SUCCESSIONAL RESEARCH AND ENVIRONMENTAL POLLUTANT MONITORING ASSOCIATED WITH BIOSPHERE RESERVES

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SECOND U.S.-U.S.S.R.
SYMPOSIUM ON
BIOSPHERE RESERVES
MARCH 10-15, 1980
EVERGLADES NATIONAL
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MAN AND THE BIOSPHERE

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Miles A. Hemstrom and Jerry F. Franklin
Technical Editors

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United States and Soviet cooperation in the area of biosphere reserves is nearly as old as the biosphere reserve concept itself. A bilateral project on biosphere reserves was established under the agreement on Cooperation in the Field of Environmental Protection in 1974 (Project 02.05-41). Exchanges of information and visits between professional personnel have taken place regularly since that time. The largest of these was centered around the First U.S.-U.S.S.R. Symposium on Biosphere Reserves held in Moscow and other regions of the Soviet Union in May 1976. This symposium focused on the biosphere reserve concept and on considerations in selecting sites and development of research and monitoring programs (Franklin and Krugman 1979). This symposium provided the basis for subsequent development of cooperative programs between the two countries.

The Second U.S.-U.S.S.R. Symposium on Biosphere Reserves was held March 10-15, 1980, at the South Florida Research Center of the National Park Service, a facility located within Everglades National Park, Florida. Six Soviet and approximately 30 American scientists participated in the technical sessions and field trips. The Soviet delegation was led by Vladimir E. Sokolov, head of the A.N. Severtsov Institute of Evolutionary Animal Morphology and Ecology, and included V.V. Krinitskiy of the U.S.S.R. Ministry of Agriculture, L.M. Filippova and F. Ya. Rovinskiy of the U.S.S.R. State Committee for Hydrometeorology and Control of the Natural Environment, and P.D. Gunin and S. Veyisov of the U.S.S.R. Academy of Sciences.

Advances in the biosphere reserve programs of both countries were reflected in the selection of topics for the second symposium. The organizers wanted to move beyond general discussions to the development and implementation of specific environmental monitoring and ecosystem-oriented research projects. Consequently, the central topics of the second symposium were the study of natural and man-induced successional processes and the development of environmental pollutant monitoring programs.

Successional information is critical to all biosphere reserve programs--research, pollutant monitoring, and management. Changes induced by human activities need to be recognized and separated from those changes reflecting "natural" processes. Similarly, trends due to climatic fluctuations need to be distinguished from those reflecting intrinsic developmental changes in the ecosystem. Furthermore, this successional knowledge needs to be synthesized in mathematical models so that it can be used to predict rates and direction of change. Successionally oriented papers presented at the symposium provide basic philosophical perspectives on succession and approaches to research and modeling.

Environmental pollutant monitoring programs are developing rapidly in both countries as a part of national and international efforts. The design and initial results of some of these programs were a major topic of symposium papers on pollutant monitoring. A specific objective of the bilateral project is, of course, the development of a program with common objectives (e.g., in terms of selected pollutants) and technologies (e.g., sampling devices and analytical procedures).

The papers and discussions at the second symposium have furthered the objectives of comparable ecosystem research and environmental pollutant monitoring efforts on biosphere reserves in the United States and the Soviet Union. They are presented in this document in the belief that they will be of value to a larger group of scientists and managers who are concerned with nature reserves and ecological research.

Many individuals and organizations contributed to the success of the Second U.S.-U.S.S.R. Symposium on Biosphere Reserves, including all of the participants. Among the organizations are the National Park Service (U.S. Department of Interior), Forest Service (U.S. Department of Agriculture), The Nature Conservancy, and U.S. National Committee for Man and the Biosphere (U.S. Department of State). Dr. Gary Hendrix and his staff at the South Florida Research Center deserve special recognition for being the sympsium's gracious hosts in the meetings and in the field.

LITERATURE CITED

Franklin, Jerry F., and Krugman, Stanley L. 1979. Selection, management and utilization of biosphere reserves. USDA For. Serv. Gen. Tech. Rpt. PNW-82. Pac. NW For. and Range Exp. Sta., Portland, Oreg.

SUCCESSION OF ECOSYSTEMS: A PRELIMINARY COMPARATIVE ANALYSIS

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Abstract

Data are presented which relate the unpredictability of rainfall worldwide to the conspicuousness of the process of succession.

The main components of succession are identified and found to be similar to those proposed in 1916 by Frederick Clements.

The six principal world biomes are shown to differ in the nature of various aspects of successional processes. The differences among biomes, it is suggested, can be used as the basis of management decision-making during the reclamation of anthropogenically altered lands.

INTRODUCTION

Recently, ecologists have revived their interest in the process and the results of succession. This renewed interest was first stimulated by Drury and Nisbet (1973), whose work was rapidly followed by a plethora of both theoretical and empirical studies. This paper is not the place to review all of the accumulated data and ideas, rather the reader is referred to any of several reviews of the topic (e.g., MacMahon 1980a, White 1979).

Herein, I want to limit my coverage to a consideration of the ways in which various terrestrial biomes, particularly their plant components, differ in the processes causing succession and in the outcomes of these processes. For such a discussion I will first introduce two models of succession. One of these models is directed to explaining why succession seems so obvious (conspicuous) in some biomes (e.g., those that are forested in the climax), while in others no marked physiognomic differences between early and late seral stages are displayed (e.g., desert and tundra). The second model takes a series of processes thought to be involved in succession (Clements 1916) and attempts to develop a general model which portrays the interactions among these processes, regardless of the biota or specific locality involved. In fact, this model is also thought to portray any compositional change, over time, of an ecosystem. Both models have been more extensively developed in MacMahon (1980a).

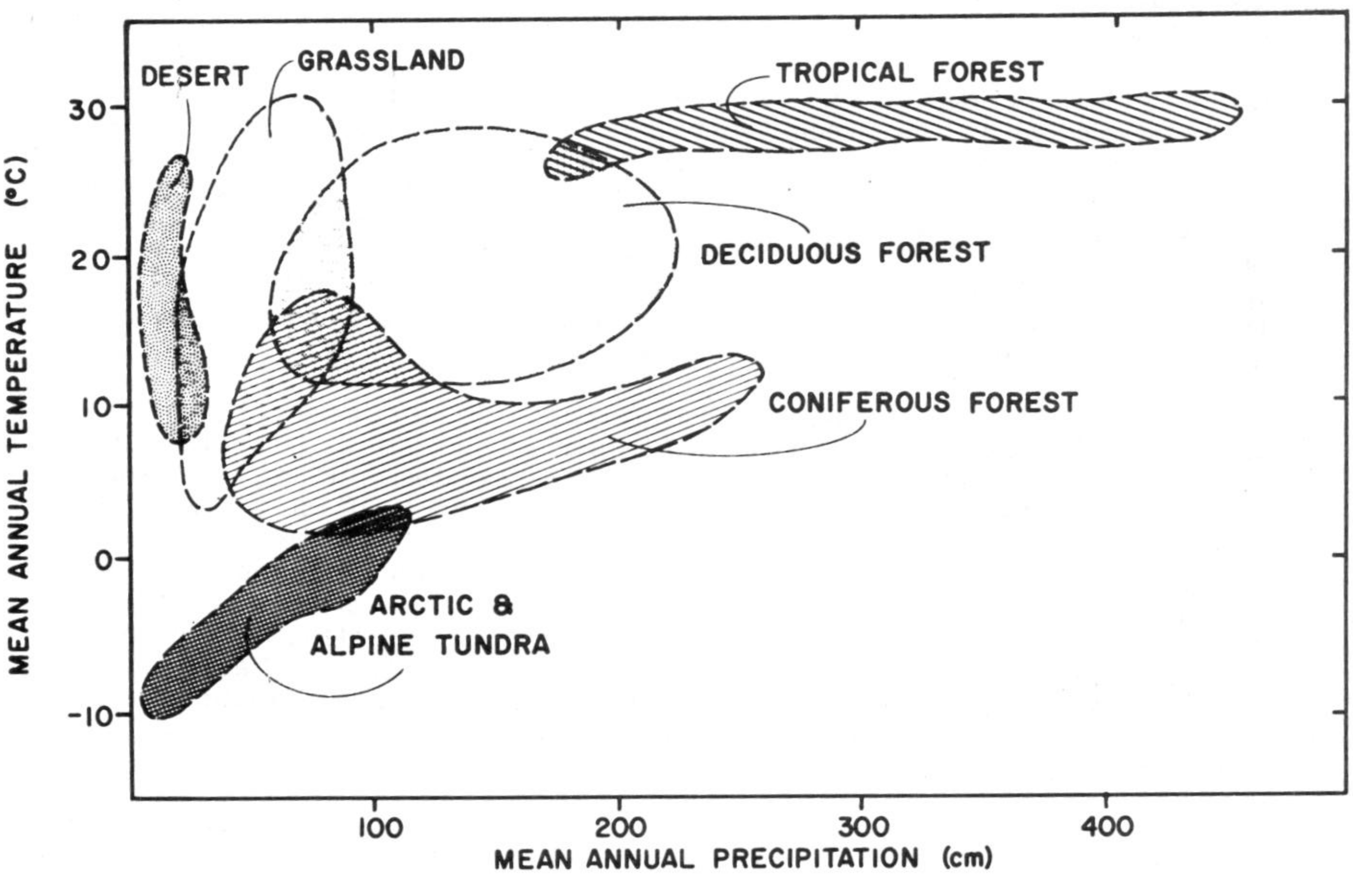
After the models are briefly described, I want to compare the processes of the second model across biome types, in an attempt to explain the first model. Additionally, the results of such an analysis suggest some management practices which might be homomorphic with natural process, and thus can be used to establish and maintain biosphere reserves.

WHY DOESN'T SUCCESSION APPEAR TO OCCUR IN TUNDRA AND DESERTS?

That unit of ecological taxonomy we term a biome is generally agreed to correlate, in a cause-effect manner, to combinations of temperature and water regimes which recur at various points on the earth's surface. Figure 1 depicts a simple, but generally acceptable, representation of such relations, and it names the broad biome types.

On this figure the two biomes which have the least conspicuous succession, tundra and desert (Whittaker 1974), seem not to be related in any close way. In both biomes workers have generally observed that after an area is disturbed, the recolonizing species are the same species as those forming the climax (Muller 1940, 1952). In other biomes, disturbance is generally followed by invasion of species not characteristic of the climax; not only does the species mix change, but the life forms of the species involved also change over the period of climax reestablishment. Thus, disturbance in forested situations is followed by

Figure 1: Depiction of the differentiation of biomes on the bases of temperature and rainfall. (Redrawn by permission, from Hammond 1972.)



invasion of annual "weeds," then in turn by perennials, herbs, and shrubs, and ultimately by a sequence of relatively distinct tree associations.

Situations where the climax dominants are also the post-disturbance colonizers are described by the term autogenesis. In contrast the term allogenesis refers to situations where conspicuous species and life form turnover occur following disturbance. Our task now is to find a correlation, presumably cause-effect in nature, which separates all biomes into one of two groups, characterized either by allogenesis or autogenesis.

While tundra and desert are not adjacent to each other in figure 1, they are most similar on the precipitation axis. It is well known that as mean annual precipitation decreases the variance of the precipitation increases. This relationship causes environments wherein species, or assemblages of species, are subjected to extreme values of precipitation. Additionally, and perhaps more importantly, the precipitation is unpredictable. While plants adapt to various types of environmental extremes (Levitt 1972), many fewer species seem capable of adapting to the combination of extreme and unpredictable environments (Grime 1977, 1979).

In figure 2, I plot weather station records for a number of localities around the world. These data are superimposed on a grid delimiting biome types as defined by Whittaker's (1975) system. Using published literature, I checked the local biome type for about 50% of the weather stations to see if the biome designations resulting from the graph were appropriate. In all cases checked this was true. Once a biome type was assigned according to the weather station data, the variation of annual rainfall (variance of the log of the mean annual rainfall) was plotted against mean annual rainfall (figure 3) for each station. Deserts and tundra are clearly lumped in this presentation on the ascending arm of the curve, while grassland and all forest types cluster sequentially on the horizontal arm of the curve.

I infer that this depiction (figure 3) suggests that the degree of unpredictability of rainfall correlates in a cause-effect manner to the highly artificial allogenic-autogenic dichotomy discussed above. The proximate cause for the dichotomy seems to involve two separate attributes. First, there is no difference between pioneer and climax species because all species which can occupy the disturbed site are similarly adapted to unpredictable environments, which occur in such areas. Thus there is not a diverse pool of variously adapted species to replace one another over time to form a sere. I hasten to note that what I say above does not infer a low species diversity (#/ha) on desert sites compared to other biomes. In fact the environmental unpredictability may actually enhance species diversity in deserts (MacMahon 1980b). Second, the harshness and unpredictability of the environment prevent organisms from significantly altering, over time, the sites they occupy. That is, the abiotic factors preclude biotic alteration of the environment, and this in turn prevents a biotically induced allogenesis.

The result of these two tendencies is that when a desert or a tundra is disturbed, it is revegetated by the climax species because they are

Figure 2: Plot of weather data (taken from Clayton 1944 and Clayton and Clayton 1947) from various world localities on an overlay of biome limits (adapted from Whittaker 1975, p. 167). D = desert, F = deciduous forest, T = tropical rain forest, G = grassland, C = coniferous forest, A = tundra. (Taken by permission from MacMahon 1980a.)

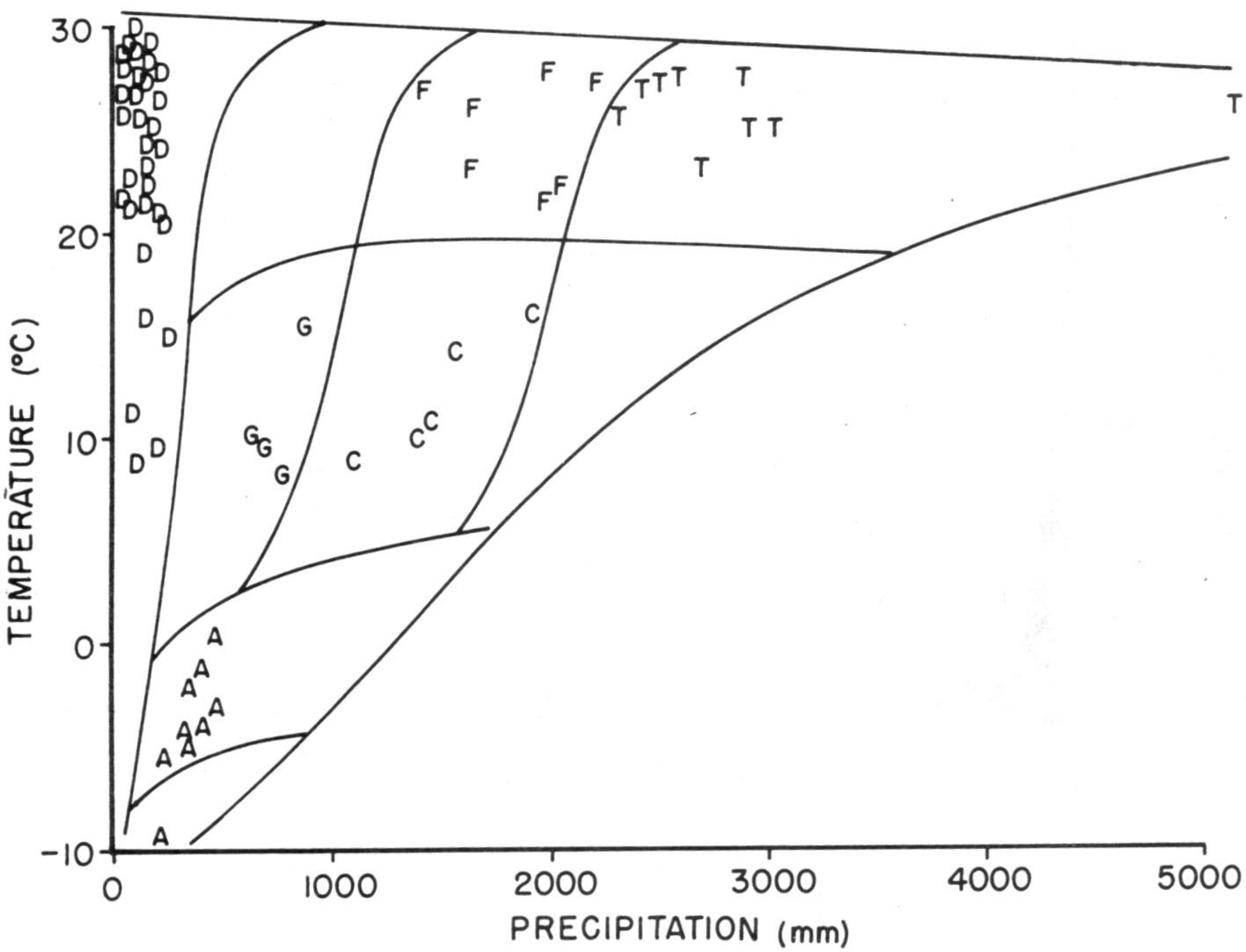
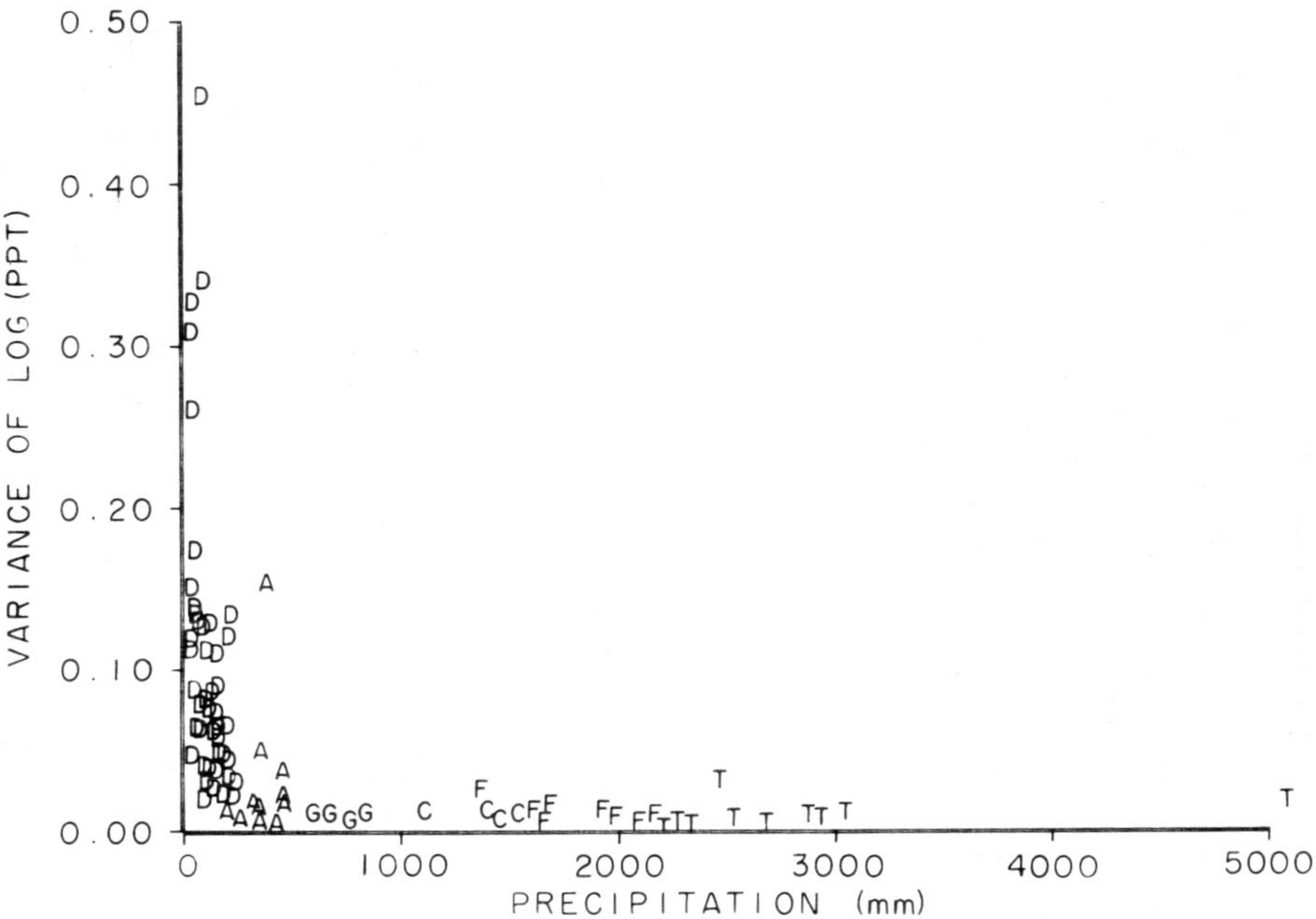


Figure 3: A plot of the variance, the log of mean annual precipitation vs. mean annual precipitation for various world weather stations. Data and biome designations are as in figure 2. (Taken by permission from MacMahon 1980a.)



geographically proximate and the only ones adapted to the unpredictable environment. When this occurs no apparent succession takes place, although, as I will develop below, I believe the same processes occur following disturbance on all sites.

WHAT ARE THE PROCESSES RESPONSIBLE FOR SUCCESSION?

Clements (1916) described three phases and six processes which occur during succession (table 1). Despite the fact that much of Clements' work has been ignored, I suggest that he clearly and correctly identified the critical parts of the succession phenomenon.

Table 1. Clements' (1916) three major phases and six basic processes of succession.

Initiation
- 1) Nudation
- 2) Migration
- 3) Ecesis
- 4) Reaction

Continuation
- 5) Competition

Termination
- 6) Stabilization

A scenario for a sere, using Clementsian terminology, would be as follows: 1) A site is disturbed, say by fire, and thus opened to invasion (nudation process). 2) Propagules of species either survive the disturbance *in situ* (residuals), or they migrate onto the disturbed site (migration process). 3) All propagules, residual or arriving *de novo*, must be able to survive the conditions of the site, establishing themselves, growing, and reproducing, if they are to be a part of that sere (ecesis process). 4) Those species surviving on the site will vie for limited resources, thus altering species proportions (competition process). 5) The various species, due to their particular attributes, may actually alter the site characteristics (reaction process). For example, they may increase soil nitrogen content by symbiotic fixation or change soil temperature by their shading effects. These alterations essentially make a different site, i.e., the properties of the disturbed site are no longer the same as they were immediately after disturbance. In fact the species mix on a site at any instant may create an environment unsuitable for their own successful reproduction and continued occupation of that site. This being the case a different set of migrants may be successful at establishing themselves and these new forms must undergo ecesis and competition. 6) This cycling of species (seral stages) will continue until all the species on a plot can exist and reproduce in the environment that they produce and maintain. This equilibrium represents the climax (stabilization process) and persists until some change in the environment (biotic or abiotic) occurs.

We can take Clements' approach and cast it in a more modern framework, that of ecological modeling, as in figure 4. A detailed discussion of this model, and of the implication of each of the processes to the vector of succession, is not appropriate here. Details of the model are available in MacMahon (1980a).

The point I wish to make is that the six processes discussed above seem adequate to describe the dynamics of the succession phenomenon. What we can then do is ask the question, "How do the six major processes occurring in succession differ among biomes?" We may also ask how these process differences affect the "conspicuousness" of succession, i.e., the apparent differences along the autogenic-allogenic continuum.

HOW DO BIOMES DIFFER IN THE NATURE OF THEIR SUCCESSIONAL PROCESSES?

Using available literature, I have attempted in a general way to characterize the successional processes for typical examples of the various biomes (figure 5). Second, I have attempted, using some numerical data and best guesses, to show the forms of the relationship between the processes and the biomes, the latter ranked by their position along the presumed allogenic-autogenic continuum (figure 6; positions derived from figure 3).

Below I discuss the various successional processes, emphasizing the variations in the importance of different factors within the various biomes. Here, I plead for understanding from the reader. I am attempting to seek worldwide patterns of successional processes at the level of the biome--a difficult task at best. It would be easy to quibble with any one minute detail of the presentation. I would hope that the reader, rather than taking too critical a purview, will be impressed, as I have been, that there even seems to be a very general pattern. The references presented are meant to suggest the correctness of the forms of the functions in figure 6. They are not meant to represent an exhaustive compendium.

Figure 4: A model of the change in the status of the components (organisms and chemicals) of a plot of ground over time. Boxes are states of the plot at any instant. Diamonds are system drivers. The circle is an intermediate variable. Dashed arrows show information flows. Letters next to control gates replace dotted lines from that point to the control for the sake of graphic simplicity. (MacMahon 1980a.)

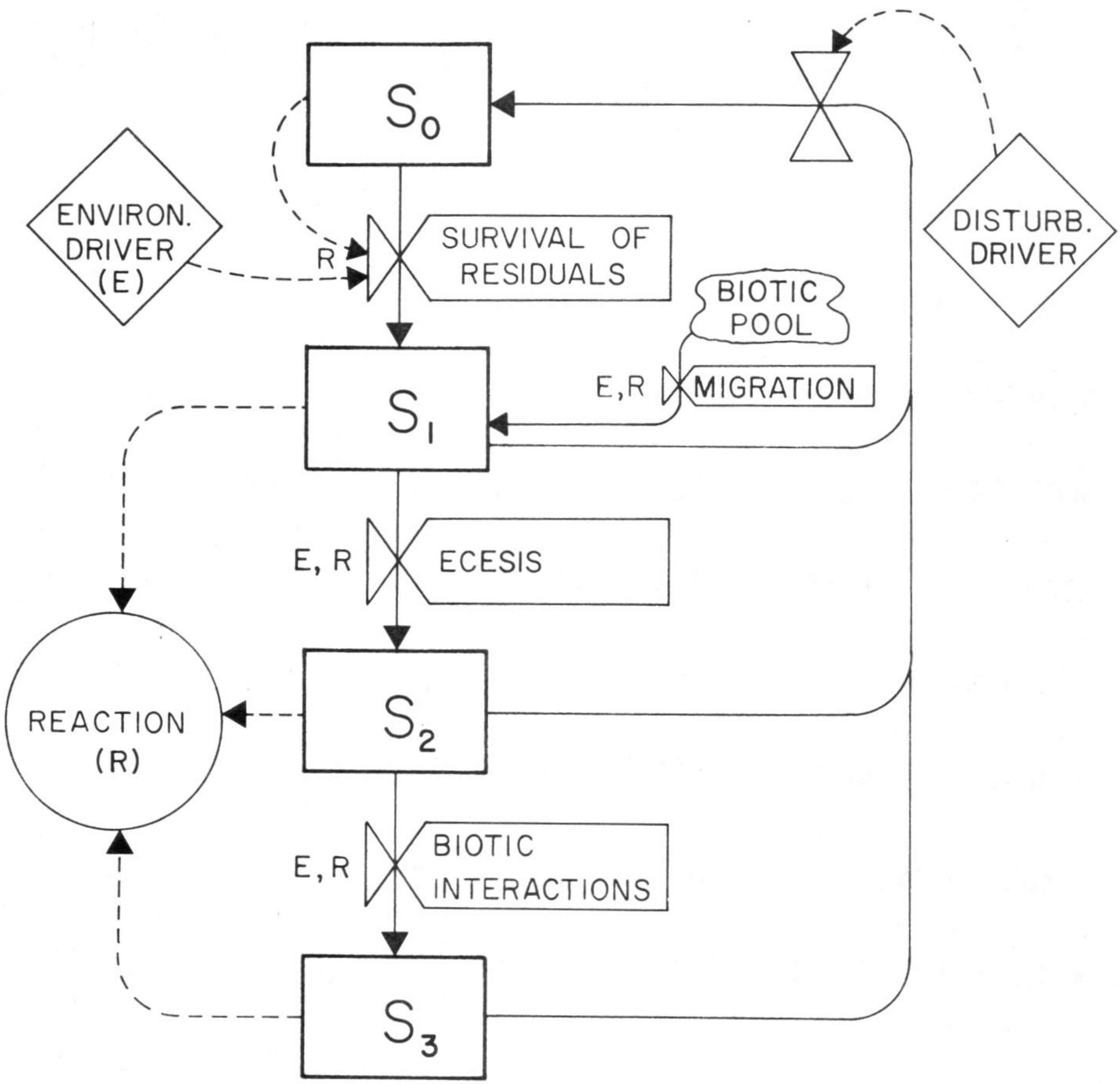


Figure 5: A comparison of the differences in successional processes across the various biomes. The sequence of biome types is from sequencing of biomes derived in figure 3. The specific comparisons summarized are NUDATION - factors most important in creating a disturbance; MIGRATION - the major type of migrules or propagules initiating site recovery; ECESIS - the constancy of and rate at which establishment occurs when propagules are available on a site; COMPETITION - relative importance of water and light as limiting resources; REACTION - the degree to which the seral biota alters a site's chemical and physical environment; STABILIZATION - rate at which the site's biota stabilize, i.e., "climax" occurs; MISCELLANEOUS - degree of physiognomic and species turnover during succession.

	DESERT	TUNDRA	GRASSLAND	CONIFEROUS FOREST	DECIDUOUS FOREST	RAIN FOREST
NUDATION	drought	cryo-planation	fire	fire/ wind	wind/ senescence	senescence/ wind
MIGRATION	seed reserves	non-seeds	seeds and non-seeds	seeds	seeds	seeds
ECESIS	periodic	slow-periodic	moderately fast	mod. fast (variable)	fast	very fast
COMPETITION	water	water	water/ light	light/ water	light	light
REACTION	low	moderately low	moderate	moderately high	high	very high
STABILIZATION	fast	fast	moderately fast	slow	slow	moderately slow
MISCELLANY	no physiog. no species	no physiog. no species	mod. physiog. high species	high physiog. high species	high physiog. high species	high physiog. high species

Deserts

Desert sites are opened to invasions by the death of older plants and perhaps by the occasional denudation of a species or life form by drought or unusual bouts of freezing. Fire, floods, wind, and even animals seem not to be the prime movers initiating secondary succession. This does not deny the cyclic vegetation pattern changes associated with the movements of unconsolidated aeolian deposits such as sand dunes (see, for example, the case in the southern Simpson Desert [Fatchen and Barker 1979]), nor the possibility that if fuel buildup occurs that a desert fire could alter succession (Humphrey 1974); I merely relegate these factors to the rare or of-little-importance category.

While it is difficult to show that desert shrubs encounter attrition significantly through senescence, the 9,400 year old Larrea clones of Vasek (1980) clearly show this possibility.

A disturbed desert site generally contains large numbers of seeds in the soil reserves, e.g., 70,000/sq m (Reichman 1978). These, coupled with other vegetative propagules, form the main source of regrowth individuals. In deserts, periods favorable to establishment, as detailed above, are unpredictable and widely separated in time. Because of this, ecesis is slow to occur. When it does occur, however, the resulting species mix is that of the climax. The time for near "climax" groupings to reestablish is 30-50 years (Vasek et al. 1975). Competition following establishment may be for water in moderately dry deserts or may not occur at all in the driest sites where the environment maintains plant populations below the level where competition is a factor (Gulmon et al. 1979; Phillips and MacMahon 1980).

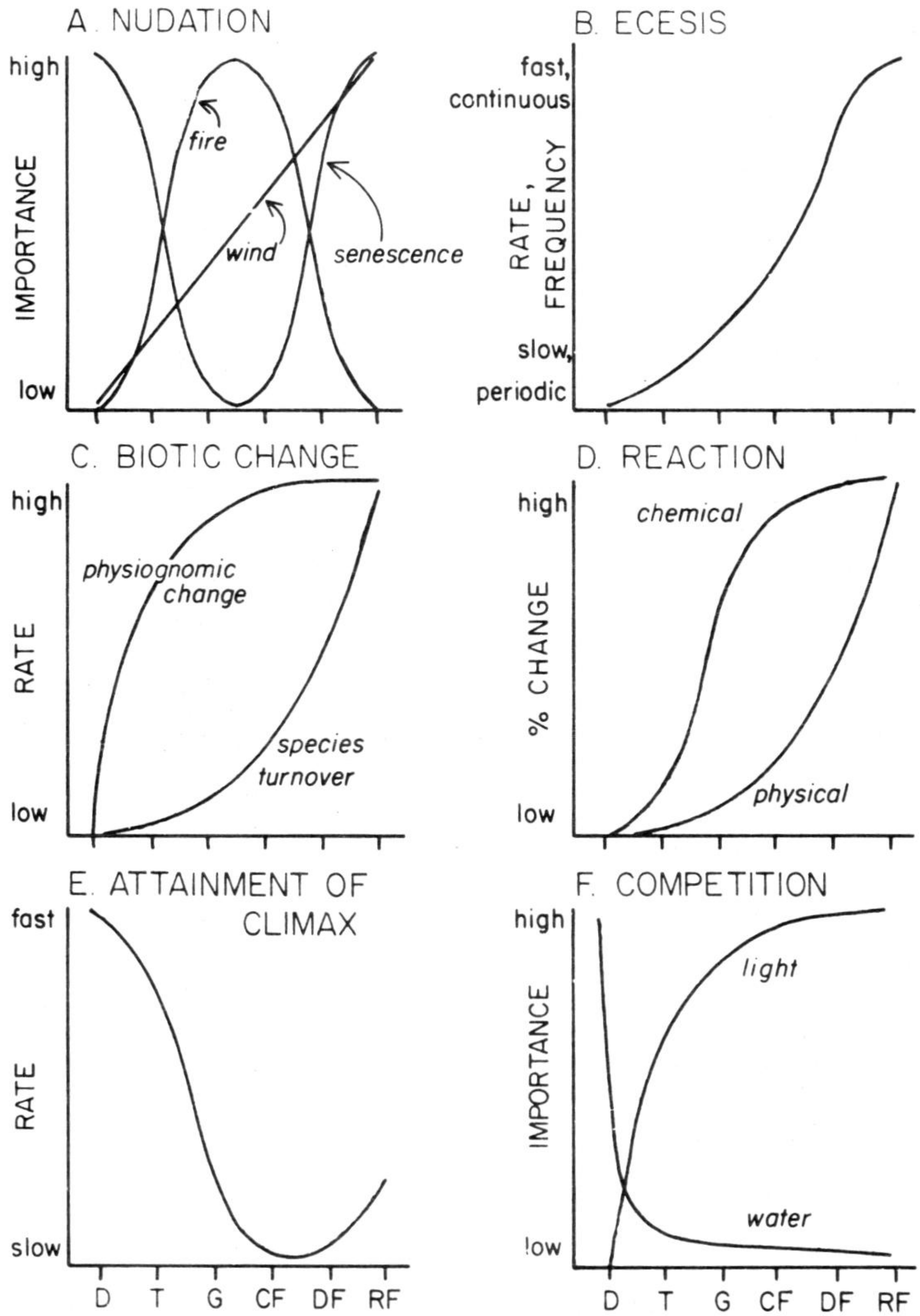
While desert plants alter the physical environment, this is a small effect compared to other ecosystems because of their sparse (less than 20%) coverage. Again, I am aware of the "island of fertility" effect of desert perennials and their role as "nurse plants" for other perennials and annuals (see review in Schimpf et al. 1980); however, compared to other ecosystems they change their environment very little.

Tundra

Tundra plants seem to live for long periods of time, frequently until they lose vigor or senesce, unless they are disturbed by soil movement caused by factors such as congeliturbation (Sigafoos 1951, Churchill and Hanson 1958, Gimingham and Smith 1970, Dahl 1975). Some cyclic or phasic changes occur in response to autogenic processes (Churchill and Hanson 1958). Thus, natural disturbances denuding large areas are not as common as in some ecosystems.

When disturbances do occur, vegetative propagules may form the major dissemules (Gimingham and Smith 1970, Bliss 1971). Diaspores frequently travel very short distances. In one study (Elven and Ryvarden 1975)

Figure 6: Hypothetical trends for some aspects of successional processes as they vary over a diversity of biomes. (Biome sequence is as in figure 3.)



87% of the diaspores collected moved less than 5 m. Large denuded areas may be slow to receive dissemules, may have low diaspore reserves in the soil, and may thus have a long establishment period. Once dissemules arrive on a site and finally establish, the "climax" species composition persists for reasons outlined earlier, though the proportions of the various species may not represent the Arctic climax mixture (Bliss et al. 1973, Webber 1978).

The addition of organic matter to mineral soils changes the soil properties, including solifluction characteristics. Despite this, the harshness of the physical environment moderates the effects of plants on the total abiotic environment, and reaction is thus moderate.

Grassland

Nudation in grasslands can be caused by periodic drought (e.g., Albertson et al. 1957) or more frequently by fires (Borchert 1950). In fact some grasslands worldwide may exist as fire-induced communities (Blydenstein 1968; Komarek 1968, 1971), though such interpretations are frequently open to question for specific sites (Beard 1953). In many areas where grazing agriculture is practiced, overgrazing, often caused by containing cattle within fenced areas, may denude the ground surface, altering the plant species mixes. Native herbivores seem not to be such a strong denuding force in Africa and North America, where they were once abundant. It is interesting that the tropical Americas seem not to have had large numbers of native herbivores. Perhaps instead of consumers feeding or grazing in the new world tropics, the plant material goes directly to decomposers, such as the numerous termites (Beard 1953).

Migration and subsequent establishment of grassland species involves both seeds and vegetative plant parts. The pattern seems to suggest, however, that vegetative parts are the more important (e.g., see Weaver and Bruner 1945). Since many prairie grasses reproduce vegetatively, it is difficult to address the problem of senescence in grasslands. Indeed it is not even clear what constitutes an individual plant in many instances. Grasses alter the chemical and physical properties of the sites they grow on quite significantly. Soil temperatures are moderated, and significant changes in the chemistry of the profile occur after grass establishment. Climax, when it occurs, may be reached in as few as 20 years or so following disturbances affecting individual plants (e.g., drought) in contradistinction to the much longer regeneration periods required where significant soil alteration has occurred.

Coniferous Forests

Coniferous forest sites are frequently denuded by fire (Kilgore 1973, Loope and Gruell 1973) although wind or ice storms can also play a significant role (Sprugel 1976, Bratton et al. this document). The opened areas are regenerated by both seeds and vegetative propagules. It is surprising that at times 40% to 75% of these are vegetative propagules (Pfister this document). For other studies significant numbers of seeds have been recovered (e.g., of 456 propagules/sq m found by Archibold [1979], 87% were seeds and 13% were roots or rhizomes), although seeds decrease percentagewise in their viability as one goes poleward (Johnson 1975). Establishment of annuals and herbaceous perennials is rapid (1-5 years), barring an extreme environment or the devastating effects of certain animals (e.g., pocket gophers and mice). Animals may also slow down the rate of conifer establishment by preying on virtually all seeds (Sullivan 1979) and seedlings during some periods (e.g., Black et al. 1979). The time course of succession in coniferous forests is quite variable, but depending on factors relating to the persistence of the meadow stage, it may take 200-1,000 years (Schimpf et al. 1980). While plants in conifer seres moderate the abiotic environment, their effects on soil changes seem to be limited to the upper layers (Schimpf et al. 1980). This may be related to the relatively shallow root systems of many of the conifers forming climax communities.

Deciduous Forests

Of all the world biome types, probably more data have accrued from studies of temperate deciduous forests than from any other vegetation. The literature is voluminous and need not be repeated here (the reader is referred to Bormann and Likens' [1979] excellent summary of the Hubbard Brook studies, which should ensure the veracity of my general statements--even though the disturbance [nudation] was clear cutting). Additionally, excellent qualitative summaries of succession are given by Curtis (1959).

Wind (e.g., Stearns 1949; Bratton et al. this document) and fire (though the rotation period may be 500-1,000 years [Bratton et al. this document]), depending on the exact site, are common causes of natural nudation. Deciduous trees, lacking a snowshed aspect, also suffer during severe ice storms (Lemon 1961). In temperate forests throughout the world, a more common disturbance is the clear cutting of timber by man. In any event denuded sites frequently contain large numbers of seeds, often more than 12 million/ha--all viable (Bormann and Likens 1979, p. 110). Frequently early establishment includes not only pioneer species but may include climax species as well, especially in deciduous forests (Drury and Nisbet 1973). The changes in the environment of a particular plot over time are significant and include those associated with the wind-caused tip-ups of nudation (Armson and Fessenden 1973) as well as the reaction of seral vegetation (Olson 1958). In some cases this is so strong that woody invaders have been hypothesized to change prairie to forest (e.g., Aikman and Smelser 1938).

The changes during forest succession are slow because the tree life form, especially when more than one tree form occupies different times in the sere, is slow to develop. Additionally the strong reaction phase, limited seasonally by winter, takes place slowly. Thus, while species richness may attain climax levels in 100-200 years, it takes 300-400 years for biomass and nutrient storage to occur and 500 years for age and size class distributions to stabilize (Bormann and Likens 1979, Bratton et al. this document).

Rain Forest

Rain forest trees, once established, may live for long periods of time, (100-1,000 years [Budowski 1970]). It may also be true that epiphyte loads of tropical trees can increase their tendency to fall down or be blown down (Strong 1977).

When openings occur, usually as mosaics rather than over large areas, it is seeds of species other than those in the canopy which are there and can germinate (Aubreville 1938, see also review in Farnworth and Golley 1974). Seeds have frequently been dispersed by animals, and soil reserves can, therefore, represent complex assemblages. Establishment of new flora is rapid because of favorable growth conditions, but since the species are not those of the canopy, unless the disturbed area is very small, there will be a long series of species replacements preceding the eventual recovery to climax (Richards 1952).

The recovery process is further complicated by the very prominent effect of the vegetation on the abiotic environment, including soil. The impacts of illumination, soil temperatures, and rainfall on an opening are so different from those in a mature forest that the rain forest, more so than almost any other community type, shows significant examples of the reaction process. In fact increased light may favor germination of early successional species rather than climax canopy forms (Longman and Jenik 1974). It has even been argued that the extreme environmental gradients from gaps to closed canopy may enhance tropical species diversity (Ricklefs 1977). Because so many changes, environmental and floral, must take place and because the mature forest trees grow slowly (Richards 1952), climax attainment takes a long time. Many details reinforcing patterns mentioned above can be found in Tomlinson and Zimmerman (1978).

THE PROCESSES

At the risk of being redundant, I should like to recap, at the process level, the trends listed in figures 5 and 6. I hope the additional emphasis will underline my general points.

Nudation (figures 5 and 6A)

In ecosystems where species are adapted to environmental extremes, chances are individuals live to maturity and beyond, finally senescing and being replaced. At the other extreme--rain forests--the favorableness of the physical environment also permits individuals to live out their life expectancy. In between, plants are subjected to perturbations which prevent them from surviving long enough to senesce.

Two of the many destructive forces common to several biomes are fire and wind. Fires do not have enough fuel to be carried in deserts and tundra, except rarely. Conversely, the most mesic sites (rain forests) are too wet to burn. Thus, it is the intermediate biomes that produce sufficient fuel and are dry enough to burn significantly often. In some such systems, like pine forests, the frequency of the burn interval may be as little as 5-10 years.

Wind as a force initiating succession increases in importance where senescing individuals, which are more susceptible to blowdown, occur. Desert and tundra senescent individuals are adapted to strong winds and are not as susceptible. Other factors play a role in the importance of wind, not the least of which is the global distribution of winds.

Migration (figure 5)

Many propagules get to a denuded site. There does not seem to be an obvious trend in the ratio of vegetative/sexual propagules which successfully colonize sites across biomes, except that vegetative reproduction seems enormously important to most biomes, with the main exceptions being the opposite ends of the biome spectrum presented, i.e., deserts and rain forests.

Ecesis (figures 5 and 6B)

The unpredictable nature of deserts and tundra enhances the delay of "good years" which permit establishment of propagules. As the environment becomes more equable, the frequency of establishment success increases.

Competition (figures 5 and 6F)

Biomes of an open physiognomy are not light limited. However, even relatively open grasslands may have some shading and thus competition for light. Obviously, this effect increases rapidly as the number of synusia or the foliage density within them increases.

Places wet enough to support overlapping synusia generally are not water limited, while ecosystems developing in zones of low and unpredictable water may force species to compete for water. In the extreme case, for example, the very dry Atacama Desert, so few plants may exist that they do not compete for water, a possibility I do not represent in figure 6F.

Parenthetically it is important to point out that I have not overlooked the potential importance of plants competing for nutrients. They were not included because the world patterns are not that clear with regard to succession. Local soil chemistry and even allelopathic effects complicate this beyond my ability to generalize at this time.

Reaction (figures 5 and 6D)

Here, I infer that while tundra and desert plant communities alter the soil chemistry of their environments, they are too sparse to alter the aboveground or belowground physical parameters to the same extent. At the other end of the spectrum, rain forests moderate the physical environment much more than any other ecosystem, but probably they do not change soil chemistry proportionately much more than does a deciduous forest.

Stabilization (figures 5, 6C and E)

Attainment of climax is very rapid in deserts and tundra and even, to a lesser extent, in grasslands because the climax species are the postdisturbance colonizers and because there is very little physiognomic change between early and late succession.

Stabilization (equilibrium) is attained much more slowly where long-lived, slow-growing species with physiognomies different from early colonizers must develop to reestablish climax. This is characteristic where the tree life form dominates and thus forests are slower to reach climax, despite faster establishment rates of plants on sites following disturbance. The more favorable growth rates of plants in the tropical environment permit faster rates in those forests as compared to their temperate counterparts.

Succession is most easily recognized where there is high species and physiognomic differentiation between early and late succession. Biomes with the greatest development of the reaction process and physiognomic change take longer to develop and are classically those sites--forests--thought to exemplify successional processes.

A WORD ABOUT MANAGEMENT STRATEGIES

This is not the place to develop management schemes for every biome. However, an example may suggest the utility of applying the theory developed above to manage perturbed ecosystems--i.e., those where the denudation is anthropogenic.

The problem of desert or tundra succession is not one of preparing a site chemically for the climax species (reaction) but rather of establishing (ecesis) the final species mix. Thus, germination and survival requirements of climax species would be the manager's concern. To the contrary, climax species in forested situations may require a modification of the disturbed site which mimics the results of autogenic reaction processes--a different management strategy requirement from that above.

Careful consideration of differences among successional processes, across different biomes, may permit man to optimize the management procedures he chooses for overcoming the effects of anthropogenic perturbations. After all it seems only reasonable that mimicking natural processes, to which plants have evolved over thousands of years, would be more efficient than erecting an artificial scenario de novo.

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MAJOR EVOLUTIONARY TRENDS, SUCCESSION, AND FLUCTUATIONS IN THE MAJOR SAND-DESERT ECOSYSTEMS

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CONSERVATION, USE, AND STUDY OF DESERT ECOSYSTEMS

The U.S.S.R. deserts cover a vast territory (about 200 billion ha) and account for 14%-15% of the whole area of the country. Despite their use for centuries, man has not caused great changes in either the nature or appearance of desert communities. In the 20th century, however, significant human impacts on desert ecosystems have occurred because of intensive development and use.

Programs for preserving natural sand-desert ecosystems should be based on landscape and climatic concepts of deserts that account for specific organizational characteristics of their ecosystems. The development of thinned-out shrubs, mainly the *Haloxylon persicum* / *Carex physodes* association, is attributed to the abundance of solar energy, high radiation and air temperature values, lack of moisture, and predominance of sand soil over significant areas. Sharp variations in climatic factors cause considerable seasonal and long-term fluctuations of life processes and, ultimately, affect fodder crop productivity. This result, in turn, complicates forecasts of pasture use and calculations of maximum permissible loadings. Weak biological cycling associated with a rather poor sand substrate (light in weight) and the hot climate make ecosystems with thin soils susceptible to fast depletion and destruction.

Consequently, sand-desert ecosystems are a category of particularly sensitive landscapes. Their life "film" is thin and easily vulnerable, and it has a lowered capability for regeneration. The disturbed cover does not regenerate for many years and sometimes for decades; the biological productivity drops abruptly, areas lose their value as pastures, and sites can turn into barren sandhills (barkhans). The limited attention paid to nature conservation in deserts is explained by the popular idea that deserts are "errors of nature" which are to be corrected by man. Such a simplified idea of the relation between man and desert did and continues to do irreparable damage to the development and transformation of deserts. Loss of some species of plants and animals and destruction of natural ecosystems are subsidiary consequences of economic development, which can make it impossible to regulate the use of natural resources and, in a number of areas, can create a real danger of intensified desertification.

All this necessitates that the problems of use, preservation, and reproduction of desert resources be studied independently, since deserts are very sensitive to external ecosystem impacts. Such a problem formulation agrees with the plan of action adopted by the U.N. Conference on Desertification Problems (August 29-September 9, 1977, Nairobi) where it was stated that desert biosphere reserves could be used as baseline stations for monitoring desertification and for training appropriate specialists (U.N. 1977).

ECOSYSTEM CHARACTERISTICS OF THE REPETEK BIOSPHERE RESERVE

The eastern Kara-Kum, where the Repetek Biosphere Reserve is located, is an alluvial sand plain subjected to aeolian processes on the surface. All principal types of sand-desert ecosystems of the Kara-Kum are present in the reserve, which has an area of 34,600 ha. There are large ridges, valley-type lowlands with *Haloxylon ammodendron*, uneven and cellular sands with *H. persicum*, barkhans with thinned-out psammophilous arboreal and shrubby vegetation, and also other ecosystem types. Although these ecosystems are observed over the rest of the Kara-Kum, the location of all of them within a small area makes the landscape of the reserve unique. It differs from other sand-desert landscapes mainly because large ridges, valley-type lowlands, and uneven sands are all present. The combination of these ecosystems determines the spatial landscape structure typical for sand deserts and the different functional roles which the ecosystems play in the large-ridge sand landscape of the eastern Kara-Kum.

H. ammodendron, which forms small areas of a "desert forest," is a very interesting and original type of ecosystem. Growing under favorable conditions--valley-type lowlands with fresh and low mineralized groundwater--*H. ammodendron* reaches 4-5 m in height (sometimes 8-10 m) and forms rather thick brushwoods. At present such haloxylons are rare in the Kara-Kum, so they present a most valuable natural example.

The ecosystems of uneven sands and barkhans are widespread in the reserve. Uneven sands are more often turfed with sedge; also *H. persicum* grows here, and unlike *H. ammodendron*, it almost never forms thick brushwoods. *H. persicum* communities include different species of shrubs: *Ephedra*--the only representative of gymnosperms, *Calligonium* sp., and *Salsola* sp. (*S. richteri* and *aellenia*). This type of ecosystem is a typical community in the Kara-Kum, where it is valuable as pasture and should, therefore, be comprehensively studied. Barkhan ecosystems contain many species--both herbaceous (*Aristida pennata*, *A. karelinii*) and arboreal (*Ammodendron conollyi*, *Eremosparton flaccidum*, *Calligonium* sp., etc.) endemics which are adapted to existence in sand and therefore are called psammophytes. These species are irreplaceable subjects for studies of plant adaptation to extreme environments.

CLIMATIC FLUCTUATIONS AND THEIR EFFECT ON VEGETATIVE COVER

Since the sand deserts of central Asia are a zonal type of the desert biome ecosystem, due to their homogeneous composition, they can be used as priority ecosystems in studies of how one or a few factors dominate in the determination of life processes and exogenous sucession of the vegetative cover. The existence of organisms in desert ecosystems is essentially limited by the lack of moisture and high temperatures which cause aridity in the environment and are a function of the climate. According to climatic zoning, the Repetek Biosphere Reserve belongs to the category of southern deserts, with distinct continental climates characteristic of extratropical continental deserts.

Besides wide diurnal temperature fluctuations, the area is characterized by sharp transitions from hot summers to rather severe winters. The mean annual air temperature is 16.1°C while that of the soil is 19°C. Mean air temperatures during the warmest summer month range from 29° to 33°C, while temperatures of the sand are 7°-8°C higher (37°-40°C). Mean soil and air temperatures in winter are about 1°C. The amplitude of diurnal air temperatures is about 20°C, and the amplitude of the sand surface temperature is 60°C for 24 hours and up to 100°C for a year.

The frost period with snow is about 10 days. Winter temperatures often drop to -10° to -30°C. The maximum air temperature recorded at the Repetek Biosphere Reserve was 50°C in July 1944, which appears to be a record for the whole territory of the Soviet Union. Sand temperatures on such days can reach 79.4°C. The minimum air temperature, -31°C, was observed in January 1969. The length of the frostless period is 235-280 days. There are 49 days with mean diurnal temperatures higher than 30°C, and 283 days with temperatures higher than 5°C. The sum of temperatures greater than 5°C is 5,719°C, and of temperatures greater than 10°C, 5,331°C (Reference Book on the Climate of the U.S.S.R., 1967). The longest season of the year in the eastern Kara-Kum is summer, which lasts more than five months (April 28 to September 27).

In the annual temperature regime of sands in the eastern Kara-Kum, two periods are noted: a period of sand warming (January-July), which is characterized by accumulation of heat in sands, and a period of cooling (July-January), characterized by gradual loss of heat from surface sand horizons.

Mean annual total precipitation in Repetek is 113 mm. Precipitation distribution is irregular both seasonally and from year to year. The analysis of the histogram of annual precipitation distribution for 50 years (1913-1917, 1926-1975) shows that years with total precipitation from 100 to 125 mm account for 22.8% of all cases. Years with precipitation below the mean (43.2%) and above the mean (34.0%) are more common. Years with very moist conditions (117-225 mm) amount to 10% of the total, and those with very arid conditions (less than 50 mm), 5% of the total. The relation between the most arid and the rainiest years is 1:10. For example, in 1917 the total precipitation was 24.3 mm, while in 1953 it was 229.5 mm.

Meteorological conditions in a particular year significantly affect the year's phytomass production in the desert area. The effect is not only upon the increase in phytomass of the shrubs, but also on aspects of their regeneration and on the abundance of herbaceous species. Periodic regeneration of plants is characteristic of the Kara-Kum. Good climatic conditions for producing seeds and for emergence and establishment of seedlings occur approximately once a decade (Nechayeva 1958).

Annual grass crops are seldom dominant in the vegetative cover. Some of them form characteristic and picturesque synusia, but only under favorable climatic conditions. During arid years the role of annuals decreases, and some species completely disappear. Because of a large diversity of species and a variable ecology, however, annuals play more important roles in the vegetative cover in some years (Nechayeva 1979). Annuals in the Kara-Kum account for 57%-63% of the species. They are divided into winter and nonwinter annuals. In relation to flowering, these groups are divided into six phenological sections: winter-spring (18 species), early spring (39 species), midspring (33 species), early summer (31 species), summer (15 species), and summer-autumn (13 species). The species composition of annuals in relation to species number and phenological sections is not constant, rather it changes abruptly from year to year depending on weather conditions. Nevertheless there are annual species which are observed yearly in herbage, although their occurrence, weight, contribution, and number vary between years.

The productivity of herbaceous vegetation, particularly for subcrown microgroups, depends on a complex of conditions: air temperature regime, precipitation during the vegetative period, and the depth of wetted soils and accessible soil moisture content. Total precipitation, total positive temperature, and their combination and distribution throughout the whole vegetation period are the primary determinants of productivity. In the eastern Kara-Kum the total positive air temperature from October to April from 1969 to 1975 ranged from 1,548°C to 2,080°C, and from February to April it ranged from 739°C to 1,117°C. Of 15 vegetation years, the following years were considered favorable in terms of moisture conditions: 1963/1964, 1968/1969, 1972/1973, and 1973/1974. Precipitation distribution during the whole vegetation year, and also during the period of growth, is important in determining herbaceous vegetative productivity.

There is a direct relation between the productivity of different herbages and precipitation amount. When precipitation for the period January-May is 80-90 mm, productivity is low; when precipitation is more than 140 mm, it is high. The same relation exists between the productivity of summer annuals and precipitation.

The soil moisture content accessible for plants is an important factor for productivity, principally annual grass crops (Togyzayev 1972). Moisture content reached 40-100 mm in rainy years (1964, 1969, 1973), but only 6-10 mm in arid years (1965, 1968, 1971, 1979).

The yield of subcrown microgroup herbages varies most of all. For instance, the terrestrial phytomass of Carex physodes in the intercrown space ranges between 77.0 and 213 kg/ha while that of the subcrown group ranges from 2.0 to 364.8 kg/ha. Consequently, the yield of C. physodes, which dominates in the herbaceous cover, increases or decreases only two or three times, while annual yields vary greatly.

Studies show that vegetative groups can be divided according to the degree of their susceptibility to variations in herbage yield. The groupings of C. physodes, which gives a relatively high yearly yield, are most stable; cereal groupings (Bromus tectorum, Erimopirum, and Shesmus) are less stable and do vary, but they yield annually; ephemeral groupings vary significantly, with very low yields in certain years; and, finally, summer annuals such as Koshia schrenka, produce yields only in favorable years.

HYDROGENIC SUCCESSION AS PRINCIPAL EVOLUTION DIRECTION

The arid climate and subsequent desert landscapes, which are characteristic of the modern central Asian plains, were established during the Pliocene (Fedorovich 1964, Kurkov 1968). Considering the Repetek Biosphere Reserve territory as an integral part of the Kara-Kum, one should note that, as a result of direct and indirect effects of the Amu Darya River and its tributaries, conditions close to those of the present were established only in the middle Pleistocene. That was the period when wind became the major factor in the formation of topographic relief, explaining the occurrence of the principal first-order relief forms: large ridges, interridge plains, and additional development of valley-type lowlands. The final ecosystems and vegetative cover adapted to modern climatic conditions formed in the late Pleistocene.

The problem of increased central Asian aridity was noted by M.P. Petrov (1966) and should be considered in two aspects: the process of climate aridization and the process of increased territorial aridity, i.e., the process by which the area has assumed characteristics of progressive aridity. The information required for correct problem-solving can be obtained from long-term observations of the dynamics of the main components of the sand desert: dynamics of sand relief forms, successional changes in the vegetative cover, and years of climate fluctuations. The reconstruction of paleogeographical conditions and the determination of the genesis and evolution of certain communities are very important.

Ecosystems of interridge and valley-type lowlands in sand deserts located on ancient alluvial plains underwent the hydromorphic stage of formation. At present only the phreatophyte formation (Haloxylon ammodendron) of all the plant communities preserves some mesophytic characteristics. Gradual increases in groundwater mineralization over most of the area and drops in the level of the freshwater tables have determined the trends in exogenic succession toward the climax sand-desert community, which is represented by a monodominant composition of ombrophytes in shrubbage and herbage which occupy different temporal ecological niches. This type of succession does not relate to climatic changes and can be called hydrogenic. The processes which take place can be characterized as drying processes. The duration and spatial distribution of the processes indicate their dominant nature and irreversibility. One should note that this type of hydrogenic succession, which is now being observed in Haloxylon ammodendron / Carex physodes communities, depends to a significant extent on successional changes close to sand ridges. The replenishment of freshwater tables with vegetation below barkhans deteriorates when ridges are gradually overgrown.

Because of local underground streams, freshwaters in the table spread over neighboring valley-type depressions that were covered with desert forests (H. ammodendron), from which water escaped as a result of evaporation and transpiration. Studies show the groundwater level has a one-vertex curve, with the maximum level in the second half of April and the minimum level in the last third of August or first third of September. From year to year the groundwater level does not reach its previous position and each year it appears to be lower. Groundwater levels in H. ammodendron communities drop by approximately 1.0 cm yearly. The absolute groundwater levels in wells show that the water level has dropped by 39-42 cm in 40 years.

Decreases in freshwater flow in valley-type depressions result in gradual increases in mineralization. Estimates are that the annual increment at some sites ranges from 70 mg/l to 150 mg/l. Therefore, changes in these two important indices of inputs to phreatophyte communities at a certain stage undoubtedly affect the vitality of H. ammodendron individuals (table 1) and finally can radically change the vital conditions of the ecosystem.

H. ammodendron communities close to the reserve are used economically. First of all they have been used for a long period of time as pastures and for cutting. Regeneration of H. ammodendron under cutting was first studied on a 1-ha experimental site within the reserve territory in 1932. Thirty seeded individuals of H. ammodendron were left. In 1952 after a corresponding check of arboreal and shrubby vegetation, H. ammodendron was again cut down except for 34 seeded individuals and juveniles (up to 2 m). Since then the whole community at this site has functioned under a reserve regime. The arboreal and shrubby vegetation was checked in 1951, 1961, 1965, 1970, and 1977 (table 2).

In 1977 the number of trees of H. ammodendron was 747 or 72.7% of the total number of trees and shrubs on the 1-ha experimental area. Of these, 507 trees or 67.9% of the H. ammodendron were in a good or satisfactory state of vitality; 193 or 25.8% were in a semidried state; and 47 or 6.3% were in a dried state.

Table 1. The state of Haloxylon ammodendron in the Repetek Biosphere Reserve.

Place	Characteristics of H. ammodendron	1967 Vitality Satis-factory	1967 Vitality Die-off	1967 Percent die-off	1972 Vitality Satis-factory	1972 Vitality Die-off	1972 Percent die-off
North Valley	High-trunk (5-7 m)	185	0	0	180	5	2
	Normal (3-5 m)	133	56	30	111	78	41
Central Valley	High-trunk (5-7 m)	141	47	25	112	76	40
	Normal (3-5 m)	105	31	22	84	52	38
South Valley	High-trunk (5-7 m)	132	12	8	136	16	12
	Normal (3-5 m)	87	33	27	44	76	63

Table 2. Density (stems per ha) of trees and shrubs after cutting experimental site (Haloxylon ammodendron / Carex physodes association), Repetek Biosphere Reserve.

Plants	1951	1961	1965	1970	1977
Haloxylon aphyllum (Minkw.) Iliih.	85	619	720	729	747
Ephedra strobilacea Bunge	29	43	75	92	85
Calligonium spp.	31	14	109	130	146
Aellenia subaphylla (C.A. Mey.) Ael.	-	-	21	22	46
Haloxylon persicum Bunge	-	-	-	5	8
Salsola richteri Kar. ex Litv.	5	24	-	-	3
Total	150	700	925	978	1,035

Source: Compiled from data obtained by V.L. Leontyev (1954), N. Jagyev (1963), A.B. Georgiyevskiy (1972), and S. Veyisov.

H. ammodendron regenerates intensively for the first 10 to 15 years following cutting and then slows rapidly in terms of new individuals while morphometric indices (height, trunk diameter, and descriptive cover) increase. Under conditions in the eastern Kara-Kum, 750 to 800 individuals of H. ammodendron per ha are apparently a limit.

H. persicum is a new inhabitant compared with H. ammodendron. This species inhabits primarily all hilly relief, i.e., it exists under less favorable ecological conditions. Its state is good.

Calligonium setosum and C. caputmedusae are second after H. ammodendron according to the number of individuals. Their vitality, determined from the experimental site, was as follows: of 146 individuals of C. setosum and caputmedusae, 97 (66.4%) were in a good state, 31 (21.2%) were in a semidried state, and 18 (12.4%) were in a dried state.

CHARACTERISTICS OF PSAMMOPHYTE SUCCESSION

Psammophyte-type successional change in a sand desert, which can differ in dynamics and be opposite in direction, was described in the literature and, until now, was considered a dominant type. This type is characteristic both of exogenic and endogenic successions. The processes which constantly bring sand and dust and determine the extent of substratum mobility in a sand desert are responsible for dynamic trends peculiar to the whole complex of natural conditions, including plant community habitat change. Consequently, heterogeneous structure and floral composition of sand massifs are related first of all to the extent of substratum mobility and the type of modern relief.

It is known that the Repetek area, as well as the whole territory of the eastern Kara-Kum, is located in a region of progressive and oscillating sand motion caused by seasonal changes in wind direction. The annual cycle of wind directions shows that north winds are dominant from April to October and south winds from November to March. This results in displacement of barkhans toward the south in summer and toward the north in winter. The annual amplitude of oscillation of the crest line is 7-9 m in high places and 18-19 m in low places of barkhan chains. Mean yearly velocity of progress of barkhan chains spreading toward the southwest is 3.1 m.

The following three dimensions of mobile sand relief forms are common in Repetek: microform - sand ripples with crests 2 cm high and 12 cm apart; mesoform - barkhan chains 2-5 m high and 50 m between crests; and macroform - aeolian ridges 20-25 m high (above valley-type depressions), 1,000 m wide at the base, and 6-7 km between ridges.

Each form is characterized by a different velocity, which is dependent on the volume. The velocity of sand ripple displacement, when wind velocity is 5-7 m/sec, is 40 cm/hr. The velocity of the progressive motion (besides seasonal fluctuations) of barkhan chains (averaged yearly) is 3.1 m, and of ridge displacement, approximately 30 cm/yr. With such velocity, barkhan chains displace completely in less than 50 years. Interbarkhan lowerings and deep hollows move simultaneously with the chains. Therefore, progressive motion of barkhan chains causes permanent changes in the position of positive and negative relief forms in the barkhan sand massif.

As a result of longitudinal displacement, the southwest terminal portion of barkhan chains approaches the top of the ridge and slides down the steep west slope, which leads to gradual displacement of the ridge toward the west. Ridge motion velocity, though insignificant (0.3 m), causes a number of changes in the natural environment of valley-type depressions. Together with a sand ridge, which gradually covers Haloxylon ammodendron, all hydrogeochemical and biogenic components also displace.

The intensive transport of sand is a major factor which prevents barkhans from being overgrown. Data from the Repetek stations show that 6-12 tons of dry sand in each linear meter of the ridge are annually transported in barkhans. When overgrown, the succession of natural and areal complexes in large barkhans takes place as a result of regular progress from a dynamic to a stable state, and sand transport decreases. For example, in the middle stage of succession in Haloxylon persicum / Aristida pennata / Bromus tectorum communities, the amount of transported sand does not exceed 0.5-0.6 t/lin m/yr. In a stationary community (Haloxylon persicum / Carex physodes), under conditions of the reserve regime, a very small amount of sand is transported (0.5 kg/lin m/yr).

The vegetative structures of sand massifs include various types of heterogeneity. In barkhans and fixed uneven sands, which are under similar climatic and lithological conditions, ecological and dynamic series of plant communities are a principal form of vegetative heterogeneity. The series includes combinations of plant communities which in certain areas present stages of changes in plant community production; they are under the influence of different exogenic processes and so do not have stable habitats. This form of heterogeneity differs from other areal elements such as complexes and microzonal series in the availability of nonformed communities and groupings (procenosis) in series composition.

Seral stages, which differ both in floral composition and quantitative species ratios when sand is definitely fixed, relate to certain types of relief and have spatial and temporal expressions. The following series are distinctly observed in the Repetek Biosphere Reserve: Ammodendron conollyi and arboreal Calligonium sp. in barkhans; psammophilous arboreal and shrub communities in uneven barkhans and small-ridge, semifixed sands; H. persicum communities on large ridges; and H. persicum / C. physodes association or H. persicum / C. physodes / Tortula on ancient aeolian fixed sands.

Years of continuous observations throughout the Repetek Biosphere Reserve show that, at all stages of development of natural and areal complexes in the succession series, there is a distinct relation among natural processes: sand transport intensity, aeolian form dynamics, morphometric values, plant composition and density, moisture storage in the root horizon, groundwater depth and mineralization, animal populations, etc.

In the sand desert under conditions of the reserve regime, gradual overgrowing of barkhans is at the center of all dynamic processes, which brings the initial ecosystems from dynamic to climax states. This long-term succession of several decades is followed by a smooth change of the ecological biogeocenosis regime. Some examples of long-term field observations are given below.

Unlike other terrestrial biomes in the zonal type desert biome, trees and shrubs (Ammodendron conollyi, Eremosparton flaccidum, and Calligonium arborescens) and perennial cereals dominate the early stages of succession in sand deserts. In subsequent stages of succession, semishrubs (Smirnovia, Astragalus unifoliolatus) and some species of perennial herbage (Aristida karelinii) along with trees and shrubs participate in the phytocenosis formation. Only in the late successional stages--climax communities--does herbage (especially sand sedge) take a major role in the phytocenosis (table 3).

Early stages of succession proceed very slowly, since plant growth is affected by many adverse natural factors (sand covering, blow outs, significant microclimatic contrasts, insufficient seeded bases, etc.). The only favorable natural condition is sufficient moisture storage in the root horizon. The subsequent stages of succession proceed relatively fast, since sands are significantly stabilized.

During succession, crown project area increases, with simultaneous root system enlargement. As a result the aboveground portions of plants significantly reduce wind velocity and the belowground portions fix sand, protecting it against weathering. At the experimental site, the number of plant species for 31 observational years (1945-1976) increased 1.5 times; the number of individuals, approximately 11 times. Crown projection area of arboreal and shrub vegetation and perennial herbage at the same site was only 1.5% in 1956 and had reached 5.9% in 1976; i.e., the project area increased four times over 20 years.

Fixing barkhans with vegetation results in a decrease of sand transport. For example, 9 t/lin m of sand per year are transported in Calligonium arborescens / Aristida pennata communities (an early successional stage), 0.5 t in H. persicum / A. karelinii / Bromus tectorum communities (a mid-successional stage), and only 3 to 5 kg/lin m in the H. persicum / C. physodes association (a climax community).

A vegetation increase leads to a reduction of moisture storage in the root horizon because of transpiration. So at the experimental site moisture storage in the 5 m layer of soil was reduced by 20.3 mm (moisture levels were determined from October 1950 to 1975). The morphological look of landscapes and morphological values of relief change as a result of growing plants. Large and medium barkhans, which are characteristic of early successional stages, become uneven small barkhans and small ridges during middle successional stages.

The soil-formation process covers still larger areas in the process of successional change. Because of high substratum mobility in barkhans, soils are practically absent. Primitive soils of several centimeter thickness are formed only under crowns of Calligonium sp. By the final

Table 3. Dynamics of barkhan vegetation, 1945-1976, Repetek Biosphere Reserve.

	1945		1956				1966				1976			
	Plant Amount		Plant Amount		Crown Project Area		Plant Amount		Crown Project Area		Plant Amount		Crown Project Area	
	No.	Percent	No.	Percent	Sq m	Percent	No.	Percent	Sq m	Percent	No.	Percent	Sq m	Percent
Ammodendron conollyi	7	11.7	7	15.2	5.7	3.6	54	26.1	39.4	12.1	159	23.1	87.4	14.8
Eremosparton flaccidum	30	50.0	18	39.1	12.5	7.9	49	23.7	31.8	9.7	102	14.8	25.4	4.3
Calligonium arborescens	14	23.3	17	37.0	132.2	83.4	32	15.4	214.1	65.6	50	7.3	356.0	60.2
Salsola richteri	4	6.7	4	8.7	8.1	5.1	18	8.7	37.4	11.4	41	6.0	50.9	8.6
Astragalus unifoliolatus	-	-	-	-	-	-	2	1.0	-	-	30	4.4	15.0	2.5
Haloxylon persicum	-	-	-	-	-	-	-	-	-	-	4	0.6	1.1	0.2
Acanthophyllum elatius	-	-	-	-	-	-	-	-	-	-	17	2.5	34.2	5.8
Aristida karelinii	5	8.3	not taken into account				40	19.3	3.5	1.1	111	16.1	9.3	1.6
Aristida pennata	-	-	-	-	-	-	12	5.8	0.2	0.1	173	25.2	11.8	2.0
Total	60	100.0	46	100.0	158.5	100.0	207	100.0	326.4	100.0	687	100.0	591.1	100.0
Total projected cover (% per ha)						1.58				3.26				5.91

Source: E.G. Mickhelson 1954. On spontaneous plant growth in Kara-Kum barkhans. Izvestiya, Turkmen Academy of Sciences, no. 4.

succession stage (Haloxylon persicum / Carex physodes association), typical sand-desert soils are already present.

H. persicum communities on ancient aeolian sands, which present a series of ecogenetic successions in the evolutionary process in the eastern Kara-Kum, compose a special, ecologically dynamic series. This type of succession, with imposed short-term zoogenic processes, has determined the cellular and hollow-type relief over the major area of the Kara-Kum.

The fact that all principal components--soils, climate, rodent activity, and vegetation--play a specific role in modern-day ecosystem formation is characteristic of ancient aeolian plains and valley-type depressions of the Kara-Kum surface.

At present these types of communities are under climax conditions and endogenic processes are not sufficiently developed. Variations of different community stages are not large and development of communities is of a wave-type nature. The slow soil accumulation of fine dust particles and the formation of a desert crust on the surface are mostly expressed and directed processes. A wave-type successional change can be due to increases of mammal numbers and does not lead to radical ecosystem reconstruction. Recently Poa bulbosa var. vivipara, a new species for the sand-desert area of the low Kara-Kum which is characteristic of ecosystems with sandy and slight loamy soils, began inhabiting the H. persicum / C. physodes communities, which are in a climax stage with pronounced crust sand and desert joints with moss.

Pastoral succession, connected with pastoral digression whether because of overuse or underuse, is an undesirable type of succession in sand deserts. Intensified cattle breeding, removal of trees and shrubs, and extensive use of modern transport devices leads to relatively fast (sometimes over several years) grass cover thinning, grass disappearance, and broken barkhans. Because this problem has been well studied and is reflected in the literature, we shall focus on the characteristics of changes in the dominant ecosystems (H. persicum / C. physodes) of the sand-desert reserve. The absence of wild hooved animals, which may be due to conditions of the reserve regime or to cessation of pasture usage by domestic animals because of the absence or low quality of water resources, has resulted in pastures being covered with moss. This type of successional change, which is being studied by desert specialists, has been found to have wide geographical distribution in sand-desert ecosystems in Turkmenistan, Uzbekistan, and Kazakhstan. The desert moss (Tortula desertorum) has a very wide ecological range and is highly competitive with flowering plants. Having formed a very dense cover over the soil surface, T. desertorum results in a significant deterioration of the hydrologic and physical properties of sands and absorbs much moisture from precipitation. It is quite evident that this process of greater aridization of desert ecosystems results in the formation of a stable climax community which has a poor species composition. The process is also demonstrative of undesirable successions, and it exemplifies one of the views of the Kara-Kum desertification.

Investigations have shown that undercrown sections of Ephedra strobilacea are the places with the most favorable conditions for T. desertorum. Moss develops well in this habitat, with individual heights to 5-6 cm, 80% to 90% cover, and presence of all vegetation stages. It is worth noting that individuals of E. strobilacea are not depressed. Further, when the sand soil surface is stabilized, such sections are sources of spores that spread to neighboring areas. Places with the second most favorable conditions for moss development are those where desert sandy crusts have formed with the active help of algae (Cyanophyta, Chlorophyta). Vegetation cover of C. physodes is depressed first in the H. persicum / C. physodes community. It is seen from table 4 that numbers of C. physodes and the terrestrial phytomass decrease 1.5 to 2 times with gradual moss development. With increases of moss cover of up to 80% to 90%, when turf thickness is 1.5-2.0 cm, individual numbers decrease three times and terrestrial phytomass values decrease 4 to 5 times.

Table 4. Characteristics of Carex physodes populations in relation to Tortula desertorum

	1974	1975	1976	1978
Vegetation length (days)	60	71	114	160
Precipitation amount (mm) from Nov. to Apr.	140.8	82.4	128.8	93.1
Sites without T. desertorum				
Individual number	549	518	593	564
Mean height	22	19	23	18
Weight	15.9	13.5	16.5	14.4
Sites with T. desertorum				
Individual number	353	351	363	331
Mean height	17	15	17	16
Weight	12.5	8.1	8.4	7.6

Unlike E. strobilacea, all the remaining shrubs, particularly H. persicum, Calligonium eriopodum, Salsola richteri, Aellenia subanphylla, and to lesser extent, H. ammodendron, are affected negatively only after soil cover accounts for 50% to 60%. The shrub cover begins to decline when some species of subcrown moss appear. The most sensitive shrub is H. persicum, primarily because it is an ombrophyte and soil under the crown is not significantly mineralized.

In conclusion, of all the communities considered, the Haloxylon persicum / Carex physodes community on ancient aeolian uneven sands is the most appropriate object for investigations of changes in background environmental conditions. This type of ecosystem covers a large area in the Kara-Kum and in central Asia and the Middle East. It is a community which has passed all principal developmental stages and approaches the climax state. It belongs to an ecosystem type with the simplest structure, and in relation to other ecosystems, it has the maximum stability.

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DISTURBANCE AND RECOVERY OF PLANT COMMUNITIES IN GREAT SMOKY MOUNTAINS NATIONAL PARK: SUCCESSIONAL DYNAMICS AND CONCEPTS OF NATURALNESS

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Abstract

One of the fundamental purposes of a national park is to preserve the native flora and fauna of the site; however, our concept of preservation and the managerial actions selected to ensure "preservation" are partially functions of our concepts of "naturalness" and our understanding of the ecological and evolutionary processes influencing the biota in question. The history of a large preserve such as Great Smoky Mountains National Park may include "natural" catastrophic events such as storms, fires, and landslides, and "man-caused" disturbances such as farming, logging, burning, grazing, and the introduction of exotic species, although these two groups may not, in all cases, be clearly distinguishable.

The purpose of this paper is to illustrate the types of disturbances important in Great Smoky Mountains National Park in pre-Columbian times, during settlement, and after the park was established. The resulting successional communities will be discussed in terms of their probable floristic origins and probable ultimate composition. Successional processes in the park will be related to managerial issues such as rare plant conservation, maintenance of grassy balds, and the role of fire.

INTRODUCTION

The popular concept of a national park has a timeless quality to it and carries the connotation of a pristine site, little disturbed by past human activity. In cases where the property was previously farmed or logged, inclusion within a park boundary implies to many people that the land is reverting to its original natural state. When we think of a national park, we often envision a mountain face: natural, magnificent, solid, unchanging.

The tendency to view park lands as static and to assume that the goal of management is to guard or maintain a stable "climax" landscape is both ecologically and evolutionarily unrealistic (White and Bratton in press; Franklin 1978). Living systems are dynamic and subject to a wide variety of natural disturbances as well as human-caused ones. These disturbances initiate compositional changes. Directional and cyclic changes occur within, as well as outside, preserve boundaries (White and Bratton in press; Miles 1979).

One of the fundamental purposes of a national park is to preserve native flora and fauna (U.S. Dept. of Interior 1970); however, the managerial actions selected to ensure preservation are functions of our concept of "naturalness" and our understanding of ecological and evolutionary processes. Since change is ongoing in all living systems, an analysis of such factors as disturbance and succession is a prerequisite to making managerial decisions for preserve areas.

This paper investigates the disturbance history of a large U.S. national park which is also an international biosphere reserve. We will separate "man-caused" disturbances from "natural" disturbances and will also analyze the interactions between these two types of perturbations in native plant communities. Our goal is to summarize dynamic processes in the landscape we study, to report long-term trends that are occurring, and to discuss management issues that are raised.

THE STUDY AREA

Great Smoky Mountains National Park (GRSM), Tennessee and North Carolina, is located at N35°37' W83°31' and is the largest wildnerness reserve (209,000 ha) in the southern Appalachian Mountains. Elevations are among the highest in the eastern United States, ranging from 256 to 2,025 m. Slopes are steep--typically 25° and greater--but unlike many western parks, bare rock is relatively uncommon, and the park is nearly entirely forested. Elevations are not high enough for climatic tree line at this latitude.

The bedrock is largely metamorphosed sandstones and shales of Precambrian age. Ordovician limestone is exposed in "windows" in the western part of the park, where solution formations such as caves and sinkholes can be found (King et al. 1968).

The climate is continental warm temperate. Rainfall increases with elevation at a rate of 6.5 cm/100 m (Shanks 1954). Annual precipitation averaged 150 cm at 445 m in the years 1947-1950 and 220 cm at 1,520 m for the same period (Stephens 1969), which is thus relatively high for the eastern United States.

The growing season (days above 0°C) averages from 156 days (445 m) to 144 days (1,075 m). Vernal species bloom as early as late February, and leaf fall may not be complete until the middle of November (Bratton 1976). Snow may be over 200 cm deep at the higher elevations, but in warm winters there is no snow pack. Temperature decreases with elevation at a rate of 5.4°C per 1,000 m (Shanks 1954).

The regional flora is diverse--1,500 vascular species, 2,200 fungi with macroscopic fruiting bodies (Peterson 1979; James Liebman, personal communication), and 350 bryophytes have been recorded within the park.

VEGETATION PATTERN

The Great Smoky Mountain vegetation pattern is a complex of broad-leaved deciduous and evergreen coniferous forests (Whittaker 1956, Golden 1974). Along a moisture gradient from mesic to xeric sites below 1,000 m, there is a continuum of communities from hardwood/hemlock cove forest to oak-dominated slopes, and finally to pine-dominated upper slopes and ridges. Species dominance also shifts with elevation--with increasing elevation on mesic sites, for example, hardwood/hemlock coves are replaced by birch/beech/maple/buckeye-dominated "northern hardwood" communities and finally by the spruce- and fir-dominated communities. At lower elevations, mesic species are restricted to concave sheltered topography but expand onto open slopes and ridges at higher elevations and from mesic to xeric sites.

Both Whittaker (1956) and Golden (1974), whose studies are the most comprehensive available for Great Smoky Mountains National Park, avoided stands with a history of farming, logging, or natural disturbance. It is to these disturbances and their effect on the park that we turn our attention in the rest of this paper.

A POST-PLEISTOCENE PERSPECTIVE

The cove forests of the southern Appalachians have often been referred to as Arcto-Tertiary relicts, implying the communities have been intact and possibly in place for millions of years (Cain 1930, Braun 1950).

Actually, it is not clear if the cove forest was present in the Appalachians during glaciations, and the most recent palynological evidence discredits the idea that coves served as refugia for deciduous species (Delcourt and Delcourt 1979). Hence, many deciduous species now in the park have reinvaded after the glaciers receded. There is also no reason to believe all elements of the present communities moved north simultaneously or were coexisting during the glacial maximum.

Although the climate has generally warmed in the last 12,000 years, there has been at least one major period during which the climate was warmer and drier than at present (the Hypsithermal, ca. 5,000 BP) and at least one period during which it was cooler and moister (the "Little Ice Age," ca. 600 BP). Whittaker (1956) hypothesized the lack of spruce/fir forest on the westernmost high peaks of the park was because of a 300-m upward shift of boreal forest during the Hypsithermal. Changes in overall climatic regime would also influence natural disturbance regimes.

Even if the climate were static, the forests of the Smokies might not be completely in phase with present-day temperature and moisture conditions. Some species might be expanding or changing their range, whereas others might be slowly disappearing. A species such as Geum radiatum, which is very rare and confined to high elevation cliffs and balds, could be a relict from alpine meadows, common in ages past but now replaced by spruce/fir forest.

PARAMETERS OF DISTURBANCE REGIMES

Ideally, one should define disturbance regimes by the following parameters:

Location--position on geographic, vegetative, elevation, moisture, and other disturbance gradients.

Frequency--number of disturbance events per time period. The inverse of frequency is the interval or period between disturbances.

Predictability--inversely related to variation around mean frequency.

Area--defined in terms of area per event or area disturbed per time.

Rotation--time interval required to disturb an area equivalent to the study area. This does not assume each site was disturbed once during the rotation; some sites may not have been disturbed while others may have been disturbed several times.

Severity and intensity--For clarity, we distinguish between these two parameters in the following way: Severity represents the impact of the disturbance on the community; thus, severity is defined in terms of community properties such as basal area, density, species, and biomass that are affected. Intensity refers to properties of the disturbance itself; in the case of fire, intensity equals heat released per area per time; in the case of rainstorms, intensity equals volume of precipitation per time period.

We have divided disturbances into three main sections: Natural, man-caused, and disturbances of mixed origin. We discuss each disturbance regime as fully as available data allow. Clearly, much remains to be studied concerning Great Smoky Mountain disturbance regimes.

NATURAL DISTURBANCES

Natural disturbances occur as a result of an interaction of climate, topography, geology, and biota (White 1979). In some cases (e.g., windstorms, icestorms, floods, droughts, and damaging frosts), climate takes the leading role, but effects are also related to the other factors. The immediate cause for some natural disturbances is the instability of the geologic substrate (e.g., karst processes and erosion on cliff faces). Finally, some natural disturbances are the result of native biota: vertebrates, insects, and diseases. Since fire may be either lightning- or man-caused, it is discussed in a later section dealing with disturbances of mixed origins.

Windstorms

Several lines of evidence can be used to model wind disturbance in Great Smoky Mountains National Park. A 37-year record of weather phenomena (Stupka unpublished data; monthly superintendent's reports, USDI, NPS, GRSM) describe 24 violent windstorms causing conspicuous, though sometimes local, damage. Areal extent of these storms is unknown. In a single mesic tract in western North Carolina, Lorimer (1976) produced evidence for a windstorm frequency of one each 50 years.

Studies on gap reproduction in mesic forests (Runkle 1979; Lorimer 1976; Barden unpublished manuscript) suggest small to medium-sized tree fall patches (25-40 sq m) occupy about 1% to 25% of stand surface area and may average at least 10% in the park. These patches are created at an average rate of about one to five tree falls per hectare per year, or 2.5% to 5% of land surface (Runkle 1979). Larger wind disturbances have not been studied, but as windstorm severity increases, frequency decreases. Some indirect evidence (Lorimer 1976, Runkle 1979) suggests that when large windstorms are averaged over time and space, they may approximate disturbance rates of 1% to 2% of the land surface per year.

Windstorms are important in maintaining habitat for the highest light-demanding species along the elevation gradient of the park. These habitat patches are also important for wildlife (McCaffrey and Creed 1969, McClellan and Frissell 1975). In general, the larger the forest opening, the greater the internal patch heterogeneity and the higher the ensuing species diversity. As there is a continuum of wind damage in stands, there is also a continuum of species from those which persist in shade to those which depend on large openings. Wind effects are a function of landscape gradients like slope position, steepness, rockiness, and soil depth; thus, frequency, predictability, and magnitude of wind disturbance vary with topography across the Great Smoky Mountain landscape. Since older trees are more prone to windthrow than younger ones, the state of the community itself also determines disturbance magnitude with a given wind strength.

Perhaps the most dramatic effect of windstorm is the maintenance of *Liriodendron tulipifera* in mesic mid- and low-elevation old-aged forests of the park. *Liriodendron* is a shade-intolerant species dependent on medium- to large-sized tree falls for its reproduction. Once established, it grows to a large size (1 - 2 m DBH) and lives long (300 years or more).

Icestorms

Icestorms have been much noted in the southern Appalachians (Abell 1934, Ashe 1918, Burton and Gwinner 1960, Campbell 1937, Carvel et al. 1956, Lemon 1961). Species differ in their resistance to ice damage. Decay fungi enter through ice damage wounds, resulting in vulnerability during windstorms.

The 1931 to 1967 record (Stupka unpublished data; monthly superintendent's reports USDI, NPS, GRSM) reports six icestorms causing tree damage at the park. In addition, there was a severe icestorm on March 24, 1969 (Runkle 1979). Only two can be located with respect to elevation--both occurred in spruce/fir and northern hardwood forests.

Although few data are available, icestorms are probably similar in their effect on the vegetation to the branch pruning and local tree fall caused by moderate windstorms, with which they sometimes interact.

Floods

Great Smoky Mountains National Park is characterized by steep topographic gradients and high rainfall. Because the park is upstream from major floodplains and is dominated by V-shaped valleys, there is little area of alluvial flooding or stream meandering. Nonetheless, heavy rainstorms are frequent, and floods have been important: 25 damaging floods have been described for the period 1931 to 1967 (Stupka unpublished data; monthly superintendent's reports USDI, NPS, GRSM). Effects include scouring of creek beds, erosive effects in stream gorges, battering and felling of creekside vegetation, and destruction of lotic communities. Disturbance is concentrated in ravines, coves, and valleys, where it affects such upper valley species as *Betula lutea*, *Tsuga canadensis*, *Rhododendron maximum*, and *Acer spicatum*, and such lower elevation species as *Plantanus occidentalis*, *Liquidambar styraciflua*, Betula nigra, and Alnus serrulata. Examples of intense rainstorms include cloudbursts of 10 to 15 cm in one hour, 30 cm in four hours, and 59 cm in two days.

Drought

Drier-than-normal periods during the growing season, ranging in length from 2 to 20 weeks, have occurred at least 19 times from 1931 to 1967 (Stupka unpublished data; monthly superintendent's reports USDI, NPS, GRSM). Late summer droughts cause early leaf abscission. Severe droughts during the growing season cause reduced growth, early leaf fall, and increased mortality (Hursh and Haasis 1931). The most significant recent droughts in the park area were in 1925 (Hursh and Haasis 1931) and from 1951 to 1954.

Drought impacts mesic species growing near their limits, e.g., Tsuga canadensis, in terms of low soil moisture (Hough 1936). It affects thin-soiled upper slopes more than other sites (Hursh and Haasis 1931). In the park it probably affects oak, oak/pine, and pine-dominated communities the most and rock outcrop vegetation the most, although some Abies fraseri mortality was noted in 1954. Drought years result in increased fire frequency.

Temperature Variability (Late Frosts)

The most noted effect of temperature variability on Great Smoky Mountains vegetation is killing frosts after warm late winter periods cause a break of dormancy. Fourteen such events have been described between 1931 and 1967 (Stupka unpublished data; monthly superintendent's reports USDI, NPS, GRSM), including three that caused widespread leaf death in upper ridge forests. Others involved death of flowers or defoliation, which was especially noted at lower elevations. All records except one were of killing frosts in spring; one upper elevation frost was noted to have killed young Rubus fruit before ripening in fall. It appears upper elevation deciduous species are especially vulnerable to frosts coming in May or June. Effects include decreased growth rates, failure of seed production, and occasional mortality. Surviving understory vegetation may experience temporary release after canopy defoliation.

Debris Slides

Debris slides affect steep slopes in a few park areas. For the southern Appalachians, Bogucki (1970) found 11 areas with major slides during the last 33 years (see also Hack and Goodlett 1960, Hull and Scott 1979, Stringfield and Smith 1936). In all areas, slides were initiated by heavy rains--eight were the result of frontal systems, and three, including the most recent ones, were the result of intense local thunderstorms. These rains also caused flash flooding and scouring of stream channels.

Two cloudbursts in the park area have caused large natural earth movements in the last 40 years. On September 1, 1951, 10 to 15 cm of rain fell on Mount LeConte in one hour, initiating over 100 individual debris slides (Bogucki 1970). On August 5, 1938, the Webb Mountain cloudburst occurred, with over 30 cm of rain failing in four hours. These cloudbursts are probably greater than 100-year events (Moneymaker 1939, Bogucki 1970). At least 15 of similar intensity have occurred locally in the park in the last 40 years, but not all initiated landslides.

Slope angle is an important factor in slide occurrence and must exceed 35° for slides to be initiated (Bogucki 1970). Biomass and regolith weight are also important when saturated with water from intense rainstorms. Violent winds against tree crowns may also work to loosen the substrate (Bogucki 1970).

Most slides occur in upper parts of stream valleys, but they can be found throughout the stream gradient. Because steep slopes and high rainfall occur together at high elevations (1,000 - 2,000 m), most slides will affect spruce/fir, northern hardwoods, and upper coves. The scar is expanded at the slide head and linearly below. Even where important, slides probably only locally exceed a small percentage of land surface.

Little is known about revegetation of landslides--Betula lutea and Acer spicatum are conspicuous where soil and rock debris accumulate. Old debris slide heads may develop into steep seepage meadows dominated by Carex and on which occur rare herbaceous plants not known in surrounding forest (e.g., Carex ruthii, C. misera, Scirpus caespitosus). Probably the mid and lower sections of slides succeed to forest more quickly and may become forested in 50 to 500 years, depending on initial site condition (e.g., amount of soil). Some vertical cliff faces may not become forested until subsequent sliding and erosion reduce steepness.

Erosional Processes on Cliff Faces and Gorges

Steep rock outcrops are subject to physical and chemical weathering, resulting in periodic loss of bedrock fragments. The presence of colluvial boulder fields in the park suggests to some that freeze-thaw riving of boulders was frequent during full glacial climates.

Effects on communities occur throughout elevation and moisture gradients wherever steep rock exposure occurs. Lichen, bryophyte, pteridophyte, and perennial herb communities are most affected, but trees on steep, rocky slopes may suffer high frequencies of windfall because of shallow soils and wind exposure and may also suffer from periodic droughts. Cliff faces are important rare plant sites, and the interruption to succession caused by substrate instability in some cases maintains an open, if spatially shifting, habitat.

Karst Processes

Limestone is restricted in the Great Smoky Mountains, but there are significant limestone ledges and sinks where limestone occurs. Collapse is an ongoing process in a number of the sinkholes--as indicated by tree growth, open mineral soil, and woody debris. Drainage changes with sink collapse have apparently eliminated the only park population of *Sparganium androcladum*.

Because limestone outcrops are located only at ca. 600 m in elevation and on mesic to subxeric parts of the moisture gradient, effects in the park are restricted. These areas do, however, possess a strikingly distinct flora and are important as rare plant habitat.

Vertebrates

Effects of native vertebrates include destruction of vegetative and reproductive plant parts, soil disturbance (important in seedbed preparation), and tree bark wounds (Linsey and Linsey 1971).

Bison (*Bison bison*) and elk (*Cervus canadensis*) were formerly present in the southeastern United States and have been credited with maintaining (or helping to maintain, along with fire) some open grasslands. This has been suggested for grassy balds in the park but is unlikely because of the small size of these areas (less than 10 ha) and the ruggedness of surrounding slopes. Bison and elk may have influenced forest structure by grazing and wallowing.

Deer (*Odocoileus virginiana*) interact with successional processes by favoring disturbed sites for browse. Recent observations indicate heavy browsing of sprout reproduction in a burned area (Harmon unpublished data).

The role of deer has varied with human-influenced changes in population size. Deer populations were low in the 1930s, and browsing was minor in postfarming areas and postlogging stands. The deer herd has since recovered and is now dense enough in Cades Cove to remove most deciduous reproduction (Bratton in press), thus selecting for the conifers, *Pinus strobus* and *Tsuga canadensis*. The deer recovery was due to extirpation of predators and protection from hunting.

Black bear (*Ursus americanus*) disperse seeds, expose mineral soil while searching for invertebrates, and damage trees and shrubs while foraging. The burrowing activities of woodchucks (*Marmota monax*) also expose mineral soil, providing a seedbed for some species.

Beaver (*Castor canadensis*) were formerly present and important in wetland dynamics along larger, low-gradient streams. Some species (e.g., *Campanula aparinoides*, *Leersia oryzoides*) may now have reduced populations due to the long absence of beaver as well as human-caused changes in wetlands. Beaver are now invading in the North Carolina side of the park, and preferential cutting of species may modify composition of streamside stands (Singer et al. in press). Much of the streamside forest in areas of beaver habitat is in postlogging or postagricultural succession.

Native Insects

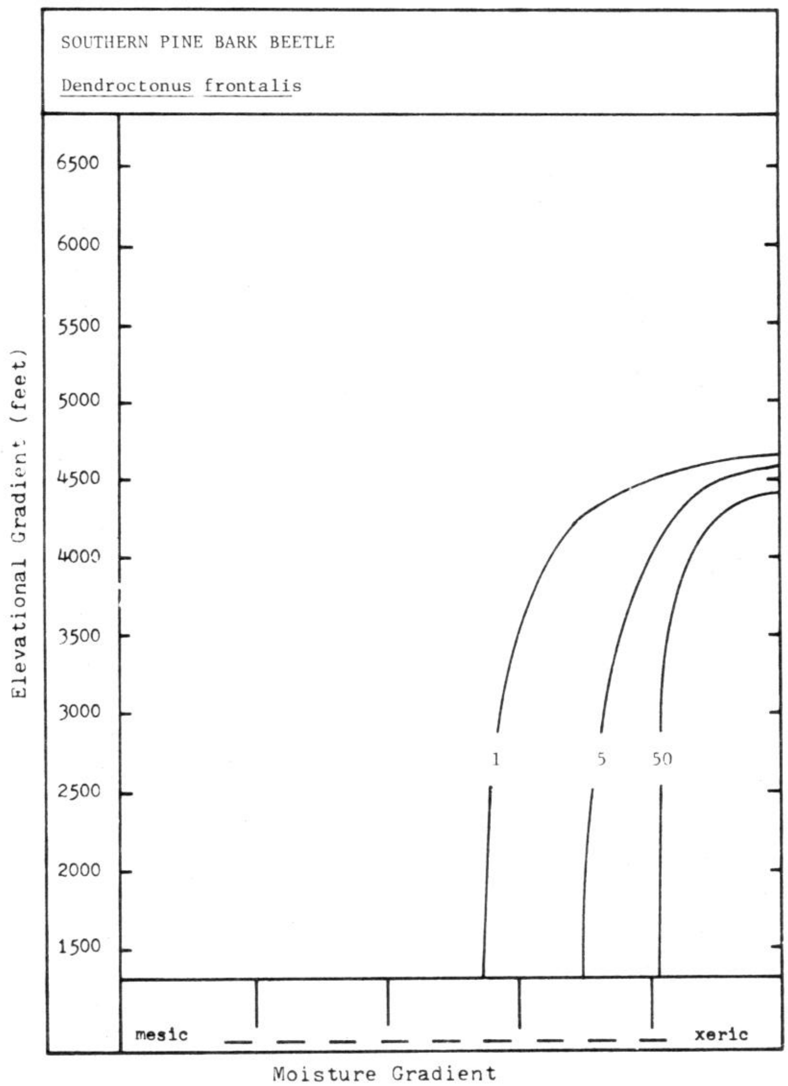
Insects disturb forests by damaging or destroying seeds or reproductive parts; by stunting, deforming, or killing shoots; by reducing tree vitality and net production by consuming foliage or photosynthate; by causing death by defoliation, photosynthate removal, and bark girdling; and by increasing susceptibility to other insect or pathogenic attack (Baker 1972, Churchill et al. 1964). Insect disturbance severity depends on the nature of the attack (e.g., cambial girdling kills more effectively than defoliation). Severity is affected by host specificity and distribution as well as by the climatic conditions (e.g., drought) which favor increases in insect populations or host susceptibility. Most attacks which kill the host usually do so by severing the transport system. Major defoliation may cause conifer death (Wickman 1978), but death to hardwoods only occurs during poor growing seasons or after two to three years of defoliation (Churchill et al. 1964). Defoliation may release understory vegetation (Collins 1961).

Kuykendall (1978) studied the historic occurrence and influence of southern pine beetle on park forests. Outbreaks are characterized by mass attacks on individual pines or groups. The host trees attacked are usually overmature, overstocked, and on xeric sites (figure 1). Deficient precipitation and warm winter temperatures enhance the likelihood of attack.

Southern pine beetle has affected southern Appalachian forests for millenia. Recent epidemic attacks were from 1954 to 1959 and from 1967 to 1976. Both epidemics declined because of low winter temperatures (Kuykendall 1978). Kills are often scattered and uneven, with pockets of mature pines escaping attack. In heavily infested areas, 80% to 97% pine basal area was removed, leaving 21% to 32% of the original stand basal area (Kuykendall 1978). Although light reaching the forest floor increases after beetle kill, pines are unable to reproduce because mineral soil is not exposed. A southern pine beetle infestation thus results in the conversion of pine forests to hardwood forests, the composition of which is a function of site. In old-field situations, *Acer rubrum*, *Cornus florida*, *Pinus strobus*, and *Oxydendrum arboreum* replace yellow pines (*Pinus echinata*, *P. rigida*, *P. virginiana*). These old-field communities probably did not exist previous to A.D. 1000 when agriculture was first introduced. Without major disturbance, these forests will reach a composition transitional between cove and oak forests.

On more mesic sites, *Nyssa sylvatica*, *Quercus prinus*, *Q. coccinea*, and residual pines dominate the post-beetle-infested forest. Without further major disturbance, *Quercus* and *Nyssa* continue to increase, while *Pinus*

Figure 1: Distribution and severity of southern pine beetle (Dendroctonus frontalis) outbreaks. Distribution on two topographic gradients and percentage of total tree stems killed are shown. (Adapted from Whittaker 1956).



decreases. Conversion to hardwood composition will probably reduce overall stand productivity on xeric sites and may also reduce organic horizon accumulations. Hardwood conversion of pine stands on xeric sites by beetles has probably occurred for thousands of years in the Great Smoky Mountains. However, constant burning by man prior to 1930 increased pine reproduction, and the area converted to pine may have exceeded or equaled that lost to beetle-kill. Fire protection has shifted this balance such that the area of beetle-kills now exceeds the area of pine reproduction. Moreover, as the remaining pine forests mature, the likelihood of insect attack will increase, thus speeding the rate of hardwood conversion.

MAN-CAUSED DISTURBANCES

There have been three major phases of land use in Great Smoky Mountains National Park: aboriginal, Euro-American (including settlement and commercial exploitation), and park preservation. These eras overlap both spatially and temporally, but they are useful divisions because of their differing disturbance characteristics.

Aboriginal (10,000 B.C. to A.D. 1800)

Over 200 archeological sites, dating back as far as 8,000 years before present, occur in the park (Bass 1977). The North Carolina portion of the park was preferred (Goodwin 1977) because of a warmer, drier climate and the abundance of mast-producing forests (Bass 1977).

During the Paleoindian period (10,000 B.C. to 8,000 B.C.), small bands of hunters and gatherers wandered throughout western North Carolina. Population densities were low and sites were used ephemerally. Few bands, if any, entered the park area during this period (Bass 1977).

Man first entered the park area during the Archaic period (ca. 8,000 B.C.). Hunting and gathering bands were thought to have followed food resources within a fixed territory (Jennings 1978). In the early Archaic (ca. 8,000 B.C.), aborigines restricted most activities to upland sites on ridges and benches and in gaps and coves (Bass 1977). By the late Archaic (ca. 2000 B.C.) valley sites, both floodplains and upper valleys, were preferred for food processing, while upland sites were only used for hunting. Aborigines probably used fire during the Archaic to drive game, enhance berry crops, gather nuts, and clear forest undergrowth. There were also accidental fires. Most influences on upland vegetation were related to fire and are discussed elsewhere. Establishment of permanent settlements increased canopy opening on upper valley and floodplain sites, but agricultural, large-scale clearing was not yet important.

Population size increased and food processing became even more important on floodplains during the Woodland period (1000 B.C. to A.D. 1000). Technological advances such as the use of ceramics and the bow and arrow as well as ceremonial activities (e.g., mound building) are dominant features of this period. Since food, firewood, and shelter demands would have increased with population size, one can infer that Woodland aborigines had a larger impact on the landscape than did Archaic aborigines. Fire frequency, as well as the size and number of settlement clearings, probably increased. Because food sources were similar to those of the Archaic period, the implication of increased population size, ceremonial activities, and technological advance is one of increased efficiency in the use of natural resources (Jennings 1978).

Extensive agriculture of maize, bean, squash, sunflowers, and other vegetables on floodplain sites was practiced during the Mississippian period (A.D. 1000 to 1650). Upland sites were used exclusively for hunting (Bass 1977). Settlements tended to be large and concentrated. Wide-scale agricultural clearing, lumbering for settlement construction, and firewood gathering increased the number of clearings in valley sites. As some sites were abandoned, succession on old fields was initiated; floodplain communities dominated by *Rhus*, *Pinus*, *Sassafras*, *Robinia*, *Liquidambar*, and *Liriodendron* became common. Increase in population size increased food demands as well as labor force. Continued use of upland sites for hunting and gathering indicates man-set fires remained important. Thus, fire frequency increased or at least remained at Woodland levels during the Mississippian. Since *Pinus* spp. reproduce well after fire, pine-dominated forests probably continued to increase in importance.

Euro-American contact after 1650 caused dramatic changes in Cherokee culture and population density (Goodwin 1977, King 1979). Increases in warfare and disease depopulated the area. By 1700 the population had already declined to between 11,000 and 22,000 (Goodwin 1977). Decreased population size implies that old-field communities increased. The introduction of free-ranging livestock after 1750 is the first known incidence of unnatural grazing disturbance in the park area, and fires were set to enhance livestock range. During the various Indian wars (1756-1794), crops and orchards were often burned by Euro-American armies (King 1979). Some of these fires probably spread onto adjacent slopes.

By 1800 the Cherokee culture was quite similar to the Euro-American culture. Between 1800 and 1834, Cherokee lands were gradually taken by American settlers, and a treaty signed in 1835 released all Cherokee land for outside settlement (King 1979).

Euro-American Settlement (1790-1930)

Cultivation. During the 1700s, Euro-American settlers moved into the lower valleys, importing metal tools, firearms, and grazing stock. The first entry rights were issued for Cades Cove in 1794, and the first legal land grant was made in 1821 (Shields 1977).

Flats above streams and areas with gentler slopes were selected for farming. In general, farming stopped at 800 m in Tennessee and 1,070 m in North Carolina. Communities cleared for fields were largely cove oak, oak/chestnut forests, and possibly low-elevation floodplain communities. In contrast to the original vegetation, postagricultural sites are dominated by yellow pines, including *Pinus virginia*, *P. rigida*, and *P. echinata*, and an assortment of hardwoods. The portion of pine to hardwood increases along the mesic to xeric topographic gradient while the importance of *Liriodendron tulipifera* declines along this gradient.

Clearing of fields is similar to natural disturbances that remove the canopy and expose mineral soil. Unlike most natural disturbances, however, surface and soil organic matter are removed by continued cultivation. Natural disturbances tend to create smaller openings than intensive agriculture and often leave root systems and seed banks intact.

Grazing. Grazing is an oft-neglected element of agricultural disturbance. In the Great Smoky Mountains, settlers allowed cattle, sheep, equids, and swine to forage in the forests. Sheep and cattle were also driven to the high ridges for summer pasturage.

Cattle and hogs used unlogged cove and oak forests, and all types of stock were kept on the grassy balds (Lindsay 1976). Densities were often high (e.g., around 2,000 head near Spence field). Although some investigators have thought the treeless state of the grassy balds was due to natural phenomena (Whittaker 1956), the initiation of a vigorous succession after national park acquisition and livestock removal indicates the grass sward (at least in its 1900-1930 state) was maintained by stock (Lindsay and Bratton 1979, in press a).

Livestock pasturage impacts on grassy balds extended into the surrounding forest. Tree reproduction in forests adjacent to grassy balds date from the time of domestic stock removal, resulting in two distinct age classes (Lindsay and Bratton in press b). Had grazing continued for 200 years, forest regeneration would have been suppressed to such an extent that the grassy balds would have expanded.

Use of Native Plants. Gathering of edible and medicinal plants has continued through all periods of human history in the Great Smoky Mountains. Park policy permits noncommercial gathering of fruits and wild leek leaves (*Allium tricoccum*), the latter being a local tradition. Unfortunately, park establishment has not prevented the gathering of the increasingly rare ginseng (*Panax quinquefolium*), roots of which are exported to China. Poaching of ornamental plants (e.g., Orchidaceae, *Rhododendron* spp., and *Epigaea repens*) also occurs.

Logging. There were two eras of logging in the park area (Lambert 1958). Between 1790 and 1900 farmers cut timber for construction and firewood. Commercial operators selectively cut desirable species (*Liriodendron tulipifera*, *Prunus seriotina*, and *Fraxinus americana*) and searched out individual trees. There was also some harvest of tanbark and acid wood (largely *Tsuga canadensis*, *Quercus prinus*, and *Castanea* dentata) for industry. These sorts of cuttings were limited to lower elevations and accessible areas, and they caused little disturbance of surrounding vegetation and local and minor soil disturbance. Individual tree cutting has effects similar to small tree gaps, but bole removal results in a loss of nutrients, nitrogen-fixation sites, and seedbed sites important for such species as Betula lutea. The effects of selective cutting are difficult to detect after the stumps disappear.

The second type of logging was based on large-scale, mechanized operations utilizing logging railroads, skidders, and booms. Lambert (1958) reports that oak and chestnut were half the saw timber produced in Swain County, North Carolina, in 1909. Spruce, fir, and hemlock were in demand after the turn of the century when railroads made these forests accessible.

This type of logging affected whole watersheds, removed most mature trees, heavily disturbed the soil, and left massive piles of slash which greatly increased the frequency of severe fires (Lambert 1958, McCracken 1978). Regeneration after this intensive disturbance tends to favor even-aged stands dominated by a few pioneer species (McCracken 1978). Usually, on lower flats and slopes, Liriodendron dominates, but on higher elevation burned sites Betula lutea and Prunus pensylvanica are most important.

In terms of spatial scale alone, logged forests have no known natural precedent. A total of 70% of the 209,000 ha of the park has been intensively disturbed by cutting and fire, whether resulting from farming or large-scale logging operations. The remaining 30%, though a fraction of the original, represents the largest block of virgin timber left in the eastern United States and is one of the most important values of the park.

Exotic Species. Euro-American man brought domestic animals and plants not native to the Appalachians. Some of these introductions, such as domestic cattle and sheep, are already gone from the natural area of the park, and others, such as apple trees and boxwood, are slowly disappearing.

None of the exotic species problems in the park, however, are related to local agriculture. The severest problems have been with chestnut blight, balsam wooly aphid, and European wild boar.

The chestnut blight, Endotheca parasitica, was originally introduced to the United States in 1919, and by 1930 it had killed most mature individuals of Castanea dentata in the park. At that time there were about 75,000 ha of oak/chestnut forest in the park; chestnuts were also found in pine and cove forests (Whittaker 1956; figure 2). The nature of Castanea replacement was a function of its original density (Woods and Shanks 1959). Where density was high, advanced tolerant reproduction and intolerant seed reproduction were important. In sites with lower densities of Castanea, encroachment by adjacent canopy trees was the dominant process. This prevented the establishment of intolerant species and the release of advanced reproduction. In general, Acer rubrum,

Figure 2: Distribution and severity of chestnut blight (*Endotheca parasitica*). Distribution on two topographic gradients and percentage of total tree stems killed are shown. (Adapted from Whittaker 1956.)

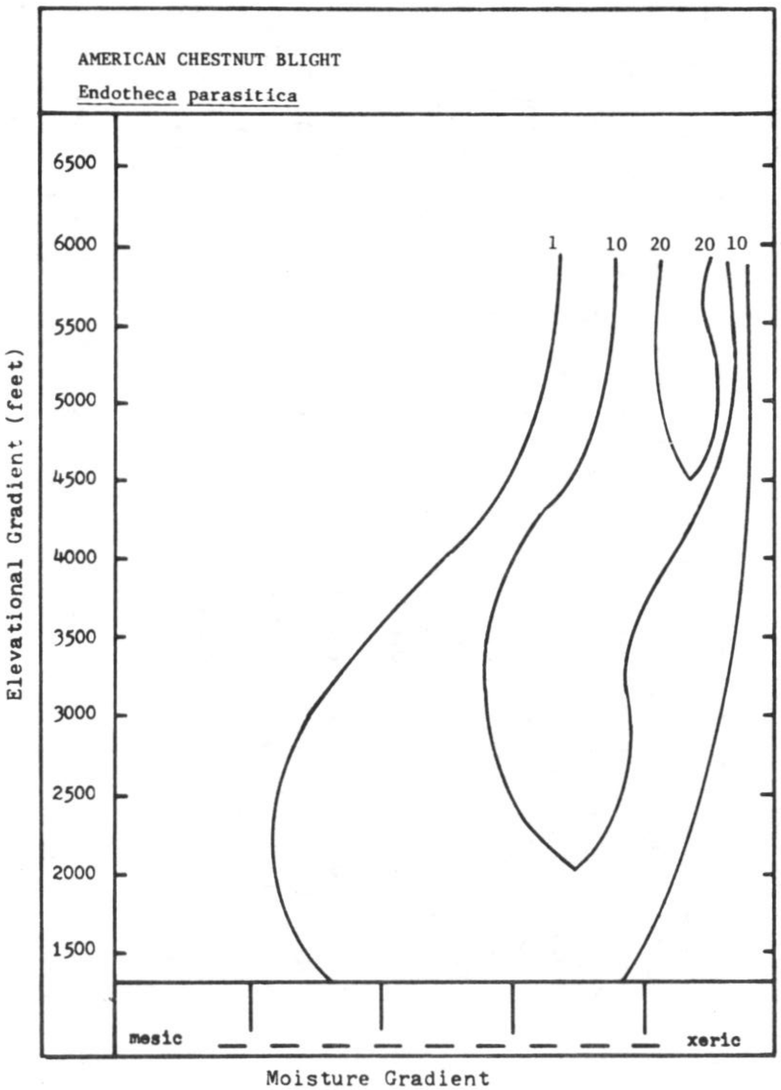
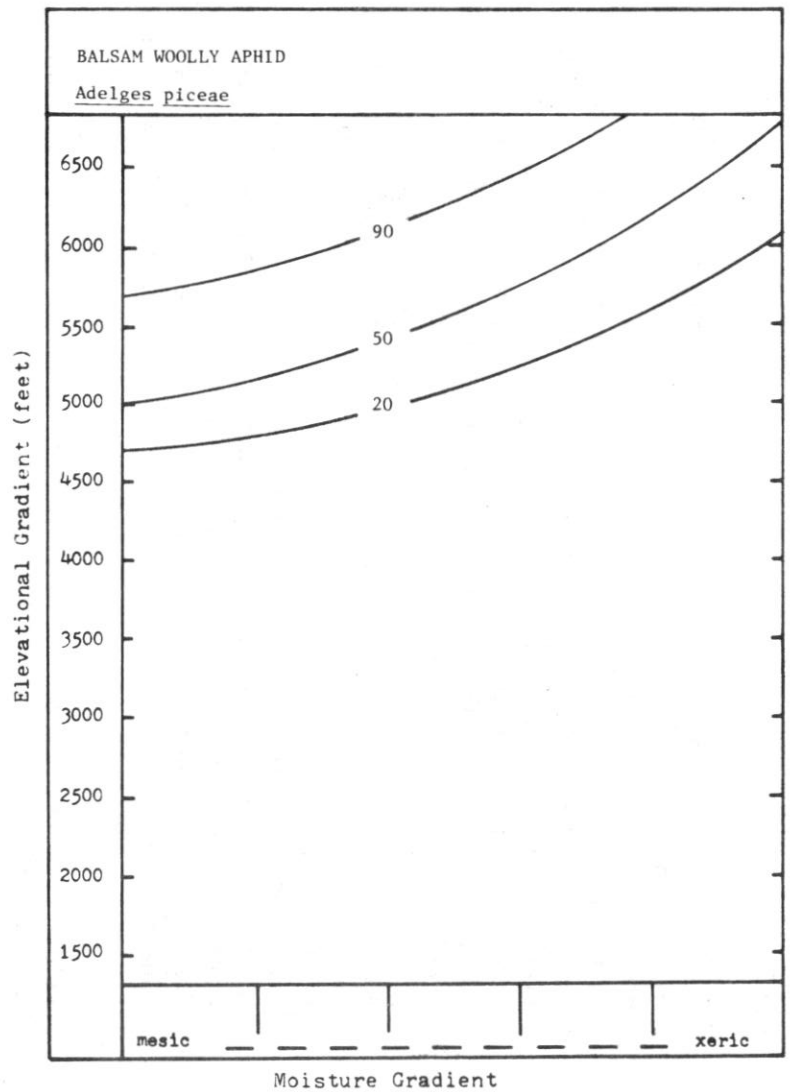


Figure 3: Distribution and severity of balsam woolly aphid (*Adelges piceae*). Distribution on two topographic gradients and percentage of tree stems killed are shown. (Adapted from Whittaker 1956.)



Quercus prinus, and Q. rubra increased in importance as Castanea declined.

Balsam woolly aphid (Adelges piceae) is the most damaging exotic insect in the park. First found in the park in 1963, the aphid now threatens to eliminate mature Abies fraseri in its 6,000 ha range (figure 3). Initial infestations tend to begin at the spruce/fir/hardwood ecotone and at lower elevations (Eager 1978). Once established, aphids spread within the stands and along the elevational gradient. Trees may take years to succumb, but death may occur in as few as three growing seasons (Johnson 1977). Fir reproduction has higher survivorship than mature trees.

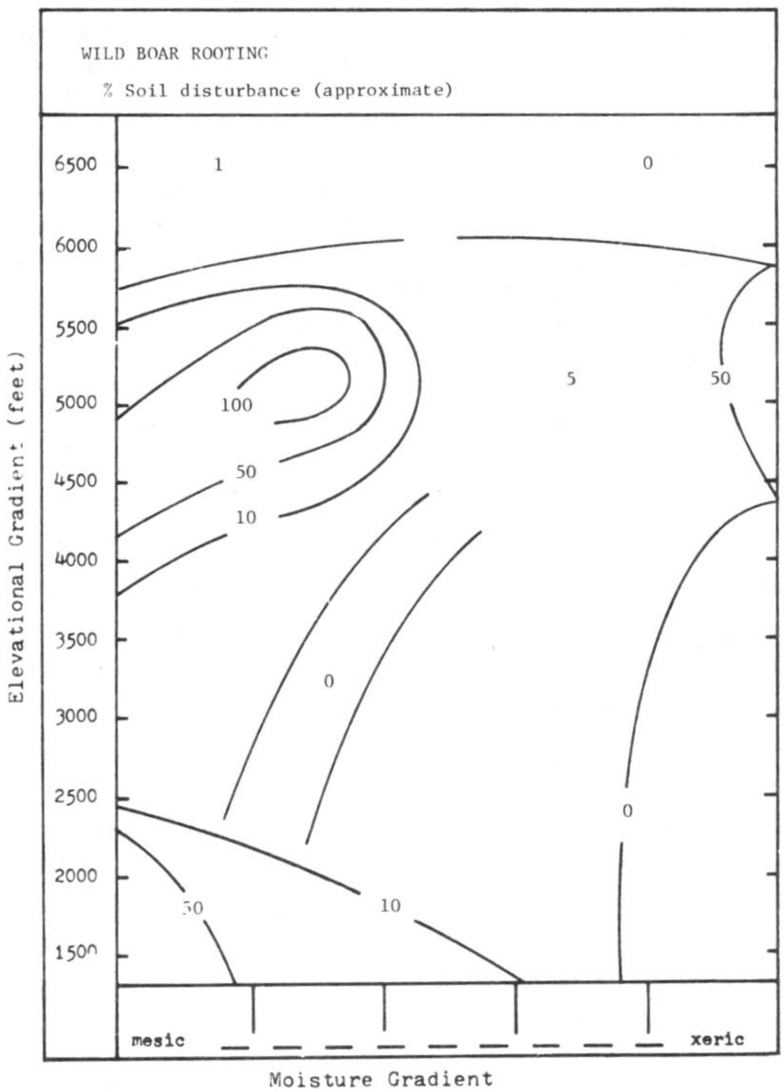
Attack by balsam woolly aphid causes an increase in light and alters microclimate in dense fir stands. Understory shrubs, herbs, and reproduction respond quickly to this disturbance by growing more vigorously (Eagar 1978). Lichens in dead fir canopies also dramatically increase after needle drop. An increase of seed reproduction has not yet been documented, but one would expect an increase in Betula lutea, Sambucus canadensis, Rubus canadensis, Sorbus americana, and Amelanchier laevis. Fraser fir may reach a mature size and reproduce before aphid attacks. If this occurs, then one can envision a mosaic of Fraser fir populations: some mature with aphids and others immature and relatively free of aphids. However, Hay et al. (1978) think it is only a matter of time before Fraser fir is entirely eliminated, removing an endemic species from the already species-poor high elevation flora. Fraser fir tends to support more epiphytic mosses and liverworts than red spruce; hence, the loss of fir may also lead to local extinctions in the cryptogammic flora. High elevation forests are most likely to be dominated by red spruce, with a minor hardwood component.

The third major exotic is the European wild boar (Sus scrofa), which entered the park during the 1940s (Bratton 1974). The hogs have slowly moved from west to east across the park and will probably invade the remaining hog-free watersheds in the next few years. Although the hogs do not directly disturb the forest canopy, they sometimes completely remove the herbaceous understory and damage tree reproduction (Huff 1978). Hog rooting is widely scattered over the topographic gradients (figure 4). Gray beech forest and successional cove forest are especially heavily impacted, while hemlock/rhododendron cove, spruce/fir, and xeric-site yellow pine stands show little or no disturbance (Bratton 1974, 1975; Howe and Bratton 1976).

Recovery after hog rooting is slow under a full canopy. Bratton (1975) noted that succession begins a few weeks after spring rooting on grassy balds but does not occur at all during a single smmer season in hog-disturbed gray beech forest. Bratton et al. (in press) found that cover of vernal flora returned to expected values after three years of hog exclusion but that species number had not returned to normal level during this period.

Looking at these three exotics together, it is noteworthy that only hemlock coves and the xeric pine forests (most of the latter have recent fire histories) have been relatively free of change in structure due to

Figure 4. Distribution and severity of wild boar rooting. Average percentage of soil surface rooted is shown on two topographic gradients. (Adapted from Whittaker 1956.)



disturbance by an exotic. It is also notable that much of the change occurred during or after park acquisition.

Preservation (1936 to Present)

The initiation of land purchase in 1927 and the establishment of the national park in 1936 ended the removal of forests within the park. Some small farmers were granted life leases, but over the last 40 years, agriculture and grazing have gradually been limited to the historic districts.

Although most of the severe human impacts have been excluded from the national park, "complete protection" of park lands from man's influence probably will never occur. To allow for tourist, recreational, and even scientific use, developments such as roads, trails, campsites, and a shelter system have been constructed. The park has an annual visitation of about 10 million visitor days, and usage is unlikely to decrease in coming years. Road building has removed the forest cover resulting in the establishment of communities of grasses and forbs, the favoring of shade-intolerant woody species, and mud and debris slides. Use of Anakeesta rock (high in iron sulfides) for fill has acidified streams below roads and parking areas in the center of the park.

Frontcountry visitor facilities have resulted in openings in the forest and the encouragement of exotic plants. Although backcountry developments, such as trails and campsites, cause less disruption in general, some forest types are vulnerable to trampling and firewood gathering. Blowdowns are common in spruce/fir forests with campsites or shelters (Saunders 1979, Bratton and Stromberg in press).

Within historic districts, the maintenance of open fields through grazing and mowing favors field weeds, including many exotics, and results in locally high populations of some native animals. Management policies have not been stable. There are also impacts on local natural communities (Bratton et al. in press).

DISTURBANCES OF MIXED ORIGIN--FIRE

Determining the degree of naturalness of fire is a matter of the interpretation of such factors as ignition source and management history. This interpretation is often difficult.

Prior to man's entrance into the southern Appalachians over 12,000 years ago (Dickens 1976), lightning was the primary ignition source. During the full-glacial period (18,000 BP) a vegetation mosaic consisting of *Pinus banksiana*, *Picea*/*Abies*, and alpine tundra communities blanketed the park area (Delcourt and Delcourt 1979). Since *P. banksiana* has serotinous cones, we can infer the presence of fire during full glacial periods.

Between 16,500 and 12,500 years ago, mixed coniferous/deciduous forests became more important as the climate became warmer and more mesic (Delcourt and Delcourt 1979). More mesic conditions may have prevented fields from drying except during drought conditions. Fire rotations may have become longer, since fire size was probably smaller.

During the Paleoindian period, fires were purposefully set, but they also accidentally escaped from campfires. Fires set by aborigines shortened the fire rotation, compared to the prehuman regime. During the Hypsithermal (5,000 BP), more xeric forests and drier conditions prevailed. Increasing human population and drier conditions probably resulted in a shorter fire rotation than previously. After the Hypsithermal, the climate became cooler and wetter. Increasing aboriginal populations may have offset the wetter climate and maintained or increased fire occurrence. When Euro-American man first contacted the Cherokee, man-set fire was an important landscape influence (Goodwin 1977). Aboriginal burning may have caused an increase of *Pinus*, *Sassafras*, *Robinia*, *Oxydendrum*, *Rhus*, and *Aralia* in area forests. The presence of *Pinus*-dominated forests on xeric sites may represent, in part, constant fire disturbance and not an edaphic climax.

Euro-American settlers between 1790 and 1930 frequently burned submesic to xeric forests below 5,000 feet with light ground fires. These communities are dominated by *Quercus*, *Castanea*, *Carya*, and *Pinus*. *Pinus* forests in the western part of the park area were burned an average of once every 11.9 years (Harmon in press a). Lambert (1958) estimated Swain County, North Carolina, was burned completely every 3 to 10 years. Settlers burned to maintain berry crops (Shields 1977), clear land, maintain livestock forage (Ayres and Ashe 1905, Lambert 1958), and aid in harvesting chestnuts (fruits of *Castanea dentata*). Accidental and arsonous fires also occurred. Repeated fires reduced canopy reproduction and soil organic horizons (Ayres and Ashe 1905). In addition, fast-growing, thick-barked species were favored by frequent burning (Harmon in press a). Some forests may have been open enough for shade intolerant species to reproduce and grow under the canopy.

Man's influence greatly expanded in the Great Smoky Mountains after large-scale logging operations were introduced (Lambert 1958). Extensive quantities of woody debris were burned between 1910 and 1930. Heavy fuel loadings combined with extreme fire conditions led to severe and widespread fires. Logging fires may have eliminated sprout reproduction and favored the establishment of light seeded or easily dispersed species. Above 1,000 m elevation the dominant replacement species are *Prunus pensylvanica*, *Sorbus americana*, and *Betula lutea*. In the highest elevations, *Abies fraseri* and grass/blackberry mixtures dominate burned sites. Below 1,000 m, replacement species on mesic sites are *Liriodendron tulipifera*, *Betula*, *Sassafras albidum*, and *Robinia pseudo-acacia*. On xeric sites, *Oxydendrum arboreum*, *Sassafras albidum*, and *Quercus* are important.

Since park establishment, there has been a noticeable decline in fire size and number (USDI, NPS, GRSM fire atlas). Under present management policies, all fires, regardless of cause, are extinguished as quickly as possible. Thus, forests which burned as often as once every three years during settlement times have not burned in over 40 years. At present rates, an area equivalent to Great Smoky Mountains National Park will burn completely every 1,000 to 10,000 years (Barden 1976). If all lightning fires were allowed to burn unhindered, the fire rotation would range between 500 and 1,000 years. When man-caused fires were allowed to burn untended, the fire rotation was as short as 20 to 50 years.

Fire suppression has increased canopy reproduction and favored the expansion of slower growing and thinner barked species (e.g., Tsuga canadensis). Short-lived genera such as Rhus, Erechtites, and Eupatorium have already declined in importance over 40 years in areas where fire has been important. Longer-lived canopy species will take longer to decline. Fire suppression also leads to increases in soil organic horizons. Therefore, nutrient cycling rates may have declined considerably since fire no longer periodically releases nutrients.

During the era of suppression, both lightning- and human-caused fires have occurred. They have differed both in number and in topographic position (figures 5 and 6). (Note that figure 5 is based on a 38-year record, while figure 6 is based on an 11-year record. If the figures were normalized for years of record, the contrast between the numbers of lightning- and man-caused fires would be increased.) Lightning fires have occurred on drier topographic positions than have man-caused ones, which occur with greater frequency near roads and park developments. Fire is of very low occurrence at the highest, wettest elevations.

DISCUSSION

The following generalizations apply to disturbances in Great Smoky Mountains National Park, as in other regions (White 1979):

> Disturbances vary in the landscape with topography, white characteristics, and community state.
>
> Species differ in their response to disturbance (in their mortality, growth rates, and ability to colonize open sites).
>
> Disturbances overlie spatial gradients of temperature and moisture in determining vegetation composition and structures.

This disturbance overlay complicates our understanding of landscape patterns: Stands with similar temperature and moisture regimes may differ in disturbance histories. Stochastic events may result in variable responses to disturbance (White 1979). This is clearly the case for fire in the park; the studies of Harmon (in press a and b) emphasize the variability of effects, depending on fire frequency, intensity, severity, and history.

Disturbance, whether natural or anthropogenic, then is an added dimension to the spatial-topographic gradients reported for the park by Whittaker (1956) and Golden (1974) and one which diminishes the

Figure 5: Number of lightning fires in Great Smoky Mountains National Park, 1942-1979 (fires suppressed). (Adapted from Whittaker 1956.)

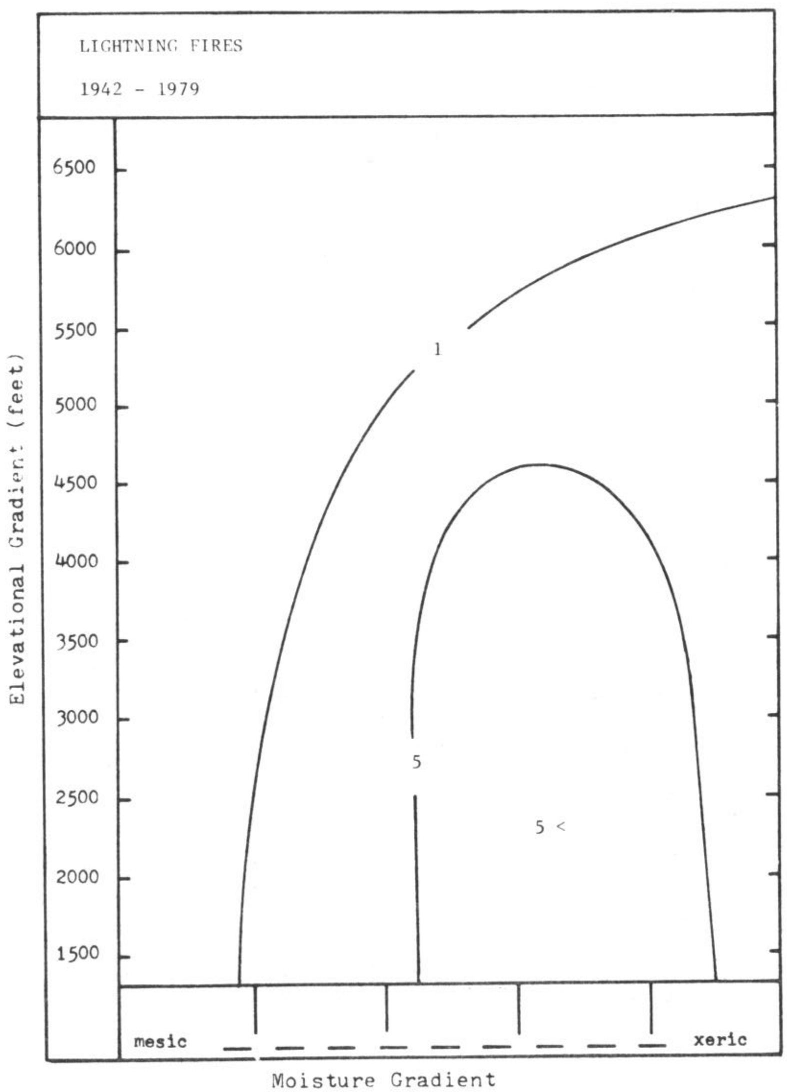
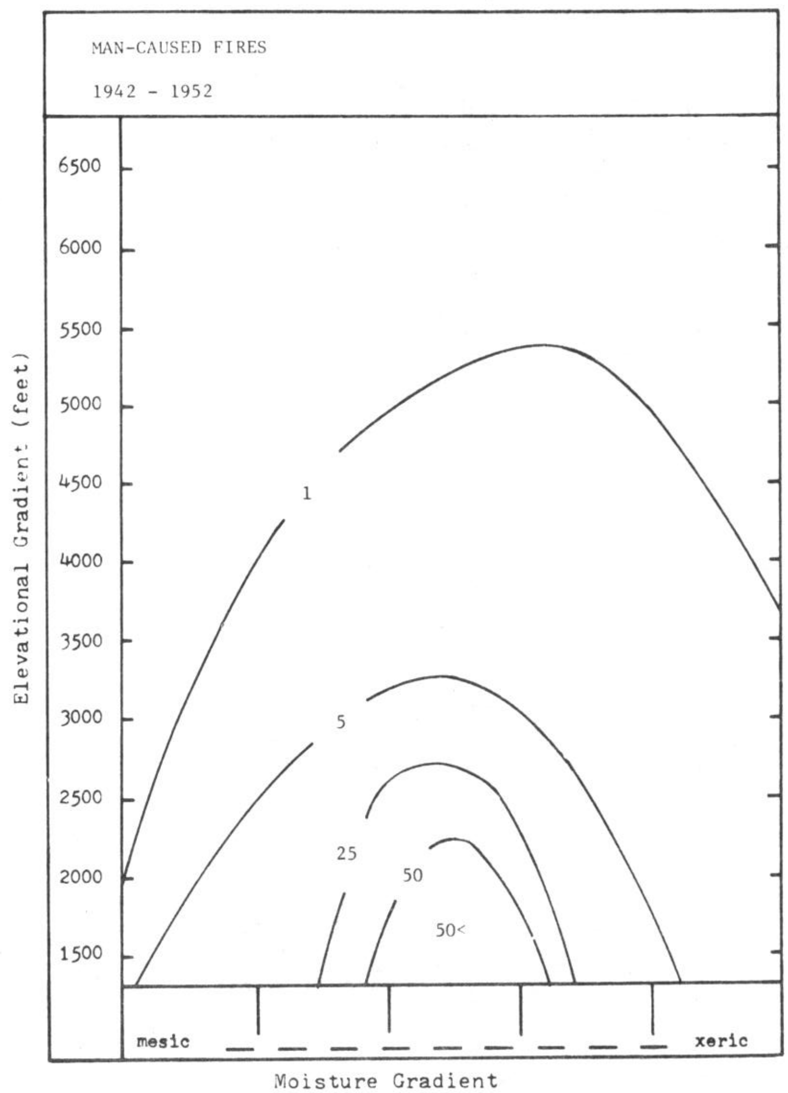


Figure 6: Number of man-caused fires in Great Smoky Mountains National Park, 1942-1952 (fires suppressed). (Adapted from Whittaker 1956.)



predictability of vegetation characteristics from site data alone. In figure 7 we have depicted the elevation and moisture gradient distribution of major disturbance-exploiting trees. The importance of these species fluctuates widely with the outplay of disturbance and succession. We have chosen those species which increase in importance with increasing disturbance severity; these are shade-intolerant, rapidly growing species. Without disturbance, shade-tolerant, slower growing species will dominate (figure 8). These two sets of species are the ends of gradients in shade tolerance; intermediate species also occur.

A final general observation is that disturbances interact synergistically. Drought- or fire-caused mortality results in greater susceptibility to windstorm; windfalls, icestorms, and pine bark beetle outbreaks increase fuel loadings and hence severity of fire; postlogging successional state influences wind disturbance over large areas. (Even-aged youthful canopies are less vulnerable to wind.) Where human impacts interact with natural disturbance regimes, as with fire, management dilemmas are posed; our management options in natural preserves are sensitive to our definitions of "natural" itself. We will return to this point later.

Importance of Park Disturbances

Disturbance importance can be assessed in terms of a number of characteristics. To compare disturbances in the park, we have chosen three characteristics (figure 9): percentage of communities potentially influenced (gradient length), percent area of the park disturbed per year, and severity (percentage of biomass affected in a typical event).

Gap formation is a process widely distributed in our predominantly forested landscape--all communities are affected. However, biomass effects and areal extent are relatively low (stated another way: ours is a landscape of relatively long-lived forests). By contrast, debris slides are very severe, but highly localized in the landscape and of low areal extent. However, these events, choosing another characteristic for disturbance assessment, are very important in terms of rare plant habitat.

There are four fire regimes indicated on figure 9: the aborigine-set fire, lightning fire, logging slash fire, and fire suppression era regimes. The aborigine-set fires were the most significant in terms of total area, but logging slash fires were more severe.

In general, anthropogenic disturbances (open circles) are more frequent than natural disturbances (closed circles). Many anthropogenic disturbances affect large areas (e.g., aborigine-set fires, chestnut blight, logging slash fires, and wild boar rooting).

Logging and agriculture, taken together, have influenced 70% of the park landscape. Much of this percentage, and the drier communities within the remaining 30%, have been much affected by changing fire regimes.

Figure 7: Distribution of representative shade-intolerant trees in Great Smoky Mountains National Park. Lines depict population limits: For SRBAMR (Sorbus americana) and PRNPNS (Prunus pensylvanica), the lines indicate lower elevational limits; for LRDTLP (Liriodendron tulipifera), RBNPSD (Robinia pseudo-acacia), and PNSSPP (Pinus spp.), the lines indicate upper elevational limits. (Adapted from Whitaker 1956).

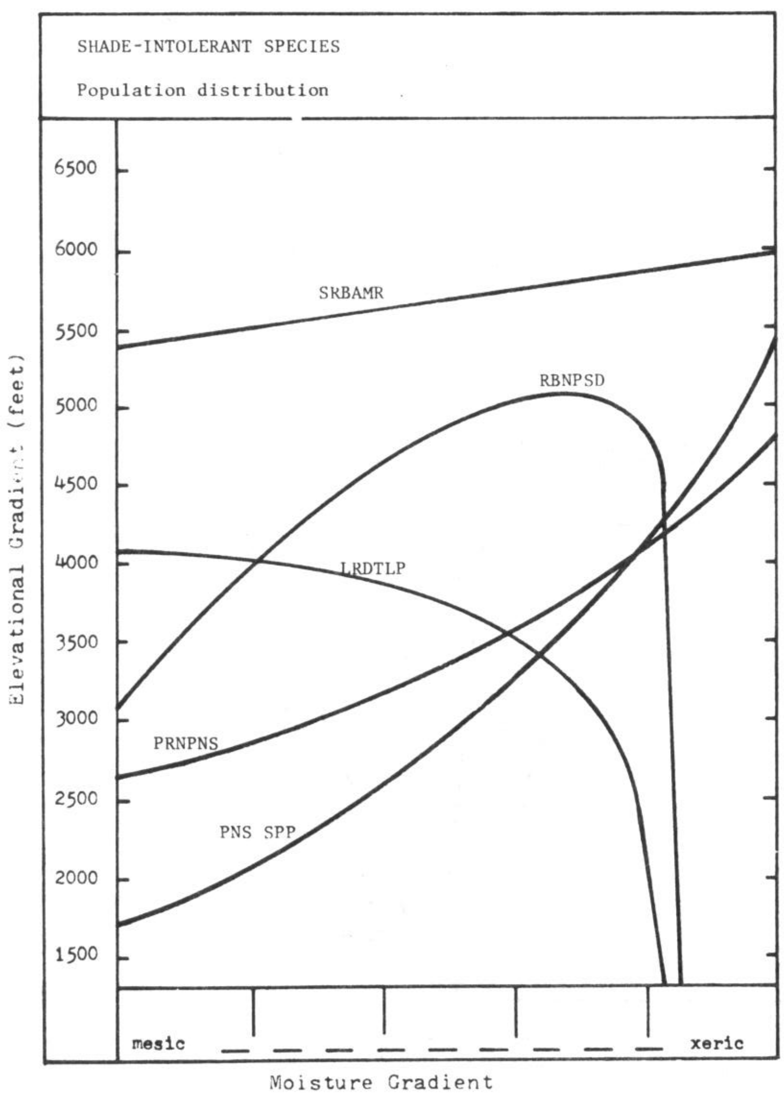


Figure 8: Distribution of representative climax trees in Great Smoky Mountains National Park. Lines depict population limits: For PICRBN (Picea rubens), the line indicates lower elevational limit; for ACRSCR (Acer saccharum), TSDCND (Tsuga canadensis), QRCPRN (Quercus prinus), and QRCCCC (Quercus coccinea), the lines indicate upper elevational limits. (Adapted from Whitaker 1956).

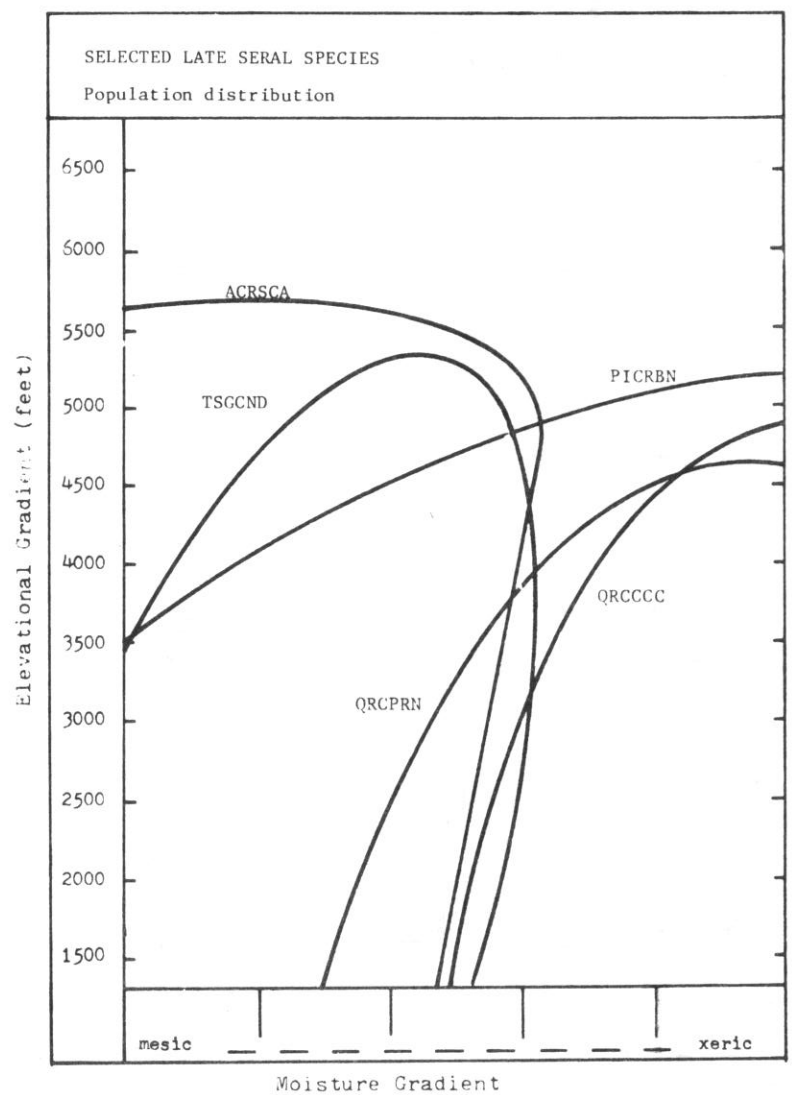
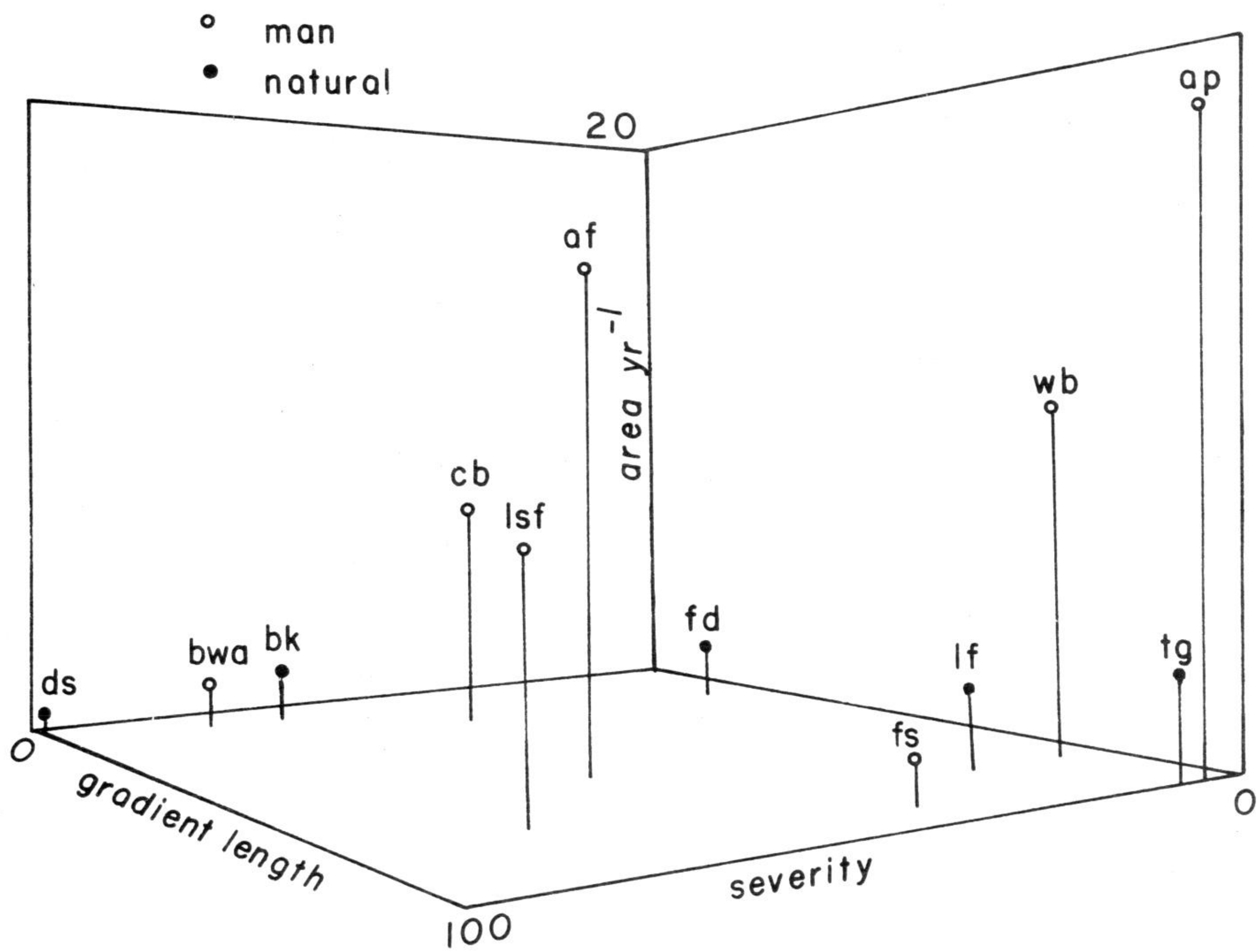


Figure 9: A three-dimensional model of disturbance importance within Great Smoky Mountains National Park. The axes correspond to (1) area affected as a percentage of the park total, (2) gradient length (or area) expressed as a percentage of the total area involved on topographic moisture and elevational gradients, and (3) severity expressed as the percentage of total biomass removed by disturbance. Disturbances are symbolized as follows: ds = debris slides, bwa = balsam woolly aphid, bk = beetle kill, cb = chestnut blight, lsf = logging slash fires, af = aborigine-set fires, fd = frost damage, fs = fire suppression regime, lf = lightning fire without suppression, wb = wild boar rooting, tg = tree gaps, and ap = air pollution. Air pollution is illustrated as influencing less than 20% of the park each year; however, the impact is probably 100% of the park.



Three exotic organisms (wild boar, chestnut blight, and balsam woolly aphid), taken together, have influenced all parts of the landscape except the hemlock/rhododendron coves and xeric pine ridges. Changing the fire regime has influenced the latter: The park's remnant old-age hemlock/rhododendron coves thus represent the only vegetation type without obvious anthropogenic impact. However, this type is potentially influenced by several general impacts: loss of native predators and large populations of deer, air pollution and the spread of pesticides in windborne agricultural dust, and visitor use. The influence of man permeates natural areas today; impacts are thus a matter of degree, not a matter of absolute presence or absence.

We should point out again our use of percent biomass removal for severity. Wild boar impacts are severe in terms of herbaceous communities, less severe in terms of our scale in figure 9. This also ignores possible long-term biomass losses, not now apparent. Air pollution is thus also rated at low severity.

As might be expected, the frequency for natural disturbances is inversely related to severity--the park landscape lacks highly frequent, highly severe disturbances. Tree species live on an average of 200 to 300 years in the park. Nonetheless, disturbance is a highly significant process for forest regeneration. The percentage of communities affected is also inversely correlated with the severity of natural disturbance. Anthropogenic disturbances show no such balance, at least in the short run. They are, in general, more severe than natural disturbances of the same frequency; similarly, they are more severe than natural disturbances with similar distributions among communities. This high severity could not continue in the long run, since the total biomass present would decline under these regimes. The anthropogenic disturbances in figure 9 have been depicted in terms of their short-term characteristics.

Cyclic and Directional Changes

Disturbances in the park landscape produce both cyclic and directional changes (see Knapp 1974). Windstorms, icestorms, floods, droughts, temperature fluctuations, debris slides, and erosional processes on bedrock outcrops all produce cyclic changes on any one site, with the landscape approximating a dynamic equilibrium in the sense of Heinselman and Wright (1973, White 1979), at least, if the possibility of long-term climatic change is excluded. The patch dynamics of these processes (Pickett and Thompson 1979) is on a small scale relative to the size of the park: All age classes of the successional sequences produced are present. We expect no large-scale compositional change and no preservewide exclusion of species or communities. Moreover, these disturbances are natural, for the most part manageable, and beneficial. (There are native species adapted to them which persist in the landscape through their operation).

Of more direct concern are the disturbances which produce directional changes. These include the anthropogenic disturbances we have outlined as well as karst processes among the natural ones. Karst processes operate in only a small part of the park landscape. Drainage changes and collapse in sinkholes could cause habitat changes and elimination of species in the park. Even if such changes were cyclic, park sites might depend, in the long run, on seed sources outside park boundaries. We suspect the park does not contain a dynamic equilibrium in terms of the geological processes in these habitats.

Fire, which has both natural and anthropogenic components, is once again difficult to assess. The recent history is one of widespread anthropogenic fire in prepark days followed by postpark fire suppression. The landscape is not now in equilibrium; the record is difficult to interpret in terms of any past equilibrium. The interaction of fire suppression and the natural outbreaks of southern pine beetle is leading to a net conversion of pine to hardwood. There may be some xeric rocky sites where pine forms a stable edaphic type (Barden 1977, Zobel 1969), but it is clear that reduced fire frequency can only lead to reduction in pine importance in the long run. Moreover, since pine requires exposed mineral soil for reproduction fire frequency is less important than fire severity for pine maintenance.

Anthropogenic disturbance has initiated directional changes as seen in postlogging and postagricultural succession and postgrazing succession on grassy balds (Lindsay and Bratton 1979). Succession has also been initiated in several wetlands, presumably because of past drainage changes and the extirpation of beaver (Castor canadensis). The extirpation of large predators and the maintenance of open habitat in several historic districts has led to local overbrowsing by Odocoileus virginiana, a native vertebrate, which is causing directional trends in tree reproduction (Bratton in press). Local gathering of native plants continues and may be causing population declines, but baseline data are only now being collected. Exotic organisms are causing directional change: Two community dominants will be lost, and severe disruption of understory vegetation has occurred, as previously discussed.

In assessing these directional changes we should be concerned with other changes in ecosystem parameters as well as compositional changes. For example, the widespread synchronization in canopy height and age in postlogging successions will influence the frequency of blowdown for hundreds of years to come. The removal of large boles in these stands and the changing size and frequency of downed wood also reflect an overall change in nutrient cycling and other site characteristics (e.g., the presence of seed sites for species such as Betula lutea, which exploits rotting boles for germination).

Bormann and Likens (1979) discussed ecosystem approach to steady state after disturbance. We extend their reasoning to mesic logged stands in the park to produce the following list of ecosystem attributes and the time required for approach to steady state: leaf area index, basal area, gross productivity, and control of soil erosion are the first parameters to return to steady state (tens of years), followed by export of dissolved substances and species richness (100-200 years), biomass and nutrient storage (200-300 years), and age and size class distributions (500 years). The mode of approach to steady state is discussed fully in Bormann and Likens (1979).

MANAGEMENT OF DISTURBANCES

Dynamic systems pose managerial issues for preservationists. Simply stated, what we preserve must change (White and Bratton in press). Implications of natural disturbance ecology for preserve management have recently been discussed by Westhoff (1971), Owen (1972), Wright (1974), Dolan et al. (1976), Franklin (1978), Pickett and Thompson (1979), and White (1979).

The situation is clearest, of course, for anthropogenic disturbances. Certainly, natural area managers should minimize human impacts, but even this situation can lead to conflicts. Currently in Great Smoky Mountains National Park, several rare plants depend on a possibly anthropogenic community--grassy balds (Lindsay 1976, Lindsay and Bratton in press). Natural succession was initiated with park establishment and the cessation of grazing; succession now threatens the open habitat and rare species. In Europe, historic anthropogenic communities are even more important in the landscape (Green 1972, Haber 1973). Should natural area managers maintain such communities? The debate is not yet concluded in Great Smoky Mountains, but it appears that two grassy balds will be maintained, while others will be allowed to succeed to forest.

Disturbance suppression is a management option that has been attempted for a variety of natural disturbances (e.g., fire, flood, insect outbreaks, and coastal erosion and deposition) but has often been found to lead to unforeseen and detrimental consequences in the long run (e.g., increased susceptibility to subsequent disturbance--Mooney et al. 1979, Johnson et al. 1976, Schroeder et al. 1976, Brown 1961). Natural system parameters are not the only constraints in determining whether disturbances should be suppressed or allowed: political pressure, danger to human life and property, impacts on air quality (in the case of fire), and threats to endangered species are also important. Whereas many endangered species are in fact maintained in the landscape by natural disturbance, some may be vulnerable to specific disturbance events. This stresses the need for understanding the biological realities of the managed systems.

Natural area management, endorsed in a general sense by the U.S. National Park Service, requires allowing, where possible, the outplay of natural processes like disturbance (Leopold et al. 1963, Stone 1965, Owen 1972). Suppression, though often practiced, is in a sense irreconcilable with this philosophy. Certainly, some park disturbances are both impossible and undesirable to manage within the natural area--debris slides, floods, windstorms, icestorms, droughts, outcrop dynamics, karst processes, and temperature fluctuations. These are natural and beneficial in the maintenance of landscape heterogeneity and species diversity.

The degree and type of managerial action with regard to fire in the park is complex. Although fire is an important influence on ecosystems, restrictions on fire occurrence will continue past the present era of full suppression (1930-1980) if a currently proposed fire management plan is accepted. Fires are legally considered as pollution sources and may be suppressed if standards are exceeded. Fires burning near park boundaries will be suppressed to reduce liability for property damage outside the park. Even with regard to fires well inside boundaries, public opinion is probably against the use of fire--this too must be overcome. Finally is the problem of the appropriate fire regime--should managers try to simulate aboriginal burning (the pre-Columbian regime)? It may not be economically feasible to burn large areas as frequently as aboriginal man did. An alternative strategy would be to maintain this disturbance regime in a few large, representative watersheds. Other watersheds might revert to a lightning-caused, fire-only status.

The exotic balsam woolly aphid and native southern pine beetle provide an interesting contrast in management. Managers attempted control of southern pine beetle in two recent epidemics through sanitation cutting and hand application of pesticide. These methods were unsuccessful, and the outbreaks declined because of natural predators and climatic conditions. Cutting of infested trees was expensive, ineffective, eliminated nesting and foraging sites for birds, and may have influenced cycling of nutrients bound in dead trees. During another major infestation, pressure from outside the park may again mount for the "control" of this insect. This pressure comes from economic interests that view the park as a refuge for an insect "pest."

Only isolated sanitation cutting has been attempted for control of balsam woolly aphid. There are no known biological or mechanical controls. The only viable management strategy at present is to avoid fire in Abies stands. Whereas fire following beetle kills in pine stands stimulates pine reproduction, fire in aphid-killed stands of fir would be disastrous for fir reproduction. Necessary research projects include the search for suitable controls and resistance development in Abies fraseri. Currently, however, the future looks bleak for Abies in the southern mountains; Castanea elimination is certainly another clear example of the lack of control options.

Wild boar (Sus scrofa) control is also difficult, and total removal is unlikely. Boar populations will only be reduced if 50% or more of the population is harvested annually. Unless some acceptable biological control is developed, boar effects cannot be eliminated by managers. High impact areas with undisturbed understories are high priority areas for protection, and exclosures are necessary. Political pressure has been brought to bear on this issue, as on the southern pine beetle issue; some interests view the park as a reservoir of boar for lands on the periphery of the park where hunting is permitted.

Two levels of management have emerged from ongoing discussions of conservationists: species-oriented management and ecosystem- or process-oriented management. Endangered species conservation has often emphasized the species level; the battle to save natural systems intact and uninfluenced has often led to rejection of single-species management. These two levels of management may sometimes complement one another (Hooper 1971, Kushlan 1979, Wilcox 1980) and sometimes conflict (Bratton and White 1980).

With regard to park disturbances, both levels are possible. Some of the natural processes are difficult and/or undesirable to manage in a large natural area--debris slides, windstorms, icestorms, droughts, temperature fluctuations, and karst processes. However, species management does have some options in these situations. Human impacts, including management, may have reduced species populations, which are then highly vulnerable to a single natural event like flooding, drought, or fire (Loope in press). Monitoring of populations and direct intervention may be necessary in such cases. In the park, past drainage changes and agriculture in Cades Cove have restricted wetland habitats and species. Reintroduction of beaver (Castor canadensis) might increase wetland habitat, but some species populations are now so restricted that they would be vulnerable to specific dam sites.

Even where management has been unsuccessful (e.g., for wild boar), managers could attempt species level management to mitigate local extinction. This could include cultivation and reintroduction of rare plants.

What is Natural?

Natural area managers in Great Smoky Mountains National Park, as elsewhere, have inherited systems which have past histories of human influence. The managing of these systems requires definition of a reference state, presumably natural and prehuman. From the definition of reference state comes the justification for management itself.

The role of aborigines in the park system is particularly vexing with regard to this question. The U.S. National Park Service has chosen the pre-Columbian era as the reference state (Leopold et al. 1963). For the park, however, the pre-Columbian era was not one of ecological consistency, particularly with reference to fire regime. Aborigine populations were changing, as was climate. In a practical sense we must choose what fire regime for which we would like to manage--how much aborigine influence we conceptualize as natural. Alternatively, we can abandon the use of fire as a management tool and allow only lightning-caused fires. Such fires will not be truly natural for decades to come, however, since current fuel levels are related to past fire suppression efforts. In addition, we may see a decline in fire-stimulated species, possibly even local extirpation. Fires may be less frequent, but due to high fuel loadings, more severe.

For specific disturbances and preserves, reference states will have to be defined in more specific terms than reference to historical eras, such as pre-Columbian. Only by making those choices can we adequately guide future policy decisions.

Monitoring

The role of disturbance in the park leads to the conclusion that monitoring of community change is essential. In addition, management regimes themselves have hardly been constant in the park: The evaluation of management changes, if it is to be done with highest confidence, requires before and after measurements. All too often, we must use control stands chosen after the fact and not strictly comparable to premanagement stands because no baseline data were collected from these sites (see discussion in Bratton et al. in press). As others have concurred, monitoring is a task integral to preserve management on ecosystem and community levels (Johnson and Bratton 1978). The importance of preserves in maintaining endangered species adds the species and population level to monitoring needs (Walters 1976, Bradshaw and Doody 1978). The occasional long-time scales of disturbance processes and population changes further underscore the need for monitoring. In addition, at least in the United States, altering management regime may require legal action--which, in turn, is dependent on data to document preserve change.

Monitoring should be oriented around the composition and structure of the natural systems, including their dynamic properties. It should always include permanent plot establishment, and it may include the collection of autecological data that will help answer questions about the mechanism of change (e.g., analysis of seed rain, seedling establishment, and survivorship data). Permanent plot and autecological data can be combined to develop and test disturbance and succession models. These models may be valuable for predicting future trends and assessing prehistoric influences on the park (e.g., aboriginal burning).

Nature Interpretation

Finally, disturbance processes, whether anthropogenic, natural, or an interaction of these types, should receive attention in interpretive and educational programs. This will foster understanding of vegetation/landscape relations and will ultimately aid visitor acceptance of natural disturbance processes themselves.

CONCLUSIONS

Scientists, managers, and interpreters must deal with the omnipresent dynamics of natural systems and the permeating influence of man. Biosphere reserves, particularly primary natural areas, are called upon to provide monitoring benchmarks against which further human-caused change can be measured. This means that natural changes and the effects of past human disturbances will have to be assessed in order for continuing human impacts, like air pollution, to be fully understood.

Scientists will deal with ecosystem change through the design of monitoring schemes and the analysis of causal factors. Scientists will be called upon to evaluate the significance of changes experienced within preserves. On the ecosystem level, managers will be called upon to mitigate human-caused changes and natural processes. Where human effects have caused extirpations or vulnerability of species to natural events, species-oriented management may be necessary. When natural and human-caused disturbances interact, or when human-caused changes are deemed desirable (e.g., the pre-Columbian aboriginal fire regime in the park), managers and scientists will have to define the crucial reference state that management works toward.

Interpreters will be called upon to foster understanding of change, anthropogenic and natural, in our systems.

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STATUS OF FOREST SUCCESSIONAL STUDIES IN THE NORTHERN ROCKY MOUNTAINS

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Abstract

The need among forest managers for information on secondary plant succession has stimulated an analysis of the status of forest succession studies in the northern Rocky Mountains. Information needs of specialists in fire, wildlife, range, recreation, silviculture, watershed, etc., are under study. Past and current studies are being reviewed in relation to meeting current and future informational needs. Study methods are being evaluated in terms of current needs and value in future analyses. Alternative classification and modeling techniques are being explored. Recent attempts to coordinate successional studies and to share knowledge are discussed.

INTRODUCTION

Ecologists have been motivated by scientific curiosity to study succession throughout the history of the science. Concepts have been developed, criticized, and modified to the point where the only current, noncontroversial statement may be that "assemblages of species on a given site do change with time." Johnson (1979) suggests five periods representing the study of succession: formative (1859-1900), developmental (1900-1930), scholastic (1930-1947), confused (1947-?), and a new view of community dynamics (?-future). Although there is some question about whether we have yet entered period five, it is readily apparent that succession has regained prominent attention in ecological circles and in several related disciplines that need sound predictions of ecological changes.

INFORMATION NEEDS

During the last decade, forest land managers have received several mandates to intensify and improve planning, production, and environmental protection. Recent legislation enforcing this direction includes the National Environmental Protection Act (NEPA) and the National Forest Management Act (NFMA). Foresters are now required by law to predict and evaluate consequences of all planned activities. Because forest management commonly requires manipulation of vegetation, scientists are increasingly being asked for new knowledge on prediction of ecosystem changes following management treatments.

Merely recognizing the general need to predict vegetative change with time and treatment does not provide much guidance for developing a research program. Information needs must be specified. One means is to list needs for information related to plant succession, as expressed by specialists in various disciplines:

Timber:
- standardization (classification) of forest cover types
- effectiveness of silvicultural systems by forest cover types and site types
- effects of undergrowth vegetation on tree regeneration and development
- site preparation methods and their effectiveness in different situations

Wildlife:
- food production (kind, quantity, and quality)
- thermal cover (kind of tree overstory and density)
- hiding cover (trees, regeneration layer, shrubs)
- stand composition and structure (especially for bird habitat)

Fire:	stand composition and structure in relation to time, vegetative community, and environmental conditions fuel (dead vegetation component) characterization and loadings in relation to time, vegetative community, and environmental conditions effects of fire frequency, intensity, and extent on vegetation and site
Range:	forage production by successional stages multiple-use interactions on forage vs. tree development and forage vs. wildlife browse utilization
Insects:	stand composition and structure in relation to hosts, alternate hosts, and parasite hosts stand development (vegetal response) following infestation identification of stands with reduced susceptibility and attempting to create similar stands with silvicultural manipulation
Diseases:	susceptibility of various communities (species composition and structural development) and sites to pathogens
Utilization:	quantity and importance of residues to stand development role of plant species in maintenance of site fertility
Soils:	role of seral communities in relation to erosion effect of silvicultural treatment on erosion--indirect and direct
Hydrology:	water use by successional stages snow accumulation and retention by successional stage and site type
Recreation:	response of plant communities to intensive visitor use suitability (potential value) of each community type for various forms of recreational use
Mining/ Reclamation:	rehabilitation of adapted species and ecotypes

It becomes apparent that successional knowledge is needed by a wide range of disciplines. Any ecologist developing new knowledge on the dynamics of community change should, at least, be cognizant of these needs. Output from new studies can be designed to meet more than one need. As ecologists fail to meet needs of other disciplines, those disciplines will develop their own studies to meet the specific needs. It is unfortunate that the information gathered in the process may be of little use to any other discipline. A grouping of specific needs into a generic framework would be useful in designing successional studies and planned output of existing and new knowledge.

CURRENT KNOWLEDGE BASE

Arno (1977) compiled an annotated bibliography of 23 northern Rocky Mountain reports on forest succession and arranged these by categories:

> Historical, general, and descriptive accounts of succession (1899-1929): four references. Although the major trends observed and recorded are generally accepted, they are too general for application to many current problems.
>
> Studies of early (0-30 years) succession (1965-1976): six references. Several forest environments are represented, and some studies include up to 10 consecutive years of permanent plot data, including pretreatment measurements of vegetation. This data base will become increasingly valuable as the studies continue.
>
> Studies of entire successional sequences (1976-1977): three references. These studies provide an additional source of good information, although they are limited either in geographic extent or range of environments.
>
> Other phytosociological studies (1962-1977): eleven references. These studies address succession only peripherally, although some of the data may be useful for further successional interpretation.

Four major components are important for applying existing knowledge to successional informational needs. They are vegetation types (before and after treatment), environmental conditions (site type, habitat type, or specified site factors), disturbance treatment (kind and intensity), and successional time frame. On the one hand, our existing knowledge base is inadequate to address all four components completely. On the other hand, it is probably more complete than for most comparable geographic areas. Three of the most important sources of data for our current study of succession are as follows:

> Forest habitat type classification: Daubenmire and Daubenmire (1968) defined 21 forest habitat types for northern Idaho; Steele et al. (1980) defined 64 forest habitat types for Montana. (Habitat types are a kind of site type classification derived from classification of potential climax natural plant community types. The habitat type represents the area of land that a given vegetation type would occupy at climax.) Although sampling was limited to later successional stages (figure 1), vegetation and environmental data are available for about 2,500 stands representing virtually all forest ecosystems in the northern Rocky Mountains. Stand ages range from 70 to 400+ years. In addition to descriptions of late seral, mature, and old-growth successional stages, the habitat type classification provides a means of controlling environmental variation in new studies of succession.

Sequential early succession: Lyon and Stickney (1976) describe early (0-10 years) succession for intensely burned sites at three different study areas, and they present a preliminary model of establishment and early succession. Revegetation from surviving species accounted for 71% to 86% of the first-year community composition (table 1). Of the species that provided the bulk of vegetative cover in the fifth postfire year, about 80% were present in the prefire community, and all were recorded in the first postfire year. (These findings have a strong bearing on approaches to modeling and prediction of succession.) Several other studies summarized by Stickney (1980) document actual vegetation change over time on permanent plots. Although generally limited to the first 10 years of secondary succession, these studies are an extremely valuable component of our successional data base. Distribution of these permanent plot studies by disturbance treatment and habitat type is illustrated in table 2.

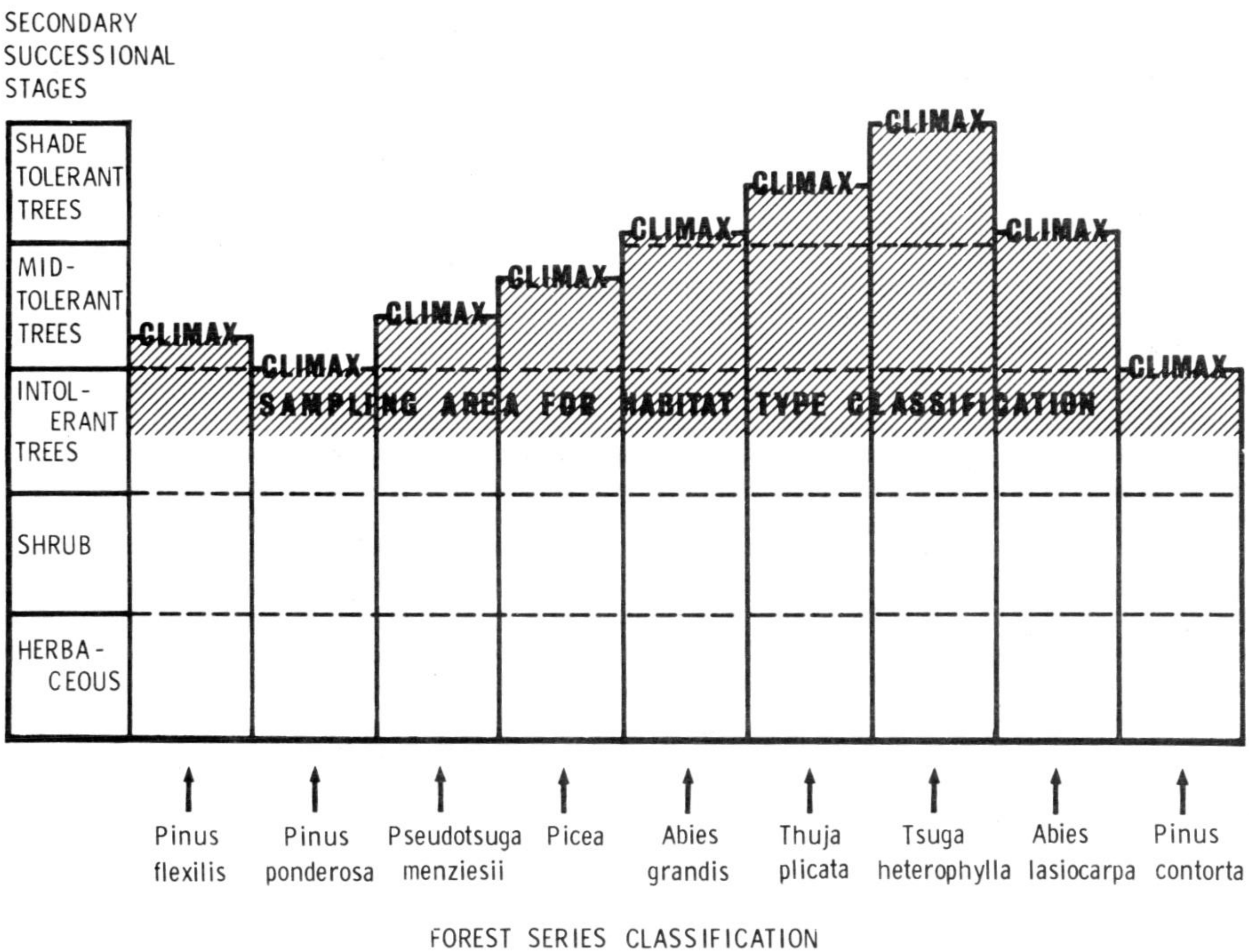


Figure 1: Generalized successional stages of each forest series, showing the types of stands sampled as the basis for our habitat type classification. (From Pfister et al. 1977.)

Table 1. Percentage composition first-year vegetation by source and survival strategy for Sleeping Child, Neal Canyon, and Sundance burns. (From Lyon and Stickney 1976.)

Item	Sleeping Child	Canyon	Sundance
Composition			
onsite sources	86	71	84
offsite sources	14	29	16
Survival strategies			
all species,			
plant parts, onsite:	75	40	60
rhizomes	33	18	33
root crowns	36	22	23
underground stems	6	0	4
seed or fruit, onsite	11	31	24
seed or fruit, offsite	14	29	16
Shrubs (only)			
root crowns	79	53	55
rhizomes	21	0	15
seed	0	47	30

Table 2. Numbers of successional study sites by major forest habitat types.

Habitat Type	Permanent Plots		
	Wildfire	Clearcut and broadcast burn	Paired plot sites (stands)
Pseudotsuga menziesii /	2		
Calamagrostic rubescens	14		
Physocarpus malvaceus		2	46 (117)
Vaccinium globulare		2	10 (27)
Abies grandis /			
Clintonia uniflora		4	
Thuja plicata /			
Clintonia uniflora		2	
Tsuga heterophylla /			
Clintonia uniflora	18	3	
Abies lasiocarpa /			
Clintonia uniflora	2	16	
Xerophyllum tenax	1		34 (99)
Menziesia ferruginea			22 (63)

Paired-plot succession: During the past three years, Arno (1979) has sampled numerous successional stands in four major habitat types in western Montana (table 2). This exploratory study seeks to fill in the data base for age gaps between the 0-10 year category of the Lyon-Stickney data base and the 70-400 year data base of the habitat type classifications. Stands were selected to sample a range of ages and silvicultural treatments (including wildfire), complemented by adjacent untreated stands as controls.

STUDY TECHNIQUES

Numerous field techniques for collection of successional data have been used, but most have serious shortcomings. Often, sample stands are located to represent a range of ages within a vegetative type. Unfortunately, the range of environments within a vegetative type may cause greater vegetation variability than the differences in ages. Use of a habitat type classification (or similar vegetation-based site classification) helps reduce environmental variability. However, even within a habitat type, one must be prepared to handle within-type variation. The "paired-plot" technique being used by Arno (1979) ensures (as far as possible within a "one-shot" sampling scheme) that the environmental conditions will be essentially equivalent for each pair. Frequently, three to five different age/treatment combinations are found close together, thereby providing efficiency in numbers of "control" plots required and the opportunity for several possible "paired" comparisons.

Repeated measurements of permanent plots installed prior to treatment are unquestionably the most reliable data (although the most difficult to obtain). We are fortunate to have early succession permanent plots for several habitat types (table 2). In addition, numerous silvicultural and mensurational (tree data only) permanent plots in northern Idaho were established 40 to 60 years ago and have been remeasured at 5- to 10-year intervals. These are the kind of data that will help make or break any successional model on tree dynamics.

Our current sampling philosophy is to obtain complete vegetative, environmental, and historical data on a range of ages and treatment types for the major forest habitat types. This data base will serve as a foundation for individual species requirements and dynamics, classification of seral communities, and models of successional development.

Although we have accumulated knowledge on individual species characteristics important for succession, this knowledge has not yet been brought together in a form usable for model development or formal hypothesis-testing. A recent paper by Rowe (1979) provides an improved version of the Noble and Slatyer (1977) approach regarding grouping of species that will respond similarly to disturbance treatments. This includes defining species attributes that are vital to reproduction and survival of the species within a community.

One of our goals has been to develop a classification of seral community types to be applied within specific habitat types. Conceptually, we want to develop a "natural" classification that will address many information needs fairly well as opposed to a "technical" classification limited to specific information needs. Several approaches to classification of seral community types are currently being considered. One promising approach consists of linking a simple classification of broad structural stages with a compositional classification based on dominant trees and undergrowth species. A description of dominant tree and undergrowth vegetation, stand characteristics, and ages are summarized for each class (figure 2). One advantage of this approach is that current timber and wildlife habitat information is also being collected within these structural classes; hence, new successional information will be easier to communicate and use. During a recent local workshop, however, it became apparent that no single classification would answer more than a few functional needs. The participants agreed that no single classification was adequate for vegetation, and perhaps a combination of several simple classifications may be more satisfactory.

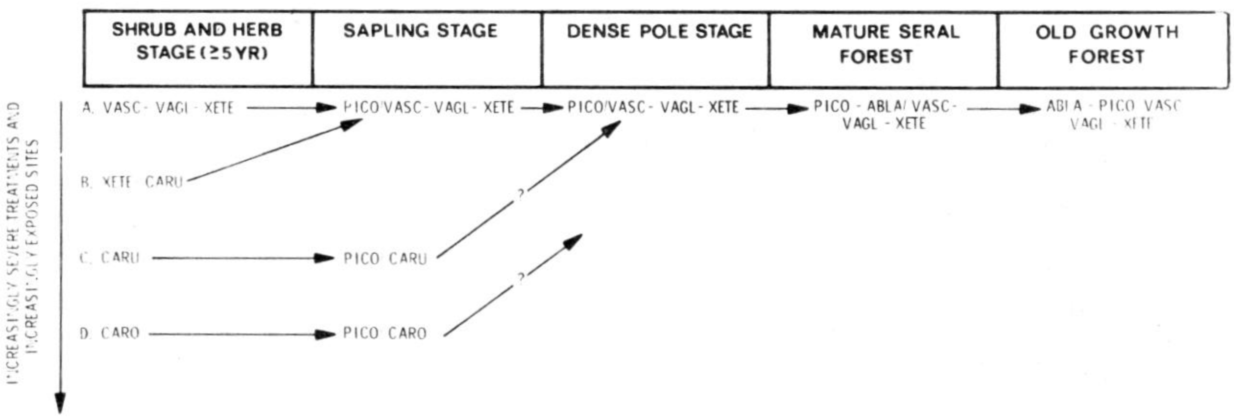
Modeling of succession is still exploratory in terms of total community development. Simple, conceptual models often accompany individual studies. Data from Arno's (1979) succession study provided a basis to develop some hypothetical models (habitat-type specific) of tree succession dynamics in relation to silvicultural treatments and fire frequency. A detailed stand prognosis model developed by Stage (1973) is being used for individual stand projections under different management regimes. Regeneration submodels under development incorporate partial undergrowth data, primarily with respect to tree regeneration. Recently, the Noble and Slatyer (1977) approach has been applied by Cattelino et al. (1979) and modified by Kessell (1979). Although further development is needed, this conceptual approach holds promise for prediction needs from available data for northern Rocky Mountain forest vegetation. As Franklin (1979) discussed, simulation of succession is an "expanding area of special pertinence."

COORDINATION NEEDS

The fragmented nature of past studies complicates attempts to assemble knowledge about ecological succession. Many masters and doctoral theses describe short-term studies of limited area and scope. Other studies are conducted within a narrow functional concept and often are not carried beyond meeting initial functional objectives.

Two notable exceptions in our study area are the long-term commitment to fundamental early-succession studies by Stickney (1980) and Lyon and Stickney (1976) in the Wildlife Habitat Research Work Unit, and paired-plot data collection by Arno (1979), who is working for both the Forest Ecosystem Research Work Unit and the Fire Effects Research Work Unit. (A parallel study is currently being conducted by Robert Steele in the Silviculture Research Work Unit at Boise, Idaho.) A concern of research administrators is how to aid continuation of long-term efforts,

Figure 2: Successional stages on the ABLA/XETE h.t. (cold phase), in west-central Montana, based upon a sample of 13 sites having a total of 33 paired communities (arrows indicate apparent directions of succession; dashed arrows are less common routes). (From Arno 1979.)



Range of values from sample stands	SHRUB AND HERB STAGE (≥5 YR)	SAPLING STAGE	DENSE POLE STAGE	MATURE SERAL FOREST	OLD GROWTH FOREST
TREE CANOPY COVERAGE	0 - 10%	10 - 50%	55 - 90%	35 - 65%	40 - 80%
DOMINANT TREE DBH	0 - 2 IN	2 - 4 IN	5 - 10 IN	10 - 15 IN	12 - 14 IN
AGE	5 - 22 YRS	10 - 45 YRS	40 - 120 YRS	120 - 200 YRS	200 - 300 YRS

LEGEND:

TREES: ABLA - ABIES LASIOCARPA
PICO - PINUS CONTORTA

UNDERGROWTH: CARO - CAREX ROSSII
CARU - CALAMAGROSTIS RUBESCENS
VAGL - VACCINIUM GLOBULARE
VASC - VACCINIUM SCOPARIUM
XETE - XEROPHYLLUM TENAX

integration between functions, and cooperation among scientists. Close coordination is essential to promote synergism and to address the complex problems of secondary succession.

Current reorganization in the Intermountain Forest and Range Experiment Station is aimed at centralizing coordination responsibility within the broad charter of the Forest Ecosystem Research Work Unit and promoting formation of teams of scientists to jointly attack problem areas of mutual concern. Forest ecosystems, fire effects, wildlife habitat, and silviculture research work units will be strong partners because of current research activities and a large existing data base. Some successional studies from other research units will also be linked to the coordinated effort, depending on data availability and inclination of participating scientists. Although this approach may face some administrative inconveniences, the goal of coordinated teams of successional scientists certainly merits a trial.

Two teams have been assembled within the last month to work cooperatively on two problem areas. The first team is working on evaluation of existing successional modeling approaches appropriate to managers' needs and data availability. Stephen Kessell is working with the team for initial evaluation and review through a combination of consultation, literature review, and workshops. This effort will help guide selection or development of modeling approaches most appropriate to various disciplinary and managerial needs.

A second team has begun a formal summary of knowledge on species characteristics (vital attributes) important for understanding successional response. This will include all northern Rocky Mountain tree species and 50 to 100 major important undergrowth species. The results of this team effort will provide a foundation for understanding the responses of individual species, a basis for grouping species with similar response characteristics, and possible input or test material for new model development.

Secondary succession is such a complex problem that no single person will likely solve more than individual pieces of the puzzle. However, a teamwork approach may accelerate understanding and solution of complex problems.

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SPACE AND TIME VARIABILITY OF THE NATURAL ENVIRONMENT IN THE CENTRAL RUSSIAN ECOLOGICAL REGION

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The term biosphere reserve denotes natural areas that are representative of the most typical biotic regions of the Earth, that are strictly preserved and removed from economic or agricultural use, and that ultimately form a worldwide network of standard biosphere areas.

The main objective of biosphere reserves is the preservation of the natural diversity of the Earth's typical ecosystems, which were created in the process of evolution, and of their abundant genetic material for science and practical use in the future. To achieve this objective, it is necessary to protect natural ecosystems from anthropogenic effects and, consequently, to let them develop under natural conditions.

Another objective of biosphere reserves is to provide areas for ecological monitoring, which is a complex of survey and control operations to measure the changeability of ecosystems under the influence of natural and anthropogenic factors. In this case a biosphere reserve may be viewed as a natural plotting board, or a screen with a sensitive surface layer, that constantly reflects all the multiformity of effects. Our periodic observations of the conditions of the ecosystems are actually photos of peculiar combinations of effects at different moments. Unbiased information on the changes of outside conditions depends on our knowledge of the characteristics of the said sensitive layer, i.e., ecosystems. One has to distinguish between signs of natural fluctuations and changes provoked by anthropogenic factors. The difficulty consists in the different sensitivities of the ecosystem components and the heterogeneity of their responses to monotypic effects. However, this difficulty has its silver lining: It ensures that any change in outside conditions is recorded in one of the elements of the sensitive layer. One has only to detect the signs: shift in the community border, replacement of species, shifting of phenological phases, morphological and physiological deviations in the organism or organ, changes in the permeability of cell membrances, etc. These indications register the results of prolonged, periodic, or single effects on a large area or on an individual organism or organ.

Let us give you examples of observations of ecological successions at three levels: the upper part of the Oka River basin (6.5 million ha), which is an ecological region of general control of the Pushchino Biosphere Station; the territory of the Prioksko-Terrasny Biosphere Reserve (5,000 ha); and a concrete ecosystem--a pine forest--within the area of the reserve.

An analysis of the cartographic survey material for a number of years showed that the forested area within the experimental square of 2 million hectares within the Oka River basin had changed during 100 years in the following way: In 1871, 20% of the total area was in forest; in 1928, 30%; in 1941, 40%; in 1951, 80%; and in 1973, 45%. The reason for these changes lies in the fact that during the period 1630-1750 the area was actually the heart of Russian metallurgy. Blast furnaces of that time used charcoal from oak and birch of the nearby forests. To protect the forests from complete elimination, the metalworks were moved to the Urals. After that the forested area increased. A sharp growth of the forested area in 1951 can be explained as the effect of World War II when part of the agricultural land was not cultivated and forests spread on formerly plowed lands, hayfields, and pastures. At present the forested area is preserved at the level of the preindustrial period of the 17th century. However, original oak groves were replaced on large areas by secondary groves of birch and aspen.

The area of the Prioksko-Terrasny Biosphere Reserve also underwent anthropogenic influences in the past. The reserve has existed for only 35 years. Up to the 16th century this territory was dominated by spruce/broad-leaved woods. Pine forests occupied adjoining parts of the Oka Valley. During the 17th century, the forests were actively eliminated as a result of war actions, metalwork, and plowing. In the opinion of N.A. Kostenshuk (1979), fire was the principal culprit in the widespread replacement of spruce forests by pine. Pine is capable of quickly invading large areas of burned-out forests.

In the process of studying ecological succession of a concrete ecosystem--a pine forest (Cladonia silvatica)--a reliable indicator was found in the soil microfauna group of mites (Oribatidae). This group is more sensitive to ecological changes than vegetation. Species structure of the Oribatidae complex characterized by Shannon's information value shows the degree of ecosystem disturbance. In the process of ecological succession, Shannon's value gradually increases from 1.50 to 2.45. The latter figure characterizes the undisturbed climax condition of the ecosystem. Besides, distribution curves of the Oribatidae number at different distances from the borders of neighboring associations help to give the direction and intensity of ecological succession (Gordeeva 1978). Strict correspondence of the degree of Oribatidae cuticle pigmentation to temperature conditions of the habitat is used to reconstruct thermal conditions of soils and ecosystems in the past.

MONITORING AND MODELING IN TANDEM: A STRATEGY TO IDENTIFY AND PREDICT SUCCESSIONAL CHANGE

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Abstract

Monitoring and succession modeling need to be more closely integrated. Newly established biosphere reserves are places where such integration can be optimally carried out by carefully planning a biological monitoring network. The network would enable the accurate parameterization of models and independent evaluation of model predictions. Alternatively, modeling helps focus monitoring so that it becomes streamlined and purposeful. When models attain adequate levels of predictability, efforts can be redirected from parameterization and testing to application of the model to management problems.

INTRODUCTION

Modeling and monitoring must be integrated to predict successional events with confidence. Each offers a unique contribution to succession research, but serious study requires their use in tandem. Modeling enables prediction through mathematics and programming. This has greatly improved our ability to study long-term processes and thereby has stimulated inquiry into succession (Waggoner and Stephens 1970, Botkin et al. 1972, Shugart et al. 1973, Johnson and Sharpe 1976, Shugart and West 1977, Noble and Slatyer 1977). Data from monitoring networks are important both in the model-building process (e.g., parameterization) and in the independent evaluation and subsequent improvement of model predictions. Without monitoring, prediction is uncertain. Without modeling, the applicability of monitoring data to succession research is diminished, monitoring becomes less focused, and the need for extensive, and often expensive, long-term monitoring continues.

MONITORING AND PARAMETERIZATION

Repeated measurement over time (monitoring) and time-specific measurement are both utilized in model-building and parameterization. Monitoring of data provides dynamic estimates of succession rates and replacement patterns. However, because succession is a long-term process and decades are required before successional change can be observed, there are few long-term data sets in existence. A middle ground is the monitoring of a variety of vegetation states (seral stages) simultaneously over a shorter time span (e.g., 5-10 years). This type of monitoring data (e.g., continuous forest inventory data) is the basis for some succession models (e.g., Shugart et al. 1973, Johnson and Sharpe 1976). Both successional trajectories (replacement patterns) and succession rates have been determined from short-term monitoring data. However, most of what is thought to be known about succession is based on a single time-specific measurement of stands differing primarily in age, rather than periodic remeasurement over time (e.g., Oosting 1942, Whittaker 1956, Heinselman 1973). Therefore, succession patterns derived in this manner are inferred and are only estimates of true patterns, since there is error in extrapolating from space to time. A number of models have utilized rates based on time-specific measurements (Bledsoe and Van Dyne 1971, Shugart et al. 1973, Johnson 1977). In other modeling approaches (e.g., Botkin et al. 1972) relationships are computed or involve stochastic components, and therefore there is less reliance on monitoring data for parameterization. However, there is no less need for monitoring data to evaluate model predictions.

Few succession models have been developed in tandem with biological monitoring programs. Approaches to parameterization have sometimes been casual; primary emphasis has been placed on mathematical formulation. Most models have been based on previous monitoring and time-specific data or on general insights from published basic ecological studies of succession. Often the data brought to bear on a given modeling problem occur in many different forms, are from different geographic locations, and have been collected at different time periods. The combined error in using general and heterogenous data to parameterize succession models has not been assessed.

The newly designated biosphere reserve network (Franklin 1977) can benefit from the numerous mathematical techniques now available to model succession (see Shugart et al. and Kessell, both in this volume) and can now optimally plan model-building and biological-monitoring activities in tandem. Many monitoring networks are still in the planning stages (Johnson and Bratton 1978). These networks of permanently marked sample plots not only provide dynamic data for use in modeling succession, but also can provide more general spatial information (e.g., other ecological trends useful in mapping, ground truth, or management). The most direct way to establish a reservewide network would be to locate sample plots at the intersections of a uniform grid system, with the grid size corresponding to desired sample intensity. In this design, communities would be sampled in rough proportion to their areal extent. This is the basic design for continuous forest inventory plot systems in the United States and Europe. However, a coarse grid would often fail to sample rare communities or species with local distributions. These communities and their associated species, some of which could be rare and endangered, are often of special interest in biosphere reserves. Therefore, an improved strategy would be to establish plots in a stratified random manner within each community. Changes in all communities, regardless of their areal extent, would be monitored. In addition to geographical and community stratification, plots could be selected to represent modal positions along major environmental gradients. It would also be necessary to install additional special-purpose sample plots to monitor the response of populations to disturbances such as fire, ice damage, and windthrow. These disturbances are often local in extent and therefore may occur infrequently on a reservewide set of sample plots.

Thus, after initial measurements on the sample plot network have been completed, an operational model could be constructed, and preliminary succession patterns could be simulated under a restricted set of conditions. These early simulations could constitute preliminary working hypotheses regarding succession in the reserve. They would be replaced by dynamic estimates as they became available. Thus, the initial modeling would proceed rapidly in a series of stages, beginning with the generation of preliminary working hypotheses. These would be significantly strengthened when remeasurements were made and rates computed. Dynamic data from a series of special-purpose plots would be used to estimate alternative successional pathways (Cattelino et al. 1979) following more local disturbances. Parameter estimates would be updated as new and long-term information on population community dynamics became available from the monitoring network.

MONITORING AND EVALUATION

The second function of monitoring is to evaluate model predictions. A basic weakness of many succession models is the lack of adequate testing. This has led to uncertainty regarding predictions and may itself be a major reason why succession models are generally not now in use by land managers. Most succession models remain untested over the full range of field conditions they were designed to simulate. Quantitative evaluation has been hampered by the general absence of long-term monitoring data and the paucity of monitoring experiments specifically devised to evaluate model predictions. Any number of specific model experiments can be devised and compared with monitoring data to rigorously evaluate model predictions. If adequate concern and effort and innovative thinking are put into the evaluation process, even difficult tests of the model can be made (e.g., accuracy of long-term simulations). Examples of innovative evaluation of models, in the absence of long-term data sets, are presented in this volume (see Shugart and West).

Monitoring and model evaluation are therefore iterative processes, where comparison of model predictions with monitoring data can identify inadequacies in model structure or parameter estimates. The use of monitoring data in the evaluation process also acts to focus monitoring so that it becomes purposeful, rather than a mindless collection of data with obscure utility. Predictability through modeling remains our primary means to eventually minimize the need for monitoring or perhaps in some cases eliminate it altogether.

Thus, the combination of model prediction, establishment of monitoring experiments, and subsequent model evaluation and modification is an iterative process which enables continuous improvement of model predictions. If there is danger of circularity in the evaluation process, i.e., data used to parameterize the model are also used in evaluation, a series of matched plots could be reserved for evaluation. Thus, evaluation correctly feeds back to parameterization. When predictions are inaccurate, parameter estimates may need to be improved by either collecting additional information on the reserve monitoring network or by establishing new monitoring experiments. Alternatively, when specific succession variables are accurately predicted by the model under a range of likely conditions, corresponding monitoring experiments can be concluded. Therefore, as the predictability and understanding of succession improves and the model reaches acceptable levels of accuracy, efforts can be redirected from monitoring and testing toward applying the improved model to management problems in or near the reserve (Kessell 1979) or to the study of succession theory.

CONCLUSIONS

The biosphere reserve program has a long-term commitment to understanding the dynamic character of ecosystems. It is this "long-term commitment" that is most advantageous in developing robust, well-tested succession models based on the close integration of modeling and monitoring. Confidence in predictions can be gained by repeatedly evaluating model output based on results from a dynamic monitoring network, one which includes often short-term, specific monitoring experiments. Dynamic data from such a monitoring network enable parameter estimates to be refined following remeasurements. When models attain acceptable levels of predictability, efforts can be directed away from testing and toward applying the model to management problems.

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VERIFICATION, VALIDATION, AND APPLICATION OF DETAILED FOREST SUCCESSION MODELS

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INTRODUCTION

Model validation is often central to the development of useful models of any ecosystem. While some theoretical applications use models in ways in which the testing of the models is not particularly germane (Mankin et al. 1977), in applied problems the utility of a model's predictions is often gauged by the veracity of the model. This is perhaps clearer when we compare ecological models with a competitor, statistical regression. In applying ecological models, the stated objective is to use a realistic model to extrapolate the behavior of the ecosystem outside the limits of observation. In developing regression equations, one adopts the position that the future behavior of a system is best determined by using simple models to interpolate between actual observations in the system. Extrapolation from statistical models is notoriously unreliable and any extrapolative methodology is difficult because of its basic nature.

Model testing is divided by some into two types of procedures:

> Verification procedures - in which a model is tested on whether it can be made consistent with some set of observations. In some cases (and in the usual usage by systems ecologists), verification procedures consist of developing a working computer program that is calibrated to a set of data. The model structure and/or parameters are sometimes altered as the model is made to agree with the observations. In this sense, linear regression is a verification

procedure in which simple models are forced to have a maximum agreement with observations by changing the parameters over an infinite range.

Validation procedures - in which the model is tested on its agreement with a set of observations that are independent from those observations used to structure the model and estimate its parameters. The degree of independence between the model and the observations prior to the validation test is as important as the degree of agreement between the model and the observations following the test.

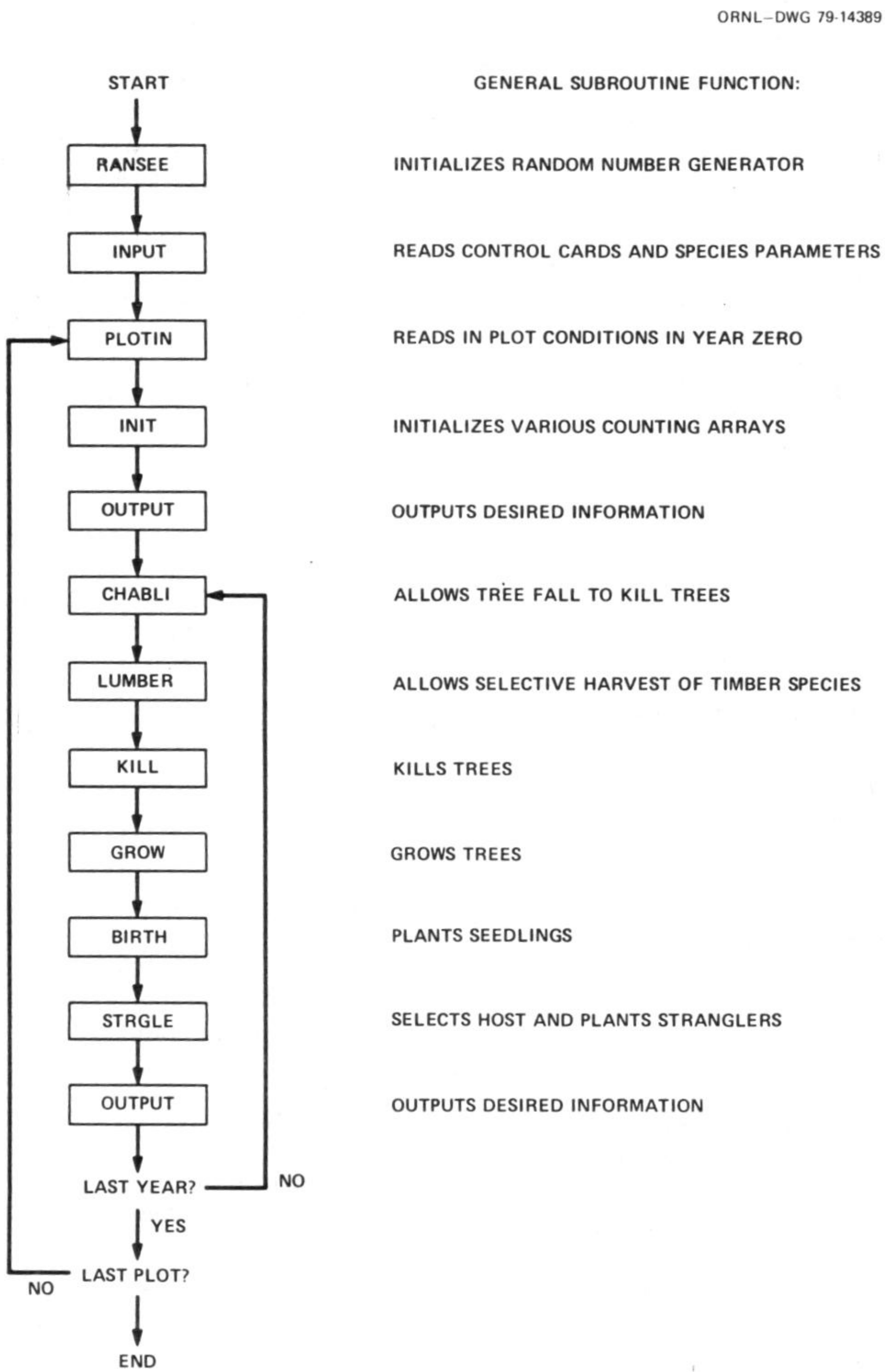
In a recent review (Shugart and West 1980), a category of ecological models called the "gap" models was identified as being particularly useful in studies of long-term ecological succession. After briefly describing the mathematical structure of a gap model, we will discuss the techniques available for validation of these models and will provide examples of such tests. We will further discuss how these models might be used to predict the consequences of man-induced change of the long-term dynamics of forest ecosystems.

GAP MODELS

Gap models function by computing the establishment, growth, and death of each individual tree on a plot of some specified spatial dimension, usually from 1/100 to 1/12 ha. Because the models simulate the diameter of each individual tree in the modeled stand, it is possible to compute the height, leaf area, and biomass of each tree from empirical relationships. Such information allows the implementation of reasonably mechanistic competition equations. The output of these models resembles the form of data usually collected in forest dynamics studies (e.g., diameter breast height [DBH] of each tree and the species of that tree for some sample quadrant). Output from the model is subject to interpretation such as that which might be used for typical sample data.

The gap models are all lineal descendants of the JABOWA model (Botkin et al. 1972), and many are also derived from the FORET model (Shugart and West 1977). Detailed descriptions of these models and program listings are available (see references and table 1). The flow diagram for order of computation for a typical gap model (figure 1) includes (for all gap models) subroutines for determining tree establishment (BIRTH AND SPROUT), growth of individual trees (GROW), and mortality (KILL). In addition, various models have subroutines that compute a variety of ecological phenomena such as fire, flood, drought, or other disturbance as they affect a given forest (table 1).

Figure 1. Flow of computations in a typical gap model. This example model is the KIAMBRAM model (Shugart et al. 1980). Each box on the diagram represents a computer subroutine.



Birth Processes

The establishment of small trees in the typical gap model is generally simulated by allowing some number of small trees to be recruited into the simulated stand as a stochastic function of stand site conditions (table 1). Small trees with a DBH of 2 cm or so are usually planted, but in some of the models, seed storage or the survival of special reproductive organs (e.g., lignotuberous sprouting in genus Eucalyptus) is also computed. Vegetative sprouting from individual trees of appropriate size and species is also included in several of the models. One of the models (the KIAMBRAM model, Shugart et al. 1980) also simulates the epiphytic, strangling habit typical of establishment of certain tropical figs (Ficus sp.).

The models taken as a whole consider 12 ecological factors that can alter the regeneration of young trees. Some of these factors are related to conditions needed for dispersal of certain species to a potential germination site. Such factors (see dispersal in table 1) include a suite of relatively straightforward model algorithms for eliminating species from eligibility for regeneration in years when a species-specific dispersal agent is absent. Several of the factors consider the state of potential germination sites in a given year (e.g., has the site been burned or flooded, or is there mineral soil present) which might serve to eliminate or amplify a given species reproduction. Other factors are concerned with seedling mortality occurring between germination and the time when the seedlings are large enough to be tallied in the model. Such sources of mortality are considered as a part of the regeneration process (e.g., deer browse), and they constitute an area in which field studies should be useful in improving the models.

Growth Processes

With the exception of the SWAMP model (Phipps 1979), which uses a tree-ring data-based growth equation, all of the gap models use a growth equation derived from offsetting the increased photosynthate production of a large tree against the increasing respiratory costs of maintaining living tissue as trees increase in size. The models all use shading from taller trees to reduce the growth of subordinate trees. In general, this effect is based on the light extinction equation referred to as Beer's Law (Kasanga and Monsi 1954, Loomis et al. 1967, Perry et al. 1969). As conditions differ from a given species climatic optimum, the growth is reduced as is also the case when there is crowding (a function of total stand biomass). The growth of each individual tree is computed annually.

Table 1. Published examples of gap models and a tabulation of biotic and abiotic features associated with the birth, growth, and death subroutines of the models.

Model--(Model documentation) Ecosystem	BIRTH												GROWTH						MORTALITY				
	Deer browse	Dispersal	Fire	Flood	Leaf litter	Lignotubers	Mineral soil	Phenology	Raised site	Seed source	Shading	Strangler	Crowding	Drought	Fire damage	Flood	Temperature	Shading	Fire	Harvest	Hurricane	Lack of growth	Tree fall
BRIND--(Shugart and Nobel 1980) Australian <u>Eucalyptus</u> forest		X	X							X	X		X		X		X	X	X			X	
FORAR--(Mielke et al. 1978) Arkansas mixed pine/oak forest	X		X		X		X				X		X				X	X	X	X		X	
FORET--(Shugart and West 1977) Tennessee Appalachian hardwood forest	X	X			X		X				X		X	X			X	X		X		X	
FORICO--(Doyle et al. 1980) Puerto Rican Tabonuco montane rain forest					X		X			X	X		X					X			X	X	
FORMIS--(Tharp 1978) Mississippi River floodplain deciduous forest		X		X	X		X			X	X		X	X		X	X	X				X	
JABOWA--(Botkin et al. 1972) Northern hardwood forest													X	X			X	X		X		X	
KIAMBRAM--(Shugart et al. 1980) Australian subtropical rain forest		X			X		X	X	X	X	X	X	X					X		X		X	X
SWAMP--(Phipps 1979) Arkansas wetlands forest				X							X		X			X	X	X		X		X	

Death Processes

Each tree is killed as a stochastic function of its species-specific expected longevity. Trees that are suppressed and are growing very slowly are exposed to an increased probability of mortality. In some cases, fire-damaged trees are exposed to increased mortality in a fashion analogous to suppressed trees. Trees may also be killed by wildfire or hurricane blowdown or by breaking under larger trees that fall in some gap models (table 1).

VERIFICATION OF GAP MODELS

Techniques for determining which information to use in parameterizing and structuring a model (verification) and which information to reserve for testing the model (validation) are at present less than a rigorous set of analytical procedures. Clearly, one should not "use up" all of the data in developing a model so that no independent test data are available. At the same time, a model cannot predict independent data unless it has some level of realism (and data) encoded into its structure and parameters. The approach in the case of gap models is to reserve the most detailed or the most unique observations for model validation and to verify the model using more qualitative observations. Two such qualitative verifications used in gap models are described below.

Patterns in compositional dynamics--One fairly straightforward verification of a gap model is to test whether it can predict the successional changes from one forest type to another. This verification procedure also provides a link between the detailed gap models and the less detailed regional forest models (Shugart et al. 1973, Johnson and Sharpe 1976). If a gap model reasonably reproduces the forest-type dynamics for some forest (e.g., figure 2), then it can be used as a source of data for the parameter estimation of the regional simulator. Figure 2 outlines such a test used to verify the BRIND model (Shugart and Noble 1980) of Eucalyptus forests in the Australian Alps. One can determine the rate of change from one forest type to another by classifying the forests simulated by the model into forest types. Figure 2 is interesting in this regard as it clearly indicates that the Australian Eucalyptus forest can have several stable vegetation types depending on the fire history of a site.

Patterns in species dynamics--A technique related to the verification procedure mentioned above and useful in ecosystems that are less exhaustively studied is the determination that the model reproduces the long-term dynamics of key species following a disturbance (figure 3). There are, at least for many forests, historical records of disturbance to forests in different areas. One would expect a succession model to reasonably duplicate the patterns obtained by piecing these observations together.

Figure 2. Compositional dynamics of various species in the alpine ash (Eucalyptus delegatensis) zone in the Brindabella Range, Australian Capital Territory, as simulated by the BRIND model (Shugart and Noble 1980).

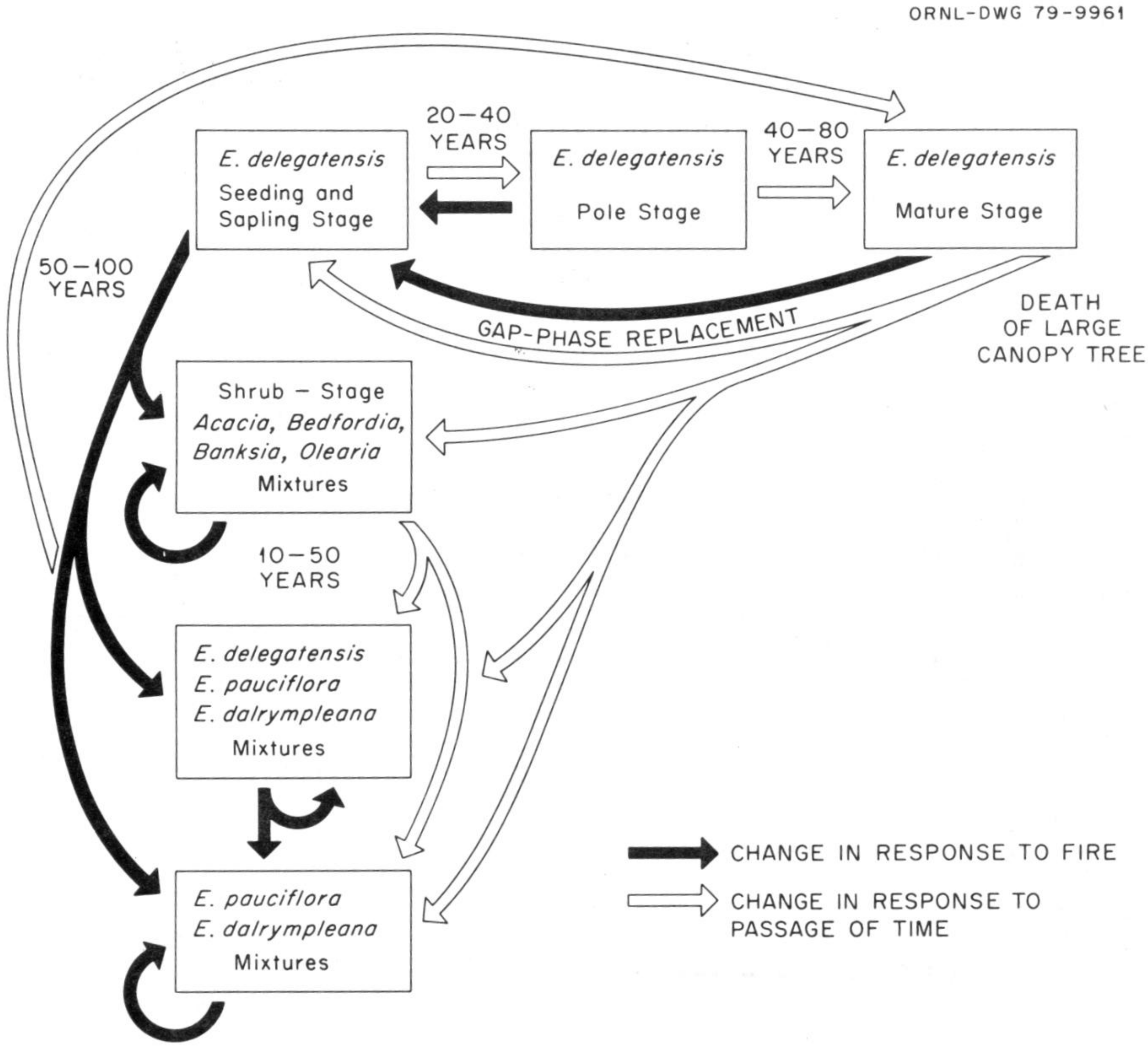
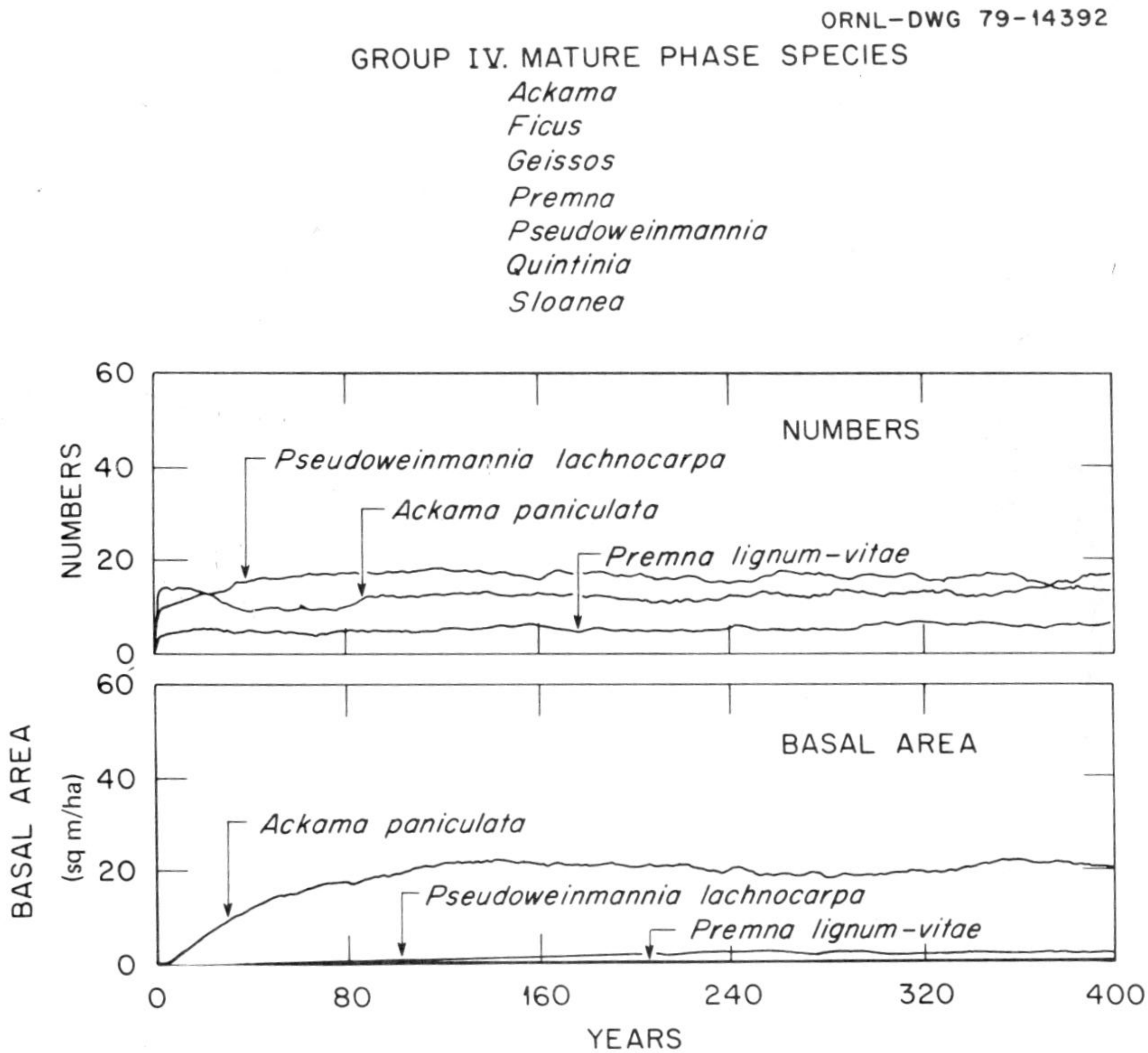


Figure 3. Number and basal area of mature phase tree species in the years following a disturbance in Australian subtropical rain forest as simulated by the KIAMBRAM (Shugart et al. 1980) model. The pattern of recruitment for these species agrees with that expected from survey data of disturbed plots with a known history and in some cases with considerable antiquity (100 years). The responses are also in substantive agreement with remeasurement data on stands for a 15-year time period.



VALIDATION OF GAP MODELS

Many of the most ecologically interesting predictions derived from gap models regard the long-term biomass and compositional dynamics of forests. There is considerable challenge to independently test these long-term predictions, particularly given the variability both of the stochastic model output and of actual field data. Nonetheless, several different validation approaches have been used to test gap models. These are discussed below.

"Brute Force" Procedures

These procedures consist of comparing model responses directly with field observations. Generally, logistic considerations in collecting samples limit the range of conditions over which the models can be tested (e.g., it is difficult to collect data that relate to assessing a change in climate). To be convincing, gap model output should be compared to field data at a detailed level of resolution. Such data should be independent of any model parameter estimation and ideally should test the model under a range of its dynamic responses.

For example, Shugart and Noble (1980) tested their simulation model (BRIND, table 1) for the *Eucalyptus* forests of the Australian Alps against independent data collected by Lindsay (1939) on the average diameter, basal area, and stocking density of alpine ash (*E. delegatensis*) in stands near Bago, New South Wales. The model simulation (figure 4) was started under an initial condition that differed from that in Lindsay's (1939) yield table. The model prediction converged to that of the yield table after 30 years and then accurately tracked the independent data set. This dynamic response is probably a stronger inferential test on the model than one that simply starts the model under the conditions at year O in the yield table and notes if the model traces the yield table. Incidentally, subsequent experimentation with the model indicates that it does, in fact, meet this latter test as well.

Doyle et al. (1980) tested FORICO, a simulation model for Puerto Rican Tabonuco montane rain forest (table 1), against independent data on the diameter frequency distribution (figure 5). Diameter frequency data have many advantages as a test data set for validating gap models. In particular, the data are highly detailed and the form of the diameter frequency curve is influenced simultaneously by birth, growth, and death processes.

Long-term Projections

Since most of the vegetation used to obtain parameters for the gap models has been disturbed by human activities, one natural test on a succession

Figure 4. A comparison of basal areas, stocking density, and mean diameters predicted by the BRIND model (Shugart and Noble 1980) and Lindsay's (1939) yield tables for *E. delegatensis*. Stocking densities at early ages are not shown for purposes of clarity but at year 10 are ca. 5,600 for Lindsay's data and ca. 2,500 for the example simulation.

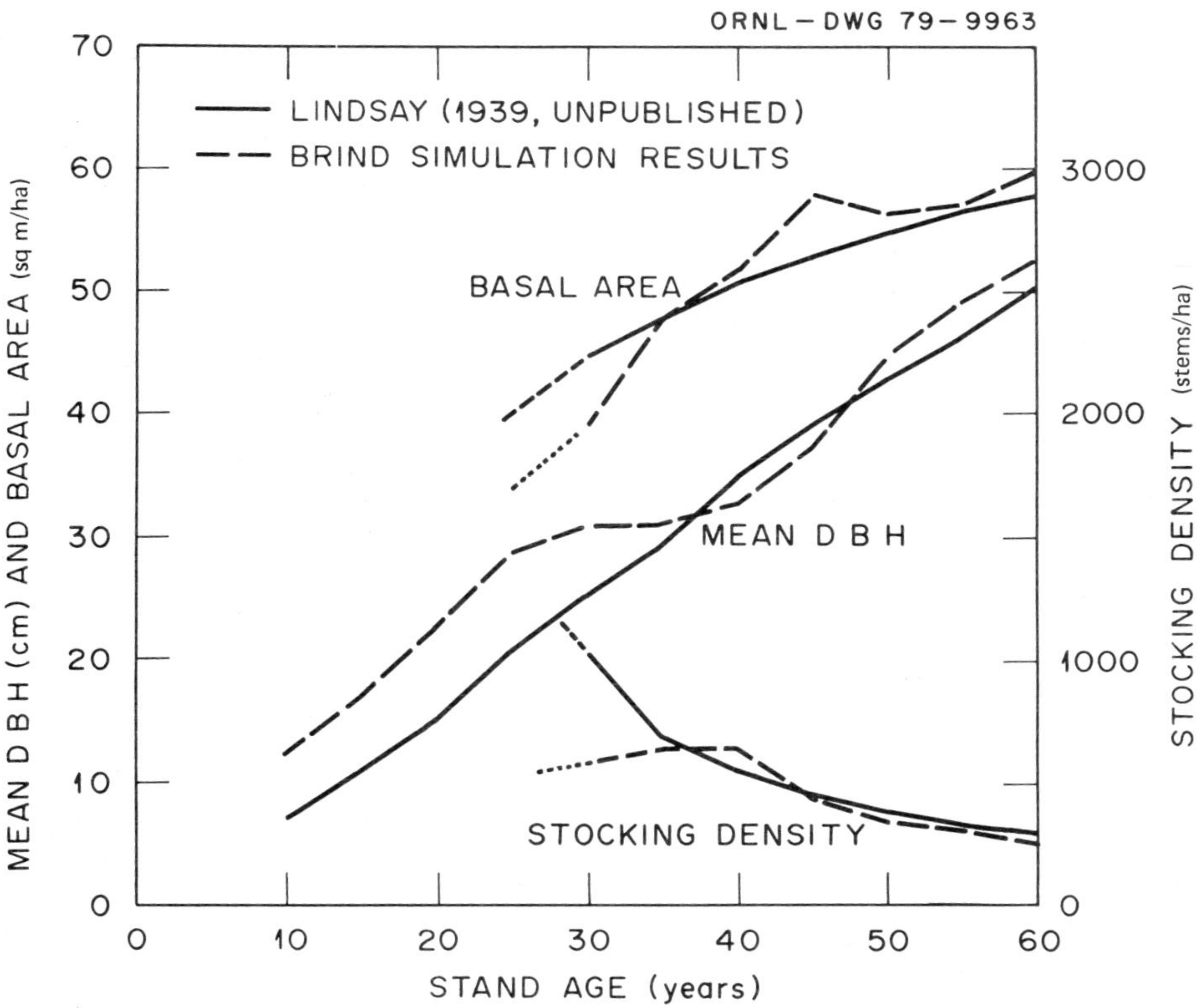
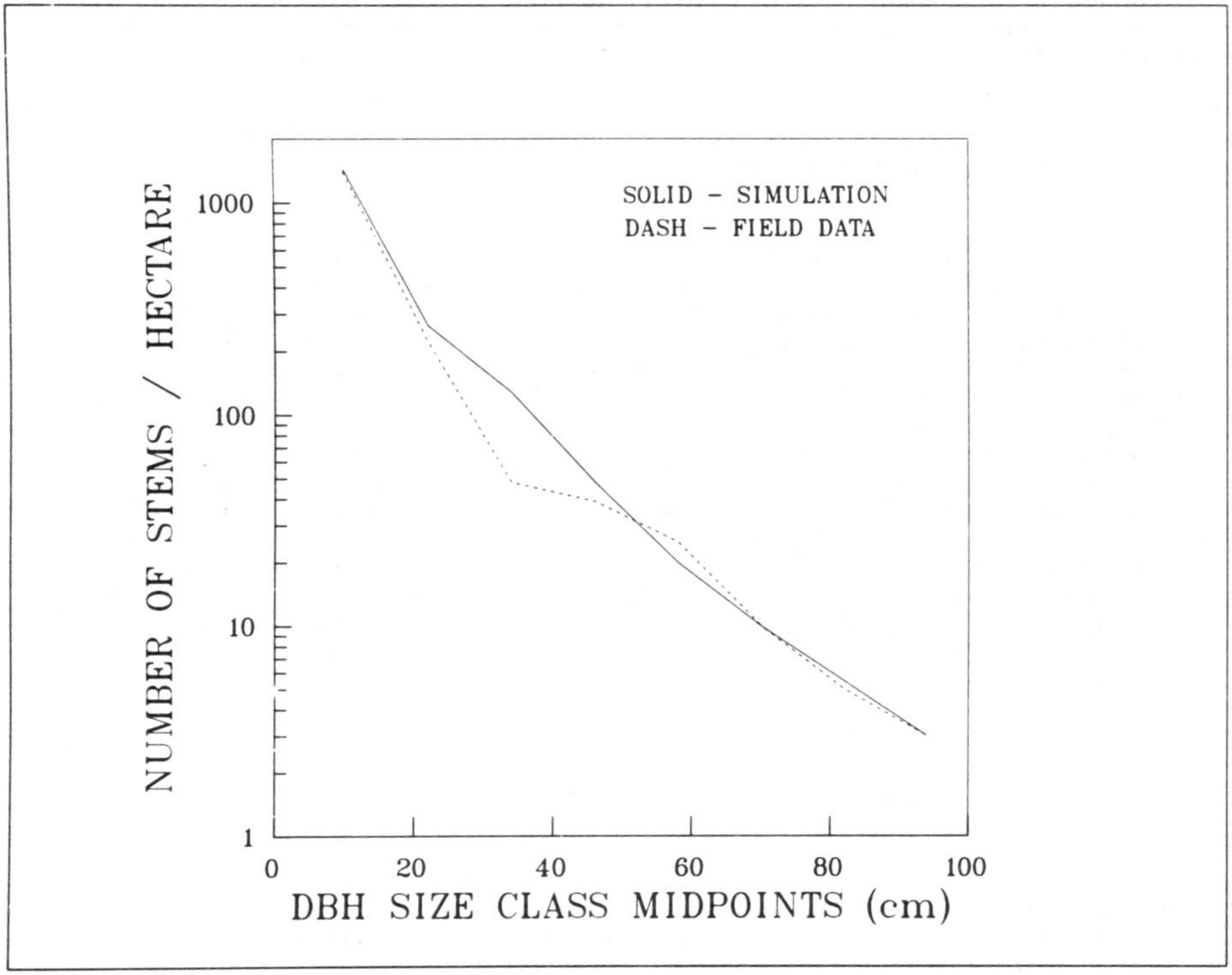


Figure 5. Comparison of measured diameter frequency distribution on a mature stand, thought to be ca. 150 years old, with minimal disturbance; equivalent diameter distribution predicted by the FORICO model (Doyle et al. 1980).



model (that agrees with extant data on forest dynamics) is to use the model to project the expected equilibrium pattern of vegetation. The resultant predictions can then be tested for consistency with what is known (either from old records or from relict sites) about the undisturbed vegetation. Horn (1976) uses such a test in comparing the species composition at equilibrium predicted by his Markovian simulator with that of a "climax" beech forest in the Princeton woods. The KIAMBRAM model (table 1) of a subtropical rain forest has also been tested in this manner, and most of the models listed have been tested to one degree or another against their ability to predict mature forest composition.

Predicting Gradient Responses

One inferential and potentially powerful test of a succession model is to run the model under a set of differing conditions that approximate some naturally occurring ecological gradient. If the model can predict patterns of vegetation along this gradient, it has then passed a reasonably severe test of the range of conditions over which it can be expected to produce reasonable results. This is particularly true if the patterns predicted are a product of higher order (e.g., competitive) interactions and not simply a consequence of the physiological ranges of the species considered. An example of this test is described by Botkin et al. (1972) in predicting the location of the deciduous/coniferous forest transition. Tharp (1978) tested her model of a floodplain forest with a similar test using a gradient of flood frequency. Figure 6 shows a similar test on the BRIND model (table 1, Shugart and Noble 1980) using a two-way gradient of fire frequency and climate change. The value of such tests is that they provide a notion of the veracity of the model over a wide range of simulation conditions.

Hindcast Procedures

Past events can be used as if they were natural experiments. Because the events occurred in the past, the procedures are called hindcast (as opposed to forecast or contemporary comparison) procedures. Shugart and West (1977), for example, used the chestnut blight as a perturbation and tested their model on its ability to predict the species composition of forests not subjected to the chestnut blight, based on historical data (table 2). Other events that might be used for such hindcast tests include other diseases, climate changes reflected in pollen records (Solomon et al. 1980), the advent of land disturbance by Europeans, and introduction or extinction of species.

Figure 6. Summary forest-type constellations for one- and two-species dominated forest types simulated by the BRIND (Shugart and Noble 1980) model at four different altitudes (expressed by the heat sum, DEGD) by four different wildfire probabilities (FRPROB). The value in a box is the percentage of instances in which the indicated species contributed 90% or more to the stand's total biomass. The values on the lines between boxes are the percentages of instances in which the two named species contributed 90% or more of a stand's total biomass. Species mnemonics are taken from the first three letters of the scientific bionomial: ACADEA = <u>Acacia dealbata</u>, BANMAR = <u>Banksia marginata</u>, EUCDAL = <u>Eucalyptus dalrympleana</u>, EUCDEL = <u>E. delegatensis</u>, EUCFAS = <u>E. fastigata</u>, EUCPAU = <u>E. pauciflora</u>, EUCROB - <u>E. robertsonii</u>, EUCRUB = <u>E. rubida</u>, and EUCVIM = <u>E. viminalis</u>.

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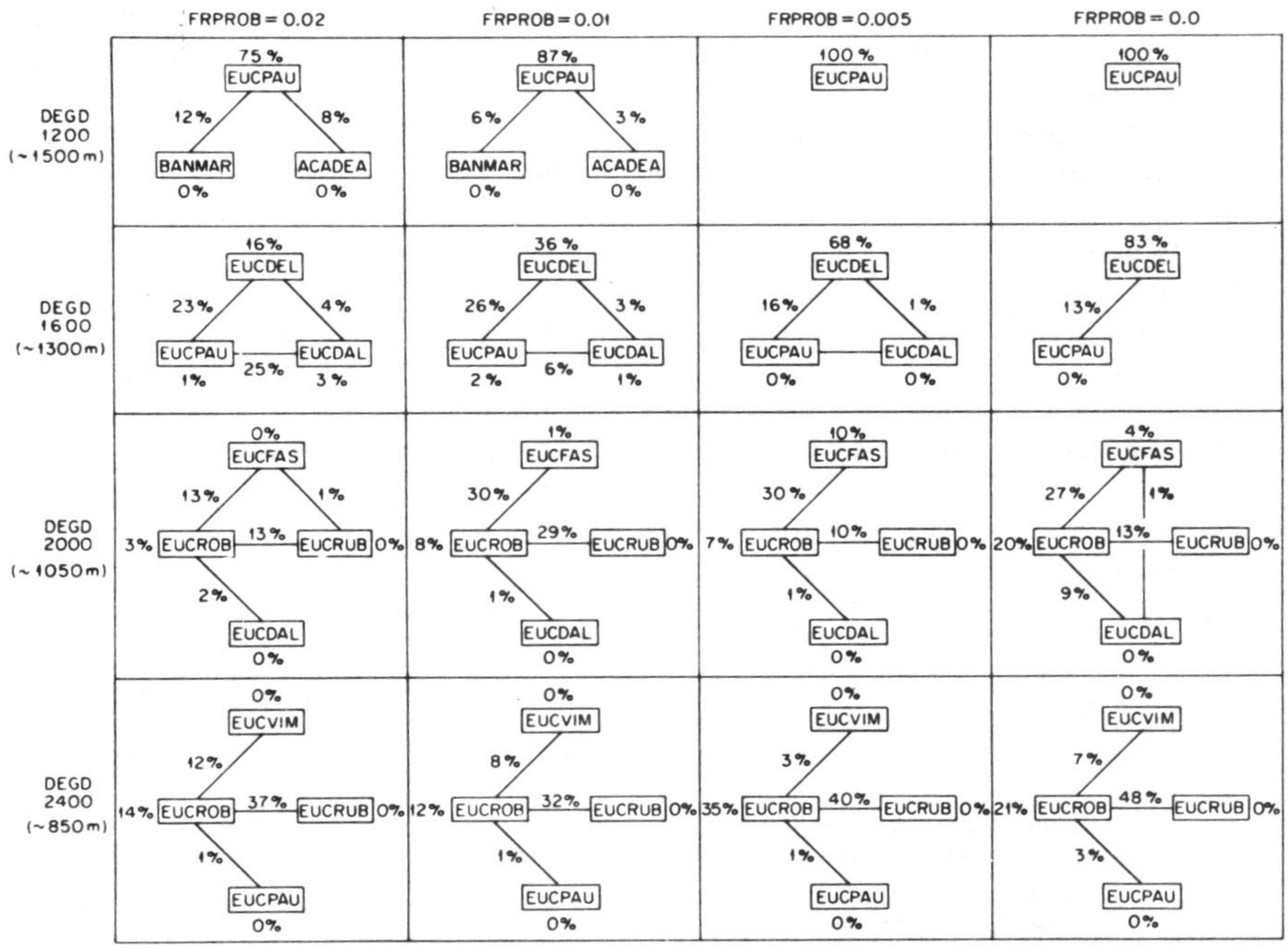


Table 2. Reproduction of a table from Foster and Ashe (1908) with the inclusion of results from the FORET model. The original table legend read, "Composition of forests in which chestnut oak forms more than 10% of the mixture, southern portion of the region, virgin growth."

[Trees 10 inches and over in diameter breast high.]

Species	Slope type					Ridge type	
	Average of 738 acres[a]		Average of 262 acres[b]			Average of 62 acres[c]	
	Number of trees	Percent	Number of trees	Percent	Percent[e]	Number of trees	Percent
Chestnut oak	6.02	16.91	7.46	16.98	10	12.54	24.34
Black oak	5.02	14.11	6.33	14.41	15	8.04	15.60
Chestnut	13.65	38.35	8.73	19.88	20	14.67	28.47
White oak	1.56	4.38	6.09	13.87	15	0.93	1.81
Shortleaf pine	1.82	5.11	0.60	1.37	1		
Scrub pine	0.85	2.39	0.33	0.75	1		
Hickory	0.82	2.30	3.14	7.15	5		
Gums	1.01	2.84	2.37	5.40	4		
White pine	1.67	4.69	0.20	0.46	3		
Yellow poplar	0.71	2.00	1.84	4.19	10	1.01	1.96
Maples	0.55	1.55	3.55	8.08	12	4.51	8.77
Hemlock	0.24	0.67	0.12	0.27	1		
Basswood	0.11	0.31	0.42	0.96	1		
Birch	0.07	0.20	0.24	0.55	1	0.15	0.29
Buckeye	0.02	0.06	0.13	0.29	1		
Cherry	0.01	0.03	0.04	0.09	1		
Beech			1.20	2.73	4	0.14	0.27
Locust			0.28	0.64	1		
Other species	1.46	4.10	0.85	1.93	1	9.53[d]	18.49
Total	35.59	100.00	43.92	100.00		51.52	100.00

[a]Polk and Monroe Counties, Tenn.
[b]Scott, Campbell, and Anderson Counties, Tenn.
[c]Harlan County, Ky., and Lee County, Va.
[d]Includes beech, gums, hickory, and locust.
[e]Values derived from FORET-with chestnut.

Accidents

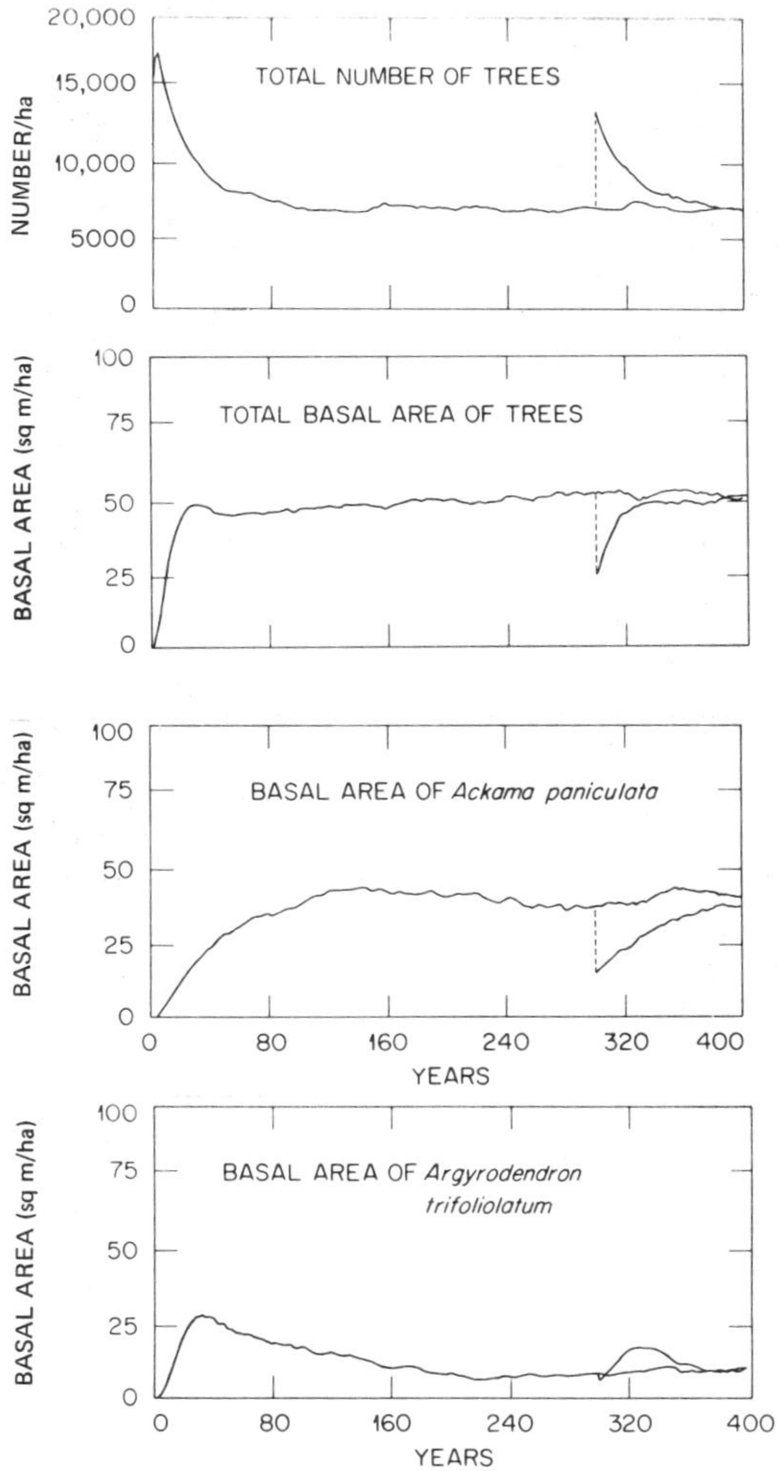
Occasionally, one will notice that, quite surprisingly, a model can predict a correct response in the face of a program error. For example, using a model that we developed for the southern Appalachian forest (Shugart and West 1977), we noticed that the model was predicting forests that to the best of our knowledge should occur in the Georgia Piedmont. Upon inspection, we found that we had accidently given the model a warmer climate than that appropriate for east Tennessee (a keypunch error on a computer card); the climate that we had given the model was, in fact, appropriate to the Georgia Piedmont. Now, observations of model behavior such as this do not constitute model experiments and rarely surface in the professional literature, but they do provide the model user with a sense of the reliability of the model's predictions. From various personal communications, it seems that these difficult-to-derive-from-intuition, anecdotal occurrences have been experienced by others who have either developed or used forest succession models. They are probably underestimated in terms of their importance as exploratory model tests.

CURRENT MODEL APPLICATIONS

Most models built strictly for forestry use are usually intended for the purpose of applications in a restricted set of specified circumstances. However, some of the succession models presented in table 1 have been used in evaluating environmental impacts on naturally occurring forests. Botkin (1973, 1977) found that the effects of altered carbon dioxide atmospheres were not manifested directly as a change in forest increment. Other effects such as plant competition and shading tended to lower the magnitude of the system response. McLaughlin et al. (1978) and West et al. (1980) performed model experiments on chronic air pollution stress expressed as a change in growth rates of pollution-sensitive trees using the FORET model. They noted that the response of growth over the long-term and in natural forests might vary in direction as well as in magnitude from what one might predict from laboratory or greenhouse studies. All of these studies identify a common problem; namely, in natural forests in which trees vary in spacing, size, and competitive responses, one cannot extrapolate directly from laboratory studies to field conditions. Forest succession models can provide and have provided a necessary adjunct to laboratory-based assessments of environmental effects.

In forest ecosystems for which we have a limited history from which to draw conclusions about the resiliency of the system to perturbation, one can use gap models to assess the effect of various management strategies. This is often true of systems that are currently being harvested at a rapid rate all over the world. That some of these models generate data much like that found in yield tables (e.g., BRIND--Shugart and Noble 1980, and figure 4; FORICO--Doyle et al. 1980, and figure 5) points to the potential role that they might have in this area. The KIAMBRAM

Figure 7. Response of the KIAMBRAM (Shugart et al. 1980) model to timber harvest at year 300 and repeated at 30-year intervals: (a) number of individuals per ha, (b) basal areas (sq m/ha) of all species, and (c) basal area (sq m/ha) for commercial species.



model (Shugart et al. 1980) has actually been used to assess the effect of a conservative forest harvest technique in the rain forests in the vicinity of the Tweed Range near the New South Wales/Queensland border (figure 7).

In many respects, the application of gap models to important problems regarding man's effect on forest ecosystems may be the most important validation procedure to which the models will be exposed. An important future application of succession models is in evaluating large-scale and long-term changes in the ambient levels of pollutants and in assessing the effects of climate change. If human activities alter the environmental conditions at a global scale, the use of models will become increasingly important as predictive tools. This is true of almost any application in which the history of observations made by ecologists on the behavior of forest ecosystems was made in an environment which had been altered in some way. At some level, this case is probably already appropriate to all forest ecosystems.

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SOME RECENT ADVANCES IN DEVELOPING INTEGRATED MODELS OF SECONDARY PLANT SUCCESSION

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Abstract

The mandate to improve fire management decision-making in western North America has required the development of new tools for predicting ecological response to different management alternatives. A result has been the development of general forest simulators, data base systems, and computerized "forest planning languages." Another result, often integrated with the above, is reviewed here; it is the recent development of new methodologies and models which predict the post-fire succession of plants and animals.

Because these models were developed to meet pressing management requirements, there were severe constraints of time, funding, and data availability. Furthermore, we sought to develop methods which both would meet local and specific information needs and could be generalized to a broad range of ecosystems. Thus our approach is somewhat different from other recent, demographic-style models.

The core model is an elaboration and refinement of a "multiple pathway" succession model originally developed in Australia by Noble and Slatyer. Our application uses it as a tool to integrate certain aspects of species populations' habitat and niche. Habitat may be determined by either a conventional classification system (such as community type, association, or habitat type) or by a community's location along continuous environmental gradients. Certain aspects of niche are then determined for major component species, including their relative tolerance to competition, their methods of reestablishment after a disturbance, and their basic life history information. The model then uses this information to quantitatively predict successional pathways followed by the postdisturbance community. These pathways are thus determined by the species' characteristics and the disturbance periodicity. Similar but qualitative predictions may be made for up to 600 species of terrestrial vertebrates using existing data bases.

Three additional components improve the utility of this basic model. The first is a model which relates overstory mortality to the intensity of the fire, which in turn can be predicted from fuel and weather parameters using existing models. Because of the core model's use of tolerance and basic life history parameters, fires of different intensities initiate different successional sequences.

The second additional component is a preliminary model which simulates the dispersal and establishment of seedlings for those tree species which are obligatory seed dispersers. For a few common tree species of this type, it thus estimates the likelihood of establishment in the postdisturbance community. Failure of one or more "adapted" species to reestablish after disturbance thus alters the successional sequences predicted by the core model.

The third additional component utilizes a data base which represents the mosaic of natural communities in the landscape, a mosaic created by both varying environmental conditions and disturbance histories. It calculates both the "mosaic diversity" and the diversity of terrestrial birds and mammals under any simulated fire regime; it also permits mapping of both the resulting mosaics and any requested bird or mammal species under any proposed fire regime. Current refinement of this model is expected to determine the effects of size, shape, and placement of the disturbance.

This work has been conducted primarily in the northern Rocky Mountains of the United States, but the models are now being calibrated for application to boreal forests in western Canada, *Eucalyptus* woodlands in New South Wales (Australia), and *Eucalyptus*/*Acacia* woodlands and heaths in Western Australia. They are also being linked with more general forest planning languages, both to provide ready access by land managers and to integrate with resource inventories, fuel and weather data bases, fire behavior models, and other management simulators.

INTRODUCTION

Recent events in several countries, including the United States, Canada, and Australia, have placed greatly increased demands upon public land management agencies; these events include increased public demands, legal constraints, economic pressures, and conflicting requirements for the preservation, conservation, and exploitation of resources. The management of natural areas such as national parks, nature reserves, and wildlife sanctuaries requires decision-making and action to maintain and sometimes to restore pristine ecosystems while providing for the public use and enjoyment of such areas. Multiple-use management, such as practiced by the U.S. Forest Service (Department of Agriculture) and other agencies, requires management programs to protect varied resources and land uses while also providing for sustained commercial resource outputs and recreation. Land management decision-making thus requires that the outcome of each management alternative be determined and weighed as part of the decision-making process. Inputs on such diverse concerns as wilderness, wildlife, endangered species, exotic species, water quality, aesthetics, recreation, sustained timber yield, and mining potential must be projected, evaluated, and presented to the public; decisions must be reached which achieve acceptable compromises, are economically feasible, and meet agency and public approval. Contingency plans for events such as unplanned fires, insect outbreaks, and changing public demands must also be considered.

Such management requires a detailed ecological understanding of how each decision will affect all major components of the ecosystem, and it presupposes the manager's ability to correctly select desired outcomes from a spectrum of conflicting demands, special interests, and legal and economic constraints. It thus requires the manager not only to choose appropriate goals but also to implement decisions which will effect the realization of those goals. Unfortunately, very few land managers possess the tools, data, and ecological understanding required to do this consistently (Kessell 1979, Kessell et al. 1980b, Franklin 1979).

These problems become especially acute in times of real or imagined emergencies, such as wildfires; sound management action requires the rapid projection of both fire behavior and its ultimate ecological effects. Once again, very few managers are able to do this adequately. As a result, management agencies have become increasingly involved with the use of modeling, simulation, large computer data bases, and information system analysis. The complexity of today's resource management problems, and the large volume of data often required in the formulation of a solution, dictates the use of such tools to handle these vast quantities of complex data, to use existing knowledge to predict the probable outcomes of various management alternatives, and to evaluate the consequences of various management alternatives without incurring the cost or consequences of implementing each option (Franklin 1979, Kessell 1978, Kessell et al. 1980b).

The developments in this area have been rapid and diverse. Specialized models and programs have proliferated in numerous areas to help solve specific management problems. Of this recent work, there are two areas of resource management simulation which I think are especially important. The first is the development of integrated "resource planning languages and simulators." These are large computer-based systems that integrate numerous models and data bases (such as resource inventories, models of floral and faunal community composition, fuel models, meteorological models, fire behavior models, and succession models) into a single, user-oriented system, often programmed by managers using simple English commands. Examples include the Glacier National Park gradient modeling system (Kessell 1976, 1979a), the U.S. Forest Service FORPLAN (Forest Planning Language and Simulator) developed in the northwestern United States (Potter et al. 1979), and the Australian PREPLAN (Pristine Environment Planning Language and Simulator) recently implemented in New South Wales and Western Australia (Kessell and Good 1980, Kessell et al. 1980a).

The second area is the development of models which predict the successional response of plant and animal communities to major periodic disturbances such as fire. Considerable recent work throughout the world has attempted to relate postfire successions to the following: preburn site, community, and weather conditions; fire behavior, intensity, duration, and periodicity; the attributes and adaptive characteristics of the species populations; the placement, shape, size, season, and timing of the fire; and chance factors. Considerable progress, and a number of new models, have emerged. Some of the results have already been incorporated into the resource planning languages noted above and are in operational use by land managers in the United States and Australia. Despite numerous unresolved problems and frequent disagreement among researchers, a sound synthesis of postfire plant and animal succession is rapidly approaching.

This paper reviews one such approach toward this synthesis developed by the author and his colleagues. While the original work was conducted in coniferous forest communities of the northwestern United States (Montana), the general modeling approach is currently being calibrated, tested, and applied to boreal forests of northwestern Canada, *Eucalyptus* woodlands in New South Wales, and *Eucalyptus* / *Acacia* woodlands and heaths in Western Australia.

MODELING SUCCESSION IN A MANAGERIAL CONTEXT

Background

The past few years have produced many significant advances in our understanding of and ability to predict postdisturbance plant succession, including the understanding of basic successional processes, the adaptive characteristics of species populations, the demography of interacting populations, the effects of disturbance periodicity and intensity, the influence of entire vegetation patterns and mosaics upon component communities, and the ability to integrate successional processes with other ecological and managerial concerns, models, and data bases. As a result, a number of modeling approaches have emerged.

Despite both real and superficial differences, these models share a fundamental component; they abstract and apply information on the habitat and niche of interacting and competing species populations. I think the habitat and niche concepts provide a useful approach to comparing and contrasting some of these modeling approaches.

Habitat refers to the distribution of communities and species populations in the environmental context, mosaic, or space (Whittaker et al. 1972). Succession models require habitat inputs not only because different communties include different species populations, but also because of the adaptive and demographic variation exhibited by a single species throughout a range of communities. Some approaches deal with habitat explicitly as a model input, while others address it implicitly by developing different models for different communities. The stratification of habitat may be accomplished by community classification, gradient analysis, or ideally a combination of the two methods (Franklin 1979, Kessell 1979b).

Niche refers to the way a species goes about "making a living," and is characterized by the community resources occupied or utilized (niche is here used in the restrictive sense of Whittaker et al. 1972). From a successional viewpoint, this is an expression of the species resource utilization, adaptations, and demography in the context of other competing species populations and the community's resources. Recent succession models deal with several aspects of niche, including species tolerance to temporal and spatial variability, modes of persistence through or establishment after a disturbance, and basic life history traits.

Let us consider three basic kinds of succession models, their utilization of habitat and niche considerations, and the kind of knowledge and data required by each approach. I shall give these the generic names of empirical models, demographic-prognosis models, and selected attributes/multiple pathway models.

Empirical models are derived from maximum information on historical successional development and minimal information on species characteristics. This is not to imply that they are necessarily crude or incomplete; much recent work (such as Lyon 1971 and 1976, Lyon and Stickney 1976, Kessell 1979a) has demonstrated that the predisturbance community composition is an excellent predictor of postdisturbance processes. They are, however, very dependent upon an extensive data base developed from sampling communities over time after a disturbance and/or sampling a variety of such communities at different stages of recovery. This approach assumes that future successions will resemble past ones for similar communities subjected to similar disturbances; it is nearly powerless to deal with new disturbances and/or periodicities which occur without historical precedence. These models may represent a single community, a range of communities, or various points on an environmental gradient continuum.

At the other extreme, demographic-prognosis models place minimal reliance on historical successional data but are very dependent on knowledge of the niche characteristics of component species populations. Such models may require twenty or more parameters describing each species; examples would include maximum age, height, and diameter; tolerance to annual meteorologic variation; and probabilities of germination and mortality (Botkin et al. 1972, Shugart and West 1977). They usually simulate succession by growing, killing, and replacing individual plants and thus are limited to modeling small areas (usually 0.1 ha or less). In some of these models, habitat may be used to a certain extent to determine the species niche attributes. The most attractive feature of demographic-prognosis models, from a land management standpoint, is their lack of dependence on a voluminous field data base represeting different stages of succession. Limitations include their dependence on detailed species characteristics, their significant computer requirements, and their restriction to modeling small areas.

Selected attributes/multiple pathway models represent a compromise between these two extremes, and thus exhibit some of the advantages and limitations of both empirical and demographic-prognosis models. They utilize key niche characteristics such as relative tolerance, method of persistence and regeneration, and basic life history characteristics; as a result, both predisturbance stand composition and disturbance periodicity affect the resulting predictions (Noble and Slatyer 1977 and 1980, Cattelino et al. 1979). Habitat is usually included as one of the determinants of each species' selected attributes. While species presence and absence can be predicted from the species attributes, predisturbance composition, and interdisturbance periodicity (Noble and Slatyer 1977, Cattelino et al. 1979), quantification of the results currently requires calibration from field samples (Kessell and Potter 1980). These models have also recently been used to integrate new components, such as disturbance intensity and seed dispersal probabilities, as described below.

Other important recent work has dealt with the mechanisms of succession (such as Connell and Slatyer 1977) and has viewed succession as an ecosystem (rather than community) process (Bormann and Likens 1979, Odum 1969, Whittaker 1975).

Goals of this Study

The new modeling work reported here was conducted under a cooperative agreement between Gradient Modeling, Inc., and the U.S. Forest Service during 1978-1979. The general purpose of the study was to develop a methodology which could use existing or readily obtainable data to predict the postfire succession of all overstory species (trees), important understory species (grasses, forbs, and shrubs), birds, and mammals. More spcific goals included the following:

> stratification of communities either by the Montana habitat-type system of Pfister et al (1977) or by a method compatible with that system

inclusion of the effects of both fire periodicity and fire intensity on the postfire successions

quantification of plant species importance during succession

demonstration of the model for several major forest communities which occur in the Lewis and Clark National Forest in Montana

inclusion of the model in the FORPLAN system as implemented on that forest (so that the utility of the succession models could be evaluated by land managers)

presentation of the results as a set of guidelines which instruct managers in other localities on how to calibrate the system to their own areas and how to use the resulting models <u>without requiring access to digital computer facilities</u>

We also imposed upon ourselves an additional goal, not required under the cooperative agreement:

development of a methodology which could be adapted to diverse ecosystems, including <u>Eucalyptus</u> / <u>Acacia</u> communities in Australia, and would not be restricted to the coniferous forest communities for which it was to be developed

These goals and constraints exerted a considerable influence upon our choice of methods. For example, previous succession work in nearby Glacier National Park (Kessell 1979a) demonstrated that a simple empirical approach (as reviewed above) would be inadequate for meeting the study goals; such an approach does not consider adequately the effects of fire intensity and fire periodicity in many communities. Both the demopgraphic-prognosis and selected attributes/multiple pathway modeling methods have proved effective for modeling postfire plant succession (Noble and Slatyer 1977, Cattelino et al. 1979, Kessell 1979a, Shugart and Nobel 1980, Shugart et al. 1980), and each method required data which were obtainable but not readily available.

We decided that an elaboration and refinement of the selected attributes/multiple pathway style of model would be most appropriate for meeting the study goals, and especially appropriate for including the effects of fire intensity and periodicity, the probabilities of seed dispersal, and birds and mammals. While its application to land management is facilitated through the use of computer-based resource planning languages, such an apprach can be developed and applied in the absence of computer facilities. It does not provide the ready quantification of changes important to species through succession that is available from a demographic-prognosis style of model, but such quantification was ultimately obtained by calibration from field data. The development of this integrated model is described below.

DEVELOPMENT OF THE INTEGRATED MODEL

The General Model

The general model is an application of the selected (or vital) attributes/multiple pathway succession model developed in Australia by Noble and Slatyer (1977) and applied to North American coniferous forest communities by Cattelino et al. (1979). Let us consider the two fundametal components of this model:

successional community "states" which result from different successional pathways or responses

transition ages (from one state to another) which are determined both by the species' attributes and the interdisturbance periodicity

Successional States and Pathways. While succession is usually conceptualized as a process of continuously changing species patterns and community characteristics, it is convenient to view the community as making transitions from one state to another (Clements 1916). One thus divides the continuum into a suitable number of states based upon the available information and the resolution required (Kessell 1979a, 1979b). Figure 1 shows a very simple model of this process. The solid lines show that a postdisturbance community of intolerant pioneer species (state A) gives way to a midseral community of both intolerant and tolerant species (state B), and is eventually replaced by a sustaining community of tolerant "climax" species (state C). The sustaining nature of state C is indicated by the closed solid arrow; state C does not make a transition to a new state in the absence of further disturbance. A more detailed model might include numerous states which reflect changes in species importance as well as species replacements.

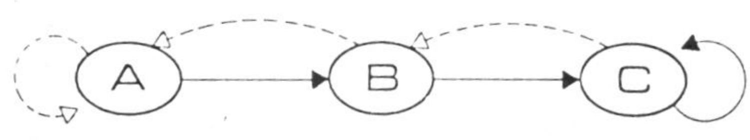


Figure 1. A simple model showing successional transitions in the absence of further disturbances (solid arrows) and those caused by additional disturbances (broken line arrows).

This simple approach models community changes following an initial disturbance, and it can also be used to show the effects of additional disturbances. We thus add broken line segments to show the results of subsequent disturbances. In this and all subsequent models illustrated, transitions which occur without additional disturbance are indicated by solid directed line segments, while those transitions resulting from additional disturbances are shown by broken line segments. Thus in the model shown in figure 1, a second disturbance of state A retains the community as state A, a disturbance of state B causes a transition back to state A, and a disturbance of state C causes a transition back to state B.

Modification and expansion of this approach are discussed later in the paper, and include more numerous states to show quantitative changes in species composition, different postdisturbance pathways resulting from disturbances of different intensities, and different transitions for overstory vegetation, understory vegetation, and/or animals.

Transition Ages, Species Attributes, and Disturbance Periodicity. Application of this approach to specific communities requires that the times at which nondisturbance transitions occur and the critical events which trigger different transitions be determined from actual observations of species populations and communities. Furthermore, the determination of ages at which certain transitions occur (such as the loss of a species from the community) requires certain information on the adaptive and life history characteristics of the component species. These are modeled according to the system proposed by Noble and Slatyer in 1977; their later scheme (1980) refines and expands this earlier work. However, we can satisfactorily demonstrate the method and its application using the simpler approach.

The Noble and Slatyer (1977) system defines a set of species attributes that are vital to the reproduction and survival of a species within the community. They define the following three attributes as most important to a species' success on a site subjected to periodic disturbances, such as fires:

the method of arrival or persistence of propagules at the site following a disturbance

the conditions in which the species establish and grow to maturity

the time taken to reach critical stages in their life history

The first attribute, method of arrival or persistence, describes how a species survives a disturbance. Four basic mechanisms are recognized by Noble and Slatyer:

persistence by the arrival of widely dispersed seeds (D species)--seeds are dispersed from the surrounding undisturbed areas and are assumed to be available at all times persistence by seeds with long viability that are stored in the soil (S species)--not all of these seeds germinate after the first disturbance, and the seed pool may persist through a series of disturbances without replenishment

persistence of seeds with short viability that often survive the disturbance within protective fruits or cones that are stored in the canopy (C species)--in this case, seeds are available only if the adults were present before the disturbance

persistence by part of the individual surviving the disturbance and recovery by vegetative regrowth (V species)

The next attribute describes the conditions necessary for establishment. The following three mechanisms are recognized:

ability of the species to establish at any time, with adults of the same species and of other species occurring at the site--these species can tolerate competition (T species); as used here, tolerance can apply to light, soil nutrients, or other physiological requirements

ability of species to establish immediately after a disturbance when competition is usually reduced--these species are intolerant of competition in established communities (I species)

inability of species to establish immediately after a disturbance, but ability to become established once mature individuals of either the same or another species are present--these species have some requirement that is only provided by established communities (R species)

The third vital attribute of life history plays an important part in the replacement sequence and in describing the role of a species after a disturbance. There are four critical events within the life history of a species that are arranged in order of occurrence following a disturbance (time 0):

the replenishment of sufficient propagules to survive another disturbance (p)

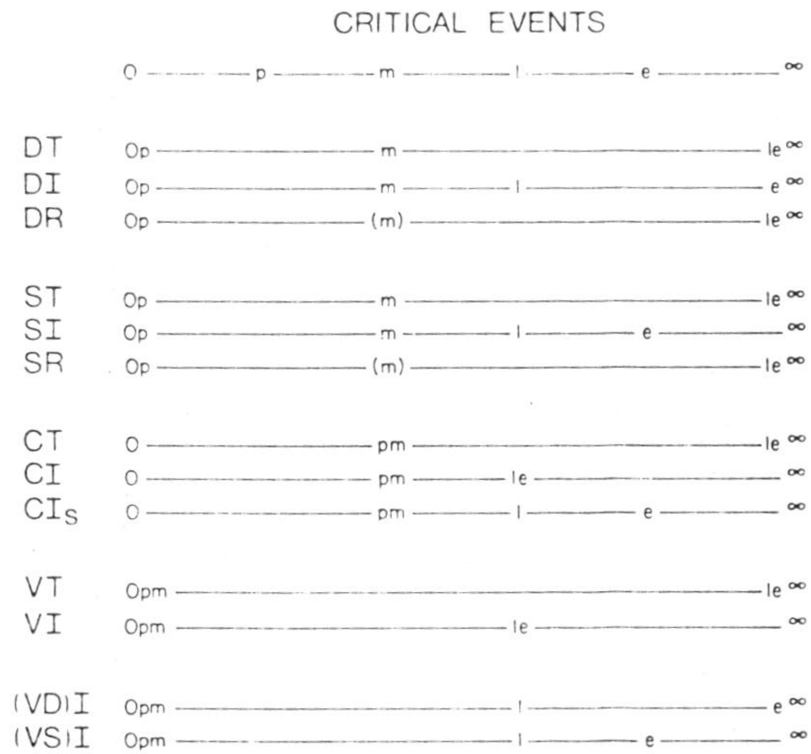
maturity (m), when individuals have recovered or grown sufficiently to be regarded as established--maturity by this definition is the time when the individual is able to contribute propagules into the pool that will enable the species to persist through another disturbance

senescence and loss of the species from the community (l)

loss of propagules from the site so that the species is extinct (e)

By combining the first two vital attributes of a species (method of persistence and conditions for establishment) with its critical life history events, these life history characteristics can be represented as shown in figure 2. Note some of the successional traits shown by this

Figure 2. Life history characteristics for various combinations of the first two vital attributes (from Noble and Slatyer 1977).



characterization. For example, D (dispersal) species always have event p (replenishment of propagules) occur at time 0, since propagules are assumed to disperse from surrounding communities. Intolerant dispersal species (DI) are locally lost in the absence of further disturbance, while DT and DR species are not; but all D species can reestablish after another disturbance.

Stored seed (S) species also have event p occur at time 0, but unlike DI species, SI species will ultimately lose their stored seed pool and thus can become extinct on the site. However, ST and SR species will not become extinct, since new populations are contributing new propagules to the pool.

Cone-stored seed species (C) are generally assumed to produce seeds with short viability, and thus event p does not occur until maturity (m) of the new generation (when the new plants produce seeds). CT species do not become extinct, but CI species do so after a sufficiently long period (equal to their longevity) without disturbance. This is because after the population dies, its intolerant status prevents further reproduction and replenishment of the seed pool.

Vegetative species (V) have events p and m both occur at time 0, since a mature individual is simply continuing to grow (or resprout) after the disturbance. VI species become extinct after a sufficiently long period without disturbance (again, it is equal to the population's longevity) while DT species do not become extinct.

Note that the (VD)I and (VS)I events are shown for species which can persist by either the V or D, or V or S, mechanisms, respectively. The CI_S species was added to Noble and Slatyer's (1977) original scheme by Cattelino et al. (1979) to account for species such as serotinous Pinus contorta (lodgepole pine); this species' seeds are viable in some communities for perhaps 20 years beyond the population's longevity.

These "vital" or "selected" attributes of Noble and Slatyer thus abstract some fundamental aspects of each species population's niche that determine the species' successional response. Habitat enters the picture both directly and indirectly. In the first case, different successional models are usually developed for different communities; in the second case, the attributes of a given species often change as a function of habitat (Kessell 1979a, Cattelino et al. 1979). For example, Abies lasiocarpa (subalpine fir) populations in Glacier National Park are usually tolerant in high elevation communities but intolerant in low elevation communities; Abies' reproduction is by dispersal in low elevation stands but may also be vegetative in higher subalpine communities.

Applications of the Model. Let us now apply these species attributes and life history representations to the successional states and transitions diagrammed earlier. Consider a simple forest which includes three tree species: Abies lasiocarpa (subalpine fir), Pseudotsuga menziesii (Douglas-fir), and Pinus contorta (lodgepole pine). For purposes of illustration, we shall assume that Abies is tolerant and regenerates from dispersed seeds (DT species); therefore once established in the postfire community, it remains there indefinitely. Pseudotsuga in this community is also a seed dispersal type but is intolerant (DI); it ultimately will fail to reproduce under the Abies and Pseudotsuga canopy, and given a sufficient interfire period will be lost from the community. Pinus is also intolerant and is assumed to regenerate only from seeds stored in serotinous cones (CI_S). We shall further assume that, for this particular community, Pseudotsuga has a longevity of 300 years, Pinus has a longevity of 200 years, and the Pinus seeds remain viable for an additional 20 years after the individual's death.

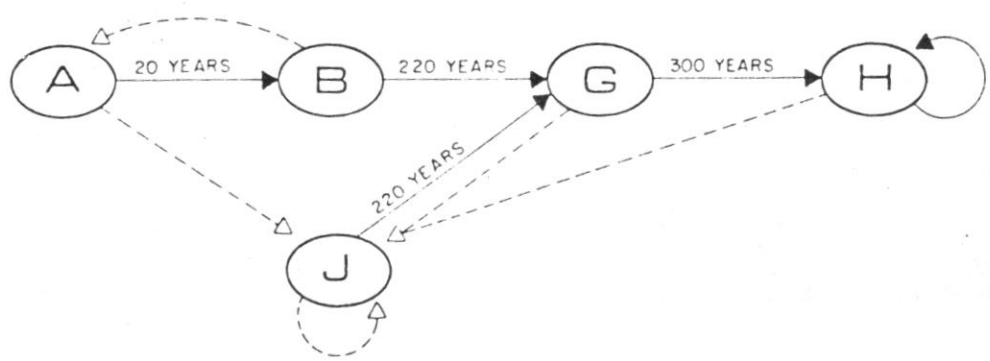


Figure 3. Application of the selected attributes/multiple pathway model to a forest community of three tree species. The successional patterns are explained in the text.

These critical life history events thus produce the model shown in figure 3. State A includes all three species, but a second disturbance of state A causes a transition to state J and the permanent loss of Pinus. If state A is undisturbed for 20 years, a transition is made to state B. State B also includes all three species, but if disturbed it will return to state A (after 20 years, Pinus has reached maturity and replenished the seed pool). If the community endures 220 years without another disturbance, it reaches state G; Pinus is lost and the community consists of Abies and Pseudotsuga. A disturbance now will result in a transition to state J; Pinus has been permanently lost from the community. If the community endures 300 years without a disturbance, it reaches state H; Pseudotsuga is lost from the present community, and the forest is pure Abies. Because it is a dispersal species, Pseudotsuga will reestablish after the next disturbance, resulting in transition to state J, but Pinus will not. Since state J represents the loss of Pinus and retention of Abies and Pseudotsuga, it reverts back to state G. If state J is disturbed, it remains as state J.

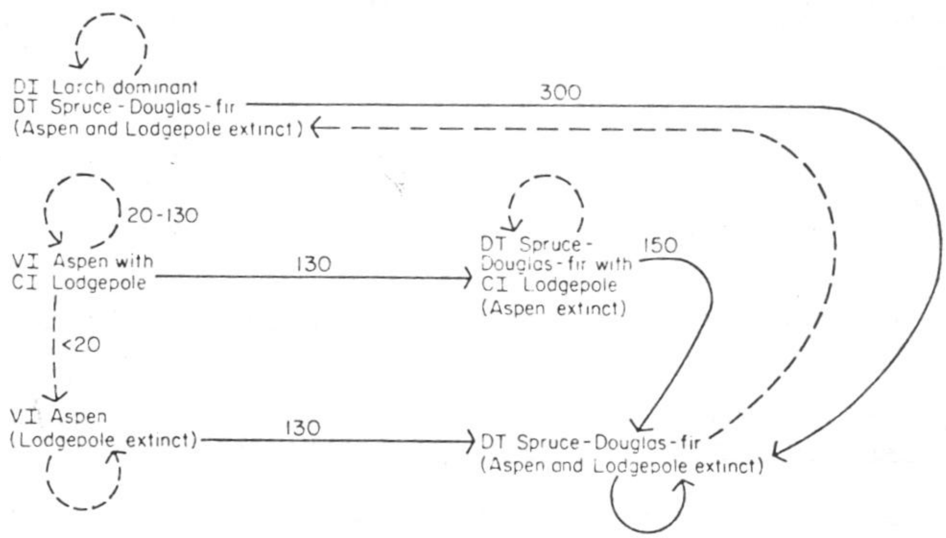
Another example is an aspen community sampled in Glacier National Park by Kessell (1979a) and modeled by Cattelino et al. (1979) and Kessell (1979a). Normal fire periodicity for these communities is about 50 years; the stands are usually a mixture of Populus tremuloides (aspen), Pinus contorta (lodgepole pine), Pinus ponderosa (ponderosa pine), Pseudotsuga menziesii (Douglas-fir), Picea glauca x engelmannii (spruce), and Larix occidentalis (western larch). When burned under normal fire periodicities, the succession includes all of these species, with either Populus tremuloides or Pinus contorta predominating the early seral communities.

Yet fires with different periodicities have been described to cause the loss of Populus tremuloides and/or the loss of Pinus contorta and/or a dramatic increase in Larix occidentalis (Kessell 1979a). A model developed from species attributes accounts for these varying successional pathways.

Populus is a VI species with a life span of about 130 years (thus extinction occurs at 130 years). Pinus contorta is a CI species with a life span in these communities of about 150 years, while Larix is a DI type with a much longer life span of 300 to 400 years. Both Abies and Pseudotsuga are DT species which are dominant only in old communities.

As shown in figure 4, several successional pathways are possible. If the community is burned with both Populus and Pinus contorta present from 20 to 130 years after the last fire, both species will be present after the fire. But if this same community is burned during the first 20 years, before P. contorta reaches maturity, the species will be lost from the community; Populus' importance will increase as a result. An interfire period in excess of 130 years will cause the loss of VI Populus from the community; burning in excess of 150 years will also cause the loss of P. contorta and a dramatic increase in Larix. Ultimately all of these successions will lead to an Abies / Pseudotsuga climax forest if fire is excluded for a sufficiently long time. But note that loss of P. contorta and Populus, with the seral dominant now being Larix, requires a much longer time to reach this climax (300 to 400 years instead of 150 years).

Figure 4. Multiple pathway model of an aspen, lodgepole pine, and mixed conifer community shows how different fire periodicities can cause the extinction of aspen and/or lodgepole pine.



Further examples of applications of this basic model are given by Noble and Slatyer (1977, 1980), Kessell (1979a), and Cattelino et al. (1979).

We have been pleased with the versatility of this general and simple model in describing successional processes in a wide range of communities in Australia and North America. However, managerial needs required modification and improvement so that the model could accomplish the following:

describe quantitative changes in species populations rather than mere presence or absence

respond to disturbances (fires) of different intensities

handle the situations where a dispersal type (D) species does not in fact disperse from adjacent communities

include birds and mammals

reflect fire effects in the context of a mosaic of communities rather than just within a single homogeneous community

These needs led to the development of new components which are used in conjunction with the basic model.

Linkage with the Fire-Intensity Model

The desire both to describe species changes quantitatively, and to include the effects of fire intensity, led to a refinement of the basic model described above. This refinement was developed for nine major coniferous forest communities (habitat types of Pfister et al. 1977) in Montana. Seven of these which occur in the Lewis and Clark National Forest were given special attention:

> Pseudotsuga menziesii / Symphoricarpos albus (includes Agropyron spicatum, Calamagrostis rubescens, and Symphoricarpos albus phases)
>
> Pseudotsuga menziesii / Vaccinium globulare, Vaccinium globulare phase
>
> Abies lasiocarpa / Linnaea borealis (includes Linnaea borealis, Xerophyllum tenax, and Vaccinium scoparium phases)
>
> Abies lasiocarpa / Vaccinium globulare
>
> Abies lasiocarpa / Vaccinium scoparium (includes Calamagrostis rubescens, Vaccinium scoparium, and Thalictrum occidentale phases)
>
> Abies lasiocarpa - Pinus albicaulis / Vaccinium scoparium
>
> Pinus albicaulis - Abies lasiocarpa

These communities were sampled to obtain structural information and floristic composition; that methodology is detailed by Kessell and Potter (1980). The data were augmented with information available from Pfister et al. (1977 and personal communication) and Stephen Arno (unpublished), and for two community types with data from nearby Glacier National Park (Kessell 1979a). These nine communities include a maximum of six tree species and 25 important understory species. The trees include Abies lasiocarpa, Picea glauca x engelmannii, Pseudotsuga menziesii, Pinus contorta, Pinus albicaulis, and Pinus ponderosa, but not all six species occur in any one community type.

Each tree species except Pinus contorta regenerates from dispersed seeds (D species). Relative tolerance and intolerance is a function of both the species and the community type. P. contorta regenerates primarily from seeds stored in serotinous cones, and therefore was modeled as a CI species; it can be lost from these communities under certain fire periodicities.

Modeling these communities required two major changes to the basic model described earlier. The first was inclusion of more states to show quantitative changes in species composition through succession. The second was inclusion of different pathways to be followed as a function of fire intensity.

Based on field studies in adjacent areas (Kessell 1979a), we estimated that fires which kill over half of the overstory are "severe" fires which cause major successional transitions. Those which kill less than half of the overstory are "mild" fires which cause little or no change in overstory species composition and minor changes in understory species composition. (An exception occurs in early stages of succession where the young overstory is predominantly P. contorta; here a "severe" fire is one which kills the entire overstory population.)

The crucial value of fire intensity which causes 50 percent tree mortality is a function of the height and species distribution of the overstory; we found that it could thus be modeled as a function of community type and stand age (Kessell and Keane 1980, Kessell and Potter 1980). Fieldwork was conducted to measure the vertical distribution of tree foliage in these communities. This allowed, for each age class of each community type sampled, the determination of the scorch height required to kill approximately 50 percent of the canopy. Scorch height is the height above the ground at which living foliage will be killed by a fire; Van Wagner (1973) has shown it to be a function of Byram's (1959) fireline intensity. Byram's intensity in turn can be calculated using existing fire behavior models (such as Rothermel 1972) as a function of fuel, weather, and site conditions. Since fuel information was also obtained for these communities (Kessell and Keane 1980, Potter et al. 1979), it is therefore possible to relate both scorch height and tree mortality directly to weather distributions. This work is described in more detail in Kessell and Keane (1980).

The successional pathways resulting from different fire scorch heights are easily incorporated into the basic model. Figure 5 shows the basic succession model (from figure 1) modified to include a critical scorch height of 10 m. A fire in state A, regardless of its scorch height, will retain the community as state A. A fire in state B causes a transition to state A only if the scorch height is greater than or equal to 10 m; a lower scorch height retains the community as state B.

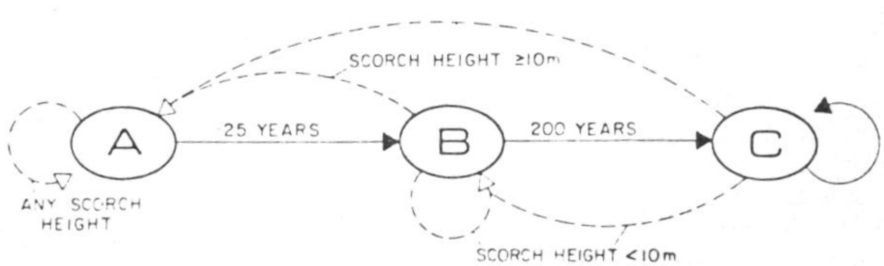


Figure 5. Elaboration of the basic succession model to allow different fire scorch heights to determine different successional responses.

Table 1. Matrix relating species composition to successional states for the Abies lasiocarpa / Vaccinium globulare habitat type. The successional state numbers correspond to the model shown in figure 6. Importance values are expressed on a seven-point scale where blank = less than 1%, 1 = 1% - 5%, 2 = 6% - 25%, 3 = 26% - 50%, 4 = 51% - 75%, 5 = 76% - 95%, 6 = over 95%. Importance values for trees over 1.4 m tall are relative density; all other importance values are absolute cover. (From Kessell and Potter 1980.)

	Succession Model States												
Overstory Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Trees Over 1.4 m Tall													
Abies lasiocarpa			1	3	4	5	5	5	6		2	4	4
Picea glauca x engelmannii			1										
Pinus albicaulis					1	1	1	1					1
Pinus contorta	5	5	5	4	3	1							
Pseudotsuga menziesii	2	2	2	2	2	1	1			6	4	2	2
Tree Seedlings													
Abies lasiocarpa	2	2	2	2	2	2	2	2	2	2	2	2	2
Pinus albicaulis					1	1							
Pinus contorta	3	3											
Total Canopy Cover	2	2	4	4	4	3	3	3	3	4	4	3	3
Understory Species													
Shrubs & Subshrubs													
Alnus sinuata	1	1								1			
Juniperis communis			1	1							1	1	
Lonicera utahensis	1	1								1			
Rosa spp.	1	1								1			
Spiraea betulifolia	1	1	1	1	1	1	1	1	1	1	1	1	1
Symphoricarpos albus				1								1	
Vaccinium globulare	1	1	2	2	2	2	2	2	2	1	2	2	2
Berberis repens			1								1		
Total Shrub Cover													
Forbs & Grasses													
Calamagrostis rubescens	4	4	3	3	1	1	1	1	1	4	3	3	1
Carex geyeri	2	2	1	1	1	1	1	1	1	2	1	1	1
Festuca scabrella	1	1								1			
Other Gramineae	1	1								1			
Antennaria racemosa			1								1		
Arnica spp.	2	2	2	2	2	2	2	2	2	2	2	2	2
Chimaphila umbellata					1								1
Epilobium angustifolium	1	1								1			
Valeriana sitchensis					1								
Total Forb & Grass Cover	4	4	4	3	2	2	2	2	2	4	4	3	2

Similarly, a scorch height of 10 m or more in state C causes a transition back to state A; a lower scorch height causes a transition to state B.

We may now use this approach to develop the model of the nine Montana forest community types shown in figure 6. As noted earlier, we increased the number of states to show quantitative changes in species composition through succession. The pathway from state 1 to state 6 is succession with seral Pinus contorta; the pathway from state 10 to state 13 is succession without seral P. contorta. States 7 through 9 show late succession and climax development beyond the longevity of P. contorta. P. contorta may thus be lost by burning a stand before the species reaches maturity and produces seeds (the first 20 years after a fire--state 1), or by allowing an interfire period in excess of 220 years (and thus loss of the species and viable seeds--state 7). Once the species is lost, it can not be regained. As in previous models, solid lines show transitions in the absence of further disturbance, while broken lines show transitions due to subsequent disturbances. The numbers plotted on the solid lines show the approximate age of the community (postfire) at which the transition occurs.

Calibration of this model to individual community types requires the development of tables which relate species composition to state numbers. An example, for the Abies lasiocarpa / Vaccinium globulare habitat (community) type, is shown in table 1; tables for the other eight communities are incuded in Kessell and Fishcher (1980). The critical scorch heights shown in figure 6 were determined from the fire intensity study noted above (Kessell and Keane 1980); they are shown in table 2 as a function of community type.

Table 2. Critical scorch height values for the seven Lewis and Clark National Forest habitat types (determined by Kessell and Keane 1980). Values determine the successional pathways followed by the model in figure 6. Habitat type codes are the first two letters of genus and species (PSME/SYAL - Pseudotsuga menziesii/ Symphoricarpos albus).

	Critical Scorch Heights (m)				
Habitat Type Code	A	B	C	D	E
PSME/SYAL	1.8	5.5	6.1	6.1	12.2
PSME/VAGL	2.1	6.4	9.1	10.4	10.4
ABLA/LIBO	3.1	6.4	12.5	13.1	13.7
ABLA/VAGL	2.1	6.4	9.1	10.4	10.4
ABLA/VASC	2.1	6.4	9.1	10.4	10.4
ABLA-PIAL/VASC	2.1	6.4	9.1	10.4	10.4
PIAL-ABLA	2.1	6.4	9.1	10.4	10.4

The model shown in figure 6 was developed for the understory species. The overstory species model is different only in that mild fires (scorch height less than the critical value) retain the community in the same state rather than retrogress it by one state. Note that predicting the presence or absence of overstory species, as well as the determination of successional pathways, was done solely by reference to the vital attributes and life history information utilized by the Noble and Slatyer system. However, the quantification of both overstory and understory species importance as shown in table 2 was determined by field sampling the various states for each community. Some of the transition ages shown in figure 6 are due to critical events in the species' life histories, including the maturity of Pinus contorta at age 20, the loss of P. contorta at age 220, the loss (in this particular community type) of intolerant Pseudotsuga at age 300, and the loss (in this community) of Pinus albicaulis at age 350 years. Other transition ages were selected for convenience as determined by the rate of species changes and the availability of field data. Also note that this general model was adequate for representing the nine community types studied but that it requires field calibration to each community type.

Linkage with the Seed-Dispersal Model

Another shortcoming of the general model presented earlier is its assumption that dispersal (D) type species will always disperse from adjacent undisturbed communities. Obviously this will not always happen, especially when the disturbance area is very large. A related problem is caused by species such as Pinus contorta; although frequently modeled as a CI species, it often exhibits a dimorphism. Serotinous P. contorta does function as a CI species, but nonserotinous (open cone) individuals should be treated as the DI type. In many natural populations, the serotinous individuals predominate. However, if unable to reproduce as a CI species due to loss from the preburn community, it may reestablish (usually much less well) as a DI species. This problem was described by Cattelino et al. (1979) for a birch, lodgepole pine, and mixed conifer community in Glacier National Park using the data of Kessell (1979a). As shown in figure 7, several transitions cause the loss of CI P. contorta; the species is retained in the community only if DI P. contorta can establish after a fire. This situation clearly demonstrates the need to determine the likelihood of each species' dispersal to and establishment in the postfire community.

Potter et al. (1980) have recently reported the first attempt at constructing such a stochastic model of seed dispersal and seedling establishment; the work was conducted in the Montana coniferous forest communities described earlier. The model currently deals with four conifer species and was developed to link with the succession model described in the last section. The model is preliminary in nature, makes a number of assumptions, and is not yet fully linked to the succession models. However, it does in my opinion show the direction of research required to effect this ultimate integration with succession models.

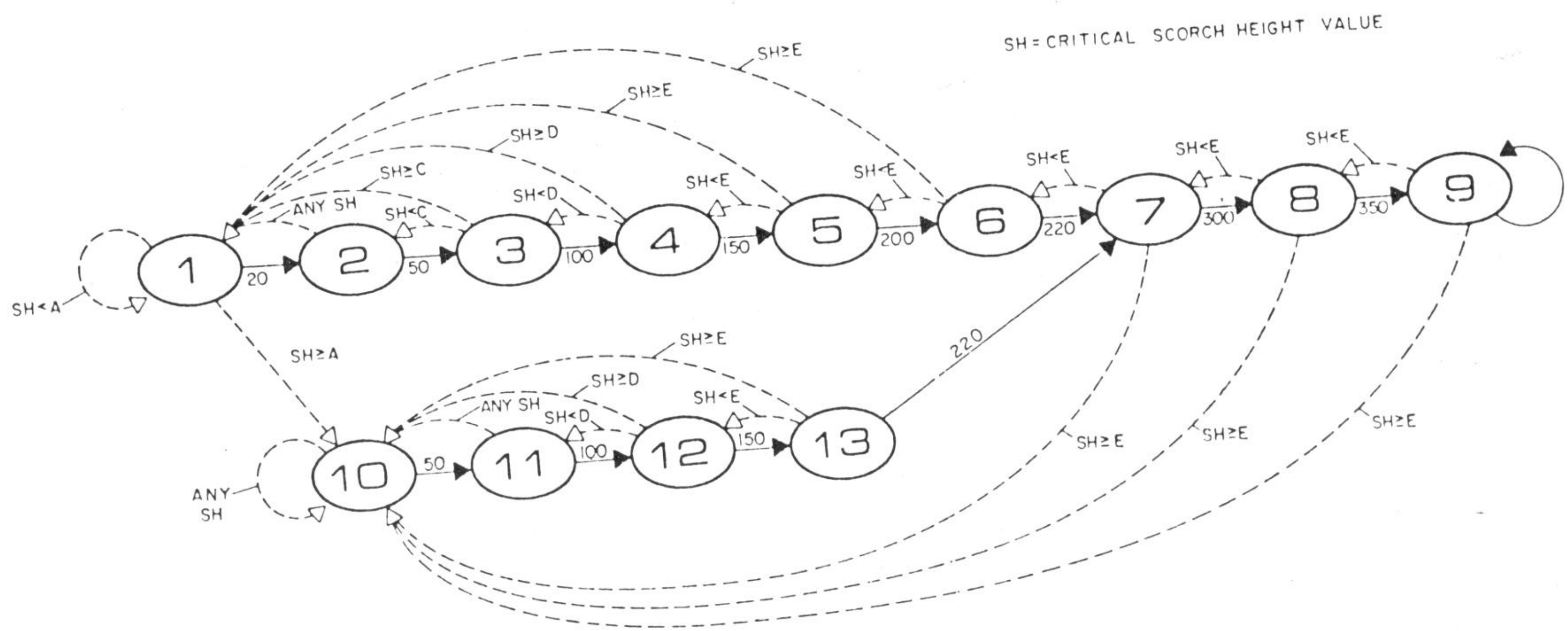


Figure 6. The full floristic succession model for the nine Montana forest community types. Transitions in the absence of further disturbances are determined by stand ages (years) shown on the solid line segments; transitions due to further disturbances are a function of stand age and fire scorch height. The critical scorch height values are given in table 2, while sample species composition changes for each state are shown in table 1 for the Abies lasiocarpa / Vaccinium globulare type. (From Kessell and Potter 1980.)

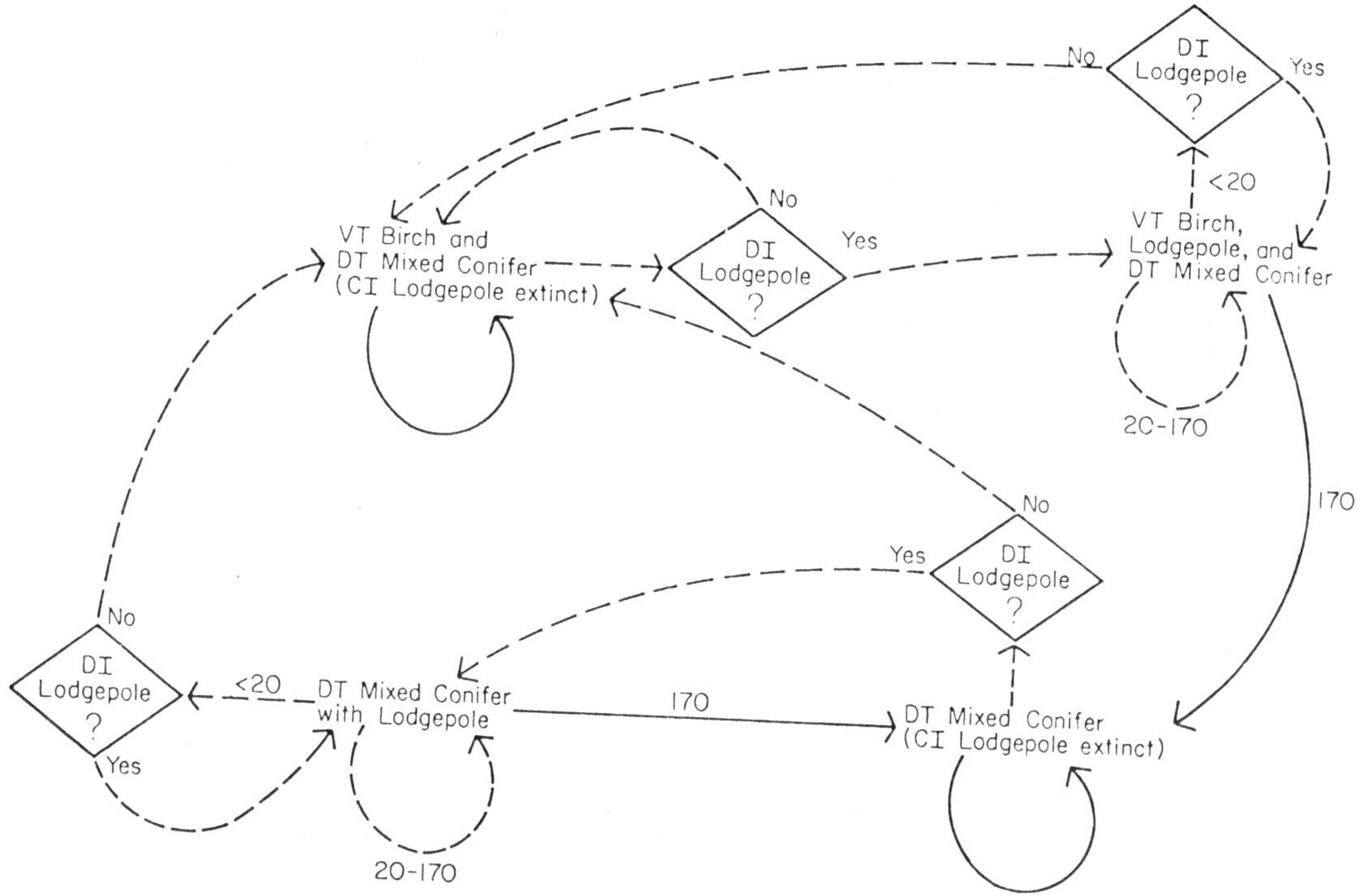


Figure 7. Succession model of a birch, lodgepole pine, and mixed conifer community in Glacier National Park shows several situations where lodgepole pine (Pinus contorta) is perpetuated only if it can establish as a DI species (from Cattelino et al. 1979).

The model was developed as a vehicle to integrate the results of several different research projects. Studies of seed crop production, seed dispersal, seed predation and mortality, and seedling survival were integrated to predict postdisturbance seedling densities over a five-year period. A stochastic model was developed; it uses several Monte Carlo methods in the placement of seed source trees, determination of cone crops, and determination of predation factors.

Seed trees are randomly located to preselected densities for each species. Stochastic variations in cone crops, and thus seed crops, are modeled using available research data (see Potter et al. 1980 for details). Seeds are dispersed primarily by thermal upslope winds using a dispersal equation developed from empirical data. Predation factors, again from empirical data, diminish these totals; microsite variations are added stochastically. Surviving seedlings are then predicted by applying literature values of seed to seedling ratios to the dispersed seeds remaining after predation. The result is the first-year seedling densities. Survival over a five-year period is then predicted using published mortality curves.

Further details are available from Potter et al. (1980). A single test of this preliminary model (comparing predicted and observed seedling densities in a five-year-old clearcut in the Lewis and Clark National Forest) showed generally good agreement; obviously further development and testing are desirable. It is hoped that continued development of this type of dispersal and seedling-establishment model will allow us to attach probabilities to seedling establishment, and thus the successional responses, of the species being modeled.

Linkage with the Mosaic and Animals Model

The development of this component was prompted by the desire to include birds and mammals in the succession models, and the desire to model disturbance effects on entire landscape mosaics rather than just within single homogeneous communities. The model has been described in detail by Potter and Kessell (1980); a brief overview will be given here.

The model uses as input a grid of user-defined size and resolution; for each grid element, the community type and stand age are recorded. For example, a user in the Lewis and Clark National Forest might wish to model the 256-ha area shown in figure 8. On the left of figure 8, the distribution of six major habitat (community) types over this area are shown; on the right, the area's fire history is shown. The user selects the desired grid size for input to the model; in this example, a 200 m x 200 m (4 ha) grid was chosen. This produces an 8 x 8 matrix of community types and stand ages which approximates the original mosaic, as shown in figure 9; a better approximation is obtained by using smaller grid elements.

The model includes an algorithm which "recaptures" the number and size of "patches" in the mosaic, where a single patch is defined as a

Figure 8. Community type map and fire history for 256-ha sample area. The community type map is on the left; digital type codes are 142 = Pinus ponderosa / Festuca idahoensis, Festuca scabrella phase; 281 = Pseudotsuga menziesii / Vaccinium globulare, Vaccinium globulare phase; 313 = Pseudotsuga menziesii / Symphoricarpos albus, Symphoricarpos albus phase; 720 = Abies lasiocarpa / Vaccinium globulare; 732 = Abies lasiocarpa / Vaccinium scoparium, Vaccinium scoparium phase; 820 = Abies lasiocarpa - Pinus albicaulis / Vaccinium scoparium. The fire history by stand age classes for the same area is on the right; age classes are 1 = less than 2 years since overstory fire; 2 = 2-10 years since overstory fire; 3 = 11-39 years since overstory fire; 4 = 40-79 years since overstory fire; 5 = 80 - 159 years since overstory fire; and 6 = more than 159 years since overstory fire. (From Potter and Kessell 1980.)

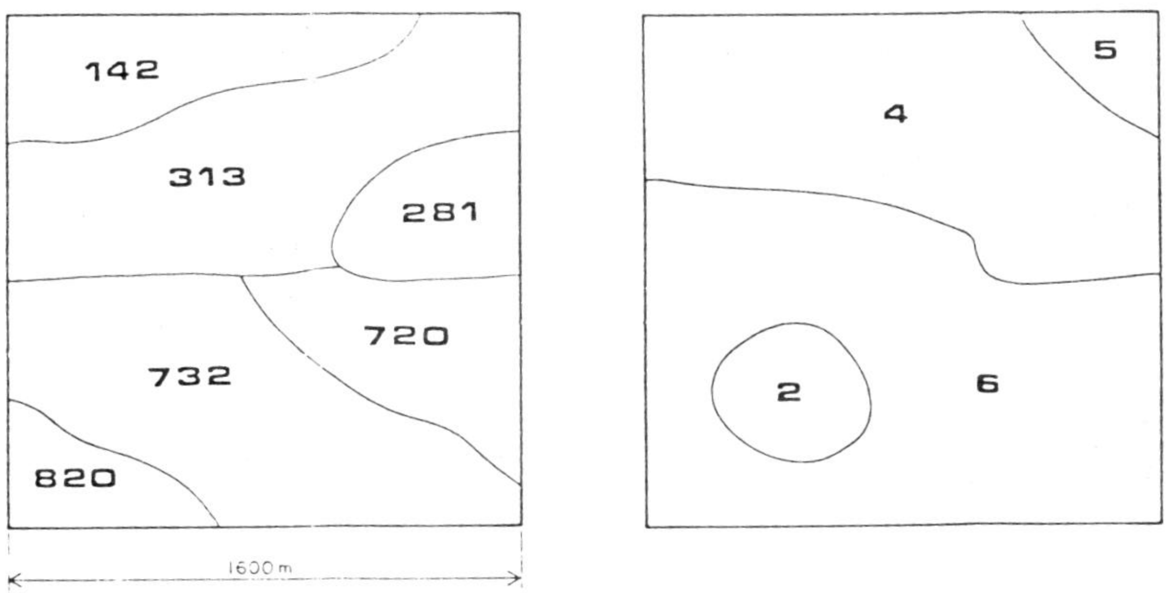
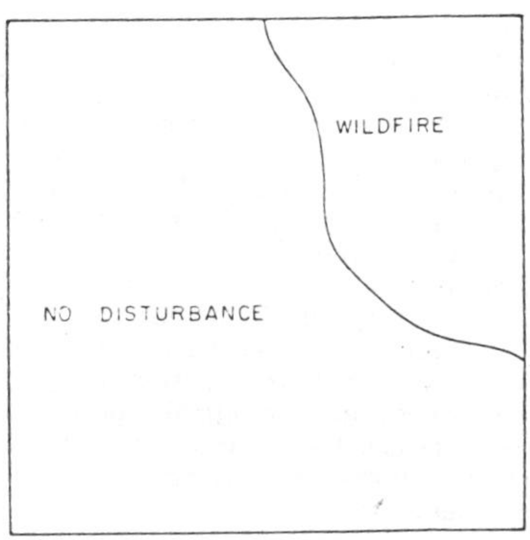


Figure 9. The digital matrix of community type and stand age produced when the area shown in figure 8 is coded on a 4-ha grid. (From Potter and Kessell 1980.)

	1	2	3	4	5	6	7	8
1	142 4	142 4	142 4	142 4	142 4	142 4	313 5	313 5
2	142 4	142 4	313 4	313 4	313 4	313 4	313 4	313 5
3	313 4	313 4	313 4	313 4	313 4	313 4	281 4	281 4
4	313 6	313 6	313 6	313 6	313 6	281 4	281 4	281 4
5	732 6	732 6	732 6	732 6	720 6	720 6	720 6	720 6
6	732 6	732 2	732 2	732 6	732 6	720 6	720 6	720 6
7	820 6	732 2	732 2	732 6	732 6	732 6	732 6	720 6
8	820 6	820 6	820 6	732 6	732 6	732 6	732 6	732 6

Figure 10. The area of a potential wildfire to be simulated with the mosaic model. Community types and stand ages are shown in figure 8. (From Potter and Kessell 1980).



contiguous area of the same community type and stand age class. Diversity algorithms compute the mosaic diversity using standard measures; the area of each patch is its importance value for diversity calculations. The model also includes a data base which relates the habitat utilization of all terrestrial birds and mammals to community type and stand age class; this work adapted the recent work of Thomas et al. (1977) in Oregon to the local Montana national forests. Utilizing these data, the model calculates the mosaic diversity of birds' and mammals' habitat utilization for both feeding and reproduction; each species' importance value is the total area where its feeding or reproduction habitat utilization, respectively, is scored either moderate or high.

The manager can also simulate the changes in mosaic diversity and in animal diversity which result from disturbances such as fire. Suppose a manager wants to know the short- and long-term effects of burning the area shown in figure 10. He states the location of the fire; the program resets the stand ages in this area to zero and recomputes the mosaic and animal diversity. He can also simulate these diversity values at future specified times; all stand ages are simply advanced the required number of years and diversity is recalculated. Table 3 shows the results of this simulation. The area shown in figure 10 was burned, and the diversity of the mosaic, bird feeding habitat, bird reproduction habitat, mammal feeding habitat, and mammal reproduction habitat were computed for the preburn state, the immediate postfire communities, the 10-year postfire communities, and the 50-year postfire communities.

The model also allows mapping, by both feeding and reproductive habitat utilization, of any nominated species; habitat utilization is mapped as low (L), moderate (M), or high (H). Figure 11 shows the effects on mule deer and black bear habitat utilization of the fire described above (in figure 10). Note that immediately after a fire, both species lose reproductive habitat but gain feeding habitat. After 10 years, bear reproductive habitat is nearly back to preburn levels, and deer reproductive habitat has been improved over preburn levels. Feeding habitat for both species has also been improved. After 50 years, the general situation for these two species is similar to the preburn conditions.

It is not yet possible to fully link the mosaic model with the succession models described above because of a present lack of succession data for all major plant species in the area's range of communities. Currently the mosaic model can handle any community type or bird or mammal species found in the Lewis and Clark National Forest, while our best succession model represents only seven of the major vegetation types. However, such a linkage should be possible in the future when more detailed successional information for a wider range of communities becomes available. We also think the mosaic model will serve as a useful vehicle for integrating the effects of disturbance size and shape, and that it could prove especially valuable for determining fire effects on animals which utilize ecotones or other ecological boundaries. Its ability to map mosaics, bird species, mammal species, and ultimately plant species, as well as their diversity, under any proposed fire regime should make it very useful to forest managers.

Figure 11. Computer-generated maps of potential feeding and reproductive habitat utilization by mule deer and black bears show the effects of the wildfire mapped in figure 10. The three levels of habitat preference are L (low), M (moderate), and H (high). The mosaic model provides such maps for any terrestrial bird or mammal species in Lewis and Clark National Forest. (From Potter and Kessell 1980.)

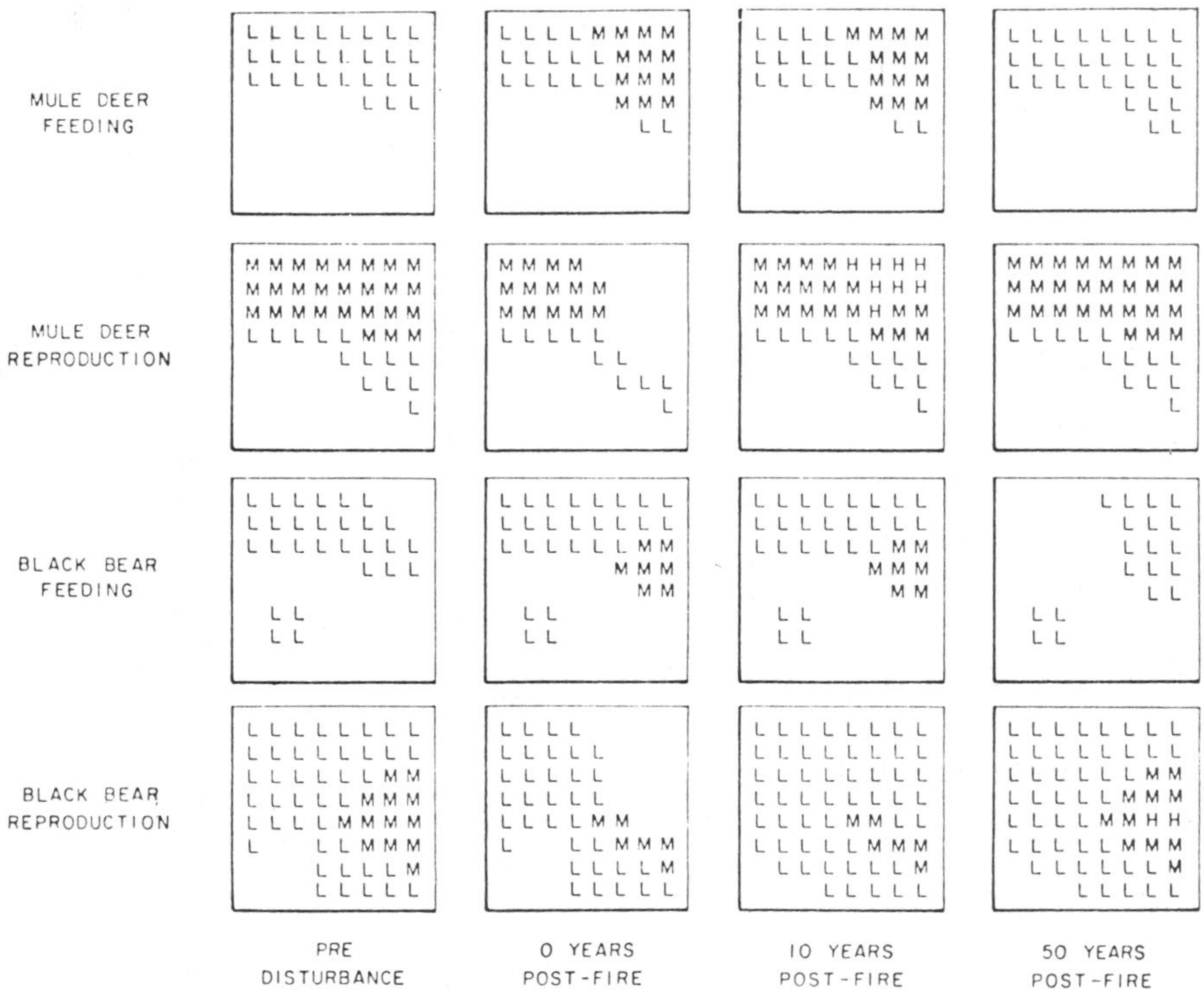


Table 3. Diversity of the habitat (community) type. Diversity measures are H' (Shannon-Weaver information index), e to the H' (base of natural logarithms raised to the H' power), C (Simpson index), and 1/C (reciprocal Simpson index). (From Potter and Kessell 1980.)

	Predisturbance community	0 years postfire	10 years postfire	50 years postfire
Community Mosaic				
H'	2.06	2.23	2.23	2.23
e to the H'	7.83	9.34	9.34	9.34
C	0.146	0.126	0.126	0.126
1/C	6.87	7.91	7.91	7.91
Bird Feeding				
H'	5.18	5.18	5.47	5.31
e to the H'	177.	178.	237.	203.
C	0.006	0.006	0.005	0.006
1/C	161.	158.	209.	176.
Bird Reproduction				
H'	4.65	4.75	5.02	4.75
e to the H'	104.	116.	151.	116.
C	0.010	0.010	0.007	0.010
1/C	95.7	103.	135.	102.
Mammal Feeding				
H'	4.09	5.62	5.46	5.31
e to the H'	59.7	276.	236.	202.
C	0.019	0.004	0.005	0.006
1/C	53.9	240.	208.	174.
Mammal Reproduction				
H'	4.77	4.74	5.00	4.73
e to the H'	118.	115.	148.	113.
C	0.009	0.010	0.008	0.010
1/C	106.	99.8	128.	97.1

DISCUSSION

Despite the significant recent advances in our understanding of succession, there is still a great deal of work to be done before we can fully utilize succession models for widespread land management decision-making. One problem is that good succession models and data bases are simply not yet available for most of these areas. Most efforts reported at this symposium have been conducted in areas of small geographic extent for which a good data base was already available or was consturcted during the study. Application to new areas is certainly possible using existing and tested models, but this can not be accomplished without the collection of new data for local calibration, fine-tuning, and validation.

Another problem is our inadequate understanding of the characteristics, adaptations, and interactions of many species populations. Much progress has been made in this area recently; much more remains to be done. Too many models must estimate, extrapolate, or simply guess these parameters. Another related problem is modeling the compound effects of disturbance intensity, periodicity, and frequency. Australian land managers ask "But what will happen in the long-term if we prescribe for this community a mild fire every five years?"; and we have no reliable answer.

I also think we must go beyond modeling vegetation and animals per se. Recent work has included predicting the succession of flammable fuels and has proved very useful in fire management decision-making; this paper also reviewed an attempt to deal with entire landscape mosaics and not just single communities. However, we have not yet dealt effectively with succession modeling at an ecosystem level; and long-term effects on watershed quality, productivity, and nutrient pools and cycles are not well understood.

Another important and frequently overlooked problem is the need to provide new tools and models to managers in a readily usable form. One good approach has been the development of integrated resource management planning languages and simulators; these computer-based systems place numerous models and data bases at the manager's fingertips. Yet not all managers and agencies have ready access to digital computers and integrated systems. This places additional burdens on the researcher to also provide results in the form of guidelines and other media which can be applied in a noncomputer environment.

I expect the development, implementation, and application of tools for ecologically oriented land management will dominate environmental research for the next decade. A significant portion of this work will be concerned with selecting alternative management approaches to disturbance, especially fire, grazing, insect outbreaks, and timber harvest. I expect significant advances in four areas.

The first area is the application of existing tools and understanding to new geographic areas; many, many parks, reserves, and forests can greatly improve their ability to manage disturbances by applying the available technology.

The second area will be the continued improvement of our understanding of succession and the resulting improvement in our models and methods. One development in this area will be a greatly improved understanding of species adaptations; I expect to see more catalogs of species characteristics and the development of "successional taxonomies." Another will be better models that isolate critical inputs and threshold values; models that currently require 25 inputs per species may be streamlined to require only a fraction of this number. An important part of this process should be the joint determination by researchers and managers of precisely how much resolution and accuracy is required for land management decision-making.

A third area of progress will be the development of models which describe the multiple ramifications of management actions. Managers will be asking questions such as:

What is the role of dead material in providing future plant nutrition?

How do disturbances affect nutrient budgets, cycles, and stores?

How are special critical habitats such as logs and snags degraded by new management practices?

We will also need to pay close attention to the interactions of different kinds of disturbances. How should we revise our fire management plans when faced with an unexpected insect outbreak?

The fourth and last area is one where I anticipate some especially exciting progress; it is the increased development and refinement of large computer-based systems which will provide managers with instant access to a range of comprehensive data bases and models. The recent implementation of such systems in North America and Australia has demonstrated their utility to and acceptance by managers. New advances in both software and hardware are occurring at an incredible rate and offer real promise for major advances in this area.

In conclusion, I have attempted in this paper to present my views on the succession modeling needs of land managers, views that have rapidly evolved as I have become more and more involved in land mangement research. I have also attempted to review some recent developments which in my opinion demonstrate a useful approach to meeting managerial needs. Much good work has been done in the last decade, and a great deal more remains to be done in the next. It should be an exciting time.

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SOME ASPECTS OF TERRITORIAL ORGANIZATION OF BIOSPHERE RESERVES AND THEIR ROLE IN ECOLOGICAL MONITORING

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The program to create a global network of biosphere reserves, that is, natural territories representing characteristic samples of Earth biomes, was aimed at conserving all the inherent diversity of ecosystems, species, and genetic resources, and at systematically collecting long-term observations of the main characteristics of the environment and the condition of its natural components. It was intended that the main attention should be on undisturbed climax zonal formations in order to characterize the condition of the selected section of the biosphere at the natural or background level and to find out global changes of these formations.

Such ecological monitoring has inherent significance in evaluating the condition of the region's natural resources. In addition, this ecological monitoring is necessary as a specific reference point while estimating the character and degree of ecosystem changes under different kinds and degrees of human impact. This implies activities related both to the pollution of the environment and destruction of ecosystems as well as to their clearing, restoration, recultivation, and increase in productivity.

The specific character of a biosphere reserve is determined either by the presence of a natural zone of sufficient size that natural systems of ecological integrity can be conserved, or by the fact that the natural conditions of the complexes in this zone are self-regulating. The primary functions of territorial elements of a biosphere reserve are to protect the natural zone from human alterations and to support the restoration of damaged portions of the ecosystem. If there is no natural zone in a biosphere reserve and if there are no ways to reestablish its natural condition, then the basic task of obtaining background information on the condition of the biosphere reserve can not be adequately carried out.

These comments indicate the necessity of identifying three main zones, or territorial/structural elements, in a biosphere reserve: natural, buffer, and restoration. Scientific research and, especially, ecological monitoring are carried out in all zones of a biosphere reserve; a prohibition on the collecting of such scientific information would contradict the main purpose for establishing biosphere reserves. The methods of scientific observation in a natural zone must, of course, exclude any disturbances to the course of natural processes or at least prevent disturbances to the maximum extent possible. That is why the conducting of experimental studies in the natural zone is unacceptable, even if it reduces the value of the studies.

The buffer zone surrounding the natural zone must absorb human impacts and thus protect the main part of the reserve. The size and management regime of the buffer zone depends on the size and condition of the natural zone and also on the intensity of human activities in surrounding areas. Monitoring in the buffer zone yields information about the condition of the natural ecosystems, which are exposed to gradually decreasing amounts of human impact.

The restoration zone of a natural ecosystem is composed of ecosystems whose naturalness has been disturbed but not destroyed by man and which can be restored to their original condition with human assistance. The proportion of such areas is different for different biosphere reserves. In some reserves there are almost no disturbed areas; in others they comprise a significant portion of the whole territory. Restorable ecosystems include forests which were previously marked for wood cutting and areas where populations of animals are abnormal in numbers, structure, and behavior. Monitoring in areas of restoration enables us to characterize the processes of restoration of natural conditions and to evaluate ongoing changes in the concerned ecosystems.

In comparing natural and seminatural ecosystems with man-made ecosystems, specifically those that exist in artificial landscapes and are actively transformed as a result of efforts to intensify production, studies of the intermediate characteristics found in the same ecosystems under conditions of a stable or traditional form of utilization can be very useful. These ecosystems may be agricultural lands (fields with vegetation), forests, or lands used for hunting or fishing. It is clear that areas which are not utilized under present conditions may be left solely for research studies of the biosphere reserve. Ecosystem monitoring in this zone characterizes a transitional and historical condition. The data are of great importance, however, in reconstructing the complete series from natural systems to modern man-made cultural systems.

A single uniform list of measured parameters is set for monitoring in all zones of a biosphere reserve. Species which are sensitive and which biologically concentrate materials can serve as indicators of ecosystem conditions. Such species are the first selected for observation. The selecting of parameters which are measurable with sufficient reliance, or at least with quantatively estimated errors of observation, is one of the most complex tasks in biological monitoring. This is the problem of monitoring very dynamic and unstable objects which are in different communities and under different ecological conditions. All this is related to the methodology for distributing experimental (stationary) sites for observations, carrying out the repeated, parallel observations, and selecting sites sufficiently representative with regard to the territory of the biosphere reserve and to the whole region.

Experience shows that extrapolating average data, obtained without necessary replication from small areas, faces serious, and in some cases, insuperable difficulties in reliability evaluation when applied to the large territory. Consequently, uniform methodology in collecting quantitative data is critical so that reliable indices of variation over time can be obtained. It is probably preferable to limit the number of fixed indices but to increase the number of experimental sites and frequency of observations.

Ecological monitoring can be adequately arranged only under unified management of all zones of the biosphere reserve as a total territory. It is difficult to present in a single global system all different types of biosphere reserves ("united," "concentrated," "non-complete," etc.), and it is very difficult to compare the data from monitoring a conglomeration of reserves which are managed and supervised by different agencies.

There is no doubt that biosphere reserves need to be established in regions that lack unaltered natural systems and that represent technological landscapes and biomes in order to conserve genetic diversity and to provide monitoring sites, but such reserves should be separated from natural biosphere reserves. Cultural ecosystems, created by man for benefits under maximum utilization, may exist in the region. Usually these areas have their own concerns, such as changes of cultivated species, forest cutting and planting, and use of fertilizers and pesticides. The importance of cultural areas, along with methods of their management and monitoring orientation, is that they have their own peculiarities which must be defined without equating their regime and monitoring with natural zones or biosphere reserves.

These differences make it quite reasonable to create a category of biosphere research stations along with biosphere reserves. These stations could coordinate monitoring of the reserve territory with monitoring of the territories exposed to intensive and thus nonstable use regimes which are defined by economic technological levels. A system of such biosphere stations is now being established in the Soviet Union. It includes independently operating biosphere reserves with their specific tasks, territorial structure, and unified management, and also experimental research sites established on intensively used lands.

So that all major biomes in the U.S.S.R. are represented by biosphere reserves, it is proposed to further develop a network of biosphere reserves and research stations on the basis of existing reserves: Astrakhanskiy, Burguzinskiy, Voronezhskiy, Darvinskiy, Okskiy, Tchernomorskiy, Slitere, Aksu-Djabagly, Karpatskiy, Altaiskiy, Badhizskiy, Tchentralno-Lesnoy, Zakatalskiy, Bordjomskiy, and others.

INITIATING A PROGRAM OF LONG-TERM ECOLOGICAL RESEARCH

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Abstract

Answers to many ecological questions depend on long-term data, and the National Science Foundation is initiating a 10-year program for ecological research. Contributors--research scientists, research institutions, the lead agency, and cooperating agencies--must be able to make predictable long-term commitments of personnel, funds, and physical resources to this program, and they must be coordinated to make the effort successful. Effective planning depends on optimizing communication among contributors. Communication is the primary constraint upon program initiation. Many past and current efforts have contributed to the research initiative. Perceived problems center upon the unpredictability of the collaborative, cooperative, and comparative arrangements necessary for this system to function in a network fashion.

INTRODUCTION

It has long been asserted that the answers to many ecological questions can best be derived from data accumulated over an extended period of time. Many such questions depend upon variables which change either slowly, or by significant quanta at infrequent or irregular intervals. The experiences of the U.S. International Biological Program served to corroborate this assertion. Current environmental issues such as global carbon dioxide, acid precipitation, and production of adequate foods further emphasize the acute requirement for long-term ecological data.

The objectives of long-term ecological research projects are multifaceted and cannot be conveniently categorized as basic, problem-oriented, or applied. The degree of overlap and complementarity is too great. Besides, such adjectives really apply to the motivations for research and not to its execution. The fundamental requirements for all such projects are essentially the same. They center upon the continuity of research resources and professional scientific effort over extended time periods.

The constraints operating upon this long-term initiative act upon the scientists, their research institutions, and funding agencies. The following considerations represent major difficulties for all parties:

> Research projects must be planned and those plans communicated coherently.
>
> Project proposals must be reviewed and evaluated in a competitive fashion and based upon peer input.
>
> The most meritorious proposals must be funded in a way which will demonstrate a good faith commitment to long-term continuity.

Different aspects of these considerations must be addressed by scientists, officials of research institutions, and funding agency administrators.

What follows is an analysis of several themes which underlie the initiation of this research effort. The themes include the following:

> Motivation - What do the participants want?
>
> Planning - How can the progression from concept to operation be scheduled?
>
> Contributing Factors - What past and current resources, or events, have served as antecedents for the new effort?
>
> Constraints - What are the relatively uncontrollable influences acting in the process?
>
> Shortcomings - What are the already perceivable faults in the initiative?

MOTIVATION

A meaningful analysis of the objectives for such a program can be performed by assessing the requirements of contributors (both individual and institutional) to the program. Scientists are interested in elucidating questions of a long-term ecological nature with respect to specific ecosystems. Research institutions seek to develop their resources for the performance of research. Sponsoring agencies wish to advance this method of fostering scientific inquiry. Cooperating agencies (e.g., titleholders of appropriate physical sites, employers of potentially contributive personnel, or vendors and users of products), by one associative means or another, desire to add to and receive from the effort. In addition to achieving their primary objectives, each of these contributors is motivated by fiscal considerations and by the prospect of success and recognition.

Each contributor possesses an agenda of requirements upon which its participation is contingent. Scientists and their institutions require money. They require not just money alone but also some form of warranty that predictable supplies of money will be available over sufficient periods to justify their initial investments and commitments. The sponsoring agency, and also cooperating agencies, are required to demonstrate that their resources are used effectively. Fundamentally, these requirements all reduce to mutual needs for predictable long-term commitments of personnel, funds, and physical resources. Each contributor must approach planning for those commitments from a different angle, yet they must be willing to communicate frequently and openly so that all the parts mesh and the effort can move forward.

PLANNING

One may get an idea of the planning process that is involved in any research effort from development of the National Science Foundation's long-term ecological research effort. The description below comprises several stages of development that have been discernible:

> Stage 1. An indefinte period during which an idea was generated or a need was realized. It was a low-key interactive period involving the research community, potential cooperators, and the sponsoring agency. By the time this stage neared completion, the interaction had changed and the origination of the idea was not attributable to any single source.
>
> Stage 2: A short period during which the basic, but unrefined, concept was accepted by the sponsor as a planning item and the first formal interaction with the research and user communities took place. The output was a report from the community to the sponsor (Botkin 1977).

Stage 3: A longer period during which the concept was refined. The research community participated actively in the refinement and identification of conceptual and methodological problems. During this period forces were generated within the community and within the sponsoring agency which tried to redirect the effort, change its emphasis, subdivide it, or kill it. Other formal reports (Botkin 1978, TIE 1979) were generated, along with preliminary versions of implementation documents.

Stage 4: A period which often paralleled stage 3. This period was one of extensive interaction among all contributing parties and might be characterized as the "recognition of the bandwagon." By the time it was concluded, the majority of enduring relationships between the primary sponsor and cooperating agencies were confirmed. It was also a period during which antecedents of the new initiative were recognized and perhaps incorporated into the new concept (TIE 1977).

Stage 5: A period during which the primary sponsor made a formal commitment to the effort. The result was an announcement of the commitment to the research community (NSF 1979). Further fiscal planning took place in the sponsoring agency, leading to clarification of its intentions regarding the effort and the development of contingency positions.

Stage 6: A period during which the research community prepared formal research proposals and submitted them to the sponsoring agency. This was when the research community formally allied itself with cooperating agencies (especially landholders and employers of collaborative personnel). At the same time the research institutions were forced to initiate or update and reaffirm collaborative ties with cooperating agencies in order to arrive at administrative agreements satisfactory to all parties. Concomitant with the proposal preparation exercise by the research community, the sponsoring agency decided upon the specific review mechanisms for evaluation of the resultant proposals.

Description of further events is purely conjectural since our experience does not extend byond stage 6. Additional remarks are limited to some anticipated events and outcomes.

Stage 7: Proposals are evaluated by peers.

Stage 8: Further information is solicited regarding top-rated proposals.

Stage 9: Awards are made and work initiated by the first subset of awardees.

Beyond this anticipatable progression, the intentions of the National Science Foundation as a sponsoring agency lie in the following directions:

continuing initiation of new projects for a number of years as funds allow

promoting the concept of a network interaction among operating sites

continuing the effort for approximately a 10-year experimental period

evaluating the accomplishments of the effort at the end of the experimental period

CONTRIBUTING FACTORS

When anyone or any organization embarks on a new effort, it is quickly discovered that nothing is entirely new. As previously mentioned, antecedents of the research initiative were identified in stage 4, and many contributors significantly affected the development of the National Science Foundation's long-term research concept.

In my view, the most important antecedent for the long-term research project has been the fact that large tracts of land, representing a broad diversity of ecosystem types, have been set aside in the United States.

Some of these are specifically dedicated to research purposes, and most of them are amenable to the performance of research. The titleholders to these lands are distributed over all levels of government, the private sector, and academic institutions. The existence of the land base has been one of the strongest reasons for the effort.

The Man and the Biosphere Program (MAB) has been a significant antecedent. Stemming in large part from the International Biological Program, MAB has served effectively to focus attention upon the value of biosphere reserves. Other MAB topics have served to reinforce the international need for long-term environmental data sets. The experimental ecological reserve studies, sponsored by the National Science Foundation and still ongoing, comprise a core of criteria to be applied to the selection of sites for long-term studies. The National Atmospheric Deposition Program, administered by the U.S. Department of Agriculture, has provided a device upon which to center the necessary meteorological measurements for long-term research sites. There are undoubtedly other antecedents, but these provide sufficient examples.

Other contributing factors to the foundation's effort need to be recognized. The research community in its attitudes and responsiveness is foremost. Community interest and receptiveness has been very high since the first formal efforts began. Their participation in a series of three workshops provided the major guidance for subsequent developments. They identified the need for and insisted that the foundation provide an aegis for support of individual long-term research pursuits as well as for larger site studies. They emphasized the requirement that even site-centered studies be focused upon real and tenable long-term research questions in order to prevent their becoming simply descriptive.

CONSTRAINTS

In addressing constraints I have chosen not to focus upon obstacles such as selling the concept to top administrators and securing funding, but upon factors which often serve as noise generators within the system. In a communications sense, noise is a disturbance which interferes with or prevents the reception of information.

In the opening section of this presentation, three specific communication junctions were cited: preparing a proposal, evaluating proposals competitively, and making awards which connote long-term continuity of funding. There are other, perhaps equally important, junctions, but these three serve as an exemplary set because they are sequential and they involve all the collaborators.

In the first case, a scientist must take the initiative. He must simultaneously communicate effectively with cooperating agencies (often the landholders) regarding the extended dedication of a site to research and with his own institution regarding its extended commitment to the project. Likewise he must be able to assess and guide the collaborative efforts of other scientists from his own institution and possibly from cooperating agencies. The result should be a proposal which states the project's scientific objectives and demonstrates how all the contributors will work in concert to achieve those objectives.

In the second case, a manager within the sponsoring agency must take the initiative. He must devise, from a limited number of options, a proposal evaluation regime which will rely primarily upon peer scientist input, be fair to all proposers, and identify the best proposals from among the total available set. To do so he must make evaluation criteria clear to reviewers as well as proposers and be able to demonstrate the reasonableness of those criteria while making them rigorous enough to separate proposals into qualitative subsets.

In the final case, the sponsoring agency, both through its managers and through its public communication outlets, must demonstrate to the communities of scientists, research institutions, and cooperating agencies that it is willing to make good on its promise to give the overall effort a fair trial by providing adequate money and time for the experiment.

We are now about to embark upon the first true test of the effectiveness of all these critical communication links. The result will undoubtedly be instructive.

SHORTCOMINGS

It is too early in the initiation of this long-term research effort to enumerate all the faults. However, a number of problems are already apparent, including the following:

Time is always insufficient for all parties concerned. The necessity of choosing between doing something substantial or doing nothing at all often characterizes the official start of such efforts.

Standardization and comparability of sampling protocols, analytical methods, data management techniques, and reporting requirements among those sites to be funded have not been effectively dealt with.

The site network concept itself is still open to question, especially with respect to the degree of integration and the form it should take.

Extensive use of data by parties other than those directly involved in site operation will continue to be problematical. A favorable outcome will depend upon data reliability, comparability, and the information requirements of many as yet unknown research questions and problems.

It is to be hoped that fundamental site characterization, extant data assemby and synthesis, and site-specific research questions will provide an early focus for the effort and provide the time necessary to come to grips with the more complex issues.

I would, however, be remiss in closing this section before stating and underscoring a problem which may be of paramount importance. It will be difficult, even unwise, for the National Science Foundation to attempt to underwrite this long-term research effort alone. An important measure of the success of the experiment will be the actual level of contribution made by other federal agencies to the operational costs of the exercise.

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FIELD PERTURBATION EXPERIMENTS:
AN ALTERNATE APPROACH TO THE
ASSESSMENT OF HUMAN EFFECTS
IN TERRESTRIAL ECOSYSTEMS

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Abstract

The National Environmental Policy Act of 1969 (NEPA) was initially interpreted as requiring full disclosure of the environmental impacts of a federal action. Because of the limitations of time, money, and manpower, the requirement that all impacts be considered has led to a superficial analysis of many important impacts. Data collection has largely been limited to the enumeration of species because this information can be applied to the analysis of any problem. The Council on Environmental Quality (CEQ) has provided a solution to this problem by reinterpreting NEPA as requiring analysis of those impacts which have significant bearing on decision-making. Because the assessment of resources can now be concentrated on a few critical issues, it should be possible to perform field perturbation experiments to provide direct evidence of the effects of a specific mixture of pollutants or physical disturbances on the specific receiving ecosystem. Techniques are described for field simulation of gaseous and particulate air pollution, soil pollutants, disturbance of the earth's surface, and disturbance of wildlife. These techniques are discussed in terms of their realism, cost, and the restrictions which they place on the measurement of ecological parameters. Development and use of these field perturbation techniques should greatly improve the accuracy of predictive assessments and further our understanding of ecosystem processes.

INTRODUCTION

The terrestrial ecological information contained in environmental impact statements and assessments has largely been limited to species lists, irregularly supplemented by indications of distribution and relative abundance. This information contributes little to the analysis of terrestrial ecological impacts because the responses of natural species to any specific anthropogenic stress are extremely limited. Extrapolations from studies of other species are difficult because taxonomic similarity does not imply similar sensitivity. This difficulty is compounded by a variation in sensitivity due to a variety of environmental factors, including soil, climate, and population parameters. In addition, toxicants, noise, and other perturbations occur as mixtures which may produce synergistic and antagonistic responses. The number of combinations of species, environmental conditions, and toxicant mixtures is so large as to overwhelm the resources of traditional laboratory toxicology. Because these problems prevent assessment of impacts at the level of the individual organism, the assessment of effects at the population, community, and ecosystem levels (higher levels) from species lists are also precluded.

This dismal situation cannot be remedied by simply collecting more and better data concerning population and community level properties of the proposed receiving systems. Theories predicting population, community, and ecosystem level responses to perturbations such as the diversity-stability hypothesis are either currently discounted or are too vague or poorly supported to serve as assessment tools. Ecosystem simulation models provide tools for extrapolating proximate responses but cannot predict those responses.

The result of this incapacity is that genuinely predictive assessment of terrestrial ecological effects has been limited to actual acts of destruction. These include complete destruction of natural systems as in right-of-way management and destruction of individual organisms, in hunting, or in selective timber harvesting. Even these assessments are typically limited to the level of ecological organization directly affected. Assessments of hunting generally do not consider community level effects. Assessments of right-of-way management and other community manipulations do not consider ecosystem level effects such as energy and nutrient transfers between the managed and unmanaged communities. Assessments of construction projects seldom look beyond the local ecosystem that is destroyed to effects on hydrology or radiation balance.

Anthropogenic perturbations such as emissions of toxicants, water vapor, noise, and behavioral disturbance affect the rates of ecological processes. These effects are acknowledged in impact assessments but are seldom quantified. In the absence of information which permits even rough quantification of effects, assessors typically assume that there will be no significant effects if all legal requirements are met. This strategy often fails because the primary regulatory emphasis is on the protection of human health. This regulatory bent is demonstrated by the recent increase in the secondary ambient air quality standard for ozone to levels at which significant phytotoxic effects occur (Heagle et al. 1979b).

The logical and direct solution to the problem of assessing secondary effects and nonlethal primary effects is to perform experimental perturbations of the proposed receiving system. These would consist of either simulations of proposed perturbations such as the various field fumigation techniques or imposition of the actual perturbation on a small scale. This option has been largely precluded in the past by the judicial mandate to make impact statements "full disclosure documents." Only a species list can give the appearance of having considered all ecological components, thereby satisfying the requirement that all effects be disclosed.

The full disclosure problem is eliminated by the new NEPA regulations (CEQ 1978) which have the goal of "distinguishing the important from the trivial." This goal is to be accomplished through scoping, "an early and open process for determining the scope of issues to be addressed and for identifying the significant issues related to a proposed action." This emphasis on analysis of a limited number of highly important issues should permit resources to be concentrated on a few site-specific field experiments. This document will review a variety of field experimental techniques which are available, their relevance to energy technologies and the NEPA process, and their cost.

EXPERIMENTAL TECHNIQUES

This section considers techniques for the simulation of the major classes of terrestrial perturbation resulting from the development and conversion of energy resources. Techniques are considered in terms of their realism and adaptability for use in a wide range of ecosystem types.

Gaseous Air Pollutants

All of the early field fumigation systems were closed chambers resembling small greenhouses into which filtered or contaminated air was pumped. Closed chambers are poor simulators of natural conditions because they drastically alter radiation balance, temperature, humidity, precipitation, and access by insects and pathogens. Closed chambers are, however, still potentially useful for short fumigations. Small portable chambers can be placed over plants in the field and fumigated for a few hours using mobile equipment (Cocking 1973, Treshow and Stewart 1973, Hill et al. 1974). The plants or plots are marked and later examined for signs of response. Miller and Yoshiyama (1973) developed small closed chambers which are self-ventilating owing to convection through 2.4-m stacks. Because they are portable and self-operating, these chambers are suited to studies of ambient pollution at remote sites and could be adapted to delivery of air polluted by compressed gases. With some ingenuity, a closed chamber can be devised for almost any vegetation, including epiphytic lichens on tree trunks and branches (Anderson 1976).

Examination of chronic pollutant effects requires the use of more elaborate systems to avoid serious alteration of the plant's environment. There are two general types of systems currently available, open-top chambers and tube arrays. The most popular form of open-top chamber is the one developed by a cooperative program of the U.S. Environmental Protection Agency, U.S. Department of Agriculture, and North Carolina State University, referred to as the EPA-type chamber (Heagle et al. 1973). It consists of a cylindrical frame 2.4 m high and 3 m in diameter, covered with a clear flexible plastic film. The lower portion of the chamber is double walled and perforated on the inner wall, forming a plenum to dispense filtered, polluted, or ambient air. This air is delivered by a duct and fan from any of a variety of air treatment devices. A similar chamber was developed independently by the Boyce Thompson Institute for Plant Research (Mandl et al. 1973). The Boyce Thompson chamber consists of 2.74-m diameter hoops of rigid fiberglass stacked 1.22 m high. The air delivery plenum, which consists of perforated plastic tubing fastened around the chamber wall, can be raised as the canopy grows.

The first tube-type system was the zonal air pollution system (ZAPS) developed by the Corvallis Environmental Research Laboratory for the study of sulfur dioxide effects on rangelands (Lee and Lewis 1978). ZAPS consists of a half hectare array of perforated rigid plastic tubes suspended above the vegetation surface receiving compressed sulfur dioxide contaminated air. A 61-m buffer is provided between arrays to reduce cross contamination. Miller et al. (1977) have developed smaller versions of ZAPS which incorporate a number of refinements, including the ability to be raised along with canopy growth. The ZAPS system is not capable of delivering filtered air to exclude ambient pollutants, so it can be used to study the effect of air pollution increments but not background pollution.

The Tennessee Valley Authority has developed an air-exclusion system to study effects of power plant emissions on crops (Jones et al. 1977). The TVA system consists of perforated flexible plastic tubes which are laid on the ground between rows of crops and inflated with charcoal-filtered air when ambient sulfur dioxide concentrations reach a predetermined level. The inflated tubes fill the space between the rows, saturating the foliage with purified air, and then subside to the soil surface at the end of the pollution episode. This type of system could also be used to deliver polluted air.

A hybrid tube and chamber system was developed at the Lawrence Livermore Laboratory (LLL) and consists of rows of flexible plastic tubes like the TVA system that are surrounded by a low, rectangular, clear fiberglass wall that is 0.6 m x 7.5 m x 3 m (Shinn et al. 1977). The LLL system combines the even delivery of tube arrays with some reduction by the walls of wind interference.

Each of these field fumigation systems has peculiar advantages and disadvantages. Closed chambers are highly flexible in terms of the range of conditions to which they can be applied and are typically simple to build and easy to install and operate. Because they are closed, control of air quality is nearly absolute. Their major disadvantage is the large effect of the chamber on the physical characteristics of the test environment (chamber effect), which can significantly alter the susceptibility of the test organisms to stress. This characteristic limits their utility to studies of responses to brief, infrequent episodes of fumigation, such as those that result from the impact of a poorly dispersed plume with the ground.

Opening the top of fumigation chambers greatly diminishes chamber effect while a large measure of control is retained over the test atmosphere. Heagle et al. (1979a) performed extensive measurements on an EPA-type chamber which indicated that chamber effects were smaller than are believed necessary to affect pollutant sensitivity (0.56° - 0.86°C higher temperatures, 88% light transmission, 1.47-3.07 km/hr air speed, and no measurable change in relative humidity).

Reported performance of the original Boyce Thompson chamber is comparable (Mandl et al. 1973), but Kats et al. (1976) found light intensities of only 45%-75% of ambient in a Boyce Thompson type chamber. Heagle et al. (1979a) summarize seven years of experience with EPA-type chambers and indicate that chamber effect causes a slight but significant increase in plant height but it "rarely" affected yield. Howell et al. (1976), however, found significant reductions in soybean yield due to chamber effect. The major factor is probably the "rain shadow" created by the chamber walls, but this problem requires further study. A second technical problem with open-top chambers is the ingress of ambient air, particularly into filtered air chambers. This problem may be reduced by adding a simple baffle to the top of the chamber (Kats et al. 1976), but results have been inconsistent.

The ZAPS-type systems provide the least interference with natural conditions and the least control of dose. Because these systems are open, concentrations of the pollutant vary widely depending on wind speed, relative humidity, solar radiation, and temperature stability class (Lee et al. 1979). Coefficients of variation in sulfur dioxide concentrations at a central monitoring point averaged over entire seasons of continuous fumigation ranged from a low of 0.33 on a high fumigation rate plot up to 2.00 on a low rate plot (calculated from Lee et al. 1979). Although the geometric means of sulfur dioxide concentrations on the control plots are low (0.2-1.6 pphm), occasional high concentrations have resulted from winds carrying sulfur dioxide from the treatment plots. These problems are considerably reduced by fumigating only when the predominant wind direction is approximately perpendicular to the line of plots (Miller et al. 1977). While the variation in dose associated with ZAPS-type systems is probably too high for purposes of standards setting, it is not large relative to the variation in dose delivered by a real plume. The variation in response to climate factors may in fact make ZAPS a better simulator of plume effects than chambers which are either on a relatively constant dose or off. Miller et al. (1979) found that variation in sulfur dioxide concentration in their system during individual fumigation episodes was similar to variation observed during measurements near real point sources.

The TVA and LLL systems have a number of advantages for the study of low-growing row crops in terms of control of air delivery and little interference with natural conditions. However, because the delivery tubes lie on the ground, they cannot be adapted to natural vegetation, with the possible exception of desert shrublands.

Many questions concerning the relative performance of these field fumigation systems can only be resolved by side-by-side comparisons. Such comparisons have been planned by the EPA for the National Crop Loss Assessment Program. Meanwhile, numerous modifications of the basic chamber and tube designs can be made to improve their performance or adapt them to particular situations. Movable open-top chambers could be used like closed chambers for intermittent fumigations in order to minimize interference with natural conditions during, as well as between, fumigations. Low walls could be used with ZAPS-type systems to obtain the air control advantages of the LLL system in studies of natural systems. Chambers have been used to fumigate small individual trees or portions of trees, but the responses of a forest to fumigation have not been investigated. Howard Odum's (1970) forest respirometer demonstrated that even plots from a mature tropical forest can be enclosed in an open top chamber. ZAPS-type systems could be built in tiers to fumigate forest plots. It should be remembered that the variance associated with all of these fumigation systems is not large relative to the variance of most field ecological measurements, and the combined variance of perturbation and measured response is small relative to the uncertainty of any assessment of gaseous emissions not based on a field fumigation.

The discussion above suggests the importance of the temporal pattern of exposure to pollutants in designing an experimental fumigation system. Experiments must rely on atmospheric dispersion modeling to indicate realistic temporal and spatial patterns of pollutant concentration. This information must then be combined with knowledge of the biotic communities potentially exposed in order to determine which conditions must be simulated. More than one system type or mode of operation may be used if both near- and far-field effects are thought to be important or if structurally different plant communities must be tested.

Precipitation

Precipitation scavenges pollutants, including gases, aerosols, and particulates, from the atmosphere. Contaminated rainfall has been simulated in the field by using a variety of sprayer nozzles, irrigation sprinklers, and watering cans. A portable sprinkler system developed by Shriner et al. (1977) delivers realistic droplet size and intensity with uniform, reproducible rates of application to a 5.76 sq m area. Through the use of roofs which slide over the plots when a switch is wetted by rain, plots can be exposed to only artificial rain without modifying the physical environment.

Rain simulators have been used in combination with a ZAPS-type fumigation system (Irving and Miller 1977) and are being used with open-top chambers at Oak Ridge National Laboratory and the Boyce Thompson Institute to study the combined effects of acid rain and gaseous pollutants. Real rain could be collected and dispensed in order to generate three treatments equivalent to the filtered, ambient, and polluted air treatments. While acidity is the primary concern in rain experiments, it may be important to consider other rain contaminants, including rain entrained particles (Whitford 1968).

Atmospheric Particles

Atmospheric particles and aerosols are difficult to realistically generate, dispense, or control in experimental systems. Filtered open-top chambers exclude most particles, but the unnatural upward air movement in these chambers must result in unrealistic rates and patterns of deposition. Chamber effects make comparisons of filtered chambers with open plots questionable.

Particles larger than 5 m aerodynamic (resistance) diameter (D_a) settle relatively rapidly and may not be expected to settle approximately below the point of release in reasonably still conditions. Simulated fallout particles consisting of 44 to 88 μm particles were uniformly spread by a modified and motorized fertilizer spreader which ran on raised tracks (Dahlman et al. 1969, Witherspoon and Taylor 1970). Particles smaller than 5 μm D_a behave as aerosols and therefore travel farther from the point of release, whether a stack or a field dispenser. Laboratory systems for dispensing fine particles utilize the Wright dust feed mechanism (Wright 1950), which can be combined with cyclone separators to produce a stream of fine particles free from large, secondary aglomerations (Raabe et al. 1979). Such systems should be adaptable to field chambers. An alternate mechanism for dispensing aerosol particles in the field was recently developed by Battelle Columbus Laboratories (Van Voris and Toole 1979).

For preoperation experiments, sources of ash and similar particles other than dust must be pilot plants or plants similar to the one being assessed and using a similar fuel. Stack-emitted particles are best represented by particles collected from the stack. A system has been developed to collect kilogram quantities of size-fractionated particles from stacks (McFarland et al. 1977). An alternate strategy is to use material collected in electrostatic precipitators or bag houses. This material must be sorted because the fine particles which escape such systems have higher concentrations of organic and metallic compounds than the average of those that are retained. Raabe et al. (1979) describe a size classification system developed for this purpose. Particles may be modified to simulate the emissions from a new technology by absorbing substances onto the particle surface (Miguel et al. 1979). Completely synthetic aerosols can be generated from solutions fed through a vibrating orifice (Wedding and Stukel 1974). This approach is particularly useful for studies of sulfate aerosols and other aerosols which form from droplets in the atmosphere.

Soil Pollution

Energy development may result in the contamination of soil by a variety of nonairborne pollutants. These include spilled natural and synthetic fuels, pesticides and herbicides used on rights-of-way or biomass plantations, "land-formed" wastes, and leachates from wastes or stored solid fuels. All of these may be simulated by applying the contaminant directly to the soil/vegetation surface, but experimental designs are considerably complicated by considerations of dose, frequency, and collateral treatments such as tillage, fertilization, and revegetation.

Oil spills on land have received considerably less attention than spills on water. Most terrestrial oil spill research has been carried out in connection with Alaskan and Canadian oil pipelines (Deneke et al. 1975, Miller et al. 1977). These experiments have included the spraying and flooding of taiga and tundra vegetation and soil with relevant crude oils. Similar experiments concerning the fate and effects of various liquid fuels in other ecosystem types would aid assessment of technology and the development of clean-up protocols.

Most pesticide and herbicide studies have consisted of laboratory toxicity and degradation studies or the monitoring of actual commercial applications. Examples of controlled field experiments are described in the following references: Barrett 1968, Shure 1971, Robel et al. 1972, and Graf et al. 1976. These studies, like the oil spill studies, provide few technical problems for simulation of real perturbations. Grow et al. (1973) developed a truck-mounted sprayer which delivers accurate pesticide doses for field experiments.

Land-farming is the disposal of solid organic wastes by incorporation into the soil. Most of the waste which is suitable for such disposal is municipal sewage sludge or animal wastes, and most of the relevant field research has considered these materials (e.g., Loehr 1977, Kelling et al. 1977, Koterba et al. 1979, Sidle and Kardos 1977). Land-farming is also used for the disposal of sludges, filter cakes, waste oils, and other organic wastes derived from energy industries. Experiments to investigate the effects of waste oil disposal with tilling and fertilization have been conducted by Kincannon (1972) and Watts et al. (1978). The wide range of responses reported in the relatively voluminous literature on land disposal of fecal materials clearly demonstrates the need for site-specific and waste-specific experiments.

Nearly all studies of the leaching of solid wastes and the fate and effects of leachates have consisted of laboratory leaching experiments which provide material for laboratory studies of toxicity or simply monitor existing landfills. The need for preoperational experiments which are more realistic than laboratory leaching is becoming more widely recognized. Boegly (1979) and Skogerboe et al. (1979) are conducting leaching experiments in field lysimeters consisting of large containers which are loaded with waste and soil. A more direct approach is the filling of small trenches or single landfill cells with waste and the monitoring of leachate collected in wells or tension lysimeters. This small-scale demonstration approach is appropriate for site-specific studies in which case realism is more important than experimental flexibility. Ecological effects should be studied in the biotic communities established on the fill material, and in downslope communities which may be exposed to leachate.

Heat may be added to soils by a variety of energy-related technologies. The effects of a hot, buried, oil pipeline on arctic soil and vegetation were investigated at the University of Alaska's heated-pipe test facility (Scarborough and Flanagan 1973, McCown 1973). The feasibility and effects of using soil as a sink for power-plant waste heat and thereby decreasing water use and aquatic ecological perturbations while possibly increasing crop yields have been studied by Boersma et al. (1974), Allred et al. (1975), and Stanley et al. (1978). The use of buried high-voltage electrical transmission lines will also involve considerable soil heating or, in the case of superconductors, soil cooling. Soil heating can have significant effects on vegetation and the soil biota due to changes in evapotranspiration rates, growing season, soil freeze/thaw cycles, and the rates of microbial processes occurring in the soil.

Surface Disturbance

Because of the large body of theory and experience concerning terrestrial ecological succession, the effects of most surface disturbance are broadly predictable on the basis of a description of the preexisting community. However, disturbances which drastically alter the character of the substrate, such as disposal of mine, mill, or dredge spoils and tailings, can unpredictably alter the course of succession. Such novel substrates may require considerable management in order to establish a self-maintaining community and prevent excessive erosion.

Reclamation experiments present no great conceptual difficulties, and the technical difficulties have to do with obtaining substrate to test early in the decision-making process. Most reclamation experiments are simply attempts to establish vegetation on material which has proved resistant to standard revegetation techniques. As soon as sufficient disturbed substrate becomes available, proposed and alternate revegetation techniques should be compared for the stability of the vegetation produced and its ability to support wildlife or livestock. Such experiments may be modeled on standard agronomic field trial designs. The literature in reclamation research is too voluminous to summarize here except to recommend four symposium volumes (Shaller and Sutton 1978, Thames 1977, Wright 1978, and Vories 1976) and two bibliographies (Goodman and Bray 1975, and Bituminous Coal Research, Inc. 1975).

Less drastic disturbances may require investigation when the source of disturbance is novel such as air-cushioned vehicles or when the system affected is poorly understood such as tundra or desert. The best examples of studies of this type are the experiments conducted in connection with oil and gas development in the arctic. Investigations of the response of tundra vegetation to varying intensities of disturbance by different types of vehicles revealed responses ranging from promotion of plant growth to long-term scarring of the surface (Rickard and Brown 1974, and Challinor and Gersper 1975).

Wildlife Disturbance

Disturbance of wildlife can result in habitat abandonment, reproductive failure, or physiological stress because of arousal and flight. The severity of the responses to a particular activity depend on the importance of the habitat involved and the sensitivity of the particular organisms. Sensitivity varies greatly between populations of a species owing to differences in their history of human contact (Geist 1971). Disturbance simulations may simply consist of observations of the distance at which animals flee from an approaching human (Stalmaster and Newman 1978). Animals may be experimentally exposed to noisy equipment (Freddy et al. 1977), or noise-making devices may be utilized to simulate particular development activities (White and Thurow 1979). While flight distance is the parameter which is most easily obtained and interpreted, much more complete knowledge of effect can be obtained by observing physiological parameters such as heart rate or population parameters such as reproduction rate. Physiological responses can be monitored by radio-telemetry (Freddy et al. 1977, Ward et al. 1976).

RELATION OF FIELD EXPERIMENTS TO OTHER ACTIVITIES

Field experiments must be coordinated with other assessment activities. Before experiments can be planned, a preliminary field and literature survey must characterize the receiving system, the review of the project plans must identify potential sources of perturbation, and the scoping process must identify the important issues.

Results of field experiments must be available for the NEPA assessment. The time available prior to the assessment depends to a large extent on the policies of the federal and state agencies involved; the Nuclear Regulatory Commission, U.S. Department of Energy, and predecessor agencies have traditionally required a minimum of one year of field data. Some federal agencies have required two or more years of field data for specific projects or classes of projects in order to estimate year-to-year variance. The CEQ regulations (1978) encourage the setting of time limits on the NEPA process and include in the list of considerations the "state of the art in analytical techniques" and the "degree to which relevant information is known and if not known the time required for obtaining it." They require that any time limits be "consistent with the purposes of NEPA." Thus, field experiments should be planned to run for at least one year prior to the first assessment and should run longer if necessary to support choices between alternate designs or actions.

Field experiments should typically continue beyond this first assessment in order to elucidate chronic effects as early as possible in the course of development. Slips in development schedules are the rule rather than the exception, and they may permit considerable time for data collection before disturbances begin. Federal agencies are required to prepare supplements to environmental impact statements if "there are significant new circumstances or information relevant to environmental concerns and bearing on the proposed action or its impacts" (CEQ 1978). This requirement implies an obligation on the part of federal agencies to continue to obtain relevant information after issuance of an impact statement if the information could be reasonably expected to affect the outcome of the assessment.

Field experiments may continue during project operation as a supplement to field effects monitoring. While field measurements of responses to an operating facility are more realistic than similar measurements in perturbation experiments, they may not demonstrate ongoing effects. Uncontrolled variation in environmental factors and in project operation frequently mask stress-induced ecological responses, resulting in false conclusions of no effect. Field experiments may better control extraneous operational and environmental variation while becoming progressively more realistic by coupling the characteristics of the experimental perturbation to in-plant and ambient monitoring.

PARAMETER SELECTION

Selection of response parameters for field experiments is limited by time availability, by the amount of space which reasonably can be perturbed, and by interference from the perturbation devices. Experimental results often must be available after the first year of data collection. However, population and community level responses of multicellular organisms to sublethal stress do not appear until at least the second year, when perturbation effects are reflected in reproductive success. It is necessary, therefore, to monitor the proximate responses which will later be reflected in population and community level (ultimate) responses. Proximate responses include toxicant uptake and accumulation, leaf chlorosis, gas exchange rates, blood chemistry, and behavior. In addition, soil microbes and some invertebrates reproduce with sufficient frequency to show population or community responses in the first year. For example, the fastest and clearest responses measured on the ZAPS sulfur dioxide fumigation plots have been the sulfur content of leaves, followed by the activity of hydrogen oxidizing bacteria, plasmolysis in lichens, early leaf necrosis, seed viability, mycorrhizal infection, and leaf chemistry of grasses (Preston and Gullett 1979). After two or three years of fumigation (ZAPS II and I, respectively) the population and community responses that would be directly reflected in range production are only beginning to be apparent.

Population, community, and ecosystem level ultimate responses must be monitored in the first year along with the proximate responses in order to detect acute responses such as mortality. In cases where acute responses do not predominate, ultimate responses should be monitored for three to five years to quantify chronic effects. Although proximate responses can indicate that a system component is being affected, the body of empirical and theoretical ecology is not sufficient to allow confident extrapolation from proximate to ultimate responses. The ultimate response parameters for experiments are selected using the same criteria of importance and sensitivity as apply to monitoring (Suter in press; Sanders and Suter in press).

The size of the area experimentally perturbed can limit the range of parameters monitored owing to minimal area requirements for display of the phenomena of interest and the requirements of sampling. For example, existing open-top chamber designs are marginally large enough (approximately 7 sq m) to display plant and small insect population and community level responses in grasslands but could support little destructive sampling. Population and community parameters of most grasslands and shrublands, including those of animals at least as abundant as common small mammals, can be studied on half hectare plots. Communities with low diversities and moderately high productivity such as marshes and planted pastures would require somewhat smaller plots, but very low productivity or high diversity and high patchiness would require larger plots. Large, long-lived species such as forest trees can only be studied in terms of individual level responses; and large, highly mobile species, unless restrained, can only be studied in terms of behavior.

The area requirements of ecosystem level studies are quite variable. The current standard for experimental ecosystem studies is the whole watershed study which allows integration of all processes within natural boundaries (Bormann and Likens 1979, Best and Monk 1975, Corbett et al. 1978). However, many ecosystem parameters such as movement of minerals between litter, mineral soil, and plants can be measured in a few square meters.

Some constraints are placed on parameter selection by the equipment used to induce the perturbation. The ZAPS fumigation pipes, for example, prevent the study of livestock grazing on the plots exposed to sulfur dioxide. A more general problem is the effect of plot enclosures. The effects of walls on physical parameters have already been discussed, but they may also affect the response of mobile organisms. Walls have been used to restrict the movement of small mammals and to produce a uniformly stressed study population (Barrett 1968, Johnson and Barrett 1975). Enclosure has been shown, however, to drastically affect the population dynamics of small rodents in 0.8-ha plots (Krebs et al. 1973). Mandl et al. (1973) intended that their open-top chamber would permit free passage of insects and pathogens. It seems likely, however, that a 2.44-m wall around a 2.16-m plot with filtered, upward moving air would have significant effects on movement of insects and pathogens. For studies of natural systems, walls used to limit air movement should be kept as low as possible and should be raised just above ground level to permit movement of animals. The problem of monitoring stress effects on animals moving to and from plots can be handled by separate accounting of resident and transient individuals (Chilgren 1979). Alternately, when enclosure or chamber effects are not expected to be significant, use of both unwalled and walled controls can establish the absence of effects. When this double control demonstrates effects of enclosure on the stress responses, as in Howell et al. (1976), it is impossible to quantify the stress response.

COST

CEQ has required that "if the information relative to adverse impacts is essential to a reasoned choice among alternatives and is not known and the overall costs of obtaining it are not exorbitant, the agency shall include the information in the environmental impact statement." The clarity and force of this requirement is mitigated only by the qualifier concerning costs. The cost of constructing and emplacing fumigation systems and a rain simulator are listed in table 1. Because the costs of equipment or supplies for most ecological sampling are minimal, the primary additional cost is the salary for one full-time technician to maintain and operate the system and to perform the sampling. Costs of the other types of perturbation experiments will vary, but they should be lower because special equipment is not necessary to simulate the perturbation. These costs are low relative to the $750,000 to $1,500,000 that is typically spent to gather data into an environmental report for a power plant or strip-mine lease.

Table 1. Costs of perturbation equipment in 1979 dollars.

Item	Costs $\times 10^3$	Source
ZAPS-type fumigation systems	$40-$50 per set of 4 plots*	E.M. Preston Corvallis Environmental Research Lab. and J.E. Miller Argonne National Lab.
Open-top chambers	$1.2-$2 per chamber	Heagle et al. (1979) and D.S. Shriner Oak Ridge National Lab
Rain simulator	$0.15-$0.2 per 2.4 m x 2.4 m plot plus $0.8 per water delivery system	Bob Philbeck North Carolina State U.
Movable rain-exclusion roof	$3 per roof	J.M. Kelly Tennessee Valley Authority

*Includes the pollutant gas monitoring system.

CONCLUSION

The scoping process required by the new NEPA regulations provides a procedural context which encourages an experimental approach to assessment. Given the low predictive power of contemporary ecology, the regulatory requirement that information be obtained which permits a reasoned choice between alternatives amounts to a mandate for an experimental approach to assessment. Techniques are available to simulate most energy-related perturbations at reasonable cost. While none of these field simulations is perfect, the gain in realism obtained by perturbing the actual receiving system more than compensates for the loss of control associated with leaving the laboratory. Even a seriously flawed experiment is more easily interpreted than unaccompanied lists of species, and moderate competence in the design and execution of experiments would result in a quantum advance in impact assessment.

Widespread use of field perturbation experiments would also greatly contribute to the advancement of pure ecology. The best way to gain an understanding of any dynamic system is to observe its response to displacement from equilibrium. The field experiments of Joseph Connell, Robert Paine, and Charles Krebs have an importance to ecology far exceeding the resources expended. A large body of such experimental results should prove invaluable.

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GEOSYSTEMS MONITORING: AIMS, OBJECTIVES, METHODS, AND ORGANIZATIONAL PRINCIPLES OF IMPLEMENTATION IN THE KURSK BIOSPHERE RESERVE

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The Kursk Biosphere Reserve was created from the Central Chernozem State Nature Reserve (CCNR), which was named after Prof. V.V. Alekhin, and the Kursk Field Experimental Station (KFES) of the Institute of Geography of the U.S.S.R. Academy of Sciences. It is located in the forest/steppe zone, in the center of the most thickly populated and economically developed part of European U.S.S.R. (Gerasimov and Grin 1976). Its creation has two bases. The first is preservation of an area of meadow/herb (northern) steppe and residues of the indigenous oak forests (dubravas) which have been unaffected by human activity within surrounding intensively used territories, a unique situation for practically all of Europe. The second is the fact that the natural geosystems of the CCNR are well-studied and directly adjoin seminatural geosystems that have been modified in differing degrees by human activity. This extensive knowledge is primarily a result of long-term intensive work in this region by the Institute of Geography (Grin et al. 1979).

Over nearly 20 years consecutive expansion and intensification took place in the scientific program on functional regularities of the central forest/steppe geosystems. Three stages of evolution of the KFES scientific program can be identified:

inventory, including landscape-typological estimation of the region, inventory of different types of resources and of the spectrum of anthropogenic impacts, identification of the leading functional mechanisms, etc.--(practically finished)

study of special mechanisms in the functioning and spatial/temporal forms of interaction of major geosystems--(basis of present investigations)

modeling of geosystems, including developing partial and general functional models of major geosystems and basic mathematical modeling--(now being developed)

These studies rest on a number of theoretical concepts, based on the constructive geosystem ideas of A.A. Grigoriyev, D.L. Armand, and I.P. Gerasimov, and the results of studies by A.A. Nichiporovich, U.K. Ross, H.G. Tooming, and other scientists. The most essential concepts derived during these studies are the following:

notion of geometabolism and its rate

notion of effectiveness of geometabolism and of its individual links

concept of "harmonious combination" of resources in geometabolic processes

idea of compensational mechanisms of environmental resource use by biota

notion of the environment-forming and -regulating function of biota in a geosystem

Specific features of radiation and thermal balance formation and of the regimes of natural and agricultural forest/steppe geosystems are already well known from completed investigations at the KFES. Water balance and the relation of human agricultural activities to erosional and hydrochemical processes have been studied for all of the geosystems in the investigated region. The first results from complex experimental studies of water-balance and hydrochemical cycles under conditions of urban landscapes were obtained here. Investigation of spatial/temporal mechanisms of groundwater formation at the geosystem level, and later on, development of a comprehensive water component model of the forest/steppe landscape, were also placed on the agenda. Parallel to these studies, detailed measurements of biological productivity of the forest, steppe, and agricultural geosystems were performed.

Present-day studies at the KFES are connected by integrated experiments, based on the unities of time and place. First, "landscape profiles" are being compiled; second, complex biogeophysical and biogeochemical investigations are being undertaken of agricultural geosystems and partly of steppe geosystems. These experiments simultaneously fix radiation and thermal characteristics (including photosynthetic active radiation [PAR], microclimate, water-balance, and biogeophysical features of vegetation cover) and biogeochemical characteristics of the soil/vegetation cover. As far as we know, these studies of the matter-energy cycles in geosystems are the most comprehensive in our country.

At this stage many interesting facts have been discovered. To prove some new hypotheses, it was important to gather corresponding measurements. For instance, it was found that the environmental resources (heat and moisture) are absorbed and retained most fully by forests and least by agricultural or anthropogenic geosystems.

The absorbed resources are utilized (transformed into bioproduction) most effectively by steppes, second by forests, and third by anthropogenic geosystems. This result is true for only a cycle of one year. For a shorter time interval, i.e., the period of growth of an agricultural crop, the most effective resource use is by the agricultural system. But because the duration of an agricultural crop is very short, considerable time remains before sowing and after harvesting when heat and moisture are wasted.

The amount of experimental data collected at the KFES is already large enough to provide the initial information for definite models (including mathematical ones) of geosystem functions which are reasonably comprehensive. Geosystem modeling, as we have already mentioned, is a line of study at the Kursk station. Here investigations on developing special structural/functional models are being carried out (water-balance model - A.M. Grin and V.A. Tuleneva; steppe and agricultural phytobiota model - V.D. Utekhin, V.P. Kashkarova, N.G. Tsarevskaya, and E.A. Denisenko; energy and water/heat-balance model - Yu. L. Rauner, L.M. Ananiyeva, I.P. Ananiyev, N.N. Samarina, et al.). First specific numeric models have been realized (see Grin 1976a). In the future a comprehensive structural/functional model of the major natural and anthropogenic geosystems will be elaborated.

Experience from studies at Kursk shows that organization of the comprehensive complex of biogeophysical and biogeochemical investigations at even a single "point" is a rather complicated organizational and technical problem. In particular, realization of such experimental programs in the field geosystem required extensive organizational efforts by the Institute of Geography and the engagement of a considerable number of specialists and supplementary staff. Also, we developed remote sensing technologies for estimating biogeophysical and biogeochemical parameters of geosystems, employing aircraft from planes and helicopters to space satellites and piloted spaceships. This line of study has recently been initiated at the KFES. The most important advantages of remote sensing techniques are found in the principal "noncontact" measurement process, the areal character of the measurements of geosystem parameters, and the possibility of frequently repeating the measurements.

The first results of remote sensing studies at Kursk have already been summarized. The collection of papers on matter and energy resources of the major central forest/steppe geosystems (Grin 1976b) has been published, and they analyze potentialities of different remote sensing methods (multizonal aerophotographs, spectrometry, and active location) for interpreting the characteristics of the soil/vegetation cover of agricultural and natural geosystems. The general conclusion is that it is necessary to combine different remote sensing technologies to interpret the greatest possible spectrum of functional characteristics of a geosystem.

The Kursk Biosphere Reserve was created not only to organize environmental monitoring in central Russia, but also to develop programs and methods for geosystem monitoring that could be used throughout the national monitoring network.

As we understand it, the aim of geosystem monitoring is to observe the definite parameters of essential components and processes that take place within a geosystem and that determine by their fluctuations the structure and function of the geosystem as an integrated natural body. Examples of such parameters are the coefficients of effective absorption and utilization of major energy and material resources by the geosystem's biota, the rate of biotic cycling, the ability for self-purification, and amounts of "compensational" resources necessary for surviving under extreme conditions. Geosystem monitoring is not only for determining the pollutants in the geosystem (as is done in the case of impact monitoring), but also for observing the movement of pollutants in the material cycle, i.e., their participation in geosystem metabolism (Gerasimov 1978).

As stated by I.P. Gerasimov, an especially important task is monitoring the change in the natural ecological equilibrium. For quantitative estimation of these changes, the first approximation should use three indices: balance and rate of biological production and intensity of exchange of mobile biogenes. The role of these characteristics is covered in detail by Gerasimov (1978). Let us consider the possibilities of using them in geosystem monitoring.

The schemes of biological exchange in natural and anthropogenic geosystems of the Kursk Bioshere Reserve (for virgin steppe and grain crops) are shown in figure 1. They vividly illustrate the thesis of Gerasimov on the nature of disturbances to geosystem ecological equilibria under anthropogenic impacts: Geosystem balance is sharply disturbed under increased rates (or more accurately, relative rates) of bioproduction owing to the displacement by man of natural consumers of primary production. Quantitative indices of balance of the studied geosystems are shown on the left in table I. It can be supposed that the indices of natural geosystems are close to optimal.

The theory, suggested by Gerasimov and confirmed by the available experimental data, shows the controlled transformation of geosystems under human influences. This theory poses the following problem to scientists: When do changes in ecological equilibria in geosystems become irreversible? Evidently, there are critical values of the indices of balance which, when exceeded, prevent restoration of an equilibrium. The values of the indices depend on the intensity of anthropogenic pressures on a geosystem and, moreover, on the type of human use. The amount of anthropogenic pressure that causes the critical index of balance value to be exceeded is the ultimate permissible pressure of a given type of use on a geosystem.

These problems are very complicated. They require more detailed experimental and theoretical investigation. First of all, in each biosphere reserve different natural geosystems and their anthropogenic modifications need to be studied as to the balances of live and dead phytomasses and zoomasses in order to calculate the indices of balance and to attempt to give at least the approximate critical values of the indices and the ultimate permissible pressure. Also, the system for determining indices of balance needs to be further developed. Eventually, a final theory of geosystem stability, which ensures accurate calculations of critical indices and ultimate permissible pressure values, will be possible only by

Figure I. Exchange of organic matter in the natural (steppe) and anthropogenic (grain crops) geosystems at the Kursk Biosphere Reserve. 1--mobile biogenes, 2--biomass (a-aboveground, b-belowground), 3--primary production, 4--secondary production, 5-balance of production, 6--rate of production, 7--intensity of exchange of matter, 8--biogenic indices of exchange, 9--disturbance, 10--decrease in parameters, 11--increase in parameters, 12--weakening of exchange, 13--withdrawal of mass.

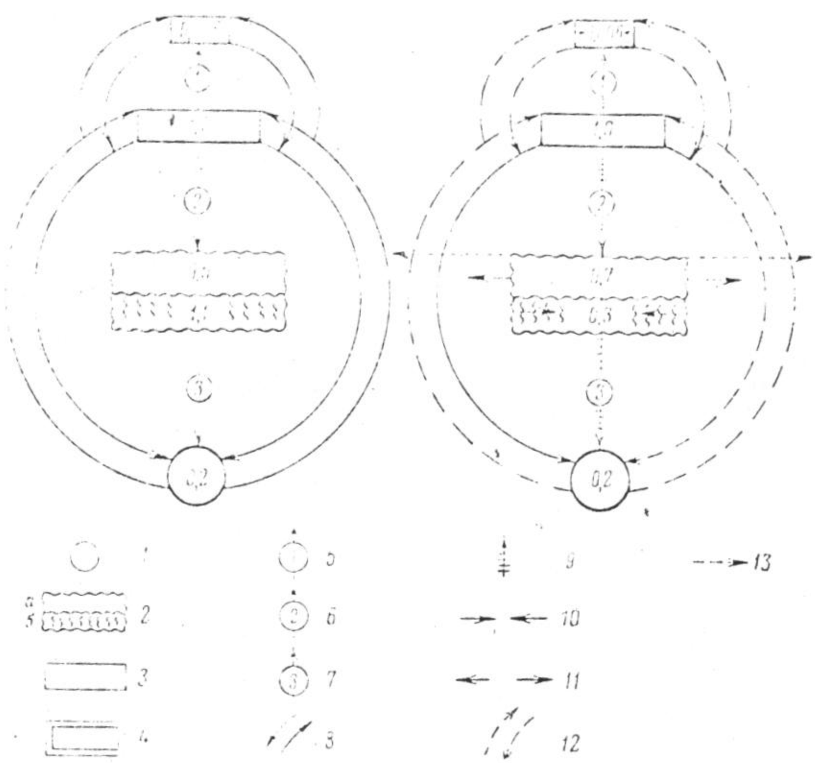


Table 1. Geosystem indices of equilibrium and of production effectiveness, Kursk Biosphere Reserve; natural (steppe) and anthropogenic (grain crop) geosystems.

	Indices of balance			Indices of effectiveness			
				Absorption		Assimilation	
Geosystem	Balance of bioproduction	Rate of bioproduction	Intensity of exchange	Solar radiation	Water	Solar radiation	Water
Natural (steppe)	0.056	1.06	1.12	0.4	0.4	0.03	0.03
Anthropogenic (crop)	0.006	1.00	1.00	0.2	0.2	0.04	0.05

employing methods of mathematical geosystem modeling using experimental data collected at the biosphere reserve.

The notion of effectiveness of geosystem functioning is also of practical and theoretical importance. Usually this notion refers to the effectiveness (efficiency) with which abiotic environmental resources (energy, water, and minerals) are used for biological production. Effectiveness depends on the level to which these resources are absorbed by a geosystem's biota and on the degree of assimilation, i.e., biological transformation of absorbed resources. Natural and anthropogenic geosystems differ both in the total effectiveness of resource-use and in the degree to which they are absorbed and assimilated. A priori these differences are difficult to forecast because of a lack of corresponding theory. Experimental studies carried out in anthropogenic and natural geosystems in Kursk, as mentioned above, show that assimilation of radiation and moisture is higher and absorption is lower in cropped areas than in natural geosystems; final effectiveness of crops in the years of observation was also lower than in natural environments (table 1, indices of effectiveness).

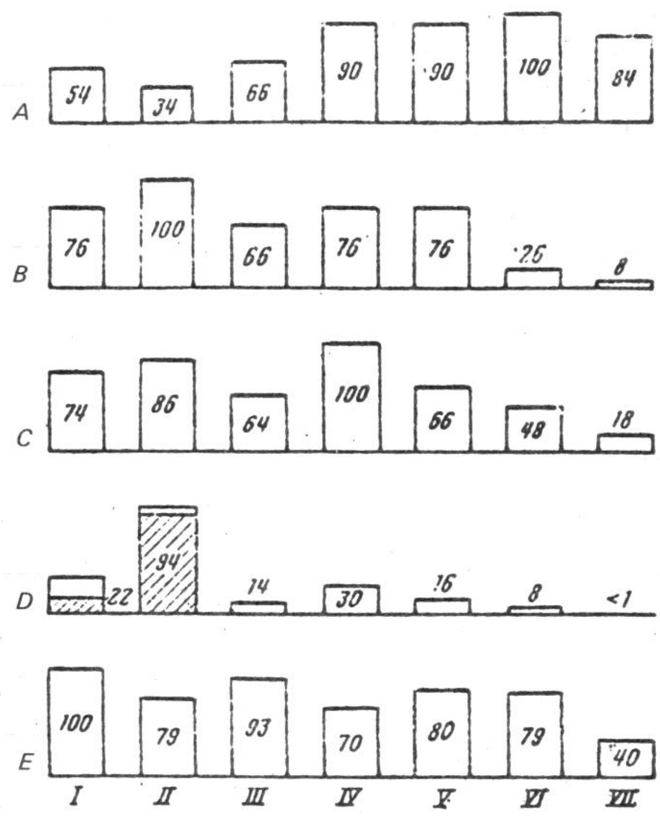
Interesting information for achieving one more objective of geosystem monitoring--determining trends of anthropogenic transformation of steppe geosystems--is also provided by data on modification of the structure of their organic matter, depending on the intensity and the character of economic pressure. As a case study, the results of experimental investigations at the Derkul station of the KFES, located in a true steppe in the northeast Ukraine, were analyzed (Zlotin et al. 1979).

In typology, according to systematic composition and amount of organic matter, the zonal type of herb/sod/cereals steppe is closest to virgin rangelands under moderate grazing by horses and to natural haylands (figure 2). For many centuries all the virgin steppes of the Russian plain experienced periodic change in grazing and haymaking. The present appearance of conserved virgin areas is determined primarily by the type of economic use made during the last decades. Investigations have shown that in the periods that virgin steppes were used for haymaking, it was mainly the structure of animal populations that changed, and because of that the role of the detritic link in the biological cycle has increased somewhat.

Increases in anthropogenic pressures, as well as full cessation of economic use (under the absence of wild ungulate animals), are reflected first of all in the structure of vegetation cover and animal populations. In both cases associations are formed that are not typical for the zonal conditions of typical steppes and, evidently, are less resistant (in long-term dynamics) to the external environmental factors.

Increases in anthropogenic pressures influence the total reserve of organic matter, composed mainly of humus, and total phytomass to a considerably lower degree. However, the structure of organic matter substantially changes. Increases in grazing pressures lead to relative increases in zoomass. However, in agrocenoses, especially annual ones, the share of phytomass and soil organic material sharply increases.

Figure 2. Structure of organic material in natural and anthropogenic ecosystems (in percentages of maximal store in the compared set of ecosystems). A--green parts of phytomass, B--roots, C--total phytomass, D--total zoomass (shaded portion corresponds to the share of domestic animals in biomass), E--humus in the layer A + AB. I--reserved steppe, II--rangeland under moderate grazing, III--rangeland under intensive grazing, IV--virgin haylands, V--triennial crop of alfalfa (man-made haylands), VI--triennial crop of Bromus, VII--spring crop of barley.



Phytomass resource structure of aboveground and belowground parts also changes. Increased grazing pressure results in decreased aboveground mass and increased belowground mass. Haymaking, especially substitution of virgin by man-made haylands, has an opposite effect. The mass of belowground parts of plants is decreased most in man-made haylands composed of cereals and in areas cropped annually for grain.

Anthropogenic changes in phytomass structure are very important for the character of the biological cycle and material balance within a given ecosystem. In the studied set of ecosystems, increases in grazing pressure are reflected to a considerably lesser degree in the outflow of vegetation materials from the ecosystem than in haymaking. This is especially the case with man-made haylands and annually cropped areas, where over three-quarters of the aboveground phytomass is annually withdrawn from green mass production.

The amount of vegetation matter annually withdrawn from the biological cycle accounts for 10% of the total phytomass reserve on rangelands intensively grazed by horses, about 20% on virgin haylands and perennially cropped areas under alfalfa, over 40% on perennially cropped areas under Bromus, and over 70% on annually cropped areas of cereals. However, it should be stressed that these results cannot be extended to all types of rangelands. It is known that excessive increases in pressures on rangelands grazed by bovine animals and sheep result in the disappearance of several valuable fodder species from the grass cover, decreasing the total ecological value of rangelands.

The character of biological cycles is, evidently, also affected by changes in the trophic structure of animal populations, resulting from the type of economic use of an ecosystem. In rangeland ecosystems the role of transformation of live vegetation matter is important, while in hayland ecosystems the role of the detrital link increases. Apparently the rate of biological exchange in steppe ecosystems does not depend on the type of economic use, judging by the ratio of live and dead matter in the aboveground phytomass. Only absolute restrictions in economic use lead to sharp decreases in the rate of exchange and to an accumulation of dead residues.

The availability of mineral nutrients in soil can be used as a conventional criterion to characterize the level of potential biological productivity of an ecosystem. In Chernozem soils, reserves of nitrogen, phosphorus, and potassium in forms fit for assimilation usually correspond to the total reserves of organic material in the soil. Hence, humus content can be viewed (within limits) as one such criterion. Humus reserves are the largest in the ecosystems which correspond most closely to the indigenous steppe type--virgin rangelands under moderate grazing and haylands. High humus content of virgin haylands is possibly accounted for by their former periodic use for grazing. Withdrawal of organic matter in periods of haymaking was compensated by the subsequent grazing regime. Many years of intensive grazing by horses, plowing, or use for perennial grass crops reduced humus content by 20% (figure 2). Evidently, in man-made haylands, expenditures of soil organic matter are impeded by grassland cropping systems with rotations of pulses and cereals. Finally, long-term use of fields for grain crops decreased the humus content by 60%.

Substantial losses of humus in the annually plowed areas are also characteristic of meadow steppes located to the north. This results not only from decreases in organic matter coming into the annual exchange, but also from increased water and wind erosion. Thus, even extremely rich cultivable lands of the steppe zone require application of fertilizers and rational agricultural practices to preserve their fertility.

In concluding the analysis of the studied set of ecosystems, it should be stressed that full cessation of economic activity on the existing virgin steppe, with its long-existing disturbed animal population structure, would result in disruptions in the structure and functioning of ecosystems as serious as under intensive economic use. Therefore, absolutely reserved areas cannot serve as standards of indigenous steppe ecosystems. Apparently, these can be provided only by areas under moderate grazing by horses.

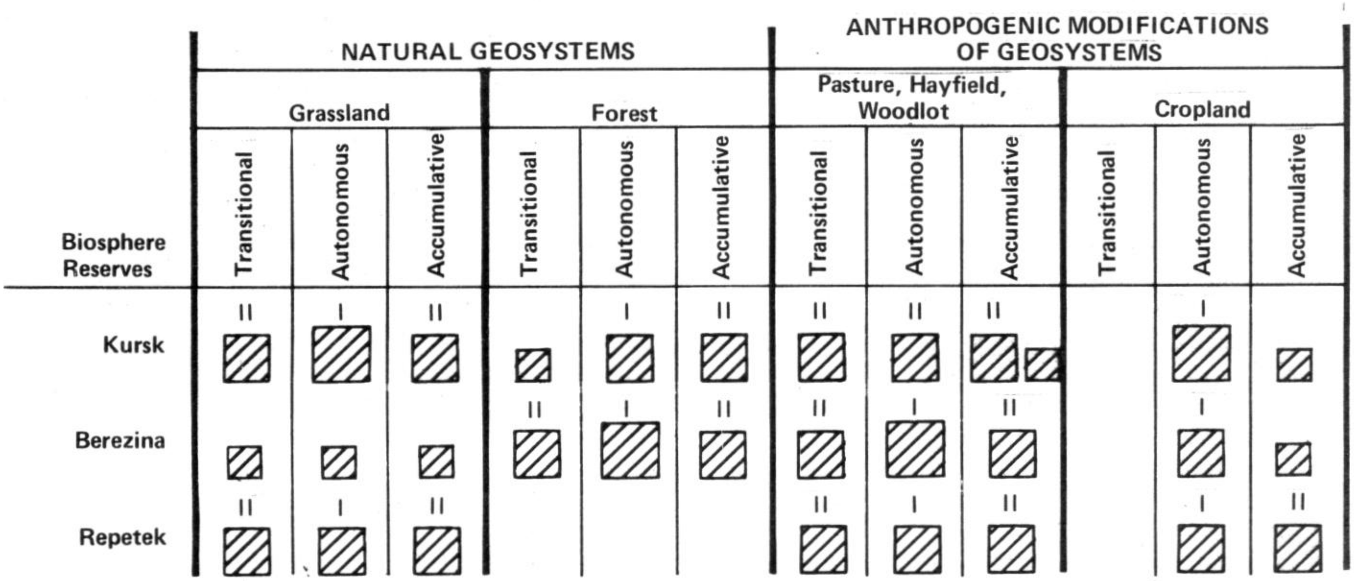
At the Kursk Biosphere Reserve, observation methods take into account the characteristic durations of individual processes and phenomena, the measurement of parameters with accuracy sufficient for definite quantitative estimations, the inclusion of anthropogenic as well as natural factors that determine the conditions of geosystem functioning within the sphere of observations, and the wide employment of noncontact (remote sensing) measurement methods which provide data on observed processes unaltered by measurement devices. On the basis of these principles a draft program of geosystem monitoring was developed and suggested for use not only at Kursk, but also at other biosphere reserves in the U.S.S.R. (Grin et al. 1978).

The scientific selection of objects for observation determines the success of geosystem monitoring more than it does for other types of monitoring systems. The objects selected for observation should ensure the following: within a biosphere reserve, the comparability of natural (standard) and anthropogenic (derived) geosystems (i.e., selection of "analogous" geosystems); and within different biosphere reserves, the comparability of different regional geosystems (i.e., selection of "homologous" geosystems). An inventory of geosystems should precede selection of objects in each reserve. To ensure comparability, these inventories should use a uniform scheme. The simplest variant of the inventory should classify geosystems according to their essential geophysical and geochemical parameters--energy and mass exchange. An example of such an inventory for the biosphere reserves that were studied is presented in figure 3. In the cells of the scheme the conventional gradations of the areas of different types of geosystems are shown.

Objects of geosystem monitoring in biosphere reserves should characterize the typical for the regional combination of geosystems and should be comparable in intraregional and interregional aspects. In addition, it is desirable to observe the most widespread primary geosystems. An inventory of geosystems helps to fulfill these conditions.

From practical considerations it is expedient to define the hierarchy of the objects to be observed for geosystem monitoring, subdividing them into two major classes. Class I objects should be observed as part of a

Figure 3. Inventory of major geosystems at Kursk, Berezina, and Repetek biosphere reserves. Horizontal--analogous geosystems; vertical--homologous geosystems; I and II--classes of observation objects. Area of squares in cells corresponds to the scale of areal spread of geosystems.



maximal program, while class II objects should be observed as part of a minimal program. In addition various supplementary observations can be made of objects of intermediate classes. The suggested set of geosystems for locating sites for monitoring of both classes in three biosphere reserves is shown in figure 3.

Geosystem monitoring cannot be successful without correct correlations with other types of monitoring programs, and above all with biospheric background monitoring. Objects for background monitoring should be located, if possible, within the monitoring sites for geosystems, or at least in the most representative sites. Territorially fixed observations for background monitoring should be the minimum carried out in the areas of class I objects for geosystem monitoring.

In addition to hydroclimatic data, information from background biospheric monitoring must include the dynamics of parameters of major components of the natural environment--relief, soil, vegetation cover, and animal populations. To obtain this information periodic mapping of the above objects will be required, along with annual registration of the composition of vegetation groupings and the complexes of animal populations in the same areas and along the same routes. The two last types of observations, which are not labor-consuming but are highly informative owing to indicative qualities of the biota species composition, should be carried out at all sites where monitoring of class I and II objects is carried out.

The suggested program of geosystem monitoring can not be too rigid; still, it has a comparatively "hard" core--the basic concept of criteria of geosystem equilibrium. In addition, some common principles of organization of geosystem monitoring, particularly at biosphere reserves, should be observed: 1) continuity of observations in time, 2) parallel observations in natural and anthropogenic geosystems, 3) technical improvement and automatization of observations, and 4) insurance in the natural reserves of the necessary correlation between the biospheric monitoring and the traditional "annals of nature."

Observation regimes for geosystem monitoring should be similar at all biosphere reserves. They should be carried out in such a way as to produce a minimal impact on the nature of the reserved zone; this is especially important because of the unlimited repetition of observations. In addition observations should not be too labor-consuming or expensive because of the economy and because the reserved zone must be protected from excessive numbers of visits.

The discussed program of studies at biosphere reserves can not be implemented without fundamental methodological investigations. The latter can be subdivided into "organization of monitoring" and "technology of monitoring."

The first category includes problems of distributing sites of observations, repetition, periodicity, selection of the observed parameters, and methods of processing data. These problems generally require employment of mathematical methods, primarily theories of probability, information, and mathematical statistics. Optimal selection of the observed parameters and, especially, processing of data for forecasting can not be fulfilled without developing mathematical models of the studied geosystems.

The second category covers problems of developing and introducing modern technologies for geosystem monitoring. These are, first of all, remote sensing methods which allow observations of a variety of geosystem parameters (listed in table 2). Potentialities of remote sensing methods (including aerospace methods) are constantly expanding. Their advantages in terms of covering broad spans of space and time by observations are widely known. Therefore, use of remote sensing technologies at biosphere reserves should be actively developed.

Despite the progress of remote sensing technology, ground observations will always occupy the leading place in geosystem monitoring programs. Hence, methods of ground observation should also be advanced. Methods adapted for work in field conditions should be actively introduced; field branches of geography (biogeophysics and biogeochemistry) have fallen substantially behind laboratory branches of the science in this respect. Technological development is proceeding toward automatizing measurements, integrating detectors, introducing telemechanical devices, and integrating registering devices with computers. Introduction of computerized data processing is, irrespective of the method employed for collecting these data, a primary task for methodological progress at biosphere reserves.

Since Soviet scientists understand geosystem monitoring in general as observation, control, and management of geosystems (Gerasimov et al. 1976), it is important for geosystem monitoring at the stage of "control" not only to estimate correctly the deviation of some geosystem parameters from a "standard" (zero point), but also to determine whether this deviation is a product of human impacts or whether it results from natural development of the observed geosystem (natural trend or successional changes of condition). In the forest/steppe geosystems observed at Kursk Biosphere Reserve, typical natural changes are the periodic advancement of forests onto steppes and forest retreat in virgin steppes under the influence of natural climatic fluctuations. Such successional changes of dominating vegetative associations can be forecast, and in reserved dubravas, violent outbursts of phytophages (Tortricidae) that jeopardize the very existence of the oak forest have been registered.

The previous studies by the KFES on the territory of Kursk Biosphere Reserve have revealed mechanisms for several of these phenomena. Thus, if background hydrometeorological conditions are normal, then forests advance onto steppes, simply because forests are better than steppes at absorbing natural resources and, as a result, expand their area. However, the ability of the steppe geosystem to use resources more effectively enables it to "survive" in extreme situations.

It is impossible to implement the higher form of geosystem monitoring--management of geosystem conditions--without developing functional models. During implementation of the first two stages of geosystem monitoring (observation and control), on the basis of a system's approach and conceptual modeling of the structure and processes of geosystem functioning, the conditions are created for formation of a

Table 2. List of observed and measured parameters of geosystems at biosphere reserves, fixation of sites and periodicity of observations.

Measured parameters	Fixation to sites and objects of observations	Periodicity of observations	Notes
	Background biospheric monitoring		
Meteorological	Class I	According to program of State Meteorological Stations (SMS) of class I and special observations for the tropo-sphere system	
Hydrological	Class I	Full program of SMS	
Geomorphological	Total area	10 years	Mapping, using remote sensing
Geobotanical	Total area	10 years	The same (including forest and rangeland management)
Geobotanical	Classes I & II	Annually	Description of stationary plots
Zoogeographical	Total area	10 years	Mapping
Zoogeographical	Classes I & II	Annually	Registering the animal population of major species along profiles and at stationary plots (according to type specified at present by "annals of nature")
Pedogeographical	Total area	10 years	Mapping, using remote sensing
	Geosystem monitoring		
Reserves of live and dead phytomass:	Class I	Monthly	By traditional methods
Annual aboveground parts, live and dead mass	Class II	Annually at the maximum	By traditional methods
Perennial above-ground parts, live and dead mass	Class I	Annually	By methods of taxation
Total aboveground phytomass	Total area	Monthly	By remote sensing methods
Aboveground dead organic matter (litter)	Class I	Monthly	By traditional methods
Belowground parts, ive and dead mass	Class I	Monthly	By drilling method with minimal disturbance of soil cover

Measured parameters	Fixation to sites and objects of observations	Periodicity of observations	Notes
Production of phytomass annual dead matter, and mineralization of dead organic matter	Class I	Annually	Calculated using data of observations
Reserves of live and dead zoomass			
Vertebrates, alive and dead	Class I	Annually	Using data on registration of population and its studies within the frame of bioecological monitoring
Invertebrates, populating leaf cover and annual above-ground parts of plants	Class I	Monthly	The same
Invertebrates, populating perennial aboveground parts of plants	Class I	Annually	The same
Invertebrates of the litter (herpetobionts)	Class I	Monthly	The same
Soil invertebrates (pedobionts)	Class I	Monthly	Using drilling materials for for determining the below-ground phytomass
Production of zoomass and its annual dead mass	Class I	Annually	Calculated using data of observations
Stores and production of microorganism mass	Class I	Annually	By available methods
Parameters of biogenes exchange			
Energy reserves (caloricity); water and chemical elements in phytomass and zoomass	Class I	Simultaneously with defining biomass	Selection of samples, with further laboratory analysis
Absorption of carbon dioxide from air by vegetation cover (gross photosynthesis), assimilation of carbon dioxide (net photosynthesis), expenditure of carbon dioxide for respiration by plants	Class I	Continuously during period of vegetation	By automatic detectors
Expenditure of carbon dioxide for respiration by aboveground heterotrophs	Class I	Continuously during period of vegetation	By automatic detectors
Expenditure of carbon dioxide for "soil respiration"	Class I	Continuously	By automatic detectors

Measured parameters	Fixation to sites and objects of observations	Periodicity of observations	Notes
Water expenditure for transpiration	Class I	Continuously	By automatic detectors
Input and expenditure of nitrogen, phosphorous, potassium and other biogenes	Class I	Annually	Using data from energy reserves (above)

Bioecological monitoring

Botanical, zoological, microbiological		According to special programs	

data bank, control indices, and primary models, which serve as bases for creating imitational models of the main geosystems in biosphere reserves. Some positive experience of creating such models has, as was stated above, already been accumulated at Kursk Biosphere Reserve.

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THE PROGRAM OF ECOLOGICAL MONITORING IN BIOSPHERE RESERVES

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INTRODUCTION

The modern development of society and the associated intensive anthropogenic effects on the environment have both positive and negative consequences. The positive consequences of the transformation of nature ultimately include the growth of material benefits and cultural values and an increase in the human life span. The accompanying negative consequences include a tendency to destroy nonrenewable natural resources, pollution of the natural environment, and decreasing natural possibilities for the reproduction of renewable resources.

Man's technological capabilities are now such that the effects on the environment of actions that were once local now attain a continental or even global scale. This makes it necessary to eliminate very quickly the negative consequences (both future and existing) of anthropogenic actions. One of the priority tasks in this area is the creation of a system of monitoring to provide, on the basis of a few observations and investigations, an adequate evaluation and prognosis of the consequences of anthropogenic activities. The scale of such a monitoring system should be global and multiyear, and its content should be ecological, i.e., it should reflect all the basic aspects of anthropogenic effects on ecological systems.

The proposals contained in this article are based on the results of theoretical and experimental studies we have conducted over the last two to three years. They are directed toward the creation of a complex program for monitoring environmental pollutants and their ecological consequences in natural biosphere reserves (Izrael 1976; Izrael et al. 1977, 1978a, 1978b, 1978c).

The content and specific characteristics of the monitoring program are explained by the tasks that we initially posed for a monitoring system and by the nature of the information that was obtained. The information system was not part of a management system, but it did constitute an essential condition for developing effective programs for regulating environmental characteristics (Izrael 1976).

The program we propose is primarily oriented toward prognosis and not simply toward ascertaining observable conditions. It is obvious that the prediction of changes in the state of ecosystems under the influence of anthropogenic activity on a global scale is not possible either through field observations or through experiments. Thus, work on constructing appropriate prognostic mathematical models occupies a prominent place in the program.

Because of high noise levels it does not appear possible to define through field methods, within reasonable periods of time, the effects of background pollutants on the natural fluctuations in the states of ecological systems. Therefore, the second important feature of the program we propose is experimental studies on the effect of pollutants of background intensity on biota under the controlled conditions of an abiotic environment.

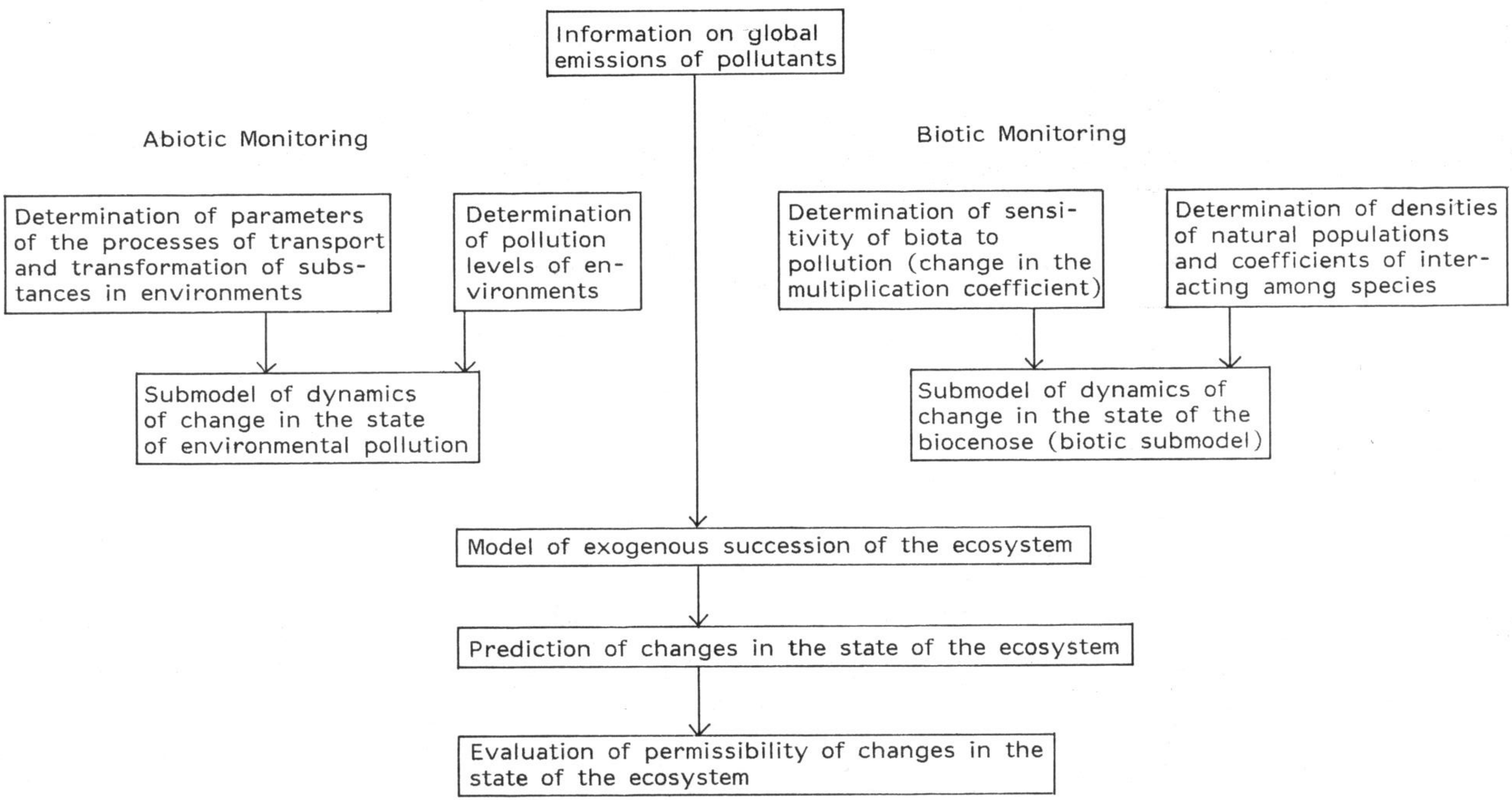
The program of ecological monitoring in biosphere reserves has been developed to bring out the global and regional consequences of anthropogenic activity. Such a program contemplates a broad complex of biological, geophysical, and geochemical studies. Considerations of the actual material, and of available methodological and instrument resources, necessitate a careful and rigid selection to formulate the list of recommended observations.

The ecological monitoring program that we propose is divided into abiotic monitoring and biotic monitoring (figure 1). The abiotic monitoring program assumes systematic multiyear observations of the pollution levels of all environments (air, precipitation, natural water, soil, and biota), as well as corresponding geophysical observations (Izrael et al. 1978c). A list of priority pollutants has been developed for monitoring in natural reserves, and these observations have already been carried out for several years. The biotic monitoring program includes nature studies and theoretical and experimental investigations. The object of the experimental program is to determine the sensitivity of individual species in a given ecosystem to the effects of low, close-to-background concentrations of pollutants. This can be done only through experiments with the individuals of various species in special facilities where constant environmental conditions (ecostats) can be maintained and through the use of highly accurate equipment that can register quite small changes in state levels.

The objective of these experiments is the construction of "dose/effect" curves that reflect changes in a multiplication factor resulting from the influence of the low levels of pollutants observed in the geophysical monitoring program. We selected the multiplication factor as an integral indicator of the state of the biota because changes in it reflect all changes in the characteristics of the state of an individual or species which are significant from an evolutionary perspective.

Since an adequate evaluation and prognosis of the state of an ecosystem requires information about the sensitivity of all species in that ecosystem to pollutants, and since it is impossible to obtain this information through experiments on individuals of all species in the ecosystem, certain representative species must be selected for experimental studies and the

Figure 1. Scheme of complex ecological monitoring of environmental pollution



results then interpreted for other species in the ecosystem. The selection of experimental subjects and the extrapolation of results to other species can usefully be carried out in coordinates of the phylogenetic tree and in such a way as to minimize the main error of extrapolation. In selecting species for experimental studies, preference should be given (all things otherwise being equal) to species which play an important ecological role in the community.

Effective prognosis of ecosystem states also requires information not relating to the effect of pollution on biota. This is quantitative information on the ecological interrelationships among species (predation, parasitism, etc.) and is presented in demographic terms. Quantitatively characterizing interactions of this type is a complex research task that involves the simultaneous recording of the densities of interacting species and their mortality structure. At present it is still impossible to identify unified methods of obtaining this kind of data and to recommend an appropriate regime of systematic observations and experiments. This is a task to be undertaken during the next few years. For now, however, it is necessary to organize a unified presentation both of available data and of demographic data on biotic parameters that will be obtained during the monitoring program.

Adequate evaluation and prognosis of anthropogenic changes in ecological systems on the basis of the collected information will require the creation of a series of mathematical models to describe natural biological and geophysical processes. The current methodology for constructing models of biotic responses to pollutants is, in effect, the modeling of exogenous succession. Such models, which are contiguous with circulation models of polluting substances in natural geophysical environments, permit the prediction of quantitative and qualitative transformations in natural ecosystems resulting from anthropogenic pollutants (Izrael et al. 1978a and 1978b).

Thus, the initial parameters of these models will be data on predicted levels of environmental pollutants, experimental data on the sensitivity of the biota to the action of pollutants at these levels, and data on the ecological interactions among species in the ecosystem under consideration. From these models we will be able to determine what species in the ecosystem will disappear or sharply diminish in number and in what sequence.

The proposed monitoring program will enable us to evaluate the background state of environmental pollution and its biological effects, to identify those species most sensitive to pollutants for each type of ecosystem, and to make an approximate prediction of changes in states of biocenoses resulting from changing levels of anthropogenic influence.

ABIOTIC MONITORING

The abiotic monitoring program of background observations will require the following:

a list of the chemical substances subject to measurement in the atmosphere, water, soil, and biota

a list of the hydrometeorological and geophysical parameters subject to measurement

a determination of the periodicity with which observations and measurements are to be carried out

In selecting the chemical substances in the environment to be studied at background stations, the following factors should be taken into account: the substances entering the environment as the result of anthropogenic activity, and their abundance and persistence; the possibility of their transmission through food chains, accumulation in the human body, and influence on ecological systems; their transformation into more dangerous substances; and the possibility of changing their content in the environment. Observations on the biogenic elements nitrogen and phosphorous are very significant in carrying out a biological monitoring program.

In accordance with the above criteria, it is appropriate to include the following substances in a program of observations at background stations:

air--sulfur dioxide, ozone, carbon dioxide, aerosol (concentration by weight), lead, cadmium, arsenic (in particles), mercury vapor, DDT and 3,4-benzopyrene

rainfall and other precipitation--mercury, lead, cadmium, arsenic, DDT, 3,4-benzopyrene, nitrogen (total content), phosphorous (total content), and the anions and cations recommended for determination at World Meteorological Organization (WMO) observatories (sulfates, nitrates, chlorides, and ions of ammonium, magnesium, potassium, sodium, and calcium)

surface water--mercury, lead, cadmium, arsenic, DDT, 3,4-benzopyrene, nitrogen (total content), and phosphorous (total content)

soil, ground deposits, suspended alluvia--mercury, lead, cadmium, arsenic, DDT, 3,4-benzopyrene, nitrogen (total content), and phosphorous (total content)

biota--mercury, lead, cadmium, arsenic, DDT, 3,4-benzopyrene, nitrogen (total content), and phosphorous (total content)

The measurements of hydrometeorological and geophysical parameters should include those measurements necessary to monitor the climate, as well as those necessary to interpret data on the concentration of pollutants in various media and to study biogeochemical cycles and the circulation of chemical substances. Such parameters include the following:

meteorological observations--wind velocity and direction, atmospheric pressure, air temperature, humidity, and precipitation

changes in the intensity of solar radiation (direct, scattered, total), including the UV region

changes in the components of the heat balance and characteristics of turbulence

hydrological observations--changes in the levels and discharge of water, water temperature, the discharge of suspended alluvia, tests of water for turbidity, chemanalysis, and tests of alluvia and bottom deposits

observations of the moisture and heat balance of the soil

Because there is not enough current information on the temporal variability in background concentrations of pollutants in natural environments (principally in air), the proposed program incorporates an excess of observations and sampling rates. This additional information can then be adapted to the data gathered at the background monitoring stations. So far observations at the monitoring stations indicate that atmospheric and precipitation tests should be conducted more frequently than the sampling of a specific environment, such as the soil and plant cover, which changes rather slowly with respect to the content of pollutants. Surface waters on dry land can occupy an intermediate place in this respect.

Table 1. Background observations made during an abiotic monitoring program.

Test no.	Observations and tasks	Period of observation and tasks
1.	Atmospheric sampling to determine content of mercury lead cadmium arsenic DDT 3,4-benzopyrene sulfur dioxide near-surface ozone	Integral sample once every 24 hours

Test no.	Observations and tasks	Period of observation and tasks
2.	Sampling of precipitation and snow cover to determine content of mercury lead cadmium arsenic DDT 3,4-benzopyrene nitrogen (total) phosphorous (total) anions and cations (WMO program)	Precipitation--integral sample once every ten days; snow cover--once a year before the onset of melting
3.	Sampling of surface water and bottom deposits to determine content of mercury lead cadmium arsenic DDT 3,4-benzopyrene nitrogen (total) phosphorous (total)	Surface water--six samples per year (onset, midpoint, and decline of high water; summer and winter midlevel; flood period); bottom deposits--one a year (summer midlevel)
4.	Sampling of soil and vegetation to determine content of mercury lead cadmium arsenic DDT 3,4-benzopyrene nitrogen (total) phosphorous (total)	Twice a year--beginning and end of growing season
5.	Meteorological, hydrological, and actinometric observations	Daily

BIOTIC MONITORING

The multiplication coefficient of a species, independent of its density, was chosen as the control factor in evaluating the state of a species under given environmental conditions. Changes in this factor in response to changes in the levels of environmental pollutants indicate an appropriate integral characteristic of the biotic response to pollution. Moreover, this indicator may be used to predict the exogenous succession of natural ecosystems as they respond to changes in the levels of environmental pollutants.

In accordance with the task of an ecological monitoring system, the proposed program will consist of the following three subprograms:

> <u>subprogram A</u>--to evaluate the current state of the biota and to identify regularly recurring changes in the multiplication coefficients of species (from the priority list proposed below)
>
> <u>subprogram B</u>--to predict responses of the biota to pollutants and to provide information to accurately establish the field of sensitivity of the biota to anthropogenic pollutants
>
> <u>subprogram C</u>--to record through field methods the state of the biota

It should be noted that the accomplishment of these three subprograms is interconnected and interdependent. The subprograms may be considered independent only at the first stage of implementation, when the optimal aggregates of the biological species under study are first approximated. At the second stage, observations and studies will be corrected on the basis of information obtained primarily in subprogram B.

Optimally, the proposed program in the long term should be developed as a step-by-step plan. Subprograms A and B will be unified in terms of instruments and methodology so that certain given types of ecostats can be used to create and maintain given abiotic conditions. Because of the conditions under which these studies are to be carried out, subprogram A, which will be less time-consuming and complex, must be implemented by a special staff at a background monitoring station under the direction of the scientific curator's organization at the natural reserve. Subprogram B, which will be more complex and time-consuming, should be implemented in a single national scientific center. Subprogram C should be implemented by the staff of the reserve and by specialized biological scientific expeditions.

<u>Subprogram A--Evaluation of the Current State of the Biota</u>

This subprogram is based on a continuous recording of changes in the multiplication coefficient of the test species population, independent of the species density.

In the first stage of implementing this subprogram, the study should be limited to species from the following groups, which should be selected on the basis of their representativeness, abundance, and sensitivity to the influence of pollutants:

Protozoa	(subkingdom) protozoa
Bacteriophyta	(subkingdom) bacteria
Cyanophyta	(class) blue-green algae
Rhodophyta	(class) red algae
Chlorophyta	(class) green algae
Chrysophyta	(class) golden algae
Bacillariophyta	(class) diatoms
Phaeophyta	(class) brown algae
Lichenophyta	(class) lichens
Bryophyta	(class) mosses
Gymnospermae	(class) gymnosperms
Angiospermae	(class) angiosperms

The control factor, as already indicated, is the multiplication coefficient, which is independent of density. For protozoa, bacteria, and algae, the concrete factor is the relative increase in the quantity of an evacuated culture, reduced to standard time units. For mosses, lichens, and higher plants, the concrete factor is the relative increase in biomass, reduced to standard time units.

The periodicity of measurement for each concrete species is individual and depends on the duration of a generation. In the process of sampling the concrete species at each background station, all the parameters of the abiotic medium (temperature, humidity, illumination) regulated in the ecostat growth chamber should be fixed at levels typical for the growth period of the concrete species in the region of the given station. During the experiments, these characteristics should be maintained without change. The pollution levels of the media used in the experiment (air, water, soil) correspond to the current background state of pollution in the region.

The measurements are to be made at background monitoring stations in each natural biosphere reserve. The scientific curator's organization will select one concrete test species from each of the groups listed above. In selecting this species, the abundance of the species in the ecosystem of the region, the development of appropriate experimental methods, and the sensitivity of the species to the influence of pollutants and its role in the ecosystem of the region should all be considered, and preference should be given to those species most promising in these respects.

Table 2. Background observations of the states of biota.

Tested group	Control factor	Period of observation (no. of tests/year)
Protozoa	Relative increase in numbers (per day)	12
Bacteria		12
Algae		12
Mosses	Relative increase in biomass (per year)	1
Lichens		1
Higher plants		4

A proved change (increase or decrease) in the control parameter (the multiplication coefficient) and the presence of a corresponding stable tendency together indicate a change in the state of the control species population in the region of the background station as a result of a change in pollution.

Subprogram B--Monitoring the Responses of Biota to Pollutants

This part of the program is to be implemented by a scientific center, and it will consist of performing a set of experiments to measure the multiplication factor of species under various states of environmental pollution by discrete pollutants; the remaininig abiotic conditions will be fixed. The measurements in this part of the program will be directed toward predicting the states of biota, and they will differ from the measurements performed in subprogram A in that they will be "one-time." Once the value of the multiplication coefficient, independent of density, has been accurately measured, experiments on that selected species may be discontinued.

Experiments with each of the selected species are to be carried out, as under subprogram A, in ecostat growth chambers. All abiotic conditions except concentrations of pollutants will be set at typical mean levels for the environment of the given species.

Experiments to measure the multiplication coefficient for each of the species are to be performed separately for each of the pollutants from the priority list. Each species should be tested with various concentrations of the given pollutant, beginning with the present-day background concentrations of the pollutant. Concentrations of the remaining ingredients should correspond to the existing background.

Within the proposed program it will be necessary to study the effect on the biota of the priority pollutants in accordance with the abiotic monitoring program. A principle in the selection of a system of test species is to use data on the sensitivity of the test species to minimize error in extrapolating responses of the biota as a whole to pollutants. The choice of test species already supposes a scheme of extrapolating data on sensitivity to pollutants from the set of test species to the set of all species. Choosing the optimal alternative in the selection of a system of test species will ensure the smallest average error in such extrapolation. A successive testing plan which is close to optimal can already be proposed.

Table 3 lists a set of classes, from each of which one species should be selected at the corresponding stages of developing subprogram B. At successive steps the recommended classes are most representative with respect to species for their systematic groups--superkingdoms, kingdoms, subkingdoms, and classes (types), respectively.

From the classes in the list, the scientific center is to select concrete species for testing, taking into consideration the feasibility of the

Table 3. Classes from which test species are selected at each stage of implementation of subprogram B, and their systematic position

Systematic Position				Recommended Class
Superkingdom	Kingdom	Subkingdom	Class/Type	
STAGE 1				
Procaryota	Mychota	Bacteriobionta	Bacteriophyta	Eubacteriae
Eucaryota	Animalia	Metazoa	Arthropoda	Insecta
STAGE 2				
Procaryota	Mychota	Bacteriobionta	Bacteriophyta	Eubacteriae
Eucaryota	Animalia	Metazoa	Arthropoda	Insecta
Eucaryota	Fungi	Mycobionta	Mycota	Ascomycetes
Eucaryota	Vegetabilia	Embryobionta	Angiospermae	Dicotyledoneae
STAGE 3				
Procaryota	Mychota	Bacteriobionta	Bacteriophyta	Eubacteriae
Procaryota	Mychota	Cyanobiota	Cyanophyta	Hormogoniophyceae
Eucaryota	Animalia	Protozoa	Protozoa	Sarcodina
Eucaryota	Animalia	Metazoa	Arthropoda	Insecta
Eucaryota	Fungi	Myxobionta	Myxomycota	Myxogastres
Eucaryota	Fungi	Mycobionta	Mycota	Ascomycetes
Eucaryota	Vegetabilia	Rhodobionta	Rhodophyta	Florideophyceae
Eucaryota	Vegetabilia	Phycobionta	Bacillariophyta	Pennatophyceae
Eucaryota	Vegetabilia	Embryobionta	Angiospermae	Dicotyledoneae
STAGE 4				
Procaryota	Mychota	Bacteriobionta	Bacteriophyta	Eubacteriae
Procaryota	Mychota	Cyanobionta	Cyanophyta	Hormogoniophycea
Eucaryota	Fungi	Myxobionta	Myxomycota	Myxogastres
Eucaryota	Fungi	Mycobionta	Mycota	Ascomycetes
Eucaryota	Fungi	Mycobionta	Lichenophyta	Ascolichenes
Eucaryota	Vegetabilia	Rhodobionta	Rhodophyta	Florideophyceae
Eucaryota	Vegetabilia	Phycobionta	Pyrrophyta	Peridineae
Eucaryota	Vegetabilia	Phycobionta	Chrysophyta	Chrysomonadophyceae
Eucaryota	Vegetabilia	Phycobionta	Bacillariophyta	Pennatophyceae
Eucaryota	Vegetabilia	Phycobionta	Phaeophyta	Phaeozoosporophyceae
Eucaryota	Vegetabilia	Phycobionta	Xantophyta	Xanthococcopyceae
Eucaryota	Vegetabilia	Phycobionta	Euglenophyta	Euglenophyceae
Eucaryota	Vegetabilia	Phycobionta	Chlorophyta	Conjugatophyceae
Eucaryota	Vegetabilia	Phycobionta	Charophyta	Charophyceae
Eucaryota	Vegetabilia	Embryobionta	Psilotophyta	Psilota
Eucaryota	Vegetabilia	Embryobionta	Bryophyta	Bryopsida
Eucaryota	Vegetabilia	Embryobionta	Lycopodiophyta	Lycopodiopsida
Eucaryota	Vegetabilia	Embryobionta	Equisetophyta	Equisetopseda
Eucaryota	Vegetabilia	Embryobionta	Polypodiophyta	Leptofilipsida
Eucaryota	Vegetabilia	Embryobionta	Gymnospermae	Coniferopsida
Eucaryota	Vegetabilia	Embryobionta	Angiospermae	Dicotyledoneae
Eucaryota	Animalia	Protozoa	Protozoa	Sarcodina
Eucaryota	Animalia	Metazoa	Mesozoa	Orthonectida
Eucaryota	Animalia	Metazoa	Spongia	Demospongia
Eucaryota	Animalia	Metazoa	Coelenterata	Authozoa
Eucaryota	Animalia	Metazoa	Ctenophora	Ctenophora
Eucaryota	Animalia	Metazoa	Platyhelminthes	Cestoidea
Eucaryota	Animalia	Metazoa	Nemathelminthes	Nematoda
Eucaryota	Animalia	Metazoa	Acanthocephala	Acanthocephala
Eucaryota	Animalia	Metazoa	Nemertini	Nemertini
Eucaryota	Animalia	Metazoa	Mollusca	Castropoda
Eucaryota	Animalia	Metazoa	Phoronoidea	Phoronoidea
Eucaryota	Animalia	Metazoa	Bryozoa	Bryozoa

Systematic Position				Recommended Class
Superkingdom	Kingdom	Subkingdom	Class/Type	
Eucaryota	Animalia	Metazoa	Brachipoda	Brachipoda
Eucaryota	Animalia	Metazoa	Annelides	Polychaeta
Eucaryota	Animalia	Metazoa	Onychophora	Onychophora
Eucaryota	Animalia	Metazoa	Arthropoda	Insecta
Eucaryota	Animalia	Metazoa	Echinodermata	Asteriodea
Eucaryota	Animalia	Metazoa	Chaetognatha	Chaetognatha
Eucaryota	Animalia	Metazoa	Pogonophora	Pogonophora
Eucaryota	Animalia	Metazoa	Hemichordata	Enteropneusta
Eucaryota	Animalia	Metazoa	Tunicata	Ascidiacea
Eucaryota	Animalia	Metazoa	Vertebrata	Pisces

corresponding measurement methods, the ecological significance of the species, its sensitivity to environmental pollution, its abundance, and other factors.

The information obtained in this phase about the sensitivity field of biota with respect to environmental pollution changes (dose/response) can in itself serve as the basis for a simple approximate prognosis. To obtain a more precise prognosis, data on interactions among species will be required in addition to this information (see "Introduction").

Subprogram C--Field Checks of the States of Biota

This subprogram is dictated by the need to correct the errors and inaccuracies which arise during the evaluations and prognoses of the states of biocenoses undertaken in subprograms A and B. Periodic verification of predictions of the states of biota through modeling requires traditional counts of the numbers of selected natural populations. Those biological species which are recognized as most sensitive to the influence of pollutants should be checked during subprograms A and B.

Conducting a correct and optimal count requires having information on the autocorrelation function of the distribution of population density in space and time for the particular species. Data on autocorrelation functions of this kind for especially sensitive species (or for species suspected of this property before subprograms A and B have been performed) should be systematically collected and preserved in the scientific center. The results of traditional counts can serve as the basic material for such assessments.

This subprogram will be carried out and is in fact already being carried out by the staff of a natural reserve and during specialized biological expeditions. It is only necessary to unify the data format and the methods of their statistical analyses.

CONCLUSION

The described program of complex ecological monitoring of pollutants will be implemented, and is already being implemented in part, in natural biosphere reserves of the U.S.S.R. We realize that it is still far from optimal, and with respect to its biotic aspects, it has still not passed the test of experience, though it has been theoretically substantiated. However, we have no question about its basic propositions and approaches. Beginning from practically nothing, we hope that in a few years the proposed program will be steadily perfected and will be able to provide us with the information so necessary for managing the quality of the environment--predictions of global environmental pollution and its ecological consequences.

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RECOMMENDED POLLUTANT MONITORING SYSTEM FOR BIOSPHERE RESERVES

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Abstract

Biosphere reserves have been established worldwide as a part of the UNESCO Man and the Biosphere Program. Part of this program is the development of a relatively inexpensive pollutant monitoring system that can be used in a variety of biosphere reserves and that can produce data that are comparable between reserves. The Environmental Monitoring Systems Laboratory, in cooperation with the U.S. National Park Service, has been working on the development of such a system for the last two years. This paper presents some conclusions and recommendations for the design of a pollutant monitoring system. Pollutants of concern were primarily those which had a real or suspected long-term transport characteristic.

Types of samples collected include those of air, water, soil, vegetation, and forest floor. Sampling design is covered, including layout of sampling blocks, subsampling, sample handling, and preservation.

Analytical procedures were chosen for their ability to detect suspected pollutants and for their cost-effectiveness. Multielemental analytical techniques were used whenever possible. Multiorganic analytical techniques were also used where available.

Mathematical models were applied to help determine the optimum monitoring system design. The modeling technique is briefly described, and results are shown using lead as an example.

Finally, current international cooperative efforts in the area of pollutant monitoring on biosphere reserves are reviewed.

INTRODUCTION

The Environmental Monitoring Systems Laboratory of the U.S. Environmental Protection Agency is developing a multimedia, integrated pollutant monitoring system for biosphere reserves. This system, which will eventually be used as part of the Global Environmental Monitoring System (GEMS) (Wiersma et al. 1978a and 1978b), is based on the basic principle of monitoring systems design as laid down by Schuck and Morgan (1975), Morgan et al. (1979), and Munn (1973). We have used their systems approach to design a monitoring system for individual biosphere reserves.

Munn stresses the need for a systems approach to the design of a global monitoring system and expands on the need for background monitoring stations:

> The point of view has sometimes been advanced that there is no point in monitoring insignificant concentrations of even potentially harmful substances at remote stations. This philosophy is not always valid, however, because threshold concentrations that cause biological effects are not absolutes. In many parts of the world, biological systems are in delicate equilibrium with their natural environments through the process of adaptation. Minute increases in the concentrations of particular substances may have significant effects, particularly if there are accumulating organisms in the food chains. . . .
>
> Another justification for measuring on the global scale is in connection with trends and cycles. In the first place, there is likely to be less day-to-day variability at remote stations, so that long-term trends and seasonal cycles are easier to detect. Secondly, a network limited to a single region does not permit separation of regional from global effects. This separation is of particular importance if the trends are due to natural geochemical phenomena.

Our reasons for using biosphere reserves for pollutant monitoring are as follows:

They serve as locales for background reference levels of certain pollutants.

They provide a frame of reference against which changes in impacted areas can be measured.

They may reflect changes of a global nature long before such changes are obvious in more impacted areas. In other words, they can serve as an early warning system for pollutants transported over long distances.

THE GLOBAL FRAMEWORK

An understanding of both the Man and the Biosphere Program (MAB) and GEMS will help to establish the context within which a pollutant monitoring system will operate on the reserves.

Man and the Biosphere Program

MAB was authorized in 1970 at the 16th general conference of the U.N. Educational, Scientific, and Cultural Organization (UNESCO), and the U.S. MAB Committee was established in 1972. The program has four major objectives:

> to study the general structure and functioning of the biosphere and its ecological regions
>
> to make systematic observations of changes brought about by man on the biosphere and its resources
>
> to study the overall effect of changes upon humans
>
> to provide public information and education needed about these subjects (Risser and Cornelison 1979)

MAB is divided into 14 project areas, of which project area 8 (MAB 8) is concerned with biosphere reserves. The need for biosphere reserves was outlined by an expert panel in 1973 (Programme on Man and the Biosphere 1973). The panel recommended that a set of criteria be developed for selecting and establishing a network of baseline stations in undisturbed, representative biome areas.

In May 1974, a task force set up the criteria for selecting and establishing biosphere reserves and defined the objectives as follows:

> to conserve for present and future human use the diversity and integrity of biotic communities of plants and animals within natural ecosystems, and to safeguard the genetic diversity of species on which their continuing evolution depends
>
> to provide areas for ecological and environmental research consistent with the previous objective, including particularly baseline studies both within and adjacent to these reserves
>
> to provide facilities for education and training (Programme on Man and the Biosphere 1974)

To date, over 144 reserves have been established in 35 countries, including 33 in the United States.

Global Environmental Monitoring System

The recognition of the need for a global monitoring system for pollutants in remote or background areas preceded the establishment of biosphere reserves by several years. Lundholm (1968) defined the need for such global stations as follows:

> Society is to an ever-increasing degree demanding information on how production in the natural environment is and will be affected by pollution. One reason why the value of the ecologist has not been sufficiently recognized by governments is that often he did not have the basic environmental information on which he can assess changes and base recommendations for action or advance warnings on the effects of man's activities on the natural habitats.
>
> There is an urgent need to create a kind of an early warning system based on long time series of environmental data from strategically situated stations or sampling areas. In order to follow the changing situation in the biosphere we need a network covering the globe. As the interest is focusing not on the local variations, but on the background levels and changes, the number of stations (or sampling areas) in such a network can be kept rather low. . . . The aim is to erect a global network of baseline stations (sampling areas) devoted to monitoring biotic as well as abiotic factors in the environment. The purpose is to have a means of assessing short term and long term changes caused by a selection of factors, including many forms of pollution. The erection of network is motivated mainly by the threat of pollutants.

The Swedish Natural Science Research Council (Ecological Research Committee 1970) and the U.S. Ad Hoc Task Force on the Global Network for Enviromental Monitoring (GNEM 1970) also called for the establishment of a global monitoring system. The administrative framework for GEMS was established in Stockholm, Sweden, at the U.N. Conference on the Human Environment. GEMS was part of Earthwatch, an activity of the U.N. Environment Program (UNEP).

An interagency working group (Task Force II, Committee on International Environmental Affairs 1976) was established in 1974 to list what should be monitored, including recommendations for the structure and operation of a U.N. global environment program. This working group set up Earthwatch with four integral components: monitoring (GEMS), research, evaluation, and information exchange. This working group also established the principle that these activities were to be carried out, wherever possible, in cooperation with ongoing and planned activities:

> Earthwatch reference sites would be expected to provide a coherent, integrated base of benchmark data and information on physical, chemical, and biological conditions for determining long-term trends of environmental processes. These sites should include selections from ongoing and planned activities, such as, (a) World Meteorological Organization (WMO) baseline and upper atmospheric programs; (b) hydrology stations; (c) lake biome programs; (d) Man and the Biosphere (MAB) biome programs; (e) open ocean baseline sites; (f) river outflow stations; and (g) inventory programs including those for deserts, forests, wet lands, and grazing lands.

From the above, it is obvious that MAB was conceived to serve as an important component of Earthwatch. Martin and Sella (1976) listed the goals of GEMS as follows:

> to establish an expanded human health warning system
>
> to assess global atmospheric pollution and its impact on climate
>
> to assess the extent and distribution of contaminants in biological systems, particularly food chains
>
> to assess critical environmental problems related to agriculture and land and water use
>
> to assess the response of terrestrial ecosystems to pressures exerted on the environment
>
> to assess the state of ocean pollution and its impact on marine ecosystems
>
> to develop an improved international system, allowing for the monitoring of factors necessary for understanding and forecasting disasters and for implementing an efficient warning system.

The incorporation of the biosphere reserve concept (or remote areas set away in perpetuity) with the terrestrial component of GEMS was specifically called for by the International Environmental Programs Committee (1976) of the National Research Council of the United States. Franklin (1977) also listed the biosphere reserves as a component of GEMS. The International Coordinating Council of the Programme on Man and the Biosphere (1978) officially recognized the link between GEMS and the biosphere reserve system. The council recommended that

> coordinated monitoring activities in biosphere reserves be developed in conjunction with the Global Environmental Monitoring System (GEMS) of UNEP, and with associated worldwide monitoring activities in the fields of climatology,

atmospheric pollution, and environmental health sponsored by WMO and WHO

UNEP provide support to developing countries to enable them to undertake appropriate monitoring activities in selected biosphere reserves

Recently at a U.N. meeting in Geneva, steps to effect these recommendations were taken. UNEP/GEMS agreed to establish three biosphere reserves as part of the terrestrial components of GEMS. These reserves were to be located respectively in the U.S. the U.S.S.R., and possibly Chile as representative of a developing country. A tentative design for monitoring was established, including the monitoring of basic ecological processes as well as of pollutants.

In summary, GEMS is using the biosphere reserves as part of its terrestrial monitoring component. The program is designed to monitor pollutants and basic ecological processes.

RECOMMENDED DESIGN PRINCIPLES

This paper sets out recommended design criteria for a pollutant monitoring system for biosphere reserves. The specific design principles we applied are discussed below and include the following:

The monitoring system is multimedia.

A systems approach is used to relate the environmental media and aid in final design recommendations.

The monitoring system is pollutant oriented.

Every effort is made to eliminate the influences of local pollution sources in the reserve.

Quality assurance procedures will apply at all phases of the project.

Multimedia

A monitoring system should be able to trace a pollutant from a source to a sink or exit point. In most terrestrial remote areas the pollutant input to the reserve site is by means of air currents. The ultimate sources, while in most cases easily associated with man's activity in general, are currently difficult to locate. Therefore, input should be measured in the form of atmospheric concentrations, deposition, and rain. Output from most biosphere reserves will be streams and rivers draining the area and the loss of pollutants by means of this route can be determined by sampling representative drainages. The identification of the potential sinks and pathways of movement of the pollutants requires sampling in other environmental media.

Currently, our sampling covers air, deposition phenomena, water, soil, forest litter, and a variety of vegetative species. Animal specimens, terrestrial as well as aquatic, were not collected because of the difficulty of collection and of getting a representative sample. This does not mean that under more intensive monitoring programs such samples would not be appropriate. Different species of plants are collected to determine if one or more species stand out as effective biomonitors of pollutants.

Finally, the multimedia monitoring approach sets the stage for interpreting man's impact on his environment, particularly when detailed data on ecological processes on the various sites become available.

Systems Approach

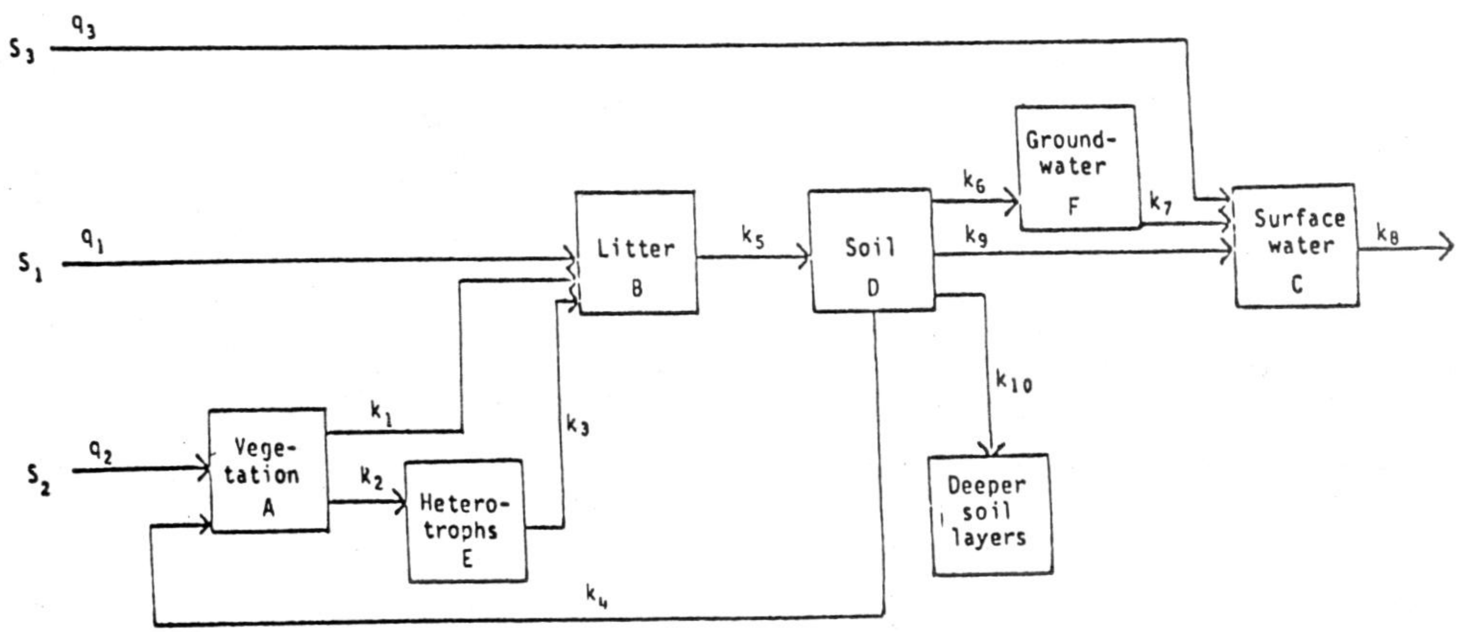
Munn (1973) states that it is essential that GEMS be designed in such a way that interactions between media can be studied, permitting delineation of the pathways of biogeochemical cycling. This requires a systems approach and is as applicable to the design of a system on a reserve as it is to putting the entire GEMS system together. A promising technique for accomplishing this is the use of kinetic models. Theoretical bases of these models have been described in detail by O'Brien (1979), Miller and Buchanan (1979), and Barry (1979). Wiersma (1979) applied this approach to the analysis of the biosphere reserve monitoring project in Great Smoky Mountains National Park.

This approach starts with a schematic representation of the system to be monitored. It must be emphasized at the outset that what is intended is not a predictive model, but merely a heuristic tool to help design and evaluate the system of interest. The kinetic analysis approach does this by forcing one to consider the system as a whole at the time the monitoring program is being conceived. Doing this also sets up a procedure for carrying out the data analysis.

Figure 1 is a schematic representation of the Great Smoky Mountains system. It represents a cross between what is practical to monitor and an approximation of the system of interest. Once this is done the components of the environment that need to be sampled are readily apparent. Basic statistical procedures are now employed to design representative sampling in each identified compartment. The specifics of the sampling that was carried out for the various compartments identified are described by Wiersma et al. (1978b and 1979).

Once a schematic representation of the system is in hand, the equations approximating the dynamics of the system are derived. The differential equations for the Great Smoky Mountains Biosphere Reserve, represented in figure 1, are given below:

Figure 1: Schematic diagram of movement and distribution of lead in Great Smoky Mountains National Park.



$$\frac{dQ_A}{dt} = q_2 + K_4Q_D - Q_A (K_1 + K_2)$$

$$\frac{dQ_B}{dt} = q_1 + K_1Q_A + K_3Q_E - K_5Q_B$$

$$\frac{dQ_C}{dt} = q_3 + K_7Q_F + K_9Q_D - K_8Q_C$$

$$\frac{dQ_D}{dt} = K_5Q_B - Q_D (K_4 + K_9 + K_6 + K_{10})$$

$$\frac{dQ_E}{dt} = K_2Q_A - K_3Q_E$$

$$\frac{dQ_F}{dt} = K_6Q_D - K_7Q_F$$

These equations can be solved in several ways. Computer simulation techniques are applicable under both steady-state and non-steady-state conditions. Matrix algebra can also be used to solve the system of equations. If steady-state conditions are assumed, conventional algebraic techniques are applicable. The system in the Great Smoky Mountains Biosphere Reserve was run using lead as a test case, and it assumed steady-state conditions. The steady-state equations (expressed as concentrations) are given below:

$$C^*_A = \frac{q_2 (K_9 + K_6 + K_{10}) + K_4 (q_1 + q_2)}{M_A (K_1 + K_2) (K_9 + K_6 + K_{10})}$$

$$C^*_B = \frac{(K_4 + K_9 + K_6 + K_{10}) (q_1 + q_2)}{K_5 M_B (K_9 + K_6 + K_{10})}$$

$$C^*_C = \frac{q_3 (K_9 + K_6 + K_{10}) + (q_1 + q_2) (K_6 + K_9)}{K_8 M_c (K_9 + K_6 + K_{10})}$$

$$C^*_D = \frac{q_1 + q_2}{M_D (K_9 + K_6 + K_{10})}$$

$$C^*_E = \frac{q_2 K_2 (K_9 + K_6 + K_{10}) + K_4 K_2 (q_1 + q_2)}{K_3 M_E (K_1 + K_2)(K_9 + K_6 + K_{10})}$$

$$C^*_F = \frac{K_6 (q_1 + q_2)}{K_7 M_F (K_9 + K_6 + K_{10})}$$

Symbols used are defined as follows:

C^*_i = Steady-state concentration of lead in compartment i

M_i = Mass of compartment i

Q_i = Quantity of lead in compartment i

q_1 = Amount of lead deposited on ground surface per hectare per year

q_2 = Amount of lead deposited on overstory leaf surface per hectare per year

q_3 = Amount of lead deposited on open surface water per hectare per year

The rate constants (K_i) are estimated from literature. When unavailable from the literature, laboratory techniques such as microcosms are useful.

The equations are solved and the calculated values compared against the measured values from the monitoring program. The results of this exercise for lead are shown in table 1. In this case there is close agreement between calculated and measured values.

Certain facts stand out from this analysis concerning the final design of the monitoring system. First, if plasma emissions were the analytical technique of choice for water analyses, then water sampling for lead may be discontinued because the input to the Great Smoky Mountains Biosphere Reserve would have to increase 25 times before the lower detection limit of the plasma emission system was exceeded. On the other hand, forest litter appears to be a good sampling medium because it appears to "concentrate" lead. Similar types of analyses would have to be run for other representative pollutants before a final monitoring program could be designed. The advantages of this systems approach are as follows:

It forces the designer to consider the system as a whole rather than as a series of distinct environmental components.

It forces an analysis and consideration of the physical, chemical, and biological factors affecting pollutant transport and distribution in the system.

It sets up an analytical procedure for data analysis at the time the monitoring system is designed.

It shows the functional relationship between pollutant levels in different environmental media.

It identifies points where sampling design could be changed to provide for a more efficient monitoring system.

It identifies gaps in the current knowledge of physical, chemical, and biological factors influencing transfer of pollutants and provides guidance to controlled studies addressing pollutant kinetics.

Table 1. Comparison of calculated steady-state levels with field measurements from Great Smoky Mountains National Park.

Component	Calculated level	Measured level
C^*_A - Vegetation	148 mcg/g	34 to 40 mcg/g (Moss samples from understory)
C^*_B - Forest litter	239 mcg/g	273 mcg/g
C^*_C - Surface water	0.002 mg/l	None detected by ICPES (detection limit - 0.05 mg/l) None detected by SSMS (detection limit - 0.001 mg/l)
C^*_D - Soil	18.5 mcg/g	16 mcg/g
C^*_E - Heterotrophs	Not calculated	Not measured
C^*_F - Groundwater	0.0005 mg/l	None detected by ICPES (detection limit - 0.05 mg/l) None detected by SSMS (detection limit - 0.001 mg/l)

Pollutants

The selection of a limited number of pollutants to measure in background areas has been a common recommendation by many scientists concerned with monitoring systems development in background areas (Munn 1973; Task Force II, Committee on International Environmental Affairs 1976; Ad Hoc Task Force on GNEM 1970). Virtually all the pollutants suggested had a potential for long-term transport. However, advances in chemical analytical techniques allow us to reconsider this approach. For example, trace element techniques for a variety of media are now multielemental (Jaklevic et al. 1973, 1976; Dzubay and Stevens 1975, and Anderson et al. 1975).

Spark source emission spectroscopy will give 26 elements per sample at one analysis. It is primarily useful for samples such as vegetation and forest litter. X-ray flourescence will measure over 20 trace elements on air filter pads at one time, and inductively coupled plasma emission spectroscopy will give 26 elements at one analysis for water samples. Spark source mass spectrometry will give estimates for virtually all elements in water samples. Neutron activation is another useful multielemental technique.

When using these techniques, speed of analysis is greatly increased, thereby reducing costs significantly. In addition, data analysis is simplified because the data output from these multielemental analytical systems can be readily placed on computer tape. However, detection limits are sometimes slightly higher than detection limits for the same element analyses by atomic absorption spectrometry. In addition, precision may be less with multielemental techniques. The initial purpose of measuring pollutants on reserves may allow for a decreased degree of analytical precision as well as decreased detection limits in the interest of cost.

Certain trace elements may still have to be analyzed with specialized, highly sensitive techniques. These would be elements of proven long-range transport capabilities and significant toxicity to ecosystems.

Multiresidue techniques for trace organics are not as advanced as multielemental techniques. Also, they are more expensive than multielemental techniques. Multiresidue techniques are available for the major types of pesticides in most environmental samples. The techniques are routine enough that they can be recommended for use as part of a biosphere reserve monitoring program and were used in our studies.

Multiorganic residue techniques (nonpesticide) are currently available for media such as air, water, and fish tissues. However, they are probably not suitable for biosphere reserve monitoring at this time because of their limited availability, the rapid development and evolution of these techniques, and their high costs ($900 to $1,500 per sample).

The number of samples required depends on the desired confidence limits and the amount in sampling error. In our studies we arbitrarily desired a sampling error of plus or minus 10% at the 95% confidence level. For example, if witch hobble, shown in table 2, was chosen as a sample species and strontium as the element, it would be necessary to collect approximately 23 samples. Similar estimates can be made for all species and elements. During field sampling and analysis, the number of samples used would probably be controlled by the sample/element combination, with the greatest variability tempered by the resources available.

For samples that exhibit a large coefficient of variation such as the manganese in rhododendron, the number of samples required to meet precision levels as stated would be approximately 100. A decrease in precision of only 2% would reduce the number of samples required to 71. Our conclusion concerning the required number of vegetation samples for a biosphere reserve monitoring system is that the number required for our desired confidence level is reasonable, and a cost-effective system can be designed.

Table 2. Coefficients of variation for elemental levels in vegetation samples collected in Great Smoky Mountains Biosphere Reserve.

Sample		Elements (%)				
		Mn	Mg	Al	Sr	Ba
Rhododendron	- site 11	21.4	38.5	51.4	30.4	22.3
Rhododendron	- site 12	13.5	39.8	25.9	26.0	22.1
Rhododendron	- site 14	15.3	50.4	22.3	37.8	17.3
Witch hobble	- site 13	20.5	30.9	22.6	23.9	11.9
Nettle	- site 11	27.2	54.2	66.8	28.7	31.1
Christmas fern	- site 12	18.5	10.8	21.9	23.2	26.1
Wood fern	- site 13	10.6	64.6	20.0	34.6	12.1
Yellow birch	- site 14	34.2	45.4	30.9	24.9	26.6

Another consideration in determining the number of samples collected is the interaction of analytical error with field sampling error. All vegetation and litter samples in our studies were analyzed in triplicate and replicated nine or ten times on each sample site. With this type of design, analysis of variance techniques to determine the variability from the analytical error versus that from field sampling was accomplished (Snedecor and Cochran 1967). The estimated variance of the sample mean per determination is given by the mean square between blocks divided by the total number of determinations. This in turn can be partitioned into the various components that contribute to this variance of the individual sample mean per determination. For example, for cobalt in forest litter, 2.2% of the variation per determination is due to analytical error, 11.1% is due to subsamples from within each site, and 86.7% is due to variation between the sites. For lead in forest litter, the estimated variance of the sample mean per determination is broken into the following relative contributions: 1.9% from analytical error, 7.4% from variability within a site, and 90.7% from variability between sites, despite the fact that the precision limits of acceptance for lead are plus or minus 50%. This is an example that, as large as the analytical error may be, the field error is much greater. Therefore, to reduce field study error and to increase the reliability of estimating trace element levels, more effort should be expended on collecting samples in the field and less on reducing or improving analytical precision. Similar types of calculations were made for all elements in the forest litter; however, no deviations from the above pattern were noted.

Remote Sites

Selected sampling sites should be free of local contamination. Sampling should be at least 5 km from the nearest road used by automobiles and other vehicles. Special care should be used in selecting the air monitoring sites. Suggested criteria for locations of air sampling sites used in a previous study (Wiersma et al. 1979) were as follows: at least 8 km from the nearest road that had any automobile traffic, at as high an elevation as possible, and in a cleared area whose diameter was at least five times the height of the surrounding forest.

Quality Assurance

Field sampling must be as representative as possible. Terrain considerations sometimes preclude totally random sampling. In these cases, a grid sample is sufficient. Soil samples collected should be made up of a composite of a number of subsamples. Details on how this sampling was accomplished in the field are given by Wiersma (1979) and Wiersma et al. (1978a, 1979a).

Handling of samples should be minimized. Vegetation and forest litter samples collected for trace element analyses are processed in the following manner to avoid excessive handling. Clean polyethylene bags (supplied by Clean Room Products) were used to collect samples in the field. These were then placed inside another bag and sealed. They were shipped to the laboratory where immediately upon receipt the bags were opened (sample not removed) and placed in a drying oven at about 60°C for approximately 24 hours. After drying, the samples were taken into the laboratory and the vegetation broken up by hand. The technician used a new pair of surgical gloves to handle each sample. A subsample was placed in an unused 73 cc plastic vial. Two Teflon balls were put in the vial and the vial placed in a Spex mill. The vegetation sample was ground to a powder inside the vial. The Teflon balls were removed and washed. An aliquot of the powder sample was sent to the analytical laboratory where it was analyzed directly. The remainder of the powdered sample (in the same vial) was archived.

This procedure obviously would not work for organic samples. Samples for pesticide analyses were placed in prewashed Teflon bottles, but because of the requirement for extraction, the sample handling was unavoidably increased.

Soil samples were composites of 10 subsamples. They were placed in clean bags when possible. Soil samples for pesticide analyses were placed in Teflon containers. More handling of soil samples was required because they required sieving and acid digestion. Specific details are given in Wiersma et al. (1979a).

Water samples for trace element analyses were dipped from streams and small rivers. Polyethylene bottles were used that had previously been cleaned. Samples were acidified in the field with a small amount of ultrex nitric acid. Trace organic analyses were sampled with special resin filters operated in the field or collected in 5-gallon carboys and extracted in the laboratory. The specific procedures are described by Wiersma et al. (1979a).

Air samples were primarily for trace metals. Details of this sampling are given by Wiersma et al. (1979b). To check for trace elements on air filters, three different analytical techniques were used: X-ray fluorescence, atomic absorption spectrometry, and scanning electron microscopy (SEM). Since the air sampling locations were remote, low trace element concentrations were expected. The low sample flow rates (1,000 cc/min) dictated special care in handling the sampling heads. Whenever possible, stainless steel filter holders were used. Filter holders and filters were washed and cleaned in a laboratory facility designed to have minimal trace element contaminants. They were triple-bagged in clean bags and not opened until ready to be used in the field. The sample heads were sent for AA analyses wrapped in clean plastic bags. They were not disassembled until in the laboratory. This type of handling was not necessary for samples sent for SEM analyses.

All phases of sampling are interrelated. While the extreme measures instituted above are good sampling procedures for any remote area, they were necessitated in part by the low volumes of air sampled. This was a direct result of the need to use low power consumption air pumps that were operated by batteries (Brown et al. 1979). Therefore, if flow rates could be increased or sample times lengthened, the reliability of the sample could be increased. New power sources are currently being investigated. These include remotely located solar panels and metal hydride fuel cells.

Wherever possible, quality assurance procedures were applied to samples submitted for analyses. The soil sample extracts were submitted with a minimum of 10% quality assurance samples. These included spiked samples, acid blanks, and replicates. Vegetation and litter samples also contained up to 10% quality assurance samples. Samples were submitted in ascending numerical order. The contractor was required to analyze the samples in the order submitted. Every tenth sample alternated between a National Bureau of Standards certified sample and a replicate sample. This latter sample was always taken from a large quantity of dried, powdered lettuce. The purpose of the repeated use of the same sample was to detect instrument drift. Prior to the submission of field samples, vegetative standards obtained from the National Bureau of Standards with certified trace element levels were submitted as quality assurance samples. Based upon the results of these standards, expected precision limits were calculated for this analytical technique (see table 3).

Table 3. Precision limits for spark source emission spectrometry.

Elements	Maximum allowable percentage deviation from a known value or COV of replicates
K, Ca, Mg, Cu, Mn, B, Sr, Ba, Al	20%
P, Na, Zn, Fe, Cr, Ag, Ti, V	40%
Li, Pb	50%

Minimum detection limits:

Element	ppm	Element	ppm	Element	ppm
P	50.0	B	0.2	Sr	0.2
Na	1.0	Al	0.1	Ba	0.2
K	150.0	Si	1.0	Li	0.3
Ca	1.0	Ti	0.5	Ag	0.1
Mg	50.0	V	1.0	Sn	0.3
Zn	5.0	Co	1.5	Pb	1.0
Cu	0.2	Ni	0.5	Be	0.2
Fe	0.6	Mo	0.2	Cd	3.0
Mn	0.1	Cr	0.2		

Similar quality assurance procedures were applied to other media. Where known value samples were difficult to obtain, two different analytical procedures were used on the same sample or on paired samples collected at the same location.

Data handling is also an essential part of quality assurance. Where possible, manual handling of data was avoided, particularly if large quantities of data were involved. For some of the analyses (trace elements in litter and vegetation), data were placed directly on magnetic tape. This included all field samples, all quality assurance samples, and internal machine check samples. These were then placed on an interactive computer system. Data files could be edited and analyzed from remote terminals. This procedure eliminates several data-transcribing steps and immeasurably speeds up the analysis of data.

CONCLUSIONS

Monitoring pollutants in background areas (i.e., biosphere reserves) is of value for both U.S. governmental environmental agencies and international environnmental agencies.

Pollutant monitoring on biosphere reserves can serve as an early warning of pollutant dispersal.

Pollutant monitoring on biosphere reserves can give background estimates of pollutants and serve as a technique for determining long-term environmental trends.

Biosphere reserves are beginning to fulfill the terrestrial monitoring requirements of GEMS.

Monitoring of pollutants on biosphere reserves is practical and can be carried out in a cost-effective manner.

Monitoring on biosphere reserves should be multimedia.

A systems approach is useful in designing and analyzing a monitoring project on biosphere reserves.

Pollutant kinetics are an essential part of the systems approach to monitoring.

Extreme care is necessary to ensure sample representativeness.

Extreme care should be taken to prevent sample contamination.

Sample variability is manageable on biosphere reserves.

Multielemental techniques are cost-effective when semiquantitative screening of pollutants is desired.

Multiresidue techniques for organic compounds are suitable for routine use when pesticides are measured, but are not ready for other organic compounds.

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THE RESPONSE OF THE NATIONAL ATMOSPHERIC DEPOSITION PROGRAM TO THE GROWING PROBLEM OF ATMOSPHERIC DEPOSITION

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Abstract

The recognition in the United States that atmospheric deposition poses a serious threat to aquatic and terrestrial ecosystems has resulted in increased awareness of the need for deposition monitoring and effects research. The declining fish populations in lakes in the Scandinavian countries, in Canada, and in the Adirondack Mountains of the United States has been directly linked to acidity increases resulting from deposition of acidic matter in both wet and dry deposition. The National Atmospheric Deposition Program (NADP) has established a national monitoring network to measure both wet and dry deposition and is conducting research into effects on agricultural crops, forests, and freshwater lakes and streams. Twelve of the sites in the NADP deposition monitoring network are located in national parks that are designated as biosphere reserves and support MAB-8 monitoring objectives.

INTRODUCTION

It has been only in the last two or three years that widespread concern has been expressed in the U.S. about the problem of atmospheric deposition, particularly acidic precipitation. In 1975 the First International Symposium on Acid Precipitation and Forest Ecosystems was held at Ohio State University (Dochinger and Seliga 1976). This symposium, attended by scientists from the U.S., Canada, and Europe, highlighted the significance of acid precipitation and its long-range implications. In 1976, Gene Likens, Cornell University, published a review article titled "Acid Precipitation." In this article Likens summarized what was known at that time about acid precipitation, particularly in Europe and North America. This article and proceedings of the first international symposium were responsible for alerting a broad spectrum of the scientific community to the fact that we in the U.S. indeed were experiencing an increase in acidity of precipitation, particularly in the northeastern U.S., and that there was potential for serious environmental damage.

The U.S. at that time had mounted only sporadic efforts to determine precipitation pH, so little historical data was available. Attention was first drawn to the problem of acid rain by the studies in Europe, particularly in the Scandinavian countries. A network for the monitoring of precipitation chemistry was established in the late 1940s in Sweden by Egner and Eriksson. In the 1950s this was extended to include much of western Europe. Using the European network data, Oden showed that since the mid-1950s, precipitation in northwestern Europe has not only become increasingly acidic but very widespread geographically. Hydrogen ion concentration increased by a factor of 200 over a 20-year period. It was also established that sulfur (and nitrogen compounds) in the atmosphere were the primary contributors to the strong acid content of precipitation. In Sweden it was demonstrated that more than 70% of the sulfur in the atmosphere could be traced to anthropogenic sources and that 77% of this sulfur originated outside Sweden. Thus, the concept of long-range transport of pollutants and their deposition in areas hundreds of kilometers from the source was introduced. A 1977 study by the Organization for Economic Cooperation and Development confirmed quantitatively the implications from trajectory analyses done by Oden in 1967-68. Further, it was determined during this period of increasing acidity of precipitation that there has been a decline in the pH of thousands of lakes and streams in Norway and Sweden and that the increased acidity had resulted in the decline of various fish species, particularly trout and salmon.

In contrast to the European data, the data on acidity of precipitation in the U.S. has been limited. Information was developed by Junge for a brief period during the 1950s. In this case, pH was not measured but was calculated from the chemical composition of the precipitation. From 1960 through 1967, the Public Health Service and the National Center for Atmospheric Research initiated measurements of pH throughout the U.S. Samples of wet precipitation only were collected monthly at 30 stations. Cogbill and Likens assembled data from a number of sources and calculated pH values for the eastern U.S. for the period 1972-1973. When compared with the data from 1955-1956, the data from 1964-1966 and 1972-1973 showed not only a decreasing pH in the northeastern U.S. but also a widening distribution of pH values less than 5. In the 1976 review, Likens pointed out the similarity between the situation in Europe and the growing acidity of precipitation in the U.S. Also recognized was the fact that several hundred lakes in the Adirondacks appeared to be undergoing acidification, with declining fish populations.

In 1976 most of the concern over this problem was still confined to the scientific community. As a result of this concern, a group of scientists from the academic community and a number of federal agencies assembled in Washington, D.C., in 1976 under the leadership of Ellis Cowling and with the support of the state agriculture experiment stations and the U.S. Department of Agriculture. The purpose of this meeting was to discuss action that should be taken to determine the magnitude of the problem of atmospheric deposition and potential long-term effects on forests, streams, lakes, and agriculture. Out of this meeting and several succeeding meetings grew the North Central Regional Project on Atmospheric Deposition 141 (NC 141), later to become known as the National Atmospheric Deposition Program (NADP). This program, organized through the state agricultural experiment stations, developed a plan entitled, "Chemical Changes in Atmospheric Deposition and Effects on Agriculture and Forested Land and Surface Waters in the United States" (Cowling et al. 1978). This plan outlined a program to meet the objectives listed in table 1. The first and most urgent objective was to develop a much needed regional deposition chemistry monitoring network covering the entire U.S.

During this period, there was a growing awareness in Canada of the problem of atmospheric deposition and acid precipitation. In 1975, the Canadians initiated a network of approximately 50 stations across Canada to sample precipitation on a monthly basis. This Canadian Network for Sampling Precipitation (CANSAP) served as a guide for the establishment of the NADP monitoring program. After much discussion over sampling techniques, frequency, methods for obtaining the chemical analyses, the location of monitoring stations, and many other questions which were important to network design and operation, the NADP network was initiated in 1978 with approximately 20 stations. These 20 stations were primarily supported by the state agricultural stations and the U.S. Forest Service, with additional financial support from the U.S. Department of Agriculture and the U.S. Geological Survey. During the first year of operation, the network doubled in the number of operating stations, with most of the increase coming in stations east of the Mississippi River. Late in 1979 the U.S. Department of the Interior committed major support to the monitoring network through the Bureau of Land Management and the National Park Service--these new monitoring stations were located primarily west of the Mississippi River. Support for the network was also obtained from various state agencies and private institutions. More recently, the U.S. Environmental Protection Agency (EPA) committed its support to the monitoring network by requesting that the NADP incorporate the EPA/National Oceanic and Atmospheric Administration (NOAA)/World Meteorological Organization (WMO) sites into the NADP monitoring network. These sites will be transferred to the NADP early in 1980. In addition, EPA plans to support an additional 30 to 40 sites over the next one to two years.

Table 1. NADP objectives.

Establish an atmospheric deposition network to determine spatial and temporal trends in the supply of beneficial nutrient elements and potentially injurious substances in precipitation and dry particulate matter deposited in various regions of the United States.

Determine the relative importance and contribution of precipitation, dry particulate matter, aerosols, and gases to the total atmospheric deposition in various states and regions in the United States.

Develop optimal procedures for collecting precipitation and dry particulate matter.

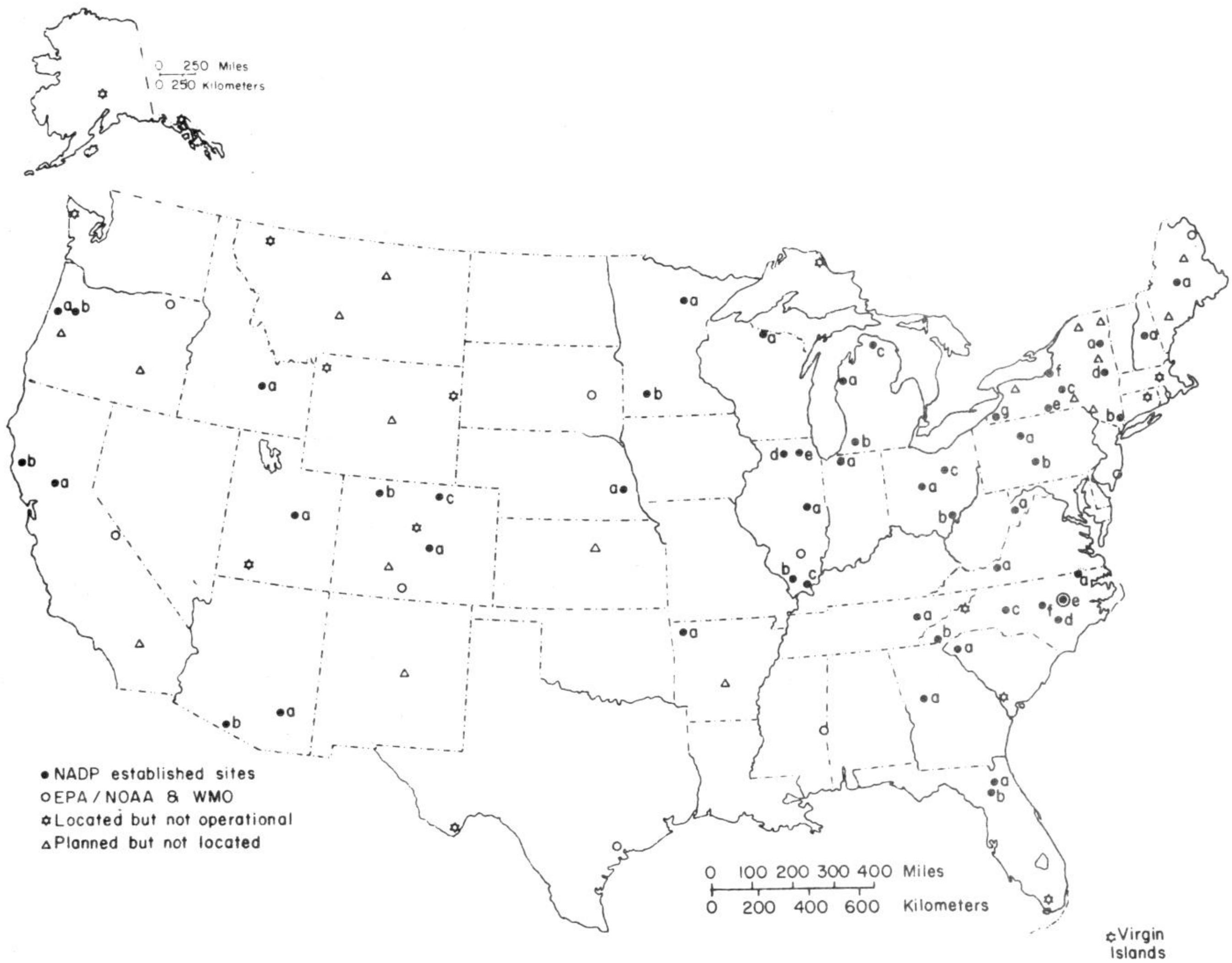
Determine the stability of certain constituents of precipitation during collection, transport, and storage prior to analysis.

Investigate the transport and transformations of atmospheric constituents.

Organize and coordinate research in the state agricultural experiment stations and other research institutions and agencies on the effects of changes in atmospheric deposition on (A) the productivity of agricultural crops, forests, rangelands, wetlands, and surface waters; (B) the health and productivity of domestic food animals, wildlife, and fish; and (C) the corrosion of metals, painted surfaces, masonry, and other materials in machinery or structures.

A review of the objectives for the NADP reveals that the establishment of an atmospheric monitoring network was a necessary first step in determining the effects of atmospheric deposition on forests, agriculture, lakes, and streams. Simultaneous with the development of the monitoring network, the NADP actively pursued the identification of research needs to quantitatively assess the potential for increased atmospheric deposition and the potential for the deterioration of the aquatic and terrestrial environments. These research needs, particularly as applied to acid rain, were published in a 1978 report to the Council on Environmental Quality (Galloway et al. 1978). This report was a basis for a presidential initiative for research and monitoring in the U.S. The national plan was outlined in President Carter's 1979 environmental message, which called for the expenditure of some $10 million to fund the necessary research and monitoring programs. A number of bills are now pending in Congress that will provide increased support for research and monitoring. Indeed the effort of NADP scientists and others has aroused the awareness of the public, which has prompted action by both the legislative and administrative branches of the government. As a result of the widespread recognition of the problems of acid precipitation, a major research effort has been mounted by the EPA. In August 1979, the NADP, through Dr. Ellis Cowling at North Carolina State University, was awarded an initial grant of $500,000 from EPA to organize and coordinate research to determine the magnitude and distribution of both long- and short-term effects of the increased acidity of precipitation. It is

Figure 1. NADP monitoring network



expected that this program will double or triple in size over the next 18 to 24 months. Future research will address not only the effects of acidic rain but the economic impact and steps that can be taken to minimize or reverse serious negative impacts.

CURRENT AND FUTURE PLANS

The two primary objectives of the NADP, the development of a national/regional atmospheric chemistry monitoring network and the development of a research program to assess the potential effects on terrestrial and aquatic systems, have been successfully initiated. I would now like to discuss the status of these two efforts and the plans and projections for the future.

NADP Precipitation Chemistry Monitoring Program

This program, begun in July 1978, now has approximately 45 operating stations, and within the next 12 to 18 months it is projected that this will increase to approximately 100. Figure 1 indicates three categories of stations: those that are currently operating, those with assigned locations but not currently operational, and those that are planned for a given state but which have not yet been assigned locations. On this map, the EPA/NOAA/WMO stations that will be soon transferred to the NADP network are represented separately. The location of each site is selected so that the data represents, to the extent possible, the chemical composition of regional wet and dry deposition. No attempt is made in the NADP network to determine the impact of a single or "point" source such as power plants or major industrial complexes. A total of approximately 80 locations are designated on the map.

To ensure comparability of data, each station in the network is operated according to a prescribed monitoring plan (see table 2). Samples are sent to a single laboratory--the Central Analytical Laboratory operated by the Illinois State Water Survey--where the listed constituents are measured. The chemical analysis data, along with data provided by field personnel, are assembled for each station and in the future will be recorded in a central data bank. Several features of the operation of this program are of particular significance and require further discussion.

Administration of the NADP Monitoring Network. The research and monitoring efforts of the NADP are now supported by all federal agencies that have responsibilities in the areas of atmospheric and water chemistry and those agencies that, because of their land management role, have responsibility for determining the potential environmental effects on terrestrial and aquatic ecosystems. My responsibility as NADP coordinator extends to both the operation of the monitoring network and its future expansion. Policy for the network operation is determined by the Technical Committee, which is currently made up of about 50 scientists who represent all agencies and institutions that participate in the NADP monitoring and research programs.

Table 2. NADP monitoring plan.

Equipment

Sampler: Aerochem Metrics wet fall/dry fall
Container: 13-l plastic pails
Rain Gauge: Belfort recording
Other: pH and conductivity meters

Field procedures

Sampling frequency:
Wet precipitation - weekly - Tuesday at 9:00 a.m.
Dry fall - every even-numbered month

Field measurements:
pH measurement and conductivity
Sample weight and temperature

Field Observations:
Type of precipitation - rain, snow, etc.
Date and amount of precipitation event

Samples are mailed in sealed collection containers to the Central Analytical Laboratory

Laboratory measurements

pH, conductivity, alkalinity, Ca^{++}, MG^{++}, Na^{+}, K^{+}, NH_4^{+}, NO_3^{-}, $SO_4^{=}$, Cl^{-}, $PO_4^{\equiv}$

Three subcommittees--Network Site Criteria and Standards Committee, Methods Development and Quality Assurance Committee, and Data Management and Analysis Committee--are responsible for developing recommendations related to network operation and monitoring protocols to be presented to the Technical Committee for approval. A fourth subcommittee, the Effects Research Committee, is involved with planning of the effects-research activities of the NADP research activities. Operating through Colorado State University, the coordinator thus implements policy as formulated by the subcommittees and approved by the Technical Committee. This has permitted a major national monitoring network to be organized in a relatively short period of time and at minimal cost. The organization of the monitoring program is unique in that it represents a truly interagency, intergovernmental, and interinstitutional effort to support a single national monitoring network. By jointly setting the objectives and monitoring procedures, agencies or institutions can jointly meet their information needs. In this way the need for multiple agency regional monitoring studies has been substantially reduced.

Quality Assurance Program. No monitoring program can provide comparable and quality data without the development of a comprehensive quality assurance program. To ensure that the NADP monitoring network provides quality data, the U.S. Geological Survey has designed and is now administering a quality assurance program. This includes the assessment of the field procedures at each site, as well as the chemical analysis carried out at the Central Analytical Laboratory. Quality assurance data will be published semiannually along with the chemical analysis data so that those using the information will be able to assess data reliability. In addition to the USGS quality assurance program, the Central Analytical Laboratory also maintains its own internal quality assurance program to monitor the performance of each of its analysts. It is believed that these combined programs will ensure that the NADP data are of the highest possible quality.

Another phase of the quality assurance program will be initiated some time in 1980. This will involve a joint study with the CANSAP program to determine the comparability of the CANSAP and NADP data. CANSAP has a monthly sampling schedule, while the NADP has a weekly schedule. Duplicate sampling will be carried out at six sites, three Canadian and three U.S., each using paired CANSAP and NADP samplers. This program will be continued over a period of several years or until sufficient data is obtained to provide statistically valid comparisons. It is hoped that eventually the level and trends of atmospheric deposition over the entire North American continent can be assessed by combining data from these two networks.

Data Management. Another important aspect of a national monitoring program is the accessibility of data to scientists studying effects of atmospheric deposition, problems related to long-range transport, atmospheric chemistry, etc. A data management system is now being developed and will be operated by EPA at its laboratories in Research Triangle Park, North Carolina. This computerized system is currently in the developmental stages and the first trial data input should be sometime in the next several weeks. When fully operational, this EPA data system will contain data not only from the NADP monitoring program but also from the CANSAP and several other ongoing localized regional monitoring studies in the United States and Canada. This data system will be accessible from interactive remote computer terminals and available to all scientists who have a need to use this information. To provide data on a more current basis, the NADP will publish its complete data base quarterly. This will be available to all participating agencies and scientists as well as to other users of atmospheric deposition information.

Future New Site Development. As pointed out in figure 1, a number of new stations will become operational in the coming months. In addition, we are working to increase the number of monitoring sites in the southern and western United States where the number of stations is inadequate. Of particular interest to this audience is the establishment of monitoring sites by the National Park Service. Twelve national parks that are designated as biosphere reserves are scheduled to become monitoring sites in 1980 (table 3). The establishment of these stations represents the development of the initial stage of the monitoring to be carried out in U.S. biosphere reserves.

Other Plans. Initially it was recognized that how, when, and where atmospheric deposition should be monitored and what should be measured had not been agreed upon by the scientific community. The potential effects of atmospheric deposition were not fully understood and thus information required to assess such effects could not be uniquely determined. For this reason it was decided that the protocol to be followed in the monitoring program would be continuously reviewed in light of new information generated from effects-research studies. This NADP decision recognizes the importance of coupling monitoring and assessment programs with effects-research studies to ensure the applicability of the monitoring data to research needs. Questions such as site locations, sampling frequency, chemical constituents, and importance and measurement of dry deposition are undergoing continuous study to determine if changes need to be made.

An assessment is being made to evaluate the total number of sites required in a given region or state. We are contemplating the possibility of designating certain sites as members of a core or benchmark network. It is envisioned that this core network will involve 40 to 50 sites that are the most critical to the assessment of atmospheric deposition on a national basis. Such sites would possibly receive increased attention in the quality assurance program, and in the future they might carry out additional monitoring studies.

Table 3. National Park Service monitoring sites in U.S. biosphere reserves.

Site location	Approximate start date
Rocky Mountain National Park	3/1/80
Everglades National Park	3/1/80
Big Bend National Park	3/17/80
Organ Pipe Cactus National Monument	3/17/80
Great Smoky Mountains National Park	3/17/80
Olympic National Park	4/14/80
Sequoia/Kings Canyon National Park	4/14/80
Isle Royale National Park	5/12/80
Glacier National Park	5/12/80
Mount McKinley National Park	6/1/80
Yellowstone National Park	6/1/80
Virgin Islands National Park	6/1/80

Another question relates to the chemical species in atmospheric deposition which are measured. It was recognized that metals, particularly heavy metals, represent a potentially serious threat to the environment both from the point of view of human health as well as effects on terrestrial and aquatic ecosystems. The U.S. Geological Survey quality assurance program is to assess the current sampling procedures for the determination of heavy metals deposition. If the current sampling procedures are demonstrated to give satisfactory results, then a group of 15 to 20 heavy metals will be added to the analytical measurements made on each sample.

Probably the most important question facing us at this time is the adequacy of the dry-fall sampling technique. It will be necessary to determine whether the sampling technique employed (13 l pail) represents the actual fallout of dry particulate matter and the escavaging of particulate material by vegetation. The importance of this question is recognized when one realizes that possibly half the sulfate deposited is a result of dry deposition. Current research indicates that these aerosols and particulates contain ammonium salts and that a large portion of the sulfate is as ammonium sulfate and ammonium bisulfate. The ammonium ion can potentially release two hydrogen ions or protons when incorporated into the soils and subsequently taken up by the biota. Ammonium sulfate is thus potentially twice as acidifying as an equivalent amount of sulfuric acid. In fact, it is estimated that it is on the average 1.5 times as acidifying. It is therefore of critical importance that we not only develop methods for assessing the dry fallout of particulates and aerosols but also that we understand the composition of these materials, particularly the deposition of ammonium ion as ammonium sulfate, bisulfate, or ammonium nitrate. In addition, there is the question of whether or not dry particulate matter should be destructively analyzed to determine the total chemical composition or leached with an aqueous solution and the solution subsequently analyzed. These are several of the questions that will require answers, and the results will influence future procedures for monitoring wet and dry fall.

THE NADP RESEARCH PROGRAM

The purpose of the NADP and of the current initiatives within the U.S. federal government is to determine the extent of atmospheric pollution and the effect of the deposition of these chemical substances on the health of aquatic and terrestrial ecosystems. Obviously these questions have far-reaching consequences with respect to the world's production of food and forest products, as well as the maintenance of the stability and aesthetic values of our natural ecosystems. The research needs as outlined in the report to the Council on Environmental Quality focused on the determination of the sensitivity of various aquatic and terrestrial systems to atmospheric inputs. A major point was made that atmospheric inputs can be both beneficial and detrimental. Obviously the addition of nitrates, sulfates, calcium, magnesium, ammonia, etc., contributes to the reservoir of essential nutrients necessary for plant growth. However, the input of these substances along with other materials, particularly hydrogen ion, pose both short- and long-term detrimental threats. The most spectacular detrimental effects are observed in freshwater ecosystems where surrounding geology and soils provide little buffering capacity. In the U.S. and Canada this has been most noticeable in the "Canadian shield" regions covering eastern Canada and portions of the northeastern and northcentral U.S. It is believed by most scientists that these aquatic systems are most sensitive and could be expected to display significant alterations. While many terrestrial systems appear to be more tolerant and capable of neutralizing such effects, it is projected that there probably will be long-term detrimental effects on the soils and that if acidity continues to increase, there can be direct damage to vegetation. Both these factors could have serious consequences for forest, range, and agricultural productivity.

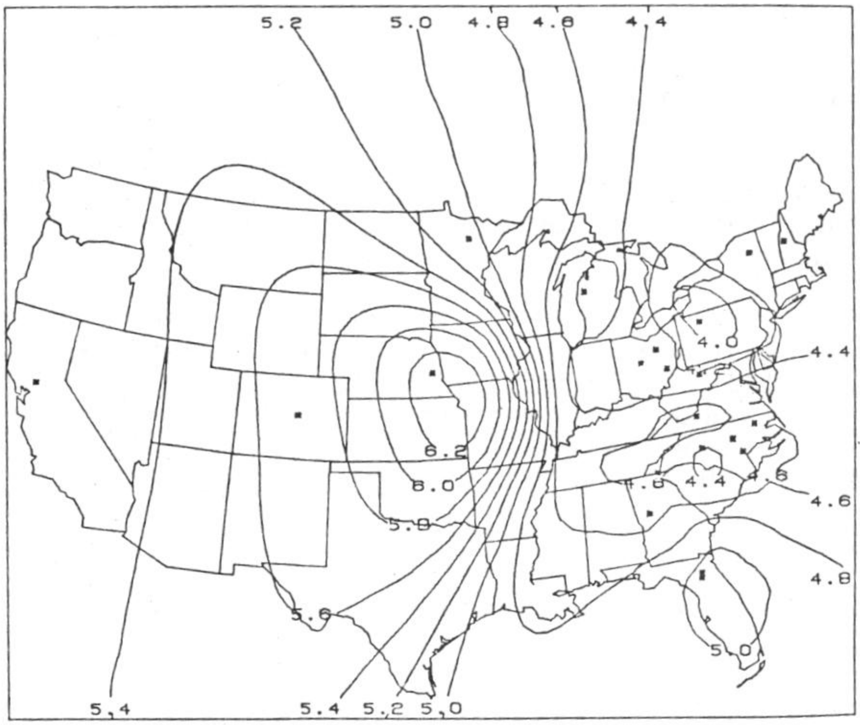
Questions related to impacts on aquatic ecosystems, forest productivity, agriculture, and soils (long term) are the subject of current NADP research programs. The research administered through the EPA grant to the NADP at North Carolina State University is focusing on problems related to freshwater streams and lakes and to long-term impacts on soils. Additional research will be instituted to look at total watersheds and the coupling of terrestrial and aquatic systems. Factors such as mobilization of metals from the soils and their impacts on streams and lakes will be measured. A smaller amount of effort is going into the direct effect of acid rain on vegetation, particularly agricultural crops. It is expected that in the next several years these research programs as well as research efforts of other agencies will be greatly expanded.

SUMMARY

The scientists involved in the NADP contend that atmospheric deposition monitoring and subsequent research to determine effects requires close coordination. It is the research needs that determine the type of information required and how it should be measured. As our research efforts produce a greater understanding of the effects of atmospheric deposition, it will undoubtedly be necessary either to adjust our monitoring programs to provide additional data or to revise the way in which we collect wet and dry deposition. In addition it has been pointed out that wet and dry deposition contains substances that are beneficial as well as detrimental to the productivity of both natural and managed ecosystems. It is important that not only do we measure acid deposition and its effects but also that we measure other major constituents in atmospheric deposition because it is the combined effects that determine the environmental response. For example, it may be that the detrimental effect of acid precipitation on forest productivity is masked by the increased inputs and availability of nutrients such as nitrate, sulfate, and calcium. The long-term effects of acidity on soils is not a simple function of the hydrogen ion but is also related to the input of other ions, particularly sulfate. Therefore, it is important that research be designed to look at total deposition effects as opposed to focusing on a single component such as hydrogen ion.

The limited quantity of data collected to date by the NADP monitoring efforts does not permit significant conclusions to be drawn at this time. It can be stated, however, that the preliminary analysis of the data, particularly what has been collected in the eastern and northeastern parts

Figure 2. pH and sulfate isopleths for the continental United States.



MEASURED PH MEDIAN
NATIONAL ATMOSPHERIC DEPOSITION PROGRAM (NADP)
CAL - ILLINOIS STATE WATER SURVEY
DATE: 29 JUN 79 WET SIDE. CAL LAB TYPE- W

SO4 DEPOSITION(MG/M**2/WK) MEDIAN
NATIONAL ATMOSPHERIC DEPOSITION PROGRAM (NADP)
CAL - ILLINOIS STATE WATER SURVEY
DATE: 29 JUN 79 WET SIDE. CAL LAB TYPE- W

of the U.S., does support the earlier predictions of a continuing trend in increasing acidity and a widening geographical distribution of low pH precipitation. Figure 2 shows pH and sulfate deposition contours plotted for the U.S. from July 1978 to February 1979. Data from only 20 sites are included. It is our belief that a minimum of five years of data is required to make any realistic statements regarding trends.

Data from research about the effects of atmospheric deposition in the U.S. are even more limited than data regarding composition and trends in deposition inputs. Based on research that has been done, the following tentative conclusions can be drawn concerning effects:

> Freshwater lakes and streams in areas with poorly buffered soils are most vulnerable. Significant acidification has been demonstrated in eastern U.S. and Canadian lakes with subsequent loss of fish populations. Other vulnerable areas of the U.S. are in the southeast as well as the Rocky Mountains and West Coast mountain ranges.
>
> Acidity of atmospheric deposition has probably not reached levels that will bring about measurable direct impacts on vegetation. Selected studies indicate that such effects may be seen when precipitation reaches pH 3 or less.
>
> Soils over a long period of time will probably undergo loss of nutrients. In addition there may be impacts on microbial and other biological soil processes. These effects should be particularly evident in poorly buffered soils, which occur in mountainous and forested regions of the U.S. This could have serious long-term implications for forest productivity.
>
> Most agricultural soils are supplemented with fertilizers and, if necessary, lime. These supplements far exceed the inputs from the atmosphere, and thus agricultural soils will probably not be drastically affected by atmospheric deposition.
>
> Materials such as limestone and man-made materials that are used in construction and statuary erode as a result of atmospheric deposition. A related problem is the corrosion of metals, particularly iron. Although not quantitatively defined, it is evident that this is a serious and growing problem.

These and other questions for which we have only partial or no information demonstrate the need for a continuing and expanding effort in monitoring the chemical composition of atmospheric deposition and expanded research programs to determine subsequent impacts. It is already evident, however, based on our incomplete understanding, that we need to substantially reduce the atmospheric inputs of sulfur and nitrogen compounds worldwide. The same may be true of heavy metals. This will have serious implications with respect to meeting the world's future energy needs.

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ENVIRONMENTAL MONITORING IN NATIONAL PARK BIOSPHERE RESERVES

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Abstract

Networks in the remote natural areas of parks/biosphere reserves are the early warning systems that can detect small-scale change in environmental conditions before they become catastropic changes affecting human health and environmental quality.

A model is proposed by which long-term monitoring in biosphere reserves can proceed within the limits set by law. Parks/biosphere reserves are to be linked by a series of monitoring processes that are conducted in the same way and on the same time scale. In addition, each park/biosphere reserve can conduct activities according to specific needs.

Methods for ecological monitoring have been refined so that physical constraints imposed by remote areas do not limit field sampling. Multielemental sampling and analysis techniques have yielded extensive savings in labor, time, and costs and have increased the probability of detecting change.

INTRODUCTION

Since the First U.S.-U.S.S.R. Symposium on Biosphere Reserves in Moscow in May 1976 (Franklin and Krugman 1979), we have made progress toward focusing the varied opinions into a definition of what we mean by long-term ecological or environmental monitoring in biosphere reserves (Herrmann et al. 1978, NSF 1979, MAB 1979). We have also learned quite a bit since Moscow about how to go about detection of change both as related to physical and life cycles and perturbations of them (Wiersma and Brown 1979).

There is value at this time in reiteration of some of the important aspects of monitoring and also in talking about the success of present U.S. efforts in a few core reserves. Man's activities are affecting life within the biosphere by disrupting cycling of energy and chemicals in some unknown ways. Since the last U.S.-U.S.S.R. symposium we have tested field methods, determined levels of effort, and specified quality control measures. We have also refined the list of suggested measurements required to unravel those effects, both individual and synergistic, that we do not understand (Wiersma and Brown 1979, Herrmann et al. 1978, Galloway et al. 1978). In some areas we have implemented these measurements, in others we have planned our implementation strategy based on five overriding management principles: cost-effectiveness, utility, quality, flexibility, and replicability.

In testing this strategy, three conclusions have surfaced and deserve consideration:

> For cost-effective monitoring of chemical cycles, there is no substitute for multielemental sampling and analysis techniques. Savings in labor, time, and funds are great, and the probability of detecting chemical change is high.
>
> Results are only as valid as the quality of the experimental methods from which they were derived. The chain of methods is weakest at the field level, and sampling errors are greatest where there is maximum human activity (i.e., field sampling error). The major analysis of causes of variability should focus on field sampling techniques. Laboratory variability can be controlled.
>
> Even in the most remote areas of biosphere reserves we have found there to be no logistic constraints to those chemical and biological activities tested. Extra effort from field-workers and special design consideration are required, however.

Research has documented the severe effects that factitious acids from atmospheric and terrestrial sources have on aquatic organisms (Pough 1976, Schofield 1976, Huckabee et al. 1975). Little has been done, however, to document the hypothesized but barely perceptible disruptions of the carbon cycle, nitrogen cycle, and other major chemical cycles of the biosphere. Similarly, little is known about the effects of these changes on crops, forests, wetlands, and grasslands, and within urban areas. A network of related long-term system and cycling studies which have received broad scientific support is now proposed with some confidence. The components of the network have these things in common: They are representative, receive long-term protection, currently maintain a permanent record of the state of environment, and contain areas where conditions of least disturbance are found; in short, these criteria define the biosphere reserves. Detection of change in these representative areas provides an early warning system of possible severe damage to the environment or to human health.

The detection/monitoring system for acid rain is one example of an early warning device which involves establishing receptor sites along gradients of urban to remote, arctic to tropical, arid to humid, and sea level to high elevation areas, including all major biotic provinces. In this way we plan to assess the direct effects of impingement and the indirect effects of hydrologic and atmospheric transport. In theory pollutant effects can be traced back to well-defined discharge sources. Our present low level initiatives involve varying degrees of accuracy and uncertainty which will undoubtedly become more accurate as more of the network becomes operational and longer data bases become available for analysis.

SHAPING THE CHARACTER OF U.S. MONITORING EFFORTS

The U.S. Congress over the years has set standards through legislation by which each federal agency with stewardship over land has gauged its commitment to preservation and conservation. The National Park Service concern for preservation and its approach toward biosphere reserves can be related to a number of these pieces of legislation, beginning with the Yellowstone Act of 1872 and subsequently the Organic Act of 1916. Important pieces of later legislation are the National Park Systems Act of 1971, the Endangered Species Acts of 1966 and 1973, the Wilderness Act of 1964, the Clean Air Act as amended 1977, and the Clean Water Act of 1977 (table 1).

Legislation becomes extremely important when the designs of long-term monitoring programs in park/biosphere reserves are considered and subsequently implemented. The Park Service is mandated by law to manage each of its areas in a specific manner; management may be either very restrictive or very liberal relative to preservation of, or activities on, a given tract of land. The removal or alteration of many natural resources in park areas is usually prohibited, preventing most manipulative research. These restrictions are limiting as to how data are collected but not as to the type of monitoring data that can be collected in remote natural areas. Wiersma et al. (1978) have demonstrated in both Great Smoky Mountains National Park and Olympic National Park (core biosphere reserves) that portable pollutant monitoring equipment can be employed in nearly any situation to gather dependable data for even the most sophisticated chemical analyses.

Table 1. A partial listing of U.S. conservation/preservation laws.

National Park Service Organic Act of 1916 (16 U.S.C. § 1 et. seq.)

National Environmental Policy Act of 1969 (42 U.S.C. § 4321 et. seq.)

National Historic Preservation Act of 1966 (16 U.S.C. § 470)

Wilderness Act of 1964 (16 U.S.C. § 1131 et. seq.)

National Wild and Scenic Rivers Act, as amended (16 U.S.C. § 1271 et. seq.)

National Trails System Act (16 U.S.C. § 1651 et. seq.)

Endangered Species Act of 1973 (16 U.S.C. § 1531 et. seq.)

Marine Protection, Research, and Sanctuaries Act of 1972 (16 U.S.C. § 1402 et. seq.)

Clean Water Act (Federal Water Pollution Control Act as amended 1977) (3 U.S.C. § 466 et. seq.)

Noise Control Act of 1972 (42 U.S.C. § 4901 et. seq.)

Clean Air Act, as amended (42 U.S.C. § 1857 et. seq.)

Safe Drinking Water Act (42 U.S.C. § f-j)

Toxic Substance Control Act (15 U.S.C. § 2601)

Legal documents and legislation establishing individual parks

Legislation not only dictates the levels at which scientific activities are allowed on federal lands but provides the best and only insurance that remote natural areas will remain remote and will not be eroded by changes in land use philosophy. The parks/biosphere reserves incorporate the concepts of wilderness, preservation, and research natural areas that will allow and encourage long-term observations. These are the core sites where sensitivity to and direction of change can be recorded, studied, and compared to those areas yielding to the needs of man.

THE PRESENT STATE OF U.S. BIOSPHERE MONITORING

We have adopted a systems modeling approach for the park/biosphere reserve monitoring network. It is not unlike the models proposed for long-term ecological monitoring sites (NSF 1979, MAB 1979). Each park/biosphere reserve in the net is linked to every other one by a series of monitoring processes that are conducted in the same way and on the same time scale. The core system includes collection and analysis of atmospheric deposition, and terrestrial, aquatic, and biological parameters are sampled as well. By employing uniform methods of collection and analysis, and strict quality control, we can be sure that the results from parks can be compared, replicated, and extrapolated to nonpark areas. These data are available to a variety of agencies, institutions, and industries for use in answering research and policy problems.

Underneath this layer of common, networkwide monitoring there will continue to be park-specific work that relates directly to general research and resource management needs. The preservation of natural areas requires active management of the total resource, which in turn requires studies of alternative actions. Some of these studies are now coordinated with multielemental chemical collections. Pertinent examples of other specific work include monitoring of rare plant population fluctuations in Great Smoky Mountains National Park, exotic mountain goat populations and their effects on high elevation flora in Olympic National Park, and atmospheric fluoride levels and plant responses in Glacier National Park. A voluminous amount of research is ongoing in the parks/biosphere reserves, as evidenced by the studies in progress in 1977 (USDI, NPS 1979; see table 2). Plans are underway to edit and organize ecological and land use data from parks and other biosphere reserves into a hierarchical format at the Ecosystem Analysis Data Center at Oak Ridge National Laboratory (Watts 1979).

COOPERATIVE INTERAGENCY EFFORTS SPONSORED BY THE NATIONAL PARK SERVICE

Uniform wet-fall and dry-fall atmospheric deposition collectors in 12 U.S. biosphere reserves are being installed as a part of the National Atmospheric Deposition Program (NADP). The national network provides the Park Service with a controlled structure for sampling, data analysis, and quality control, and it may in the future provide the capability for testing exotic and organic substances. From this program the Park Service and others will be able to study what and how atmospheric substances are impinging on natural resources. Pollutant monitoring pilot studies cosponsored by the Environmental Protection Agency (EPA) in Great Smoky Mountains and Olympic involve chemical assays of air, water, soil layers, and vegetation. These studies are slated to be expanded to more parks in the future. Methods involve careful field sampling techniques and high resolution laboratory analyses on a yearly basis to assess levels, patterns, and trends of environmental pollutants and their metabolites. In this program the testing of multielemental analysis techniques has increased the speed of analysis and significantly reduced costs. The methods employed greatly increase the probability of noticing unnatural changes in chemical cycles and of understanding unusual chemical results. In Great Smoky Mountains, in the southeastern U.S., the pilot study began in 1976. In Olympic, in the Pacific Northwest, the first collecting year was completed in 1979. In Glacier, on the Canadian border, studies are programmed to begin in 1980-81, with studies in other parks/biosphere reserves expected to follow. First year sampling in

Table 2. Independent research studies in U.S. biosphere reserves, 1977.

National park/ biosphere reserve	Terrestrial ecology	Aquatic ecology	Geology	Meteorology	Marine studies	Human studies	Total
Big Bend	8	0	5	0	0	0	13
Channel Islands	20	0	1	0	7	2	30
Everglades	31	3	23	0	5	3	65
Glacier	25	2	4	0	0	1	32
Great Smoky Mountains	109	8	6	0	0	4	127
Mount McKinley	14	0	2	1	0	3	20
Organ Pipe	7	4	1	0	0	1	13
Olympic	8	0	1	0	1	1	11
Rocky Mountain	45	1	9	0	0	2	57
Sequoia/Kings Canyon	35	4	8	1	0	4	52
Virgin Islands	9	0	0	0	3	0	12
Yellowstone	29	8	19	1	0	2	59
Totals	340	30	79	3	16	23	491

Great Smoky Mountains involved ten sample sites. These ten replicated sites were chosen following a block design based on elevation, aspect, forest history, and age. After the initial analysis was completed it was determined that two sampling sites were sufficient to obtain adequate chemical data.

Data from Olympic have so far yielded low levels of pollution encroachment. These results are important both to establish a base line and to aid the park in understanding how external pollutant threats will have an impact on park resources. Decisions on acceptable pollutant concentrations must be based on knowledge of ambient levels and the nature of effects. Management level monitoring work in Olympic has involved the placing of permanent plots to study vegetational change. These are linked with population studies of exotic mountain goats and disturbance studies of high elevation flora. A long-term pollution and ecological monitoring system for Olympic that integrates monitoring on many ecosystem levels is projected to be fully functional within five years. Nutrient uptake and cycling, Landsat II images recording physical changes over time inside and outside the park, stream water quality, and population studies at both the organism and ecosystem level will be included in addition to NADP and pollutant monitoring.

Park-specific activities at Glacier include water quality monitoring, which has been undertaken in cooperation with the U.S. Fish and Wildlife Service since 1978. Monitoring of population changes and movements of large mammals has been undertaken for up to 12 years. A new colony of bald eagles, which began wintering in Glacier to take advantage of an exotic cutthroat trout population, is being observed (the species is recognized as threatened).

The dependency of the Everglades upon freshwater sheet flow makes it vital that hydrologic processes be understood. Extensive monitoring efforts are underway on all levels to increase knowledge and provide a base for management decisions. Fresh, marine, and estuarine water distribution, including inflows, outflows, and saltwater incursions, are monitored by the in-park research facility. Chemical analyses are aided by several agencies, including the U.S. Army Corps of Engineers, U.S. Geological Survey, and the Water Management District, and are coupled with careful and extensive animal population studies. Fresh and marine fish populations, alligators, crocodiles, minks, and native birds are being monitored for changes in distribution and numbers. Permanent vegetation transects and plots have been established. Atmospheric deposition monitors are being installed.

Great Smoky Mountains has been in the vanguard of long-term biosphere monitoring studies. Even before the establishment of an in-park research facility, permanent plot work and primary productivity work were being done. Monitoring plans call for 700 permanent vegetation plots which can be relocated for sampling. Included are some 300 relocatable plots dating back to 1938. Water quality, flow, and weather data are sampled using standardized techniques, and special studies include remote water quality monitors in two streams. Fish population monitoring in cooperation with the U.S. Fish and Wildlife Service has been going on since 1935 and will continue. The monitoring of exotic wild boar populations and movement has been active since 1974. Other animals whose trends are being followed in varying levels of detail include black bears and several species of salamanders.

Long-term multilevel monitoring is getting underway at Isle Royale and Pictured Rocks. Isle Royale is setting up NADP monitors as part of proposed activities for biosphere reserves. This work complements primary long-term research on plant nutrient cycling being conducted by Robert Stottlemeyer. The U.S. Geological Survey has been collecting base line drainage data at Isle Royale for 16 years, and routine analysis covers some 80 substances, including common minerals, trace elements, and pesticides.

It should be emphasized that most of the monitoring in national parks is done in collaboration with other agencies and institutions. As a consequence we hope the results have much broader application than to Park Service activities alone.

CONCLUSIONS

The National Park Service has begun to meet its MAB responsibility by establishing a network of remote areas for the study of ambient pollutant and other chemical levels. While it can no longer be said that these areas are pristine, they are some of the least altered areas in the United States. It is necessary to realize that man has tinkered with every facet of the Earth's environment, including those pristine spheres thought to be external to our influence. We must monitor our effects and analyze the changes, not only to preserve the integrity of remote natural areas, but also to ensure man's own health and safety. The network monitoring system is one step toward meeting these responsibilities.

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MATERIALS ON COMPLEX BACKGROUND MONITORING IN SELECTED SOVIET BIOSPHERE RESERVES

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INTRODUCTION

During the First Soviet-American Symposium on Biosphere Reserves (May 1976 in Moscow), specialists of both countries outlined approaches to the complex monitoring program for natural media contamination. It turned out that proposed programs and monitoring methods were much alike (Izrael et al. 1977, Gasilina et al. 1977, Morgan et al. 1977). At the following meetings of the task force on biosphere reserves (October 1978, U.S.A.) and at the International Symposium on Monitoring (December 1978, U.S.S.R.), Soviet and American specialists reported on the results of the first observations conducted according to the program of background monitoring in biosphere reserves. This paper discusses the background observations that have been conducted during the last few years in biosphere reserves in the Soviet Union.

Monitoring stations, consisting of observational proving grounds, sampling points, and small laboratories, have been created for the stationary perennial observations and measurements under the background monitoring program in each biosphere reserve; meteorological and hydrological posts are included in these stations. Preliminary research expeditions to the reserve areas and surrounding regions were conducted to select the representative sampling points.

Stationary observations have been performed at the Borovoje background station (in northern Kazakhstan) since 1976. The program provides daily measurements of particulates, sulfur dioxide, mercury, lead, cadmium, arsenic, 3,4-benzopyrene, and hydrocarbons in the atmosphere; the same materials (except for particulates and sulfur dioxide) are measured in atmospheric depositions, soils, waters, and herbage. In addition, ozone and sulfates in the atmospheric layer near the ground, and DDT with its derivatives in all media, are measured in all biosphere reserves during the research expeditions.

BACKGROUND MEASUREMENTS

Atmospheric Sulfur Dioxide and Sulfate

Table 1 presents generalized measurement data for sulfur dioxide and sulfates in the areas of four biosphere reserves located in different zones. It was determined that sulfur dioxide background concentrations varied from 0.02 to 3 mcg/cu m in the summertime. Minimum concentrations were registered in the Caucasus Biosphere Reserve. As a rule, sulfur dioxide concentrations in the atmosphere change at the time air masses or meteorological elements change. With increasing humidity sulfur dioxide concentrations usually decrease. Measurements of sulfur dioxide throughout the day showed the maximum concentration in the daytime.

Table 1. Generalized background measurement data of sulfur dioxide and sulfate in the atmospheric layer near the ground (mcg/cu m).

Background station	Observation period	Sulfur dioxide	Sulfate
Borovoje	Whole year	0.2-8.1	-
	Summertime	0.2-0.8	0.7-7.8
Sary-Chelek Biosphere Reserve	August-September 1976	0.5+3	-
Berezina Biosphere Reserve	June-July 1978	0.4+1.5	-
Caucasus Biosphere Reserve	September-October 1976	0.08+0.3	3+5
	June-July 1979	0.02+0.2	2+10

Many years of measurements of sulfur dioxide in the air at the Borovoje background station show a pronounced annual variation. Winter maxima are connected with increases in sulfur dioxide discharges from heating systems and with decreases in the speed of sulfur dioxide oxidation.

The parallel measurements of sulfur dioxide and sulfate aerosols show a correlation in their concentration changes. According to absolute quantities, the correlation of sulfur dioxide and sulfate is more or less than 1. This indicates an absence of big local sources of atmospheric pollution in the background measurements in the examined areas.

Ozone

Interpreting ozone measurements in background regions is difficult because the ozone levels could be the result of vertical transportation from upper atmosphere layers and advective transportation of polluted air masses from urban areas. Ozone could serve as an indicator of anthropogenic atmospheric pollution if the nature of its origin could be exactly determined in the region of observation.

Ozone concentrations in Berezina Biosphere Reserve from June 15, 1978, to July 24, 1978, varied from 20 to 125 mcg/cu m. The daily ozone analysis showed that the average maximum ozone concentration in July (115 mcg/cu m) differed from the corresponding data in June (52 mcg/cu m). The synoptical conditions analysis showed that ozone concentrations of over 90 mcg/cu m were obtained mainly during west and southwest winds. Additional considerations of ozone's nature were obtained from the correlation of maximum (daytime) and minimum (nighttime) average hourly ozone concentrations. If the atmosphere had not been polluted, the high levels of nighttime concentrations would correspond with the daytime ozone concentration levels. This is because the products of photochemical reactions resulting in ozone generation during the daytime and its decomposition during the nighttime (nitrogen oxide, unsaturated hydrocarbons, radicals) were absent. The correlation of daytime and nighttime concentrations was 0.72 in June, but in July it was -0.33. The factors contributing to ozone concentrations in July were advective air transportation from urban regions, although generally the maximum concentrations during the whole observation period were within the limits of background values known from literature.

Measurements of ozone concentrations in the Caucasus Biosphere Reserve (altitude 1,600 m) from July 5 to July 27, 1979, showed that ozone varied from 40 to 120 mcg/cu m. The daily ozone run typical of background regions was also determined there. The meteorological data analysis did not allow detection of a relationship between air mass advective transportation directions and ozone levels in the near-ground layer. Simultaneous measurements of sulfur dioxide and nitrogen oxide concentrations also had very low values that could be characterized as background. In this case, vertical ozone transportation from upper layers of the atmosphere was the likely cause of ozone generation.

Mercury

Mercury is unlike the other heavy metals. The atmosphere contains mercury mainly (more than 90%) in a vaporous form (Braman 1974, Jonson and Braman 1974).

Three years of stationary observation data from the Borovoje station showed that mercury contents in the near-ground layer of the atmosphere did not vary much from year to year. More than 90% of all average daily concentrations ranged from 2 to 24 ng/cu m. Average daily concentrations up to 50-60 ng/cu m seldom occurred. Such concentrations remained no longer than a day and could occur two or three times a month, but only during summer.

Although most concentration values were within narrow limits, the typical seasonal change for vaporous mercury contents in the atmosphere was obvious. Summertime concentrations were two to three times higher than during winter. The main source of atmospheric mercury is the burning of fossil fuels. But when the temperature falls below 0°C, mercury condenses in a solid phase, resulting in the reverse annual run indicated by experimental observations.

The amount of mercury in precipitation, which has been measured for several years at Borovoje station, is near the amount in surface water--0.02 to 0.25 mcg/l. The amount of mercury is also near the known natural background in water, ground sediments, soils, and vegetation.

Lead, Cadmium, and Arsenic

Unlike mercury, lead, cadmium, and arsenic of natural and anthropogenic origins are present in the atmosphere as submicron aerosols capable of long-distance transport (Chester and Stoner 1973a and b). The amounts of examined metals in the near-ground air layer are characterized by the following ranges: lead--2-30 ng/cu m, cadmium--0.2-1 ng/cu m, and arsenic--1-5 ng/cu m. These ranges include 90% of all average daily concentrations characteristic for areas distant from industrial sources (Janssens and Dams 1975).

There is a typical annual run in the atmospheric concentrations of these metals, with a maximum during the winter because of more intensive burning of fossil fuels.

Lead, cadmium, and arsenic distribution in the lithosphere is presented by the ratio 100:1:3 (Goronovskiy 1974).

Based on measured concentrations at the Borovoje station, the correlation of lead, cadmium, and arsenic in atmospheric aerosols is 80:1:4; thus, the region is characterized by small arsenic amounts in aerosols.

3,4-Benzopyrene, Hydrocarbons, and DDT

Average monthly concentrations of 3,4-benzopyrene and benzoperylene at the Borovoje station varied from 0.02 to 0.95 ng/cu m and from 0.01 to 9.8 ng/cu m. A distinct annual run of these components shows the average monthly concentrations in winter are several tens of times higher than in the summertime. Extended precipitation generally reduces levels of benzopyrene and benzoperylene in the atmosphere near the ground to minimal values.

Eleven nonsubstituted polynuclear aromatic hydrocarbons (PAH) containing from four to seven benzene rings (tetraphene, 1,2-benzopyrene, dibenzanthracene, fluoranthene, pyrene, naphthobenzopyrene, coronene, anthanthrene, perylene, benzopyrene, benzoperylene), as well as the series of substituted homologues of benzofluorene, naphthalene, phenanthrene, chrysene, and pyrene (including 3-methylpyrene), have been determined at the background station in winter. More than half of these hydrocarbons are carcinogenic. During the summer the PAH quantity and diversity is minimal because of PAH degradation processes caused by ultraviolet rays and different oxidants. The amount of all PAH ranges from 0.57 to 7.5 ng/cu m, with the amount of low-ring PAH (pyrene) an order of magnitude larger than for many-ring materials (benzopyrene, benzoperylene, coronene, anthanthrene).

The amounts of benzopyrene and benzoperylene in the near-ground layer of the atmosphere in Sary-Chelek Biosphere Reserve from August to September 1976 were 0.29±0.1 and 0.13±0.07 ng/cu m. This was close to amounts of these components at the Borovoje station during the same period (0.30±0.07 and 0.11±0.02 ng/cu m).

The amounts of benzopyrene and benzoperylene in the near-ground layer of the atmosphere at Berezina Biosphere Reserve in June and July 1978 were 0.06±0.03 and 0.20±0.1 ng/cu m. Values at the same period at Borovoje were 0.025±0.006 and 0.06±0.01 ng/cu m.

The amounts of benzopyrene and benzoperylene in the near-ground layer of the atmosphere in Caucasus Biosphere Reserve in September and October 1978 were 0.02±0.01 and 0.05±0.02 ng/cu m, which was less than during the same period at the Borovoje station (0.09±0.04 and 0.20±0.06 ng/cu m).

The total amount of hydrocarbons in aerosols and in precipitation was determined from 1976 to 1979 at the Borovoje station. Aerosols and precipitation contained polar and nonpolar hydrocarbons, including aliphatic, aromatic, and polynuclear compounds. An annual run of hydrocarbon concentrations was detected in aerosols, with a maximum during the winter. Aerosols sampled in winter included hydrocarbons with a number of atoms from C_{15} to C_{32}, but summer aerosols had numbers from C_{20} to C_{32}. The average monthly hydrocarbon concentrations measured at the Borovoje station during summers from 1976 to 1979, using the infrared spectrophotometry method, ranged from 0.25 to 2.6 mcg/cu m. The maximum hydrocarbon concentrations (6.7 mcg/cu m) were measured in Berezina Biosphere Reserve; the minimum (0.1 mcg/cu m), in Caucasus Biosphere Reserve.

The average hydrocarbon concentrations in precipitation at the Borovoje station varied from 0.89 mg/l (1976) to 0.32 mg/l (1978); the hydrocarbon concentrations were from 0.26 to 0.24 mg/l in precipitation in the Berezina and Caucasus biosphere reserves.

The observations in the Borovoje region showed that DDT and the other chlororganic derivatives were present in the near-ground air layer as aerosols and gases. The correlation of these phases was approximately equal in the summertime. The average daily background concentrations

Table 2. Conjugate correlations between pollutant amounts.

Components	Observation periods	Correlation factor
lead/cadmium	June 1976-August 1979	0.77±0.07
lead/3,4-benzopyrene	June 1976-March 1979	0.63±0.11
lead/particulates	June 1976-August 1979	-0.40±0.14
lead/sulfur dioxide	June 1976-August 1979	0.57±0.11
3,4-benzopyrene/ sulfur dioxide	June 1976-March 1979	0.62±0.11
3,4-benzopyrene/ hydrocarbons	June 1976-March 1979	0.84-0.17
3,4-benzopyrene/ particulates	June 1976-March 1979	-0.43±0.15
cadmium/sulfur dioxide	June 1976-August 1979	0.46±0.13
particulates/cadmium	June 1976-August 1979	-0.40±0.14
particulates/sulfur dioxide	June 1976-August 1979	-0.52±0.12
particulates/lead	winter (November-December 1976; January, February, November, December 1977 and 1978; January-February 1979)	0.35±0.26
particulates/cadmium	winter, same as above	-0.28±0.28
particulates/ 3,4-benzopyrene	winter (November, December 1976; January, February, and December 1977; January, February, and November 1978; January, February 1979)	-0.25±0.33
particulates/ sulfur dioxide	winter (November, December 1976; January, February, and December 1977; January, February, November, and December 1978; January, February 1979)	-0.09±0.31

varied in the limits 0.2-0.5 ng/cu m for DDT, 0.05-0.2 ng/cu m for DDT and DDE, and 0.2-0.4 ng/cu m for lindane. The amount of DDT in surface water and precipitation was 3-5 ng/l.

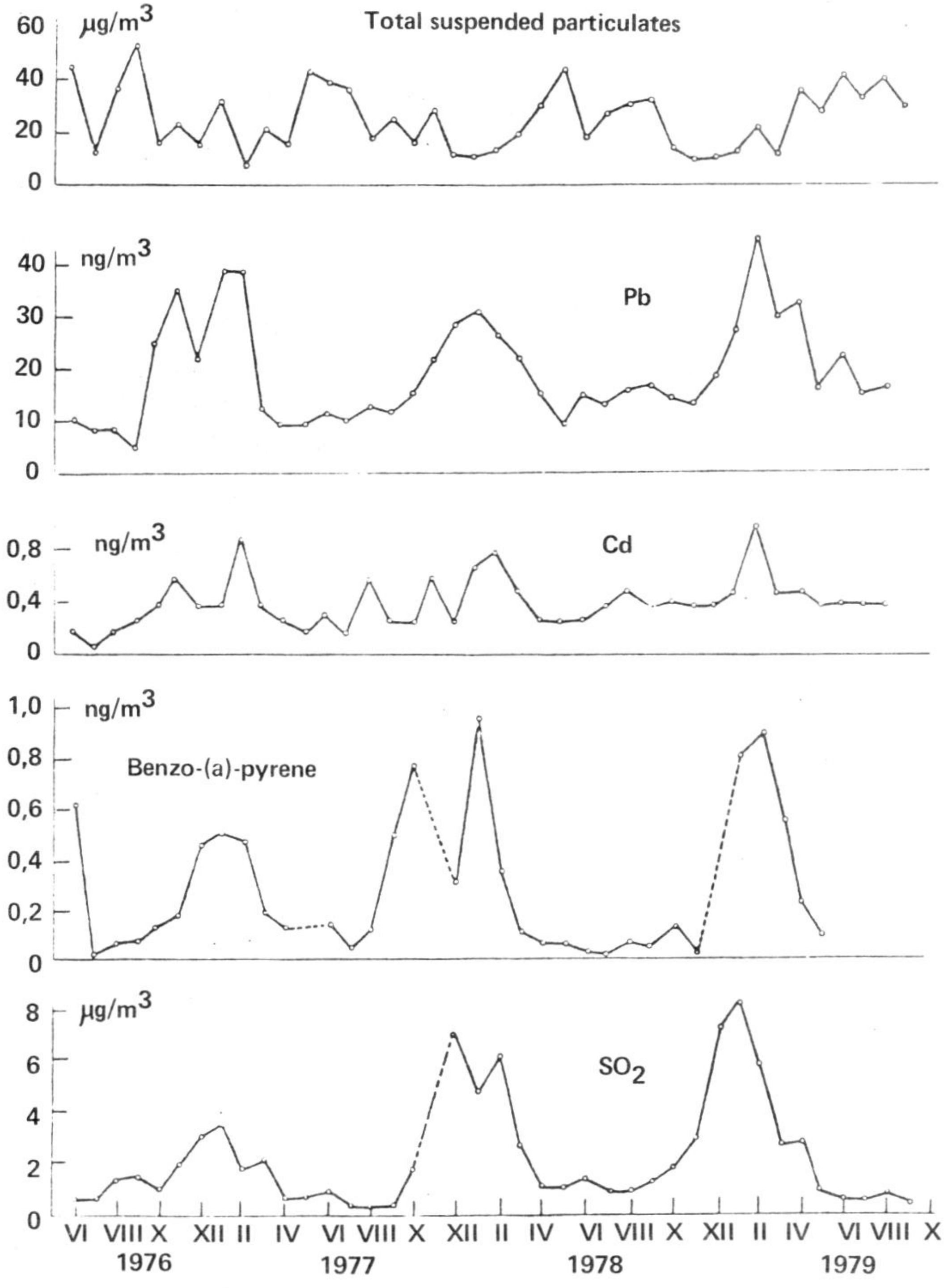
The dynamics in amounts of priority pollutants in the atmosphere, based on three years of systematic observations at the Borovoje station, is shown in figure 1.

Mutual relations between separate substances are presented in table 2 as correlation factors along with their standard errors. Satisfactory correlations (0.57-0.84) for the whole period of observation exist between lead and cadmium, lead and 3,4-benzopyrene, lead and sulfur dioxide, 3,4-benzopyrene and sulfur dioxide, and 3,4-benzopyrene and hydrocarbons. Poor correlations (0.35-0.46) exist for lead and particulates (during winter) and for cadmium and sulfur dioxide.

Particulate matter in air is likely to be from anthropogenic sources in winter when the ground surface is covered by snow, and its concentration is likely to have a good correlation with concentrations of metals, 3,4-benzopyrene, and sulfur dioxide. However, in winter there is a poor correlation between concentrations of particulates and lead and practically no correlation with cadmium, 3,4-benzopyrene, and sulfur dioxide; this fact shows different sources of pollutants.

These data characterize current background or natural pollutant levels in Soviet biosphere reserves.

Figure 1. Average monthly concentrations of particulates, lead, cadmium, 3,4-benzopyrene, and sulfur dioxide in the near-ground layer of the atmosphere; the Borovoje background station.



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