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OVERVIEW OF NUTRIENT CYCLING RESEARCH AT COWEETA HYDROLOGIC LABORATORY

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Abstract--A research program at the Coweeta Hydrologic Laboratory, North Carolina, is investigating effects of perturbation or manipulations on nutrient cycling and productivity of forested watersheds. The experimental approach is to explain whole ecosystem behavior, as revealed by watershed nutrient and water budgets, by reference to internal ecosystem processes. Research is designed to examine the emergence of higher level ecosystem properties from lower level component processes. This report describes the general scope of the research at process levels, and relates dynamics of internal processes to ecosystem level response. The research is organized around a general theory of ecosystem relative stability, based on the complementary aspects of resistance to disturbance and resilience following disturbance. The research is a cooperative effort between the U.S. Forest Service and the University of Georgia.

Research on nutrient cycling at Coweeta has centered around the use of small watersheds as basic ecological units. Bormann & Likens (1967) drew ecologists attention to advantages of the small watershed approach. Studies of nutrient cycling at Coweeta were initiated in 1968. We are using the small watershed approach as a means of elucidating basic ecosystem phenomena, and as a sensitive indicator of long-term consequences of land management practices (Johnson & Swank, 1973; Swank & Douglass, 1975). The research has been a cooperative effort between The University of Georgia and the U.S. Forest Service with major aspects funded by the National Science Foundation. Significant funding was provided through the Eastern Deciduous Forest Biome of the U.S. IBP.

The purpose of this overview is to describe the scope of nutrient cycling research at Coweeta and the underlying guiding philosophy. Current research is a blend of objectives concerned with ecosystem theory and of practical aspects of forest management. The training objectives of university research have played a significant role in our studies as well. Graduate and postdoctoral students have made and are making significant contributions to research at Coweeta. The mix of personnel has been diverse and has changed during the years. We feel that one of our major strengths has been the variety of scientific disciplines involved with various aspects of the work. Orientation of diverse specialities around a common set of objectives has been a necessary requisite for this work.

DEVELOPMENT OF RESEARCH OBJECTIVES

Nutrient cycling research at Coweeta initially was built upon several unique advantages afforded by that site: (1) a 35-year background of hydrologic and climatological monitoring; (2) a well-documented history of experimental watersheds; and (3) data on a variety of watershed manipulations and basic hydrologic processes, which provide a base for interpreting studies of nutrient transfers. Further, the Coweeta watersheds of various sizes and elevations afford the opportunity to assess scalar and elevation dependence of research results. A summary of the Coweeta watersheds, treatments, vegetation types, and sizes is given elsewhere in this workshop (Swank & Douglass).

Initially, the research at Coweeta concentrated on cation input-output budgets with basic objectives of characterizing cation losses from manipulated watersheds (Johnson & Swank, 1973). Beginning in 1968, four watersheds were selected for intensive study: a grass-to-forest successional watershed (WS 6), a seven-year-old coppice watershed (WS 13), a thirteen-year-old white pine watershed (WS 17), and a mature hardwood forest watershed (WS 18). Simultaneously with input-output budgets, various internal processes were measured, including aspects of primary production, consumption, and decomposition. Research projects emphasized basic ecosystem processes on the hardwood watershed (WS 18), and attempted to assess how they had been altered by comparision with manipulated watersheds. Nutrient budgets provided a means for evaluating holistic ecosystem responses to management practices. Studies at the process level attempted to relate internal nutrient dynamics to observed changes in input-output budgets. Budgetary analyses were also made on a variety of other watersheds in the Coweeta basin (Swank & Douglass, 1975).

This research provided essential information on nutrient cycles in Southern Applachian watersheds. We established basic patterns of nutrient circulation, evaluated effects of applied management schemes, and suggested possible mechanisms of biotic regulation of nutrient output (Waide & Swank, 1974). Also, these results suggested that, following manipulations, nutrient cycles recover rapidly at the ecosystem level to nominal unperturbed levels. The treatments of three of the watersheds were not observed to have produced major alterations in input-output dynamics at the time the studies were conducted. Background data collected during this research have been summarized in several recent publications (see Howell, et al. 1975). A major synthesis covering this data base is now in preparation, as a part of the concluding efforts of the EDFB-IBP.

Current research has shifted in emphasis, from essentially descriptive or exploratory research on previously treated watersheds, to implementation and intensive study of two ecosystem perturbations. The perturbations are being utilized as a means of evaluating specific hypotheses concerning ecosystem behavior and a general theory of relative stability (Webster, et al. 1975). The two perturbations include a clear-cut by cable logging as a major, acute, man-induced alteration of ecosystem behavior, and a aturally occuring defoliation by the fall cankerworm, which is being examined s a low-level, chronic disruption. Results of these experiments are intended o provide a partial test of our underlying theory of ecosystem stability. ata are being interpreted in terms of ecosystem response to these two classes f perturbation and in each instance we are testing specific hypotheses bout the nature of the responses. These hypotheses have been proposed at everal hierarchial levels, allowing for generalization at population, com- unity, and process levels.

Results of our research have had and will continue to have implications or forest management practices. Cooper (1969) argued, as have others, that he only level of ecological theory that will provide the necessary guidelines or proper resource management is the ecosystem level. Yet, he noted that the cological basis on which most current management practices are based remains enerally a collection of facts about isolated populations, not a "set of redictive statments about integrated systems." Evaluation of management ractices in the context of basic ecosystem research is one of the major enefits from the continuing interaction of Forest Service and university ersonnel in these studies.

There are at least two major questions concerning the management of atersheds for timber resources. First, what are the consequences of specific anagement practices? Nutrient cycling studies on manipulated watersheds are roviding important answers to this question (Bormann, et al., 1967, 1974; ohnson & Swank, 1973). Second, what are the effects of current levels of imber utilization on sustainable productivity? Removal of vegetation, on a ong-term rotation, is a neglible loss of nutrients from the watershed in elation to soil nutrient pools. But, what is the long-term effect on nutrient vailabliity and nutrient pools? Current experiments and associated modeling tudies are providing at least partial answers (Waide & Swank, 1975).

THEORETICAL BASIS AND ORGANIZATION OF RESEARCH

ierarchial organization of watershed ecosystems

The overall approach to this research is to explain ecosystem-level behavior, as revealed by net element and water budgets, by focusing on internal element cycling processes. Underlying this approach is a general concept of an ecosystem as a hierarchial system. Research is designed to examine how higher-level ecosystem properites emerge from lower level component processes. Also, the approach is designed to evaluate a general theory of ecosystem relative stability, based on two complementary aspects of stability: resistance to disturbance as a function of system mass, and resilience following disruption as indicative of ecosystem metabolism. This relative stability approach allows for the analysis of ecosystem response to specific perturbations, as well as the ecosystem-level balance between mass and turnover rates as an evolutionary response to a given set of environmental variables.

It is a basic tenet of the theory of hierarchially organized systems that system behaviors are "nearly decomposable" as regards their frequencies of operation (Simon, 1973). That is, given the range of behaviors or responses which may be defined or identified for any system, it is possible to arrange these behaviors according to the frequencies with which they occur. Behaviors characteristic of higher organizational levels generally occur with lower frequencies (i.e., have long time constants). Conversely, lower organizational levels within the system typically exhibit higher-frequency behaviors (i.e., have short time constants). Responses at intermediate levels of organization have intermediate frequencies. In ecological studies, systems are usually conceptualized so that attention is focused at a single organizational level. Behaviors attributable to higher levels occur very slowly relative to the level of focus, and thus appear as constants in the system description. Lower-level behaviors occur so rapidly that only their steady state properties appear in the system description. This suggests that a given system conceptualization can effectively "seal off" higher and lower levels of behavior, concentrating on one specific level.

The relationship of organizational levels and frequencies of behavior to the watershed-level research at Coweeta is conceptualized in Figure 1. Ecosystems may be studied at a variety of levels, with relative behaviors arranged from processes with very long time constants (climatic shifts, geomorphic processes) to those with relatively short time constants (diurnal cycles, cell turnover). Our major focus on watershed-level research is at intermediate

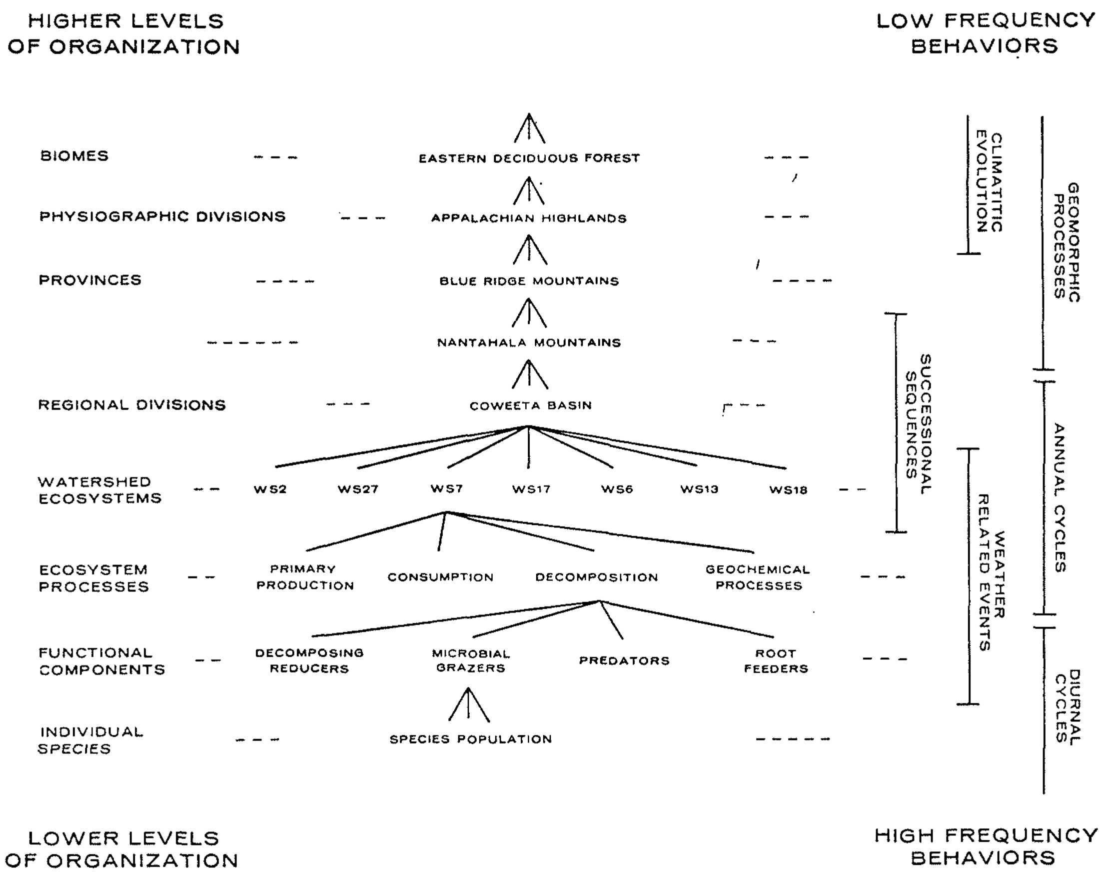

Figure 1. Organizational and temporal levels of resolution in ecosystem research.

frequencies, ranging from processes which occur somewhat more often than seasonally (e.g. weather related events), to those at the frequency of successional sequences. In Figure 1, the hierarchial levels being emphasized are shown expanded. At the highest level we are concerned with input-output relationships of individual watershed ecosystems. The lowest level of focus is identified as "functional components", which represent groupings of individual species populations having a similar functional role in ecosystem elemental cycles.

Above the level of functionalcomponents, we view the next higher level of ecological organization as being composed of the four integrative ecosystem processes of primary production, consumption, decomposition, and geochemical phenomena (short term weathering and erosional events). Because of the smoothing of behaviors which has occurred at the functional component level, process behaviors are more regular. At this process level, the various functional components which together comprise a given ecosystem process, interact to accomplish resource transfer and storage.

Research at Coweeta has been concerned with the definition of functional components in forest nutrient cycles and on identification and measurement of relationships between the functional components. In all cases our objective is the explanation of behaviors observable at the process and ecosystem level. The research is examining the manner in which lower level processes are intergrated or smoothed to produce the emergent behaviors at the ecosystem level.

Stability of watershed ecosystems

Ecosystem-level units such as watersheds have long been presumed to be stable, at least in some sense. Ecologists have sought relationships between ecosystem stability and diversity of organisms. It is now fairly well accepted that no compelling evidence, mathematical or ecological, exits to support the specific hypothesis that diversity itself fosters stability (May, 1973; Goodman, 1974). Recent papers have suggested that it is environmental characteristics, especially the availability of nutrient resources which regulates ecosystem stability (Pomeroy, 1975; Webster *et al.*, 1975). In any case we assume that watershed-level ecosystems are stable, and prefer to ocus our research not on stability per se, but rather on relative stability.

Relative stability concerns system response to disturbance, and dis-)lacement from nominal, steady state levels of function. Two aspects of :his response may be identified (Patten & Witcamp, 1967; Child & Shugart, 972; Holling, 1973; Marks, 1974; Waide et al., 1974; Webster et al., 1975). he first concerns the resistance of an ecosystem to displacement. An ecosystem that is easily displaced from steady state functions has low esistance, whereas one that is difficult to displace is highly resistant and is, in this sense, very stable. The second aspect of relative stability con-:erns return to the reference steady state, or resilience. An ecosystem that eturns to its original condition rapidly is more resilient, more stable in :his sense, than one that responds slowly.

In this view of ecosystems two alternatives are thus identified for ecosystem persistence in the face of environmental variation. Persistence to lisplacement results from the elaboration and maintenance of massive ecosystem structure, an obvious characteristic of forested watersheds. Resilience ollowing displacement is related to ecosystem metabolism, and therefore re-lects both inherent tendencies for the dissipation and re-formation of ecosystem structure. In the closed biogeochemical cycles of the biospheres, :he structural and functional characteristics of ecosystems are determined by ealized balances between factors favoring resistence and resilience. lutrient cycling thus becomes a central issue in the consideration of nechanisms of ecosystem relative stability.

The measurement of the various parameters of nutrient cycling, within :he context of a general theory of ecosystem relative stability, forms the ramework for the experimental approaches now being pursued at Coweeta. The major propositions are two: (1) Compared with other regions, ecosystem nutrient cycles in the southern Applachians are highly resistant to dis-:urbance. Effects of ecosystem perturbation should be less pronounced than eported for several other sites. (2) Compared with other regions, nutrient cycles in the southern Applachians are similarly highly resilient, and should recover rapidly from perturbation as a result of successional events which re-establish nutrient conservation.

RESEARCH AT FUNCTIONAL COMPONENT AND PROCESS LEVELS

Data collection at Coweeta is organized around several major areas of research, at process or functional component levels. Within each area various types of research are underway. Most are related to nutrient cycling, and all are organized so as to allow cross-comparisons of results. Space limitations do not allow for descriptions of the research at these levels. Table 1 provides a list of references to publications describing work at process or functional component levels at Coweeta.

Table 1. Publications Describing Process or Functional Component Research at Coweeta.

Process or functional component	References
Stream Chemistry, Input-output Budgets	Swank & Douglass, this Workshop
Water and Nutrient Transport Studies	Best & Monk 1975, Johnson & Swank 1973
Vegetation Analysis	Day & Monk 1974, Spring 1973, Iglich 1973
Litterfall Analysis	Cromack & Monk 1975
Canopy Insect Studies	Crossley *et al*. 1975
Forest Floor Processes	Waide *et al*. 1975; McGinty 1976, Todd *et al*. 1973, 1975; Cornaby and Waide 1973
Forest Floor Arthropods	Gist and Crossley 1975, Cornaby *et al*. 1975
Stream Processes	Webster, this Workshop; Wallace *et al*. 1976

INTEGRATION OF PROCESS LEVEL RESEARCH

The research efforts at process and functional component levels can be ntegrated in several ways. The research is concurrent in time and space, aking comparisons of response at different levels realistic. The hier-rchial view of organization allows for the explanation of the emergent roperties at a given level in terms of the interactions of its component rocesses. The two major components of relative stability, resistance and esilience, are applicable as responses to perturbation at process levels as ell as at ecosystem levels, which provides a further means of interpreting cosystem response in terms of process level response.

At Coweeta we have depended upon modeling studies as an integrative rocess. Modeling and systems analysis have played a major role in our ast research at Coweeta, and we anticipate that they will continue to do so n future studies. Modeling has largely provided a means of synthesizing and rganizing our data on a variety of nutrient cycling processes in a compatable nd comparable framework. Such modeling has helped with the definition of unctional components in forest elemental cycles, and with the identification nd quantification of pathways of elemental transfer among components. Most f our past studies have concerned previously perturbed or unperturbed atersheds, and essentially were based on assumptions about the steady state ature of elemental cycles of those ecosystems. We are now initiating studies f watersheds currently being perturbed, either by our own efforts or atural perturbations. As we continue to improve our understanding of cosystem regulation, we will revise our models of forest elemental cycling o incorporate new information. We expect that our models will continue to epresent evolving hypotheses about the functional regulation of nutrient ynamics in southern Appalachian ecosystems.

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DISCUSSION

ıbrose: Could you take nitrate or orthophosphate and tell us what patterns you've ın as the water goes from rainwater through the litter into the ground and into the eam and do these patterns vary seasonally?

ınk: The data that we have concerning change in nutrient concentration as it comes as rainfall and passes these various monitoring stations has been restricted mostly to .cium, magnesium, potassium and sodium.

dd: As far as the nitrate values, yes, they vary quite a bit as far as vegetation and o season. The highest rates of nitrate are obviously in the wintertime when the nts are not as actively taking up the ammonia as they are so we get a higher rate of rification and a loss of nitrate from the than we do in the summertime.

nk: If you take potassium concentration in rainwater as one, you pass that water ough the canopy and catch it before it hits the litter and it goes to about 7. Pass it ough the litter and it goes to 8 or 8½, pass it though 25 cm. of soil it goes to 4 and it ꞉s out of the stream at about 4. The amount of water passing each of these nitoring points varies markedly. Calcium that's in rainwater as 1, pass it through the ıopy it goes to 3; pass it through the litter it goes to 5 or 6. There is a greater bilization of calcium out of the litter while potassium has a greater mobilization ꞉e it is leached out of the canopy. Magnesium is more like calcium than it is like assium. Sodium bounces around. There is a great deal of difference in the ıcentration of each of these elements depending on where you monitor movement of ꞉er through the system.

brose: What is the temperature of the water seasonally? What is a good range? In winter would it be low enough to inhibit life?

ɔster: Four to nineteen degrees C, 73/74 for stream water.