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# H.T. Odum and the Luquillo Experimental Forest

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> How does the forest operate, develop its patterns, retain information in its memory sites, and transmit the great message to the future? (Odum, 1970a, p. x)
>
> The rain forest achieves complexity, high metabolism, and stability over geological time periods without surges and waste. Can we find in this example the clues for designing our own equally effective systems of man and nature? (Odum, 1970b, p. A5)

## 1. Introduction

H.T. Odum visited the Luquillo Experimental Forest (LEF) for the first time in 1944 (Lugo, 1995b) and from then until his death he actively studied the forest. The centerpiece of this intellectual activity is a classic in tropical literature . . . "A Tropical Rain Forest" (Odum and Pigeon, 1970) sometimes referred to as the "rain forest book" and as Odum often referred to various of his books by their color instead of their title . . . the "green book". The green book was published as a result of Odum's tenure as Chief Scientist at the University of Puerto Rico's Puerto Ricao Nuclear Center, from 1963 to 1966, and where he conducted experimental irradiation of the rain forest.

The objective of this article is to place H.T. Odum's research at the LEF in context and then to review his contributions to tropical ecology using the broad scope of the green book. Attention will be drawn to key aspects of the book and quotes that are particularly revealing. In addition, some background related to Odum's earlier research and to his work after LEF will be related to his LEF research and publication of the rain forest book. The huge quantity of scientific findings contained in the rainforest book make it impractical to review them one by one. Instead, I suggest that ecologists, interested in understanding tropical forests, should read it. Readers will acquire a quantitative, holistic viewpoint of the phenomena that power these magnificent forests. Consider the following descriptions of the rain forest at El Verde:

> A deep green rain forest is a prodigious volume of cells, leaf proteins, enzymes, high energy compounds, macromolecular organelles, nucleic acids, and the genetic information by which the cumulative designs of long evolutionary storage are maintained and transformed to the future. (Odum, 1970f, p. G3)
>
> Viewed from above, the rain forest leaves form a deep foliage bed evenly distributed. Spreading like a sheet over the ground below is a mat of small roots important to mineral cycles. These are joined through centers of structural and respiratory activity in the trunk-root base. (Odum, 1970h, p. I243)
>
> I take the view that a soil is a self-maintained structure of the ecosystem of which it is a principal part, rather than an external factor that one characterizes after one cuts down the system and changes the soil. (Odum, 1970g, p. H8)

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Almost every aspect of H.T. Odum's scientific career had its roots in the rain forest book, even the concept of energy quality (later called EMERGY) as shown by the following quotes:

> Energy dominance may not be proportional to structural dominance ... greater energy control may be exerted by the low-calorie (but concentrated) specific work actions of respiratory consumers among animals. Should dominance of a population be defined by the total energy flow in that group or by the larger energy flow that is controlled by the work of that group? (Odum, 1970h, p. I233)

> The importance of a species is measurable not only by its own energy budget but in the energy power flows which it may control. (Odum et al., 1970c, p. E5)

## 2. Before the green book

In 1957, Odum received a grant from the Rockefeller Foundation, which funded six field trips to Puerto Rico to study mangroves and the tabonuco (*Dacryodes excelsa*) forest at the LEF. The mangrove research resulted in the first paper to report in situ metabolism measurements and a comprehensive description of the structure and function of this forest type (Golley et al., 1962).

Research in the tabonuco forest eventually led to the comprehensive rain forest radiation study reported in the green book. Both studies took place in the Luquillo Mountains, which Odum (1970c) described as follows (p. B3):

> Rising 3500 ft (1050 m) into the trade winds over eastern Puerto Rico (18°19′N, 65°45′W) is a basaltic mountain whose orographic effects produce regular rains and cause a lush tropical forest to drape deeply dissected ridges and river ravines with a rich green carpet.

The earlier Rockefeller study reflected six aspects of Odum's research strategy that he followed throughout his scientific career.

1. He collaborated with many people both from mainland United States and Puerto Rico. Engineers were often among his collaborators because Odum sometimes incorporated large-scale structures in his research. For the Rockefeller study, he constructed towers and used scaffolds to gain access to the canopy. The giant cylinder, enclosing a whole tabonuco stand, that was used to measure forest metabolism became one of Odum's signature examples of large-scale ecological measurements (Odum and Jordan, 1970).
2. The research was always quantitative and oriented toward whole ecosystems, including plants, animals, and microbes.
3. There were always innovations to the methodology for studying the ecosystem. For example, evaluating color shades in Ektachrome slides to estimate pigment diversity in the canopy and calibrate results with direct measurements of pigmentation (Odum and Cintrón, 1970).
4. He presented all the data (even outliers, because those might reflect a new discovery) and he would document his work to assess future change in the ecosystem. The green book contains large quantities of raw data, including actual charts with output tracings from measuring equipment. He recognized the relevant literature and analyzed his results, as others would, to demonstrate both the strength and general applicability of his research, as well as departures in interpretation or flaws in the reasoning of others.
5. He generalized results to several scales of organization, from the individual to the whole biosphere with attention to the role of humans.

Not all the work in Puerto Rico appeared in journals. Odum was successful in publishing his research results from Silver Springs (Odum, 1957) and the Pacific islands (Odum and Odum, 1955) in the journals of the Ecological Society, but he was unsuccessful in publishing those from the LEF. A trend started in Puerto Rico by which most of Odum's research was published in books, proceedings, or other type of literature. This was unfortunate because it limited the dissemination of his ecosystem-level ideas. Today, it is amusing to Odum's students (yet, a sad commentary on scientific acceptance of new ideas) to find ecologists arguing about primary productivity and ecosystem-level research, subjects that in our view were resolved by Odum decades ago. At the time, however, they were not popular subjects and thus of-

ten rejected by peers. As an example, Odum's review of a book on primary productivity clarifies the concept of primary productivity in forests (Odum, 1964), a subject that was recently revisited at a meeting of the scientists associated with Long-Term Ecological Research Programs of the National Science Foundation. In my view, there was no improvement at that meeting on Odum's succinct discussion of the issue in 1964.

Three papers summarize Odum's research at the LEF prior to publication of the green book (Odum, 1962; Odum et al., 1963, 1970f). A paper presented at the Lockwood Conference on the suburban forest and ecology (Odum, 1962) is a classic of the tropical literature (Lugo, 1995a) because of the scope of the paper and the new ideas that it contained about rain forest structure, function, and management. In 1962, there was no precedent in tropical ecology for the scope of analysis of a tropical forest that Odum presented. Moreover, as was characteristic of much of his work, he used fundamental ecosystem analysis in the paper to develop new ideas about the relation between humans and the biosphere. The field of Ecological Engineering originated with this paper (and followed through in Odum, 1970h), as did his energy diagram symbols (Lugo, 1995a). The Lockwood Conference dealt with issues of urban forestry, which are now becoming increasingly important to ecologists.

## 3. The green book

The green book contains 1667 glossy pages and weights 25 kg. The book's 114 chapters are organized in nine individually lettered and numbered sections. The nine sections are: the rain forest project (A), the rain forest at El Verde (B), the radiation experiment (C), plants and the effects of radiation (D), animals and the effects of radiation (E), microorganisms and the effects of radiation (F), cytological studies within the irradiated forest (G), mineral cycling and soils (H), and forest metabolism and energy flows (I). The book contains many photographs (color, infrared, black and white, and hemispheric) of the forest and of every aspect of the research activity and equipment In addition, the book contains many maps, even of the distribution of rocks on the forest floor, and isopleths of leaf holes (Odum and Ruiz-Reyes, 1970).

Table 1
Examples of organisms included in the green book (Odum and Pigeon, 1970)

| | |
|---|---|
| Insects | Fleshy fungi |
| Walking sticks | Myxomycetes |
| Wood boring insects | Actinomycetes |
| Termites | Microfungi |
| Microarthropods | Mycorrhiza |
| Mosquitoes | Soil microflora |
| Ectoparasites | Lichens |
| Snails | Epiphytic algae |
| Nematodes | Epiphylls |
| Viruses | Bryophytes |
| Rats | Ferns |
| Reptiles and amphibians | Bromeliads |
| Birds | Trees and shrubs |

The list is not comprehensive and the book index identifies the pages corresponding to any group.

When initially sold at $10.00, the green book was quite a bargain. The book received an excellence award from government editors but most tropical ecologists ignored it. Today, as tropical ecology catches up with the ecosystem approach, the green book is in demand. A second printing resulted in its issuance in three paperback volumes. However, currently the green book is out of print and no longer available.

In addition to his work as Director of the Rain Forest Project, Odum was responsible for authoring or co-authoring 22 papers (589 pp.) and he drafted all the abstracts in the green book. Of these papers, five are must-read articles for tropical ecologists (Odum, 1970f,g,h; Odum et al., 1970a,b). Tables 1 and 2 contain a listing of the groups of organisms and examples of topics in the green book. These lists and examples are illustrative rather than exhaustive and they support my statements about Odum's tropical research.

The Atomic Energy Commission funded the rain forest research for about 4 years, at a total cost of about 1 million dollars—a real bargain under any criteria. The following quote from the green book explains the objectives of the rain forest project:

> The aim of the project was to learn how a rain forest works as a system and under stress, including populations, mineral cycles, metabolism, and operations of the complex living structure, by concentrating new and old techniques and many investigators on one small area. (Odum, 1970a, p. ix)

Table 2
Examples of topics included in the green book (Odum and Pigeon, 1970)

| | |
|---|---|
| Five weather regimes of El Verde | Calendar of phenological events |
| Microclimate of the forest floor | Grazing control mechanism |
| Climate diagrams | Sounds of animals |
| Nuclear volume vs. radiation effects | Ecomix |
| DNA content by species | Hydrogen cycle |
| Soil profiles | Uptake of fallout by epiphytes |
| Root biomass | Analog computer simulations |
| Forest floor microcosms | Leaf pigment diversity |
| Vegetation profiles | Color slides used to estimate pigment diversity |
| Leaf life history | Margalef ratios |
| Size of stomata | Chlorophyll |
| Seedling taxonomy and ecology | Classification of rain forests |
| Energy quality | Chemical specialization theory |
| Auxiliary energies, such as dry air | Self-design process |
| Dollar flows | Genetic ecological homeostasis |
| Chemostat | Virus cycles |

The list is not comprehensive and the book index identifies the pages corresponding to any topic.

Consistent with this project objective, Odum defined the ecosystem in a unique way:

> The ecosystem can be thought of as a program of energy modules in which each category of storage, operation, or species is a group of statements. (Odum, 1970b, p. A7)

For those interested in historical trivia that emerge from careful analysis of the green book, I recommend the following:

- The acknowledgement sections not only account for Odum's collaborators and his influence on others, but they also reflect tension among collaborators, as evidenced, for example, in Odum's acknowledgment of cytologists in the introduction to section G. The research in Puerto Rico trashed the popular nuclear target theory used to explain radiation sensitivity of organisms in the laboratory.
- The co-authors of Odum's chapters reflects his selfless attitude towards authorship and how he used co-authorship to reward and encourage collaborators. In my experience, for example, I was associated with three manuscripts in the green book, and while I conducted field research for all of them, at that stage of my career I was not capable of developing those manuscripts. Odum was the main force for the manuscripts, even for the paper based on my Masters thesis (Lugo, 1970) and deserves full credit for bringing them to fruition. Similarly, other graduate students, workers, technicians, and even well-established scientists, benefited from Odum's contributions to manuscript development.
- Odum introduced each section of the book. In these introductions he reviewed all the papers of the section plus other relevant information from the literature and combined these with his fabulous insight of how ecosystems function, or should function. These introductions, in some cases, were manuscripts in their own right and I encourage ecologists to read them to experience a level of synthesis of ecological information that one seldom finds in the literature today. Three of my recommended must-read papers in the green book are introductions to sections, and one is the overall summary of the book:
  - Introduction to section G: microscopic order in the forest (pp. G1–G14).
  - Rain forest structure and mineral-cycling homeostasis (pp. H3–H52).
  - Effects of gamma radiation on the forest at El Verde (pp. D3–D75).
  - Summary, an emerging view of the ecological system at El Verde (pp. I191–I289).

Odum papers are chock full of questions that reveal his inquisitive mind and reflect his sense of wonder, discovery, and admiration in the presence of the complexity of natural systems. Consider, for example, . . . "*What would the Luquillo Forest be like with a population of men feeding on lizards, snails, and coqui's?*" (Odum et al., 1970c, p. E8)

### 3.1. Four areas of Odum's interest

I selected four topics of ecological research that today are receiving increased attention by researchers in the tropics to illustrate Odum's interests in the 1960s when he conducted research at the LEF. The topics are disturbance ecology, microbial ecology, species invasions, and the carbon cycle.

*3.1.1. Disturbance ecology*

As was customary in the 1960s, ecosystem studies focused on balanced or mature natural systems. Much of the discussion about the LEF centered on its maturity and indeed, Odum developed and simulated balanced carbon budgets. However, in spite of this, Odum made numerous observations and contributed much to theories of disturbance ecology from his work at the LEF. For example, he was the first to interpret the canopy characteristics of the tabonuco forest as resulting from trade winds and hurricanes (Odum, 1970g). On page I260 Odum discusses the energy basis of stress from the biochemical to the community levels of organization. The following quote further demonstrates his clear understanding of disturbance events:

> The rain forest is often cited as a vegetational system without such great stresses as regular drought, frost, or sharp changes requiring adaptational programs. However, . . . [there] are extremely heavy rains, very acid leaching associated with heavy rain and carbon dioxide production in the litter, saturated conditions in the soil requiring many root adaptations for oxygen supply, and soft soil strengths requiring tree foundation adaptations as stilts, buttresses, and root-rock intermingling. (Odum, 1970h, p. I260)

All of Odum's insights about disturbance came together in Fig. 1, which effectively summarizes the response of the forest to radiation and hurricanes. We relearned Odum's insights 25 years later when

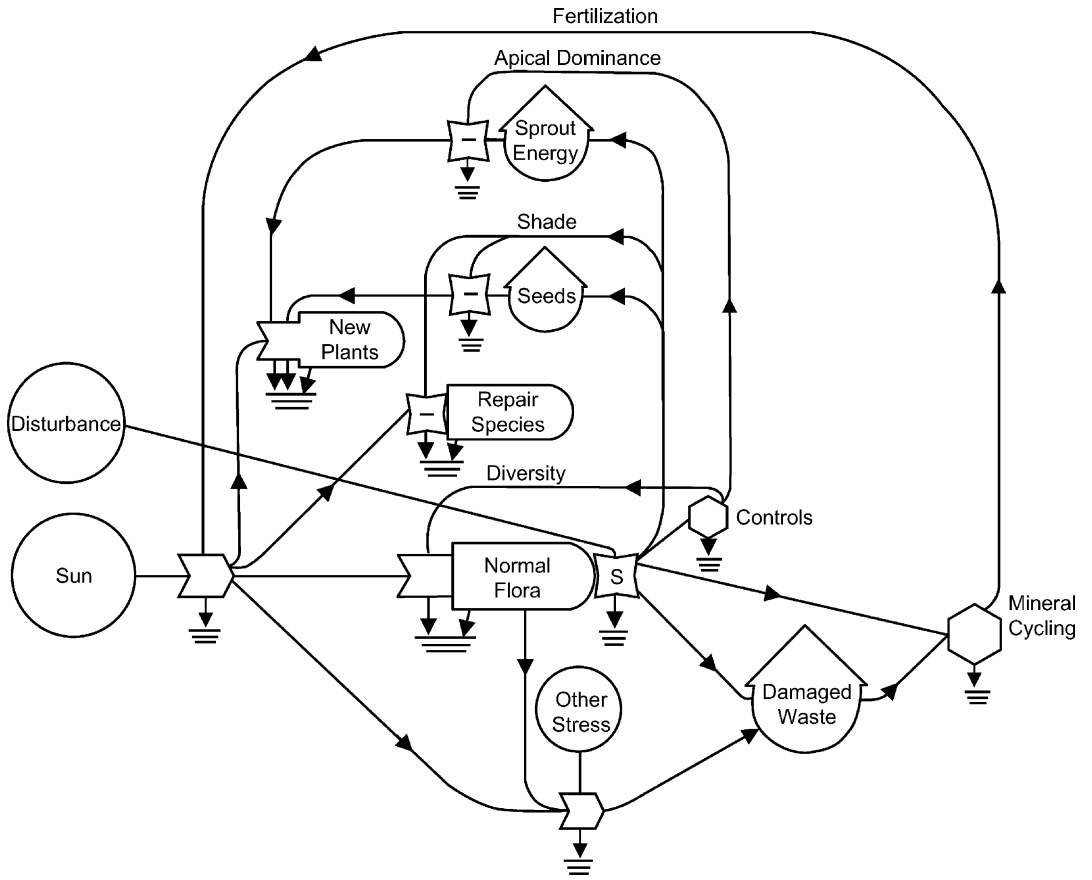


Fig. 1. Energy diagram showing repair mechanisms at the ecological level of organization and some switching actions of stress in releasing accelerated metabolic activity (Odum, 1970h). I made two changes to the original of this figure: changed the γ radiation label to "disturbance" and connected the output of "other stress" to "damage waste". This figure depicts our understanding of hurricane effects on the tabonuco forest.

Hurricane Hugo leveled the forests in 1989. The critical insights of this diagram are:

- The accumulation of organic debris on the forest floor due to leaf, branch, and tree falls.
- The role of disturbance in switching-off the normal controls of the forest (e.g., apical dominance and shade).
- The recycling of damaged forest parts.
- The resulting fertilization effect, and outburst of sprouting and seed germination.
- The positive influence, or reinforcement action, that the disturbance event has on the forest.
- The invasion of the site by new species.

### 3.1.2. Microbial ecology

Most of the energy flow in the rain forest is through the litter/soil subsystem dominated by small and microscopic organisms. Odum noted that the rapid turnover rates of these organisms was critical to the processing of organic materials, recycling of nutrients, and recovery from stresses, including ionizing gamma radiation. He also believed that the more species present in the liter/soil subsystem, meant that less organic matter passed away without use (Odum, 1970e). His analysis led him to suggest that: "*The secret of forest management may be in these populations [microorganisms], which can control the larger plants by the timing and location of their regeneration of minerals*" (Odum, 1970e, p. F7).

Of particular excitement at the time, was the realization that minerals in airborne radioactive fallout from bomb testing were reaching Puerto Rico and were being absorbed by epiphytes (Odum et al., 1970e; Kline and Odum, 1970; Kline, 1970). Accordingly, considerable attention was given to microbial ecology during the rain forest project. Odum's descriptions of the microbial world are most interesting and suggest a multi-scale approach.

> The great mass of microscopic order stands in spite of the disorder-generating processes of the biosphere that are continuously shaking the structure towards randomness. (Odum, 1970f, p. G3)

> The green forest attains a quiet order at the macroscopic level even though it is a seething, selecting, noisy struggle with much error at the microscopic level. (Odum, 1970f, p. G12)

### 3.1.3. Species invasions

Odum reinterpreted the concept of island biogeography within a context where energy was required for moving and organizing species (Fig. 2). He realized that organization was an energy demanding process and that the species–area curve had an energy basis that determined the saturation level of the curve (Odum, 1970h). He also recognized that the invasion of species was facilitated by disturbances, which he termed stresses. Odum interpreted species invasions quantitatively using energy constraints, and emerging patterns that relate species invasions with disturbance, ecosystem age, and available resources. Elsewhere in the book, he suggested that shade adaptation in the forest was possible by species substitutions rather than by changing the chlorophyll content within one tree's leaves (Odum and Cintrón, 1970). The principle that emerges is that species turnovers in forests are in response to changing conditions that are subject to study, understanding, and manipulation.

### 3.1.4. The carbon cycle

Odum was the quintessential carbon budget specialist in ecology. His background in biogeochemistry originated with his dissertation on the global strontium cycle. During his many years of ecosystem studies, his work on aquatic, marine, estuarine, and terrestrial ecosystems involved carbon budgets. In Puerto Rico, Odum documented the carbon budget of the rain forest in detail (Fig. 3). Gas exchange measurements, in the field, were conducted at many levels of organization and on different forest compartments (Odum et al., 1970g, Odum and Jordan, 1970) to document carbon fluxes. He also used allometry, biomass determinations, soil pits, and a few assumptions (Odum, 1970h). Of even greater interest was the experiment with microcosms, which showed that different combinations of soil, plants, and animals stabilized at different atmospheric carbon dioxide concentrations. Odum concluded many years prior to publication of the popular Gaia theory:

> The physical properties of the atmosphere of the earth are a result of biological evolution as much as vice versa. . . . since carbon dioxide is implicated in the thermal-radiation balance on the earth in relation to ice-cap maintenance, it is not unreasonable to suspect that ice ages may be caused by the relative

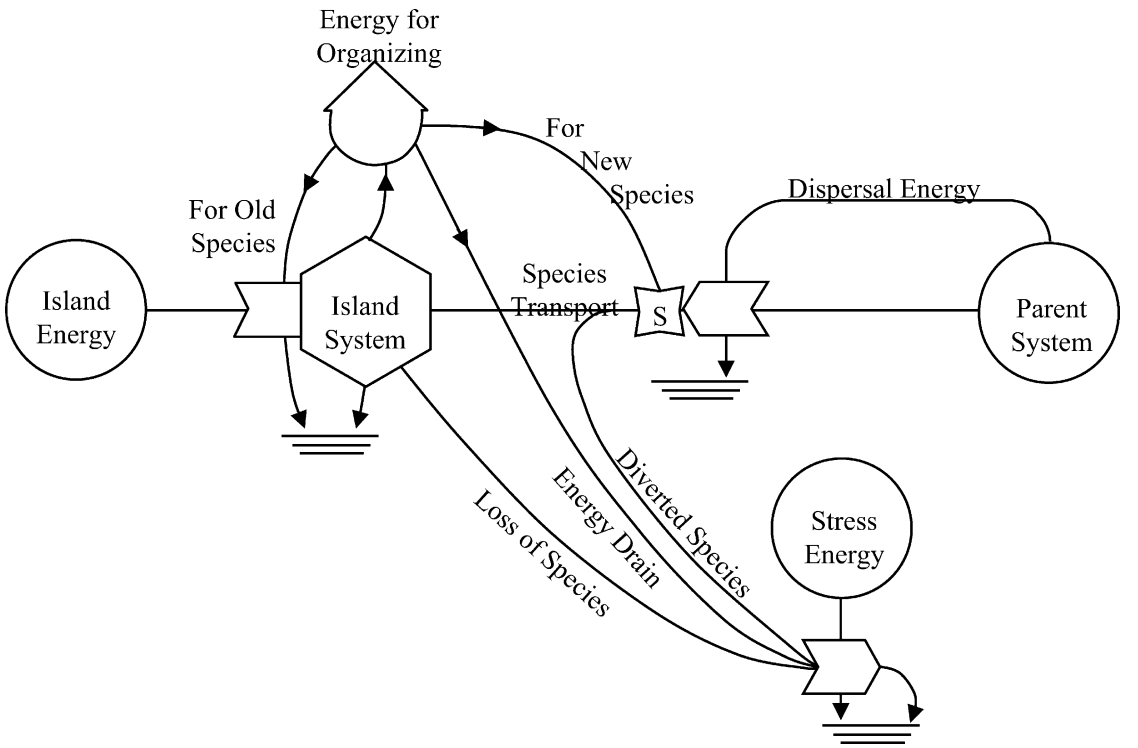


Fig. 2. Energy diagram of theory of species colonization of isolated systems. Energy flows are derived from parent landmass, from island budget of energy excess of that required to organize existing species (Odum, 1970h).

> evolution of plants and animals and their excesses or deficits in organic-matter production. (Odum and Lugo, 1970, p. I47)

## 4. After the green book

Most of Odum's writings after the publication of the green book contained the imprint of his work in the LEF. Throughout his scientific career, Odum pursued a line of thought about man and nature, considering them to be one, integral parts of a whole, instead of the "trap" that humans were apart from nature. He was convinced that theory was best generated from field observations and throughout his career he brought his considerable experience in the field to bear on whatever new ideas he was developing. As far as the work in Puerto Rico, he formally revisited the green book on many occasions, but in particular, for the 50th anniversary of the USDA Forest Service Institute of Tropical Forestry in 1989. Odum was always a close collaborator with the Institute, first through Dr. Frank Wadsworth and later under my leadership of the Institute. For the 50th anniversary, Odum (1995) developed and simulated 12 mini models of tropical forests at four scales, including: a single forest stand, landscapes with many stands, tropical forests at an international scale, and tropical forests in the global carbon budget. Each of these topics was present in the green book, but by revisiting them, Odum provided much embellishment after 20 years of progress in simulation modeling. He used powerful tools of computer simulation that he introduced in the 1950s (Lugo, 1995a) elaborated on in the green book (Odum, 1970d,g,h; Odum and Lugo, 1970; Odum et al., 1970d) and brought to full realization in the early 1980s with publication of his seminal text "Systems Ecology" (Odum, 1983). The simulations of rain forests closed the loop on much of Odum's conceptual thinking and theoretical work begun in the LEF and first published in the green book. I finish this essay with the summary points made by Odum

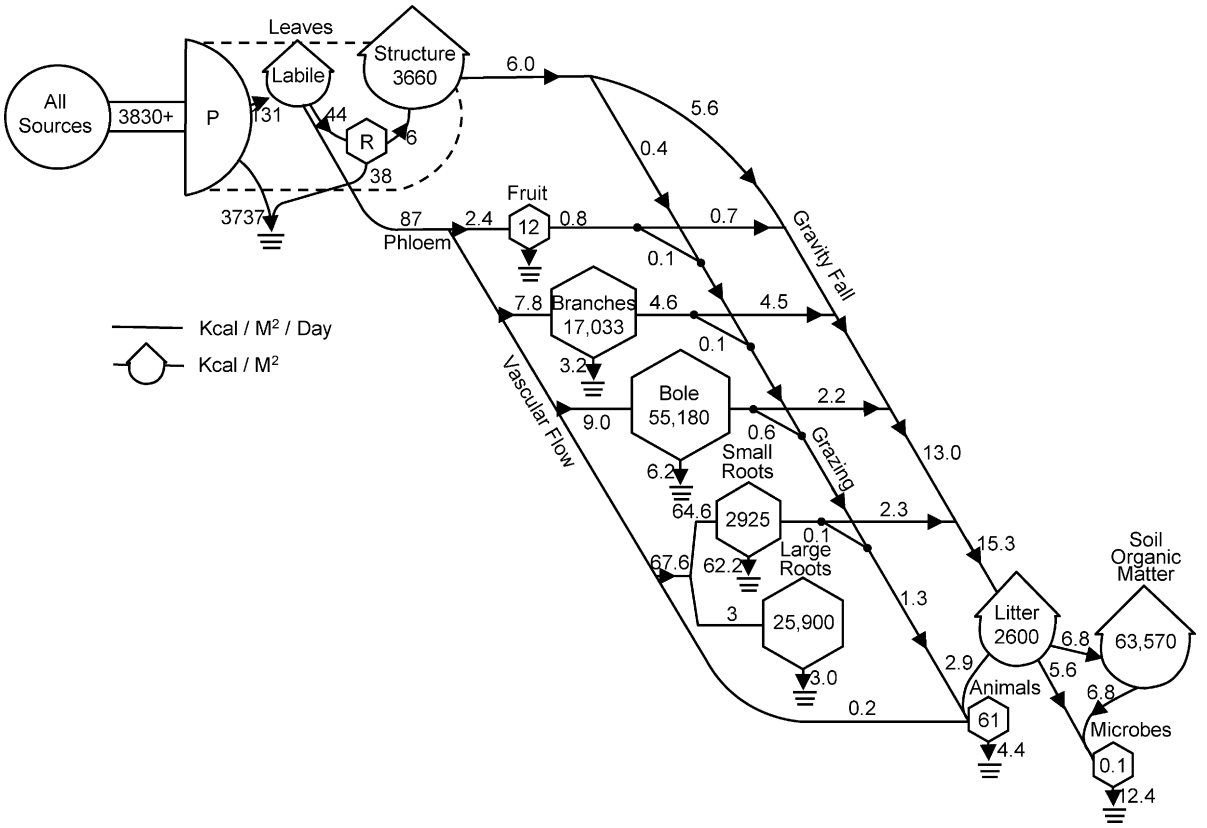


Fig. 3. A network energy diagram of the main power flows suitable for budget balancing but with control circuits lumped as compartmental respiration (Odum, 1970h).

(1995) in the manuscript for the 50th anniversary celebration.

1. Tropical forest restoration is a world priority for sustainable economies, stabilized atmospheric carbon dioxide, and preparation for a prosperous way down from the present system. The world economic–environmental pattern can be prosperous during a time of declining use of fossil fuels provided we make a smooth transition from high-intensity, fuel-based systems to those with a greater role for environmental production.
2. Simple overview models are able to generate some of the special features of tropical forests such as seasonal changes, differences in island forests, patterns of succession, nutrient conservation, roles of seeding, and gap-generating oscillations.
3. For more equity in developing tropical forests, products should be used in the home country or exchanged for products with equal EMERGY.
4. Intensity of tropical forest utilization systems that are appropriate now, are indicated by EMERGY investment rations of 7.0 in developed countries, 2.5 on the average for the world, and less that 1.0 in rural tropical forest areas.
5. Lower intensity versions of various tropical forest utilization systems will become prevalent as the EMERGY–investment ratios of the world decline again as fuels and other minerals become relatively less net yielding.
6. In the lower energy future, products will draw a higher percentage of EMERGY from the environment and less from purchased fuels, goods, and services. The yields and costs will be less, and efficiency greater.

7. Maximum long-range production may require rotation of lands following the natural hierarchical pattern generated by steady production and pulsed consumption.
8. Preservation of high-diversity gene pools in complex forests is a major need for maximizing economic contributions, especially as the fossil fuels decrease.
9. Utilization, as much as possible, of the natural cycles and homeostasis prevents nutrient limitations and maximizes production potentials.
10. Natural patterns of hierarchy are represented by timber-age distribution and by the distribution of gaps.
11. Patterns of tropical forest management may retain the hierarchical structure by adapting size and frequency of cutting to the hierarchical gap distribution found in nature.
12. Coupled pulsing of production and consumption models can generate spatial hierarchy where time between pulses is proportional to the area of the gaps generated.
13. Photosynthesis of tropical forests may be stimulated by the increase of carbon dioxide from the consumption of fossils fuels, but the mini model suggests that the area of vegetation must be restored to return carbon dioxide to lower levels.
14. A reasonable management of world tropical forests requires their use to be organized in sustainable cycles to maximize the EMERGY use of national and regional systems in which they are embedded, contributing more to the world economy in the long run that when left to the excess of market economies (Odum, 1995, pp. 390–391).

These summary points neatly depict the current state of the debate about tropical forest conservation. They illustrate how fundamental science leads to practical approaches to solving intractable problems. Science illuminates debates and through understanding, provides scientists with the freedom to generalize, which in turn provides ecosystem managers with the freedom of action. Through out his career, Odum's science was always "top down" as he liked to describe his macroscopic view of whatever system he was studying at the time. His approach was always to reveal general principles based on measurement and observation of real systems which were in turn used to develop insights for management. While Odum studied many types of ecosystems throughout his career he returned often to the LEF in Puerto Rico, developing a rich tapestry of papers that express a profound understanding of the system and its dynamics and providing, many years of research opportunities for generations of scientists to come through the questions and observations he left unanswered.

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