A History of the Ecosystem Concept in Ecology

More Than the Sum of the Parts

Frank Benjamin Golley

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ABBREVIATIONS

AEC	Atomic Energy Commission
BES	British Ecological Society
CNRS	Centre National de la Recherché Scientifique
EDFB	Eastern Deciduous Forest Biome project
ELM	Grassland system model
ENCORE	European network of catchments for ecological research
FAO	Food and Agriculture Organization
IBP	International Biological Program
ICSU	International Council of Scientific Unions
IGY	International Geophysical Year
IUBS	Union of Biological Sciences
IUCN	International Union for the Conservation of Nature
MAB	Man and the Biosphere program
MEDECO	Mediterranean Ecological Society
NAS	National Academy of Science
NSF	National Science Foundation
PERT	program evaluation and review technique *(sys. eng.)*
RANN	Research Applied to National Needs
RES	Regional Environmental Systems
SIL	*Societas Internationalis Limnologiae Theoreticae et Applicatae*

SREL	Savannah River Ecology Laboratory
UNESCO	United Nations Educational, Scientific, and Cultural Organization
WHO	World Health Organization

this period. The growth, excitement, and advance
of the founding ideas coupled by analogies to other
time. Ecologists were not questioning the cultural
king within them. It was not until later, when
tioned in American culture, that ecosystem theory
ount of criticism that could no longer be ignored.

CHAPTER 5

The International Biological Program

By the mid-1960s ecosystem studies had reached a level of worldwide activity. Ecosystem studies were a popular, even dominant, form of ecological research. While teams of researchers at national laboratories and other centers studied whole forests or lakes, individual researchers examined processes within systems, such as the rates of primary production, transfers between trophic levels and populations, and the rate of organic decomposition. An unorganized body of theory was available to stimulate research. Eugene and Howard Odum, Margalef, Slobodkin, and others viewed ecosystems from a variety of perspectives, frequently reasoning analogically from physical, chemical, or biological systems to ecosystems. The condition of ecosystem studies at this time might be characterized by Claude Levi-Strauss's term *bricolage,* which refers to the construction of an object or a theory from a variety of unrelated, found materials. The *bricoleur* arranges these and creates something new and unexpected from the disparate materials. Ecosystem theory was constructed from thermodynamics, from physical equilibrium theory, from information theory, from evolutionary theory, from field natural history, and so on. In 1965 it did not yet form a coherent, organized body of knowledge.

It was suggested by several systems ecologists that the way through this stage of science development was to employ systems theory to design models to organize the information about ecosystems. Olson, Patten, and Van Dyne at Oak Ridge were most enthusiastic about this approach, and they predicted a substantial advance in both the understanding and utility of ecosystem theory using systems ecology. Actually, the discipline faced two alternatives, although the choice was not clearly recognized by the community at the time. On one side was the system ecology approach, which constructed ecosystem models from the information about its components and linkages. These models represented the ecosystem type in a general way and would prove useful in predicting ecosystem performance under changing environmental conditions. On the other side was the approach pioneered by Howard Odum at Silver Springs. The ecosystem was considered as an object of research. Its input and output properties were determined and then the components were examined to explain the conversion of inputs into outputs by the system. In the next ten years, these two alternatives were tested in a scientific experiment carried out mainly in the United States. The opportunity for the test was an international scientific program called the International Biological Program. In this chapter I present the IBP from the perspective of its impact on ecosystem science.

Only one part of IBP, biome studies, was focused on ecosystem studies. *Biome* was a word coined by Frederic Clements to refer to broad, regionwide associations of plants and animals, such as tundra, boreal forests, and so forth.[1] The size and complexity of the IBP biome program as it existed preclude a detailed examination of each project. Rather, my strategy will be to focus on one program—the grassland biome project—and then to contrast selected features of the other studies within that project. In this way we will be able to identify some of the key factors that influenced ecosystem science and that led, or did not lead, to a new stage of development.

THE DEVELOPMENT OF THE INTERNATIONAL BIOLOGICAL PROGRAM

The International Biological Program became a major vehicle for ecosystem studies, but when it was first conceived by Sir Rudolph Peters, an English biochemist and president of the International Council of Scientific Unions (ICSU), as a biological imitation of the International Geophysical Year (IGY), he visualized a project in nucleic acids (Peters, 1975). The idea was first put forth in March 1959 after a meeting of the ICSU executive committee in Cambridge, England, when Peters, Lloyd Berkner, an American physicist and past president of ICSU, and Giuseppe Montalenti, president of the International Union of Biological Sciences (IUBS) and a geneticist, were returning to London on the same train. The idea spread rapidly, and in 1960, at the ICSU's next executive committee meeting, Montalenti presented a formal scheme for the IBP (Waddington, 1975). The overall theme chosen was "The Biological Basis of Human Welfare." A preparatory committee was formed, which met in March 1961 and drew up a proposal with three project areas: human heredity; plant genetics and breeding; and studies of natural communities that were liable to undergo modification or destruction. At the IUBS's general assembly meeting later that year, the committee's proposals were considered and a resolution was passed affirming that the program's aim would be "toward the betterment of mankind." The three specific areas for action would be conservation, human genetics, and improvements in the use of natural resources.

The planning committee met again in May 1962 in Morges, Switzerland, at the headquarters of the International Union for the Conservation of Nature (IUCN), where the final organization of the IBP was developed. Seven sections were organized. Three focused on terrestrial productivity; these included general productivity, metabolic processes, and the conservation of threatened communities. A fourth section was concerned with productivity in fresh water and a fifth with productivity in marine environments. A sixth section dealt with human adaptability both physiologically and genetically, and the seventh, titled "Use and Management," focused on aspects of applied biology outside of the interests of the World Health Organization (WHO) and the Food and Agriculture Organization (FAO) of the United Nations. The program was launched at the first general assembly of the IBP in Paris in 1964. Here it was resolved that the program should contribute to "the optimum exploitation, on a global basis, of the biological resources on which mankind is vitally dependent for its food and for many other products." The program was to have a finite life, terminating in 1972, but was later extended to 1974.

A book on the origin and development of the IBP (Worthington, 1975) follows the twists and turns that were required before the final compromise program was designed. Unlike the geophysicists, the biologists did not have a material global object on which to focus a global program. Biologists were required to create a global purpose from abstract needs and concepts. Peter's nucleic acid idea was quickly dropped, because he concluded that the field was "fully stretched." Montalenti's interest in human populations, in contrast, was converted into a program on human adaptability. Academicians Andrey Lvovich Kursanov, a plant physiologist, and Vladimir Aleksandrovich Engelhardt, a biochemist, the Russian members of the ICSU executive committee and the ICSU planning committee, pressed to have the program deal with the rational use of plant and animal resources with the aim of raising the standard of human life. This theme was reflected in the program's title and by its emphasis on productivity. Conrad H. Waddington thought that the study of the way solar energy is processed by the biological world to form complex molecules, which are used as human food should be a theme of the IBP. A conservation theme had been proposed early in the planning.

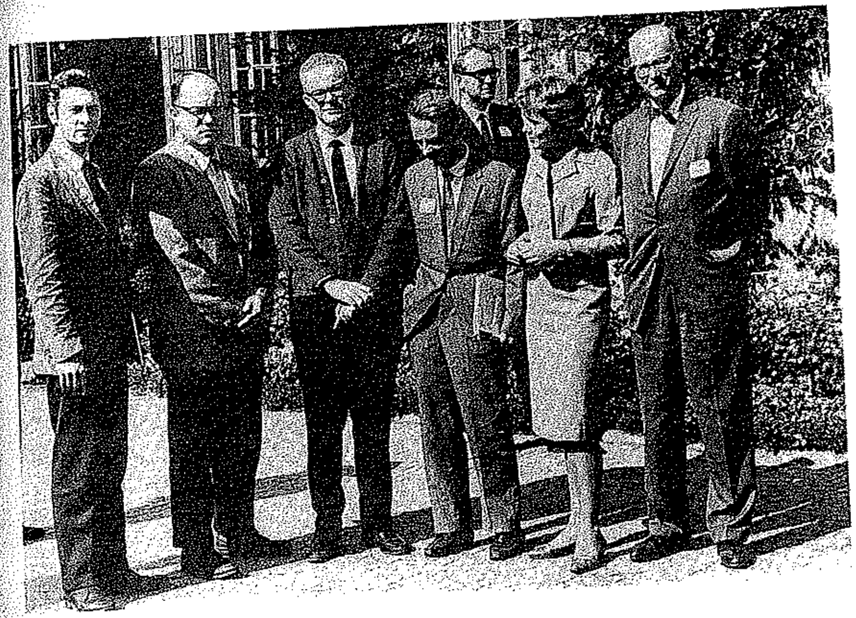
Thus, the themes of conservation, human adaptability, and use and management were grouped with an overall focus on biological productivity as a basis for human well-being. In retrospect, this focus made good sense. Productivity was a scientific concept that had been well developed by the early 1960s. It would attract scientists in agriculture, forestry, and fisheries, as well as those in basic ecology and fundamental studies in plant and animal biochemistry and metabolism. Also, it was broad enough to cover the different interests of the various national members.

The IBP was a complex program with projects in many areas of biology. Ultimately, however, it developed into a largely ecological program. The production part was developed in two phases. The first phase, from 1964 to 1967, was characterized by a series of planning meetings, the development of methodology handbooks, and the beginning of some limited research projects. The second phase, from 1967 to 1974, was marked by a growing dominance of the biome programs, which gradually became so active that the name IBP became in some people's minds synonymous with biome studies. The scientific director of the IBP, E. Barton Worthington (1975, 64), writing in the synthesis volume, states the matter well:

> It is this ecosystem approach which distinguishes much of the IBP research from what had dominated ecology before. Essentially it consists of the careful selection of a number of variables—biological, chemical and physical—about which data are collected, quantitatively as well as qualitatively. Thereby the ecosystem can be analyzed in order to ascertain which factors and processes are important in causing the dynamics of the whole. In this, the application of system analysis to biological systems has been one of the major innovations developed during IBP. Some would go further and say that it has been one of IBP's major achievements.

International programs do not evolve in a vacuum. The organizers must have good reasons for devoting the immense amount of time and effort required to plan a program and to convince fellow scientists and funding sources that the work is needed and will yield productive results. The original impetus for the IBP was, apparently, the desire to obtain some of the same benefits that had accrued to the earth sciences from the International Geophysical Year. These included the creation of international networks of collaborators, the collection of data on large-scale systems, and obtaining the attention of decision makers.

In addition, large communities of scientists were already at work, or were capable of beginning work immediately, and were eager to organize internationally. The freshwater biologists, for example, by 1962 had presented a report



5.1 Participants at the IBP Terrestrial Production project organizational meeting in Jablonna, Poland, 1966. From left to right, F. B. Golley, R. G. Wiegert, D. A. Crossley, Jr., Kazimierz Petrusewicz, Alicja Breymeyer, and Francis Evans. The man in the rear is unidentified. Photo property of the author

on the opportunities for limnology in the IBP,[2] prepared by Wilhelm Rodhe, a Swedish limnologist. This report was considered at the fifteenth Congress of *Societas Internationalis Limnologiae Theoreticae et Applicatae* (SIL). The marine biologists were also thinking globally and had several international programs under way.[3] The IBP, in their case, focused on topics not adequately covered in these other programs. For these fields and for the conservationists, IBP provided an opportunity to build better linkages between national communities, collect data globally, and to look for patterns on a global or regional scale.

The terrestrial group began with a meeting in September 1963, organized by Paul Duvigneaud, a plant ecologist and biogeochemist from Belgium. Attending were mainly plant ecologists and vegetation scientists interested in global patterns. Yet the official orientation of the terrestrial scientists did not continue in this botanical direction. In 1966, a meeting on the secondary productivity of terrestrial ecosystems was convened in Jablonna, Poland, under the leadership of François Bourliere, a French mammalian ecologist and professor of medicine in Paris. This meeting included many scientists working on ecosystem processes (fig. 5.1), and after long discussions,[4] the participants addition to the official U.S. group, the Conservation Foundation, the Nature Conservancy, the IUCN, the National Science Foundation, the Ecological Society of America, the IUBS, and several ICSU special committees. At the Paris meeting, James B. Cragg, an English zoologist and chair of a committee including Heinz Ellenberg from Germany and forest ecologist J. D. Ovington from England, proposed the formation of a production terrestrial (PT) group. Their proposal included the following statements: "Nevertheless studies of organic production and decomposition at different trophic levels seem to provide a unifying factor and should be a fundamental part of every project in terrestrial ecology. Analysis of dry matter can provide basic data on energy flow, protein production, mineral cycling, environmental pollution, etc. The interrelationships between production and biological diversity, community structure and the living organisms of different communities can be examined as well as environmental factors such as climate and soil."[8]

The U.S. delegation returned home and began the development of the program. A U.S. national committee was formed, chaired by Professor Roger Revelle of the Harvard Center for Population Studies.[9] Revelle was a distinguished scientist, a member of the U.S. National Academy of Science, and a capable organizer. He was assisted by Byerly and Cain as cochairs. Subcommittees or subsections corresponding to the IBP themes were also formed. The terrestrial productivity group was chaired by Eugene Odum, freshwater production (PF) by Arthur Hasler, and marine production (PM) by B. H. Ketchum. In late 1965, Donald Hornig, director of the Office of Science and Technology of the U.S. government, wrote Leland Haworth, director of the U.S. National Science Foundation, asking NSF to coordinate an interagency committee on the IBP. Haworth appointed Harve Carlson, director of the NSF Division of Biological and Medical Sciences, as the chair of this coordinating committee. In 1965, the subcommittees began planning their research programs.

The U.S. IBP organization had the same problem as the international organization in determining how to design a program that would be attractive to all biologists. Although the proposed program initially was broad, including various studies on topics of interest to U.S. biologists, one effort focused on ecosystems directly. The Analysis of Ecosystems program grew from a series of meetings of the subcommittees concerned with production ecology.

The first meeting of the terrestrial productivity group took place in May 1965. The participants included Robert Whittaker, whose most recent work had been at the ecosystem study site at Brookhaven National Laboratory in New York; Larry Bliss, a plant ecologist from the University of Illinois with experience in the tundra; Frank Pitelka, from the University of California at Berkeley, who was also interested in tundra; and Van Dyne, the modeler and former animal production scientist who was at Oak Ridge National Laboratory. A report was written with contributions from each member. The first draft emphasized research on productivity, training ecologists to carry out the IBP studies, and interaction with scientists in Latin American countries.

As chair, Eugene Odum worked on this draft report and gradually forged a document that was designed to be a national program statement. His report had two special features. First, through contact with the freshwater production committee, Odum's group had developed the idea of focusing research on large areas containing both freshwater and terrestrial habitats. This focus was what ultimately created a very different type of research project.[10] The report proposed as its general objective studying "landscapes as ecosystems," with emphasis on production and trophic structure, energy flow pathways, limiting factors, biogeochemical cycling, and species diversity. It stressed that these studies were not to be confined to natural areas only. The second feature was a proposal to use systems analysis as a mechanism for integrating the results of the study.

Eugene Odum was concerned that the IBP should develop "new thinking at the ecosystem level." In the final program statement, the second guideline was titled "Development of New Methods and Approaches": "Probably the most important role that the PT program can play in the U.S. National IBP effort is that of catalyzing new ideas and techniques which will make it possible to evaluate whole landscapes within the framework of man's dual role as a manipulator of, and a functional component in, ecosystems. The PT program differs from that of the other IBP subcommittees in that it seeks to establish a new science of landscape ecology that can provide a 'pure science' basis for landscape planning in the future."[11] This statement was typical of the Odum thought process and expression, and it was prescient.

The terrestrial productivity program statement was to be considered, along with the freshwater production program, at a general meeting of interested ecologists at Williamstown. This meeting was scheduled from 28 to 31 October 1966, and it grew in size until the organizers had to limit the participants based on the availability of hotel rooms. In transmitting the PT program statement, Odum wrote Bliss in July 1966, "Since I have not seen Hasler's final statement, be sure our statement about cooperation with PF in planning, and in hiring a full-time man, jibe with his program statement."[12]

The meeting was a grand success! A new, expanded view of ecosystem research emerged amid a spirit of cooperation and fellowship, helped in no small part by Pitelka, who at the piano led the group in evening song. The final report from this meeting merged the PT and PF committees into a single

Species Groups	Habitats: Tundra	Boreal Forest	Temperate Forest	Grassland	Tropical Forest
Vegetation					
Small mammals					
Large grazing mammals					
Granvorous birds					
Social insects					
Soil organisms					

5.2 A matrix developed to organize research in terrestrial productivity of the International Biological Program, approved at the Jablonna, Poland, organizational meeting in August 1966. Groups of organisms were to be compared within and across habitats.

agreed to a program designed as a matrix (fig. 5.2). At the top of this matrix were placed the major ecological formations of the world, indicating the principal habitats of animals. Emphasis was on temperate regions, although the tundra, taiga, and tropical forests were included. The rows of the matrix consisted of groups of organisms. Over Duvigneaud's objections, vegetation was treated as a group, as were insect herbivores, social insects, small mammals, large grazing herbivores, granivorous birds, and so forth. In this way, terrestrial productivity included within the IBP some of the subdivisions of biology focusing on taxa, along with ecological subgroups interested in the properties of ecosystems, such as the flow of energy, productivity, and the decomposition of organic matter. This plan went beyond a focus on secondary productivity,[5] since it included vegetation as part of the matrix and treated it as the primary producer component of the ecosystems.[6]

This scheme represents the biologically oriented ecologists' definition of a global program. The emphasis was on groups of organisms studied across habitats and regions. It took a biogeographic approach to the problem. Processes were not emphasized, except as they were represented by organism groups.

THE U.S. PLAN

The Jablonna matrix lasted as the accepted plan for all IBP terrestrial studies for about one month. Ecologists in the United States met about a month after the Jablonna meeting at Williamstown, Massachusetts, and developed an IBP of their own, which over years gradually influenced and changed the international focus.

The United States was part of the IBP almost from the beginning. George Ledyard Stebbins, secretary general of the IUBS and a Davis, California, plant geneticist, offered his ideas about potential objectives at the first meetings to organize the IBP. He had queried American biologists about their interest in forming an IBP, although with not very useful results,[7] according to Waddington (1975). When the special committee for the IBP was formed by ICSU, Stanley Cain, a Michigan botany professor and at the time (1965–68) assistant secretary for Fish, Wildlife, Parks and Marine Resources of the U.S. Department of the Interior, was chosen as a member. Arthur Hasler of the University of Wisconsin, George K. Davis, a Florida nutritionist and biochemist, and Bostwick H. Ketchum from the Woods Hole Marine Laboratory in Massachusetts were also involved in planning from about 1964. The U.S. National Academy of Science (NAS) provided a special IBP planning grant of $50,000 a year for four years, from 1965 through 1968. Even so, Waddington felt that the American community of biologists was the most difficult group to have become involved in the program. Waddington commented: "The idea of studying the energy balance of ecosystems had therefore got to thread its way between adherents of the 'central dogma,' who couldn't care less but were apprehensive it might take away some of their public funds, and an opposite party whose line was that 'we *are* field biology, and productivity is not an American problem'" (Waddington, 1975, 9). In 1963, after a meeting in Washington, D.C., arranged by T. C. Byerly, a U.S. Department of Agriculture animal biologist, Waddington was sufficiently disturbed by the hostility of senior American biologists to participation of the United States in the international program that he wrote to a number of his friends, such as C. H. Müller, Tracy Morton Sonneborn, Sewall Wright, Ernst Mayr, Theodosius Dobzhansky, and James Ebert, all distinguished American biologists, asking for advice and support. The response from Ebert was that a well-designed international program would be supported (Waddington, 1975). This support eventually resulted in a financial grant from NAS and in the organization of IBP planning committees.

U.S. IBP ACTIVITY BEGINS

Although Waddington's concern about U.S. participation in the IBP may have been correct in 1963, by 1964 interest had begun to burgeon. The U.S. delegation to the first General Assembly in Paris consisted of nineteen people, with T. C. Byerly and S. A. Cain as cochairs. The delegates represented, in program focusing on the analysis of ecosystems, with Fred Smith, a professor at the University of Michigan and a theoretical ecologist, as director.

The terrestrial productivity program statement for this new effort said that "the primary purpose of the IBP is an understanding of ecosystems, including man's own." The general objectives of this program were:

1. to study whole systems, such as drainage basins and landscapes, through team effort

2. to study interactions between components

3. to emphasize primary production, trophic structure, energy flow pathways (food chains), limiting factors, interactions of species, biogeochemical cycling, species diversity, and other attributes that interact to regulate and control the structure and function of communities

4. not to restrict the studies only to natural areas. Ecological succession was to serve as a background in which general objectives could be pursued

5. to consist of collaborative studies in major biomes, in drainage basins, where terrestrial and aquatic studies can be simultaneous

6. to catalyze new techniques, developing theory from small field and laboratory studies

7. to involve systems analysis techniques for examination of existing data on ecosystem processes by sensitivity analysis as an aid in allocating resources for integrated system studies, for rapid organization and analysis of data collected by electronic recording equipment and for analysis and integration of results designed to test and develop theory

8. and finally, to establish centers to store and distribute information collected at the different study sites.[13]

A list of sites in six biomes of North America where work could be carried was also compiled.

Following the Williamstown meeting, Larry Bliss took over the chair of the terrestrial productivity group from Odum. His November 1966 letter to Odum describes Odum's role in developing the PT program.[14] "Your good influence has prevailed in the union of the two subcommittees and in the adoption of the ecosystem theme throughout the program." Yet Bliss was concerned about the communities response. He continued, "I talked with John Wolfe yesterday and he feels we will do well if we can establish one or two good ecosystem studies and that there will be considerable opposition for this program from biologists, to say nothing of other vested interest groups." Wolfe, of course, spoke from the experience of having established the Atomic Energy Commission ecosystem programs.

Nevertheless, the program developed rapidly with a virtual blizzard of meetings in 1967. In February, the U.S. national committee met and approved the plans developed at Williamstown. Also in February a meeting in Chicago considered the criteria to be used for selecting sites for studies. In May, the NSF granted two years of funding for program management, which meant that an office could be established. Also in May a meeting was held on the role of system analysis in the Analysis of Ecosystems program. At this meeting it was decided to focus system analysis first on a grassland site, since the grassland was relatively well understood ecologically and was structurally simpler than forests. In late June, Fred Smith, in a progress report, estimated that the cost of the "Program on Drainage Basins and Landscapes" has been "guessed at $45,000,000."[15] By October, the Pawnee grassland site near Fort Collins, Colorado, had been selected and Van Dyne was appointed director of the project. At this time the first Grassland Working Session was held to design the general scheme of work, which would include both intensive studies at Pawnee site and extensive studies throughout the grassland biome in North America. A smaller group also began discussions on the formation of a tundra study.

Finally, Congress member Emilio Daddario of Connecticut, chair of the subcommittee on Science, Research, and Development of the Committee on Science and Astronautics in the U.S. House of Representatives, held five hearings on the IBP. These hearings included testimony from a number of scientists and were favorable to the program. It appeared that a special funding initiative for the IBP might be provided by the federal government. Philip Johnson, a member of the PT committee and the faculty of the University of Georgia, wrote the Georgia faculty in January 1968 that "the impetus IBP is fostering in ecology cannot simply stop in five years. Ecology will by then have become 'big science' with all the attendant pros and cons."[16] Fred Smith said, "Whatever the causes, a revolution among ecologists is under way, and the IBP is in the middle of it."[17]

The U.S. Analysis of Ecosystems program provided an opportunity for substantial advances in ecosystem studies. It would make a large amount of new funds available to an already well-funded community. It would permit the organization of academic researchers into teams like those at the national laboratories and would focus them on problems of large spatial scale. And finally, it would permit systems ecology to develop its potential organizing and predictive functions.

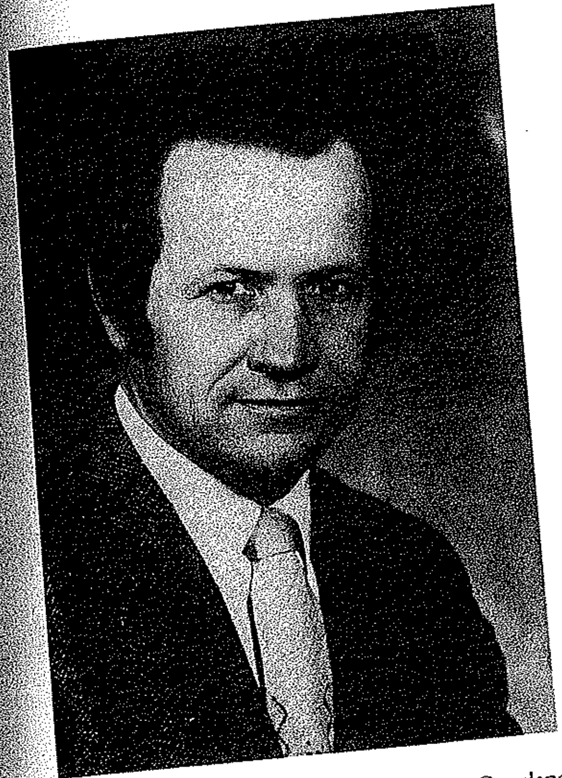
The Grassland Biome

In October 1967, the Committee for the Analysis of Ecosystems met in Fort Collins, Colorado, and approved a proposed research program for grasslands. The IBP biome programs were under way.

The selection of Van Dyne (fig. 5.3) as director was an important formative factor in the entire Analysis of Ecosystems program. George was thirty-five years old at that time. He was born in southern Colorado into a relatively poor ranching family. As a bright person, he saw the opportunity to better his life with a university education. He began his education at Pueblo College and finished it with a doctorate from the University of California, Davis, in animal nutrition with an emphasis on biometrics and biochemistry. While at the University of California, he taught himself computing techniques by studying and experimenting at nights and on weekends at the computer center. His academic positions included teaching animal husbandry and range management at Colorado State University and Montana State University. He moved to Oak Ridge National Laboratory as an ecologist and was jointly appointed associate professor in the University of Tennessee department of botany.

George Van Dyne brought a familiar American personality type to the IBP: the workaholic. The standards he respected were quantitative, large, and fast. To him, success was largely judged by the amount of money paid—earned or received—from the granting agency; by the number of publications achieved; and by similar measurable criteria. By the time he had reached Oak Ridge, he had authored sixty-seven publications on animal husbandry; according to his bibliography, many of these were reports and experiment station documents. Although many of the publications had coauthors, for almost all he was the senior author. Van Dyne was not inclined to manage an organization by direct personal relations; rather, like the prototypical American business person after whom he patterned himself, he depended on memos, PERT charts, and tables of organization.

Although Van Dyne was selected to be biome director because of his enthusiasm and understanding of modeling, his personal characteristics meant that the IBP grassland program was going to be active in a quantitative way. Van Dyne performed according to expectations. By December 1967 he had organized and sent a 370-page proposal to the National Science Foundation for a grassland program. This work was to extend from April 1968 to March 1969 with a cost for this proposed work of nearly $2 million! The proposal contained the resumes of more than eighty investigators and consultants and over sixty research projects. The work was structured within the Lindeman ecosystem paradigm, with overviews of abiotic factors, and studies of producers, consumers, and decomposers. It contained considerable detail about the ecology of



5.3 George Van Dyne, director of the U.S. Grassland Biome program. Photograph courtesy of Bernard Patten

animal species. Guided by the aims of the national committee, the study included both intensive research at a single site and extensive studies throughout the grassland region. The experimental design and systems procedures were not well developed, but there were organization charts and schedules of work. The proposal ended with a twenty-two-page document on ecological modeling. In this article Van Dyne revealed that he was not interested merely in using modeling to integrate the work, he was interested in creating a new form, or at least, a new application of ecological modeling. This form would be probabilistic and nonlinear.[18]

The initial proposal was not funded. Rather, a revised proposal was requested by NSF. Van Dyne submitted this revised proposal in February 1968 requesting $700,000 for the period April 1968 to June 1969. The reduction in cost was achieved by postponing the start of the comprehensive program, the aquatic studies, and some of the subprojects, delaying some hiring and focusing more attention on the initial modeling. Construction would begin on a building for the project on the Colorado State University campus, and field facilities construction also would get under way.

In June 1968, $400,000 was received from NSF and AEC for the remaining months of the year. This allowed Van Dyne to bring Donald Jameson, a range scientist with a botanical orientation and an interest in system modeling, to Colorado as the manager of the intensive site and to give research contracts to twenty-five scientists. Further, it permitted the program to look beyond the intensive site study toward the comprehensive program. It provided funding for a first meeting of investigators from other grassland sites held at Manhattan, Kansas, in late June.

This was quite an achievement. In nine months Van Dyne and his staff had written two large proposals, involved many investigators across the western United States in the program, implemented the general program plan of the national committee, began to think through the modeling of grasslands, and set up a management system appropriate to a small corporation. It appeared that choosing the grassland as the first biome and Van Dyne as the biome director were the right choices. Clearly, the speed and enthusiasm of the Van Dyne group created a model for other biomes to emulate or reject.

Van Dyne was an enthusiastic spokesperson for ecological modeling. In Washington at NSF, he repeatedly argued that this approach was the way to understand and manage studies of large complex systems. Officials at NSF, especially the assistant director for Biological, Behavioral and Social Sciences, Eloise Clark, were not fully convinced of the ecosystem approach or the utility of models. This was unfamiliar ground, and there were no lack of ecologists who declared that the work outlined could not be done. Van Dyne, in his enthusiasm, overstated his case, and although he obtained support for the program, his exaggerated claims for ecological modeling later came back to haunt him.

In January 1969, Van Dyne, after receiving almost half a million dollars for the period January 1969 to August 1969, submitted another proposal to NSF for the continuation and expansion of the grassland program. This proposal was 675-pages long; in it, he requested $2.2 million for the period September 1969 to December 1970. In the proposal, the full program was described. The broad objectives were to study the "various states of the grassland ecosystems to determine the interrelationships of structure and function; to determine the variability and magnitude of rates of energy flow and nutrient cycling, and to encompass these parameters and variables in an overall systems framework and mathematical model." The research strategy was to employ a systems analysis approach and to isolate and examine the factors and components through the following questions:

1. What are the driving forces making grassland ecosystems operate?

2. What are the major and minor components of grassland ecosystems, and what are the changes in magnitudes of these components over time?

3. What are the important families or groups of processes that cause the interaction, coupling, or linking of the components of the ecosystem one to another?

In the proposal, systems modeling began to receive more attention. Systems analysis is discussed and several important positions taken,[20] including:

A systems approach is the only known method of attaining the objectives of our project.

To our knowledge, no person or group has developed models of entire ecosystems.

Since mathematical modeling of ecological systems is an art in its infancy, we recognize the importance of recording the steps we use in model development and redevelopment. This implies a continued series of reports or publications on stages of modeling.

Most of our participating scientists are not skilled mathematicians. Yet their input into model development is essential. They must recognize the responsibility and accept the challenge.

The functioning of an ecosystem is dependent upon its structure.

These quotations reveal some of the thinking that went into the plans. Much of it was from Van Dyne, and the demand for commitment—because of the significance and value of the exercise—was definitely his. This was the Achilles' heel of the program. Van Dyne was one of the U.S. IBP biome program designers. He tried to follow the plan developed by the national committee in the abstract, and at the same time, create a new kind of program for ecology. He selected the systems model as the key organizing idea, and then with this organizing idea in mind, chose to move toward the program objectives using modern concepts of business management. The resources were not adequate to the task, however, and the people in the project could not be managed as in a private corporation.

The language used in the proposal was a new language for many ecologists. It expressed goals in mechanical systems science terms. How did one translate the word *components* into organisms; *forces* into ecological processes, such as energy flow and mineral cycling; or *coupling* into ecological interactions? Traditional ecologists recruited for the biome programs could interpret the goals in a variety of ways, depending upon the way they decoded this new language.

The National Science Foundation was not willing or able to provide all the funds requested in the several grassland proposals. Within NSF, research is ordinarily funded through a complex program of peer review. The process is linear, with about thirty steps, and involves mail reviews as well as a panel discussion in Washington, D.C. Nonetheless, when a research request exceeds a certain set amount (which was $500,000 during the time of the IBP), additional steps are required. The National Science Board, the policy committee of the foundation made up of the heads of corporations and universities and widely respected scientists, must approve the decision to fund a project. Thus, a proposal the size of the grassland biome proposal had to go through a review process within the ecology program and be approved by the assistant director before being presented to the National Science Board. The board meets at regular intervals, and it requires advanced scheduling to be on the agenda.

One begins to see the complexity of funding this type of work. A proposal might, according to Van Dyne (1972), consist of 100,000 to 200,000 words. It would be reviewed internally two or three times and be rewritten. It would then be reviewed by the U.S. IBP Grassland Biome Scientific Coordinators, an advisory group, then by the Analysis of Ecosystem central staff, and the U.S. IBP Coordination Committee. Only at this point would it be sent to NSF and enter its review system.

The amount of money requested in a proposal was the aggregate from proposals solicited from many individual investigators, adjusted by the Van Dyne management group, and then reviewed and defended up through the committee and peer review system. Although the cost base for the program was determined by many people, the initial request was a compromise between what might be done and what should be done to meet the biome goals, as interpreted by Van Dyne, within the limits of what the participants felt was possible. This was an entirely new kind of venture for ecological science and no one really knew what the National Science Board would do. Therefore it surprised many that the project received about 50 percent of the funds requested in the first case and 80 percent in the second. Still, even this relatively large amount of funding required scaling back the work that was proposed and created management problems. Van Dyne was faced with the prospect of telling people who had been selected to be part of the proposed research group that they would not be funded or that their funding would be much less than required for the work. Further, the funding process was segmented. Van Dyne was required to write a supplement three months after the first proposal was approved in order to obtain all the funds granted for the first period.

Van Dyne (1972, 125), in his no-nonsense, businesslike way, determined that these shortfalls and delays in funding would delay meeting project objectives:

> At the outset, we contemplated the completion of a final report in 1,250 working days for a five-year first phase of our program. Yet the calculated duration of the project in the PERT analysis was 1,740 days! Obviously there can be some trade-off between time and dollars. Yet, using our estimates of funding and completion times for activities, it was clear from this analysis this program could not be completed in time. What was feared by many, i. e. that the late start and slow funding in the U.S. IBP, was that IBP would not be able to meet its commitments within the original planned time span through 1972. This preliminary analysis suggested that the final report for the initial phase of our grassland research program could not be completed until between December 1973 and June 1974. Interestingly, and coincidentally, the IBP has recently been lengthened in many countries through June of 1974. We still have a chance!

Not only were the resources inadequate to meet the plan and the method of funding the science Kafka-like, there was also a fundamental problem with staff. The terrestrial ecologists attracted to the biome studies were generally individualists and had never experienced the constraints of a rigid organizational framework. Most were used to the constraints of the classroom or experiment station. Their performance had been judged on the basis of their independent work, and frequently their field work was done alone under arduous conditions. Each competed with others for resources, students, prestige, and recognition. The cooperation that occurred between scientists from the same graduate programs or the same background working on similar problems was frequently expressed in male drinking parties with numerous stories and kidding. The grassland biome proposal and Van Dyne's papers on the project used the male pronoun almost exclusively in referring to scientists. In large part, this was a male world and competition was more the rule.

The biome program assumed that individual scientists could be brought together in a team, focused on a common goal, and that the common goal would be more important than individual goals. That is, the program managers felt that the natural tendency for research to spin off in unpredictable directions could be countermanded through management. Even though the grassland biome began at a time when the popular culture of the United States was supportive of cooperative activity of all kinds, older scientists tended to be less affected by these trends than were students who were caught up into the movements of the day. Although their motivations for becoming involved with the biome program were mixed—a need for funding, interest in a new kind of science and activity, attraction to ecosystem studies, an interest in modeling, or a response to George Van Dyne—people did voluntarily join the project. The problem was to keep them involved, happy, and productive. This proved exceedingly difficult to do.

Van Dyne (1972, 1980) discussed some of the management problems of large-scale ecological work at the same time he was struggling to make the grassland biome program work. These problems included the conflict between the goals of individual research projects and the goals of the model. Ordinarily, a research scientist sets up objectives, collects data, writes an article, and sets new objectives. All the decisions about goals, design, data analysis, and interpretation are made by the individual scientist. In the biome program, these steps were open to comment and control by others. An individual's goal might be redefined in a imaginative, exciting way through discussion with a group of peers, but equally it could be altered through coercion. It was possible for a scientist to become only a highly trained technician working for a modeling group. One solution to this problem was to hire students to do most of the actual fieldwork. As a consequence, the quality of the data suffered. Although Van Dyne, from the perspective of modeling activity and the search for trends and patterns, was able to accept some increase in experimental or observational error, the biome scientists were not, and they became concerned about the quality of the research. After an Ecological Society of America symposium in 1972, when these problems were aired publicly, Nelson Hairston made highly critical remarks about the research to the National Academy of Science IBP Coordinating Committee.

Hairston's complaints represented a growing body of opinion in the ecological community. Many scientists who were unable or unwilling to join teams began to defend the approach of the individual scientist. Some of the reservations expressed about the IBP when it was first proposed were repeated. The biome programs were believed to be a threat to the individual. It was thought that the large biome research budgets took money from individual ecological research. In a biomelike project, which remained outside of the IBP, led by Gene Likens and Herbert Bormann, the individual nature of the research was emphasized. The high productivity and excellence achieved by their studies at Hubbard Brook were widely used as evidence by others that individual research on ecosystems was more productive than team research.[21]

The debate on how ecological science should be conducted became more virulent during the IBP, and it began to work against ecological science, since decision makers who were not ecologists could not be sure which side was

correct. Young and liberal Americans were attracted to the concept of community and cooperation. Conservative Americans defended individualism. These inherent differences in political outlook were exaggerated by the debate over the morality of the Vietnam War: thus, the public enthusiasm for ecology during the age of environmentalism, which might have been converted to support new and grandly conceived ecological programs, was frustrated and diffused. As a consequence, ecological support from the federal government, including additional funds for the IBP, increased only at the inflation rate (Golley, 1980). During this same period, support for the other environmental sciences, where these debates did not occur—such as geology, marine science, and atmospheric science, increased rapidly at rates well above inflation. Although it is not possible to assign exact causation in this situation, it seems clear that the debates among distinguished members of the ecological community on how to best do ecological research had a negative effect on the overall funding of ecology. In the debates, one side tended to discredit its opponents' position by pointing out weaknesses in their research designs, and NSF Assistant Director Eloise Clark, a biophysicist, was troubled by the contrary advice she received. Hence, her support for the biome program, which was crucial at the level of the National Science Board, was not deeply founded.

Van Dyne was an effective competitor. He presented dozens of lectures all over the United States explaining how the biome program was organized and what he expected from the research. He and his team wrote voluminously. He instituted an in-house series of publications, *The Technical Report Series,* which was meant to inform the research group and eventually included almost three hundred titles. Articles also began to appear in peer-reviewed journals. A grassland seminar program moved between the universities in Colorado and Wyoming, both of which had grassland biome research groups.

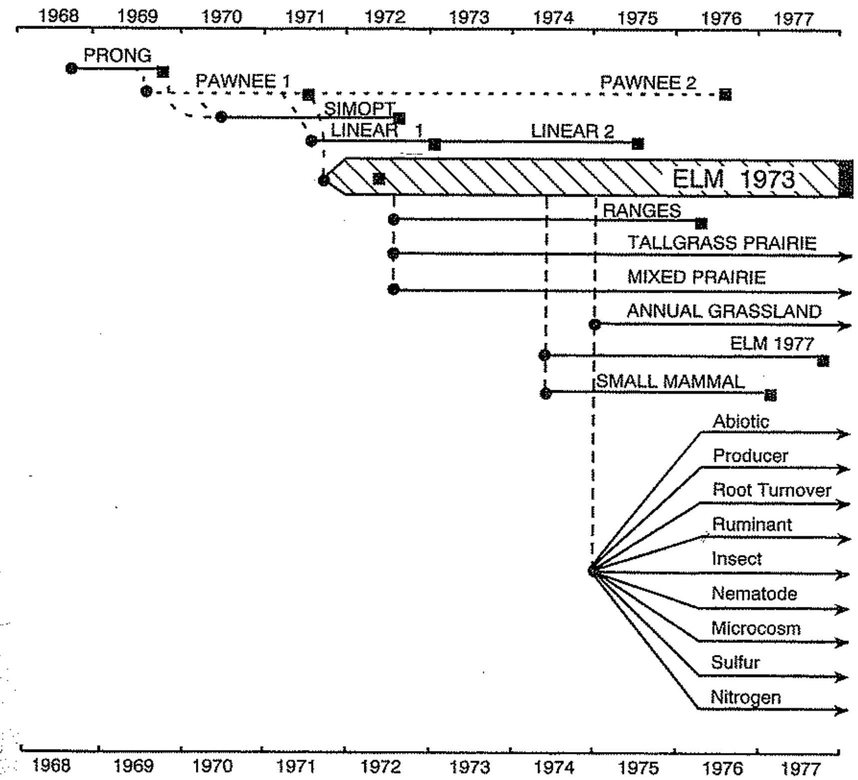
In 1969, Norman French was hired as comprehensive site coordinator and the third member of a three-man management team. French was a mammalogist from the AEC Nevada test site program of the University of California at Los Angles, with extensive experience studying desert rodents. French developed active programs at about ten other sites throughout the North American grassland.

Although specialists were brought in to organize and direct detailed studies on their subjects and to organize a modeling team able to take the data and build models to predict the performance of components, the program lacked people between the specialists and the modelers able to interpret the data. If this had been a small project, Van Dyne might have been able to play this role himself, but he was dealing with hundreds of people. A decision was made to hire a group of integrators. It brought into the project another group of senior scientists to add to the team of Van Dyne, Jameson, and French. The 1973 organization chart of the grassland program indicates that these integrators were F. M. Smith, abiotic factors; J. E. Ellis, consumers; D. C. Coleman, decomposers; J. K. Marshall, producers; M. I. Dyer, rate process studies; G. S. Innis, systems analysis; and J. H. Gibson directed services and administration.

Van Dyne worked progressively harder for longer hours, took more trips, and wrote more reports and articles. One staff member recalled that the team received about four memos a day from the director. Yet Van Dyne could not overcome the internal conflicts and contradictions of the program. Don Jameson was the first to leave. In 1971 he received funding for an applied grassland program using a systems analytical perspective from a new NSF program, Research Applied to National Needs, or RANN. Van Dyne, however, did not want to accept a project organized and run separately from the main project. He considered it a deviation from the plan and an expression of unacceptable independence by Jameson. Thus, Jameson left the project, and the task of directing field activities was added to French's other tasks.

Obviously, Van Dyne needed some relief from the pressures of the project, and in 1972 he planned to take sabbatical leave during the next academic year. He planned that he and his wife would visit Europe and spend part of the time in England, where the IBP was headquartered. He went alone. His wife left him, giving him an apparently unexpected blow, which he found extremely hard to accept. Yet the leave seemed to be effective in restoring his equilibrium. He made several trips back to Colorado to check on the program and contribute to the third large proposal, which was being developed under the direction of integrator Dyer, a former Fish and Wildlife Service biologist who was a specialist on the interaction of birds and vegetation. Upon its completion, Van Dyne signed it, and it was sent to NSF, reviewed, and funded.

Upon Van Dyne's return, he reread and reconsidered the proposal and became outraged. He declared it to be counter to the entire pattern of biome development. He immediately went to Washington. At NSF, he demanded that the proposal be withdrawn and that full authority to return the project to its objectives be given to him. His request was denied, and he returned from Washington in a foul mood. His first action when he arrived in Fort Collins was to call the entire staff together and tell them that the project and their employment was reaching its end. He said that he would begin making plans to lay off staff and that they should begin to look for other employment. He labeled this outburst "save six for pall bearers," envisioning a much-reduced program with only six senior staff to work on parts of the large program. One can imagine the consternation this action produced. Here was a group that had successfully written a proposal that produced over two million dollars for each of three years



5.4 Evolution of the ELM model of the IBP grassland program. The black boxes represent reports on the model, and the arrows indicate that the work was unpublished in 1978 (Van Dyne, 1978, ix).

being told by their director that the project would end and to start packing their bags.

Today, in rereading these proposals, it is difficult to see what aroused Van Dyne's ire. The June 1973 continuation proposal requested $7.6 million for the period from January 1974 to December 1976, and it continued the earlier development of research in its three hundred pages. There was, however, a discussion about the end of the program: "Our current plans, to obtain the model-experiment feedback and interaction in a more quantitative way, call for detailed modeling, model sensitivity analysis, and synthesis activities in the 1973 and 1974 period to be followed by a final comparative field validation study sequence in 1975 to 1977 [fig. 5.4]. This period would be followed by a final phase of coordinated model development, model experimentation, and synthesis in 1978 and 1979. Although publications have been emanating from the Grassland Biome study throughout its duration, a major terminal reporting and publication phase would begin in 1980" (pp. 9, 10).[22]

Apparently, Van Dyne had a different conception about the life of the biome program that he had not shared with his staff. I suspect that he envisioned the grassland biome becoming an ongoing, long-term study at Colorado State University, probably funded by a diversity of sources, and gradually becoming oriented to applying a tested and validated grassland model to regional problem solving. This was a perfectly reasonable and valid dream, and to a large degree it has come true because the Natural Resource Ecology Laboratory continues its grassland studies. Putting an ending date in the 1973 proposal that could be used to terminate the funding of the large centralized effort was, however, perhaps in Van Dyne's mind a self-defeating and disastrous strategy.

By taking sabbatical leave in 1972–73, Van Dyne lost firm control of the program. His private vision of the future of the grassland program was not reflected in the statement that the program would end at the end of the decade. By leaving a group of able senior scientists to carry on biome management, he allowed the development of individual research initiatives and the evolution of group camaraderie in program direction. The former central control was weakened fatally. His outright repudiation of the proposal of June 1973, his attempt to reassert control, and his reaction to his own failure to convince NSF to return control solely to him further weakened any respect for his authority.

Nineteen seventy-four was the crisis year. NSF made a special site visit led by Eloise Clark, which apparently went well. The overall modeling activity under George Innis and the various component programs under other senior staff were strong and were following interesting scientific questions. Nevertheless, the rancor between Van Dyne, supported by those who respected his leadership and shared his goals, and other senior staff who wanted independence and a more open, collective leadership persisted. In March, Van Dyne was asked by Colorado State University to resign as biome director. Jim Gibson, who had been in charge of administration, was asked to serve as the project director, and the senior staff became directors of their projects. David Coleman received the first independent research grant (the second in the history of the program) in 1975; William Hunt received a second in 1977; and since then the group has continued to be funded through a variety of sources.

Van Dyne moved to the range science department at Colorado State University where he began a new modeling program, still focused on the grassland. He also retained connections with the biome program, and he was carried on their reports as an investigator until 1976. In 1981 he died unexpectedly of a heart attack; he was forty-nine.

Evaluation

In evaluating the impact of the IBP grassland biome program on ecosystem studies, one finds that there were many difficulties. The material developed by the program is voluminous and scattered. Nevertheless, three syntheses have appeared. The first was edited by Innis (1978a) and reports on the development of the systems model, which was called ELM. The second was edited by French (1979) and reports on some of the comprehensive studies. The third, edited by Paul Risser and co-workers (1981), is concerned with the true prairie ecosystem. In addition, two other volumes appeared in the Cambridge University Press IBP synthesis series and present comparisons of grasslands internationally. These volumes provide a foundation for an evaluation of the program.

We can analyze the program in several ways. First, from an economic point of view, we might audit its productivity in terms of the literature and graduate degrees. These parameters could be linked to its intellectual product. Second, we might ask, Did the project succeed in doing what it proposed to do at its outset? Third, we might question whether the program contributed to our understanding of ecosystems? Did it enlarge the conception? I will briefly explore each of these paths of analysis.

The IBP grassland project, through 1976, received $16.3 million in funding, uncorrected for inflation (table 5.1). We have only cumulative publication records through 1974, since those publications prepared in 1975 and 1976 appeared one or two years later and, as far as I know, were never included in a list of IBP publications. The publications, taking the raw lists from the proposals and correcting for duplicates, indicate that the production of titles held reasonably steady over the life of the project. There were from fifty-seven to seventy-six titles published annually. A count of listed titles, however, exaggerates the production, since it includes abstracts of talks published in program editions of bulletins, book reviews, and other minor writing. Nevertheless, these lists are what reviewers in NSF were given by the research team, and it represents the material by which the project chose to be judged. Besides published titles, the project produced 98 theses or dissertations during this period and 293 technical reports. The senior, (doctorate or equivalent) staff available to direct the research, prepare articles, and direct students increased over the life of the project. In the most active phase, there were about twenty person-years of senior staff time allocated and paid for. Of course, this amount does not include any volunteer time given to the project.

These data provide a basis for an economic analysis of the grassland project. From 1968 to 1974, the average cost for each published title was nearly $43,000, and for each published title plus thesis title, over $33,000. A few years earlier (1965), at the Savannah River Ecology Laboratory (SREL), I determined

Year	Dollars $ × 10⁶	Senior-Staff Person-years	Titles Published	Theses and Dissertations
1968	0.85	3.35	—	1
1969	1.80	6.00	59	3
1970	1.80	10.47	72	7
1971	1.80	14.25	60	29
1972	2.94	20.10	26	27
1973	3.09	21.55	57	21
1974	2.5*	23.38	71	10
1975	2.6*	20.00	—	—
1976	2.5*	19.25	—	—

* requested amount
— no data available

5.1 Resources and production of the IBP grassland biome project, based on grassland biome project proposals and reports (University of Georgia library archives)

that the cost of each published title for the laboratory was approximately $10,000. The SREL costs did not include the construction of a building and other facilities, the operation of a multistate network of scientists, nor a large computer program as required in the IBP. These comparisons suggest that the grassland program was not excessively costly for its size and organization. Further, the number of publications produced by senior scientists was three-and-a-half titles per person-year, which is a reasonably strong rate of publication, especially for a new program. Thus, an economic evaluation of the grassland project suggests that it was productive given the resources available to it.

An economic analysis of basic research is unsatisfactory for several reasons. It is exceedingly difficult to determine the inputs. For example, Van Dyne never received his full salary from the grassland biome when he was biome director. How does one calculate the twenty-four-hour-a-day attention he gave to the project in terms of person-years or dollars? It is also difficult to establish outputs and their value. Some research has immediate value because it creates new directions and new paradigms. Other research has lasting value because it is foundational, providing baseline data that will always be used. Yet other research builds our understanding of a topic and adds to our knowledge. These thoughts bring us to our second form of evaluation.

The statement of objectives in the original proposal for the grassland biome (December 1967) is complex. It acknowledges that the purpose of the IBP was to examine the biological basis of productivity in human welfare. It then states that the project would be concerned with primary and secondary productivity and how those levels are affected by man. The immediate goals were identified as an analysis of "energy flow, nutrient cycles, trophic structure, spatial patterns, interspecies relations and species diversity." To reach the ultimate goal, the project would have to be involved in the analysis of structure, function, and the interaction of these processes in grassland function. The statement concludes: "The focal point of this research is to improve our understanding of entire systems. Throughout this study, the whole system will be kept continuously in view. No matter how narrow or detailed some of the projects may be, their relation to the whole will be the dominant theme."[23]

Finally, after over a hundred pages of detailed discussion of the aims and goals of the study of the abiotic environment and three trophic levels, ecosystem modeling is presented as the synthetic tool of the project. Models would serve not only to synthesize data but to organize and guide the research.

In the second proposal (January 1969), the objectives were made more general with the addition of the following three questions: (1) What are the driving forces making grassland ecosystems operate? (2) What are the major and minor components of grassland ecosystems and what are the changes in magnitudes of these components over time? (3) What are the important families or groups of processes which cause the interaction, coupling, or linking of the components of the ecosystem one to another?[24]

Thus, one of the main objectives was the development of a grassland ecosystem model. A series of models were produced (see fig. 5.4) (Van Dyne, 1978). The first several models were limited in scope. For example, several developed by Patten (1972) and W. G. Cale (1975) were linear models. In 1971, however, the team began developing the ELM model. ELM was a total system model focusing on biomass dynamics, which would be representative or applicable to sites in the grassland. The model addressed four questions:

1. What is the effect on net or gross primary productivity as the result of the following perturbations: (*a*) variations in the level and type of herbivory, (*b*) variations in temperature and precipitation or applied water, and (*c*) the addition of nitrogen or phosphorus?

2. How is the carrying capacity of a grassland affected by these perturbations?

3. Are the results of an appropriately driven model run consistent with field data taken in the Grassland Biome Program, and if not, why?

4. What are the changes in the composition of the producers as a result of these perturbations? (Woodmansee, 1978, 270)

Woodmansee (1978) reviewed and critiqued the ELM model program. His analysis suggests that the model was relatively successful, especially as an integrating and communicating device. It was less successful in answering the questions posed by Innis. For example, prediction of the impact of nitrogen addition on primary production was not verified (Breymeyer and Van Dyne, 1980, 398). The model predicted 161 grams dry weight per square meter of peak live biomass, and 290 were observed in the field. Woodmansee felt that these failures may have been owing to using Liebig's law of the minimum in the model, by which he meant that in the model the impacts from an environmental factor were applied one at a time when actually a synergistic response was probably operating.

Yet, these investigators built a successful ecosystem model, which fit the field data in many aspects. It was a model of a point in space, with time as the varying factor; it was also structurally conservative, using Lindeman's trophic levels as the key structural feature; and it did not easily respond to questions. It seems that every question required its own model. The ELM model did not so much produce answers as it led to questions. The model has not been used in the management of livestock grazing, apparently, because of its complexity, and the fact that it used a code that has gradually become outdated.

Thus, the idea of whole-ecosystem modeling, which was certainly a widely accepted and attractive idea in 1968, as tested in the ELM model did not have the impact expected. This was due partly to the rapidly expanding field of model building—the ideas of 1968 became outmoded rapidly. Partly, it was also due to social factors operating in the research team. The replacement of Van Dyne and Innis's later move to Utah allowed the direction to shift to components of the model, with the result that construction of a series of component models began (see fig. 5.4). This type of model fit more closely the strategy of the research community. Finally, the team was not asking the ecosystem model ecosystem questions. Rather, all the questions addressed components—productivity, cycling, and species impacts. The theory of ecosystems was not tested. Rather, it was accepted and used to build models and direct research. This is made especially clear in the second synthesis book edited by French. In this volume, a successful effort is made to compare data across sites within the comprehensive program. For example, in a chapter authored by French, R. K. Steinhorst, and D. M. Swift (1979), trophic pyramids for each

site were compared. It was concluded that these pyramids did not vary over time but were significantly different between sites, thus justifying the identification of different types of grasslands. Questions about the validity of trophic pyramids apparently were never asked.

Thus, there was a basic contradiction in the IBP grassland biome study. The goal was a study of the whole system, yet the scientific questions were couched in terms of the behavior of trophic levels and components. No one, including Van Dyne, seemed to see this problem. It was at least partly due to the development of models without a spatial component. The ecosystem can be conceived as a spatial object and its behavior understood mainly as change in space over time.

Yet, the program was successful at the component and process level. Success came from adapting to findings and the experience as they unfolded. Trouble came from the conflict between the unbending direction of Van Dyne, which he hoped would lead to something new and useful, and the adaptive strategy of the senior scientists who were responding to the answers they were getting in the field. Possibly, if Van Dyne had been allowed to carry the program through to completion on his terms, something different would have happened. As it was, ecosystem modeling and research shifted from whole-system studies to component studies, and these have been supported continually ever since.

Van Dyne's dream of a new way to express ecological insight, which would be directly practical, was never achieved. His own evaluation of this failure was focused on the agencies supporting the effort. According to him, NSF and others never had the vision, confidence, or capacity to support the test. Van Dyne never influenced enough of his fellow ecologists to create the necessary pressure on the agencies to meet his expectations. Indeed, the history of the grassland biome program and the synthesis volumes indicates that the scientific community had little stomach for tight organization to meet abstract goals and little imagination about what might be needed for management of the biosphere. Instead, they relied on the tried and true methods of individual investigators, meeting together, discussing their work, and writing articles. The academic ecologists' viewpoint prevailed.

The grassland biome project was only one of five efforts to carry out ecosystem studies in the IBP. How did these other projects face such problems?

THE OTHER BIOME PROGRAMS

Besides the grasslands, biome projects were organized in the tundra, deserts, coniferous forests, and deciduous forests. An unsuccessful effort was made to launch a tropical forest biome study. Each biome was organized and developed individually. The characteristics of the biomes reflected their leadership, organization, the environmental features of the biome, funding availability, and the state of prebiome knowledge. For this reason, it is difficult to compare one project with another. Even so, the criteria used in evaluating the grassland biome will be employed for other biomes. These criteria are the effectiveness of the organizational structure, project productivity, and relevance to ecosystem studies.

No biome program other than the grassland biome program followed the original plan of a central site, with satellite comparative sites. This form of a spatial context was lost, partly because of the cost and effort to organize satellite programs—the central programs were never supported at the level requested—and partly owing to a change in program conception. The grassland model was to be an abstract general model that could be modified with data from other sites. In this way specific site-controlled problems could be addressed with a universal ecosystem model. The other biome programs tended to copy the grassland program, and when questions about central modeling were raised, attempts to construct a single-biome model were abandoned.

Rather, each biome discovered that local, site-controlled differences were a crucial elements of its system and needed to be considered in any general scheme. The tundra biome program focused its work at Point Barrow, Alaska. The work of the desert biome program was carried out at several sites, with the one at Curlew valley, Utah, assuming something of a central location. The coniferous forest biome program had two sites, the Cedar River basin near Seattle and H. J. Andrews experimental forest in Oregon. The deciduous forest biome program had five sites. In each of these biome programs, the number of sites reflected a compromise between the inclusion of ongoing ecosystem programs in the biome, a need to create a central tendency of the biome for theoretical modeling purposes, the past experience of ecologists, and the existence of banks of information.

The biome programs also deviated from the central organization of the grassland program. There were no other leaders with the personal characteristics of Van Dyne. The tundra program was led by Jerry Brown, a soil scientist with the U.S. Army Cold Regions Research and Engineering Laboratory at Hanover, New Hampshire. This biome program relied on the remoteness of the site, the compression of research into a few summer months, and the experience of working together in the field to organize research. The pattern was fundamentally no different from former arctic studies at Point Barrow. The desert biome program was led by David Goodall, a systems modeler formerly from Australia and before the IBP, a professor at the University of California at Irvine, and by Fred Wagner, a professor of wildlife biology at Utah State University. Goodall did have strong opinions about modeling and tried to control the centripetal tendency of the biome program but the diversity of the desert environment and the individualism of the researchers defeated him. The coniferous forest program was led by Stanley Gessel, a professor at the University of Washington School of Forestry. This biome program incorporated scientists from the School of Forestry and the U.S. Forest Service who were used to organized and directed research; it did not suffer from organizational problems. The biome research was located at two centers that functioned almost independently. Finally, the eastern deciduous forest biome program was led by Auerbach, the manager of the environmental science program at Oak Ridge National Laboratory. In Auerbach, the IBP probably had the most experienced manager of ecology work in the United States. He had organized and guided the development of his program into one of the foremost in the world. For Auerbach, the problem was that he had numerous well-organized and active ecosystem programs in the biome. Only a few of these were willing to be part of the project, and they exercised an independence that was impossible to curtail.

The consequence of this variety was that the Analysis of Ecosystem program operated on expediency, taking advantage of the earlier development of ecosystem studies and allowing the scientific community to organize itself to meet its own goals and seek its own advantage. Given the strong opinion of individualist ecologists that biome organizations were fundamentally inefficient, supported mediocre science, and were politically suspect, it is obvious that the organizers of the Analysis of Ecosystems program made the appropriate decision. Yet, the compromise meant that ecology lost its opportunity to organize hierarchically and use funds to benefit the entire community. The argument that there was a right level of organization for ecological research and that those studying ecology at other levels were misguided at best, or intellectually dishonest at worst, was ultimately destructive to ecology as a science and prevented it from achieving its potential in the decade of the environment (1965–75).

The Analysis of Ecosystem program began in 1967 with the intention of applying a systems approach to ecological studies. The systems approach was intended to organize research, as well as to produce predictive models that could link the theoretical studies of ecosystems to applied environmental and resource problems. Systems ecology did advance with the IBP projects, partly as a result of focused and increased support, attraction of modelers and mathematicians such Goodall, Innis, and others to the ecosystem concept and the interaction of field scientists, modelers and programmers, and applied researchers. Their interaction produced a tremendous amount of argument but also a check on a too strong reductionism and too abstract modeling. A major argument that was not adequately resolved during IBP was the degree of disaggregation of the ecosystem needed for accurate models of real-world systems. The trophic-level concept was the disaggregation theory of choice, with the levels being decomposed into groups of like-acting species populations. This level of decomposition satisfied neither the community ecologist, who was concerned with interactions between single-species populations, nor the evolutionary ecologist, who argued that selection occurred at the level of the individual organism and that higher levels were abstractions. Regardless of the validity or lack of validity of these opinions, it was not possible to represent many populations in a ecosystem model, let alone individuals, and stay within the capacity of the computers and the imagination of the modelers. Scott Overton, of the Coniferous Forest Biome program at Oregon State University, proposed that models be constructed of subsystems and that the linkages between subsystems be made clear and realistic. With this structure, one could attend to those subsystems of interest and their linkages and ignore others. Overton's idea of disaggregation was never operationalized during the IBP, except in his models of the coniferous forest.

Systems models were most useful in organizing research and showing researchers how systems were constructed. The development of predictive models was less successful. The grassland program produced the ELM model, which was a total grassland model, and the tundra biome produced word models of the tundra. The tundra word model described the tundra ecosystem in a few paragraphs. Although both of these were effective within limits, the ELM model was not sufficiently adaptable, being strongly controlled by its structure and formatting. The other programs created practical models that focused on processes, such as nitrogen cycling, or on components, such as decomposer populations in the soil. These models proved highly effective, and the growth of ecosystem modeling is derived from their success. Every biome program produced useful models at levels of scale below the entire ecosystem.

The Analysis of Ecosystem program had a large impact on ecosystem studies, independent of the science of ecology, which was mainly through the institutionalization of ecosystem studies in the United States. First, funding, which amounted to about $57 million over the life of the program (Fred Smith had predicted the cost would be $45 million) was transferred intact to a new program in the division of environmental biology of NSF. The program was called "Ecosystem Studies," and it continued to provide funding for ecosystem work after IBP ended. The consequence of this action was that the new source

of support garnered by IBP was kept for ecological science and the partly completed biome projects could be ended by synthesis activity over several years rather than abruptly terminated and lost. All the biomes produced synthesis reports of some type as a consequence.

Second, the biome program also provided support for a new set of academic centers and opened the possibilities for ecosystem studies directly to the universities beyond the earlier connection through ABC national laboratories. These new centers included the University of Georgia, Colorado State University, Utah State University, San Diego State University, and Oregon State University. These centers expanded ecological research across the United States, opening many new opportunities for ecologists of all types and linking theoretical ecologists with applied ecologists. In most cases, these programs have become institutionalized within universities and continue activity today.

Finally, the biome programs involved over 1,800 scientists. Many of these people became familiar with ecosystem studies through the IBP and then they continued this type of work afterward. The time of the IBP coincided with development of environmental management programs in the states, the federal government, and in the private sector of the economy, and many of those trained in the biome programs found employment in environmental management and protection. Even though departments of ecosystem studies or graduate programs in ecosystem studies did not become common, the value of this type of training became widely recognized and many students were encouraged to do theses on the processes or components of ecosystems.

The impact of the IBP biome program on the development of ecosystem theory was marginal. One might say that the IBP carried bricolage to a new level of activity and scale. There were enough theories or concepts in the literature so that almost any project could be underpinned theoretically. The programs were not designed to sort out competing or contradictory ideas. Rather, they were driven, at least initially, by the idea that ecologists could construct a mechanical systems model built on the concepts of trophic levels, the food web, or the food cycle, and then represent the dynamic behavior of the components by data from organisms or populations that are surrogates of the component. This "bottom-up" or "design-up" approach did not prove possible or useful. Further, the biome projects did not effectively promote landscape ecology, as Odum has hoped. The biome was the setting for site research but was not really addressed as such in an effective manner.

Did IBP contribute to ecosystem studies? Yes, definitely. Did it achieve the objectives set at its start? No, not entirely. Did the field advance theoretically? No, not significantly. Did it build the institutional, manpower, and structural base for further advances? Yes. Did it further ecological knowledge? Yes, decidedly. The corpus of literature produced by the IBP stands as testimony to its contribution to all aspects of ecological science. Finally, Did it contribute to the solving of ecological problems? Yes, in many cases it did so directly. But possibly it is the indirect contributions it made in creating practitioners, methods, and information that was even more impressive.

CHAPTER 6

Consolidation and Extension of the Concept

The U.S. biome program dominated, and in many peoples minds characterized, the IBP. Yet the biome program continued the mixed research approach that had characterized ecosystem studies in the post–second world war period. The movement in the IBP period was so rapid, so many investigators were involved, and their motivations so different that the little coherence was obtained even within single biome programs.

Actually, the biome program created an opportunity for ecosystem studies to break out of a confused situation, an opportunity to test approaches to studying ecological systems. The test was conducted unknowingly within the IBP, but it was through a comparison of the paradigmatic IBP biome project, the grassland biome project, and another program outside the IBP biome that made this test visible and understandable. This other project was called the Hubbard Brook project since it was located at Hubbard Brook Experimental Forest.

The test involved approaching ecosystem studies from the components, which would then be linked together into a system in a computer model-driven theory or as a natural object that could be studied using conventional scientific methods. In this latter case, the ecosystem object would be observed, a pattern of behavior established, and questions about the origin of this behavior posed. These questions would then require that the ecosystem be dissected into components or subsystems and their linkages and their behaviors observed and *cal Monographs* (16[4]). The articles on the dynamics of marine production by George Clarke and on the production of fish populations by William Ricker were exceptionally important and are cited by many later authors. Macfadyen cites Ricker's article as the source that attracted him to the problem of productivity.

25 As far as I know, Macfadyen is the first to emphasize that energy flow is unidirectional. The assertion that energy flows and materials cycle became a central tenet of ecology.

26 There were many attempts to compute the productivity of the entire earth. Gordon Riley's (1944) estimate was $146 \pm 87 \times 10^9$ tons, for an energetic equivalency of $13.6 \pm 8.1 \times 10^{20}$ calories. He calculated the mean efficiency of conversion of solar energy to carbon energy as 0.09 percent. Riley quotes several earlier estimates by German scientists.

27 The Savannah River Ecology Laboratory evolved from E. P. Odum's research project. In 1962, the laboratory was established and a resident staff hired. Before 1962, research was carried out mainly by graduate students working out of the University of Georgia, Athens. An exception was in the period 1956–58 when Robert Norris was the resident Ph.D. ecologist at the Savannah River Plant under the Odum program.

28 This idea repeats that of Tansley (1922, 25) in which he states that "all living organisms may be regarded as machines transforming energy from one form into another."

29 The number of ecologists in the Ecological Society of America during this period was approximately two thousand (Burgess, 1977).

Chapter 5: The International Biological Program

1 A biome is a biotic community of plants and animals, considered at a large geographic scale. The word *biome* is synonymous with formation or bioregion. According to Carpenter (1939), Clements proposed the term at the New York meeting of the Ecological Society of America as a synonym for biotic community. In 1932 Shelford applied it to large-scale communities.

2 In 1962, at the meeting of the International Association of Theoretical and Applied Limnology, in Madison, Wisconsin, W. Rodhe, who was the convener of the freshwater section of the IBP, presented a plan for freshwater studies. The delegates approved his plan. In 1965, at the next meeting in Warsaw, Poland, V. Tonolli asked for continued support of the IBP.

3 According to Rhodes W. Fairbridge (1966) the most recent era of marine exploration was termed the "era of international research cooperation." It began with the IGY (1957–59), and included the International Cooperative Investigations of the Tropical Atlantic and the International Indian Ocean Expedition.

4 Like many IBP meetings, this one was an exciting experience for the participants. For many it was their first opportunity to meet scientists from East to West, across cold war boundaries. Kazimierz Petrusewicz, [illegible]

emy of Science Institute of Ecology, was the host. The problems of defining the principles of production ecology required ad hoc night discussions, which attracted the serious attention of many participants. The fact that these discussions led to an eventual agreement added to the conviviality of the meeting. This spirit also made the selection of themes and choice of research topics easier. François Bourliere chaired the final formal meeting and by a process of voting with a show of hands, settled the difficult questions. Given the wide differences of opinion among botanists, zoologists, and scientists from different national groups, it was largely through Bourliere's leadership that a consensus was reached quickly.

5 At the Jablonna meeting, the interest of the scientists was largely in organisms, not habitats. The habitats provided a basis for comparison of the biota; it did not form the strongest element in the program. This orientation was continued through the IBP as studies of small mammals, granivorous birds, social insects, and so forth.

6 Vegetation was treated as the animal's food and habitat by the animal ecologists at Jablonna. Duvigneaud pointed out that vegetation can be subdivided vertically into strata, horizontally into life forms, and conceptually into species groups. A botanist could not be satisfied with PT committee's treatment of vegetation as equivalent to small mammals and social insects.

7 The survey of the U.S. scientific community by the NAS was carried out by an ad hoc committee chaired by Stanley Cain. American opinion was sampled by telephone and correspondence. One hundred and sixty-two scientists were consulted directly, and their names represent many of the most prominent and active ecologists, including L. C. Bliss, Francis Evans, Stanley Gessel, Donald Lawrence, Eugene Odum, H. T. Odum, Jerry Olson, William Osburn, Frank Pitelka, Arnold Schultz, L. B. Slobodkin, Robert Whittaker, and George Woodwell. In addition, the Ecological Society of America published a questionnaire in its bulletin (1963, 44:146–9) and had received 119 returns by February 1964. This questionnaire elicited suggestions for projects. Further, forty-one professional societies associated with the NAS Division of Biology and Agriculture were asked their opinion. Of the total respondents to the NAS telephone survey (162), 98 answered yes to the question, Should the United States participate in the IBP? 50 answered yes, if; and 7 answered no. The committee commented that the reluctance and opposition to an IBP arose from (1) the fear that the United States might be called upon to pay for the foreign programs, (2) the need for new money to be found, otherwise the ongoing programs would suffer financially, (3) that American research freedom might be placed in an international straitjacket, and (4) that efforts toward standardization might stifle originality (NAS/NRC 1944).

8 Proposal in the University of Georgia Archives, Odum, box 1.

9 In 1967 Roger Revelle was replaced by Frank Blair, a professor of zoology at the University of Texas.

10 Eugene Odum attributes the suggestion to Hasler. Neither Hasler nor Bliss recalls the source of the idea, but Hasler emphasized the concept "that lakes are mirror images of the landscape around them" (Beckel, 1987, 31), and he suggested that he might well have expressed this view when the organization was in a formative stage (Halser, letter to Golley, 21 Dec. 1988).

11 University of Georgia Archives, Odum, box 1.

12 Ibid.

13 Proposal for a PT and PF program, 31 Sept. 1966. University of Georgia Archives, Odum, box 1.

14 Ibid., box 13.

15 Progress Report, Analysis of Ecosystems, 27 June 1967 by Fred Smith. University of Georgia Archives, Odum, box 13.

16 Letter from Philip Johnson to the faculty at the University of Georgia Institute of Ecology, 8 Jan. 1968. University of Georgia Archives, Odum, box 13.

17 First Annual Report "Analysis of Ecosystems," 11 Nov. 1967. University of Georgia Archives, Odum, box 13.

18 Proposal to the NSF by Colorado State University, Dec. 1967, pp. E1–22. University of Georgia Archives, U.S. IBP Grassland Biome, Budget 1968–69, proposal 1968–69, Progress Report, Continuation Proposal 1969–70.

19 University of Georgia Archives, U.S. IBP Grassland Biome, Budget 1968–69, proposal 1968–69, Progress Report, Continuation Proposal 1969–70.

20 Proposal for Continuation of research grant GB-7824 from Colorado State University, 135–156. U.S. IBP Grassland Biome, Budget 1968–69, proposal 1968–69, Progress Report, Continuation Proposal 1969–70. University of Georgia Archives.

21 For example, the premature review of the IBP biome studies by Mitchell, Mayer, and Downhower (1976) contrasted the productivity of publications from the Hubbard Brook project with those from three IBP projects.

22 Proposal for Continuation of research grant GB-31862X and GB-31862X2 from Colorado State University, June 1973. U.S. IBP Grassland Biome Continuation Proposal 1974–76, Progress Report 1973, Annual Report 1974–75. University of Georgia Archives.

23 Proposal to the NSF by Colorado State University, Dec. 1967. University of Georgia Archives. U.S. IBP Grassland Biome, Budget 1968–69, proposal 1968–69, Progress Report, Continuation proposal 1969–70.

24 Proposal for Continuation of Research grant GB-7824 from Colorado State University. U.S. IBP Grassland Biome, Budget 1968–69, proposal 1968–69, Progress Report, Continuation Proposal 1969–70. University of Georgia Archives.

Chapter 6: Consolidation and Extension of the Concept

1 The background about the development of the Hubbard Brook project comes from remembrances of Herbert Bormann printed in 1985, and Likens, 1985.

2 Likens et al., 1977. The 1975 review of the three biomes (Battelle Columbus, 1975) lists 107 articles published by the Hubbard Brook team.

3 Introduction to the Ellenberg *Festschrift* by Wolfgang Haber, 9–13, in Schmidt, 1983.

4 For example, see Kato, Tadaki, and Ogawa, 1978, in a special issue of the *Malayasian Nature Journal* for a report on plant productivity at Pasoh.

5 See Colwell (1973), in an unpublished technical report available in the University of Georgia Archives, IBP Collection, *Origin and Structure of Ecosystems.*

6 See the review by Cody and Mooney (1978), for a general discussion of convergence.

7 The society is called the Mediterranean Ecological Society (MEDECO) and meets at approximately two-year intervals.

8 Mar, 1977. This was a review funded by NSF for purposes of evaluating the RES program.

9 Di Castri returned to UNESCO in 1990.

10 Herrera et al. (1978) presents a useful summary and a list of relevant supporting articles to the San Carlos project.

Chapter 7: Interpretations and Conclusions

1 John Algeo (1988) describes numbers of *eco-* words that have become current in American literature and speech. These words include *ecotage, ecofix, ecopornography, ecodisaster, ecodefense, ecofact, ecomenu, econote,* and so on. The usage almost always implies some connection with the environment. Thus, *ecodisaster* would mean a serious event in which a disaster occurred in the environment, causing environmental disturbance. The use of *eco-* for environment comes from misuse of ecology as a synonym for environment by the American media beginning in the late 1960s. Apparently, the shorter word *ecology* fit the column width of a printed page better than the longer word *environment.* Newspapers especially were impervious to repeated attempts by ecologists to correct this misusage. It is now fixed in the language.

2 The list is that of Sukachev and Dylis (1964), 16, which is cited in their discussion over the advantages of using biogeocenosis in place of ecosystem and facies.

3 For example, the human body was referred to as "that magnificent machine" in a popular television film. Houses are termed "machines for living" in architectural writing. This conception may have originated in the form of a clocklike mechanical world, stimulated by the discoveries of Galileo, Descartes, and Newton, among others, and continues today in the form of a computer or space colony (Ferré, 1988). Although in the environmentalist literature there is strong condemnation for using a machine metaphor for living objects or ecosystems, nevertheless the metaphor has wide popular appeal.

4 Weiner, 1988, 132. See also ...