Institute of Ecosystem Studies
The New York Botanical Garden
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LONG-TERM ECOLOGICAL STUDIES:
AN ILLUSTRATED ACCOUNT OF THEIR DESIGN, OPERATION, AND IMPORTANCE TO ECOLOGY

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SUMMARY

Long-term studies have made essential contributions in ecology. Because of constraints imposed by funding agencies, research institutions, human behavior, and the brevity of professional careers, the successful completion of a long-term study offers a series of special problems not encountered by scientists who do short-term studies. This report is a discussion of some of these problems, which were described to us by approximately 100 ecologists involved in long-term studies. We reached these scientists by site visits, interviews, and questionnaires. Although we hoped to use the information we gathered to develop a "how to" guide for doing long-term ecological studies, this proved to be impractical, and our report instead concentrates on raising and discussing problems, rather than solving them.

One element that is clearly critical to the continued survival and success of a long-term study is dedicated guidance by one or a few project leaders. The importance of other elements is less clear. Some issues frequently mentioned by ecologists who do long-term studies include designing the study to be as simple as possible, the role of experimentation, whether having clearly defined objectives is valuable, when to terminate a long-term study, the protection and management of research sites, the choice of measurement variables, the collection and management of data, sample banking, management of personnel, the role of graduate students in long-term studies, the importance of monitoring, short-term justification for long-term studies, serendipity, and the role of synthesis and mathematical models. Our report also describes the kinds of situations in which long-term studies may be especially useful, and offers a brief critique of short-term alternatives for investigating long-term phenomena. Although our report is not definitive, we hope that it will help to spark discussion about the design, execution, and importance of long-term studies in ecology.

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INTRODUCTION

Most ecologists agree that long-term studies are invaluable, yet ecologists do long-term studies only rarely. This paradoxical situation is due to constraints imposed by funding agencies, research institutions, and human nature, all of which make long-term studies much more difficult to do than conventional short-term studies. The Institute of Ecosystem Studies long-term studies group arose from a suggestion made at a Friday TGIF session that a study of the design, operation, and productivity of existing long-term studies might help ecologists conduct long-term studies more successfully. Gene Likens set up our committee in September, 1984, to gather information about existing long-term studies in ecosystem ecology with the hope that we could relate features of the design and operation of these studies to their longevity and productivity. In simple terms, we hoped to produce something like a list of rules, suggestions, and prohibitions about doing long-term studies that would enhance the productivity of such studies.

It was apparent almost from the start that this original objective was naively overambitious, for several reasons. To begin with, long-term studies in ecology are numerous and not always easy to ferret out; the ca. 125 studies that we uncovered are, in our opinion, a small and biased sample of all long-term studies in ecology. It is particularly difficult to unearth long-term studies that have been unproductive or discontinued. To get a complete or representative sample of ecological long-term studies would require much more work than we are able to devote to the project. Without such a complete or representative sample, it is impossible to offer rigorous, statistically supported answers to the question of what design features of long-term studies are related to their productivity. A second fundamental problem is that most of the widely known long-term studies in ecology were not designed consciously as long-term studies, but rather grew to be long-term studies. It is difficult to describe or analyze a design that may have been nebulous or evolving until well into the long-term study. Conversely, the studies that have been set up as long-term studies, with a deliberate design, have arisen chiefly during the past decade and have not yet developed a "track record" (Fig. 1).

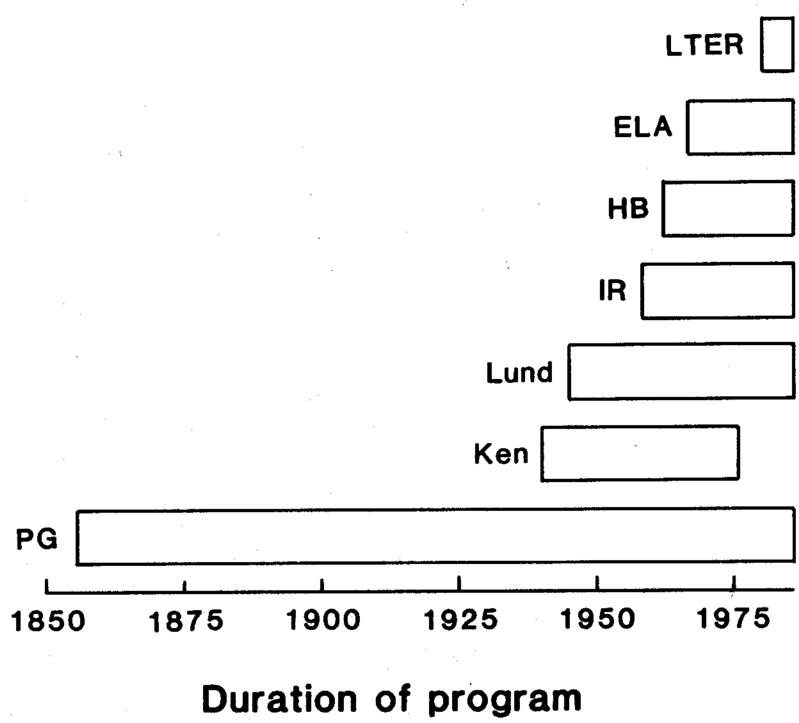

Fig. 1. The duration of some well known long-term ecological research programs. From top to bottom: LTER = the National Science Foundation Long-Term Ecological Research program (Callahan, 1984); ELA = the Experimental Lakes Area (Schindler, 1973); HB = the Hubbard Brook Ecosystem Study (Likens et al., 1977; Bormann and Likens, 1979); IR = studies of populations of large mammals on Isle Royale (Allen, 1979); Lund = studies of the phytoplankton of the English Lake District (Lund, 1978); Ken = studies of bird populations in Illinois (Kendeigh, 1982); PG = the Park Grass experiments at Rothamsted (Lawes Agricultural Trust, 1984).

Finally, it is necessarily somewhat arbitrary to define "productivity" quantitatively. (We use the term loosely in this report to mean the useful products of a long-term study, including - but not necessarily limited to - publications, educational services, input to public policy, and development of major scientific ideas).

For these reasons, the committee abandoned its original hope of being able to state, unambiguously, how the design and operation of a long-term study affects its productivity. Instead, we have used the information gathered from questionnaires, site visits, and interviews to construct a narrative account of the features of long-term studies that scientists and our committee believe to be of importance. We hope that this account will be useful in two ways to ecologists interested in long-term studies. First, it provides a listing of the topics considered to be of major importance by the people who are actually doing long-term studies. These topics could serve as a sort of checklist, admittedly incomplete, of topics that ought to be considered by a scientist who is beginning a long-term study. More importantly, we hope that the ideas contained in this paper could serve as a nucleus for discussions about various aspects of long-term studies, and thereby help ecologists conduct better long-term studies.

Methods

Our initial list of long-term studies in ecosystem ecology was derived from a request for information sent to 50-75 ecologists in the fall of 1984. Once we had agreed upon a list of long-term studies to be investigated, we gathered information about these long-term studies by two means: questionnaires and direct interviews or site visits. After considerable wrangling, and with the help of Marque Miringoff of Vassar College's sociology department, we produced a questionnaire containing 22 simple questions (see appendix) that we sent to 95 scientists who are doing (or recently did) long-term studies. The responses from the 76 questionnaires that were returned are summarized in the appendix. In addition, we visited Rothamsted Experimental Station in England; the University of Michigan, Ann Arbor; the Freshwater Biological Association in England; Merlewood Research Station in England; the H.J. Andrews Experimental Forest, Oregon; the Cedar Creek Natural History Area, Minnesota; and the University of Georgia, Athens; met with Drs. L. Roy Taylor, Durward Allen, Moshe Shachak, Arthur Hasler, Gene Likens, and John Eaton at the Institute of Ecosystem Studies, and interviewed Dr. David Schindler by telephone.

What is long-term, anyway?

Before proceeding, it may be helpful to define "long-term." There are at least two answers to the question: "How long must you continue a study before it is considered a long-term study?" The more obvious, and more satisfying, answer is that a study is long-term if it continues for as long as the generation time of the dominant organism or long enough to include examples of the important processes that structure the ecosystem under study. According to this class of definitions, the length of a study is measured against the dynamic speed of the system being studied.

A completely different approach is to define a long-term study simply as a study that has continued for a longer time than most ecological studies. Thus, we might consider a 5-year study of pelagic bacterial communities to be long-term just because few such studies extend for more than a year, and because the longer study has revealed attributes of the system that were not obvious from short-term study. Although this definition of long-term seems unsophisticated, it offers some advantages over the first definition.

For example, Gause's classic experiments on competitive exclusion in *Paramecium* took only about 20 days, but covered many generation times for *Paramecium* and clearly elucidated the dynamics of the system under study (Fig. 2). At the Hubbard Brook Experimental Forest in New Hampshire, ecologists have been studying the recovery of a forest ecosystem from clearcutting for 20 years, perhaps 1/20 of the time required for the forest to reach steady-state (Bormann and Likens, 1979). By the first definition of long-term, Gause's work is long-term and Bormann and Likens' is not. By the second definition, as by the common understanding of long-term, the Gause study is not long-term, but the Hubbard Brook study is.

Note that by accepting the second definition of long-term, we are accepting human instititions and constraints (e.g., human life span, funding cycles, graduate education), not the pace of natural processes, as the chief determinants of the length of ecological studies and the chief obstacle to conducting long-term studies. It is not intrinsically hard to study an ecological system for several generation times of the dominant organism, but it is intrinsically hard to study an ecological system for several funding cycles or several human lifetimes.

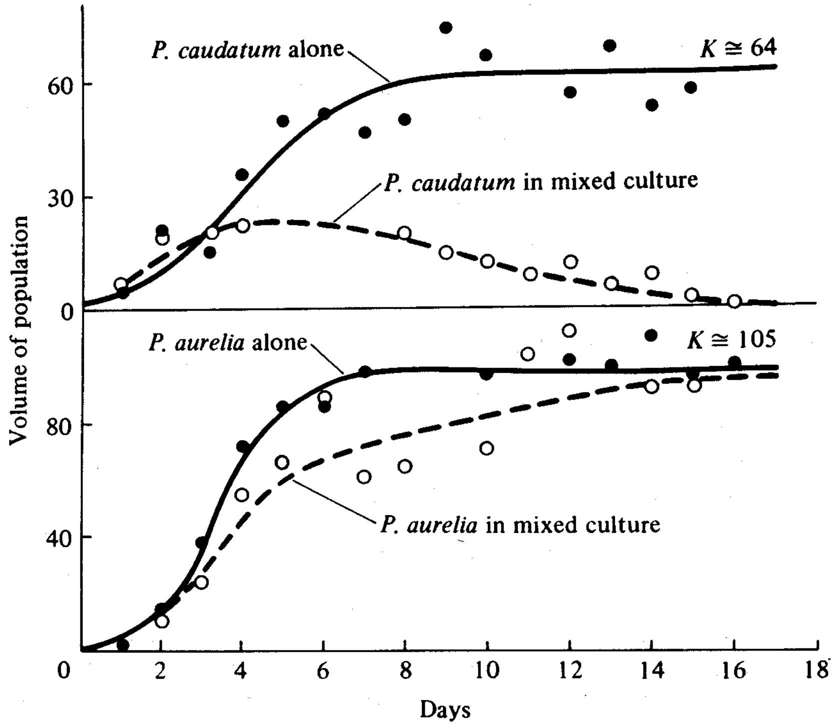

Fig. 2. Competitive exclusion in a laboratory experiment with two protozoans. From Pianka (1974), after Gause.

Contributions of long-term studies

There is widespread sentiment among ecologists that long-term studies have made great contributions to ecology; recently several prominent ecologists have called for more attention to be paid to long-term studies (e.g., Ehrlich, 1979; Likens, 1983; Wiens, 1984; Coull, 1985a; Taylor, 1986), and a special program (LTER) was set up by the National Science Foundation to fund long-term studies (Callahan, 1984; Halfpenny and Ingraham, 1984; Webster et al., 1985). Probably most ecologists already have accepted long-term studies as a useful approach in ecology. Nonetheless, it may be useful to list briefly some of the areas in which long-term studies have made especially important contributions.

Societal concerns. Long-term ecological studies have provided society with critical data on a number of practical issues. Long-term studies demonstrated the efficacy of inorganic fertilizers and showed that continued use of ammonium fertilizers caused detrimental effects by acidifying the soil (Lawes Agricultrual Trust, 1984), documented the response of lakes to sewage pollution (Edmondson and Lehman, 1981) and acidification (Schindler et al., 1985), demonstrated declining concentrations of lead in the environment following the reduction in use of leaded gasoline in the United States (Likens, 1983), and resulted in the discovery of acid precipitation in North America (Likens et al., 1972). The U.S. Geological Survey long-term records of streamflows throughout the United States have provided invaluable information for wise development and use of water and land. Many other examples exist.

Ecological theory. Long-term studies have made important contributions to the development and testing of ecological theory. We will cite only a few examples. C.O. Tamm's (1948, 1956) long-term studies of survival and reproduction of perennial herbs helped to inspire the field of plant demography (Harper, 1977, pp. 557-569). Elliott's (1984a-b, 1985a-d) elegant 18-year study of a brown trout population has provided useful data for testing models of stock recruitment and population regulation, and Pimm (1982a, b) turned to long-term records of British bird populations to answer a question (about population regulation) that was critical to the formulation of general models of food web structure.

General ecological knowledge. Perhaps the greatest contribution of long-term studies has been simply the knowledge that they have given us of the workings of selected ecosystems. Ecological systems that have been the subject of long-term studies have provided ecologists with many of the important ideas and paradigms that form the core of modern ecology. Some examples include the rocky intertidal, where Paine's studies have spanned 23 years (e.g., Paine, 1984); Isle Royale, where 28 years of study have shown us much about the population ecology and behavior of large mammals (Allen, 1979); Lawrence Lake, Michigan, from which 15 years of observation provided much of the material for a textbook of limnology (Wetzel, 1983); and large, multidisciplinary studies such as the Hubbard Brook Experimental Forest, the Experimental Lakes Area (ELA), and the Coweeta Hydrologic Laboratory, which have provided much of our understanding of basic ecosystem behavior.

Education. Long-term studies have played an important role in education. Many graduate students, undergraduate students, and technicians have received training as part of ecological long-term studies. For example, 56 graduate theses and 11 undergraduate theses were completed as part of the Hubbard Brook Ecosystem Study between 1961 and 1984, and dozens of students were involved with the project as technicians, volunteers, and so on (P. Likens, 1985). In this respect, long-term studies are no different from any other research activities. In addition, many long-term studies offer tours to classes or to the general public to demonstrate either general ecological principles or specific research projects. These tours may provide a valuable educational service to the public by providing a tangible example of what science is and does. Rothamsted gives tours to thousands of visitors each year; such educational tours now provide a major justification for continuing the Park Grass experiments at Rothamsted (L. Roy Taylor, pers. comm.).

Drawbacks of long-term studies

There are some obvious disadvantages to conducting long-term studies that should be considered before beginning a long-term study. Perhaps the chief difficulty with doing a long-term study is the continued commitment of money, time, staff, facilities, etc. that is required. The commitment or research resources to a long-term study will prevent a scientist from pursuing other lines of research. Furthermore, it may take much of a scientist's time and energy to provide these resources (finding funding, finding and keeping staff, justifying the project in the short term, etc.). A second difficulty for funders and administrators, as well as scientists, is to keep a project from falling into an unproductive complacency if funding and job security are provided over the long term. Furthermore, pressing environmental problems often require prompt answers, while the results from a long-term study may take years to decades to come in. Finally, long-term studies are restricted by practical considerations to time scales no longer than a few decades to a century or two. Questions about longer time scales must be approached by means other than direct long-term studies.

CONCLUSIONS

Despite the difficulties described in the introduction, we were able to reach clear conclusions in three areas concerning the conduct of long-term studies: the importance of a study leader, the importance of special features at long-term study sites, and the diversity of approaches used by ecologists to conduct long-term studies. We discuss these in the following section. Other potentially important issues are treated in the lengthy "Discussion" section that follows.

Successful long-term studies have dedicated leaders

Every successful long-term study that we studied has had associated with it one (or a few) good, dedicated scientist who has devoted much time and energy to the long-term study. These leaders are so deeply involved with their long-term studies that in many cases the leader's name has become synonymous with the project. Just as with any kind of scientific study, long-term studies require creativity and care in their design and execution. In addition, scientists involved in long-term studies have special problems in maintaining the project's funding, personnel, data collection, and output continuously over a long period. In our opinion, there is no special formula that solves all of these problems. Instead, we believe that the leaders of long-term studies have used their energy and creativity to solve these problems in diverse ways; in fact, in ways that appear unique for each long-term study.

The importance of a leader raises some obvious problems for the continuity of projects that extend for more than a professional lifetime. What happens to a long-term study when its leader dies or retires? It is difficult to provide an answer to this important question, since most ecological long-term studies were begun only recently (Fig. 1) and are still directed by their original leaders. In some cases, the project simply ceases. S.C. Kendeigh's 27-year-long studies of bird populations (Kendeigh, 1982) ended when he retired in 1976, and Francis Evans believes that no one will take over studies of the Evans old field when his work ends. In a few cases, leadership of a long-term study has been passed on to a younger colleague. For example, Rolf Peterson now leads the project that Durward Allen began on the mammals of Isle Royale, and Colin Reynolds and Ivan Heaney are continuing J.W.G. Lund's long-term study of phytoplankton in the English Lake District. It is perhaps significant in both of these cases, though, that the original leaders are still alive and active professionally.

One long-term study that is old enough to have confronted the problem of changing leadership is the classical experiments at Rothamsted. In 1843, John Lawes and J.H. Gilbert began the first long-term agronomic study on Broadbalk field at Rothamsted. For the next 46 years, these and other experiments were supervised by Lawes. In 1889, Lawes provided for the continuation of his agronomic experiments by setting up a trust of £100,000, administered by three trustees (chosen by the Royal Society) and a trust committee of nine, to manage the experiments. Lawes died in 1900, and Gilbert in 1901. Since Gilbert's death, there have been only five directors of the Rothamsted Experimental Station, none with a tenure shorter than ten years. Rothamsted has received government funding since 1911, and the Lawes Agricultural Trust now provides only a small fraction of Rothamsted's funding. It seems likely that Rothamsted has been able to persist because of Lawes' long tenure (> 50 years), his foresight and care in setting up the trust, the low turnover of senior staff, and the simplicity of its design (see below).

Some long-term studies have been done on uniquely attractive sites

Many, but not all, of the sites where long-term studies have been conducted have some special feature that has been important to the long-term study done there. The E.S. George Reserve in southeastern Michigan is surrounded by an 11-foot-high fence. Although the fence was not built for research purposes, researchers saw that the fence made it possible to make complete censuses of deer population that is contained on the 600-hectare site. The combination of a special feature (the fence) and researchers who saw and took advantage of the feature has resulted in a well known long-term study on deer at the George Reserve (McCullough, 1979). Likewise, the Experimental Lakes Area in Canada (Johnson and Vallentyne, 1971) provided limnologists with the opportunity to manipulate whole lakes for scientific purposes. This remarkable advantage has certainly helped the ELA conduct some of the best limnological long-term studies ever done (e.g., Schindler et al., 1985). Many other sites of successful long-term studies have analogous advantages.

However, it is equally important to note that many long-term studies have been done on sites that did not offer any obviously unique advantage. The classic experiments at Rothamsted did not depend on any special features of the site at Harpenden. Likewise, Francis Evans' long-term study of an old field at the George Reserve could have been done at many other sites around Ann Arbor. Of course, once a long-term study has been started, even at an unremarkable site, the accumulating long-term data provides an important special feature that makes the site especially attractive for further research.

Successful long-term studies have been done in a diversity of ways

We gathered information about how ecologists have done long-term studies in the hope that we could relate features of the design and execution of long-term studies to their longevity and productivity. Instead of discovering any clear relationships, we were struck by the great diversity of ways in which ecologists have designed and conducted long-term studies. Successful long-term studies have been done using various funding sources, experimental (or non-experimental) designs, motivations and questions, personnel, systems of data collection and management, and so forth. This diversity is itself an interesting feature, for it means that the challenges of long-term studies have been handled in a number of specific ways, depending upon the nature of each individual research project and the availability of various resources. However, this diversity also obscures any relationships between design and productivity in long-term studies, especially in the absence of a large, statistically representative data set. We do not believe that design is irrevelant to the ultimate productivity of a long-term study, but we are unable to support any recommendations concerning optimal design of long-term studies.

The remainder of this report deals with these details of the design and execution of long-term studies. Our discussion and recommendations are based on the opinions of scientists who are involved in long-term studies and on our opinions. We hope that these opinions and illustrations will help to generate useful discussion about the design and execution of long-term studies, but is should be kept in mind that the opinions expressed in the following section are not backed by hard data showing relationships between the design and the productivity of long-term studies.

DISCUSSION

Motivation of long-term studies

It is possible to recognize several classes of motivations for starting long-term studies. In many cases, investigators have wanted to learn about the particular *system* under study. An example might be Charles Goldman's detailed work on Lake Tahoe (Goldman, 1981). Alternatively, the scientist might be interested in answering some general *question*. Robert Paine told us that he began his long-term studies on the rocky intertidal because he was interested in the role of predation in structuring ecological communities. A third motivation to begin a long-term study might be to answer a perceived *societal need* (USGS gage stations). Of course, any specific long-term study is motivated by some combination of these three factors.

A somewhat arbitrary classification of our questionnaire responses (Appendix) suggests that about 80% of our respondents were motivated primarily by system-oriented questions, 20% by general ecological questions, and societal needs provided an important motivation for 21% of our respondents. It is possible that ecologists will move toward more of a question orientation as ecological knowledge advances.

What kinds of questions are long-term studies good at answering?

Long-term studies seem to us especially suited to exploring four major classes of ecological phenomena (Fig. 3).

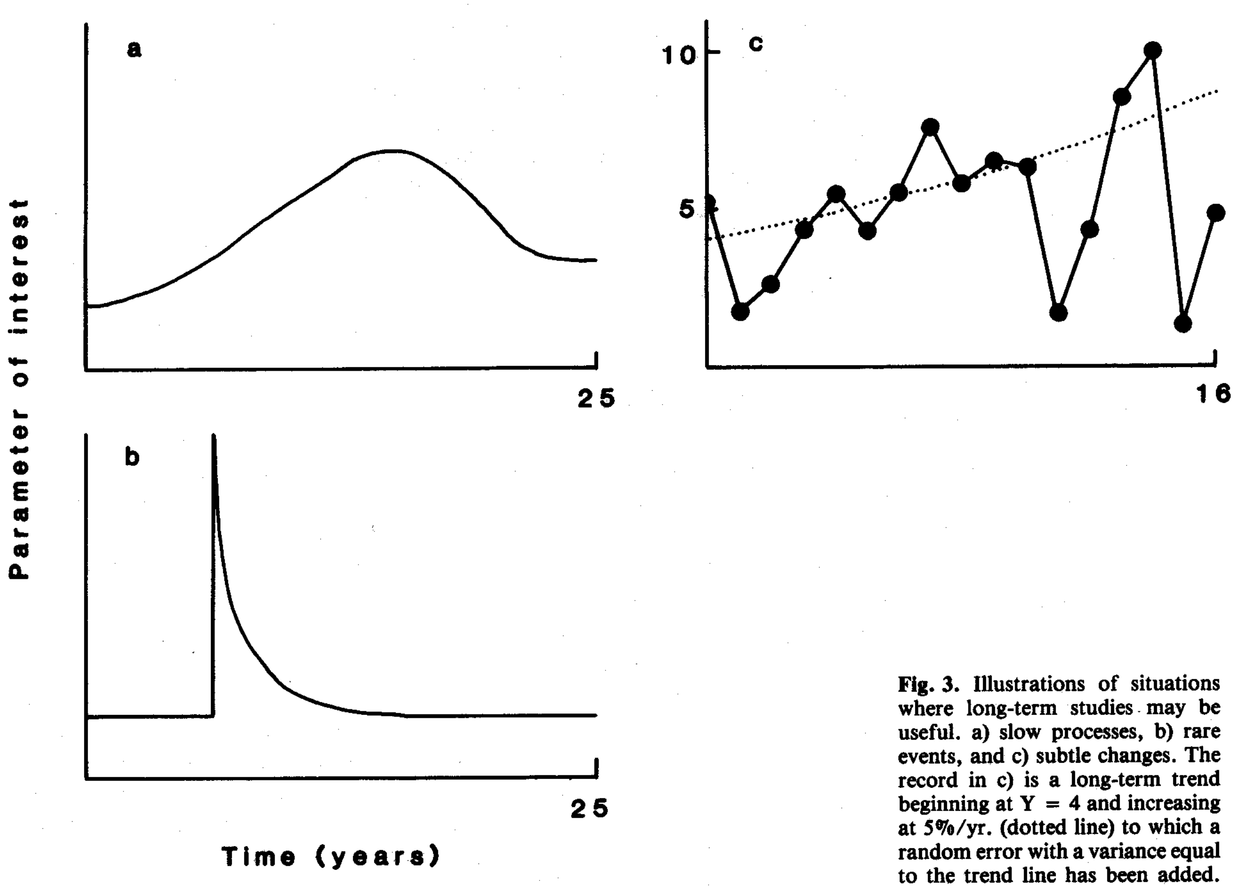

Fig. 3. Illustrations of situations where long-term studies may be useful. a) slow processes, b) rare events, and c) subtle changes. The record in c) is a long-term trend beginning at Y = 4 and increasing at 5%/yr. (dotted line) to which a random error with a variance equal to the trend line has been added.

i) *Slow processes.* Many important ecological phenomena occur on time scales longer than the 1-3-year funding cycle or, in fact, longer than a human lifetime. Long-term studies obviously can contribute greatly to the understanding of these phenomena. Some prominent examples of slow processes are forest succession, invasions of exotic species, soil development, wood decomposition, and vertebrate population cycles. There are many long-term studies of slow processes (e.g., Christensen and Peet, 1981; Pickett, 1982; Gill et al., 1983; McCune and Cottam, 1985).

ii) *Rare events.* Many important ecological phenomena occur irregularly with return times of more than a few years. Although one can conduct a short-term study following the occurrence of one of these phenomena, it is impossible to know the frequency, context, and ultimate ecological significance of rare phenomena without conducting a long-term study. Examples of important but rare phenomena include catastrophes such as fires, wind storms, or floods, population eruptions such as disease or outbreaks of insect "pests," year-class phenomena in fish, and environmental "crunches." Some long-term studies that have contributed to our understanding of rare events include the numerous studies following the catastrophic eruption of Krakatoa (Thornton, 1984) and Crook and Shields' (1985) work on infanticide in barn swallows.

iii) *Subtle processes.* We have in mind here an ecosystem process that is changing over time in a regular fashion (e.g., monotonic change, a step-function, a cycle), but where the year-to-year variance is large compared to the magnitude of the long-term trend (Fig. 3). A short-term study will be unable to discern the long-term trend, or, even worse, will suggest a completely incorrect conclusion about the magnitude and direction of the change (notice the many points in the record shown in Fig. 3c that show a decline with time). A short-term record simply lacks the statistical power to detect subtle long-term trends (e.g., Ricker, 1975, p. 277). Situations of this kind are especially common in the real world. The utility of long-term studies has been suggested for detecting subtle changes in algal communities in response to changing loads of P to New York's Finger Lakes (Trautmann et al., 1982), in acidity of rainfall (Likens et al., 1984), and in the biogeochemistry of an aggrading forest (Likens, 1983). Many other examples exist.

iv) *Complex phenomena.* A long-term study may provide the necessary statistical degrees of freedom to conduct multivariate analyses of complex phenomena. This approach has perhaps been used most widely to assess the importance of environmental factors to population growth and recruitment in economically important insects and fish. Multivariate analysis of a long-term record allows a scientist to determine which of many potentially important, intercorrelated environmental factors are related to the population parameters of the species of interest, and to make a preliminary estimate of the strength of such relationships. Ricker (1975, pp. 279-280) and George and Harris (1985) provided examples of this use of a long-term record (see also Beeftink, 1979, and Austin, 1981).

Short-term approaches to long-term phenomena

There are at least four classes of short-term studies that can provide insight into the long-term behavior of ecological systems: retrospective studies, substitution of space for time, use of systems with fast dynamics as analogues for systems with slow dynamics, and modeling. Such short-term studies can be (and often have been) used in place of long-term studies in cases where limitations of time, money, or personnel make long-term studies impractical to conduct. It is important to remember that such short-term approaches are in no way incompatible with direct long-term studies and can be valuable complements to long-term studies, extending the temporal and spatial scales of the investigation and allowing the ecologist to explore a wider range of ecological phenomena than might be practical in a direct long-term study.

i) *Retrospective studies.* In some cases, ecosystems record their past condition and behavior in a form that can be read by astute ecologists. Familiar examples include tree rings and lake sediments. In the ideal case, a good paleolimnologist can tell a great deal about the long-term behavior of a lake and its watershed from a relatively short-term study of lake sediments, for example. There are several obvious strengths and weaknesses to retrospective studies. On one hand, retrospective studies often allow ecologists to explore time scales that are too long to investigate directly with long-term studies (e.g., 10^3 - 10^5 yrs in paleolimnology). Furthermore, retrospective analyses can be meshed nicely with long-term studies. For instance, a direct long-term study of a forest or lake can be extended by retrospective analyses (e.g., Wetzel and Manny, 1978; Likens, 1985) in a way that is not possible for a long-term study of a stream, which probably has left little in the way of a record of its past behavior.

On the other hand, retrospective analyses have some serious drawbacks, especially if used in isolation as a replacement for long-term studies. The raw material for a retrospective study is the record left by the ecosystem; only the persistent structures have remained for the ecologist to analyze. Unfortunately, many important processes and conditions leave no trace of their occurrence. Furthermore, past conditions, environments, and processes must be inferred from the record left by the ecosystem, often with considerable uncertainty. Finally, retrospective analyses often have poor resolution of short-term events (e.g., on time scales of < 1 year).

Despite these criticisms, it is clear that retrospective analyses have made important contributions to our understanding of the long-term behavior of ecosystems (e.g., Hutchinson et al., 1970; Henry and Swan, 1974; Oliver and Stephens, 1977) and can be an invaluable complement to long-term studies.

ii) *Substitution of space for time.* This approach is perhaps best described by example. To study old field succession, an ecologist studies fields abandoned 1, 2, 5, 10, and 30 years ago and assumes the difference in plant communities among the sites is the same as the succession that occurs in a single site for the first 30 years after abandonment. Or, an ecologist finds that 5% of the forests in New York were defoliated in the past year and concludes that the average piece of forest is defoliated every 20 years. In both of these cases, there has been some substitution of space (different sites) for time (different years). Studies of this sort have made great contributions to our understanding of our long-term behavior of ecosystems, particularly in the area of succession (e.g., Oosting, 1942; Foster, 1985).

There are some obvious advantages to substituting space for time. An ecologist can gain insight into processes that occur at long time scales in a short-term study. These studies often are cheaper and easier to set up and execute than long-term studies. Unlike retrospective analysis, studies that substitute space for time allow the investigator to examine mechanisms or processes directly; an ecologist can look at seedling survival in 1-, 10-, and 30-year-old stands, for example. Finally, these studies can be set up in parallel to long-term studies, allowing ecologists to explore phenomena that are impractical to include as part of the long-term study, expand the time scales of the investigation, and, especially importantly, test the generality of the results generated at a single long-term site.

There is one very serious drawback to studies that substitute space for time: the assumption that all important events and processes are independent of space and time. Put more simply, this approach requires that all sites have the same history and environmental characteristics. Of course, many important ecological phenomena are strongly time- and space- dependent; no two sites have the same history (cf. Hamburg and Sanford, 1986). To return to our hypothetical old fields, it may be that the field abandoned 30 years ago was subject to three dry years and an unusually early frost in its first four years, while the field abandoned 10 years ago saw four years of "normal" rainfall and frost, but suffered from a beetle outbreak in year 8. To the extent that these peculiar historical events, rather than successional time, influence plant species composition, the difference between the 10- and 30-year-old fields will reflect individual histories as well as (or instead of) a purely successional trend (Buell et al., 1971; Collins and Adams, 1983). Between-site variation in environment will have an analogous effect. Of course, an ecologist can minimize this difficulty by choosing study sites that have, as far as is known, similar histories and characteristics, but can never eliminate the problem.

The results of direct long-term studies also are dependent upon the history and local environment of the study site. For example, if the Hubbard Brook studies had been done at Waterville Valley (~15 km away from HBEF) or had been done in 1953-1975 instead of 1963-1985, some of the results certainly would have been different from those actually found at Hubbard Brook. We have no way of knowing to what extent the results of the Hubbard Brook Ecosystem Study reflect generalizable ecological trends as opposed to site- or time-dependent phenomena, using only the data from Hubbard Brook.

The ideal solution, of course, to deal with site- and history-dependence is to replicate (in space and time), both in direct long-term studies and in space-for-time substitutions. A statistical analysis of the resulting data will show generalizable phenomena as the mean pattern and the influence of history and local environment as the variance about that pattern (Fig. 4). It is important to note that direct long-term studies have an important advantage in dealing with the year-to-year variation that masks general trends. If direct long-term studies are done in a parallel with a careful matched "reference" ecosystem (such as has been done at Hubbard Brook), then the year-to-year variation can be factored out, and the general phenomena of interest will be much more clear.

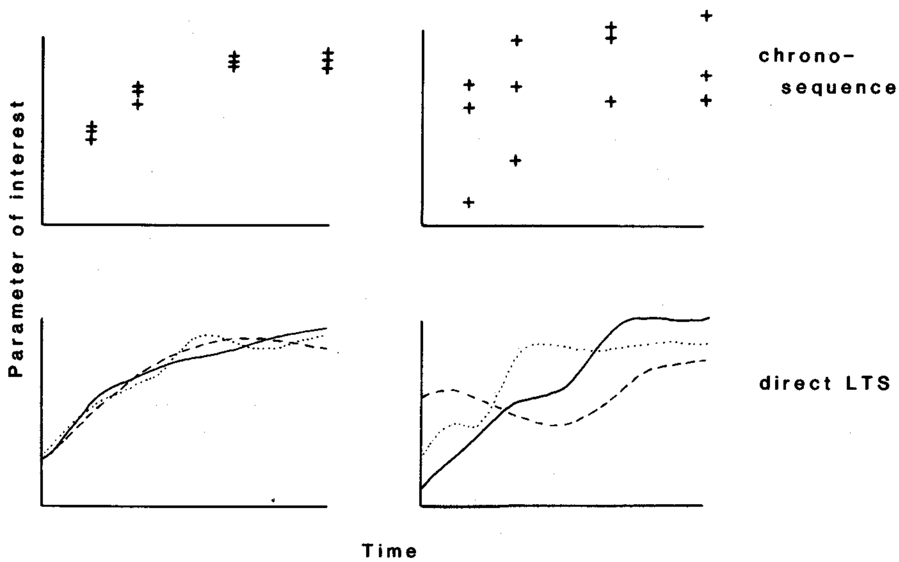

Fig. 4. The influence of history and local site factors in chronosequences and direct long-term studies. In each case, the generalizable ecological phenomenon is the mean trend and the influence of history and local factors is the variance about the trend.

Sufficient replication can be realized only rarely, because of logistical constraints. It is usually not possible to conduct direct long-term studies in parallel at 10 sites or to find, say, 50 carefully matched sites in a chronosequence. A more practical and widely used solution is to combine a direct long-term study with a broader scale space-for-time substitution.

iii) *Use of systems with fast dynamics.* When Stuart Fisher visited the Institute of Ecosystem Studies in November, 1985, he suggested using systems with fast dynamics to answer general questions about ecological phenomena. For example, a forest ecologist might wonder how disturbance frequency affects species richness of trees in a forest. To answer this question directly might require a decades-to-centuries-long experimental study of forest dynamics. However, the same general question about disturbance frequency and species richness could be posed for a system dynamically much faster than forest trees (e.g., stream algae, zooplankton) and explored thoroughly in 1-3 years. Thus, Fisher's approach could be a fast, cheap substitute or complement to any long-term study that is designed to answer a general (as opposed to system-dependent) question.

The approach is attractive, but has a drawback that severely limits its practicality. In its most naive form, there is the assumption of scale invariance; i.e., that a result generated in one system will hold for every other system. More realistically, we might expect results generated in one system to hold for "similar" systems. The trick here is to be able to recognize which systems are similar to the system we've studied. We may hope for the day when we can say "any system where 20% of the species have generation times of less than the disturbance frequency will respond to disturbances like zooplankton communities; temperate forests satisfy this criterion, so we can apply the findings from our zooplankton communities to temperate forests," but so far, ecologists have not been able to generate such rules, by and large (but note Lubchenco, 1985).

The reader may have noted that the strengths and weaknesses of system substitution are perfectly analogous to those of using small, manipulable systems (microcosms, limnocorrals, etc.) as analogues for large natural systems. Despite the many problems with microcosms and their kin, these model systems have made important contributions to ecology. Likewise, we expect that the use of dynamically fast systems will be a useful exploratory tool for ecologists interested in certain long-term processes. David Tilman's work may provide an example. His work on resource competition in algae provided the basis for a general theory of resource competition (Tilman, 1982) that is now being used to guide long-term studies on a much slower system (prairie vegetation).

iv) *Modeling.* It is of course possible to construct mathematical models to predict the long-term behavior of an ecosystem. Indeed, such models exist and have been used as an aid in the understanding of long-term ecological phenomena (e.g., JABOWA; cf. Bormann and Likens, 1979). It is probably unreasonable to expect such models to provide a detailed, realistic picture of the long-term behavior of ecosystems, because of limited knowledge of the functioning of real ecosystems and because the data used to construct and test the models will inevitably be subject to peculiar historical circumstances not easily accommodated in a model. Nonetheless, mathematical modeling can provide answers in the short term that can be useful in the design, execution, and interpretation of long-term studies.

The design of the long-term study

Several features of the initial design of long-term studies were mentioned frequently as being important to the ultimate productivity of the study. They are, in no particular order, the importance of a simple and accommodating design, whether having clearly defined objectives to the study is useful, and the role of experimentation.

Importance of a simple, accommodating design. We heard repeatedly that a study must be simple to persist over the long term. In this view, the essential measurements and experimental treatments should be straightforward and unambiguously repeatable even by staff lacking sophisticated training.

Also, several scientists stressed the importance of adopting an initial design that can accommodate studies not envisioned as part of the core long-term study as a way of increasing the utility of a long-term study. A specific element mentioned by several scientists is the importance of setting up plots that are large enough to withstand intensive research use (sampling, trampling, and plot subdivision for new treatments). L. Roy Taylor's advice was to choose a plot size that is absolutely the largest that you can handle, "and then double it." Another point raised by J.W.G. Lund, among others, is that the essential measurements that form the core of the long-term study must not be so time-consuming that the investigator is unable to set up ancillary studies to explore questions raised by the long-term study data set. These ancillary studies often make an enormous contribution to the overall productivity of a long-term study. For example, only 20% of the papers arising from the Hubbard Brook project used a long-term (> 5-yr) data set *per se* (cf. Fig. 7).

We can offer two examples of long-term studies with beautifully simple and accommodating designs. The Park Grass experiments were begun at Rothamsted in 1856 to examine the effect of various inorganic fertilizers on the yield and composition of hay (Lawes Agricultural Trust, 1984). Each year, the plots receive a specified application of fertilizer. The hay is cut each year, its yield recorded, and subsamples stored for later chemical analysis. The botanical composition of the hay is described at irregular intervals. No carefully calibrated scientific instrumentation or highly trained scientists are required to do the routine work for the Park Grass experiment. L. Roy Taylor of Rothamsted believes that this simplicity is in part responsible for the continued operation of the Park Grass project in the face of 130 years of varying scientific and societal conditions, including two world wars.

The Gisburn Forest project was set up in 1955 in the northwest of England to examine the effect of various species of trees on long-term soil development. The original design consisted of three replicate blocks, each containing twelve 1/2-acre plots: oak, Scot's pine, Norway spruce, or alder (an N-fixer) planted alone, every possible 2-species combination, a grazed reference plot (the whole area was in sheep pasture prior to the experiment), and an ungrazed reference plot. The basic design called for measurements of tree height every five years and of nutrient content of the soil. The design appears to be elegantly simple, statistically sound, and rich in possibilities to accommodate a great variety of other research projects. However, the Gisburn Forest project produced a single paper between 1955 and 1984 (Brown and Harrison, 1983), although more papers should appear soon (A.F.H. Brown, pers. comm.). Thus, although a simple and accommodating design may be desirable, it in itself is certainly no guarantee of productivity.

Importance of rigorously defined objectives. We heard two different views on the importance of having a well defined hypothesis and a rigorous statistical design in a long-term study. Members of one school argue that a good long-term study should begin with a clearly defined question or hypothesis, proceed through preliminary studies to develop appropriate methods and sampling design, and then be designed and conducted to answer a specific research question as efficiently as possible. A long-term study done more or less according to this model is Elliott's study of a brown trout population (Elliott, 1984a, b; 1985 a-d).

At the other extreme are long-term studies that were begun to find out "what's going on out there" in various communities or ecosystems, without a specific hypothesis or a sampling design that is chosen to be optimal for answering specific questions. This approach is perhaps best exemplified by Lund's 43-year record of phytoplankton populations in the English Lake District (Lund, 1971, 1972, 1978) and the 28-year study of large mammals on Isle Royale (Allen, 1979), both of which apparently were set up to see how the system behaved, without a specific hypothesis. Proponents of this approach see a specific hypothesis as being potentially restrictive while proponents of a more rigorous approach see an unfocused long-term study as being inefficient and ultimately wasteful of research resources.

Productive long-term studies have been done both in the presence and in the absence of rigorously defined questions. Perhaps the rigouous approach is more productive in systems whose basic characteristics already are known.

Importance of experimentation. Many well known long-term studies have involved experimental manipulation of large field plots (e.g., Rothamsted, ELA, Hubbard Brook, several LTER sites) and several scientists that we contacted argued strongly that manipulation is a powerful tool for investigating the workings of an ecosystem. However compelling this argument, we point out that other well known long-term studies have not involved experimental manipulations (e.g., L.R. Taylor's moth surveys, Elliott's studies of brown trout, Tamm's work on the demography or perennial herbs), and it is not clear from our limited analysis that manipulability has enhanced productivity. Nonetheless, it is clear that manipulations have led to important insights into ecosystem functions that would not have been obtained by other means, so it seems advisable for a scientist who is setting up a long-term study to consider how her study system can be experimentally manipulated.

Cooperation with real-world management programs. Large scale, whole-system manipulations often are too expensive or logistically difficult for ecologists to do frequently. At the 1985 Cary Conference (Likens, 1986), Peter Vitousek suggested a useful supplement to strictly scientific whole-ecosystem manipulations. The following section is taken from a discussion at the Cary Conference based on Peter's ideas.

There is a whole class of whole-ecosystem manipulations that ecosystem scientists have not begun to exploit. These manipulations can be classed broadly as real-world ecosystem management, and include, for instance, management of timber plantations, liming of lakes, exploitation or manipulation of fisheries, and even routine development of land for human use. These are ecosystem-level manipulations, and someone else is paying the bill. Furthermore, these ecosystem manipulations are important in themselves, since they are being done on large parts of the earth. We believe that poor communication and an adversial attitude between ecologists and the people who do these manipulations have blocked the use of such manipulations for research. We strongly encourage ecosystem ecologists to try to integrate themselves into the design and execution of these manipulations. Although management schemes may rarely approach the ideal of controlled ecosystem experimention, they should allow ecosystem scientists to collect experimental data in quantities and on scales that are economically infeasible in the traditional research environment. Furthermore, the results generated from these cooperative ecosystem experiments/management should be especially helpful when it comes time to design our long-term studies.

Before leaving the question of study design, there are three other topics worth discussing: the duration of a long-term study, access to and protection and management of research sites, and selection of variables to be measured.

How long is long enough? There are really two related questions here. First, you might ask how long you need to run a given long-term study to achieve the desired results. The answer to this question is straightforward, if you have a clearly defined objective and know something about the ecosystem under the study. The procedure for determining the necessary length of the study is analogous to the statistical procedure for determining the number of samples or plots needed in a study (e.g., Snedecor and Cochran, 1967, pp. 516-518).

A more difficult question is: when do you terminate a long-term study? Obviously, if you have a single, clearly defined objective, you terminate the study when you've fulfilled that objective. Only rarely are long-term studies so restricted in scope. More frequently, an investigator develops new ideas and objectives throughout the course of the study, and never reaches the point where he can say, "There, I've learned everything that I want to know about *that* ecosystem," and move on. In such circumstances, the study should be terminated when the rate at which new knowledge is being accrued does not justify the cost.

We do not know any general rules to determine when this point has been reached. Durward Allen thought that 10 years of study would be enough to work out the basic relationships between moose and wolves on Isle Royale. In fact, after 10 years, Allen thought he *did* understand the system well, and it was only after the hard winters of years 10-15 that Allen realized that he did not understand the system well at all. The first 10 years did not show him the diversity of behavior that the ecosystem was capable of, and he had (and *has*) no way of knowing how many years of study would be needed to uncover the full complexity of the system. Allen told us, "I can't see *any* reason for stopping this project," and offered specific reasons (the long-term stochasticity of weather, epizootics, etc.) why the Isle Royale project can be expected to continue to yield significant new knowledge. Allen's views were echoed repeatedly and strongly by other scientists involved in long-term studies. It is perhaps significant that none of the long-term studies that we studied were terminated voluntarily because the PI felt that the study no longer justified the cost. Studies were stopped by funding difficulties and retirement of the PI, but never for lack of important research questions.

Research sites: access and protection. It should be obvious that scientists involved in a long-term study need access to and protection of their research site over the long term. In most cases, this access and protection has been provided by site ownership by the research organization (university, institute, state or federal government). However, a surprising number of long-term studies have been conducted on sites not under control of the investigator or his parent organization. For example, Thomas Waters and his students have gotten access to Valley Creek, Minnesota, the site of intensive studies since 1960 (e.g., Waters, 1981), through the courtesy of sympathetic landowners. Nonetheless, it should be clear that without the guaranteed use and protection of a site that ownership (or similar legal arrangements) provides, an investigator is subject to the potentially devastating loss of, or change to, the research site. We do not know of any long-term study that had to be stopped or greatly modified due to restrictions on access or research activities imposed by a landowner. However, a sobering example is provided by Mirror Lake, New Hampshire, where Gene Likens and his colleagues have worked since 1964. In 1969, despite protests by ecologists, an interstate highway was built through the watershed of Mirror Lake, resulting in a loss of 17% of the watershed area and a 10-fold increase in concentrations of sodium in one of the lake's tributaries (Likens, 1985).

However, it is also important to point out that ownership of a research site by a researcher's parent organization does not guarantee continued access and protection for a researcher; one can think of Harvard's proposed sale of the Black Rock Forest (Trow, 1984).

Management of research sites. The management of research sites is regarded as an important concern at most long-term study sites. The reasons that active management of research sites is needed include:

i) Degradation of the research site. Sites may become unsuitable for research because of lingering effects of experimental treatments, physical trampling of sites, or distrubance due to intensive sampling.

ii) Interference between studies. Two studies may be incompatible with one another, so there must be a mechanism to avoid interference between them.

iii) Assignment of priorities to proposed studies. Because of (i) and (ii), it may be necessary to prohibit some research activities as being overly demanding of the research site.

iv) Site maintenance. Research sites usually have roads, fences, trails, machinery, etc. that need to be maintained. Also, someone needs to decide in what state the site will be kept (should roads be added/abandoned, should old fields be kept open/allowed to grow into forests, etc.).

Because of considerations like these, most long-term study sites, especially those involving many researchers, have adopted some system of site management. We found several common features of these systems of site management.

i) Records of research activities. At many long-term study sites, records are kept that show the nature and location of all ongoing and past research activities.

ii) Site manager. At many long-term study sites, there is a site manager, (often *not* the study leader) whose job it is to coordinate field research activities and site maintenance.

iii) Site management committee. Commonly (but not always), there is a committee that sets the policy for long-term site management, approves extraordinary uses for the long-term study site, and settles disputes over conflicting uses of the long-term study site.

Two other issues are sometimes mentioned but appear to have been dealt with only rarely. At some research sites, research activity has become so intense that there is serious concern that the research activity itself is having an impact on the ecosystem. We have rarely seen any action to alleviate, say, trampling effects. Second, there is the question of reuse of areas that once were manipulated. Put simply, how long does it take for the effect of an experiment to vanish? This is an important consideration wherever intensive research is conducted in a small area, but seems to have been discussed only rarely.

Choice of measurement variables. When the LTER program was set up, there was considerable discussion about the selection and measurement of ecological parameters in long-term studies (National Science Foundation, 1977, 1978; The Institute of Ecology, 1979a,b). We will not elaborate on these discussions here. However, it may be useful to make a general distinction between measurements of structure (e.g., species composition, population demography) and function (e.g., primary production, litter decay). On one hand, functional variables integrate the behavior of the ecosystem and often are of considerable interest themselves. On the other hand, because of compensatory mechanisms within the ecosystem, functional variables may be poor indicators of changing behavior of the system, including behavior in response to stress. For example, Schindler et al. (1985) have pointed out that experimental acidification of Lake 223 did not affect rates of total primary production, although there were numerous, conspicuous changes in community structure. Also, Eugene Stoermer suggested to us that measurements of function often are technically difficult to make and subject to changing methodology (e.g., methods for the assessment of aquatic primary production).

Collection and management of data

Several topics that can be grouped under this broad heading arose during our discussion: development of new methods, quality control, the problem of changing methods, sample banking, data management, and statistical methods (in the narrow sense).

Development of new methods. It is striking and perhaps significant that some scientists engaged in long-term studies have devoted considerable effort to develop new methods early in their long-term studies. For example, scientists at the ELA developed new methods for the analysis of dissolved inorganic carbon (Stainton, 1973) and phosphorus, parameters that were of critical importance in the initial eutrophication experiments at the ELA. Likewise, Lund developed new methodology for sampling and counting phytoplankton early in his study of the phytoplankton of Windermere (Lund, 1951; Lund and Talling, 1957; Lund et al., 1958). In both cases,. the newly developed methods were important in the subsequent execution of the long-term research projects.

It is tempting to speculate that a scientist who is thinking of a research project (and thus the utility of a new method) in terms of several years to decades is more likely to take the time early in a research project to work out a new method carefully. However, it is important to remember that Lund was not intending to conduct a long-term study at the time that he developed new methods; he was simply being a thorough ecologist who was engaged in an interesting short-term study. Viewed in this light, the development of new methods may have enhanced the longevity and productivity of Lund's long-term studies, rather than being a result of the long-term study.

Quality control. It is essential to the interpretation and use of long-term data sets that *all* data in the set be reliably accurate. Thus, quality control of sample collection and analysis is of great importance. It is probably significant that some prominent long-term studies (e.g., ELA, Hubbard Brook) are also known for the scrupulous care with which data has been collected. At a minimum, a scientist engaged in a long-term study should be careful to follow standard procedures for good laboratory and field practice. In addition, it may be especially important in a long-term study to archive samples (see section on sample banking), document experimental treatments and procedures for sample collection and analysis in tedious detail, mark plots accurately and permanently, and so on.

The problem of changing methodology. The constant improvement of analytical methods can pose some problems for a scientist engaged in a long-term study. Shapiro and Swain's (1983) paper provides one cautionary tale. Data produced by Chicago's water authority showed declining concentrations of silica in Lake Michigan between 1926 and 1962. This decline was used to support a widely cited hypotheses linking increasing phosphorus loads, diatoms, and silica in Lake Michigan (Schelske and Stoermer, 1971). However, Shapiro and Swain pointed out that the decline in silica concentrations coincided with a change in analytical methods in 1948 (Fig. 5). Their reanalysis of the data set showed no evidence for a long-term decline in silica concentrations in Lake Michigan. It is easy to imagine other examples where a change in methods could cause an apparent change in the data that could be wrongly interpreted as a long-term change.

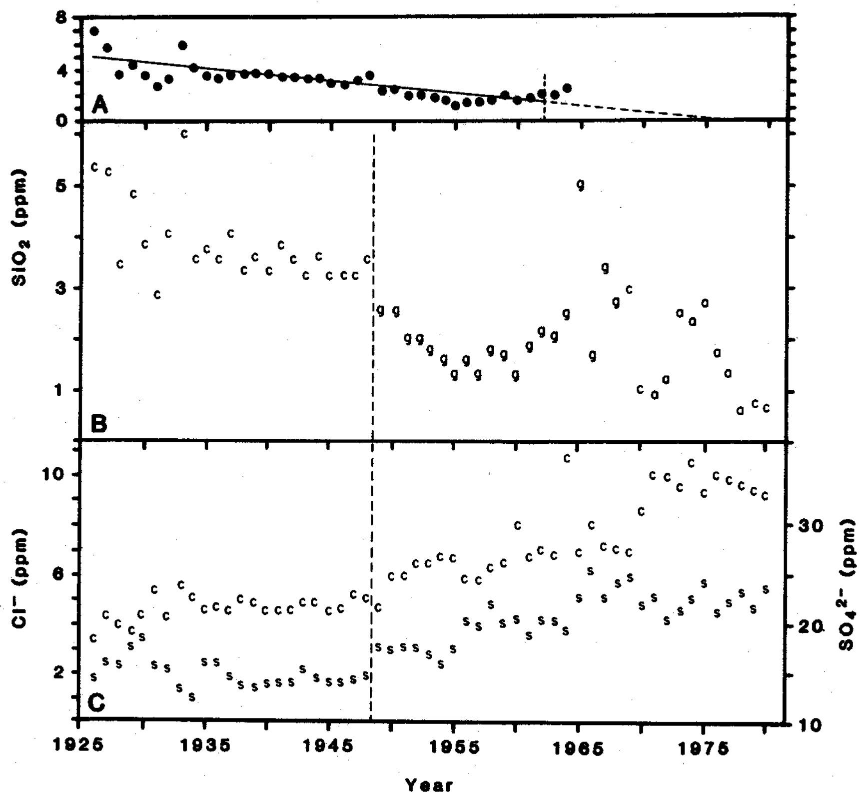

Fig. 5. Chemical factors measured in Lake Michigan at Chicago. A change in laboratories is shown by the dashed line at 1948-49. A) Annual SiO_2 averages with declining trend as published by Powers and Schelske and Stoermer. B) Annual SiO_2 averages calculated with data from the Harrison and Dever intakes. Methods of analysis: c = colorimetric, g = gravimetric, and a = atomic absorption. C) Annual averages for Cl and SO_4. From Shapiro and Swain (1983).

When changing between two methods designed to measure the same parameter, there are several obvious precautions that can be taken to reduce the chance of introducing uncertainty into a long-term record.

i) Investigators should run the two methods in parallel over enough samples and enough conditions and kinds of samples to allow for confident intercalibration of methods. (The same procedure may be desirable when changing technicians, especially for subjective or complex assays.)

ii) Investigators should keep a detailed protocol of their methods on permanent file. One of the great difficulties in correcting colorimetric pH data from lakes from the 1930's for comparison with modern electrometric pH's is that most investigators from the 1930's (as well as from the 1980's!) did not leave detailed protocols (Haines et al., 1983). What color indicator did they use? How many drops of indicator did they use? These protocols should contain even the most mundane details, so that a future investigator can repeat the methods unambiguously.

iii) Reference samples should be saved, if this is feasible (see section on sample banking).

iv) Methods should be changed as infrequently as possible. It may be desirable to build into the project some mechanism that resists changing procedures. For example, any changes in procedure at Rothamsted need to be approved by a committee.

If procedures such as these are followed, it should be possible to avoid many of the problems associated with changing methodology. A much more difficult problem arises when one method is to be replaced by a new method that measures something slightly different. For example, suppose that a limnologist involved in a long-term study has been counting bacteria from a lake (weekly, 5 depths) by epifluorescene microscopy. This procedure is widely used, but is tedious, slow, and somewhat subjective. After 10 years of study, someone develops a rapid, accurate, cheap method to measure the *biomass* of active bacteria. Even if the two methods are intercalibrated, they will never be directly comparable, because they measure different things. Should our limnologist adopt the new method? The answer to this question depends on the tightness of the intercalibration, the length of the data record collected using the old method, the relative goodness (cost, accuracy, speed, etc.) of the two methods, and the research questions for which the data are needed.

Sample banking. Scientists frequently retain samples taken as part of a study beyond the duration of that study. Samples are retained so thay can be reanalyzed to verify a suspicious datum, to provide more data by using a new technique that was developed since the sample was analyzed originally, or to provide information on some attribute of the sample that was not originally characterized. For instance, soil samples taken at Rothamsted prior to the discovery of radioactivity and kept in sealed containers were subsequently analyzed to provide an estimate of pre-atomic era background radioactivity. For these reasons, "banked" samples can be valuable, and are commonly held as part of a long-term studies.

Ecological sample banking has been the province of individual scientists, who have had to provide the space and curation of banked samples in anticipation of their eventual value. In addition to placing a burden on ecologists, this system has no provision for the long-term storage and curation of banked samples beyond the lifetime of the individual projects or scientists. As a result, samples frequently are discarded when space becomes dear or (especially) when scientists die or retire. Thus, although ecologists might wish for samples of Lake Erie water from 1920, rainwater from 1900 from the Adirondacks, or soil samples from an Ohio forest prior to the introduction of leaded gasoline, such samples are exceedingly scarce. Furthermore, ecologists do not now have any system to provide future generations with a systematic array of ecological samples.

One model for long-term banking already exists, in the form of museums that house specimens for systematics. These museums are numerous, and curate immense numbers of specimens for a long time. Solem (1975) surveyed the mollusk collections of North America; the following data from his paper (all for 1975) may be instructive. There are 26 institutions in North America that each house > 10,000 lots of mollusks, and 8 museums with > 160,000 lots each. In total, there are 3,700,000 lots of mollusks in North America, representing ca. 72,000,000 individual specimens. Many of these lots were collected prior to 1900, but collections are growing at a rate of 2.1%/year. This enormous resource is managed by 26 curators (some part-time) and a support staff equivalent to 44 full-time positions. Similarly large collections of vertebrates, insects, and plants exist.

Conventional museum specimens have been useful in some ecological long-term studies; for example, long-term changes in species lists (e.g., Strayer, 1980) or levels of contamination in the biota (e.g., Applequist et al., 1985) of well collected sites. However, systematic collections, naturally enough, are not ideal for ecological purposes. As a result, there has been a recent flurry of interest in developing "museums" to house ecological materials (Lewis et al., 1984).

Most of the authors in the Lewis et al. volume want to bank samples that can be analyzed for a broad range of substances, including contaminants such as trace organics, in the future. Consequently, sample collection and storage are sophisticated and expensive. The pilot specimen bank set up by the National Bureau of Standards (U.S.) involves collection of human livers in Teflon bags and storage over liquid nitrogen, at a set-up cost of $75,872 (1982) plus ca. $250/liver (Wise et al., 1984). Nürnberg (1984) estimated that a "medium-size" specimen bank of this sort would cost ca. $1,500,000 to build and ca. $2,500,000 per year to operate.

However valuable "clean" samples stored on liquid nitrogen will be, it is important to remember that much simpler samples may be of great use to ecologists. Dried samples may be of immense value in some ecological contexts, for example, and they are inexpensive to prepare and store. Rothamsted archives dried samples of grain and soil every year at a cost of ca. $500/year (King, 1984). In our opinion, ecologists need to do some creative thinking about developing national or international sample banks of various kinds.

Data management. Most long-term studies generate a large data set. Unless these data can be readily retrieved for subsequent analysis and interpretation, the long-term study is useless. We heard repeatedly about how important an effective data management system is to a long-term study; in particular, the data must be stored so that they can be readily retrieved and used by ecologists who are not database freaks themselves. Michener (1986) provides an introduction to database management for ecologists.

We encountered a wide variety of data management systems being used successfully by scientists doing long-term studies. Some long-term studies have invested much thought and money into large computer databases. For example, Oregon State's forestry department has a full-time Ph.D. and 2 master's-level technicians to design and manage the database resulting from studies at the Andrews Forest (Fig. 6).

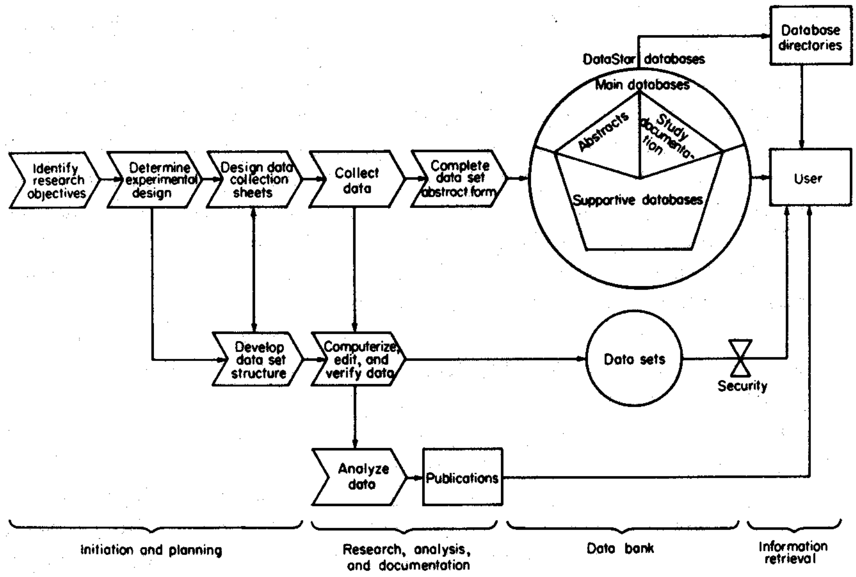

Fig. 6. Integration of the Forest Science Data Bank in the research process. From Stafford et al. (1984.)

Approximately 20% of the budget from LTERII at Andrews is devoted to data management. Data from many other studies, particularly those begun before the computer revolution, are still stored in notebooks. Surprisingly, the users of these data sets do not always regard such a system of storage as a serious liability. Ivan Heaney of the Freshwater Biological Association told us that it is quite easy to retrieve data from the notebooks containing 40 years of weekly counts of phytoplankton from four sites in the English Lake District. Apparently these notebooks provide the simple, accessible means of data storage regarded as essential by many practitioners of long-term studies.

We asked our questionnaire recipients how they stored their raw data, and received the following replies (the question allowed the respondent to check all categories that applied - see appendix): non-computer data files (77%), publications (64%), computer databases (67%), data reports (45%), and other methods (8% - including photographs, maps, theses, and a methods manual).

A related question is the availability of data collected in long-term studies to people outside of the long-term studies. Our questionnaire respondents told us that they released their data widely to scientific cooperators (84%), all scientists (61%), and even the general public (43%). Only one respondent indicated that some of the raw data from his study were unavailable for use by others. Some scientists told us that it has been troublesome to answer requests for data and they they sometimes have found others to use these data improperly. On the other hand, scientists outside long-term studies have been able to make good use of long-term study data in some cases. For instance, Tilman (1982) used data from Rothamsted's annual reports to support his theory of resource competition.

Statistical considerations. Occasionally, we heard complaints that statistical methods to analyze some kinds of data from ecological long-term studies are unavailable. This complaint perhaps applies less to long-term studies *per se* than to large, whole-system experiments, where logistical and financial considerations may prevent replication of treatments and true statistical controls. The feeling is that many basic statistical methods were developed for use on agronomic field trials (in fact, many of these methods were developed for the Rothamsted experiments by Fisher and Yates) and are inappropriate for many ecological data. Some ecologists seem to wish for a modern-day R.A. Fisher to develop statistical methods for such situations. However, the lack of replicability in many ecological field experiments may pose fundamental statistical difficulties (cf. also Hurlbert, 1984).

Personnel

Three personnel-related issues were raised frequently in our discussions: continuity of staff, the role of graduate students in long-term studies, and execution of the routine work. These are discussed briefly below.

Turnover of staff. Having a low turnover of staff was, along with continuity of funding, one of the features most frequently mentioned as contributing to the productivity of a long-term study (see appendix). There are some obvious advantages of maintaining a low turnover of staff. Staff continuity provides a mechanism to retain knowledge of procedures, so they can be recalled or repeated even without detailed written protocols. Long-term staff have developed knowledge of the ecosystem and the project that may be helpful in interpreting data and in designing further studies. Finally, long-term employees may exhibit loyalty to the project and be willing to devote extra effort when needed. One potential drawback with hiring staff for the long term is that their enthusiasm may flag in boring jobs.

Many long-term studies have long-term staff in some key positions (in addition to obvious long-term involvement of the project leaders). John Eaton, who currently oversees the laboratory analyses for the Hubbard Brook Ecosystem Study, has been with the project since 1965, although technicians for the Hubbard Brook project typically have turned over every 1-3 years. Similarly, M.P. Stainton came to the Freshwater Institute in 1967-68, and now heads the inorganic chemistry lab there. When David Schindler accepted the 1985 G.E. Hutchinson medal at the ASLO meeting in Minneapolis, he stressed that a remarkably high percentage of the ELA staff has been with the project for 15+ years. There are similar examples from other long-term studies.

It often is difficult to keep valuable staff members on with a project over the long term because of the lack of job security brought on by uncertainties in long-term funding, the low pay provided for many technical jobs, and the boredom of carrying out routine tasks over the long term.

What overrides such drawbacks in the long-term studies that have retained their staffs over the long term? It is our perception that staff members may be drawn by the feeling that they are part of an important, exciting scientific enterprise. At the ELA, all staff members are invited to participate in weekly discussions of the research, and David Schindler believes that the staff members feel that they are involved in the management of the project, and are "turned on" by the scientific research. However, when we asked others how they kept people on a project, or why they remained with a project, we did not get any clear answers.

Another obvious way to help keep staff on is to hire them on a long-term contract. The ELA is part of the Canadian government, so its employees are civil servants. However, a long-term contract cannot provide the motivation for people to stay with a long-term study so much as a mechanism.

A related thorny issue is whether long-term contracts for scientists enhance their productivity or propensity to conduct long-term studies. The Freshwater Biological Association (England) offers an illuminating example. Traditionally, the FBA has hired scientists for life following satisfactory performance in a three-year probationary period. During their tenure, FBA scientists have had considerable intellectual freedom or, as one FBA scientist put it, considerable autonomy to "ignore" advice from their governing board. It is tempting to attribute the many long-term studies done by the FBA (e.g., Sutcliffe et al., 1982; Elliott, 1984a,b, 1985 a-d; Lund, 1971, 1972, 1978; Lund and Reynolds, 1982; Craig, 1982; Macan, 1977; Crisp, 1984; to name a few) at least in part to their policies of hiring and their intellectual freedom (although, of course, we can offer no real evidence to support such a speculation) (If these factors do in fact encourage long-term studies, then it is ironic that the FBA is now being officially encouraged to do long-term studies at the same time that intellectual freedom is being reduced, and many staff are being hired on short-term contracts rather than lifetime contracts, due to severe cuts in British science budgets [LeCren, 1982; Clarke, 1985.])

The obvious argument against long-term contracts is that scientists on long-term contracts do not feel any responsibility or pressure to be productive. In fact, the FBA has been criticized as harboring scientific "dead wood" and being unresponsive to real and immediate societal needs for ecological information.

Who does the routine data collection? Sample collection and analysis form the heart of most long-term studies. These routine jobs may be done by the project leader (e.g., Evans, 1975), graduate students (e.g., the Hutcheson Memorial Forest; Buell and Forman, 1982), technicians paid either by grant funds (e.g., Hubbard Brook water chemistry) or by supporting agency (Coweeta's gage records), volunteers (e.g., L. Roy Taylor's moth work; Taylor, 1979), undergraduates, students in a class (e.g., Van Cleave, 1940), or, commonly, some mixture of workers. Members of these different groups vary in commitment to the project, turnover rates, availability, training, cost, and so on, so they will have different suitabilities for different research projects. Although it has been suggested to us that the project leaders or technicians are best for handling routine data production, this is often not practical, and it is apparent from the examples cited above that other classes of workers have been used extensively and successfully in long-term studies.

The role of graduate students. One concern frequently mentioned about long-term studies is a perceived incompatibility between long-term studies and graduate education. The argument is that graduate students, who are responsible for a large fraction of ecological research, need to find research projects of 1-3 years' duration and are therefore excluded from long-term studies.

Our committee does not see any real incompatibility between long-term studies and graduate education. We see at least three ways that graduate students can participate in long-term studies.

1. A student can do a 1-3-year study within the context of a long-term study. This is probably the most common way that graduate students participate in long-term studies (e.g., Cook, 1981; Cook and Schindler, 1984; Murtaugh, 1981a,b; Ross 1982; Ross and Wallace, 1983; among many others).

2. A student can collect and/ or analyze the routine samples that provide the backbone of the long-term study itself. Typically, the student is paid and receives experience in the operation of a long-term study, but does not participate in the analysis or write-up of the data. This is another common role of graduate students in long-term studies. If graduate students collect or analyze routine samples, special care must be taken to ensure consistency and continuity of the program between students.

3. A student can analyze and write up long-term data, even if he did not participate in the collection of data. This is rarely done, probably because scientists are reluctant to give up the responsibility of data analysis and because graduate students are expected to collect new data as part of their training. Nonetheless, it should be possible for students to assist in the analysis and interpretation of long-term data, perhaps as a complement to their main thesis research (e.g., Frye, 1978).

The best evidence that graduate students can be integrated successfully into long-term studies comes from large long-term studies in ecosystem ecology (ELA, Hubbard Brook, Coweeta), where graduate students have made important contributions. For example, at Hubbard Brook, 29% of the 394 papers published during 1971-1984 include a graduate student as an author, and an additional 5% have an undergraduate as an author. The chief role of graduate students at Hubbard Brook has been #1 (above).

The students at Hubbard Brook used long-term data sets themselves but less frequently than other workers at Hubbard Brook. Thirteen percent of the graduate student papers used a long-term (> 5-year) data set, compared to 24% of all other papers (Fig. 7).

Finally, we point out that it may be especially important to involve students in long-term studies to give them some insight into the special values and problems of long-term studies.

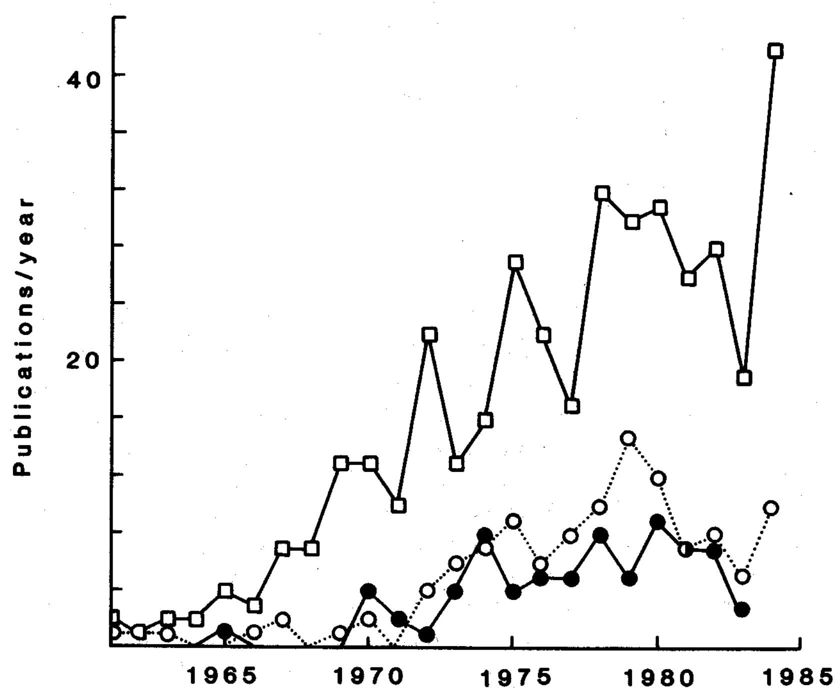

Fig. 7. Time course of publication of the Hubbard Brook Ecosystem Study: (□______□) = all publications (excludes abstracts and theses); (o........o) = publications having a graduate student as an author; (•______•) = publications using a long-term (>5-yr. record. Based on P. Likens (1985).

Monitoring

The subject of "monitoring" almost inevitably arises in discussions of long-term studies. On the one hand, many successful practitioners of long-term studies stress the importance of monitoring key parameters of an ecosystem as the core of a long-term study. For example, the research program at Hubbard Brook and Coweeta includes the regular (weekly, monthly) measurement of the amount and major-ion chemistry of precipitation and streamwater, both in experimental and reference plots. The data from these routine monitoring programs has been called "a national treasure" (Likens, 1983) and the most valuable contribution of Coweeta (W. Swank, pers. comm.) by the principals in these long-term studies. Monitoring data have provided essential support for many of the research projects and publications arising from many long-term studies (cf. Fig. 7). Furthermore, monitoring programs occasionally have led to important and entirely unexpected discoveries: e.g., the first report of acid precititation in North America was a serendipitous product of the monitoring program at Hubbard Brook.

However, monitoring has a low status in ecology, as shown by its frequent appearance as "just monitoring," or "merely monitoring." Monitoring is widely regarded as requiring little originality or intelligence to conduct and as unproductive of new scientific knowledge.

To caricature this view, we might define monitoring as a program where a second-rate scientist measures fifteen commonplace variables weekly for 10 years and produces a mass of data of uncertain quality that are never used by anyone for anything. This unsympathetic view of monitoring may be in part responsible for chronic difficulties experienced by long-term studies such as Hubbard Brook and Coweeta in obtaining funding to support their long-term monitoring programs.

We do not deny that some monitoring programs have been unimaginative and ultimately unproductive. We see this as evidence that some monitoring programs have been poorly designed and executed, just as some laboratory studies, simulation models, and whole-system manipulations have been poorly conducted, not that monitoring itself is an intrinsically flawed strategy. We believe that we are echoing the feelings of many who are doing long-term studies when we argue that the essential importance of good monitoring programs must be recognized and that such studies receive the funding that they require.

We especially like the idea of monitoring that was described to us by David Sutcliffe and Moshe Shachak. These scientists see as the essential elements of a good monitoring program:

i) The initial sampling design, variables to be measured, and methodology must be carefully chosen (just the same as in any kind of ecological study!). For example, the selection of sampling sites and frequency should be based on a preliminary knowledge of the spatial and temporal variation of the parameters of interest. It may be necessary to develop or modify methodology to conduct the monitoring program optimally; this has been done at least on a few occasions (e.g., Lund, 1951; Lund et al., 1958; Likens et al., 1967; Stainton, 1973).

ii) A scientist who is interested in and capable of interpreting the data should keep abreast of the data as they are collected. This allows for the publication of interim results, alerts the scientist to any "glitches" in the sample collection or analysis, and most importantly, allows the scientist to modify the design of the monitoring program to take advantage of his ever-increasing knowledge about the ecosystem under scrutiny.

iii) The monitoring program should be flexible. As the data come in and more is known about the ecosystem, it may be desirable to change the sampling sites or frequencies, or measured parameters. This flexibility seems to us to be one of the least appreciated aspects of a monitoring program; it provides a challenge to the scientist to make optimal use of his knowledge of the ecosystem.

Obviously, the trick here is to eliminate the unproductive or suboptimal parts of the monitoring program to make room for more fruitful ventures without destroying some part of the long-term core data that would have been of great value. Inevitably, a scientist will drop some part of a long-term monitoring program that he will later wish that he had not. For example, J.W.G. Lund (and now Colin Reynolds and Ivan Heaney) has been taking weekly samples of phytoplankton from four sites in the English Lake District since 1945. Early on, he took some pH measurements too, but discontinued them as being uninteresting. Had Lund continued his pH meaurements, they would have provided the longest continuous record of lake pH and been of great value in the current controversy on lake acidification. However, Lund probably made the correct decision based on the information available to him at the time. By advocating flexibility, we do not mean to suggest that a sampling program should be changed willy-nilly to accomodate changing fashions. As L. Roy Taylor (pers. comm.) has emphasized: "It is the *continuity* [of a long-term study] that is valuable; not the immediate interest. Otherwise, for example, Park Grass would have been vandalized by petty, superficial, ephemeral experiments decades ago."

iv) Finally, a point made by Lund and reinforced by others: the core monitoring program must not be so large that it consumes all of the time and resources of the investigator. The growing long-term record will periodically suggest questions that can be addressed by short-term experimental (or observational) studies. To make the best use of the monitoring program, the ecologist must have the time and resources to follow up on these questions.

Short-term justification for long-term studies

One of the most frequently mentioned drawbacks to long-term studies is that they must be justified in the short term or face termination. According to this view, a long-term study that does not justify its existence early on (before the long-term results come in) will lose funding or come under pressure to apply its resources elsewhere, where short-term gain is more apparent. Perhaps it is simply because long-term studies that did not produce short-term results have vanished, leaving us with those that were successful in the short term, but we are impressed by how productive long-term studies have been over the short term (Fig. 8). As Ehrlich (1979) stated: "Long-term studies need not be a gamble - discoveries made along the way

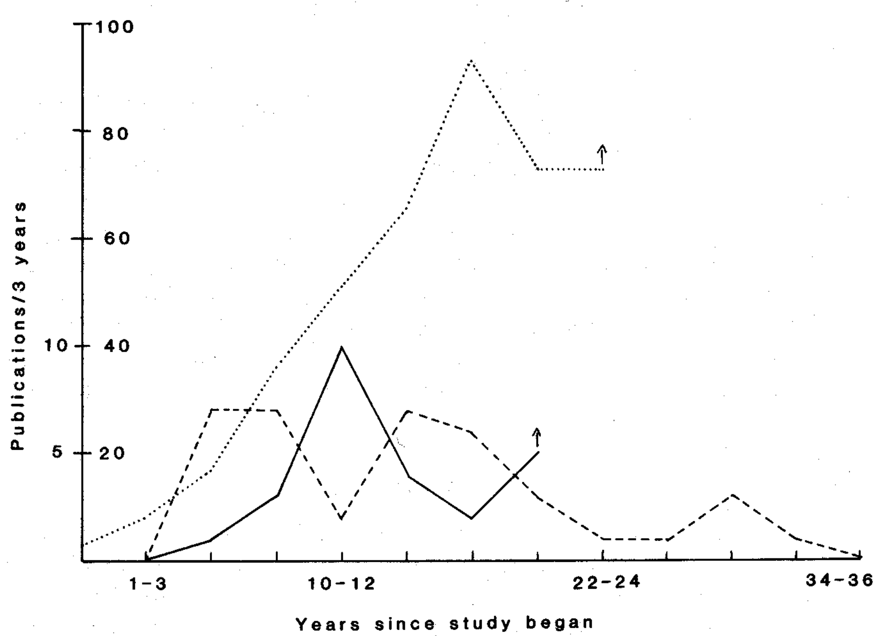

Fig. 8. Time course publication of three long-term studies: the Hubbard Brook Ecosystem Study (........); the F.C. Evans old-field study (-------); and Elliott's long-term study of brown trout (__________). Based on P. Likens (1985) on bibliographies supplied by Evans and Elliott; theses and abstracts are not included. Year 1 is the year the study began. The last point plotted for Hubbard Brook and Elliott includes only two years of publications.

provide more than enough grist for publications to satisfy deans and granting agencies." We suspect this short-term productivity means that scientists doing long-term studies have been aware of the desirability to produce short-term results, and have taken special care to do so. We do not see any general incompatibility between long-term studies and short-term productivity.

It is a separate issue whether long-term studies should be *expected* to produce short-term results. On the one hand, perhaps the necessity for short-term results forces the researcher to use his data aggressively and creatively, and keeps him on top of the growing long-term data set (cf. section on monitoring), resulting in a better, more productive research project. In this view, the requirement for short-term results helps to weed out complacency and scientific "dead wood." On the other hand, it would be a shame to prevent or stop a worthwhile long-term study simply because it would not produce results in the short term (note that the arguments here are somewhat parallel to those for and against long-term hiring policies).

Serendipity

There is a widespread perception among scientists involved in long-term studies that long-term studies often produce important serendipitous findings. Of course, short-term studies also result in serendipitous findings, and we have no objective way of knowing whether serendipity is enhanced in long-term studies. We did ask our questionnaire respondents whether their work resulted in any serendipitous findings. Although most (52%) of the respondents told us that they had made important, unexpected findings, examination of the examples given suggested that important, truly unexpected findings are relatively rare: we judged that only 18% of the respondents had made such findings, defining serendipity as an important finding that could not be (or was not) planned for in the original study design.

However, long-term studies have unquestionably produced some serendipitous findings of great importance. In some cases, scientists conducting a long-term study stumbled across a phenomenon that was total unexpected. Examples include the discovery of acid precipitation at Hubbard Brook (Likens et al., 1972), the elucidation of *in situ* production of alkalinity in experimentallly acidified lakes (Schindler et al., 1980; Schindler et al., 1985), and, perhaps most remarkably, the measurement of pre-atomic age levels of radioactivity later made on sealed samples of soil taken at Rothamsted before radioactivity itself was discovered. Alternatively, scientists have been able to assess the impact of rare events whose occurrence could not have been expected when the long-term study was designed. A good example is Goldman's observation of the effects of El Niño on Castle Lake, California (Strub et al., 1985). Finally, the results of a long-term study may, for whatever reason, trigger an important but unexpected theoretical advance. Paul Ehrlich told us that the roots of the Ehrlich-Raven work on coevolution were in Ehrlich's long-term studies on checkerspot butterfiles.

Self-evaluation

We have stressed at several points the importance of flexibility and continuing aggressive management of a long-term study. In this view, a long-term study that follows an initial design rigidly, without any modifications, is not making optimal use of increasing knowledge of the study system, improving methodology, and advances in general ecological understanding. However, aggressive management of a study implies a commitment to continuing self-evaluation. Where only a single (or a few) investigator is involved in the long-term study, this self-evaluation may simply be a regular, critical look at the project. For larger projects, it may be more difficult to perform a thorough self-evaluation. Some long-term studies have special mechanisms to insure a critical evaluation of the project. For example, the results of the ELA's whole-lake manipulations are reviewed during a series of weekly meetings held at The Freshwater Institute over the winter. All interested personnel from the ELA projects (as well as outsiders) may attend these discussions.

The role of synthesis and mathematical modeling

We already have referred several times to the value of occasional self-assessments of the long-term study as a whole. One common way that scientists accomplish this is through an overall synthesis of the results of the long-term study. This synthesis can offer a critical self-evaluation of the project, highlight important directions for further research, and provide a visible, convenient summary of the major results of the long-term study to scientists, students, policy makers, and others. Such syntheses have been done for many long-term studies that we studied (e.g., Evans, 1975; Likens et al., 1977; Bormann and Likens, 1979; Likens 1985; Allen, 1979; Coull, 1985b; Forney, 1980; Goldman, 1981; Kendeigh, 1979, 1982; Pomeroy and Wiegert, 1981; Schindler et al., 1985; and others). We see the preparation of these syntheses as one of the major responsibilities of the project leader (and indeed an important goal of any long-term study).

Mathematical modeling is sometimes used to aid, supplement, or provide such syntheses. There is a wide divergence of opinion of the importance of modeling in long-term studies (as elsewhere in ecology; cf. Pielou, 1980; Hall and DeAngelis, 1985). It would seem that a long-term study would be the perfect place to use a model in the iterative procedure described by some simulation modelers (e.g., Hall and Day, 1977), where modeling suggests research projects, the results of which are used to modify the model, and so on. In fact, models of one sort or another have had a prominent place in some long-term studies (e.g., Wiegert, 1977; Elliott, 1984a, b, 1985a-d; Patten and the Okeefenokee LTER). However, scientists involved in other long-term studies have actively rejected a central role for mathematical modeling (e.g., Schindler, 1973; Bormann and Likens 1979, p. 3). It should therefore be clear that productive long-term studies have been done both with and without mathematical models as an important element. It appears that the inclusion of a mathematical model may largely be a matter of personal taste.

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APPENDIX

Long-term study ______________________________

Respondant ______________________________

1. Why was the study initiated? ______________________________

____

____

2. Is this original objective still central to the study?

   _____ yes _____ no

   (if your answer is no, please elaborate)

____

____

3. Did the original design of the study involve an experimental manipulation?

   _____ yes _____ no

4. What year did the study begin? __________

5. Has the study been continuous? _____ yes _____ no

6. Please describe any gaps in continuity of the study and the reasons for their occurrence.

____

____

____

____

7. Who is in charge of the long-term studies?

   i. _____ an individual

   ii. _____ a special committee dedicated to overseeing the study

   iii. _____ an institution or agency

   iv. _____ other (please specify)

8. If an individual is in charge of the long-term studies, how many such people have served since the study began? __________

9. How many people work on the study?

	full time	part time
now	_____	_____
when the study began	_____	_____
rough average over the course of the study	_____	_____

10. *Rank* the importance of contributions of each of the following groups to the long-term study.

a. _____ staff scientists

b. _____ visiting scientists

c. _____ graduate students

d. _____ technicians

e. _____ secretarial and clerical workers

f. _____ undergraduate students

g. _____ other (please specify)

11. How are the raw data collected from the study stored?

_____ publications

_____ data reports

_____ computer database

_____ non-computer data files

_____ other (specify)

_____ data not stored (e.g., discarded or destroyed)

12. To whom are the raw data available? (check all that apply)

_____ general public

_____ all scientists

_____ scientific cooperators

_____ unavailable

13. What do you feel is the single most important attribute in the design of a long-term study to encourage the continued productivity of the study?

____

14. If you have a list of publications resulting from the long-term studies, please enclose it.

15. If you did not enclose a publication list, please summarize your record of publication below.

_____ number of papers in refereed journals

_____ number of books

_____ number of chapters in books

_____ other (specify)

16. How many Ph.D. theses, M.S. theses, and undergraduate theses have been completed in conjunction with the long-term studies?

_____ Ph.D. theses

_____ M.S. theses

_____ undergraduate theses

_____ other (specify)

17. Describe any extraordinarily significant finding that occurred *as a result of the long-term study* (i.e., results that were especially important in changing ecological concepts, public policy, etc.).

____

____

18. Describe any major serendipitous finding that could not have been discovered without the long-term study, but was not part of the original objectives.

____

____

19. Please summarize the approximate percentage of each type of funding in your budget, and mark the boxes showing the sources of your funding.

		government	other public	private
i. competitive grants	____ %	☐	☐	☐
ii. non-competitive grants	____ %	☐	☐	☐
iii. endowments	____ %	☐	☐	☐
iv. other (specify)	____ %	☐	☐	☐

20. How large is the annual operating budget for the study, averaged over the course of the study and (roughly) expressed in 1985 dollars?

    i. ____ less than $5,000/yr

    ii. ____ $5,000 - 50,000/yr

    iii. ____ $50,000 - 250,000/yr

    iv. ____ more than $250,000/yr

21. Please attach any reports about the design and history of the long-term studies.

22. If you have other comments about the design, execution, and importance of long-term ecological studies, please use the space below (or attach pages) to discuss them.

Thank you for your help.

Summary of the questionnaire responses

The following summary includes all of the questions that have straightforward, objective answers.

2. Is this original objective still central to the study?

   yes - 61
   no - 15

3. Did the original design of the study involve an experimental manipulation?

   yes - 37
   no - 38

4. In what year did the study begin?

   <1900 - 1
   1900-1930 - 0
   1931-1940 - 4
   1941-1950 - 7
   1951-1960 - 13
   1961-1970 - 19
   1971-1980 - 25
   1981-1985 - 7

5. Has the study been continuous?

   yes - 67
   no - 9

7. Who is in charge of the long-term studies?

   an individual - 63
   a special committee - 7
   an institution - 3
   other - 3

8. If an individual is in charge of the long-term studies, how many such people have served since the study began?

   1 - 43
   2 - 10
   3 - 4
   4 - 1
   5 - 3

9. How many people work on the study (average)?

	full-time	part-time
0	36	5
1	11	5
2	11	22
3	3	7
4	2	5
5	2	8
6-10	7	9
11-15	0	5
16-25	0	3
>25	0	2

10. Rank the importance of contributions of each of the following groups to the long-term study. (The figures listed below are mean ranks. Where the group was given no rank [= no contribution], we assumed a rank of 8).

staff scientists - 1.5
visiting scientists - 5.8
graduate students - 3.5
technicians - 3.8
secretaries - 6.1
undergraduates - 5.3
others - 7.2

11. How are the raw data collected from the study stored?

publications - 47
data reports - 33
computer database - 49
non-computer data files - 56
other - 6
data not stored - 1

12. To whom are the raw data available?

general public - 32
all scientists - 45
scientific cooperators - 62
unavailable - 1

13. What do you feel is the single most important attribute in the design of a long-term study to encourage the continued productivity of the study? (The answers have been edited somewhat to force them into categories.)

leadership - 10
good questions, goals - 7
continuity - 5
careful planning, design - 4
flexibility - 4
documentation - 4
adequate funding; manipulation; organization; consistency - 2 each
institutional base; good sampling; short-term yield; no pressure to publish; manageable size; good site; practicality; persistence; standard methods; length of study; public relations; data management; quality data- 1 each

15. Publication record (excludes abstracts and theses in the cases where we provided the numbers from a publications list).

# of pubs.	papers	book chaps.	books	others	total
0	18	31	49	37	8
1-10	19	20	11	17	32
11-20	8	5	0	2	8
21-50	7	2	0	4	10
51-100	6	2	0	0	7
>100	2	0	0	0	4
no data	16	16	0	16	15

16. Production of theses.

# of theses	Ph.D.	M.S.	B.S.
0	31	37	59
1-5	26	21	8
6-10	8	7	1
11-20	5	4	1
>20	2	2	1
no data	5	6	7

19. Summary of funding (figures shown below are mean %).

competitive grants - 47%
non-competitive grants - 26%
endowments - 5%
other - 19%

20. How large is the annual operating budget for the study?

<$5,000 - 25
$5,000-50,000 - 23
$50,000-250,000 - 15
>$250,000 - 8

Sources of information

A. Site visits

We met with the following scientists during our site visits.

University of Michigan, Ann Arbor — January 1985 (Strayer)
Dr. Francis Evans
Dr. Alfred Beeton
Dr. Eugene Stoermer
Dr. Ronald Nussbaum

Rothamsted Agricultural Experiment Station, England — October 1984 (Jones)
Dr. L. Roy Taylor
Dr. David S. Jenkinson
Dr. James McEwan
Dr. Ian Woiwod

Freshwater Biological Association, Ambleside, England — July 1985 (Strayer)
Dr. J.W.G. Lund
Dr. Malcolm Elliott
Dr. Ivan Heaney
Dr. David Sutcliffe

Institute of Terrestrial Ecology, Penicuik, Scotland — July 1985 (Strayer)
Dr. Fred Last
Dr. Philip Mason
Dr. David Fowler
Dr. Neal Cape

Institute of Terrestrial Ecology, Merlewood Research Station, England — July 1985 (Strayer)
Dr. Hugh Brown
Dr. Stewart Allen

H.J. Andrews Experimental Forest, Oregon — August 1985 (McDonnell, Canham)

Dr. Jerry Franklin
Dr. Mark Harmon
Dr. Fred Swanson
Ms. Sarah Greene
Dr. Paul Harcombe (visiting)
Dr. Art McKee
Dr. Susan Stafford
Dr. Tom Spies
Dr. Jim Sedell

Cedar Creek Natural History Area, Minnesota — June 1985 (Strayer)

University of Georgia, Athens — October 1985 (Kolasa, Berkowitz)

Dr. Eugene Odum
Dr. D.A. Crossley
Dr. Wayne Swank
Dr. Judy Meyer
Dr. Bernard Patten
Dr. Domy Adriano
Dr. John Pinder
Dr. Ken McLeod
Dr. D.C. Coleman
Dr. Paul Hendrix
Mr. Steven Schoenberg
Dr. Karen Porter

B. Interviews

These scientists were interviewed at IES by the full committee, except for David Schindler, who was interviewed by telephone by Strayer, Kolasa, and Parker; and Gene Likens and John Eaton, who were interviewed by Strayer and Parker.

Dr. L. Roy Taylor - October 1984
Dr. Durward Allen - September 1985
Dr. Moshe Shachak - October 1985
Dr. Arthur Hasler - October 1985
Dr. David Schindler - January 1986
Dr. Gene Likens - January 1986
Mr. John Eaton - January 1986

C. Questionnaires

We received questionnaires from the following scientists. 30 scientists did not return the questionnaires.

Durward Allen - the wolf and its prey on Isle Royale
Kenneth Armitage - The Kansas Biotic Succession Facility
Valerie K. Brown - insect/plant relationships during secondary succession
H. Casey - stream water chemistry in southern England
F.S. Chapin - Barrow IBP
Grant Cottam - prairie reestablishment at the Wisconsin Arboretum
Grant Cottam - succession in Noe Woods
Bruce Coull - meiofauna in North Inlet, SC
D.T. Crisp - effects of impoundment on fish populations at Cow Green, U.K.
H.C. Dawkins - ecological monitoring of woodland and open-cast spoil
W.T. Edmondson - saline lakes in the Lower Grand Coulee, Washington
W.T. Edmondson - Lake Washington
P.R. Ehrlich - Jasper Ridge checkerspot butterflies *(Euphydryas)*
J.M. Elliott - population dynamics of migratory trout *(Salmo trutta)* in a Lake District stream (UK)
Francis C. Evans - community dynamics of an old field at the E.S. George Reserve
Håkan Fogelfors - flora and vegetation in Swedish meadows (3 studies)

John Forney - fisheries and limnology of Oneida Lake, NY
Jerry F. Franklin - growth and mortality in western conifer forests
Jerry F. Franklin - successional processes in an old growth Douglas fir forest
Jerry F. Franklin - cone and seed production in true fir-hemlock forests of the Pacific Northwest
James R. Gammon - Wabash River communities
Lowell L. Getz - population fluctuations in *Microtus*
Charles R. Goldman - limnology of Lake Tahoe, CA-NV
Charles R. Goldman - limnology of Castle Lake, CA
J.R. Gosz - Tesuque watersheds, NM
Sarah Greene - growth and yield studies at Cascade Head Experimental Forest
Sarah Greene - Neskowin Crest Research Natural Area
James Halfpenny - University of Colorado Niwot Ridge/Green Lakes Valley LTER
C.B. Halpern - early stages of succession after logging and burning of Douglas fir forests in the western Cascades, OR
P.A. Harcombe - demographic analysis of tree populations, Big Thicket, TX
M. Harmon - ungulate exclosures in the Hoh rainforest, OR
M. Harmon - experiments on log decay, Andrews Forest, OR
J.L. Harper - population dynamics of species in a permanent pasture
G.F. Hartman - Carnation Creek watershed study (Canada)
Francis D. Hole - incorporation of organic matter into soils
Michael Huston - old field vegetation experiments at the University of Michigan Botanical Gardens
D.S. Jenkinson - the Park Grass experiment, Rothamsted
Dale W. Johnson - Walker Branch Watershed, TN
S.C. Kendeigh - bird populations in Trelease Woods, IL
S.C. Kendeigh - invertebrate populations in Illinois
W.K. Lauenroth - Central Plains Experimental Range LTER, CO
G.E. Likens - Hubbard Brook Ecosystem Study
Robert J. Livingstone - Apalachicola Bay, FL
John J. Magnuson - Wisconsin lakes LTER
M. Marten - the benthos of the River Fulda (Germany)
William H. Martin - tree-fall gaps in the Lilley Cornett Woods, KY
G. Richard Marzolf - Konza Prairie LTER
A. McKee - meteorological and hydrological measurements at the Andrews Forest, OR
K.W. McLeod - nutrient cycling in longleaf pine plantations, Savannah River Ecology Laboratory, SC
H.G. Miller - nutrient cycling and growth in a stand of Sitka spruce (Scotland)
G. Wayne Minshall - ecological effects of wildfire on stream ecosystems
Jennifer Owen - ecology of a suburban garden, U.K.
Robert T. Paine - structure and organization of rocky intertidal communities, WA
Bernard Patten - Okeefenokee Swamp LTER
Steward Pickett, Helen Buell, and Charles F. Leck - three studies at Rutgers' Hutcheson Memorial Forest
L.R. Pomeroy - Duplin River watershed, Sapelo Island, GA
C.S. Reynolds - phytoplankton of Rostherne Mere, U.K.
D.W. Schindler - the Experimental Lakes Project, Canada
P. Sollins - snowbrush project, Andrews Forest, OR
F. Swanson - changes in channel geometry and wood in streams
F. Swanson - inventory of small landslides
F. Swanson - movement of large earthflows in the Cascades and Coast Ranges, OR
C.O. Tamm - survival and flowering of perennial herbs
C.O. Tamm - Swedish Optimum Nutrition Experiments in forest stands
David Tilman - Cedar Creek LTER, MN
Ivan Valiela - Great Sippewissett Marsh, MA
W.G. Whitford - Jornada LTER, NM
B. Wilson - University of Massachusetts Forest