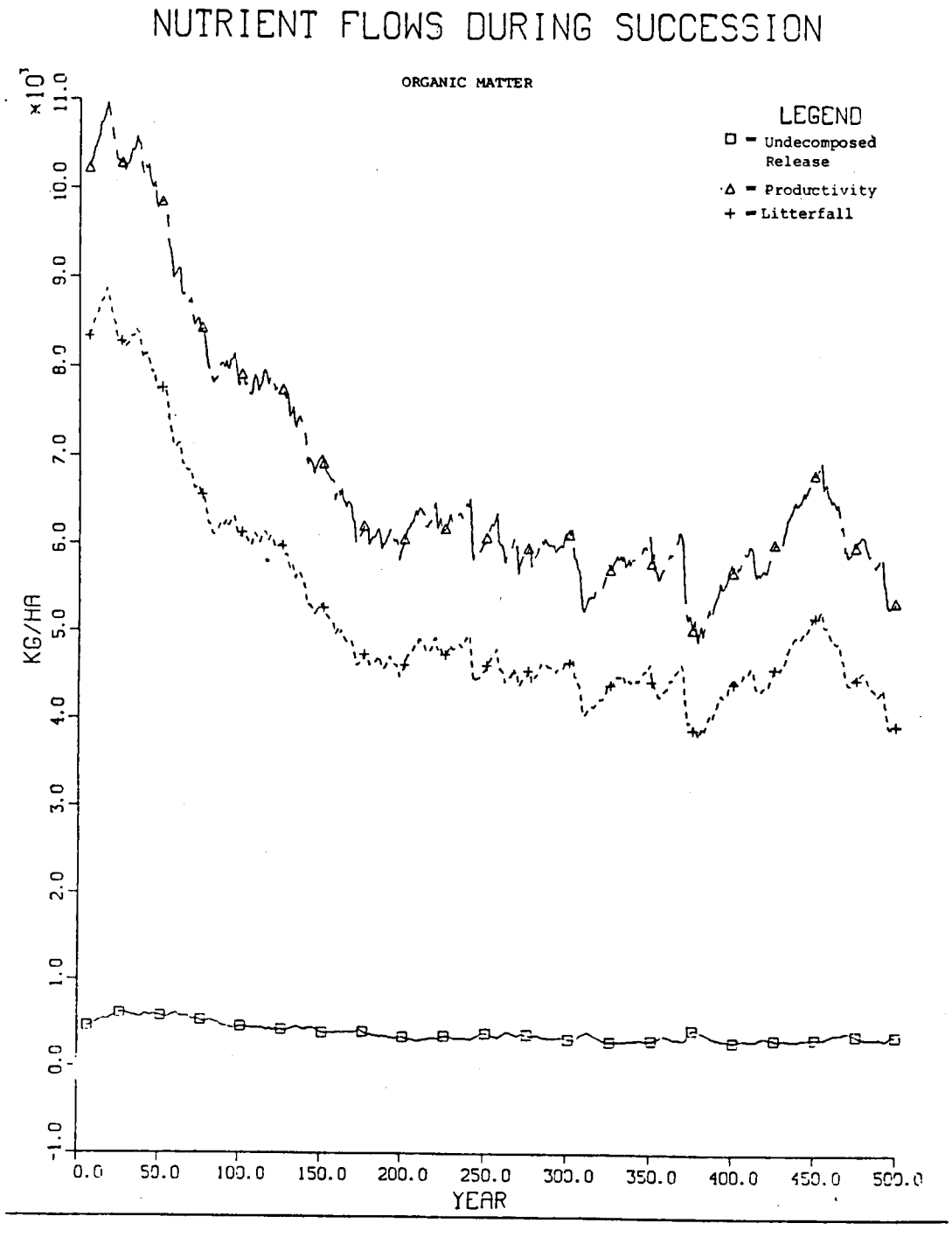

NUTRIENT FLOWS DURING SUCCESSION
ORGANIC MATTER
LEGEND
□ = Undecomposed Release
Δ = Productivity
+ = Litterfall
KG/HA
×10³
11.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
-1.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
YEAR

Figure 6

Even without this proportion of total litterfall, the magnitude of return to the forest floor was a large proportion of the organic matter fixed in the forest during the year and remained a large proportion throughout the simulation.

The amount of organic matter released from the litter layer into the soil is also shown in Figure 6. This represents the subsection of the litter deposited in the litter layer which was not oxidized to carbon dioxide by decomposer organisms during the first year following deposition, but which, due to the recalcitrant nature of the carbon molecules, became an addition to the amorphous humic pool in the soil. The litter layer release of recalcitrant carbon to the soil was low in magnitude and showed little fluctuation compared to litterfall and gross productivity quantities.

The effects of these flows on the average pools of organic matter in the WBW are shown in Figure 7. The dynamics through 500 years of simulation of the four major pools are shown: the vegetation pool (TREE), the primary decomposition pool (FLOOR 01), the secondary decomposition pool (FLOOR 02), and the soil pool (SOILFX). Each graph represents the average behavior of the pool in the forest. The values on the left of each sub-graph indicate the maximum (top value) and minimum (bottom value) average values in metric tons per hectare reached by that pool during the simulation. The graphs are begun at year twenty-five.

From a high of 158 metric tons per hectare of tree biomass, the amount of organic matter in the trees decreased gradually to less than

Figure 7. Simulated changes in organic matter pools in the four major components of the WBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

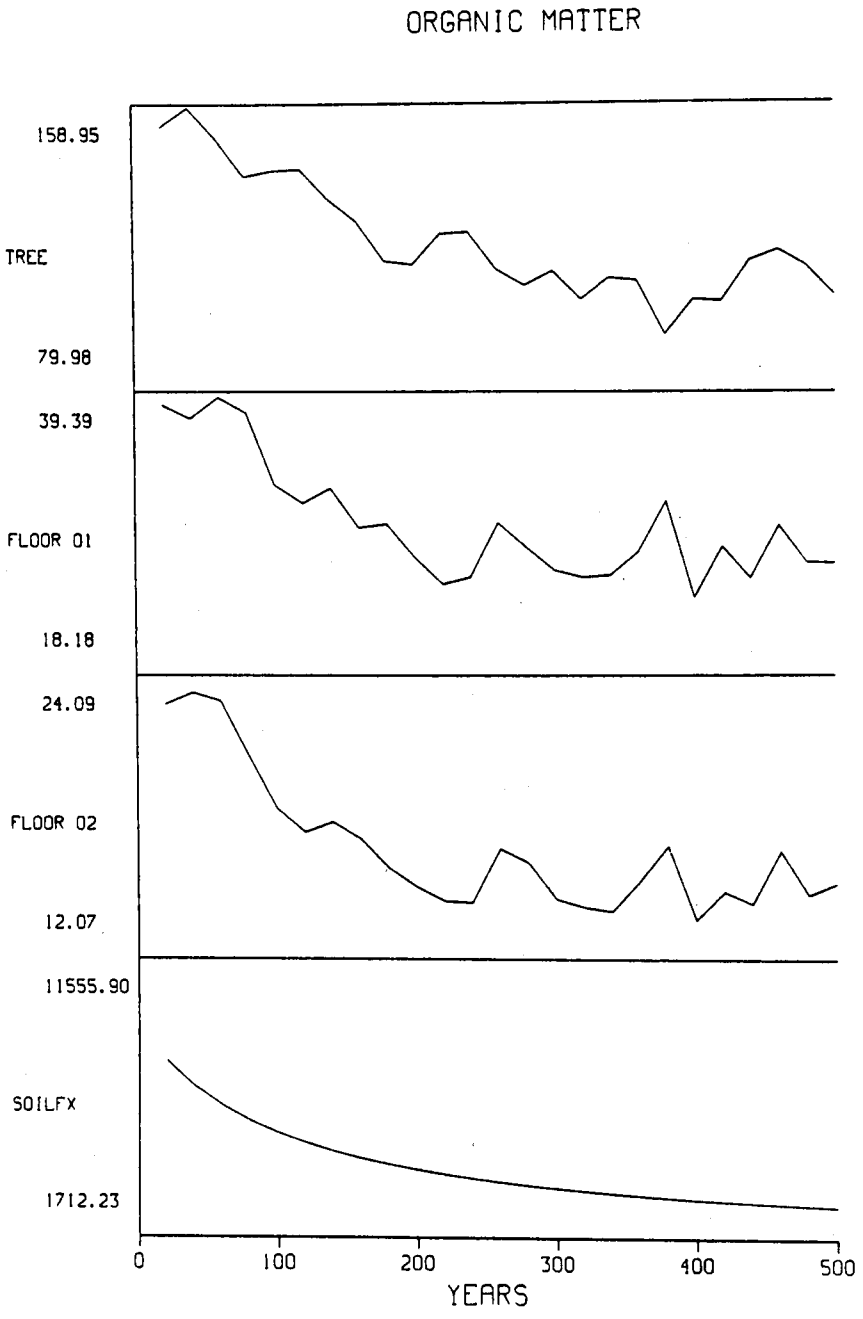

ORGANIC MATTER
158.95
TREE
79.98
39.39
FLOOR 01
18.18
24.09
FLOOR 02
12.07
11555.90
SOILFX
1712.23
0
100
200
300
400
500
YEARS

Figure 7

100 metric tons per hectare. The reduction of tree biomass and organic matter flows led to similar drops in the size of the primary and secondary decomposition pools. These pools displayed relatively synchronous behavior with respect to the timing of increases or decreases. However, periods of delays in response to the behavior of the tree components are frequent. For example, while the tree component began declining at year 50, the secondary decomposition component did not sharply decline until year 75, and the primary decomposition component remained near maximum until year 100. Similarly, when the tree component began to rise at year 200, the increase in the decomposition components did not appear until twenty-five years later. However, there were periods during which the response of the decomposition components to the tree component was rapid, such as in year 375, when a sharp dip in the tree pool was accompanied by a rapid rise in the decomposition layers in the same year.

As a result of a lack of information concerning the turnover rate of the soil organic matter pool, an assumption was made that 1% of the pool would decompose each year. This assumed rate was probably an overestimate for the WBW. However, since the soil organic matter does not affect other components or flows, error in this assumption did not affect the model behavior, but affected only the size of the organic matter pool.

The transfers of calcium are shown in Figure 8 for this simulation of the WBW. Three characteristics immediately distinguish this graph from the organic matter graph. First, the amount of calcium that has

Figure 8. Simulated changes in the quantity of calcium transferred annually in the WBW.

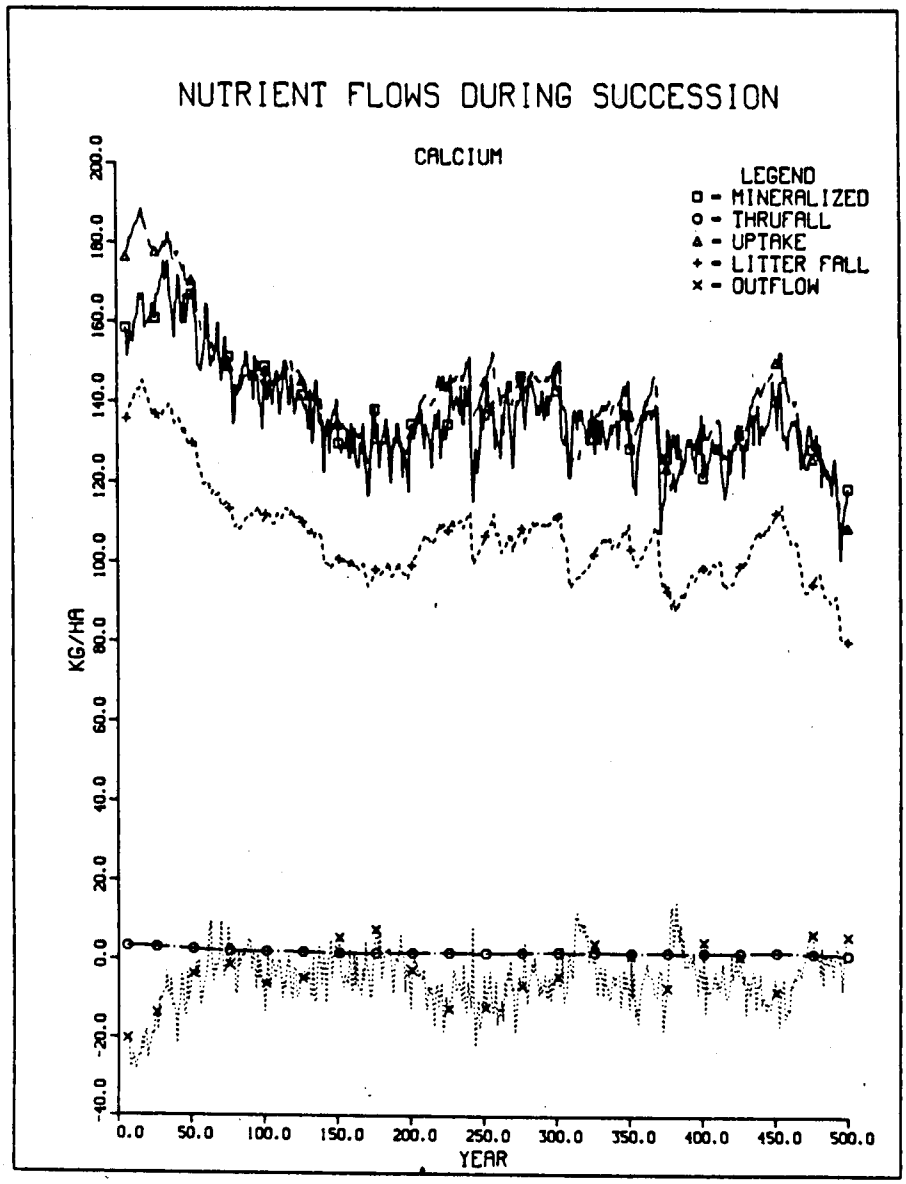

NUTRIENT FLOWS DURING SUCCESSION
CALCIUM
LEGEND
□ - MINERALIZED
○ - THRUFALL
△ - UPTAKE
+ - LITTER FALL
× - OUTFLOW
KG/HA
200.0
180.0
160.0
140.0
120.0
100.0
80.0
60.0
40.0
20.0
0.0
-20.0
-40.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
YEAR

Figure 8

been released from the litter layer to the soil (mineralized) was of comparable magnitude to the amount of the annual uptake of calcium (note that the uptake and the mineralized curves are difficult to distinguish from one another). Second, there was more year to year variability in the release of calcium from the litter layer than in the release of organic matter. The outflow values also varied from year to year. The outflow represents the quantity of calcium which was made available through mineralization from the litter layer but was not taken up by trees. Consequently, the outflow curve represents the difference between the uptake and the mineralized curves. A positive value of outflow indicates an excess of release of calcium from the litter layer over what could be used by the trees. A negative value indicates that insufficient quantities of calcium are released from the litter layer to meet tree growth requirements. In this case, the deficit is supplied by mining the exchange sites in the soil and reducing the amount of calcium on these sites.

The cause of the fluctuation in the relationship between the uptake requirement and mineralization from the litter layer is that the behavior of each flow is regulated by a different subsystem. The tree determines uptake requirement, and the complex microbial community in the litter regulates the mineralization rate. However, each of these subsystems is constrained by a somewhat different set of environmental conditions. Trees determine calcium uptake needs based on the availability of light, water and a particular combination of growth and maintenance requirements. Microbes in the litter release calcium according to the constraints of

their growth processes. For example, weather conditions in a given year might make it possible for abundant mineralization to occur while simultaneously inadequate moisture is available for optimum growth of the dominant trees. The differences in the response of the subsystem to its own set of constraints may determine whether a nutrient such as calcium (Figure 8) is in abundance. Consequently, the lack of synchrony between the two sets of constraints and between their respective effects on nutrient flow is expected. During some years the two subsystems are constrained to produce similar behavior. In these years the tree requirement for calcium is essentially met by the release of calcium from the litter layer (and output has a value of zero). However, it is more typical for the requirement to exceed the release from the litter layer (negative values of outflow). The consequence is that trees must rely on a slow draining of the soil pool of calcium to continue to meet uptake needs.

Periodically, the outflow was positive. At these times an abundance of calcium was mineralized over that taken up by the trees. At least some of the calcium excess not claimed by plant roots is lost from the rooted zone and thus lost from the system.

The litterfall curve (Figure 8) represents the quantity contributed each year exclusive of tree death and tree fall. The difference between the tree uptake and tree litterfall gives an indication of the quantity of calcium which live trees removed from the yearly cycle and placed in long-term storage. On any of the twenty-five plots where death of a large tree had not recently occurred, this difference represented the

degree of mining of the yearly cycle by the trees. Mineralization from the litter layer did not equal uptake. The contributions of the trees to the litter layer were less than the yearly uptake. Therefore, individual plots that were accumulating biomass were likely to have calcium deficits. In terms of the entire stand, however, with tree fall included the average mineralization release remained similar to the average uptake.

The reduction of calcium uptake and litterfall was much smaller than the decrease in organic matter accumulation. Some of the same long-term dynamics were apparent, however, such as the decrease in size during the periods from year 50 to year 200 and from year 450 to year 500.

As with calcium flows, the calcium pool in the trees (Figure 9) did not decrease as much as the organic matter pool. Large fluctuations in tree calcium levels occurred during the simulation, with the vegetation reaching new maximums in calcium accumulation during the middle of the simulation. The secondary decomposition layer reflected the shrinking tree pool, but the primary decomposition reached a higher level early in the simulation and remained in more or less steady state at that level. The frequent periods during which amounts of mineralized calcium were insufficient to meet the uptake requirement caused a gradual draining from the soil pool, reducing it from 5.4 metric tons per hectare to less than half that value by year 500.

Considerable variability from year to year was evident in the record of mineralization of magnesium, but the level remained in excess

Figure 9. Simulated changes in calcium pools in the four major components of the WBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

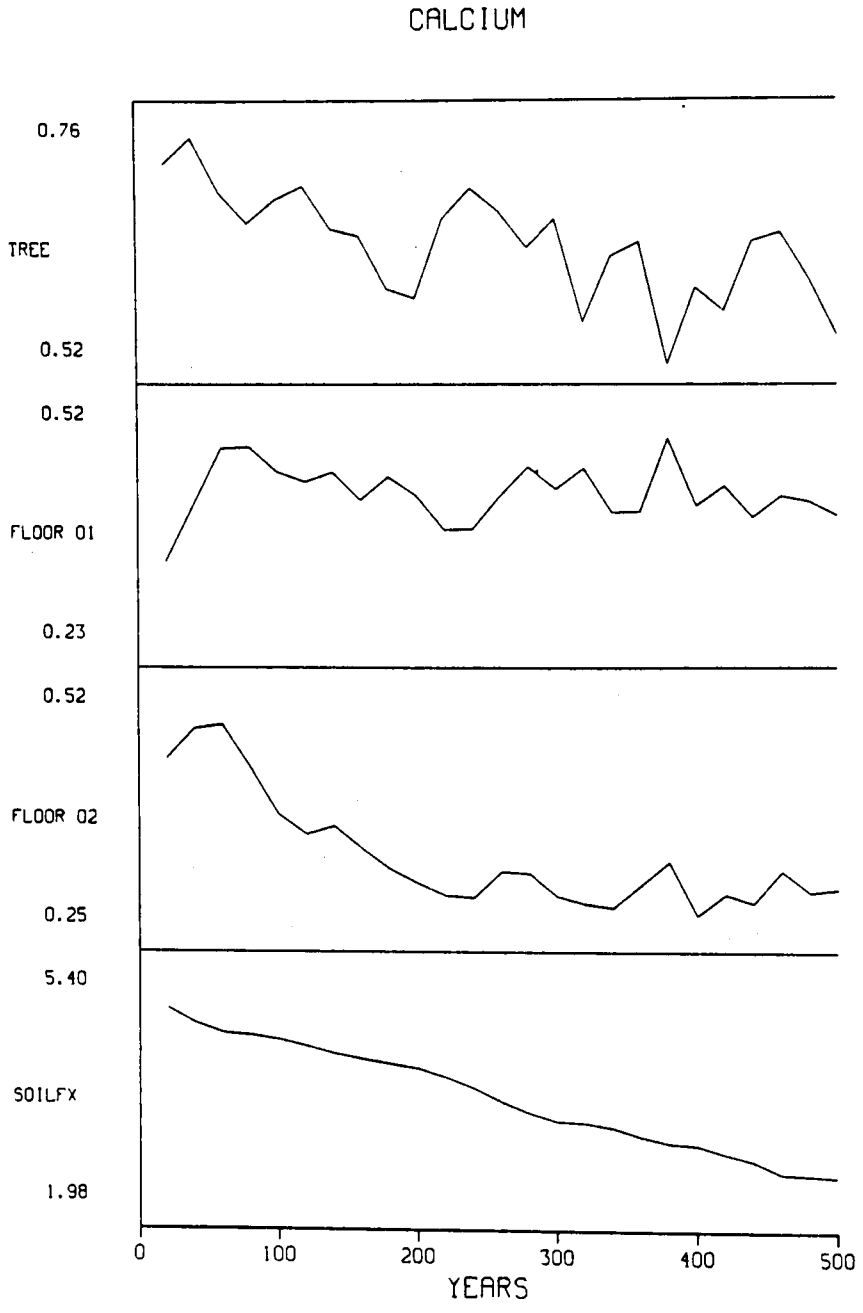

CALCIUM
0.76
TREE
0.52
0.52
FLOOR 01
0.23
0.52
FLOOR 02
0.25
5.40
SOILFX
1.98
0
100
200
300
400
500
YEARS

Figure 9

of that required by trees (Figure 10). Consequently, the outflow remained above zero. Though the general pattern of magnesium flow was similar to that of the organic matter flows, it is notable that mineralization, uptake, and litterfall reached levels during the later part of the simulation which exceeded those levels achieved during the vigorous biomass accumulation phase early in the simulation (Figure 11). A rise in all three of these flows suggests that magnesium is concentrated to higher levels in tissues of the late successional trees. Little change in the overall pattern of outflow occurred, however.

The rapid and increasing flows of magnesium toward the end of the simulation were associated with a rapid buildup of magnesium in the vegetation which began in year 400 (Figure 11). The behavior of magnesium in the decomposer components was similar to calcium behavior. The excesses of mineralized magnesium needed by plants resulted in a slow increase in the soil pool of magnesium. Precipitation and exchange reactions occurring in the soil in the presence of the abundant surplus of magnesium caused this increase.

Potassium mineralization was also consistently higher than uptake, although potassium reserve had to be utilized during several years (Figure 12). In contrast to elements previously discussed, 10% of the potassium required by the trees came from throughfall. Throughfall showed some variation with fluctuations in the size of the leaf mass, as would be expected.

Potassium component changes were very similar to magnesium (Figure 13). Buildup of potassium in the vegetation occurred late in

Figure 10. Simulated changes in the quantity of magnesium transferred annually in the WBW.

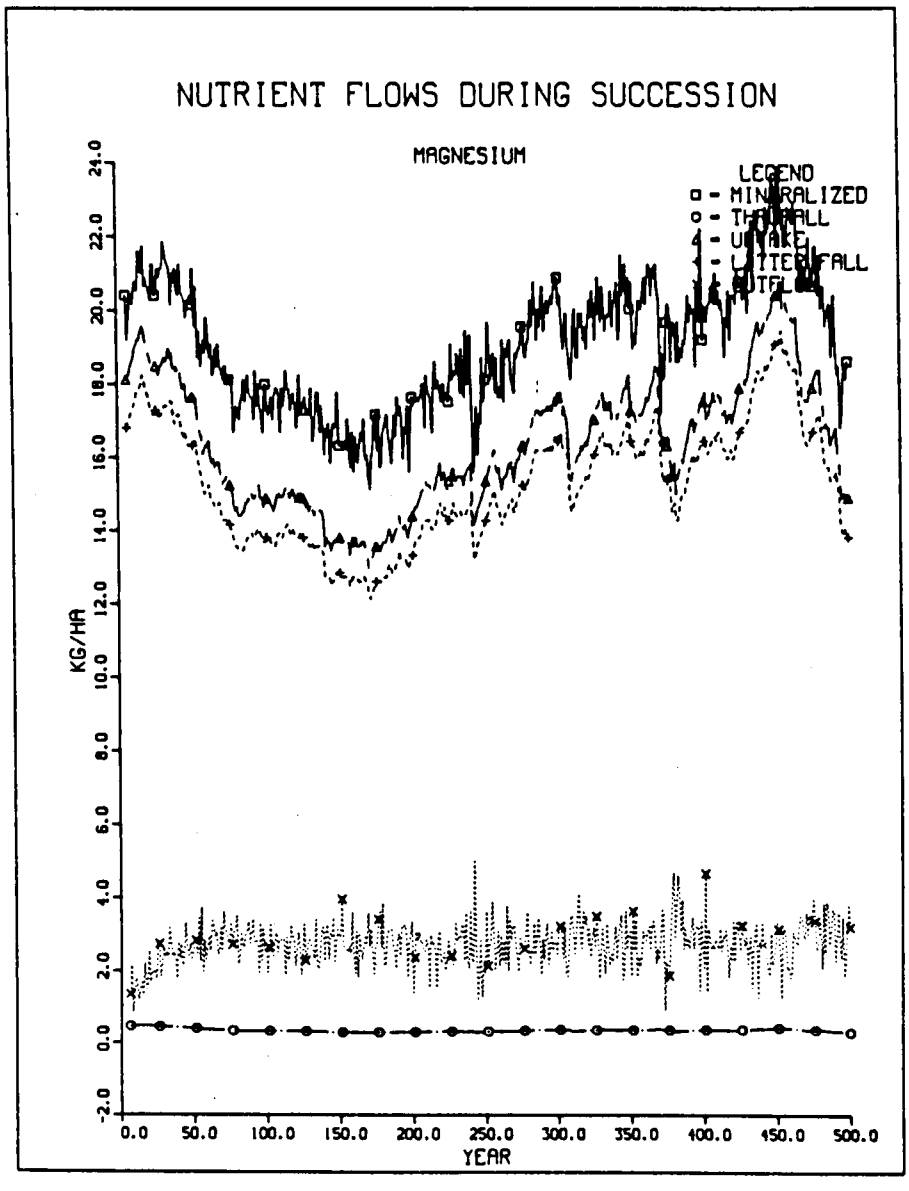

NUTRIENT FLOWS DURING SUCCESSION
MAGNESIUM
LEGEND
KG/HA
YEAR
24.0
22.0
20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
-2.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0

Figure 10

Figure 11. Simulated changes in magnesium pools in the four major components of the WBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

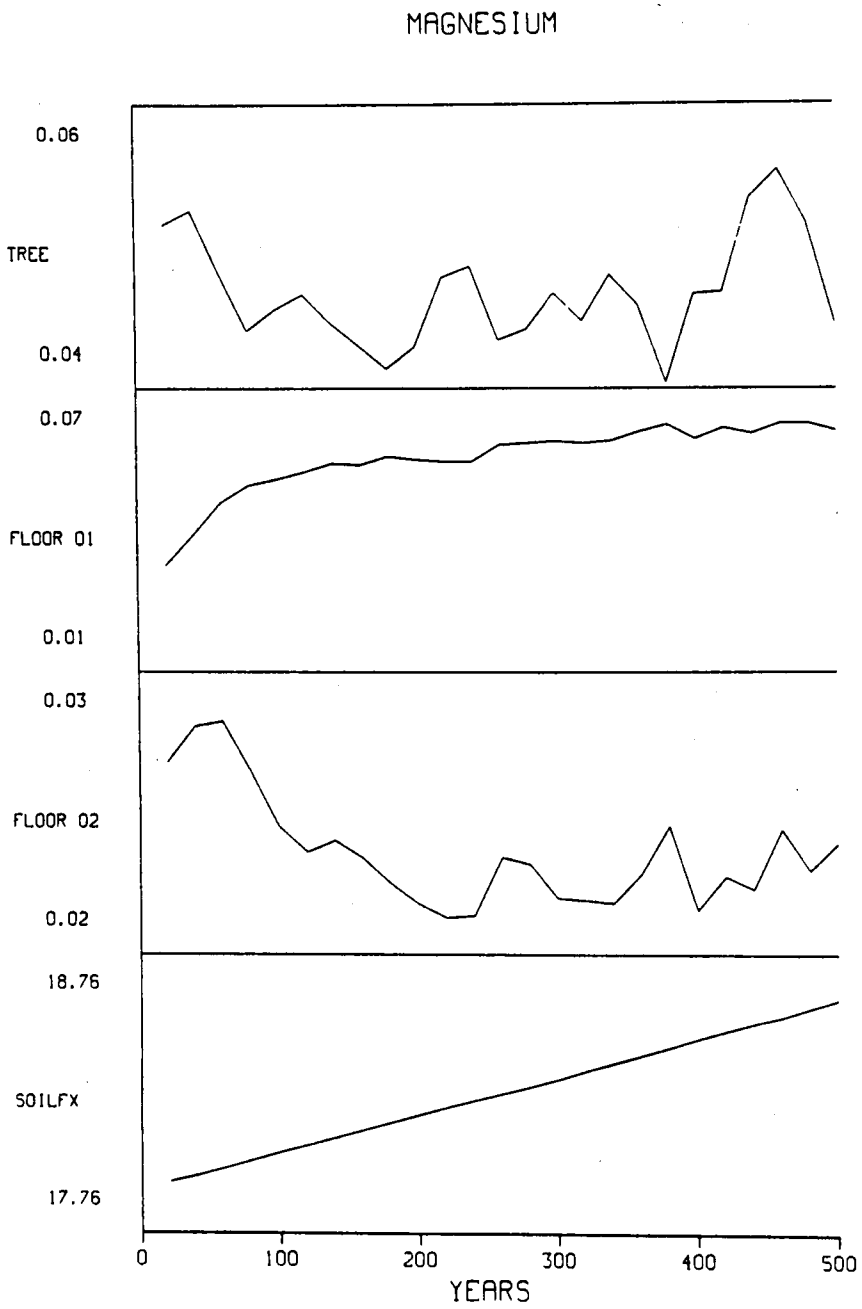

MAGNESIUM
0.06
TREE
0.04
0.07
FLOOR 01
0.01
0.03
FLOOR 02
0.02
18.76
SOILFX
17.76
0
100
200
300
400
500
YEARS

Figure 11

Figure 12. Simulated changes in the quantity of potassium transferred annually in the WBW.

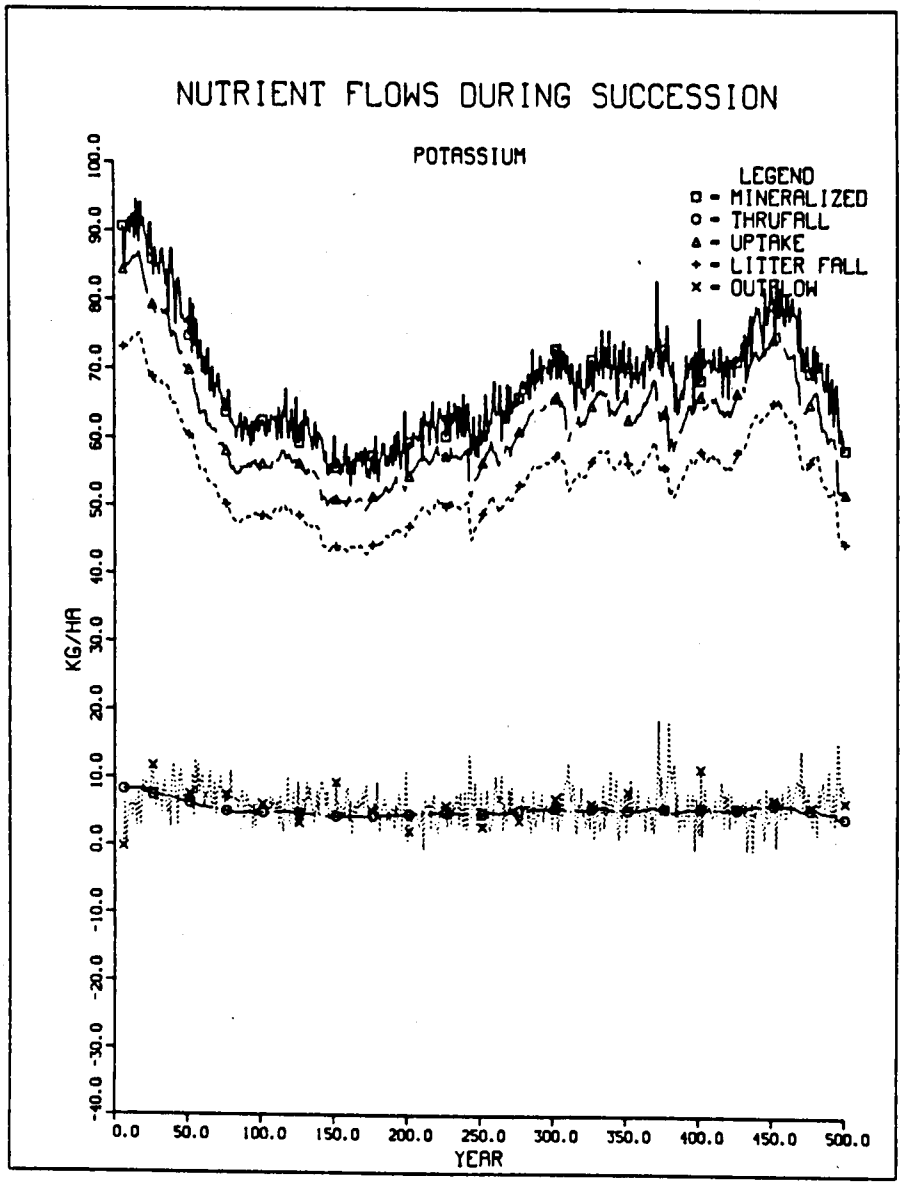

NUTRIENT FLOWS DURING SUCCESSION
POTASSIUM
LEGEND
□ - MINERALIZED
○ - THRUFALL
△ - UPTAKE
+ - LITTER FALL
× - OUTFLOW
KG/HA
100.0
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
-10.0
-20.0
-30.0
-40.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
YEAR

Figure 12

Figure 13. Simulated changes in potassium pools in the four major components of the WBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

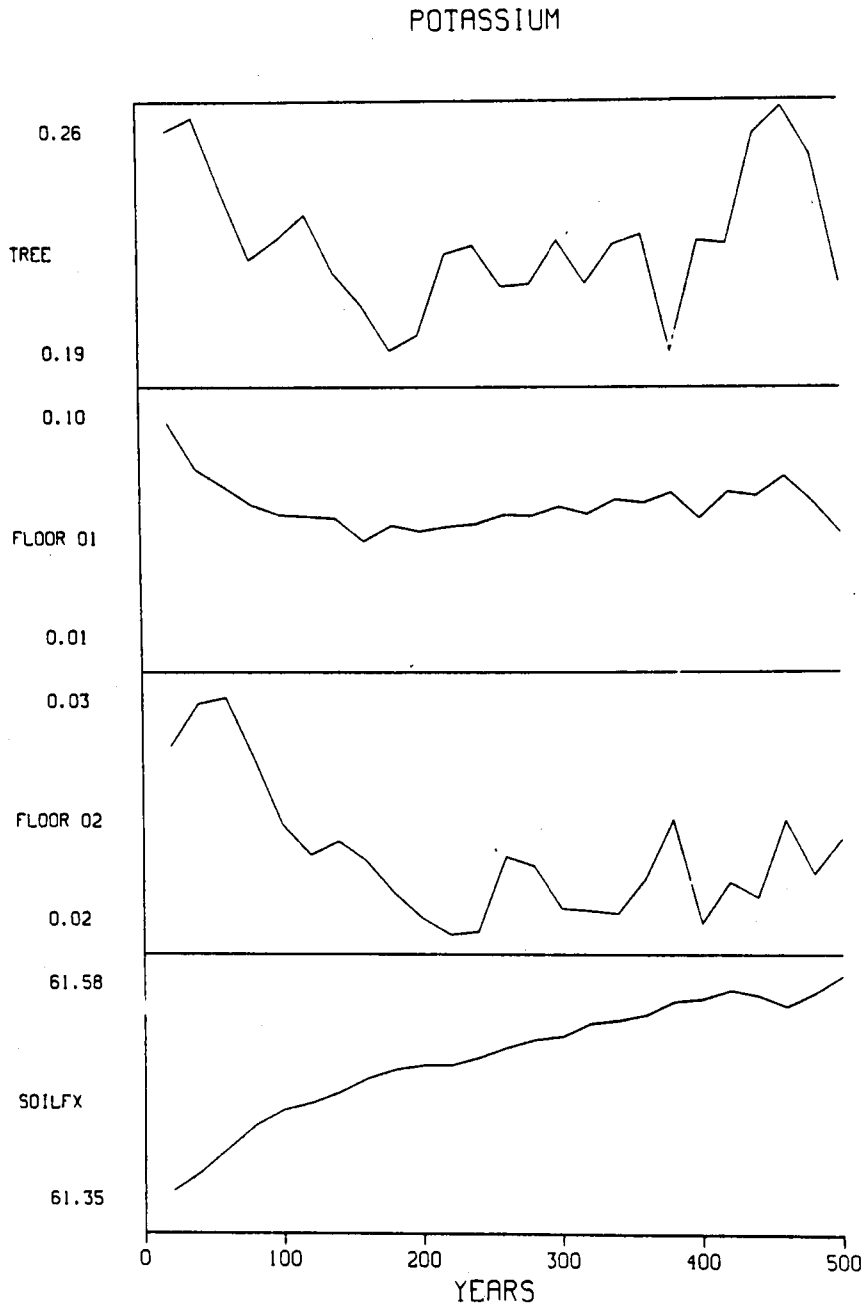

POTASSIUM
0.26
TREE
0.19
0.10
FLOOR 01
0.01
0.03
FLOOR 02
0.02
61.58
SOILFX
61.35
0
100
200
300
400
500
YEARS

Figure 13

the simulation. The primary decomposition layer reached steady state, while the secondary decomposition layer decreased in size. There was also a slight rise in soil potassium, though this pool was sufficiently large that the percentage change was relatively small.

Phosphorus (Figure 14) was mineralized in quantities far in excess of uptake requirements. Mineralized phosphorus showed the largest year to year variability of any of the elements. Beginning in year 370 and in the following few years the mineralized quantity increased by almost 50%. Phosphorus pool behavior was similar to the behavior of the magnesium and potassium pools (Figure 15).

Nitrogen showed a decline in flows during the period from year 50 to year 150 (Figure 16). During the period of decline, uptake frequently exceeded mineralization. After the decline the gap between mineralized nitrogen and uptake widened and deficits became rare. No rise in flows was observed near the end of the simulation. There was a 50 year cycle in the uptake curve which resulted in some periods when large excesses occurred.

The major nitrogen pools (Figure 17) decreased during the first half of the simulation. The continued decline in the soil component occurred despite the cessation of decline in the vegetation and litter pools. The decline of the soil nitrogen pool was not as marked as the decline in the soil calcium pool, however.

Patterns of Nutrient Cycling Dynamics on the Hannah Branch Watershed

Twenty-five plots from the mid-slope oak-hickory forest in the Hannah Branch watershed (HBW) were simulated to test the effects of

Figure 14. Simulated changes in the quantity of phosphorus transferred annually in the WBW.

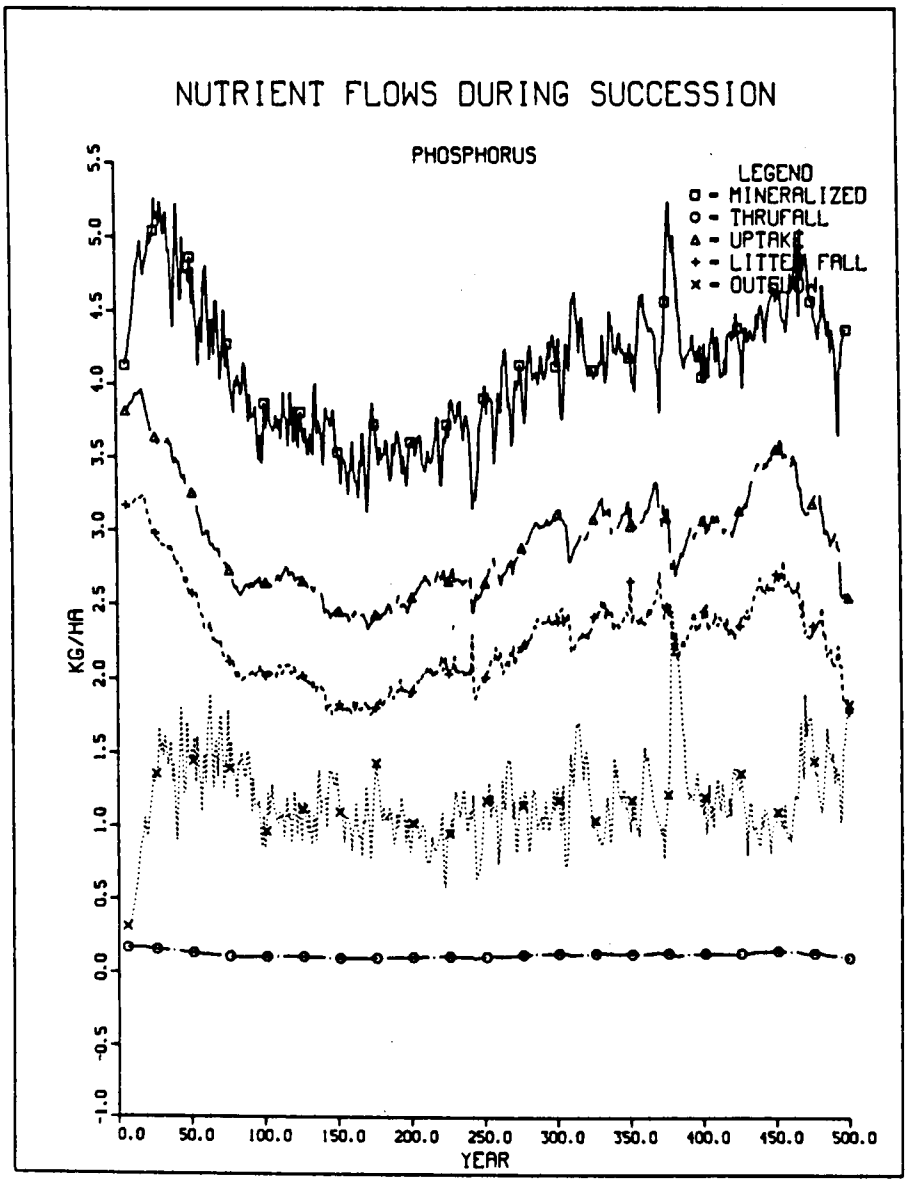

NUTRIENT FLOWS DURING SUCCESSION
PHOSPHORUS
LEGEND
□ = MINERALIZED
○ = THRUFALL
△ = UPTAKE
+ = LITTER FALL
× = OUTFLOW
KG/HA
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
YEAR

Figure 14

Figure 15. Simulated changes in phosphorus pools in the four major components of the WBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

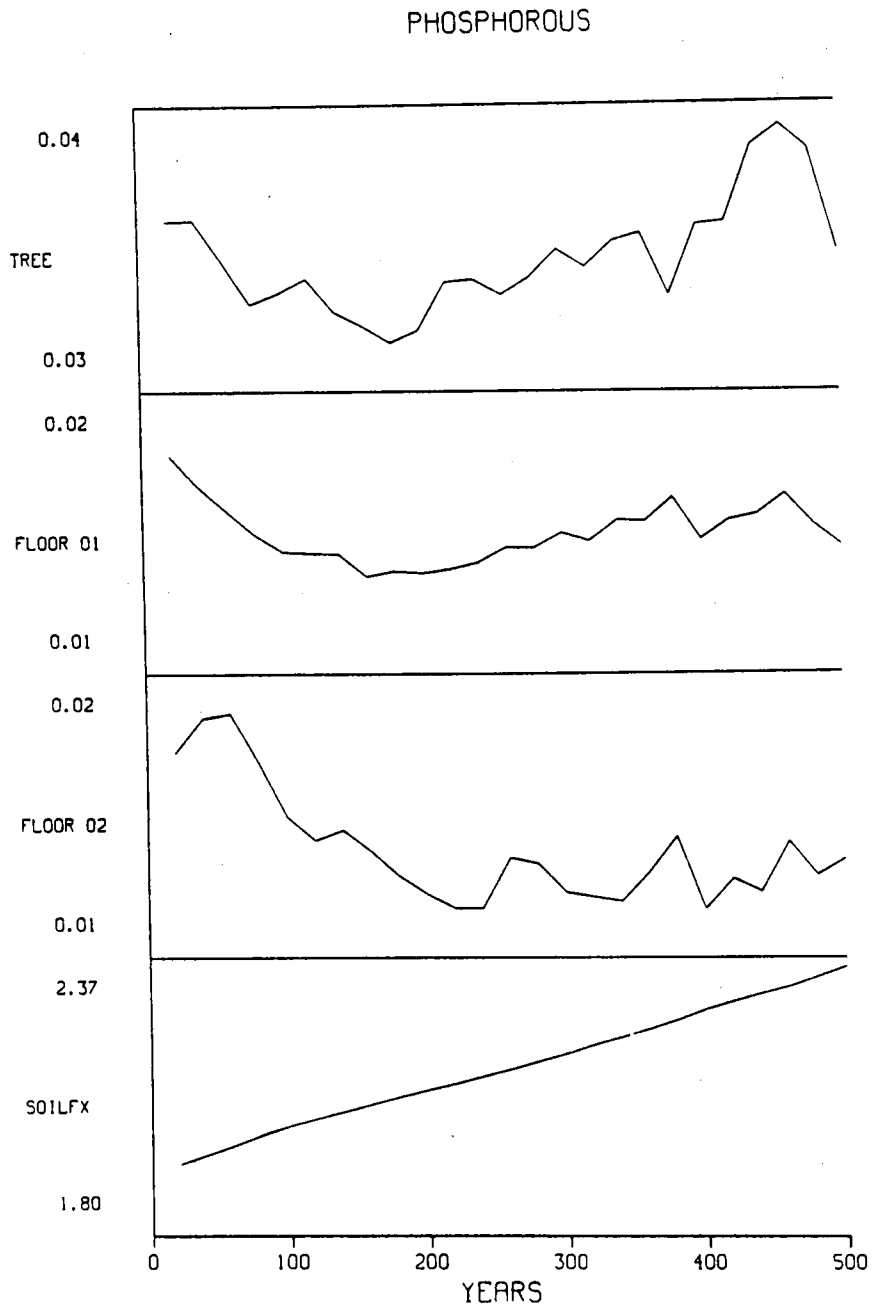

PHOSPHOROUS
0.04
TREE
0.03
0.02
FLOOR 01
0.01
0.02
FLOOR 02
0.01
2.37
SOILFX
1.80
0
100
200
300
400
500
YEARS

Figure 15

Figure 16. Simulated changes in the quantity of nitrogen transferred annually in the WBW.

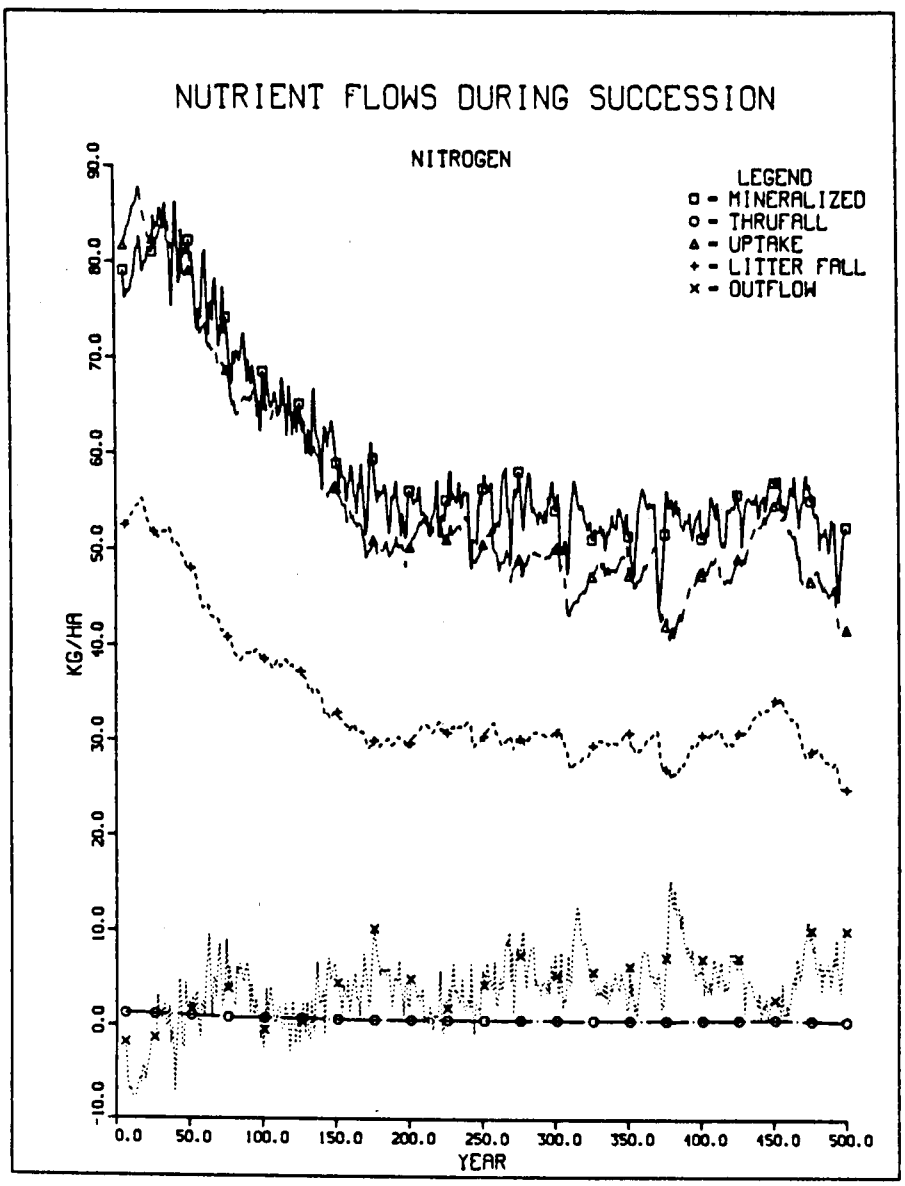

NUTRIENT FLOWS DURING SUCCESSION
NITROGEN
LEGEND
□ - MINERALIZED
○ - THRUFALL
△ - UPTAKE
+ - LITTER FALL
× - OUTFLOW
KG/HA
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
-10.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
YEAR

Figure 16

Figure 17. Simulated changes in nitrogen pools in the four major components of the WBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

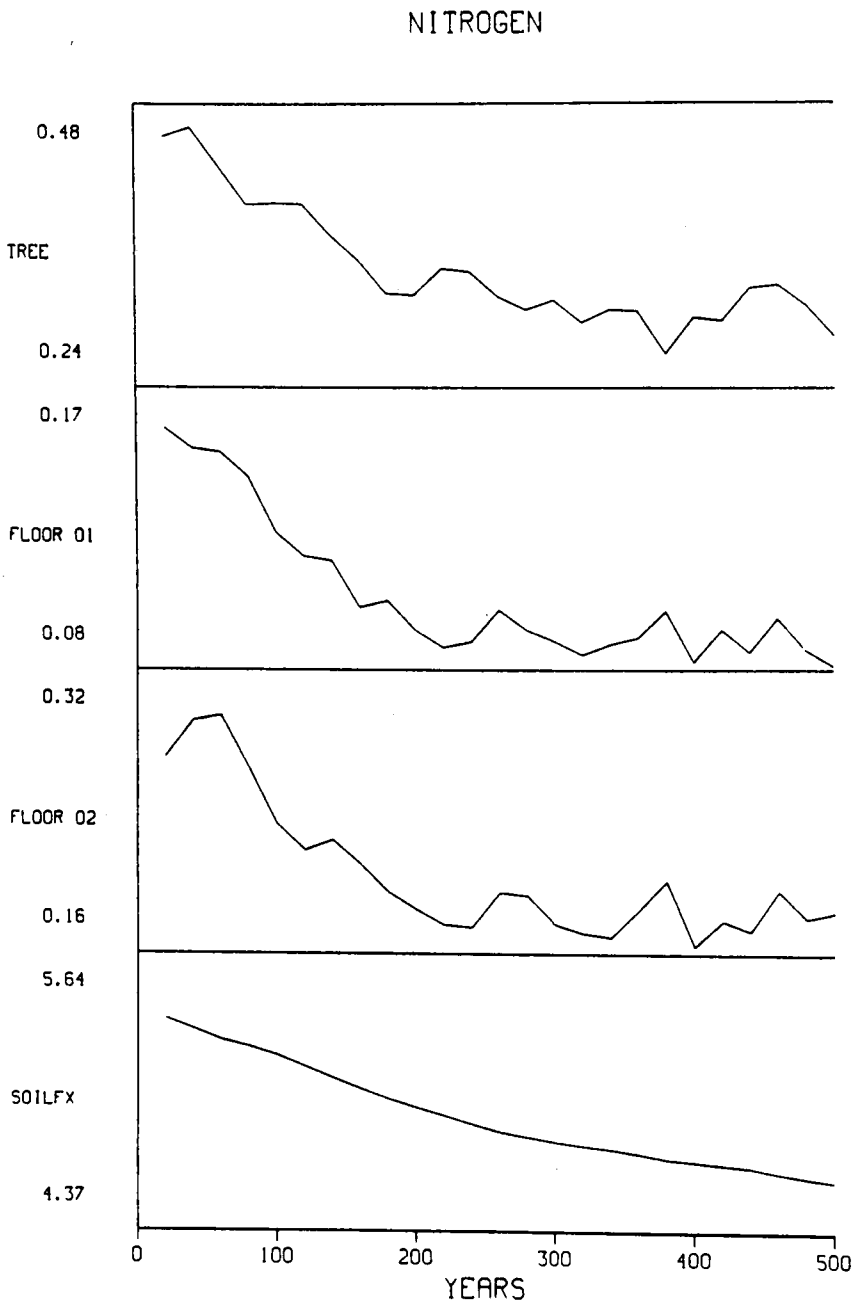

NITROGEN
0.48
TREE
0.24
0.17
FLOOR 01
0.08
0.32
FLOOR 02
0.16
5.64
SOILFX
4.37
0
100
200
300
400
500
YEARS

Figure 17

differences in climatic input and initial nutrient cycling parameters on the results obtained from the WBW simulation. The site information from Harmon (1980) and information concerning the nutrient pools and flows extrapolated from the Coweeta watershed have been previously described. Since this simulation included a composite of information from these two sites it, strictly speaking, was not a simulation of the HBW, but rather an arbitrarily constructed forest expected to be representative of the parameters appropriate for the HBW. Each of the 25 plots was initialized for simulation with tree data from actual plot data collected from the Hannah Branch watershed by Harmon (1980).

Figure 18 shows the average flows of organic matter in the 25 plots from the HBW stand. This stand contained 50% more organic matter, gross productivity, and litterfall than the WBW. The all-aged condition of the trees in the stand led to a less precipitous decline in organic matter flows during the simulation than the WBW. In addition, fluctuations in year to year amounts of organic matter transferred were large, probably caused by the death of very large individuals.

Figure 19 shows the dynamics in the organic matter pools of the HBW during the simulation. The organic matter tree pool showed a gradual decline. Some large fluctuations were evidenced between years 300 and 400. In contrast, relatively little trend was displayed by either decomposition layer. The soil pool increased throughout the simulation, probably because of an underestimate of the soil organic matter decomposition rate for this site.

Calcium flows did not show strong trends during the simulation (Figure 20). Intervals of calcium deficits were frequent. Consequently,

Figure 18. Simulated changes in the quantity of organic matter transferred annually in the HBW.

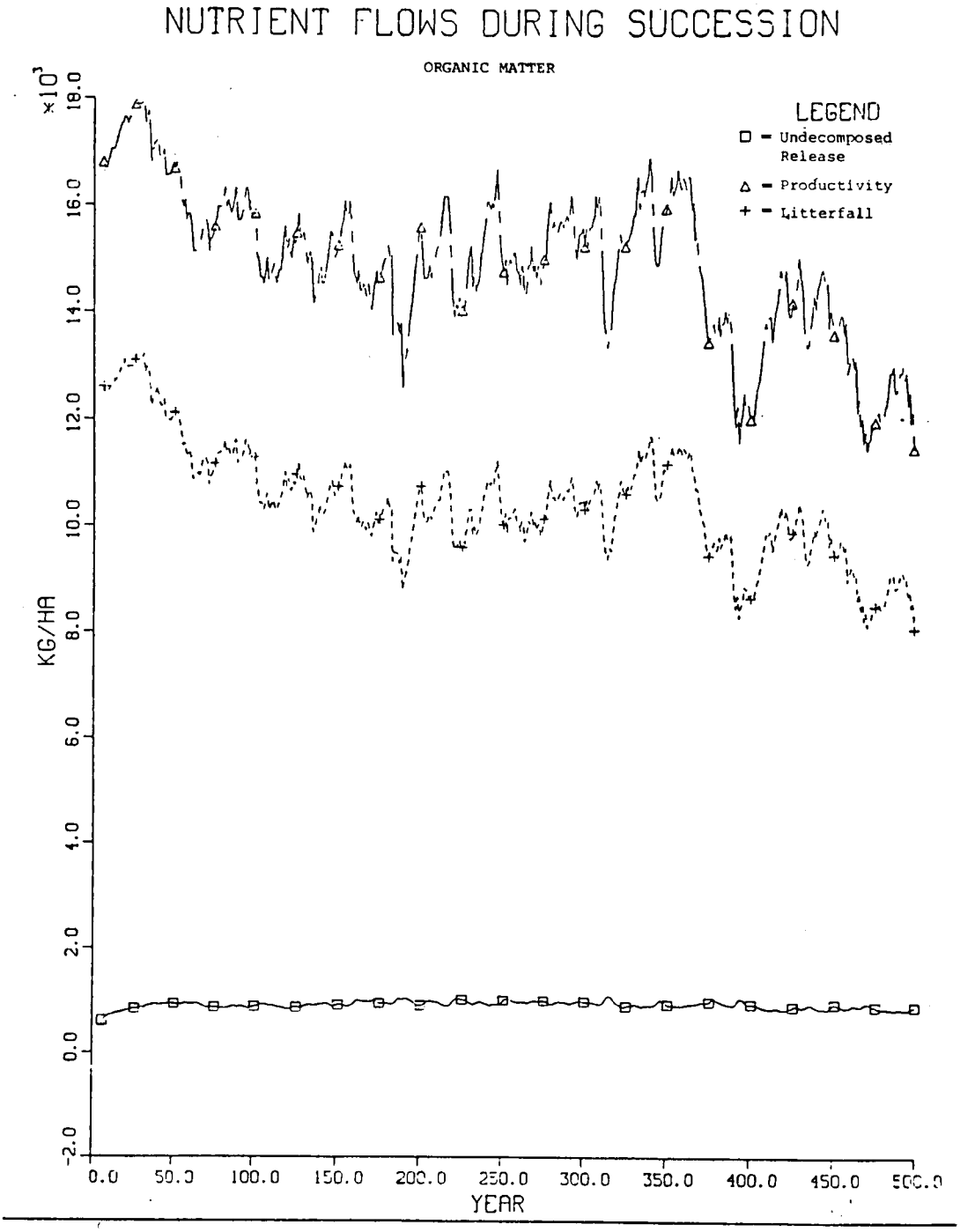

NUTRIENT FLOWS DURING SUCCESSION
ORGANIC MATTER
LEGEND
□ = Undecomposed Release
△ = Productivity
+ = Litterfall
KG/HA
×10³
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
-2.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
YEAR

Figure 18

Figure 19. Simulated changes in organic matter pools in the four major components of the HBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

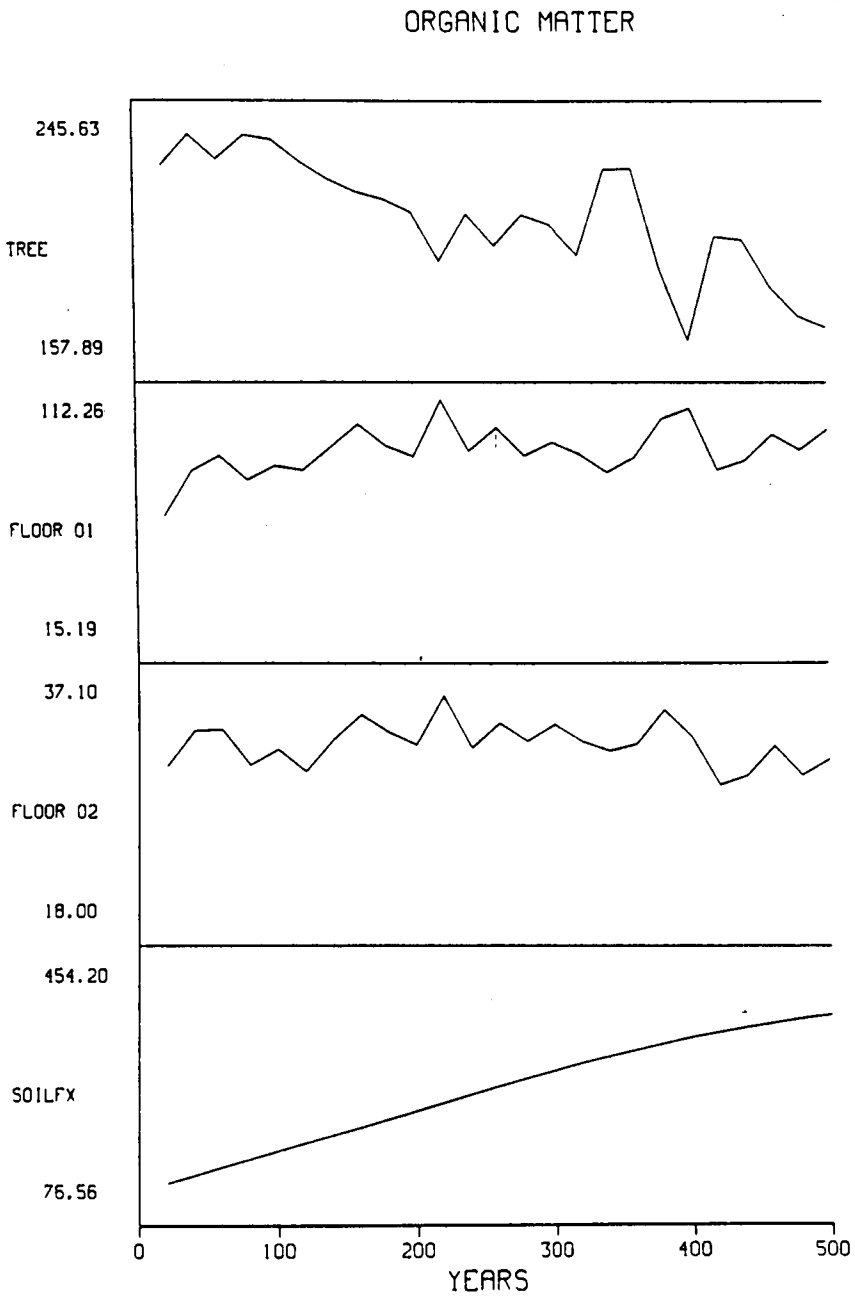

ORGANIC MATTER
245.63
TREE
157.89
112.26
FLOOR 01
15.19
37.10
FLOOR 02
18.00
454.20
SOILFX
76.56
0
100
200
300
400
500
YEARS

Figure 19

Figure 20. Simulated changes in the quantity of calcium transferred annually in the HBW.

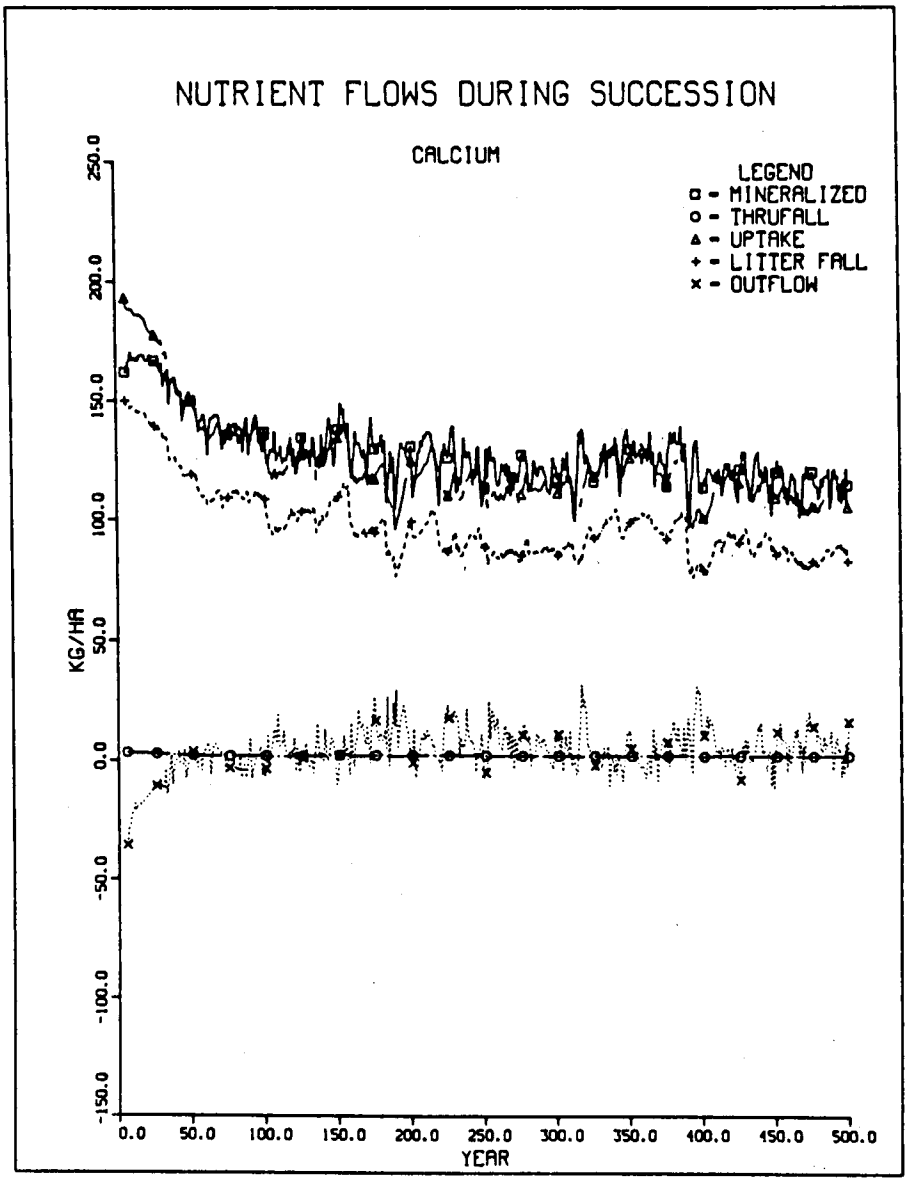

NUTRIENT FLOWS DURING SUCCESSION
CALCIUM
LEGEND
□ = MINERALIZED
○ = THRUFALL
△ = UPTAKE
+ = LITTER FALL
× = OUTFLOW
KG/HA
250.0
200.0
150.0
100.0
50.0
0.0
-50.0
-100.0
-150.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
YEAR

Figure 20

the calcium pool was drained to a low level during the simulation. However, the deficits, as expressed by outflow, were neither as frequent nor as sizeable as in the WBW simulation. This stand experienced a slower rate of calcium loss. Despite the larger organic matter flows in the HBW stand, the two stands experienced very similar quantities of calcium uptake, mineralization, and litterfall throughout the simulations.

The result of these flows in the HBW on pool sizes are shown in Figure 21. Calcium in the vegetation slowly declined. Though some increase occurred during the regrowth period between years 300 and 400, little significant variation occurred in the litter layer. However, despite the frequent periods of calcium excess, the ability of the soil to retain a portion of the calcium mineralized from the litter layer led to an increase of calcium in the soil beginning in year 175.

The yearly amount of magnesium mineralized was much more variable in the HBW (Figure 22). As a consequence, frequent periods during which mineralized releases were insufficient to meet uptake requirements occurred. However, a slight increase occurred in the soil pool (Figure 23), with soil depletion rates being more than compensated by the rates of soil retention during years of excess mineralization. The flow of magnesium mineralized from the litter layer declined during the simulation even though the primary decomposition pool slowly increased in size and the secondary decomposition pool remained near 80 $kg \cdot ha^{-1}$. Lower temperatures associated with lower decomposition rates probably caused this increase.

Figure 21. Simulated changes in calcium pools in the four major components of the HBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

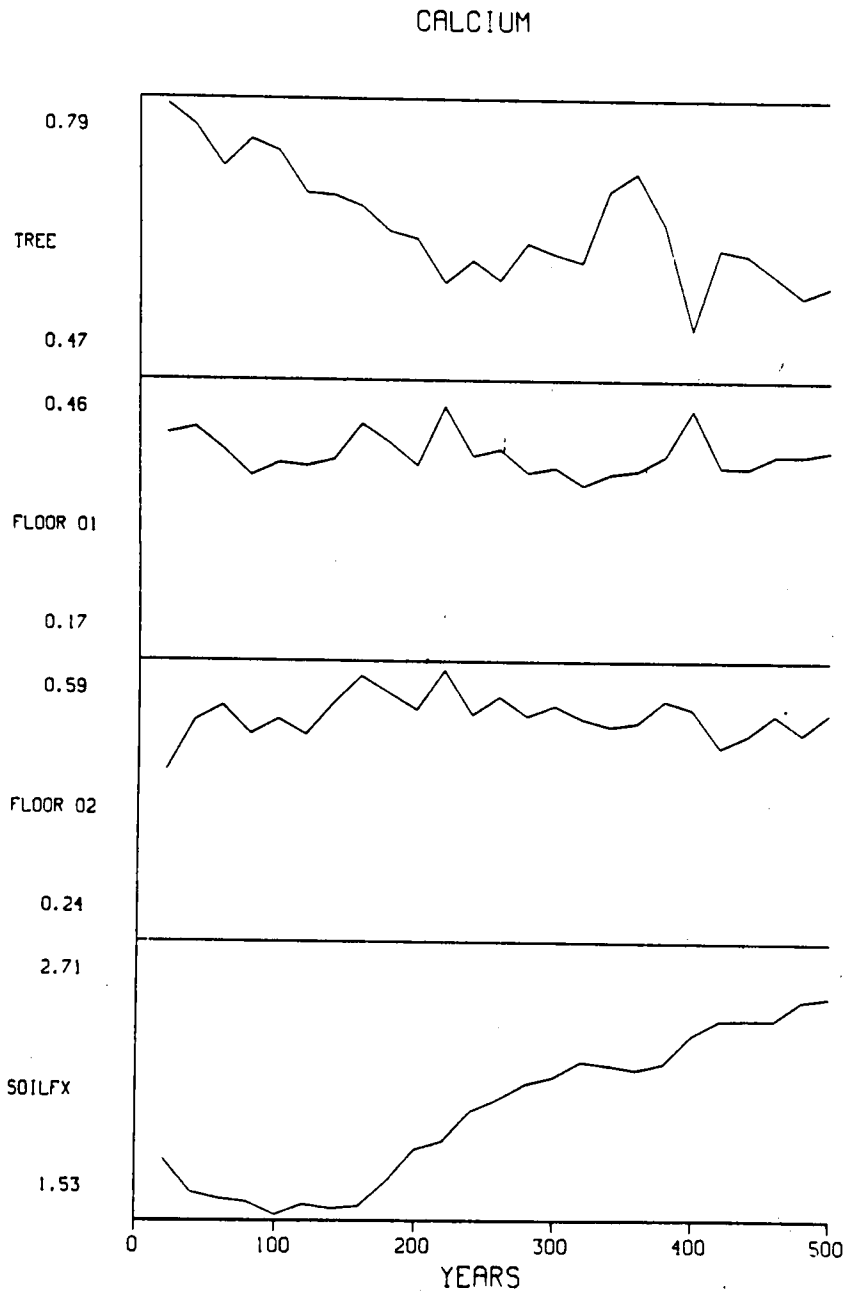

CALCIUM
0.79
TREE
0.47
0.46
FLOOR 01
0.17
0.59
FLOOR 02
0.24
2.71
SOILFX
1.53
0
100
200
300
400
500
YEARS

Figure 21

Figure 22. Simulated changes in the quantity of magnesium transferred annually in the HBW.

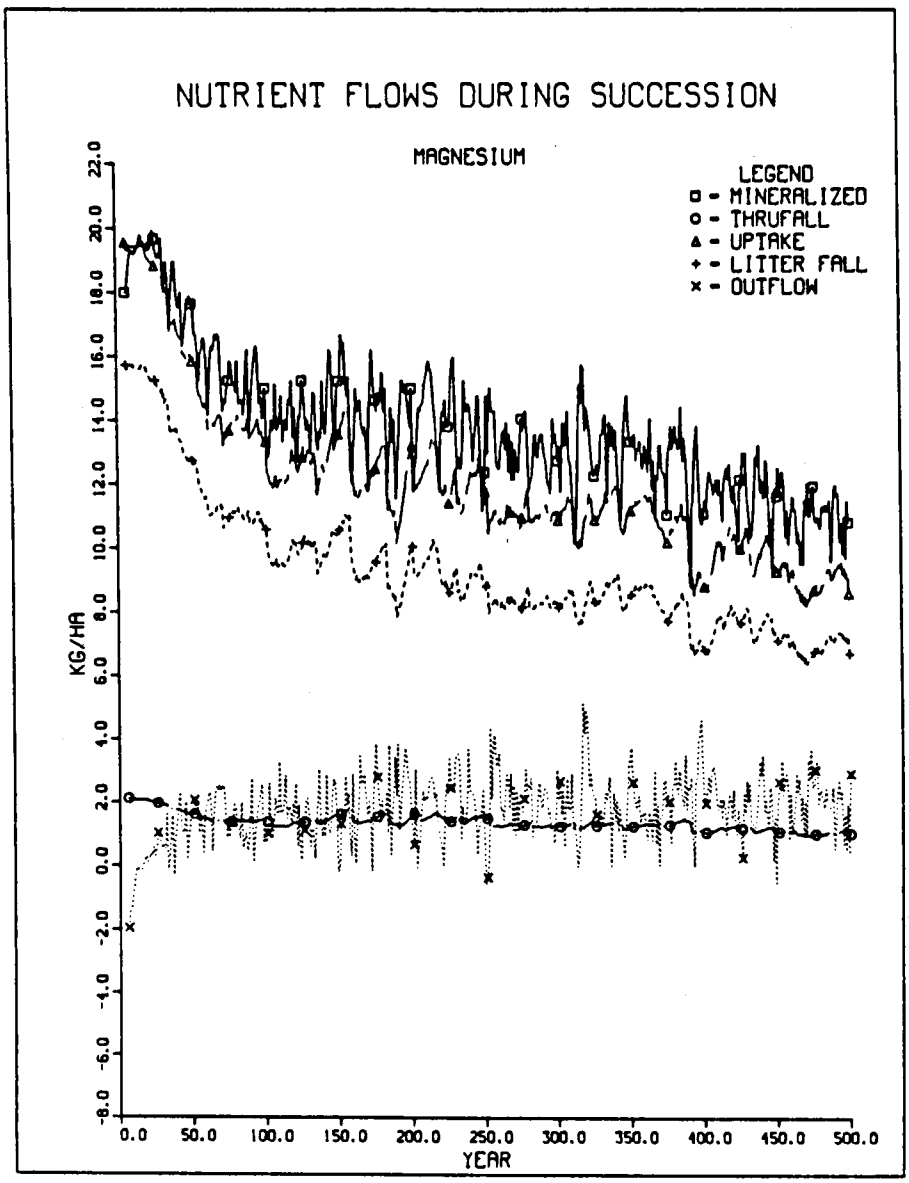

NUTRIENT FLOWS DURING SUCCESSION
MAGNESIUM
LEGEND
□ - MINERALIZED
○ - THRUFALL
△ - UPTAKE
+ - LITTER FALL
× - OUTFLOW
KG/HA
22.0
20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
-2.0
-4.0
-6.0
-8.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
YEAR

Figure 22

Figure 23. Simulated changes in magnesium pools in the four major components of the HBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

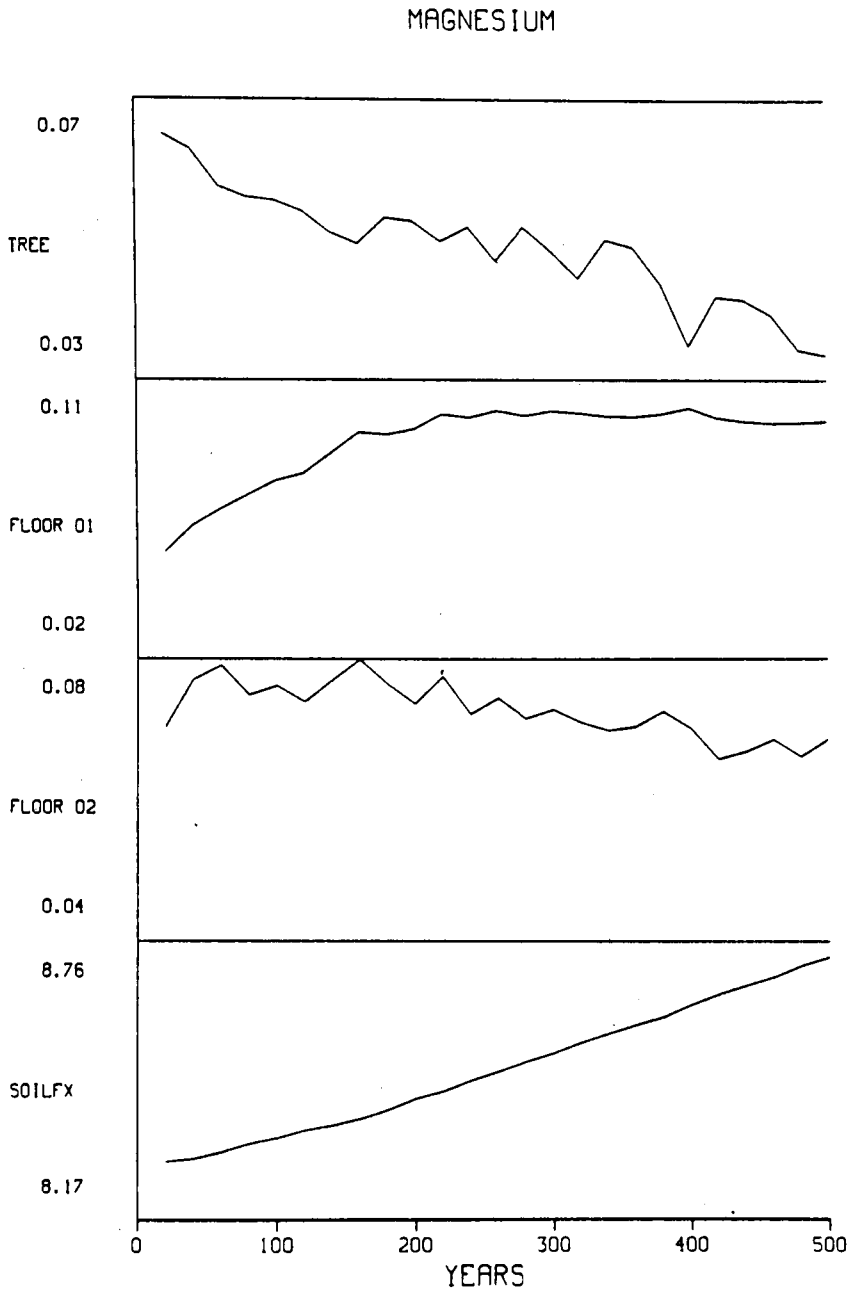

MAGNESIUM
0.07
TREE
0.03
0.11
FLOOR 01
0.02
0.08
FLOOR 02
0.04
8.76
SOILFX
8.17
0
100
200
300
400
500
YEARS

Figure 23

As a result of high levels of throughfall experienced during this simulation, potassium was abundantly available (Figure 24) and remained in excess. There was a gradual drop in the total pool of potassium (Figure 25) in the trees and a large reduction in the levels of flows in uptake, litterfall, throughfall, and mineralization early in the simulation. These patterns were not reflected in the litter layers. Primary decomposition underwent large fluctuation during the simulation, though these fluctuations were not clearly related to any particular aspect of the vegetation dynamics. Secondary decomposition layer and the soil pool slowly accumulated potassium.

Phosphorus mineralization underwent frequent and large fluctuations (Figure 26), often causing mineralized releases to be exceeded by uptake demand. Up to a 30% difference in the release from one year to the next occurred. Despite these unstable dynamics and frequent phosphorus deficiency, the immobility of released phosphorus caused quantities to build in the soil compartment by 50%, to 1.53 metric tons per hectare, during the simulation (Figure 27).

Nitrogen flows gradually decreased through the simulation (Figure 28). Initially, nitrogen uptake requirement outweighed the mineralized release annually, and reserves in the soil nitrogen pool were depleted (Figure 29). Since these reserves are not held in the soil in an exchangeable form, but rather must be released from organic complexes, the depletion of these reserves represented the conversion of nitrogen from a fixed form to a more mobile form. This latter form was more easily lost from the system if not taken up by plants. Thus, the depletion of this reserve

Figure 24. Simulated changes in the quantity of potassium transferred annually in the HBW.

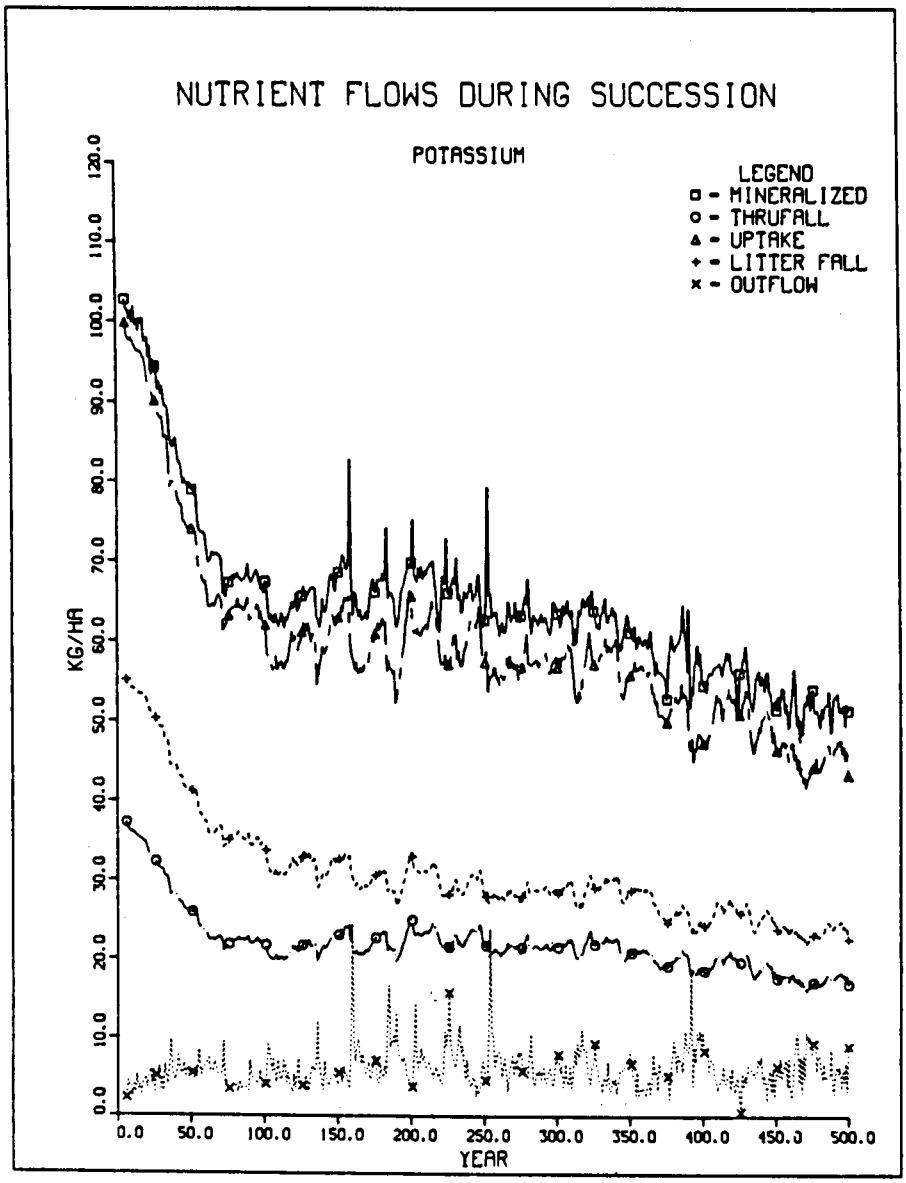

NUTRIENT FLOWS DURING SUCCESSION
POTASSIUM
LEGEND
□ - MINERALIZED
○ - THRUFALL
△ - UPTAKE
+ - LITTER FALL
× - OUTFLOW
KG/HA
0.0
10.0
20.0
30.0
40.0
50.0
60.0
70.0
80.0
90.0
100.0
110.0
120.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
YEAR

Figure 24

Figure 25. Simulated changes in potassium pools in the four major components of the HBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

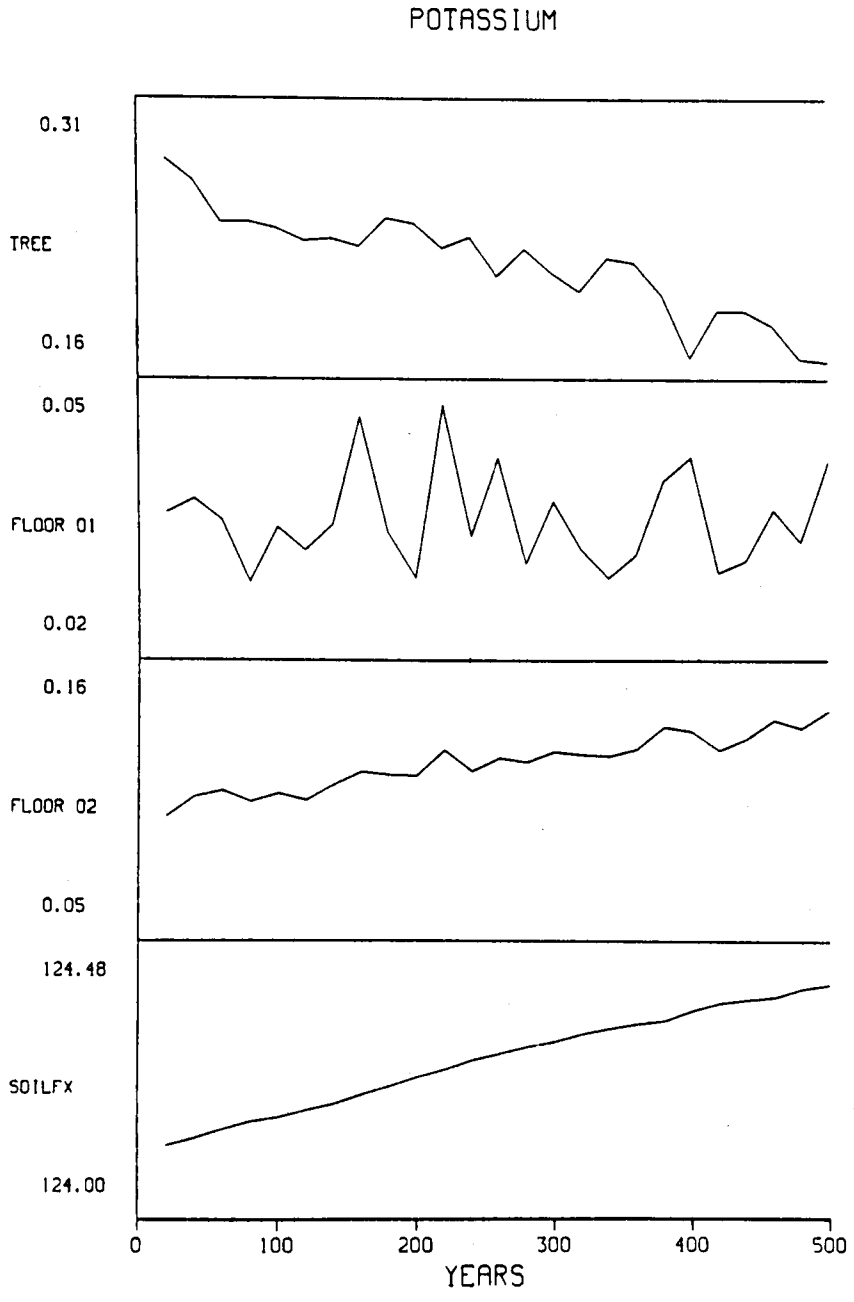

POTASSIUM
0.31
TREE
0.16
0.05
FLOOR 01
0.02
0.16
FLOOR 02
0.05
124.48
SOILFX
124.00
0
100
200
300
400
500
YEARS

Figure 25

Figure 26. Simulated changes in the quantity of phosphorus transferred annually in the HBW.

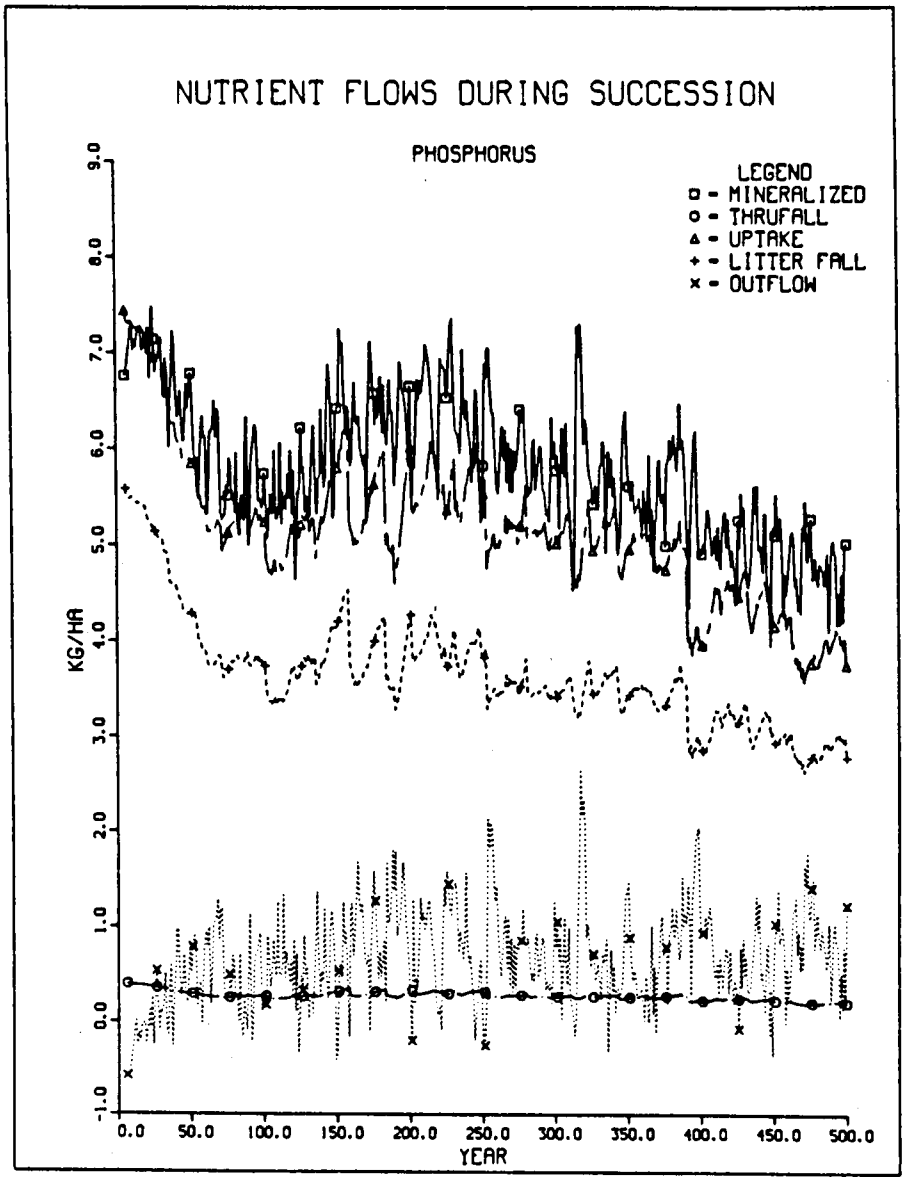

NUTRIENT FLOWS DURING SUCCESSION
PHOSPHORUS
LEGEND
□ - MINERALIZED
○ - THRUFALL
△ - UPTAKE
+ - LITTER FALL
× - OUTFLOW
KG/HA
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
-1.0
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
YEAR

Figure 26

Figure 27. Simulated changes in phosphorus pools in the four major components of the HBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

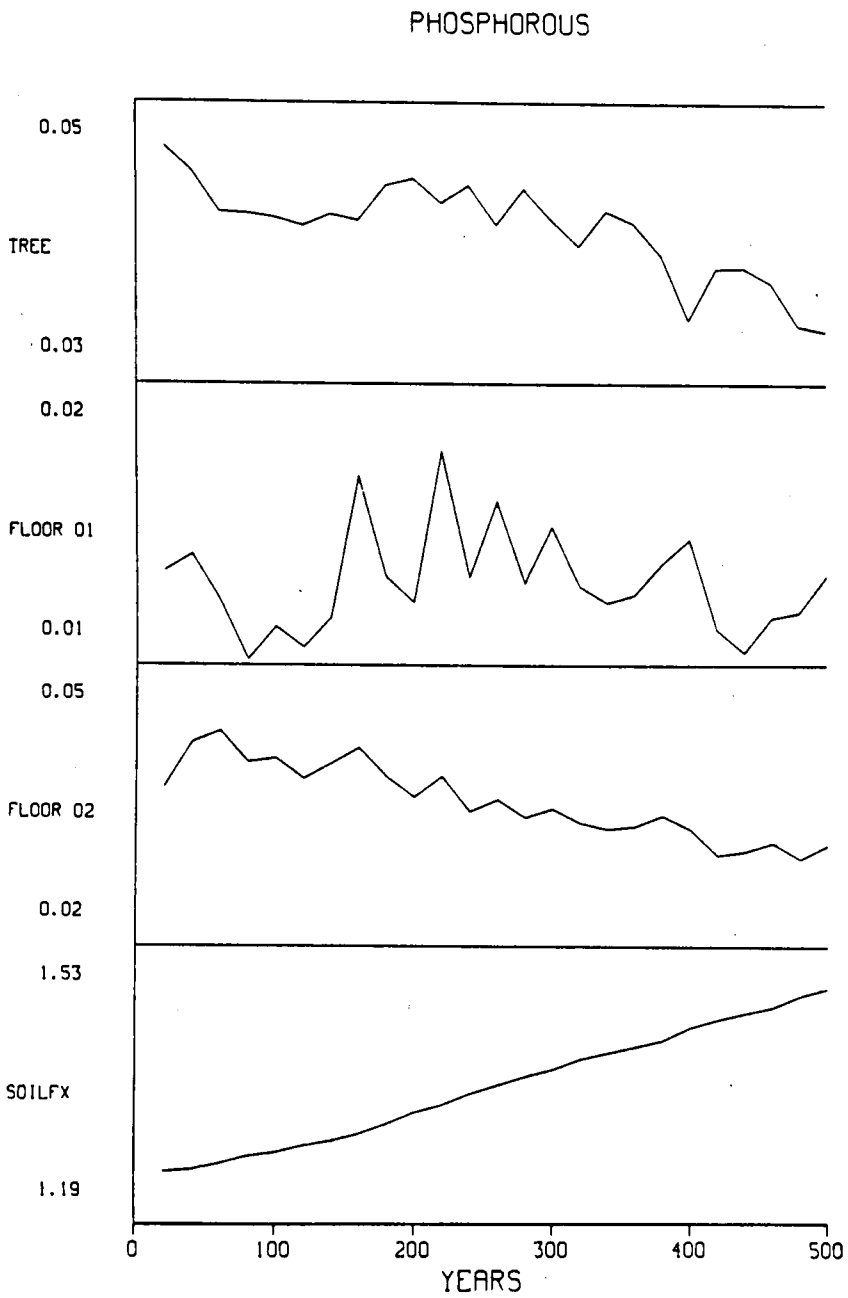

PHOSPHOROUS
0.05
TREE
0.03
0.02
FLOOR 01
0.01
0.05
FLOOR 02
0.02
1.53
SOILFX
1.19
0
100
200
300
400
500
YEARS

Figure 27

Figure 28. Simulated changes in the quantity of nitrogen transferred annually in the HBW.

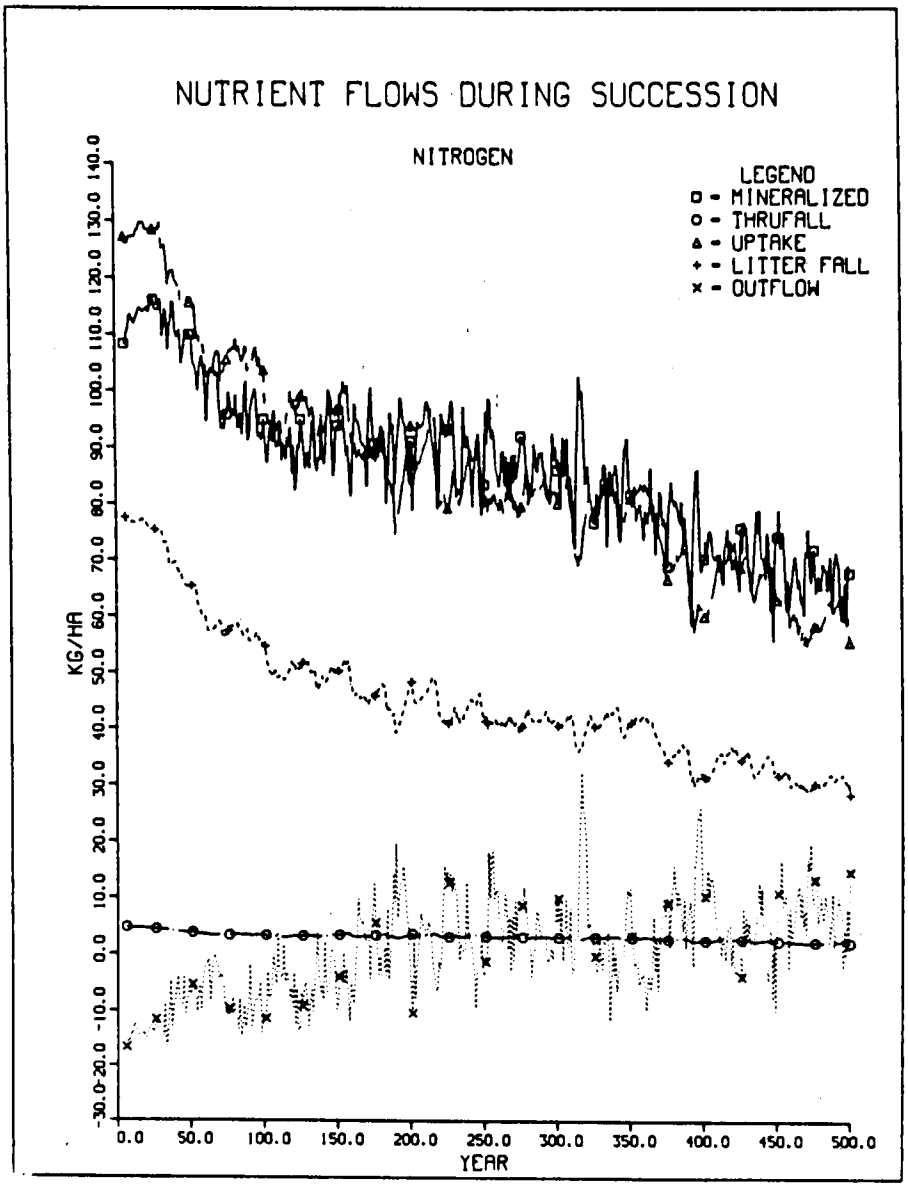

NUTRIENT FLOWS DURING SUCCESSION
NITROGEN
LEGEND
□ - MINERALIZED
○ - THRUFALL
△ - UPTAKE
+ - LITTER FALL
× - OUTFLOW
KG/HA
-30.0 -20.0 -10.0 0.0 10.0 20.0 30.0 40.0 50.0 60.0 70.0 80.0 90.0 100.0 110.0 120.0 130.0 140.0
0.0 50.0 100.0 150.0 200.0 250.0 300.0 350.0 400.0 450.0 500.0
YEAR

Figure 28

Figure 29. Simulated changes in nitrogen pools in the four major components of the HBW ($mt \cdot ha^{-1}$).

TREE = vegetation component, above and below ground;

FLOOR 01 = primary decomposition component, including dead trees;

FLOOR 02 = secondary decomposition component;

SOILFX = total soil component.

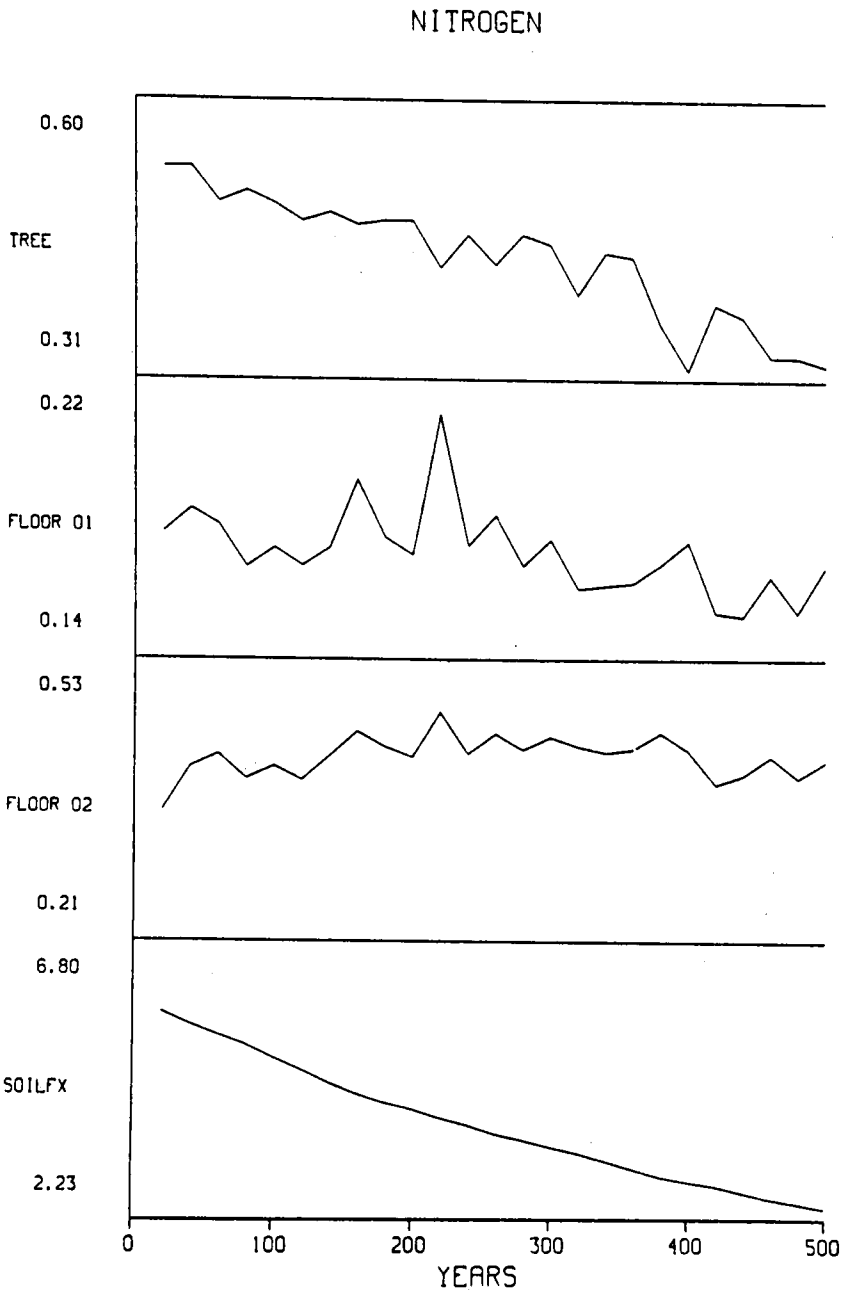

NITROGEN
0.60
TREE
0.31
0.22
FLOOR 01
0.14
0.53
FLOOR 02
0.21
6.80
SOILFX
2.23
0
100
200
300
400
500
YEARS

Figure 29

occurred when soil nitrogen was being released in years when excesses of nitrogen were already available to the plants. Late in the simulation, despite decreases in uptake requirement, nitrogen remained periodically in short supply, although excesses were also frequent.

Figure 30 shows the shift in distribution of the organic matter, calcium, and nitrogen among the four major components during the simulation. Each rectangle is divided into four regions (from top to bottom): the percentage contained in the vegetation, the portion in the primary decomposition layer, the portion in the secondary decomposition layer, and the percentage in the soil. At any one time during the simulation the percentage of the total element pool that is contained in one of these components is represented by the space between the lines. For example, at year 250 approximately 30% of the organic matter in the HBW was located in the vegetation, 20% in the primary decomposition layer, 5% in the secondary decomposition layer, and 45% in the soil component. By year 500 these percentages has shifted to 20%, 15%, 5%, and 60%, respectively.

These diagrams show that for calcium the soil became an increasingly important storage location due to decreases in vegetation percentages. For nitrogen, however, the soil became less important and increasing percentages collected in the vegetation and in the secondary decomposition layer. Due to the large soil reserves of magnesium, potassium, and phosphorus, little shift can be observed from such a diagramatic representation of the distribution of these elements.

For comparison the distribution of organic matter, calcium, and nitrogen in the WBW is shown in Figure 31. A much greater proportion

Figure 30. Simulated changes in the proportional distribution of organic matter, calcium, and nitrogen between the four major components of the HBW. (The sections, from top to bottom section of each rectangle, are: the total tree component, the primary decomposition component, the secondary decomposition component, and the total soil component.)

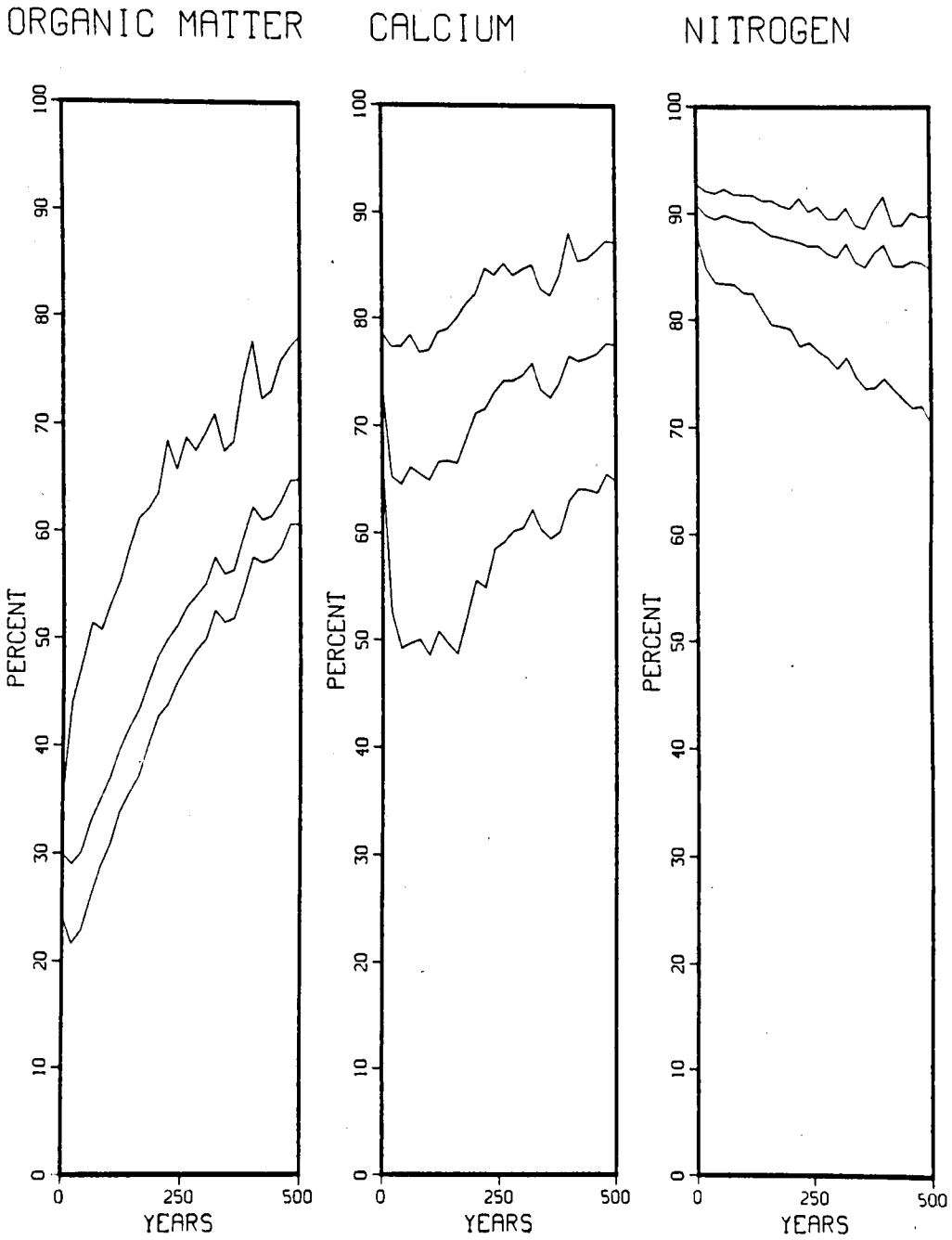

ORGANIC MATTER
CALCIUM
NITROGEN
PERCENT
YEARS
0
10
20
30
40
50
60
70
80
90
100
250
500

Figure 30

Figure 31. Simulated changes in the proportional distribution of organic matter, calcium, and nitrogen between the four major components of the WBW. (The sections, from top to bottom section of each rectangle, are: the total tree component, the primary decomposition component, the secondary decomposition component, and the total soil component.)

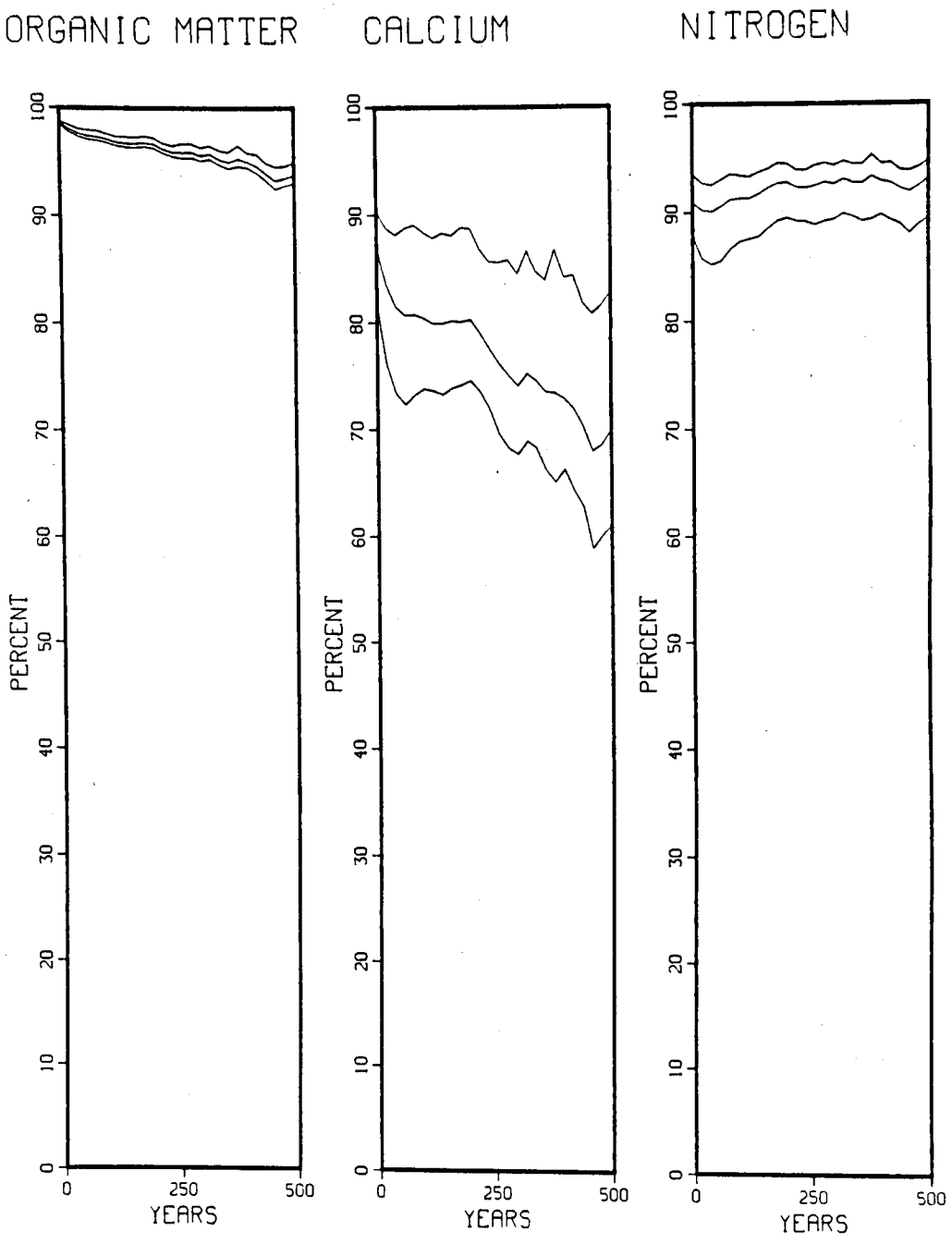

ORGANIC MATTER
CALCIUM
NITROGEN
PERCENT
YEARS
0
10
20
30
40
50
60
70
80
90
100
250
500

Figure 31

of the initial pool of organic matter was contained within the soil of the WBW. This proportion declined, with relative accumulations in the vegetation occurring during the simulation. Calcium in the soil also declined in relation to other major components. Nitrogen distribution showed less change in the WBW than in the HBW during simulation.

The Influence of Individual Species on Nutrient Retention

Since the behavior of the trees and litter layer on each plot has been demonstrated to be critical in determining total stand nutrient retention, attention must be given to the dynamics of each plot. The HBW was examined for relationships between the dominance of particular species on a plot and the rate of nutrient loss from that plot. Each simulated plot was sampled at twenty-five year intervals during the 500 year simulation and all species contributing greater than 20% to the total plot tree biomass were recorded. With twenty-five sampling intervals for each of 25 plots, each species could appear as plot dominant a maximum of 625 times. Table 8 shows the number of plots that species were shown to dominate. Red maple (Acer rubrum), shortleaf pine (Pinus echinata), white pine (Pinus strobus), chestnut oak (Quercus prinus), and black oak (Quercus velutina) emerged as frequent dominants. Table 9 examines the correlation between the occurrence of a species as a dominant on a plot and the rate of outflow of calcium and nitrogen from that plot. Only those species which had an r^2 value greater than 0.2 at the 95% level are listed. The only strong relationships were found in species that appeared as dominants infrequently: tulip poplar

Table 8. Number of plots with greater than 20% biomass contributed by the indicated species.

Species	Number of Plots
Acer rubrum	190
Acer saccharum	15
Aesculus octandra	—
Betula lenta	—
Carya glabra	6
Carya tomentosa	2
Fagus grandifolia	—
Halesia carolina	26
Ilex montana	7
Kalmia latifolia	10
Liriodendron tulipifera	5
Magnolia spp.	—
Oxydendron arboreum	1
Pinus echinata	164
Pinus rigida	16
Pinus strobus	128
Pinus virginiana	21
Prunus serotina	—
Quercus alba	32
Quercus coccinea	30
Quercus prinus	169
Quercus rubra	2
Quercus velutina	82
Robinia pseudoacacia	1
Tilia heterophyla	—
Tsuga canadensis	—

Table 9. Correlation coefficients between calcium and nitrogen outflow and individual species biomass. (Only those species with an r^2 greater than 0.2 at the 95% level are shown.)

Species	Calcium	Nitrogen
Ilex montana - Mountain Holly	-.85	.54
Kalmia latifolia - Mountain laurel	-.84	-.69
Liriodendron tulipifera - Tulip poplar	-.88	.67
Quercus alba - White oak	-.35	
Quercus prinus - Chestnut oak		-.27
Quercus velutina - Black oak	.21	.21

(Lirodendron tulipifera), and two understory species, mountain holly (Ilex montana) and mountain laurel (Kalmia Latifolia). All three were related to deficits in calcium outflow (less mineralization release than uptake requirement). Tulip poplar and mountain holly were strongly related to excesses of nitrogen, however. Consequently, plots where these species dominated would be expected to show nitrogen leaching losses. Although it was not present as a dominant in this simulation, in other simulations locust (Robinia pseudoacacia) has shown a distinct relationship to nitrogen losses, no doubt due to the nitrogen fixing habit of locust, reducing uptake and importing nitrogen into the plot. Some species do not show consistency in their relationship to outflow. In additional simulations, fast growing species such as shortleaf pine, silverbell, pitch pine and black cherry have displayed a distinct relationship to nutrient deficits, but no association was apparent in this simulation. Even slower growing species, such as white and black oak, have shown lesser degrees of association with deficits. Thus, no consistent pattern of species or species growth strategy type emerges with respect to the effect on nutrient loss.

The Influence of Processes on Nutrient Retention

Other components and processes can be identified as playing an important role in nutrient retention. A series of parallel simulations of the HBW were conducted to demonstrate the potential influence of nutrient mechanisms on nutrient retention. In each of these simulations the HBW model was modified by adding an additional mechanism. Moist

conditions and a deep fertile soul were used to eliminate drought and insufficient nutrient reserves as confounding variables. Case one was the base case in which no modification was made. In cases 2, 3, and 4 the effect of the age characteristics of the trees in the stand on nutrient retention was explored through altering the plot with simulated cutting. In case 2 tree uptake was modified by removing all trees in year 0, lowering the average age of trees on the plots to a minimum. In case 3 the average age was reduced by removing those trees with a dbh greater than 30 cm. In case 4 uptake was also altered by thinning the stand, which raised the average age of trees on the plots.

In case 5 the effect of negative feedback from a dwindling nutrient reserve was tested by initializing the plot with a soil pool twice as large as in other plot simulations. In case 6 only the nitrogen soil pool was enhanced, although not by an increase in the reserve but rather by the addition of free living nitrogen fixers, which doubled the yearly atmospheric input. Case seven included both cases 5 and 6.

Cases 8 and 9 tested the influence of internal tree mechanisms. In case 8 the tree community nutrient uptake could be reduced by shifting tissue concentrations. A tree species with lower nutrient concentrations in its tissues (and thus a lower demand) was assumed to have a competitive advantage over other species during conditions of nutrient limitation. In case 9 trees were given the capability of increasing internal nutrient translocation under conditions of nutrient limitation, allowing them to meet more of their annual needs by holding nutrients internally in autumn for reuse the following spring.

In case 10 the physical capability of the soil to retain nutrients was increased to 95% of all available nutrients for all elements. In cases 11-13 various combinations of the above mechanisms were simultaneously tested to investigate interactions.

Table 10 shows the effect of inclusion of the different processes in the models on the retention of calcium and nitrogen. These are shown as the percent change in the total soil pool during the first 100 years of simulation, when the mechanism might affect short term nutrient retention, and during the period from year 100 to year 500, over which long term retention can be evaluated. Several general conclusions can be drawn from this analysis:

1. In the base case calcium and nitrogen both drained from the system quickly during the initial phases of the simulation. Later, nitrogen loss continued while the calcium pool in the soil increased. In general, a reduction in the rate of long term nitrogen loss increased the long term calcium loss.

2. Nitrogen fixers reduced initial calcium loss, but increased long term calcium loss. The presence of fixers reduced initial nitrogen loss and proved to be the most effective mechanism for reducing long term nitrogen loss.

3. When species with low tissue concentrations had an advantage under nutrient limiting situations initial losses were reduced considerably, but long term losses were reduced only slightly.

4. Stand thinning reduced the calcium loss, but had little effect on nitrogen loss.

Table 10. Percent change in total soil nutrient pool size as related to system processes and mechanisms.

Case	Description	Calcium		Nitrogen	
		Years 0-100	Years 100-500	Years 0-100	Years 100-500
1	Basic case, mechanisms as described	-59	+28	-45	-94
2	Cut and remove all trees	-87	-100	-54	-100
3	Cut and remove large trees	-58	-100	-65	-100
4	Thin plot at year 0	-40	+60	-46	-94
5	Larger soil nutrient reserve	-22	-2	-22	-86
6	Nitrogen fixation capability included	-55	-7	-42	-46
7	Larger soil reserve, nitrogen fixation included	-46	+11	-46	-96
8	Competitive advantage given to species with lower tissue concentrations	0	-13	-25	-90
9	Translocation adaptiveness	-30	-44	-36	-66
10	Increased soil physical-chemical retention	-18	-15	-21	-78
11	Larger nutrient reserve, increased nutrient retention	-53	+6	-38	-84
12	Cut trees, increased soil retention, larger soil reserve	-27	-15	-27	-73
13	Larger soil reserve, nitrogen fixation included, translocation adaptiveness included	-47	+15	-30	-67

5. A single removal of large trees produced drastic losses of nutrients.

6. Translocation internally within trees greatly reduced short and long term loss from nitrogen pools, and reduced short term losses of calcium, but actually increased long term calcium losses.

7. Larger initial pools produced greatly reduced initial losses from both calcium and nitrogen pools, and less, but still sizeable, reductions of long term losses of nitrogen. However, calcium loss rate was increased.

8. Given extra nutrient reserves, additional mechanisms tended to increase the initial rate of nitrogen loss or calcium loss. However, these mechanisms were not simply additions of individual effects.

9. Given extra nutrient reserves, extra soil retention capabilities increased the rate of long term calcium losses, contrary to expectations.

With deep soils assumed for each simulation, species with rapid growth rates were capable of achieving near optimal growth rates during the simulation. Such rapid growth is likely to cause calcium and nitrogen to be taken up in large quantities. These large quantities, upon re-release from the litter, are subject to leaching. Rapid nutrient loss from these forests is possible under these conditions. Thus, when uptake was reduced slightly by thinning, the loss of nutrient decreased. However, when uptake was reduced greatly by cutting, and then increased by subsequent reinvasion, large losses occurred. When the uptake rate most closely resembled the mineralization rate, nutrient retention was at a maximum. The small litter layer was

unable to retain large quantities of nutrients in the system. Stand thinning reduced uptake. While calcium could collect in the soil by adsorption, nitrogen released from the litter layer passed through the soil. Removal of large trees released subcanopy species. During the high productivity periods nitrogen and calcium would be in short supply and losses from the stand were minimal. However, during the initial years of regrowth and as the trees passed the point of maximum productivity, all the nutrients that had been mined from the soil for growth would be susceptible to leaching after being dropped in litterfall. Further, when one element becomes limiting to the trees it is likely that other elements will be present in excess, resulting in higher losses for these nonlimiting elements. Nitrogen fixers increased the overall productivity of the plot, making calcium supply more limiting. Calcium loss was reduced. Translocation proved to be a very important property for nitrogen retention. Calcium loss rate was significantly reduced only by an increase in soil absorption capability. Interactions of mechanisms produced results that were largely unexpected and difficult to interpret.

CHAPTER VI

DISCUSSION

Nutrient Retention Differences

Soil calcium values in the WBW, though initially higher than in the HBW, were depleted at a rapid rate (Figure 9, page 82, and Figure 21, page 110). The HBW stand accumulated calcium during the simulation. Conversely, though the two stands initially had similar soil nitrogen pools, the HBW stand depleted this reserve much more rapidly than did the WBW stand. It could be concluded that trees on the WBW were chronically deficient in calcium and actively mining the soil calcium reserve. Further, low concentrations would consequently be expected in the outflow water from the WBW. However, high concentrations of both calcium and nitrogen could be found in leachate water in any year. Chronic nitrogen deficiency, active nitrogen mining, and low nitrogen concentrations in outflow water might be expected from the HBW. However, high nitrogen concentrations were often found in the leachate water from the HBW in any year. High outflow concentrations could have occurred during the simulations when climatic conditions caused the release of mineralizable nutrients in excess of the amount required for uptake by the vegetation. It is clear that a single year's leachate information is insufficient evidence on which to base conclusions concerning the chronic nature of dynamics within the forest. Such concentrations are likely to vary widely with fluctuations in climate and vegetational dynamics. Consequently, annual budgets are not adequate for explanation of

differing rates of nutrient loss. Further, during the early period of the WBW simulation, in any given year either calcium or nitrogen might be the limiting element, with the two periodically switching positions of shortest supply. Usually nitrogen is thought to be the element limiting to growth, and it is further thought that this limitation remains consistent year after year. Only in certain locations or after nitrogen fertilization is another element considered to be potentially limiting. The notion that the limitation on growth caused by nutrient deficiency may be transitory and a function of climatic conditions and vegetational dynamics is dramatically different from the prevailing view.

Compositional Differences

Figures 4 and 5 (pages 65 and 68) suggest that differences in nutrient retention ability could be due to the differences in composition between the stands. Although these two forests are generally classified as mixed oak-hickory, it is conceivable that the compositional differences that exist (more hickory and white oak in the WBW; more chestnut oak in the HBW) are sufficient to cause nutrient retention differences. Retention differences could be anticipated if these composition differences were associated with differences in the nutrient use efficiency. This efficiency is determined by nutrient uptake and storage in tissue among species. At the beginning of the simulation the average calcium concentration in vegetation tissue in the WBW was 0.46% compared to 0.38% for the HBW, not a significant difference. Even less difference in nitrogen concentration existed, with 0.29% for the WBW

compared to 0.27% for the HBW. Consequently, no prediction of a difference in nutrient retention would have been made based on the initial difference in nutrient concentrations. However, a concentration difference does develop for both elements, with the calcium concentration increasing to 0.65% in the WBW by year 300 while decreasing to 0.27% in the HBW; nitrogen in the WBW increased to 0.29% while nitrogen dropped to 0.23% in the HBW.

The WBW stand began the simulation as a predominantly hickory-chestnut oak forest, and experienced increasing domination by white oak as pignut hickory declined. The HBW stand remained dominated by chestnut oak, with white pine peaking in biomass by mid-simulation, followed by a growth in importance of silverbell toward the end of the simulation. Had both the watersheds remained oak-hickory dominated the difference between the nutrient cycles of the watersheds might not have developed because of the similarity in growth characteristics and nutrient requirements among the oaks and hickories. However, the increasing importance of fast growing species in the HBW could have produced differences due to the lower concentrations in tissues of these species, particularly in the conifers. A 40 cm diameter white pine stored less than one fourth the calcium in its tissues and 50% less nitrogen than a 40 cm white oak. A complicating factor is that despite the lower tissue concentration of some fast growing species, the faster growth rate increases their uptake requirement. A white pine adding tissue at twice the rate of an oak might require almost the same amount of yearly calcium uptake.

Major Pool Size Differences

Table 11 compares the organic matter, calcium, and nitrogen quantities in the four major pools, the tree, primary decomposition layer, secondary decomposition layer, and the total soil. Pool sizes in the simulations are difficult to compare to other studies since they include quantities not always measured in pool assessments. The tree pool includes both above and below ground totals. The decomposition layers include dead tree boles and roots as well as the more typically included partially decomposed leaf matter. Dead tree roots and boles swell the size of these components considerably above the values typically reported.

There was a difference in the amount of organic matter contained within the tree and forest floor components, with the HBW having considerably greater quantities. This difference is a reflection of the more nearly ideal growing conditions found in the GSMNP, largely due to a lower water stress.

Despite the great difference in organic matter content, there was much less difference between stands in the calcium content of the trees or decomposition layers. Total calcium content of trees did not decrease in proportion to organic matter accumulation. This suggests that changes in composition and/or tissue concentration resulted in an alteration of the efficiency with which the forest ecosystem utilized a nutrient to produce organic matter. The efficiency of calcium use in the WBW forest changed from 5.0×10^{-3} grams per gram of organic matter in trees in year 100 to 5.9×10^{-3} grams per gram organic matter

Table 11. Comparisons of the simulated quantities of nutrients in the major components of the Walker Branch Watershed (WBW) and the Hannah Branch Watershed (HBW) forest stands.

		Year 100	Year 200	Year 300	Year 400	Year 500
			Organic Matter ($mt \cdot ha^{-1}$)			
Total Tree	WBW	137	104	102	92	93
	HBW	243	212	207	158	163
Primary Decomposition Layer	WBW	30	22	21	18	22
	HBW	84	88	94	108	99
Secondary Decomposition Layer	WBW	19	14	13	12	14
	HBW	32	33	35	33	31
			Calcium ($mt \cdot ha^{-1}$)			
Total Tree	WBW	.69	.59	.58	.60	.55
	HBW	.72	.60	.67	.47	.53
Primary Decomposition Layer	WBW	.48	.44	.45	.43	.41
	HBW	.38	.38	.37	.45	.40
Secondary Decomposition Layer	WBW	.39	.30	.27	.25	.29
	HBW	.51	.53	.54	.53	.53
Total Soil	WBW	4.43	3.92	2.95	2.53	1.98
	HBW	1.53	1.89	2.36	2.50	2.71
			Nitrogen ($mt \cdot ha^{-1}$)			
Total Tree	WBW	.39	.30	.29	.27	.25
	HBW	.55	.52	.49	.31	.32

Table 11 (continued)

		Year 100	Year 200	Year 300	Year 400	Year 500
Primary Decomposition Layer	WBW	.13	.09	.09	.08	.08
	HBW	.17	.16	.17	.17	.16
Secondary Decomposition Layer	WBW	.24	.18	.17	.16	.18
	HBW	.49	.46	.49	.47	.46
Total Soil	WBW	5.27	4.89	4.68	4.51	4.38
	HBW	5.50	4.37	3.56	2.81	2.23

in year 500. That of the HBW changes from 3.0×10^{-3} grams calcium per gram organic matter in year 100 to 3.3×10^{-3} grams calcium per gram organic matter in year 500.

The WBW had a greater increase in the efficiency of calcium use in the vegetation. Assuming the lower calcium reserve made competition in the vegetation more acute, the result of this competition was an increase in calcium use efficiency. The greater the loss of calcium from the system, the greater the gain in efficiency. Since the calcium concentration in the tissues of each species remained constant during the simulation, the change in efficiency of calcium use was a result of competitive replacement among species. This competition could also have resulted in a replacement by age groups which were more efficient in the use of calcium. Nevertheless, this increased efficiency did not prevent the rapid loss of calcium from the system. Thus, increased calcium use efficiency was likely the result of dwindling soil pools rather than a cause of these losses.

The decline of the nutrients showed no relationship to dynamics of element storage in the litter layers. That is, the stability in the size of these litter layer pools through time was not drastically different between the two forests. In neither stand did the litter immobilization processes respond to losses from the system by increasing the pool size. Conversely, losses do not appear to be related to large reductions in the amount of nutrients immobilized in this pool. The HBW contained twice as much nitrogen in both litter layers, and considerably more calcium than the WBW layers. However, these

differences were a consequence of climatic factors and not a reason for differential losses. In fact, the cycling rate of calcium, as measured by the magnitude of input to the litter pool and output from the litter pool (mineralization), was similar in both stands. Although litterfall and mineralization release of nitrogen were higher in the HBW, uptake was also greater in response to the demand created by the larger biomass. Climatic conditions, rather than greater cycling rates, maintained the larger litter mass. Nutrients accumulated in the litter layer under cooler temperature conditions.

The greater nitrogen uptake demands were met in the HBW by larger nitrogen mineralization releases from the litter layer. This balance is much more critical than total size of the nutrient pool in the litter. Nutrient drain from a forest system is the accumulated result of many years in which uptake requirements are insufficient to withdraw excess mineralized nutrient quantities from the soil system. Nitrogen leaching will take place readily under such conditions, while for calcium the physical processes in the soil may be sufficient to hold the ions in the soil matrix.

Flux Rate Differences

Greater tree uptake did not prevent nutrient loss from the system. While the greater quantities of nitrogen being released from the litter layer in the HBW made greater tree growth rates possible, these growth rates did not restrain nitrogen loss. In addition, greater efficiency of calcium use in the WBW did not prevent calcium loss. Due to the lower calcium concentrations in tree tissues in the HBW, the greater

productivity did not cause the demand for calcium to be greater than in the WBW. In the WBW, with the same demand for calcium and, in addition, a greater efficiency of calcium use, loss of this element was not prevented.

Since nitrogen was lost from the HBW system at a faster rate, it could be hypothesized that the yearly cycling of greater quantities led to a greater nitrogen loss. Such an effect could occur if there was proportional leakage from the system. Greater nitrogen mineralization release could have been accompanied by an increased risk that the very mobile nitrate ions would be lost by leaching from the soil profile. However, closer examination shows that as the nitrogen uptake rate in the HBW decreased the rate of nitrogen loss from the system did not also decrease. This suggests that nitrogen loss rate is not directly associated with the average uptake rate. The percentage reduction of the soil pool was 20.5% from year 100 to year 200, 18.5% from year 200 to 300, 21.2% from year 300 to year 400, and 20.6% from year 400 to year 500. In other words, nitrogen loss rate remained constant throughout the simulation and did not decrease with decreasing uptake rate. Average rates of litterfall and mineralization of calcium and nitrogen remained proportional to uptake. Thus, as uptake decreased the rate at which these elements were cycling through the litter decreased, or, in other words, the pool of nutrients available for leaching was not changing in magnitude. If cycling rate were related to nutrient retention, a difference in the rate of cycling of nutrients through the two systems would be expected to cause a difference in nutrient retention.

Table 12 compares the amount of change which occurred in the size of several components and processes to the change in the soil pool. Two periods are shown, one from year 100 to year 200, during which the biomass was decreasing in both simulations, and one from year 200 to year 300, in which litter biomass decrease occurred. The magnitude of some losses of calcium in the WBW and of nitrogen in the HBW could not be accounted for by decreases in any of the key component sizes or flux sizes. The loss of nutrients from the trees was of an insignificant magnitude compared to these soil losses. Interestingly, the changing concentrations of nutrients (a result of shifting species composition) alone accounted for an increase in the pool of nutrients in the trees. The overall tree pool decreased despite this effect. Furthermore, the decrease in annual uptake was not nearly enough to account for such soil losses. Decreased average demand for available nutrients was of insufficient magnitude to provide enough excess nutrients in the soil solution to account for all of that lost.

The Balance of Tree Uptake and Litter Mineralization

Little understanding of the comparative control of nutrient loss from these systems can be found by examining the long term changes in average pool sizes or flow rates. What, then, controls these rates of loss? The balance of annual plant uptake and annual mineralization from the litter is critical to leaching processes. If quantities of a nutrient are released from the litter layer in excess of the amount that can be used by the vegetation, the surplus will be available for

Table 12. Factors contributing to nutrient losses: the percent and magnitude of change in important processes and components during two 100 year intervals during the Walker Branch Watershed (WBW) simulation and the Hannah Branch Watershed (HBW) simulation.

		Calcium		Nitrogen	
		WBW	HBW	WBW	HBW
		Year 100 to Year 200			
Soil	%	-11.5	+23.4	- 7.2	-20.5
	$mt \cdot ha^{-1}$	- .51	+ .36	- .28	- 1.13
Tree	%	-14.4	-16.7	-23.1	- 5.4
	$mt \cdot ha^{-1}$	- .1	- .12	- .09	- .03
Uptake	%	- 7.0	- 7.1	-15.4	-10.0
	$mt \cdot ha^{-1}$	- .01	- .01	- .01	- .01
Litter	%	-14.9	+ 2.0	-27.7	- 6.1
	$mt \cdot ha^{-1}$	- .13	+ .02	- .10	- .04
Concentration	%	+12.0	- 3.0	- 3.4	+ 8.4
	$mt \cdot ha^{-1}$	+ .06	- .02	- .01	+ .04
		Year 200 to Year 300			
Soil	%	-27.7	+24.9	- 4.2	-18.5
	$mt \cdot ha^{-1}$	- .97	+ .47	- .21	- .89
Tree	%	- 1.7	+11.7	- 3.3	- 5.8
	$mt \cdot ha^{-1}$	- .01	+ .07	- .01	- .03
Uptake	%	—	—	—	—
	$mt \cdot ha^{-1}$	—	—	—	—

Table 12 (continued)

		Calcium		Nitrogen	
		WBW	HBW	WBW	HBW
Litter	%	- 2.7	—	- 3.6	+ 7.0
	$mt \cdot ha^{-1}$	- .02	—	- .01	+ .04
Concentration	%	+16.1	- 3.5	- 3.5	- 3.6
	$mt \cdot ha^{-1}$	+ .05	- .01	- .01	- .02

leaching from the soil profile unless restrained by some physical-chemical process. Calcium can be held within the soil matrix either as a precipitate or at cation exchange sites. However, calcium ion loss becomes increasingly likely if sufficient anions are present in the soil solution to hold cations in solution. Nitrate is not held by physical processes within the soil matrix. In these simulations, conditions of excess mineralization of calcium and nitrogen often existed (Figures 8, 16, 20, and 28, pages 77, 98, 107, and 125). These conditions were attributable to the presence of one element in short supply, restricting plant uptake of other elements. While an element in limiting supply will likely be completely removed from the pool of leachable ions by vegetation uptake, other elements will not be withdrawn due to their comparative excess.

Since the soil was treated in a very simplified manner in which 75% of all excess calcium would be retained in the soil matrix (25% of this excess would be lost from the system) regardless of anion availability, the potential loss of calcium was reduced considerably. Little capability of physical soil retention of nitrogen was assumed (5% of all excess nitrogen would be retained). Nitrogen retention is dependent upon vegetation and litter immobilization. Since the environmental conditions often restrain the growth of these components, nitrogen retention capabilities of the system are likely to be lower than the 75% retention assumed for the calcium system. All things being equal, nitrogen would be expected to be lost in greater quantities from the system.

In the HBW annual calcium outflow (the difference between mineralization release and uptake) was greater than nitrogen outflow (5.25 $kg \cdot ha^{-1}$ calcium versus 1.41 $kg \cdot ha^{-1}$ nitrogen). A positive value of outflow indicates nutrient excess, with the higher the value the greater the excess. Variances on these average outflows were large, with a standard deviation of 8.3 $kg \cdot ha^{-1}$ calcium and 9.3 $kg \cdot ha^{-1}$ nitrogen. The annual values fluctuated widely, meaning that in any year a large number of plots were experiencing excesses of nitrogen or calcium.

The lack of a physical-chemical soil retention system allowed large losses of excess nitrogen despite a much lower average nitrogen outflow than calcium outflow. The WBW had a mean deficit of calcium outflow (-5.0 ± 7.3 $kg \cdot ha^{-1}$) and a much higher nitrogen outflow (3.82 ± 4.24 $kg \cdot ha^{-1}$). The higher variance in average calcium outflow in this stand could indicate that more of the WBW plots would be experiencing calcium excesses than nitrogen excesses in any given year, and the forest would tend to lose calcium faster despite the greater soil retention of calcium over nitrogen. Calcium was lost more rapidly from the WBW than from the HBW although the average calcium outflow was lower. Plot to plot variance was critical in determining stand nutrient loss.

An element that is consistently in short supply will not be lost from the system. Conversely, an element which is continually in excess, and is lost in large quantities because of these excesses, is not likely to be limiting to vegetation growth. Thus, the suggestion is that calcium was limiting more often in plots of the HBW and that nitrogen was more often limiting in WBW plots. There is a confounding factor,

however, and that is the influence of weather on tree growth. It is conceivable that in a given year the weather conditions could be limiting to tree growth rather than any element induced limitation. If soil microbial processes were not also limited by these conditions both calcium and nitrogen could be mineralized in excess of uptake requirements and potentially lost from the system in large quantities.

Nutrients become available by mineralization from the litter layer, by hydrogen ion replacement on the exchange sites in the soil, and by mineral weathering. The amount of yearly uptake on a single plot remains relatively similar in magnitude to the quantity of nutrient released from the secondary decomposition stage. The difference between these two quantities must be supplied by soil weathering or growth must decrease. Thus, ideally the pattern of uptake by vegetation will track the pattern of nutrient release from weathering and mineralization, or in other words, the vegetation will grab every available ion. Insufficient uptake leads to the potential of leaching loss from the system.

Constraints on Tree Uptake and Litter Immobilization

What restricts the ability of vegetation uptake to match mineralization? The answer lies in the forces which drive the two processes each year. Mineralization occurs when an ion cannot be used by the soil microbial population. Ample evidence exists showing the ability of the microbial population to outcompete higher plants for ions (Vitousek et al., 1979; Johnson and Edwards, 1979; Swift et al.,

1978). Microbial populations can respond very rapidly to changes in resource availability. The utilization of available nutrients is restricted by the environmental conditions discussed earlier. Nutrients are used by microbes, in biologically determined rates with carbon, to build molecules. When the carbon/nutrient ratio of material entering the decomposition component matches the biological needs of the microbial community, nutrients will be turning over and will be released as fast as they enter the litter. When the carbon/nutrient ratios are larger than this value, the rate of microbial processing of material will be restricted by the most limiting nutrient. Given a fixed amount of carbon, the larger this ratio, the longer an ion of nutrient will be held in the immobilized state, and the lower the frequency of the output of an ion from the litter.

In the simulations related to this study, the rate of mineralization showed large year to year variation, reflecting the response of the microbial community to patterns of moisture availability. Tree uptake, being less responsive to moisture patterns and being less capable of rapid year-to-year adjustments in growth, was unable to precisely track the pattern of mineralization. The difference between the two processes led to years when available nutrients were more abundant than the quantity required for growth. During these years excess quantities of nutrients were lost from the system. During more favorable years trees depleted portions of the exchangeable supply in the soil. Once these depleted exchange sites were restored through weathering of minerals in the soil reserve, new ions became susceptible to leaching. The result was a gradual reduction in the soil reserve.

The vegetation community is constrained in year-to-year growth behavior by the cycles of response to light, moisture, and nutrients. The cycle of light availability generated by canopy replacement dynamics is typically on the order of 100 to 200 years. Although the response to moisture availability is rapid in the model, the response to nutrient availability can vary from slow to rapid, depending upon the species' characteristics. At certain times during the gap replacement cycle the ability to respond to yearly availability of nutrients may be low due to the constraints of other environmental factors.

Predicting System Properties from Constraints

The rate of production (and consequently of nutrient uptake) in ecosystems is constrained by the input of biologically usable solar energy, temperature and moisture availability, the inputs of essential elements, the presence of abiotic reserves, the physical limits on the potential for development of active pathways of recycling and conservation, and the biology of the organic structures (Waide, 1980). The organic structures evolve to allow maximum use of resources under these constraints. It would follow then that these organic structures are predictable from the abiotic conditions which constrain them, and that the kinetics of biogeochemical processes are predictable from the structures, since the kinetics are intimately linked to metabolic rates. An example of a prediction of the rate of recycling by an ecosystem process based on abiotic resource input information comes from Meetenmeyer (1978). He developed an equation which successfully predicted

decomposition rates of fresh litter in forests in several regions of the United States from evapotranspiration data. Evapotranspiration is an integrated measure of the rate of input of three abiotic resources: light, moisture, and heat. The important point is that without knowledge of the specific organisms involved in the decomposition process, the rate of element release could be accurately predicted. Such a prediction suggests that the key factors controlling the rate of microbial nutrient processing have been identified. These factors control resources to which the microbial community is most sensitive and is adapted to utilizing at maximum rates.

The abiotic resources which drive other ecosystem functions are not as clear as those driving microbial communities. However, the similarities in the efficiency with which two systems cycle essential nutrients will still be a function of the similarities in abiotic resource input and in the degree of biological adaptation to the maximum use of the patterns of this input.

Cole and Rapp (1981) have shown that higher productivity rates in forest ecosystems can be associated with higher rates of nutrient cycling. The ability of a system to maintain high productivity levels is dependent upon the preservation of high levels of available resources. The property which imports nutrient conservation to a system is the presence of organisms which are capable of rapidly capturing nutrients when they become available. This is why soil heterotrophs have been identified as controllers of ecosystem dynamics (O'Neill et al., 1975). However, the heterotrophs are controlled by climatic conditions and their ability to

respond to nutrient abundances may be limited by these conditions. Given two forests, each capable of responding to a variety of resource availability patterns, the forest most capable of utilizing nutrients in the released pattern will retain higher quantities of nutrients within the system and thus can maintain a higher level of biomass accumulation.

Ecosystem biomass accumulation provides an example of the relationship of a system property to abiotic inputs. Ecosystems receiving similar patterns of resources in the eastern deciduous forest achieve similar maximum biomass levels regardless of species present (Cole and Rapp, 1981). The individual species respond to localized patterns of resource availability. However, maximum biomass of eastern deciduous forest types is a property of the system as determined by climate and not by variation in localized differences in resources. This property is a function of long term climatic change and can be observed to change only between broad latitudinal bands (Cole and Rapp, 1981).

Functional Components

Nutrient retention properties result from the presence of functional components which have developed to maximally utilize the pattern of abiotic input of resources. Thus, the pattern of ecosystem response to changes in nutrient availability will be predictable from the relative change in the magnitude and frequency of resource input. These functional components can be identified based on their ability to process resources at given rates and magnitudes. Redundant functional

components are components in a system which process at the same rates. The absence of components which process at the same rate in two different ecosystems will result in a difference in response which can be translated, in more traditional ecosystems analysis terms, to a difference in resistance and resilience. Long term nutrient patterns should be predictable from a knowledge of the resource response components of a system. This discussion provides a hypothesis which is neither proven nor disproven by this study. However, the hypothesis provides a direction in which to look to find the factors controlling nutrient retention.

Identifying these functional nutrient-processing components in different ecosystems is a difficult task. The problem involves identifying the set of organisms or processes that display a capability of utilizing a resource rapidly when it becomes available. Consequently, the ability of such subunits to respond is typically apparent only during transient changes in resource availability. During a given year on a particular plot in the forest such a response might be identified. However, the process of making such an identification based on a summary of the behavior of many plots over many years is unclear.

One principal long term response of the system is the change in species dominance. The replacement species are those that are competitively superior under regimes of low nutrient availability. They characteristically have lower rates of uptake. However, short term fluctuations in release, such as those induced by changing moisture conditions, seem even more likely to release nutrients in excess of

that required by the vegetation once the plant community has become composed of slower responding species.

Consequently, though the system is capable of functioning at a lower level of internal cycling, it would not be expected to retain nutrients any more efficiently. Rather, the system would be expected to function at a lower rate of productivity. The set of species that competes best in nutrient deficient conditions makes up one type of functional component of the system, that is, a component which responds best to slow releases of resources.

CHAPTER VII

CONCLUSIONS

The dry mid-slope forest of the Walker Branch Watershed showed large losses of calcium from the soil pool during 500 years of simulation. In contrast, the dry mid-slope forest of the Hannah Branch Watershed showed large losses of nitrogen and an increase in the pool of calcium within the soil. Since losses are the result of an excess of release from litter mineralization over the tree uptake requirement, the rate of tree uptake is assumed to be regulated by a limitation in the available quantity of an element which is not being lost rapidly. Consequently, the simulated Walker Branch Watershed was likely limited by nitrogen while the Hannah Branch Watershed was limited by calcium. However, this study also demonstrated the importance of variability from plot to plot and through time in assessing the causes of nutrient losses. Although a general condition of calcium limitation might exist in the HBW, in any given year nitrogen might be the element limiting to growth. Such transient conditions were likely due to the differential response of the microbial mineralization processes and the tree uptake processes to climatic and weather conditions.

Calcium retention in forests is very dependent upon physical soil retention characteristics. Nitrogen is much more dependent on vegetative characteristics. In a simplified treatment of the soil system, it was assumed in this study that the soil was capable of retaining 75% of excess calcium released from the litter to the soil and not taken up by

the vegetation. However, only a 5% retention of nitrogen was assumed. Litter immobilization and tree uptake processes are limited by climatic conditions and are consequently often prevented from contributing as much as 75% to nitrogen retention. Thus, nitrogen is likely to be lost from the system in quantities greater than calcium. However, the balance of mineralization and uptake is very dependent on the specifics of site and time. When tree uptake is very similar to mineralization release nutrients will be held tightly in the system. Many mechanisms, such as translocation alteration, tissue concentration alteration, and nitrogen fixation relationships, are capable of enhancing the adjustment of tree uptake to efficiently capture available nutrients.

The differences between the two forests were the result of the accumulated effects of short term imbalances between uptake and mineralization rather than the result of a chronic characteristic of the nutrient cycles. The differences did not clearly arise out of differences in species dominance or community structure which developed during the successional path of each forest. Neither can it be said that the greater cycling rate of the more productive HBW stand led to the differences. In attempts to assess the impact of human induced disturbance on forest nutrient retention, we must focus attention on the effect of this balance.

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VITA

David A. Weinstein was born in Highland Park, New Jersey, on March 26, 1951. He attended Highland Park High School where he was graduated in June 1969. He received a Bachelor of Arts from Dartmouth College in June of 1973, majoring in Anthropology with a special program in Environmental Science. After accepting a research assistantship at the University of New Hampshire in September 1974, he earned a Master of Science degree from the Botany and Plant Pathology Department. His thesis was entitled, "The Effect of Spray Irrigation of Sewage Effluent on a Northern Forested Ecosystem."

In September 1976 he entered The University of Tennessee with support from both a teaching assistantship and a research assistantship from the Graduate Program in Ecology. One year later he was awarded a research fellowship from the Oak Ridge National Laboratory, where the present work was conducted.

The author is a member of Sigma Xi and received the First Place award in the 1980 Graduate Student Symposium sponsored by The University of Tennessee chapter of that organization. He accepted a position of research associate at the Ecosystems Research Center at Cornell University in September 1981 and is presently employed at that facility.

He is married to Carole Whitehead of Columbia, Tennessee, the mule capital of the world.