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30. Past and Future of Ecosystem Research—Contribution of Dedicated Experimental Sites

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Most fields of science seem to profit disproportionately from the central role of one or a few outstanding institutions. This symposium recognizes one such institution, the Coweeta Hydrologic Laboratory. For 50 years, the laboratory has generated scientific information about the forested landscapes of the southern Appalachian Mountains and, particularly, about the relationship between land treatment and the water resource. Its contributions to applied sciences, such as forestry, have been inestimable. Of special relevance to this keynote address is Coweeta's leadership in the development of the young field of ecosystem science.

In many senses, Coweeta Hydrologic Laboratory is the mentor for numerous other ecosystem research sites and programs. Many have benefited from the concepts, materials, and data developed at, and from personnel based or trained at Coweeta. Dr. F. Herbert Bormann (personal communication) relates how the watershed research program at Coweeta inspired the program initiated at Hubbard Brook. As a student at Duke University and then as a young assistant professor at Emory University, Bormann became impressed with the whole ecosystem approach to research at Coweeta. Later, struggling with approaches to biogeochemical research as a professor at Dartmouth, Bormann recalled that, "years of experience with Coweeta quickly made it apparent that small watersheds with monitored hydrologic input and output could be used as vehicles to study whole system biogeochemistry." Subsequently, the Hubbard Brook ecosystem study was born. When watershed research was initiated at newly established H. J. Andrews Experimental Forest in Oregon, many methods and concepts were adopted from Coweeta. I used a Southeastern Forest Experiment Station paper from

Coweeta in analyzing Andrews stream hydrographs during my first summer with the Forest Service.

In this chapter I will make some personal observations on ecological research during the last 15 years, with particular reference to the role that has been played by Coweeta and similar sites. I will consider accomplishments in ecosystem research, factors that have contributed to these accomplishments, and implications for future progress in ecological research. These are, of course, my personal views, with all of the implied biases and experiences.

Accomplishments in Ecosystem Science

Recent years have seen astonishing progress in our understanding of ecosystems and how they function. There have been numerous discoveries, many of them that were clearly surprises. In the following sections I review some of my favorite examples.

The magnitude and dynamics of belowground processes in forest ecosystems has been documented. A rule of thumb assigned approximately 20% of the live forest biomass to belowground. Not appreciated were the turnover rates in fine roots and mycorrhizae, nor the fact that highly disproportionate amounts of photosynthate, typically around 50%, must be directed to maintenance of these intensely dynamic belowground tissues. Further research is showing that the belowground energy requirements are highly variable (from perhaps 10 to 70% of the photosynthate) and that this variation is related to site conditions. In more favorable environments, such as highly fertile sites, the proportion devoted to belowground maintenance is less. The implications of this emerging body of information for development and interpretation of silvicultural practices, such as fertilization, is only now beginning to be developed.

The importance of interactions between forest canopies and the atmosphere has emerged. Many such interactions have, of course, been appreciated for some time; for example, the role of the canopy in interception and transpiration processes (Chapter 9, this volume). Fog drip and cloud moisture have been viewed as significant in some local ecosystems. But, the complexity and extent of these condensing/precipitating surfaces was not fully appreciated; good measures of the surface areas did not even exist. A report by Swank and Helvey (1970; see also Chapter 22, this volume) was one of the first watershed scale experiments illustrating the dynamic relationship between the quantity of forest foliar surface, evapotranspiration, and streamflow. We know that there may be an incredible 400,000 m^2/ha of foliar surface in coniferous forests of the Pacific Northwest, and that the canopy can dramatically increase water yields where fog is common (Harr 1982). It is only recently that we have begun to understand the importance of plant canopies in cycles of several elements and as a site for deposition of pollutants. It is certainly no accident that much of the forest decline that we are seeing is in cloud forest zones (see, e.g., Lovett, Reiners and Olson 1982). The topic of canopy-atmosphere interactions is one that we have only begun to understand.

Ecosystem research has enumerated the numerous and complex interactions between forests and streams as illustrated throughout this volume. Vegetative influences on stream chemistry, light, and temperature regimes have been quantified and incorporated into predictive models. We now recognize the importance of riparian vegetation to aquatic organisms in providing energy resources diverse in quality and quantity (Chapter 19) as well as in their delivery in time and space. Our view of woody debris in aquatic ecosystems has reversed from a negative to a positive influence. The importance of wood in creating habitat diversity, contributing to spatial stability, and providing retentiveness are all recent (or, at least, rediscovered) concepts (Chapter 21).

Some of the ecological roles of coarse woody debris, standing dead trees, and down boles have been identified and quantified in terrestrial environments. The extent and importance of these structures simply was not appreciated by most ecologists. This was even true in the Pacific Northwest, where 150 Mt/ha of coarse woody debris is common in forests and where > 500 Mt/ha may occur in an intact stand. If you doubt the degree to which these structures were unappreciated, the International Biological Programme's (IBP) woodlands synthesis volume did not even have a data set category for down dead wood on the forest floor (Reichle 1981). Today we recognize the fact that wood structures are as important dead as alive—important to animals as food and habitat, to geomorphic processes, in carbon and nutrient cycles, and as sites for nitrogen fixation (Harmon et al. 1985).

Advances in our appreciation of the nitrogen dynamics in forest ecosystems have been substantial, particularly of the scale and sources of nitrogen additions. Early forest soil textbooks had little to say about nitrogen additions other than a general suggestion that lightning and freeliving blue green algae were probably primary sources. The role of woody leguminous and nonleguminous plants with nitrogen-fixing microbial associates has been identified during the last two decades. Many of these plants, such as *Alnus*, *Ceanothus*, and *Purshia* in the west and *Robinia* in the east (Chapter 12), appear to have critical roles in maintaining productivity of temperate forest sites because of the high levels of nitrogen fixation. Especially impressive has been the discovery of the numerous routes for nitrogen accretion—fixation in forest canopy lichens, in rotting wood, in decaying leaf litter, and in the root rhizosphere. No doubt many additional pathways of nitrogen additions and losses remain to be identified and quantified.

The ecological importance of nongrowing season photosynthesis has been recognized. This has particular importance in the forests of the Pacific Northwest, where over 50% of the net photosynthesis can occur outside of the growing season and partially explains the prodigious growth rates possible during the cool, short summers. This phenomenon is very important on a variety of habitats, including the extremely productive coastal *Picea sitchensis* and *Sequoia sempervirens* regions and sites, which suffer significant summer drought. Nongrowing season photosynthesis is obviously an important factor in the superiority of evergreen conifers over deciduous hardwoods in the western environments (Waring and Franklin 1979).

The importance of vegetative regrowth in preventing nutrient losses following catastrophic disturbances has been discovered. The Hubbard Brook experiment provided the most graphical demonstration of this phenomenon (Likens et al. 1978), which has been explored and quantified in a variety of other environments including Coweeta (Boring et al., Chapter 12). Indeed, several theoretical constructs have been developed around this phenomenon (Bormann and Likens 1979).

There have been many other ecological discoveries that are illustrated by papers in this symposium. There is the tight linkage between hydrologic and nutrient cycles

(Chapter 4). There have been discoveries about the paths and rates of sediment processing in stream ecosystems including the recognition of the long-lasting effects of delivering such materials to streams (Chapter 21). The denitrification process is emerging as important in some ecosystems. Differences in water usage between hardwoods and conifers have been quantified with results that are surprising in the magnitude of the differences (Chapter 22). The eastern white pine-hardwood comparison has been repeated in the Rocky Mountains with similar results; although responsible processes differ, quaking aspen has less impact on water yield than either Engelmann spruce-subalpine fir or lodgepole pine forests. Unsaturated soil water movement has been shown to be important in maintaining stream flow (Chapter 8). The fact and importance of biological regulation of the sulphur cycle has been demonstrated for forest soils (Swank et al. 1984; Chapter 18). The role of insect populations in regulating nutrient cycles has been demonstrated at an ecosystem scale (Swank et al. 1981).

The list of important discoveries is long and would dramatically expand if we moved beyond considerations of temperate forests to grasslands, deserts, tropical forests, taiga, and tundra. We have progressed in our understanding of ecosystems. This knowledge is having a major impact upon our ability to predict system responses and modifying the way that forest ecosystems are being managed. And, we have had numerous surprises along the way, which has several implications for the science. While surprises have made the research fun, they are also reminders of the need to expand our scientific frameworks, to deal with problems of faulty logic and inadequate observations, and to appreciate the importance of research at discipline boundaries.

Factors Contributing to Advances in Ecosystem Research

What are some factors contributing to these discoveries? Doubtless each of us would have our own list of favorites. Here are some of the factors from mine.

The existence of long-term data bases has contributed significantly to ecosystem research. For example, the data on baseline stream chemistry at Coweeta made it possible for an alert research team to discover the effects of the fall cankerworm defoliation on nitrogen losses from a watershed (Swank et al. 1981). Other long-term stream records indicate that southern Appalachian forests may be in the early stages of acidification (Swank and Waide, Chapter 4). Similarly, the long-term watershed records confirmed and quantified the reduced water yields that followed conversion of hardwood to white pine forest. Note the serendipitous nature of the first two examples and the unexpected magnitude of the third.

All of the discoveries mentioned in the preceding section came from research programs with a holistic point of view—a whole ecosystem perspective—and most were generated by interdisciplinary research teams. Pioneering programs such as Hubbard Brook made a significant contribution, not just of scientific findings, but in helping to make ecosystem science a respectable undertaking. New concepts and methods were contributed by creative scientists, such as Eugene Odum with his textbooks and stimulating treatises; especially "Strategies of Ecosystem Development" (Odum 1969).

The International Biological Programme (IBP) made a special contribution to the advances of the last 15 years. The Biome projects were grandiose in concept and unrealistic in some of their goals, but they were holistic. These projects cracked many black boxes and forced many groups to at least attempt to address whole ecosystems. IBP created a new appreciation of the importance of decomposition processes and organisms. Belowground processes, land and water interactions, and coarse woody debris have surfaced as major topics because of Biome programs. What young assistant professor, on his or her own, would have selected the labor-intensive, methodologically difficult area of root production and turnover to build a career? What National Science Foundation panel would have funded such work? There had to be the impetus and support of a large, holistic research effort to stimulate such topical areas. The IBP set the stage for subsequent generations of more tightly structured ecosystem proposals, experimental and hypothesis-based efforts, which exploit and generate fertile topics.

Few advances in ecosystem research have been the products of isolated scientists or results of laboratory studies. Almost none are the consequence of null hypotheses or outgrowths of ecological theory.

Musings on Ecological Theory

I would like to diverge momentarily with some of my thoughts on ecological theory. Let me say at the outset that I do believe that the development of theoretical constructs has been important in the progress of ecology. They have helped ecologists to move from a pedantic and dominantly descriptive science to one with greater rigor and structure; as Paul Risser (personal communication) has commented, at least the theories have prompted ecologists to reconcile their observations with those made elsewhere.

My criticisms concern primarily the relatively narrow body of work increasingly (and unfortunately) referred to as "community ecology": the world of broken-stick models, r- and k-selection, Lotka-Volterra equations, and competition as the structuring angel of all communities (or not, depending on your point of view). For many years I was in awe of these theoreticians, who so effectively dominated what has been known as ecological theory. Although much of the theory seemed nonsensical and failed when I attempted to apply it to communities of plants or to ecosystems, I assumed the fault lay with my perception of the real world and not with the theory.

In fact this body of ecological constructs has proved of marginal value, a fact increasingly acknowledged by theoreticians themselves. I attended a conference on application of ecological theory to societal problems several years ago, at which an eminent theoretical ecologist acknowledged a reliance on ecological knowledge of organisms and communities, and not on theory, when giving advice on solutions for real world problems. Much current ecological theory addresses special cases and lacks broader application. Other ecological theory addresses biological phenomena which are interesting, but of limited consequence in the behavior of ecological systems. I think that we may be doing our students and ecological science a disservice with an excessive emphasis on such theory.

Indeed, we may have done a disservice to our science with several other of our recent emphases. Use of the null hypothesis in ecology can be useful; it has, for example, encouraged rigor in the design and exposition of research. But, an exclusive reliance on this approach conditions one to think in terms of absolutes instead of probabilities or proportional contributions of several processor factors. The disparagement of natural history research, which is the ultimate source material in ecology, has been unfortunate. Mediocrity is not a necessary condition of natural history research, nor brilliance uniformly represented in theoretical efforts. Species do make a difference, particularly where they fill a unique structural or functional role within an ecosystem. Consider the character of Sierran mixed conifer forest with and without giant sequoia, as one example.

I wish that we would teach ecological students to think more broadly. We have often created a view of the natural world that is strongly deterministic, filled with the best adapted and highly coevolved organisms. We provide a world that is almost devoid of surprises. I view the world as having a lot of randomness, one in which there are many successful strategies, many unfilled niches and, perhaps, organisms more capable of utilizing resources than those currently present. Anyone doubting the last point should review the status of cheatgrass in the shrub-steppe of the Pacific Northwest or the aggressiveness of lodgepole pine above the original timberline in New Zealand.

In my view, the most useful ecological paradigms will have to accommodate the great diversity inherent in the world's ecosystems. Key processes and controlling factors will vary across ecosystems, and this must be recognized in our paradigms. MacMahon (1981) illustrates one approach in his contrasts of successional processes in different biomes, from desert to rainforest. Processes of denudation, migration, establishment, competition, and site modification differ in patterns, rates, and intensity in each biome.

Tree mortality in mature forests of the Pacific Northwest provides a regional example of how dominant processes vary on a probabilistic basis. In coastal Sitka spruce-western hemlock forests, wind accounts for about 80% of the mortality. In the Douglas fir-western hemlock forests of the Cascade Range, wind accounts for 35 to 50% of the mortality. In further contrast, only 15 to 20% of the mortality is attributable to wind in interior ponderosa pine forests. Mortality due to insects and disease has a reverse relationship.

Almost any successional scenario seems possible depending upon the physical setting and the organisms. Productivity and system complexity can decline with time, as when muskeg succeeds forests in boreal regions. Disturbances can accelerate succession as well as retard it, as illustrated by the effects of catastrophic wind in eliminating overstories of a shade-intolerant species, such as Douglas fir, and releasing understories of shade-tolerant species, such as western hemlock and Pacific silver fir. Species diversity may peak early in a sere, or late, or at some intermediate point.

Some of the existing ecological models provide another approach to ecological paradigms. Models such as JABOWA and FORET allow us to use our knowledge of species ecology and of environment to generate probabilistic outputs. They allow us to synthesize our natural history information into a usable form. Note that such models can integrate the fields of physiological ecology, population biology, and ecosystem science.

We need to get on with the process of developing more robust ecological theory. I suspect that some of the greater advances will come from collaborations between various subdisciplines in ecology, such as the ecosystem and population scientists. I doubt that much usable ecological theory will consist of simple mathematical formulae. Ecological science is not physics, and it is time to stop trying to fit it into that mold. Ecological theory must incorporate the realities and unpredictability of the natural world.

Future Directions in Ecosystem Research

What about future directions in ecosystem research? We need to continue to encourage development of tightly structured hypotheses and definitive experiments, particularly as we look in detail at subsystems and processes. We see such trends in the proposals submitted to the National Science Foundation, such as in increased numbers of exciting proposals dealing with soil chemistry as it affects nutrient cycling, productivity, and ecosystem response to pollutants.

We need to continue to adapt new technologies that allow us to do new things or old things better. Opportunities are being created at both the micro- and macro-levels, as illustrated by the use of optical fibers to study root growth, and remote sensing to study productivity at the global level. It is also important that we continue to incorporate other disciplines, with their fresh perspectives and exotic technologies, into ecosystem research programs.

We need to move up in our scale of study, both temporally and spatially. Heterogeneity and spatial patterns at all scales up to the landscape are an exciting topic. Larger spatial and temporal scales are presently very critical issues in terms of the relevance of ecological research to societal problems, as illustrated by concerns over cumulative effects and long-term site productivity. Some of this probably involves scaling up some of the modeling efforts and incorporating spatial patterns; juxtaposition of pieces of an ecosystem or landscape can be critical to outcomes. Much of our science has not effectively made the jump from stands or small watersheds to drainage basins. Are there thresholds at which point a landscape or a stream drainage may unravel?

Despite my harsh words about the past contributions of ecological theory, I believe that we do need to work hard at organizing our knowledge as general principles or theory as it is more broadly interpreted. This theoretical framework would include use of model structures and syntheses of major systems and processes. To be successful, a much broader and more broadly experienced ecological community will need to take an active part in formulation of ecological theory than seems to have been the case.

I am sure that we will do all of these things. They are logical, they are in our self interest, and they fit traditional biases or current trends. But, there are some other emphases that I view as equally critical and that I fear may lack sufficient attention or support.

Intensive, whole ecosystem studies must continue. Many types of ecosystems, particularly in tropical regions, still lack detailed examinations. Additional processes and compartments will be recognized as the result of such efforts. As I recall how long it took us to "see" coarse woody debris, I have no doubt that many fundamental structural and functional features of ecosystems remain to be identified; we have not even recognized all of the basic physical and chemical processes operating in these systems. The selection of additional sites for comprehensive studies will have to be done very carefully, as we cannot afford many such studies.

Natural history research needs to be returned to its rightful place as a respected element of ecological science. Such research provides us with our ultimate source material. Careful review is important in the selection of projects for support, but so is the need to nurture this type of study.

Comparative analyses of ecosystems are essential so that we can systematically examine system-to-system variability in the types and relative importance of compartments, processes, and controlling factors. Such analyses are essential to developing truly general predictive capabilities. I do not mean comparisons involving a random selection of sites; I do mean logical sets, within and between biomes that will allow us to look at responses along gradients or across environmental fields. Vitousek et al. (1979) have illustrated the power of such an approach. We must minimize the tendency to impose our local view on the world and join other scientists in developing response surfaces for regions and continents.

Collaborations of interdisciplinary teams will continue to be important – if ecosystem science is going to advance. There are too many interesting and critical questions that simply cannot be tackled individually or even by small groups. Prime examples include questions about ecosystem level responses to acid rain and other pollutants, cumulative effects of human activities on watershed- and landscape-level responses, effects of management practices on long-term site productivity, and the structure and function of old-growth forests. We must continue to train our students in the merit and art of cooperative research, and work to modify scientific institutions to recognize and reward such efforts.

Long-term data bases must be developed and maintained. They can only increase in importance with their critical role in providing critical tests of hypotheses, providing the "raw meat" for formulation of hypotheses, measuring the rates of long-term processes, providing baselines and identifying trends, and developing an appreciation of and information on episodic phenomena. Long-term data bases mean long-term experimental manipulations and permanent sample plots.

Scientific properties like Coweeta are essential to the three needs of comparison, collaboration, and long-term data bases. We must have locales dedicated to science and education with experimental capabilities, whole ecosystems available for study, and logistical support. We must have sites with long-term measurements, superior scientific leadership, and diverse scientific teams.

Many of the best locales for such research are federal properties under the jurisdiction of U.S.D.A. Forest Service, Department of Energy, and U.S.D.I. National Park Service. Coweeta illustrates the power of the governmental-academic linkage very well. Most of the highly productive ecological research programs have evolved where government and academic personnel have combined efforts at a site. Such sites can and do operate along a continuum of concept, experimentation, and application. With a good basic research program, management issues and societal problems can be addressed with understanding – essentially all research proves relevant!

Networking of the sites and research groups dedicated to long-term ecosystem research is critical. I think that suprasite synthesis is where the next generation of ecological paradigms will arise, and it needs greater attention and some fresh approaches.

Need for Stewardship

The continuity of Coweeta and comparable facilities is a shared concern and responsibility. Their existence depends upon a combined stewardship of institutions and of the scientific community. I want to express my concern about potential failures in this stewardship. Too often, the continued existence of facilities such as Coweeta must be credited to one or a few individuals. Maintaining sites and data bases have cost individuals and programs, sometimes dearly. All of the federal sites are operated out of research funds, whether such funds have come from Forest Service, National Science Foundation, or other sources. In effect, someone's research budget is paying the overhead of maintaining these sites. Someone's curriculum vitae is going to be the thinner for the time and cost involved.

The institutions responsible for the sites and programs need to lift some of the burden from individual research programs. Some of the long-term monitoring programs need to be supported "off the top", not out of local research projects. National Science Foundation needs to reconsider its unwillingness to provide support for monitoring and operating facilities. Forest Service, National Park Service, and Department of Energy need to provide support from the national level.

The scientific community must see that dedicated research sites are protected and maintained. We can actively support such properties by utilizing them and by encouraging institutional financial support.

Agencies and institutions have a particular responsibility since they provide the funds, protect the lands, maintain the facilities, and archive the data sets. Even the most valuable of facilities have been threatened with closure or disestablishment--during times of tight budgets, tenures of unsympathetic administrators, or changes in program emphasis. Many old hands in Forest Service research remember the pendulum from field to laboratory studies in the 1960s. Coweeta was repeatedly scheduled for closure in the last fifteen years. H. J. Andrews was almost dissolved in the early 1960s on the assumption that we knew all that we needed to about old-growth Douglas fir forests. San Joaquin Experimental Range, a biosphere reserve, was proposed for disposal as excess federal property in 1980.

It is to the credit of the Forest Service that none of these things happened, but they could have. In lesser instances, they did, such as the disposal of numerous structures that should have remained available as research facilities. Nor is the problem unique to the Forest Service, as scientists involved with the National Environmental Research Parks can attest.

As individuals and as organizations we need to be vigilant in the protection of these scientific resources. We must insure that the scientific community and institutions take the longer view, especially in unstable times.

Conclusion

Ecosystem science is healthy. There is a sense of excitement with many important discoveries during the last two decades and the promise of many more. There are a diversity of approaches and scales of study and a tolerance of this diversity. There is a sense of community that facilitates cooperation and collaboration. The science is relevant; findings are being utilized in the solution of societal problems.

Coweeta Hydrological Laboratory has been a major leader in this progression of ecosystem science. The scientific community looks forward to its next 50 years of contribution.

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