AMERICA'S
RENEWABLE RESOURCE POTENTIAL - 1975:
THE TURNING POINT

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INTRODUCTION

The theme of this year's conference concerns America's "renewable resource potential." If there is one keyword in this phrase, it is certainly renewable. The current generation cannot prosper at the expense of future generations by severely depleting our natural resource base. Yet the wise husbandry of natural resources is a complex and complicated process. Two basic facts combine to make resource management a difficult task. First, management decisions are made in a multidemand environment, in which the demand structure imposed upon the system may change dramatically. Second, the ecological systems which should be the objects of management decisions are complex and diverse assemblages of many species, and much basic information is lacking.

It is a premise of sound resource management that ecosystem responses to a variety of management perturbations can be predicted, controlled, and made beneficial to man if the proper information is available. Thus, it becomes essential to establish a sound conceptual framework within which to make management decisions. This framework should identify information most needed for management purposes, and also reveal basic characteristics of the ecosystems being managed.

Our purpose—in this paper is to outline such a conceptual framework which has guided much of our thinking in an integrated study of elemental cycles on forested watersheds of diverse treatment histories at the Coweeta Hydrologic Laboratory in the southern Appalachians. This basic framework will then be applied to analyses of the nitrogen cycle in two important southeastern forest ecosystem types, i.e., deciduous hardwoods and loblolly pine, to evaluate potential impacts of several forestry practices on these systems.

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ELEMENTAL CYCLES AND FOREST MANAGEMENT

The ecosystem concept is now well established in both academic and applied ecology. The ecosystem is also the proper unit for management. Ecological systems are coevolutionary units in which every species population is coadapted to all others. All populations are linked together in complex chains of causal relationships, so that not only primary but also secondary and higher-order effects of any natural or applied disturbance must be considered. Each population is a part of the environment of all other populations, and it is clear that one cannot manage forests simply by managing the trees.

The eminent ecologist G. Evelyn Hutchinson (1968) referred to ecosystems as "circular causal systems," arguing that cycles of mineral elements within biological communities organize and integrate these into functioning holistic systems. Complete appreciation of this argument reveals that patterns and processes of elemental cycling must be thoroughly assessed if ecosystem management is to succeed.

Two basic questions concerning forestry effects on elemental cycles must be considered. The first relates largely to changes in quality of surface water following forestry operations. Much progress is being made in this area, and we do not intend to mention such problems further. The second and perhaps ultimately more important question involves the "on site" response, or the sustainable productivity of ecosystems with intensive forest management. Along with sunlight and water, elemental resources regulate and may limit primary fixation of carbon by biological communities. The benefits of short rotations, complete-tree harvests, and genetically superior and highly productive tree strains will be much reduced if soil elemental pools are depleted, leading to decreased productivity over several rotations. These points are especially critical today in light of the current world outlook for petroleum and fertilizer. Thus, basic patterns of elemental cycling in forests and their stability to various perturbations must be understood.

A CONCEPTUAL MODEL OF ECOSYSTEM RELATIVE STABILITY

The concept of stability has been an important one in academic ecology; consideration of the stability of ecosystems has produced much of modern ecological theory (e.g., Woodwell and Smith, 1969). Stability is also a basic, intuitive concept in human experience, and is extremely relevant to problems of resource management.

The classical notion of stability is a fairly simple one, namely that a system's response to some perturbation of its normal operating conditions is bounded. That is, the system retains essentially the same characteristics it had prior to the application and relaxation of the disturbance. This notion can be made mathematically rigorous (e.g., Rosen, 1970; May, 1973). The intuitive concept is sufficient for our purposes, however. We have argued previously (Waide et al., 1974; Webster, Waide, and Patten, 1975), as have other authors (Child and Shugart, 1972; Patten, 1974; O'Neill et al., 1975), that ecosystems are stable by this classical, absolute, yes-or-no definition. For example, when a mixed hardwood forest in the southern Appalachians is cut, it is replaced naturally by another hardwood forest with similar species composition, basal area, biomass, and elemental cycling characteristics. Neither a savanna nor a boreal coniferous forest returns in its place. Although this example is simplistic, it demonstrates the concept of ecosystem stability.
Thus, we have suggested that what is important for study is the notion of relative stability (Waide et al., 1974; Webster et al., 1975). Two basic aspects of relative stability may be identified, in terms of ecosystem response to perturbation (Waide et al., 1974; Patten, 1974; Webster et al., 1975). The first is the notion of resistance, or displacement of an ecosystem from its nominal or unperturbed state. A system that deviates little in response to disturbance is more stable in the sense of resistance than one which deviates to a greater degree from its nominal behavior. The second, complementary aspect of relative stability concerns the concept of resilience, or recoverability. For a given level of disturbance, a system that recovers more rapidly to its nominal state behavior is more resilient and hence more stable than a system that recovers more slowly.

We suggest that these are intuitive concepts of ecosystem response to perturbation, that they bear strong relation to current ecological theory, and that they are relevant considerations for resource management. Ecosystems which are shown to be relatively less resistant should be disturbed to a lesser degree, and ones which are shown to be relatively less resilient should be disturbed less frequently, than other ecosystems which are relatively more resistant and resilient, respectively. Further, these two aspects of relative stability can be quantified and related to specific attributes of ecosystems which are measurable in field research programs.

The basic mathematical techniques for quantifying these concepts come from the engineering sciences. Experience has demonstrated that the behavior of higher-order, many-component systems can be approximated by second-order systems. The basic techniques will not be given here since they are well established (e.g., DiStefano, Stubberud, and Williams, 1967; Shinners, 1972). Several previous ecological papers have employed and discussed such techniques in analyses of characteristics of populations (Hubbell, 1973a,b) and ecosystems (Child and Shugart, 1972; Waide et al., 1974; Webster et al., 1975; Waide and Webster, 1975).

The general response of a second-order system may be described by the equation

\[ y'' + 2\zeta \omega_n y' + \omega_n^2 y = \omega_n^2 z, \]

where \( y \) is some system output of interest with \( y' \) and \( y'' \) its first and second derivatives with respect to time, and \( z \) is some system input. The two basic parameters which define the response of such a system are the natural frequency, \( \omega_n \), and the damping factor, or damping ratio, \( \zeta \). In our conceptual model of ecosystem relative stability, we have identified the natural frequency with resistance, and the damping factor with resilience. The smaller the estimate of the natural frequency, the greater the resistance and the less the system is affected by disturbance. Similarly, the farther the damping value is from 1, the less resilient is the ecosystem and the more slowly it recovers following disturbance.

Three specific indices or characteristics of ecosystem elemental cycles have been shown to influence the degree of resistance and resilience a given ecosystem exhibits (Webster et al., 1975):

1. The abiotic storage index expresses the presence or absence of large abiotic reserves of an element. This refers to pools of an element which are tied up in a relatively unavailable form (e.g., nitrogen bound in soil organic matter which decays slowly). The term abiotic
does not indicate that these reserves are not of biological origin, only that they are currently in a non-living state, and that they are in a relatively unavailable or recalcitrant form for uptake by living organisms.

(2) The index of biotic storage refers either to the proportion of the total amount of an element which is contained within living organisms, or to the turnover time of the element within biotic pools.

(3) The recycling index is a measure of the rate with which elements contained in forms available for reuse by organisms are recycled in the system. It typically might be used to indicate the turnover rate of the litter or detritus component of the ecosystem.

Previous analyses have shown that large indices of abiotic or biotic storage are typical of ecosystems which are relatively more resistant, whereas ecosystems with small pool sizes and high indices of recycling are relatively more resilient. It is conceivable that a given ecosystem might be both more resistant and more resilient than another ecosystem. However, an ecosystem cannot at once be both highly resistant and highly resilient. Webster et al. (1975) used these three indices to classify various idealized ecosystem types according to their elemental cycling characteristics. Temperate forests were identified as systems with relatively large abiotic and biotic element reserves and with relatively slow rates of recycling. In contrast, planktonic systems characteristic of open oceans were idealized as ecosystems with low abiotic and biotic storage and a high index of recycling.

This conceptual model, developed only briefly here, may prove to be a rigorous and operational approach to ecosystem analysis which is testable by observation and experimentation. Its relevance for specific management decisions will be examined by analyzing the relative stability of nitrogen cycles in two important southeastern forest ecosystem types, a loblolly pine plantation and a natural oak-hickory forest. Nitrogen was chosen as the element for consideration because of its key role in the productivity of diverse ecosystems.

FLOW DIAGRAMS OF THE NITROGEN CYCLE IN TWO SOUTHEASTERN ECOSYSTEMS

Figures 1 and 2 are flow models of the nitrogen cycle modified from Mitchell, Waide, and Todd (1975) for a relatively undisturbed oak-hickory forest located on a 12.66 ha north-facing watershed (WS 18) at the Coweeta Hydrologic Laboratory in the southern Appalachians. These diagrams provide estimates of the pool sizes (kg N/ha) for fifteen compartments in this ecosystem, as well as estimates of vegetation increments (kg N/ha/yr) and transfers of nitrogen among the various compartments (kg N/ha/yr). Sources of data and underlying assumptions used in constructing this model are discussed fully by Mitchell et al. (1975).

The data in Figs. 1 and 2 show that most of the nitrogen in this undisturbed forest is contained in large storage pools which turn over slowly. Over 80% of the total nitrogen is bound within soil organic matter, with about 11% in total vegetation, 3% in litter pools, 4% in microbial biomass, and 2% in free soil pools. Of the total estimated uptake of 112 kg N/ha/yr, only about 10% is retained in plant increments. Figure 1 also shows that a large amount of nitrogen, about 51 kg/ha/yr, recycles annually within plants. This nitrogen is withdrawn from leaves prior to abscission and stored in woody tissue until being remobilized for new growth the following spring.
Figure 1. Flow model of nitrogen cycling in an oak-hickory forest at Coweeta. Values inside large boxes represent standing crops of nitrogen (kg N/ha); values in small rectangles are vegetation increments (kg N/ha/yr); numbers on arrows represent nitrogen transfers among compartments (kg N/ha/yr). This diagram shows nitrogen transfers associated with nitrogen uptake by plants and return to litter-soil pools.
Figure 2. Flow model of nitrogen cycling in an oak-hickory forest at Coweeta. Labelling conventions as in Fig. 1. This diagram emphasizes nitrogen transfers associated with litter decomposition and nitrogen remineralization.
Gains and losses of nitrogen for this system have been described by Todd, Wald, and Cornaby (1975). Nitrogen gains include inputs by precipitation (3.4 kg N/ha/yr) and by nitrogen fixation (10.9 kg N/ha/yr). Losses were estimated as 0.08 kg N/ha/yr dissolved in streamwater, 0.23 kg N/ha/yr lost in sediments, and 18.2 kg N/ha/yr lost via denitrification. However, subsequent analyses have suggested that the original estimate of denitrification is excessive. The method used to quantify denitrification potentially could also be measuring the amount of nitrogen fixation. Hence, for each component of the litter-soil profile for which measurements were made, the estimate of nitrogen fixation was subtracted from that of denitrification, producing a revised estimate of denitrification of 10.7 kg N/ha/yr.

Although the nitrogen cycle in this ecosystem appears to be dominated by large compartments which turn over slowly, a dynamic portion of the cycle exists in the soil. As shown in Fig. 2 a much greater amount of nitrogen flows through the microbial, NO₃, and NH₄ compartments than is contained within them. Turnover rates for these three compartments are 5-6 times per year. This rapidly recycling portion of the total cycle is important in the behavior of the whole system, and may be largely responsible for the conservation of nitrogen within this ecosystem (Mitchell et al., 1975). Any analyses of nitrogen dynamics in this forest which obscure the contribution of these components to the total cycle could produce serious errors.

These data are the result of a large, integrated study of ecosystem structure and function at Coweeta as part of the U.S. International Biological Program. Other studies of forest nitrogen cycles (e.g., Henderson and Harris, 1975; Wells and Jorgensen, 1975), or evaluations of potential effects of forest operations on ecosystem elemental cycles (e.g., Boyle, Phillips, and Ek, 1973; White, 1974; Jorgensen, Wells, and Matz, 1975; Patric and Smith, 1975; Wells, Jorgensen, and Burnette, 1975), have not been based upon such a complete, fine-resolution compartmentalization of nitrogen storage and transfer. But an accurate assessment both of nitrogen dynamics in forests and of their stability to various disturbances may depend on such a complete picture of the nitrogen cycle.

In order to compare Coweeta data with those from other studies a lumped, seven-compartment version of Figs. 1 and 2 was derived by combining or eliminating several compartments (Fig. 3). The two leaf litter compartments were combined into a single compartment, and the soil organic matter, NO₃, and NH₄ compartments of the expanded model (15 compartments) were lumped into a single soil fraction in the lumped model (7 compartments). The herbivore, soil fauna, microflora, and mycorrhizae compartments were deleted from the new model. Especially important is the fact that the dynamic transfers of nitrogen among the microflora, NO₃, and NH₄ pools are now all contained within the new soil component. Thus, their contribution to properties of the total cycle has been obscured. We should emphasize that these two models of the Coweeta nitrogen cycle are based upon the same data, and that they simply represent different levels of resolution of nitrogen dynamics.

The third model of nitrogen cycling is based upon studies of loblolly pine plantations in the southeastern United States. The flow model of Fig. 4 is specifically based upon data from a plantation in the Duke Forest, in the Piedmont of North Carolina (Jorgensen et al., 1975; Wells and Jorgensen, 1975; Wells et al., 1975). This plantation was established in 1953 and was thinned at age 16 in 1968; data used here are based upon standing crops and transfers at age 16. Original data were used as reported, except for the estimate of litterfall which was adjusted to balance other transfers. Total litterfall shown in Fig. 4 is 38.3 kg N/ha/yr, compared with the original estimate of
Figure 3. Flow model of the nitrogen cycle in an oak-hickory forest at Coweeta. This diagram is a more coarsely lumped version of Figs. 1 and 2. Labelling conventions as in Fig. 1.
Figure 4. Flow model of nitrogen cycling in a loblolly pine plantation in the Duke Forest. Labelling conventions as in Fig. 1.
58.2 kg N/ha/yr. This latter value was probably not representative due to the occurrence of several ice storms during the study period (Wells and Jorgensen, 1975; Wells, pers. comm.). Inputs to the system were estimated as 5.45 kg N/ha/yr in precipitation (Wells and Jorgensen, 1975), and 1.0 kg N/ha/yr as nitrogen fixation (Jorgensen et al., 1975). The only loss considered was 0.70 kg N/ha/yr discharged in groundwater (Wells and Jorgensen, 1975).

Figure 4 shows that this forest is also dominated by large storage pools which turn over slowly. Over 73% of the total nitrogen is contained within the soil, with about 13% contained in both the vegetation and litter pools. About 13% of the total uptake of 105 kg N/ha/yr is retained in vegetation increments. The estimated amount of nitrogen recycling within plants is 17 kg N/ha/yr, about one-third of the estimate for the oak-hickory forest. Nitrogen in vegetation is about 58% of that in the Coweeta forest, while the litter nitrogen pool for the loblolly pine plantation is over twice that of the oak-hickory forest. The soil pool in the Coweeta forest is about twice that for the pine plantation. As in the lumped Coweeta model, the functionally important role of rapidly recycling pools of nitrogen in the soil is obscured by these data (Fig. 4).

In examining results of these three models, two types of comparisons will be made. First, the expanded Coweeta hardwood model will be compared with the lumped hardwood model to evaluate the effects of two different levels of resolution on predictions of system properties and responses to disturbance. This comparison should reveal the importance of the rapidly turning over pools of nitrogen in the soil relative to the total nitrogen cycle. A second comparison will be made between the lumped hardwood model and the pine model, to examine differences in properties and stability of the nitrogen cycle in oak-hickory and loblolly pine forests. These two models were conceptualized at similar levels of resolution, and such comparisons should yield meaningful results.

Two other models of nitrogen cycling in southeastern ecosystems were also analyzed, a model of an oak-hickory forest on the Walker Branch watershed at Oak Ridge, Tennessee (Henderson and Harris, 1975), and a model of a natural loblolly pine forest in Mississippi (Switzer and Nelson, 1972). Results of these two models agreed well with results from comparable forest types discussed above, but space limitations prevent inclusion of findings in this paper.

The structural indices for the three nitrogen cycles discussed above (Figs. 1 to 4) are shown in Table 1. These four indices were defined as follows: Abiotic storage is the proportion of the total nitrogen in the system which is localized within the soil; biotic storage is equal to the amount of nitrogen contained in plants, divided by total nitrogen uptake; recycling is the amount of nitrogen taken up by plants, divided by the amount of nitrogen contained in litter pools. A fourth index not discussed earlier is system turnover, which is total nitrogen in the system divided by total nitrogen taken up by plants. This index is related to the turnover time of the total nitrogen contained in the ecosystem.

Comparison of structural indices for the two different Coweeta models provides a contrast in stability interpretation (Table 1). Values for the lumped model suggest that the system has larger storage pools, and is recycling nitrogen less rapidly, than comparable values for the expanded model. These values demonstrate that system conceptualization strongly influences subsequent analytical results. Comparison of the oak-hickory and loblolly pine nitrogen
cycles shows that the pine plantation has smaller storage pools of nitrogen in both abiotic and biotic forms. Also, this forest appears to be recycling available nitrogen less rapidly than the oak-hickory forest and the system turnover is smaller than for the Coweeta hardwood forest. Based on previous analyses (Webster et al., 1975), values of these structural indices suggest that the loblolly pine nitrogen cycle is both less resistant and less resilient than the oak-hickory cycle. Also, values for the lumped Coweeta model suggest that this nitrogen cycle is less resistant, but more resilient, than do those for the expanded model.

Results of the structural indices are confirmed by results of the relative stability analyses (Table 2). These values were obtained as discussed by Webster et al. (1975), based upon the time domain algorithm of Pa Hii (1971). The state variable chosen to estimate the two relative stability indices using this algorithm was nitrogen contained in total plant biomass (kg N/ha). As seen in

<table>
<thead>
<tr>
<th>Ecosystem Type</th>
<th>Abiotic Storage Index</th>
<th>Biotic Storage Index</th>
<th>Recycling Index</th>
<th>System Turnover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oak-hickory (15 compartment)</td>
<td>.815</td>
<td>4.70</td>
<td>.833</td>
<td>34.3</td>
</tr>
<tr>
<td>Oak-hickory (7 compartment)</td>
<td>.846</td>
<td>7.19</td>
<td>.579</td>
<td>58.7</td>
</tr>
<tr>
<td>Loblolly pine plantation (7 compartment)</td>
<td>.624</td>
<td>3.60</td>
<td>.177</td>
<td>24.6</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Ecosystem Type</th>
<th>Resistance (Natural Frequency)</th>
<th>Resilience (Damping Ratio)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oak-hickory (15 compartment)</td>
<td>.106</td>
<td>.906</td>
</tr>
<tr>
<td>Oak-hickory (7 compartment)</td>
<td>.080</td>
<td>.855</td>
</tr>
<tr>
<td>Loblolly pine plantation (7 compartment)</td>
<td>.167</td>
<td>.850</td>
</tr>
</tbody>
</table>
be emphasized that although the damping coefficients for the two systems are quite similar numerically, this parameter appears as an exponent in the solution equations for the time behavior of these systems. Thus, a small difference in damping may produce a much larger difference in actual time response. Taken collectively, the structural and relative stability indices suggest that the nitrogen cycle in the oak-hickory forest is both more resistant and more resilient than in the pine forest. These results imply that management impacts on sustainable productivity may be greater for pine than for hardwoods.

EFFECTS OF DIFFERENT TYPES AND FREQUENCIES OF CUTTING ON PRODUCTIVITY OF LOBLOLLY PINE AND OAK-HICKORY FOREST ECOSYSTEMS

The previous discussions provide a conceptual and operational framework for evaluating effects of alternative forest operations on the productivity of loblolly pine and oak-hickory forest ecosystems. Both types of forest are commercially important in the southeastern U. S., and contribute substantially to total timber production of the nation. Moreover, projections of future demand for wood fiber suggest that forest management practices must be intensified in these forest types. Increased utilization of wood fiber is one method of increasing yield, but this practice also raises important questions about sustainable levels of productivity and possible disruptions of elemental cycles.

Potential effects of increased tree utilization on nitrogen cycling and productivity in loblolly pine and oak-hickory forest ecosystems were examined using simulation models of nitrogen dynamics based upon the flow diagrams shown in Figs. 1 to 4. Techniques used in constructing these models have been discussed fully in previous papers (e.g., Waide et al., 1974; Webster et al., 1975). Time-varying functions were used to simulate known changes in nitrogen uptake as pine and hardwood stands mature. All simulations were performed on an IBM 360 computer using the CSMP simulation language. Euler integrations were employed with a time step of .01 year.

Several types and frequencies of cutting were selected as alternative forestry practices, and simulations were run using each nitrogen model. Forestry operations applied to the two oak-hickory models included (1) harvest of merchantable stems, without removal of logging residue, with a "standard" 90 yr rotation length; (2) harvest of merchantable stems, with residue removal, on a 90 yr rotation; (3) complete-tree harvest, without removal of any remaining residue, on a 90 yr rotation; and (4) harvest of merchantable stems, without residue removal, on a shorter 50 yr rotation. Operations considered in loblolly pine simulations were (1) harvest of merchantable stems, without residue removal, on a "standard" 30 yr rotation; (2) harvest of merchantable stems, with residue removal, with a 30 yr rotation length; (3) complete-tree harvest, with removal of any remaining residue, on a 30 yr rotation; (4) harvest of merchantable stems, without residue removal, on a shorter 16 yr rotation; and (5) harvest of merchantable stems, without residue removal, on a 30 year rotation with thinning at age 16. Fertilization was not considered as an alternative in any simulation. As used here, residue refers to above and belowground portions of plants remaining on site after removal of forest products, plus the amount of litter present. Residue removal may include techniques such as actual physical removal or burning or both, all of which remove nitrogen from the site.

At appropriate times during simulations, as defined by rotation length, amounts of nitrogen were removed from certain plant compartments as forest products. The remainder of the nitrogen in plants was then transferred to litter or soil pools. Litter pools were then decremented by a certain proportion, typically 70%, if residue removal was specified in a simulation. Simulations of
complete-tree harvests involved removing all foliage, branches, stems, and roots above 4 cm diameter. Definition of merchantable stem followed discussions and calculations found in Day (1971, 1974), Patric and Smith (1975), and Wells et al. (1975). Proportions of roots in harvestable size classes were calculated from Harris, Kinerson, and Edwards (1975) and Wells et al. (1975). The amount of material removed from plant compartments when the loblolly pine model was "thinned" at age 16 was calculated from Wells et al. (1975). Three successive rotations were simulated for each type and frequency of cutting for each model. The amounts of nitrogen in each compartment at the end of a given rotation served as initial conditions for simulating the next rotation. In the following discussions of simulation results, yields of forest products, and amounts of residue removed, will be expressed as kilograms of nitrogen rather than as total dry matter.

The first question to ask concerning management impacts on nitrogen cycling involves the amount of nitrogen removed from the site. Amounts of nitrogen removed over the first two rotations as forest products and as residue and the yearly rate of nitrogen removal for each simulation are given in Table 3. For each ecosystem the greatest amount of nitrogen was removed in the complete-tree harvest simulation and in the simulation of merchantable stem harvest with residue removal. In the latter case, total nitrogen removed was large due to the amount of nitrogen removed as residue. Otherwise, amounts of nitrogen removed in forest products for the three types of merchantable stem harvest were similar. For the loblolly pine model, the amount of nitrogen removed in forest products in the simulation of a merchantable stem harvest with thinning at age 16 was 40 to 50% higher than in the other three merchantable stem harvests.

When comparisons are based on the amount of nitrogen removed per year, a slightly different picture emerges. Again, values for the complete-tree harvest and merchantable harvest with residue removal simulations were the largest for each ecosystem. However, removal rates for shorter rotation lengths—50 years for hardwood, 16 years for pine—were considerably larger than for "standard" rotations. For the loblolly pine model, the removal rate for the thinning alternative was intermediate between values for the shorter and standard rotation lengths.

Comparisons of nitrogen removal from the three models for similar types of cutting reveal slightly higher values for the lumped oak-hickory model than for the expanded hardwood model, totally and per year. Also, comparison of similar cuts on hardwood and pine systems reveal larger total amounts removed from the hardwood forest. However, because rotation lengths were much shorter for pine harvests, annual rates of removal were much larger for the loblolly than for the oak-hickory model. These results agree well with similar calculations reported by Patric and Smith (1975) and Wells et al. (1975).

A second effect of forest practices on these ecosystems involves changes in yield (expressed as kg N) following several simulated rotations. Table 4 presents data on such changes in yield at the end of the third rotation compared with the first rotation. A variety of rotations could have been compared. This choice allowed sufficient time for decreases in yield to develop while still representing a reasonable time interval for considering management alternatives.

For each ecosystem the smallest decrease or the largest increase in yield occurred for the merchantable harvest, without residue removal, and with a "standard" rotation length. Results of shorter rotation simulations revealed only slightly larger decreases in yield compared with standard length rotations. Largest absolute decreases in yield (36 to 95 kg N/ha) were observed for complete-
<table>
<thead>
<tr>
<th>Product &amp; Leave Residue (Y/N)</th>
<th>Nitrogen Removed (kg/ha)</th>
<th>Total Nitrogen Removed (kg/ha)</th>
<th>Product &amp; Leave Residue (Y/N)</th>
<th>Nitrogen Removed (kg/ha)</th>
<th>Total Nitrogen Removed (kg/ha)</th>
<th>Type of Forest</th>
<th>Type of Forest</th>
<th>Impact of Different Types and Frequencies of Cuts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Merchandable</td>
<td>326.3</td>
<td>0</td>
<td>No</td>
<td>326.3</td>
<td>30</td>
<td>No</td>
<td>No</td>
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<tr>
<td>Complete-tree</td>
<td>1.75</td>
<td>0</td>
<td>No</td>
<td>16.5</td>
<td>6</td>
<td>No</td>
<td>No</td>
<td></td>
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<tr>
<td>Complete-tree</td>
<td>7.5</td>
<td>0</td>
<td>No</td>
<td>20.0</td>
<td>30</td>
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<td></td>
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<td>No</td>
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<td>30</td>
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<tr>
<td>Complete-tree</td>
<td>7.0</td>
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<td>No</td>
<td>7.0</td>
<td>90</td>
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<td>0</td>
<td>Yes</td>
<td>36.8</td>
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<td>No</td>
<td>3.7</td>
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<td>3.4</td>
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<td>5</td>
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<tr>
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<tr>
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</tr>
<tr>
<td>Oak-Hickory</td>
<td>1.75</td>
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<td>No</td>
<td>16.5</td>
<td>6</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
</tbody>
</table>

Table 3: Impacts of different types and frequencies of cuts.
Table 4. Change in yield, expressed as kg N/ha removed in forest products, at the end of the third compared to the first rotation, following several types and frequencies of cutting of loblolly pine and oak-hickory forest ecosystems.

<table>
<thead>
<tr>
<th>Ecosystem Model</th>
<th>Type of Cut</th>
<th>Rotation Removal</th>
<th>Rotation Length (yrs)</th>
<th>1st Yield (kg/ha)</th>
<th>3rd Yield (kg/ha)</th>
<th>Change in Yield (kg/ha)</th>
<th>Change in Yield (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oak-hickory (15 compartment)</td>
<td>Merchantable</td>
<td>No</td>
<td>90</td>
<td>184.6</td>
<td>165.7</td>
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<td>-10.3</td>
</tr>
<tr>
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<td>Yes</td>
<td>90</td>
<td>184.6</td>
<td>151.7</td>
<td>-33.0</td>
<td>-17.9</td>
</tr>
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<td></td>
<td>Complete-tree</td>
<td>No</td>
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<td>502.6</td>
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<td>-84.6</td>
<td>-16.8</td>
</tr>
<tr>
<td></td>
<td>Merchantable</td>
<td>No</td>
<td>50</td>
<td>178.4</td>
<td>155.7</td>
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</tr>
<tr>
<td>Oak-hickory (7 compartment)</td>
<td>Merchantable</td>
<td>No</td>
<td>90</td>
<td>187.9</td>
<td>191.3</td>
<td>+3.4</td>
<td>+1.8</td>
</tr>
<tr>
<td></td>
<td>Merchantable</td>
<td>Yes</td>
<td>90</td>
<td>187.9</td>
<td>172.8</td>
<td>-15.1</td>
<td>-8.0</td>
</tr>
<tr>
<td></td>
<td>Complete-tree</td>
<td>No</td>
<td>90</td>
<td>510.9</td>
<td>475.1</td>
<td>-35.8</td>
<td>-7.0</td>
</tr>
<tr>
<td></td>
<td>Merchantable</td>
<td>No</td>
<td>50</td>
<td>179.4</td>
<td>179.1</td>
<td>-0.3</td>
<td>-0.2</td>
</tr>
<tr>
<td>Loblolly Pine (7 compartment)</td>
<td>Merchantable</td>
<td>No</td>
<td>30</td>
<td>111.3</td>
<td>118.9</td>
<td>+7.6</td>
<td>+6.9</td>
</tr>
<tr>
<td></td>
<td>Merchantable</td>
<td>Yes</td>
<td>30</td>
<td>111.3</td>
<td>83.6</td>
<td>-27.7</td>
<td>-24.9</td>
</tr>
<tr>
<td></td>
<td>Complete-tree</td>
<td>Yes</td>
<td>30</td>
<td>322.1</td>
<td>227.0</td>
<td>-95.1</td>
<td>-29.5</td>
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<tr>
<td></td>
<td>Merchantable</td>
<td>No</td>
<td>16</td>
<td>101.2</td>
<td>99.4</td>
<td>-1.8</td>
<td>-1.8</td>
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<tr>
<td></td>
<td>Merchantable</td>
<td>No</td>
<td>30</td>
<td>164.4</td>
<td>165.4</td>
<td>+1.0</td>
<td>+0.6</td>
</tr>
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</table>
tree harvest simulations. However, because total yields were larger for complete-
tree harvests, percentage decreases in yield for the complete harvests (7 to 30%) were similar to those for simulations of merchantable harvests with residue re-
moval (8 to 25%).

Jorgensen et al. (1975) argued that merchantable bole harvests, whether of short or long rotation length, would have little effect on the nitrogen cycle in loblolly pine plantations, but suggested that more intensive utilization schemes might lead to decreased yield after several rotations. Similarly, Patric and Smith (1975) argued that conventional, merchantable timber harvests would not adversely affect sustainable yield in eastern hardwoods, but emphasized that any increased levels of timber utilization must be thoroughly evaluated before being applied on a widescale basis. Data in Table 4 tend to support findings and arguments of these authors. Merchantable harvests without residue removal led to increases, or to small decreases, in yield for both the lumped hardwood and the loblolly pine model. The expanded oak-hickory model showed a larger decrease in yield. This result suggests that effects of forest operations on nitrogen cycling may be underestimated if rapidly recycling pools of nitrogen in the soil are ignored. However, the predicted change in yield is still relatively small (10%). But simulations of complete-tree harvests and merchant-
able harvests with residue removal resulted in substantial decreases in yield in the third rotation, in the absence of any fertilization treatment.

Comparisons of changes in yield for the two oak-hickory models show that the expanded model predicted greater decreases in yield in all simulations than did the lumped model. Comparison of the lumped oak-hickory and pine models reveals that decreases in yield, in both absolute and percent terms, were much greater for the loblolly pine stand. We should emphasize that, based upon comparisons of the two hardwood models, if an expanded model were available for the loblolly pine forest it might predict greater decreases in yield than shown by the model used here (Fig. 4). Reasons why the merchantable, standard rotation length simulations predicted larger increases for the pine than for the oak-
hickory forest are unclear, but may relate to the lack of a denitrification estimate for the loblolly site.

An interesting result was observed for nitrogen in litter and soil pools in two loblolly pine simulations. In both the 16 yr rotation alternative, and the 30 yr simulated rotation with thinning at age 16, yield and soil nitrogen levels declined from the first to the second rotation. However, litter nitrogen was increasing as a result of logging residue. Nitrogen in litter had increased over 80% by the third rotation in the 16 yr rotation and over 14% in the simulated thinning alternative. As this material decayed it released nitrogen to the soil, so that by the third rotation in both simulations yield and soil nitrogen had begun to increase. Thus, data for later rotations for these two simulations might reveal yield increases greater than shown in Table 4.

In general, results in Table 4 agree well with the relative stability analyses (Table 2). These analyses showed that the expanded Coweeta model was more resilient but less resistant than the lumped hardwood model, and that the loblolly pine system was both less resistant and less resilient than the oak-
hickory system. Decreases in yield are essentially a measure of the degree of deviation in response to perturbation (in this case cutting), and they relate to resistance. Hence, data in Table 4 confirm predictions of the relative sta-
bility analyses, thus suggesting that this conceptual framework may prove useful in a management context.
Table 5. Change in yield in the third rotation compared with the first rotation, for various types and frequencies of cutting of loblolly pine and oak-hickory forest ecosystems. Each value represents the actual change in yield (Table 4), expressed as a percent of the total N removed from the system in the first two rotations (Table 3.)

<table>
<thead>
<tr>
<th>Ecosystem Model</th>
<th>Type of Cut</th>
<th>Residue Removal</th>
<th>Rotation Length (yrs)</th>
<th>Change in Yield (% of N removed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oak-hickory (15 compartment)</td>
<td>Merchantable</td>
<td>No</td>
<td>90</td>
<td>-5.3</td>
</tr>
<tr>
<td></td>
<td>Merchantable</td>
<td>Yes</td>
<td>90</td>
<td>-3.2</td>
</tr>
<tr>
<td></td>
<td>Complete-tree</td>
<td>No</td>
<td>90</td>
<td>-8.9</td>
</tr>
<tr>
<td></td>
<td>Merchantable</td>
<td>No</td>
<td>50</td>
<td>-6.6</td>
</tr>
<tr>
<td>Oak-hickory (7 compartment)</td>
<td>Merchantable</td>
<td>No</td>
<td>90</td>
<td>+0.9</td>
</tr>
<tr>
<td></td>
<td>Merchantable</td>
<td>Yes</td>
<td>90</td>
<td>+1.4</td>
</tr>
<tr>
<td></td>
<td>Complete-tree</td>
<td>No</td>
<td>90</td>
<td>-3.6</td>
</tr>
<tr>
<td></td>
<td>Merchantable</td>
<td>No</td>
<td>50</td>
<td>-0.1</td>
</tr>
<tr>
<td>Loblolly Pine (7 compartment)</td>
<td>Merchantable</td>
<td>No</td>
<td>30</td>
<td>+3.4</td>
</tr>
<tr>
<td></td>
<td>Merchantable</td>
<td>Yes</td>
<td>30</td>
<td>-3.9</td>
</tr>
<tr>
<td></td>
<td>Complete-tree</td>
<td>Yes</td>
<td>30</td>
<td>-12.6</td>
</tr>
<tr>
<td></td>
<td>Merchantable</td>
<td>No</td>
<td>16</td>
<td>-0.9</td>
</tr>
<tr>
<td></td>
<td>Merchantable (thinning at age 16)</td>
<td>No</td>
<td>30</td>
<td>+0.3</td>
</tr>
</tbody>
</table>
However, each model was not disturbed equally. Table 3 shows that different amounts of nitrogen were removed from each system, and that removal occurred at different yearly rates. Thus, to test fully the relative stability predictions, data in Table 4 must be normalized to both the degree and rate of disturbance. Table 5 presents data on changes in yield in the third rotation, normalized with respect to the total amount of nitrogen removed from the system in the two previous rotations. Each value represents the absolute change in yield (Table 4), expressed as a percent of the total nitrogen removed (Table 3). Values for the expanded oak-hickory model are more negative than for the lumped hardwood model. Similarly, in all but the merchantable harvest-no residue removal-standard rotation length case, values for the loblolly pine model are more negative than for the lumped Coweeta model. These results are in agreement with the relative stability predictions, and show that for a given amount of nitrogen removed from the ecosystem, the expanded hardwood model predicts larger decreases in yield than the lumped model, and that the loblolly pine forest will be more strongly affected than the hardwood stand. The data in Table 4 could also be normalized to the annual rate of nitrogen removal, and would reveal similar comparisons to those shown in Table 5. These results substantiate predictions based on the relative stability analyses and provide further evidence of the relevance of this approach to evaluating management alternatives.

SUMMARY

We do not wish to overemphasize the exact quantitative results obtained in this analysis of potential effects of several forestry practices on loblolly pine and oak-hickory forest ecosystems in the southeastern U.S. The models used to simulate nitrogen cycling are incomplete, largely because knowledge of nitrogen cycling processes is incomplete. Moreover, results are dependent on specific data sets for the sites used as examples. However, we do have confidence in the qualitative and comparative aspects of the results, and feel that several points are worth emphasizing.

First, the relevance of the conceptual model of ecosystem relative stability to practical considerations of resource management seems to be firmly established. This approach provides an operational framework which is consistent with theoretical treatments of ecosystem behavior. The method also identifies information needed to assess effects of management alternatives on the cycling of essential elemental resources within forest ecosystems. Results of the stability analyses correctly predicted the relative effects of forest cutting on the different models considered. Also, elemental cycling indices (Table 1) were strongly related to the measures of relative stability. These structural indices can be derived from data routinely collected in studies of forest elemental cycles. They may someday prove to be useful indices for resource managers. Although experience in their use and interpretation is currently insufficient, it may be possible in the future to construct scales from these indices which are useful in predicting ecosystem responses to alternative management practices. Further research in this area is desirable.

Second, this study demonstrates the importance of system conceptualization to subsequent system analyses. The two nitrogen models for the Coweeta oak-hickory forest predicted different levels of resistance and resilience and different responses to disturbance. Yet both models were derived from the same data, but were conceptualized at different levels of resolution. Although forests contain large storage pools of nitrogen in several compartments, a rapidly recycling portion of the cycle exists in the soil which may in part control or regulate the entire cycle. Plants take up nitrogen from these soil mineral pools which turn over rapidly, rather than from large pools of soil organic nitrogen which turn over slowly. Disturbances which affect these
available forms of nitrogen and rates of uptake from them may adversely affect forest productivity, even though substantial amounts of nitrogen remain in soil organic matter. Additionally, elemental cycles are dynamic in time, although most previous analyses of forest management effects on sustainable yield have been based on static considerations (e.g., Boyle et al., 1973; White, 1974; Jorgensen et al., 1975; Patric and Smith, 1975; Wells et al., 1975). Intensive utilization of timber resources may affect the dynamics of nitrogen transfers in ways not accounted for by such static analyses. Thus, analyses of forestry effects on elemental cycling must include examination of effects on forms of nitrogen directly available for uptake, and must be based upon the dynamics as well as the statics of elemental cycles.

Third, results indicate that site yield may be slightly increased, unchanged, or substantially decreased after several rotations depending upon the degree of tree utilization. We should emphasize that these results are dependent upon specific data sets for the sites used as examples, and that the nitrogen status is relatively high for both loblolly and oak-hickory sites. Decreases in yield could be much greater on other sites where nitrogen pools are smaller. A typical management response might be to recommend fertilization to correct such changes in yield. However, fertilization may not be an economically viable alternative in all cases (Jorgensen et al., 1975). One factor not accounted for by our models is "normal" repair processes operative during ecosystem succession which act rapidly to return the system to previous levels of function. Successional woody species typically have high rates of productivity and nutrient uptake, and they may stimulate nitrogen fixation. Marks (1974) demonstrated the important successional role of pin cherry in the recovery of northeastern forests from disturbance. Black locust probably has a similar role in southeastern hardwood forests, and may especially stimulate nitrogen fixation (Ike and Stone, 1958). Many analogous species could be cited for other forested regions of the United States. But in many cases these successional species are regarded as undesirable in forest management, and practices are employed to suppress or eliminate such successional vegetation. More information is needed on natural repair processes and their role in nutrient cycling. Forest management should foster rather than suppress these natural mechanisms by which ecosystems recover from disturbance.

Finally, it is clear that points raised in this paper must be given more attention than they have been previously. Although these analyses will benefit from improved understanding of forest elemental cycles, the approach presented here can be used by forest managers to consider alternative management strategies and trade-offs involved in such decisions. Ecological as well as economic and technological information must be evaluated before increased utilization of timber resources becomes an established management practice. Especially critical are effects of such practices on elemental cycling and sustainable yield. If our results are indicative of changes in wood fiber yields in southeastern forests under intensive tree utilization, then current estimates of substantial future increases in wood fiber harvests from southeastern pine and hardwood forests must be revised. The decreases in yield suggested by our analyses may be offset by successional recovery mechanisms and in some instances by fertilization. But the net picture for sustainable yield under intensive management is unclear, and demands further analysis.

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