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A TROPICAL RAIN FOREST: PAST AND PRESENT

Report from a Workshop on Research at El Verde, Puerto Rico

June 19-21, 1984

Prepared by

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INTRODUCTION

The area around the El Verde Field Station has been the focus of studies of the lower montane rain forest ecosystem for over 20 years. El Verde is one of most intensively studied locations in the neotropics and the only neotropical site whose principal research focus has been the determination of ecosystem structure and function since its inception. As such, the accumulation of information on ecosystem processes is extensive and makes rain forest studies at El Verde unique in the tropics in their depth and breadth.

Since the initial studies of the rain forest began, the program has had a dominant focus: the experimental determination of the effects of exogenous influences on the functioning of the ecosystem. These experiments have ranged from the measurement of whole forest gas exchange with giant cylinder respirometers, through tests of the effects of ionizing radiation on community structure, to the manipulations of single species populations to delineate population parameters. Over time, the likelihood of, and interest in different exogenous influences has waxed and waned, with radiation and fallout occupying the attention of earlier workers while atmospheric inputs of pollutants from the burning of fossil fuels is currently of primary interest. During the same period, the dimensions of anthropogenic disturbances of tropical ecosystems have increased greatly, with the result that the El Verde data have become more valuable to the understanding of the resistance and recovery of disturbed tropical ecosystems.

Several generations of scientists have now passed through El

Verde, each contributing to the store of information about the site and about tropical forests in general. With changes in personnel, studies have concentrated on different aspects of the ecosystem within the framework of the overall project focus. As a result, different groups of researchers have become expert in different ecosystem processes, different exogenous inputs, or different groups of organisms. The purpose of the recent workshop on research at El Verde was to bring these experts together to consolidate knowledge of the rain forest and to plot the future course of research at this important site.

History of Research at El Verde

The Rain Forest Project began in 1963 under the direction of Dr. Howard T. Odum. The goals of the initial research were to determine the effects of gamma irradiation on the forest, to measure cycles of fallout elements in the rain forest system, and to determine circuits of energy flow and metabolic processes of the ecosystem. In 1975, the program was re-oriented to focus on the land use, climatology, hydrology, soils, and limnology of the entire Rio Espiritu Santo drainage basin.

After the completion of five years of work on the drainage basin, research emphasis returned once again to the rain forest where it continues today as the Rain Forest Cycling and Transport Program. The main objectives of this research are to delineate the major reservoirs and pathways of movement of energy and nutrients through the ecosystem in order to test hypotheses concerning the effects of energy development on rain forests. The first phase of this program emphasized the role of the fauna

in controlling fluxes in the ecosystem. The goals of the next phase of research will be determined in part on the basis of the recommendations resulting from the workshop.

In terms of current administrative organization and logistics, the Terrestrial Ecology Division of the Center for Energy and Environment Research is the entity responsible for conducting research at El Verde and for the maintenance of the site and field station with funding from the Office of Health and Environment Research of the U. S. Department of Energy and the University of Puerto Rico. The principal research program in the Division is the long-term study of the structure and function of lower montane rain forest at El Verde in the Luquillo Forest in eastern Puerto Rico.

Purpose of the Workshop

The long-term studies at El Verde, in conjunction with data on tree growth collected by the Institute of Tropical Forestry in the Luquillo Experimental Forest, represent a body of knowledge on forest dynamics unparalleled in the neotropics. Although many aspects of the ecosystem have been studied without interruption for 20 years or longer, the tenure of individual researchers has rarely been greater than 3-4 years. Workers at El Verde are able to draw on a large reservoir of published and unpublished information in designing and carrying out their studies but the experience of individual scientists is lost when they leave the project. Recognizing the importance of communication between succeeding generations of researchers, the CEER Senior Advisory Committee recommended in 1984 that the Terrestrial Ecology

Division organize a workshop to bring together scientists who had made substantial contributions to our knowledge of the lower montane rain forest ecosystem. As a result, a proposal for such a workshop was funded by DOE. The workshop was held from June 19-22, 1984, at the El Verde Field Station. The 20 participants included scientists from different epochs of the Rain Forest Project as well as the Department of Energy, Oak Ridge National Laboratories, and various universities (see Appendix 1).

Objectives of the Workshop

Four major objectives were defined by the organizers of the workshop:

- -To elaborate a sound rationale for long-term studies of ecosystem processes in the tropics in general and at El Verde in particular. This objective included the identification of unique features of El Verde, the Luquillo Experimental Forest, or Puerto Rico that were advantageous in ecological studies or that made particular experimental problems more tractable.

- -To identify weaknesses in our knowledge of the El Verde ecosystem and to highlight data sets whose continuity should be maintained. The purpose of this effort was to foster maximum use of the available data and to avoid redundancy. A further goal was to generate testable hypotheses through interactions among workers of different backgrounds.

- -To explore possibilities for the use of mathematical models in understanding the ecosystem.

- -To develop a series of recommendations on future research directions at El Verde, including the identification of priority studies and alternative sources of funding for research complementary to work sponsored by DOE.

The objectives of the workshop were achieved during a series of working sessions aimed at reaching specific goals (see Appendix 2). The agenda included a mini-symposium on current research at El Verde, a presentation of accumulated information on rain forest compartments and fluxes, and round-table

discussions on current research, gaps in knowledge of important ecosystem processes, and future research priorities.

RESULTS FROM WORKSHOP OBJECTIVES

A Rationale for Studies of Tropical Ecosystems

Managing ecosystems

Many of the world's future energy problems relate to man's ability to understand and manage natural ecosystems, particularly forests. Forests not only supply a variety of valuable products, they also serve to trap solar energy as the first step in the accumulation of biomass which can replace fossil fuels under many circumstances. As fossil fuels dwindle and demand for wood outstrips supply, managed forests will increase in importance.

An effective approach for forest management is to manipulate their natural control systems. By understanding the biology of those plants and animals involved in key control circuits, the efficiency of forests as energy traps can be manipulated. Such manipulation may serve to increase yields or to maintain them in the face of exogenous influences.

Controls of energy flow in forests may be either biotic or abiotic. Odum and Pigeon (1970; p. I-195) have identified the potential abiotic energy controls in the El Verde rain forest, most of which are atmospheric driving sources. Possible biotic controls are also known, but what is lacking is an understanding of the relative importance of the two types of control. By correlating biological activity and physical forcing functions

with energy flow, it may be possible to determine which has precedence in a given ecosystem. When this question is resolved, the manipulation of energy flow can be attempted.

Models and the study of nested systems

Systems can be defined at different levels of organization, and must be studied in the context of higher and lower organizational levels. In focusing on a system of interest, one may define all influences as outside forcing functions. This reductionistic approach reduces the ability to understand the external interplay of forcing functions (Odum 1983). For complete understanding of a system, one must model and simulate systems that are one size larger and one size smaller than the system of interest. For example, one would not profess to a complete understanding of a human individual without knowledge of the society of which the individual was part or without insight into the functioning of the adrenal cortex. Similarly, to understand the behavior of a tree species requires models of forest dynamics and photosynthesis.

A thorough understanding of the lower montane rain forest ecosystem depends on working models of subsystems, such as the decomposer community, and of regional systems, such as the Luquillo Mountains. Control functions may be exerted at different levels of organization, and evaluation of possible controls requires investigators working on different scales within the whole ecosystem context. For example, regional climatic patterns (hurricanes) may control forest structure and function on one time scale while the rate of return of nutrients

to the soil (decomposition) may exert control on another time scale.

Advantages of Puerto Rico for studies of ecosystems

During the workshop a variety of circumstances were advanced as being favorable for ecosystem-level studies in Puerto Rico. A list of the major points raised is given below.

- There exists in the Luquillo Mountains a very compact altitudinal gradient over several life zones, all of which are easily accessible. The existence of this gradient permits comparison of life zones and studies of fluxes between zones at relatively low cost.

- Historical records of forest biomass and production are available.

- Long-term meteorological data are available for many sites.

- Manipulations of forests in the Luquillo Experimental Forest are planned by the U. S. Forest Service. Such manipulations include clear-cutting, initiation of biomass plantations, and the development of line plantations, and provide the opportunity for experimental tests of hypotheses at a scale not possible under current budget restrictions.

- The simplified island biota facilitates study of the ecosystem. The relative simplicity of the component subsystems makes El Verde an ideal model for more complex mainland forest ecosystems.

- There exists detailed taxonomic work which is much more advanced than most places in the mainland neotropics.

Relevance of El Verde ecosystem studies to the mission of DOE.

There was general agreement among the workshop participants that future energy development would have marked effects on tropical forests both on a regional and global scale. Participants identified several specific effects of energy technologies, such as direct forest destruction by deforestation,

acid rain, heavy metal pollution, increased CO_2 concentrations in the atmosphere, and introduction of exotic species. The consensus among participants was that the best way to mitigate any of these potential effects was through understanding and manipulation of ecosystem controls. Given constraints of funding and manpower, research must be focused on the controls of ecosystem storages and fluxes that are primary targets of anthropogenic effects. With this in mind, a preliminary classification of such effects was attempted.

A model was proposed which identified five principal points of impact and ranked them in the following way: 1) energy resources, 2) photosynthetic apparatus/primary productivity, 3) plant structure, 4) animal structure, and 5) nutrient base. The classification assumes that all effects will ramify through the system, but that the principal point of attack can be identified for any effect. A working hypothesis was developed which states that the closer the impact falls to the primary producers, the greater the effect on the ecosystem. The classification, along with information on the type, intensity, and frequency of likely stressors, will be used to pinpoint foci for intensive studies.

The principal benefit to DOE from the El Verde ecosystem studies will be a generalizable understanding of the response of tropical ecosystems to byproducts of energy production and utilization. This knowledge will be a direct product of the ultimate objective of the research, an understanding of ecosystem controls in order to predict system response to changes in forcing functions. Further benefits from the research will include fundamental information concerning solar energy fixation

in the tropics, information on tropical forest utilization and management, contributions to the understanding of the role of tropical forests in the global carbon cycle, and further exploration of the role of forests as biological filters of atmospheric contaminants.

Making Maximum Use of the Existing Data Set

One of the major accomplishments of the workshop was to identify ecosystem storages and fluxes for which our information was deficient. The purpose of this exercise was to help determine the goals of future and continuing studies. In general, little redundancy was found between studies from different project phases at El Verde. Some ambiguities with respect to published data and methods were resolved, and a list of important gaps in our knowledge of the ecosystem was prepared. The most important items on that list include:

-information on soil and litter populations and gaseous exchange from the soil and litter

-information on cycles of C, N, P, and S.

-an attempt to balance the carbon budget for El Verde.

-fate of organic matter storages during succession and under different management plans.

-role of exotic animals in the forest.

-information on carbon flux between ecosystems.

-food web studies of canopy populations and primary consumers throughout the forest.

-standing stocks of soil nutrients.

-rates of net primary productivity under different environmental conditions.

-rates of root turnover.

-population regulation of herbivores.

-limitations on the decomposition rate.

-degree of host-plant specificity shown by herbivores.

Some of the items contained on this list are already being examined in the current phase of the program, and others will be included in planned further studies. Priorities for future studies will be set on the basis of the resources available and the need for specific information to evaluate ecosystem controls.

Participants developed a second list of projects which consisted of long-term measurements or comparisons between the forest as it existed in the 1960's and current conditions. This list included:

-growth and mortality of trees marked during the Odum studies.

-remeasurement of control center vegetation.

-remeasurement of vegetation in the cut center.

-continued monitoring of the vegetation in the radiation center.

-renewal of monitoring of meteorological parameters.

-concentrations of isotopes in epiphylls tagged during the 1960's.

-erosion in the area of the giant cylinder.

-population studies of termite nests.

The importance which the entire group placed on these studies indicates that they should be high on our list of priorities. Because several of these proposed studies require more manpower than we currently can spare, they will have to be conducted using adjunct staff, students, Oak Ridge Associated Universities participants, or volunteers.

Models as Tools in Understanding Ecosystem Structure

The participants recommended that the Terrestrial Ecology Division not devote resources to a full-scale simulation model of the El Verde ecosystem. Their feeling was that such an undertaking is beyond the capacity of both our manpower and database. It was suggested, however, that simulation models developed for other ecosystems might be adapted to El Verde and that this approach might be explored further. In particular, the group recommended establishing contact with the modeling team at San Diego State University to investigate a cooperative effort. The ecosystem simulation modelling at SDSU has over a decade of experience in DOE research in both arctic and mediterranean areas. Collaboration will be facilitated by strong existing contacts between staff members at both institutions. There is a great interest in cooperating and in trying to transport DOE funded models from other ecosystems into the tropical rain forest at El Verde.

There was also a strong and unanimous recommendation that computer models of sub-systems or processes be used to generate hypotheses and to help choose directions for future work. Drs. H. T. Odum and Richard Wiegert gave a demonstration of the development of simple computer models, and the group devised several preliminary models of ecosystem processes as an exercise. The group concluded that computer models should be incorporated into the process of determining future research directions in the early stages. Staff members will work with Dr. Odum on implementing those techniques during the summer of 1985.

RECOMMENDATIONS

The following recommendations have been distilled from the tremendous volume of post-workshop correspondence from the participants. At the close of the workshop everyone wrote up an informal serie of impressions, ideas, and suggestions. These were included in the first draft of this document. The draft was circulated to all participants, which spurred them to respond with even more suggestions. After compilation and editing for clarity and redundancy, they are set forth as our best sense of where we are, and where we should be going with research at the El Verde field station.

1. It is essential to maintain well-defined goals within the project mission defined by OHER/DOE, which is to develop an understanding of ecological processes at El Verde that can be generalized to other tropical forests. Within this mission, particular reference should be paid to the potential effects of the development of energy sources on ecosystem structure and function.

2. Ecosystem structure can be organized into a system of storages and fluxes whose values are determined by physical and biological controls. The principal focus of the program should be the experimental determination of how storages and fluxes are controlled. Models will prove invaluable in generating hypotheses, testing system sensitivity, and formulating key experimental work.

3. The tabonuco forest at El Verde can be used as a simplified model of more complex tropical ecosystems. To derive full benefit from this model, it should be viewed in contrast to simpler (plantations) and more complex (mainland) ecosystems. Emphasis should be placed on those aspects of tropical mainland ecosystems that may be too complex to study without the use of simplified models, for example, food webs.

4. Research should not be artificially limited by the boundaries of the El Verde research area. However, major ecosystem-level studies along an altitudinal gradient are not possible at the current level of funding. Some studies in the next phase are planned to take advantage of the compressed elevational gradient available in the Luquillo Experimental Forest (e. g. stream chemistry). For other studies,

comparable data may be available from other forest types within the Luquillo Mountains (Weaver in colorado; Lugo and Frangi in palm forest).

5. Priority should be given to studies that take advantage of El Verde's unique features for ecosystem studies. In particular, attention should be paid to the maintenance of long-term climatological records and to the historical data base available from earlier studies.

6. Work on frog/anole canopy predation should be continued. The dominance of these two predators makes the El Verde system unique and has important implications for our understanding of canopy insect populations and our ideas about grazing pressure on trees.

7. The general research approach should be experimental, with a mix of studies of whole ecosystem processes and specific populations. Studies of different levels of organization should always be related to ecosystem structure and function. Experimental manipulations can be either large- or small scale, depending on the resources available and the opportunities presented by coincidental natural or man-caused disturbances.

8. Simple computer models should be used from the onset to guide the research. They can serve to focus research and foster a more organized, elemental basis towards experimentation.

9. The food web studies of Phase I should be integrated, and storages and fluxes quantified wherever possible. Work should continue in this area to develop a model of the animal control system.

10. Whenever possible, experiments should be designed to take advantage of forest manipulations planned by the U. S. Forest Service. These manipulations include partial or complete harvesting, plantation establishment and maintenance, and line plantings. Close coordination should be established with Forest Service and Institute of Tropical Forestry personnel, and experiments should be organized to make use of management practices outlined in the draft Land and Resource Management Plan for the Luquillo Experimental Forest.

11. Plantations and natural forests of the same age are a valuable resource and should be used in comparative studies. They are essentially natural experiments in forest manipulation and can be used in lieu of large scale disturbance at El Verde.

12. More attention should be paid to the life histories of important autotrophs, including the temporal aspects of regeneration, spatio/temporal population dynamics, and the apparent decrease in certain species (Sloanea, Cordia) over the last 20 years.

13. Studies of the carbon cycle, especially plant gas exchange and decomposer/forest floor respiration, will take advantage of overlapping staff expertise. Future studies by CEER and the Institute of Tropical Forestry and will eventually produce an extensive data set useful in addressing DOE priorities.

SUMMARY OF MAJOR ACCOMPLISHMENTS OF THE WORKSHOP

In addition to addressing the stated goals of the workshop, a variety of peripheral and in some cases unexpected benefits resulted from the interactions of present and past staff. Participants were stimulated to pull together and scrutinize published data sets prior to the meeting and to look at data in different ways at the meeting, mainly due to the wide range of interests represented by those present. This interaction resulted in a better understanding of the quality and spectrum of available information, as well as identifying gaps in the data set. The discussions which ensued at the workshop enhanced the view of the lower montane rain forest as a reticulate system by identifying a series of unrecognized connections between different forest compartments and by allowing each person to better visualize the role of his own work within the broad ecosystem perspective.

Increased cooperative efforts between participants is a likely result of the workshop. Areas of common interest have been identified between current staff members and several other participants. Included in discussions of collaborative projects were the possibility of parallel studies of wood and leaf decomposition involving scientists at CEER and ORNL, attempts to use simple computer models in studying ecosystem compartments

in conjunction with Dr. Odum and his colleagues at the University of Florida, and the participation of University of Georgia scientists in studies of nitrogen dynamics and evapotranspiration at El Verde.

The workshop resulted in several direct implementations of new work or changes in emphases over the last few months. During summers 1984 and 1985, ORAU students have been resurveying the El Verde vegetation sites. Drs. Lodge and Lawrence are collaborating in detailed forest floor respiration measurements and its correlation to seasonal activity of fungal and microbial populations. A faculty associate on ORAU 1985 summer funds is studying root patterns and distribution. In terms of concrete interactions, both Drs. Waide and Lopez, respectively the Heads of Terrestrial and Marine Ecology, will be spending several weeks this summer working on the modelling approach with Dr. Odum at Gainesville.

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APPENDIX 1. LIST OF PARTICIPANTS

CEER

William T. Lawrence	Terrestrial Ecology Division
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Former Program Staff

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Elizabeth McMahan	University of North Carolina
Peter Murphy	Michigan State University
Ariel Lugo	Institute of Tropical Forestry
Douglas Reagan	Environmental Scientists and Engineers
Rosser Garrison	Office of the Agricultural Commissioner, Los Angeles

Other Researchers with Long-term Projects at El Verde

Warran Kaplan	Harvard University
Margaret Stewart	SUNY-Albany
Michael Willig	Texas Tech University

Observers

Michael Huston	ORNL
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