

AN INTRODUCTION TO HUMAN ECOLOGY RESEARCH
ON AGRICULTURAL SYSTEMS IN SOUTHEAST ASIA

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CHAPTER 4**The Tropical Rain Forest
as an Ecosystem**

Gerald G. Marten

Tropical rain forests are the prevailing natural vegetation in the humid tropics. Rainfall in the humid tropics generally exceeds 2,000 mm per year and is distributed throughout the year, at least eight months of the year having more than 100 mm of rain. This abundance of rainfall allows forest trees to remain green throughout the year and supports a richness of flora and fauna and a level of biological production that is greater than occurs in any other natural ecosystem in the world.

The structure of a tropical rain forest is quite distinctive. Many of the trees have a characteristic smooth bark, pointed "drip-tip" leaves, and a flaired "buttress" base. There is an overwhelming impression of greenness, the trees tending to occur in three vertical layers, though the layers are not distinct (Figure 4.1). The main layer is a dense and continuous canopy of trees that are 30 to 60 meters in height. Another layer consists of even taller trees that protrude above the canopy from place to place. The third layer is a discontinuous understory of trees below the canopy. The tallest trees are adapted to full sunlight; the understory trees are adapted to shade. The understory is dense only in spots where one of the taller trees has fallen and left a gap in the canopy, allowing direct sunlight to come through to the trees below. About 1 to 2 percent of the trees fall each year.

A few hectares of tropical rain forest may contain several hundred species of trees and thousands of species of smaller plants. There are many

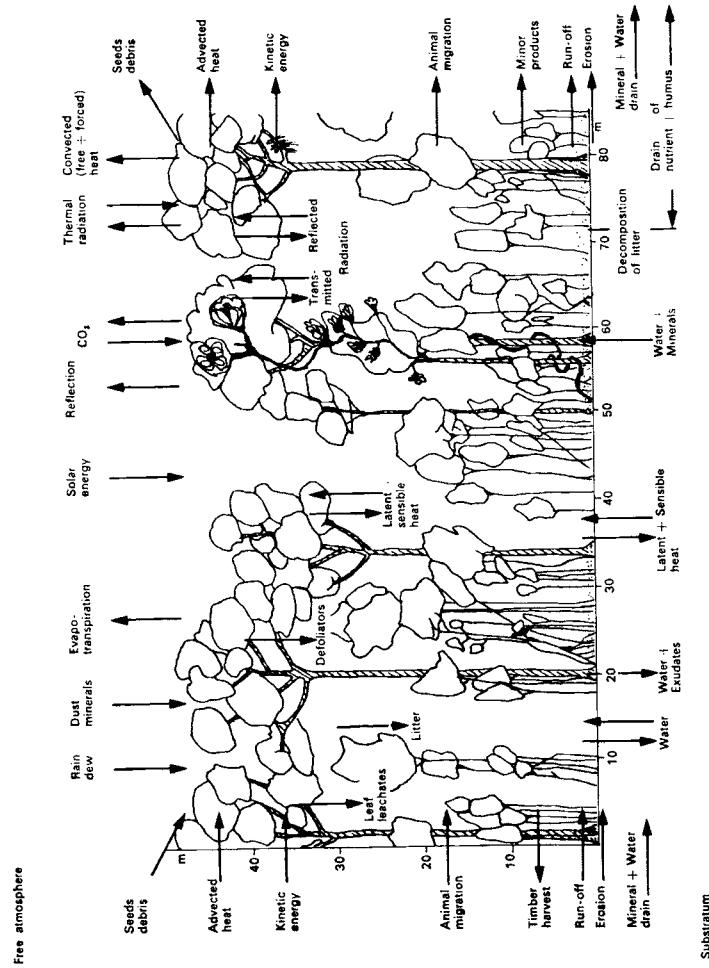


Figure 4.1. Profile diagram of a tropical rain forest showing some of the movements of nutrients and energy into and out of the ecosystem (Source: UNESCO 1978).

kinds of plants attached to the trees. Some of them, like vines, are rooted in the ground; others, like epiphytes (e.g., orchids), have their roots in the air and obtain part of their water and nutrients from the air while obtaining the rest from the tree surface on which they live. Because the forest has many overlapping trees at various heights, the sun is not visible from most points along the forest floor. In fact, a typical hectare of tropical rain forest has 5 to 10 hectares of leaves on its trees. As the sunlight must pass through so many leaves, only a fraction of the incoming light (less than 1 percent) actually reaches the forest floor. As a consequence, most rain forests have little vegetation at the ground level. Plants less than a half meter in height cover only 10 to 50 percent of the ground. Nonetheless, a variety of tree seedlings are usually found on the forest floor. The seedlings may hardly be growing, waiting for favorable conditions such as an old tree falling and opening up a patch of sunlight above them.

Associated with this diversity of plant life is a corresponding diversity of animals and microorganisms. Few of the animals are conspicuous to the casual observer because the forest supports few animals at ground level. Many animals – thousands of species of insects, hundreds of species of birds, and numerous monkeys and other arboreal mammals – are in the trees where food (e.g., leaves, fruits, seeds) is found in greater abundance. A great variety of tiny animals (e.g., mites and nematodes) and microorganisms (bacteria, fungi, protozoa) also live in the soil where they feed upon decomposing leaves, and much of the forest's biological activity takes place in the soil. Tree roots are also a major source of food for microorganisms and soil animals. Every cubic centimeter of soil contains billions of bacteria and hundreds of soil animals.

Most of the animals in the forest are specialized as to where they live and what they feed upon. Every species of tree has particular species of insects and other animals which feed upon its leaves, other species which eat its bark, and still others that feed upon its wood. Each of these, as well as the numerous species in the soil, has predators, parasites, and disease organisms that feed upon it.

This picture of a tropical rain forest applies best to lowland forests. At a higher altitude, where the lowland forest is replaced by montane forest (often called "cloud forest"), the trees are shorter (canopy 20 to 30 meters in height), the leaves are smaller, and epiphytes, mosses, and ferns are more abundant. The trees do not grow as fast, but as decomposition is slower because of lower temperatures, there is a greater accumulation of litter and humus in the top layers of the soil. The lowland rain forest is also different where the environment is drier. The trees are shorter, the canopy is more patchy (i.e., the cover is not so continuous), and the total area of leaves in the canopy is less. Many species of trees may lose their leaves during the dry season, and there are fewer species of plants and animals.

The flora and fauna of rain forests can vary even over small distances. As topography, microclimate, soil fertility, and soil drainage change from place

to place, the species of plants and animals in the forest change likewise, though the forest may appear superficially the same. The same kinds of plants tend to be found together under the same microenvironmental conditions, each assemblage of plants and associated animals forming a *community*. Forest communities in the temperate zone are often conspicuously different from each other, with distinct boundaries between them, but tropical rain forest communities tend to grade continuously into one another.

AN ECOSYSTEM PERSPECTIVE

An *ecosystem* is everything – plants, animals, microorganisms, air, water, minerals – that occurs in a given spatial area. The size of an ecosystem is defined by the observer. At one extreme, a particle of soil or a few drops of water can be regarded as ecosystems; at the other extreme, the entire planet Earth is an ecosystem. However, it is customary to refer to an area of more or less similar vegetation as an ecosystem. A stand of tropical rain forest is an ecosystem.

The numerous plants, animals, and microorganisms in a tropical rain forest interact in a complex fashion that serves to maintain the integrity of the forest. They display a diversity of biological activities, many of them associated with obtaining food and nutrition. The biological activities may be summarized in terms of two major processes (Figure 4.2):

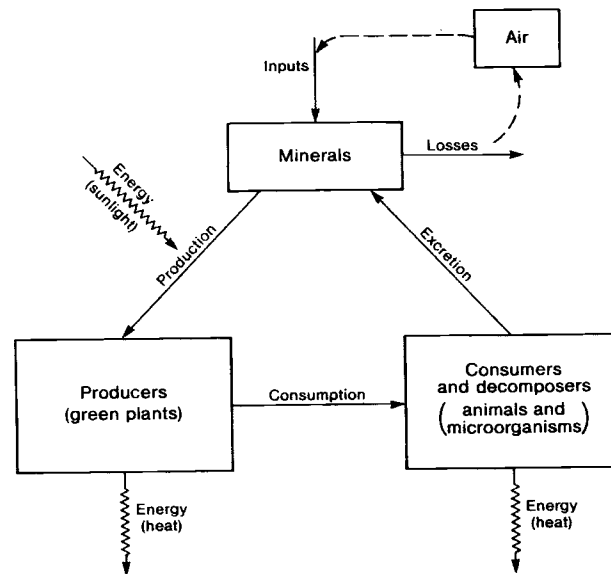


Figure 4.2. Energy flow and mineral cycling as they occur in the production-consumption cycle.

1. **Production** (also called primary production): The growth of green plants that results from photosynthesis. The carbon from carbon dioxide is joined into carbon chains that form the plants' living tissues (i.e., *biomass*).
2. **Consumption:** The metabolic activities of animals and microorganisms as they feed on plants, animals, or microorganisms and use the carbon chains in their food for their own growth. In the process, many of the carbon chains are broken apart and end up being released to the atmosphere as carbon dioxide.

Mineral Cycling

In the course of production and consumption, mineral nutrients move through the forest ecosystem in a cyclic manner (Figure 4.2). The most important mineral elements are those required for photosynthesis (carbon, hydrogen, and oxygen) and for the construction of proteins and other structural and metabolic compounds (nitrogen, sulphur, phosphorus, calcium, magnesium). Potassium and the *minor elements* (iron, copper, boron, zinc, manganese) can also be important. Minerals are transferred from the nonliving part of the ecosystem into the biological part of the cycle in the course of production. They are returned to the nonliving portion of the ecosystem whenever carbon chains are degraded (i.e., broken apart) in the course of consumption. This returns minerals to the soil where they can sustain further plant production.

These transfers of minerals take place through a variety of biological processes (Figure 4.1). Plants take up water through their roots and transpire (i.e., evaporate) water from their leaves. They take up carbon dioxide and release oxygen during the day, doing the opposite at night. Animals take up oxygen and release carbon dioxide. Some microorganisms consume nitrogen gas; others release it. As a consequence of all these activities, there is a net exchange of gases like carbon dioxide, oxygen, and nitrogen between the soil and the air above the soil, and between the forest and the atmosphere above the forest. During the day the net movement of gas may be in one direction, and at night another.

Figure 4.1 shows that mineral nutrients move through the forest not only in a gaseous form but also in tiny particles of dirt or dust and as ions dissolved in water (e.g., NO_3 , PO_4 , SO_4). Minerals enter the forest in dust and rainfall that fall from the sky above. As rainwater flows over leaves and branches, it leaches minerals from the leaves and carries them to the soil below. Minerals enter the soil solution as they are dissolved out of tiny rock particles in the soil. Streams and underground water flow into and out of the forest, carrying minerals with them. Water percolates downward, carrying minerals below the reach of tree roots.

The key feature of all these biological and physical processes is that they enable the forest to maintain its integrity. For example, trees on poor.

nutrient-depleted soils are able to continue using mineral nutrients for their growth although minerals are only slowly entering the soil system by weathering of the soil parent material. The only way the forest can retain enough minerals is by minimizing loss of minerals from the system.

Tropical rain forests on poor soils have a variety of intricate mechanisms for holding minerals within the system. Their main strategy is to hold nearly all the minerals of the entire forest system in the living organisms themselves, so only a small fraction of the minerals are "loose" in the soil, where they have the possibility of being washed out of the system. When a leaf falls to the forest floor, fungi begin to grow into it, decomposing it and causing it to disappear within a few weeks. The roots of forest trees and other plants grow into the leaf as it decomposes, and special fungi (mycorrhizae) form a living bridge between the decomposing leaf and the roots that are penetrating it. The fungi absorb the leaf's minerals as they decompose it, and minerals such as phosphorus pass directly from the fungi into tree roots. As a consequence, an atom of phosphorus from a decomposing leaf is never loose in the soil for very long before it is taken up by another plant.

Energy Flow

Energy enters the forest as sunlight and undergoes numerous physical transformations (Figure 4.1). Soil and plant surfaces absorb sunlight and emit infrared radiation; warm air carries heat energy as it passes to areas of cooler air. Heat passes between the soil and the air above, and between the forest and the atmosphere – in one direction during the day, and the opposite direction at night.

Biological *energy flow* (Figure 4.3) refers to the transfer of energy into living organisms by photosynthesis (production) and from one organism to another through the food web (consumption). The movement of energy is not cyclic like the movement of minerals. Energy is incorporated into living tissues by photosynthesis, when sunlight energy is bound into the carbon chains that green plants use for their production (i.e., growth). The carbon chains contain potential energy, which the plants can use to drive the metabolic reactions by which they grow and maintain themselves. Internal consumption of energy for metabolic purposes is *respiration*, and some of this energy is lost as heat. The net energy that goes into the growth of the plant after using energy for respiration (i.e., its net accumulation of potential energy in carbon chains) is net *primary production*.

Animals and microorganisms are *consumers*, which have a variety of ecological roles (e.g., herbivore, frugivore, predator, parasite, pathogen, scavenger, decomposer), depending upon the kind of food they eat, whether it is live or dead, and whether or not they eat it whole. Consumers that feed upon plants utilize the carbon chains in their food as building blocks to construct their own tissues, and they degrade a certain percentage of the chains in order to release energy for their metabolic needs (i.e., respiration).

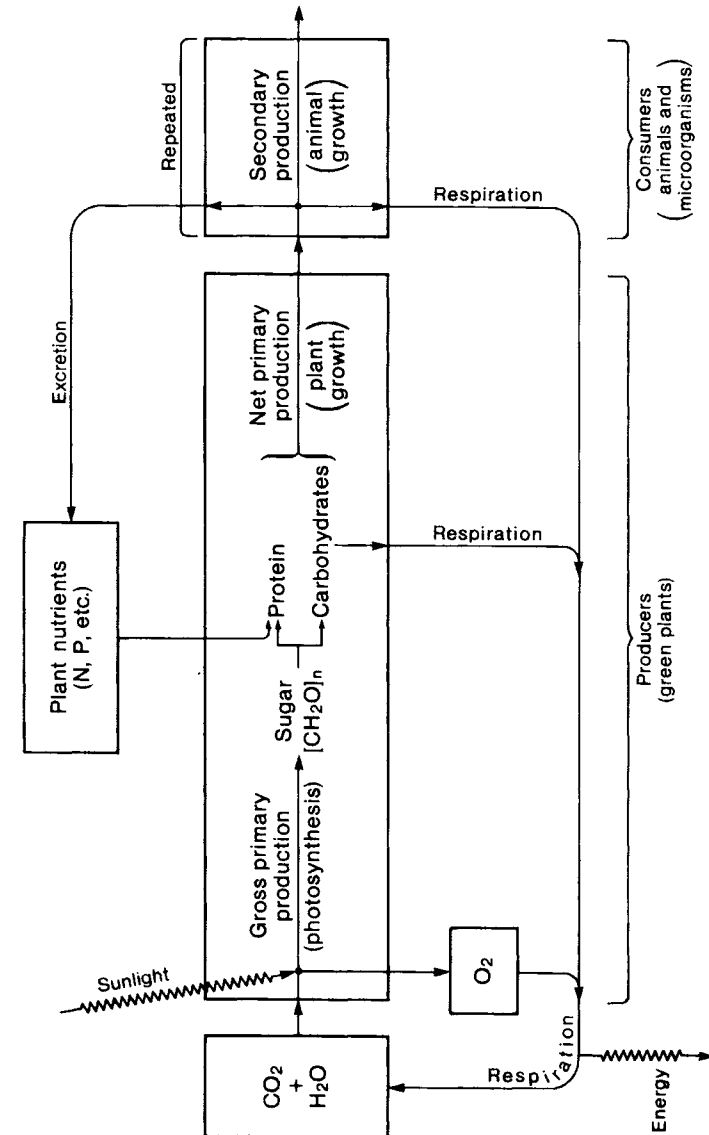


Figure 4.3. Details of energy flow through a food chain.

Minerals that are acquired in surplus of the needs of the animals or microorganisms are excreted along with other metabolic products to the environment. For example, nitrogen is released as ammonia, urea, or phenolic substances such as those passing into the soil from decomposing *Imperata* leaves, described by Sajise in Chapter 8. The rest of the energy and minerals, which are not excreted by animals or microorganisms, are retained for their growth (Figure 4.3).

The same is true for consumers that feed on other consumers. As one consumer eats another, there is a "flow" of biological energy (in carbon chains) along the food chain, and there is a loss of energy (to respiration) at each step in the food chain. The percentage of energy at one step, which passes to the succeeding step, is the food chain efficiency, typically 10 to 50 percent. Because an animal or microorganism may feed upon more than one kind of plant, animal, etc., the chains are interconnected to form a food web.

Figure 4.4 shows the pattern of production and consumption in a typical undisturbed tropical rain forest. Only a minor fraction of the production passes through animals, and only a minuscule fraction passes to humans (assumed to be hunters and gatherers). Most of the plant material falls to the forest floor to become litter, which is decomposed by soil microorganisms. Although the forest contains many kinds of animals, it does not support a large biomass of animals, in part because the plants are effective at making themselves inedible. The woody parts of the plants are indigestible to most animals because of their cellulose and lignin content. Leaves, fruits, and seeds can be more digestible, but they may also contain chemicals that make them poisonous or interfere with the animals' digestive enzymes. To counter this strategy, many animals specialize on particular species of plants, upon which they can feed successfully despite the toxicity or indigestibility. Many plants counter with highly synchronized fruiting, which sometimes occurs as infrequently as once every ten years, so that most of the time there is very little food to sustain the animal populations that specialize in feeding upon them. Not all forest trees follow this strategy, however; many bear fruit randomly throughout the year.

FOREST ECOSYSTEM ORGANIZATION

An observer of a tropical rain forest is impressed not only by the diversity of living organisms but also by the fact that all of them appear to fit in. Every species is intimately associated with certain other species. Even though every species has its natural enemies (predators, parasites, diseases), none of the natural enemies is able to eliminate it from the forest. By the same token, any organism that is not a natural member of the forest community may have difficulty surviving there.

The functioning of a forest ecosystem is related to its structure by the fact that its living components (each kind of plant, animal, or microorganism) are well adapted to the physical environment and to one another. The plants

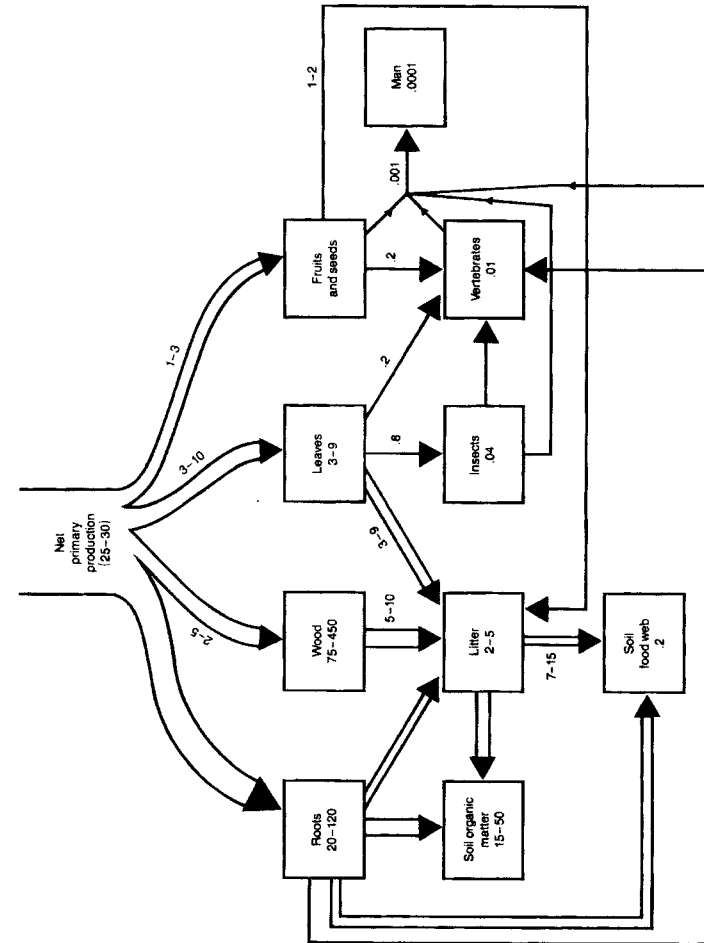


Figure 4.4. Typical flow of biomass in a lowland tropical rain forest. The numbers inside boxes represent dry matter standing crops in tons/hectare. The numbers attached to arrows represent flows in tons/hectare/year (shown where figures are available). The thickness of arrows reflects magnitude of flows (Sources: Richards 1952, Whitmore 1975, Leigh 1975).

are highly adapted to growing under the soil and moisture conditions where they are found; and the animals are adapted to obtaining the particular organisms on which they feed, and they are also adapted to avoiding their enemies. In the case of natural ecosystems such as forests, the coadaptation of the ecosystem's living components to one another is the product of a long process of evolution that has generated a highly intricate organization at the level of the ecosystem as a whole.

The organization of a forest ecosystem can be clarified by comparing it to another kind of system, a television set. A television set has some properties in common with a forest ecosystem — properties that are held in common by all systems. There are additional properties that are unique to ecosystems because of their biological organization. One of the most conspicuous characteristics of a television set is its design. It consists of many components, but each component (a particular transistor, resistor, or capacitor) is suited exactly to the components to which it is connected. If there were simply a random connection of components, the television set would blow up as soon as it was plugged in. An ecosystem has a similar design (coadaptation of components), which contributes to its continued persistence.

The television set and the forest ecosystem derive their whole-system behavior from the fact that the behavior of each component in the system is constrained by the actions of other components. Although every resistor in the television set could theoretically output a wide range of voltages, the output of each resistor depends in fact upon inputs from other components. These inputs are limited to those that generate an orderly television picture. Although all the plants, animals, and microorganisms in a forest have the reproductive capacity to multiply to enormous numbers, their populations are in fact held in check by natural enemies and other natural forces. Because uncontrolled populations would exhaust their food supply, possibly destroying themselves and the system, the ecosystem ensures its persistence by evolving feedback mechanisms for regulating the biological populations within it. Details of population regulation are discussed by Marten in Chapter 6.

There are, however, some important differences between ecosystems and television sets. Ecosystems have a higher level of redundancy than television sets, and this gives them a greater reliability. Because television sets are designed to be constructed as economically as possible, there is only one component for every function. (In this regard, many agroecosystems tend to be similar to television sets.) If a component is removed, the television set ceases to function. In the case of ecosystems, there is a considerable overlap of function between different organisms. If a single species is removed from a tropical rain forest, the forest may continue to function almost as though nothing has happened. In addition, the biological components of an ecosystem are adaptive. A resistor in the television set has the same operating characteristics regardless of the rest of the circuit, and once soldered into

place it cannot change the connection it has to the rest of the components. In contrast, some predators in the forest may switch from one kind of prey to another whenever one prey becomes scarce and the other becomes abundant.

We have seen that a tropical forest is organized in space because of vertical stratification of the trees and because the community of mutually adapted plants, animals, and microorganisms can be different according to different environmental conditions at different sites. Forest ecosystems are also organized in time to persist despite periodic environmental disturbances or perturbations (e.g., fires, typhoons, drought), which might otherwise eliminate them. Ecosystems persist by means of change, an orderly progression in the species composition and structure of the ecosystem (i.e., a change in plant and animal communities) known as *succession*. If a portion of the forest is destroyed by fire, or if a patch of forest is opened up by a falling tree, a different group of plants and animals replace the old forest. Over the years these plants and animals will in turn be replaced by others in a process that eventually leads to the same forest as before. The mature forest and the successional stages leading up to it constitute a total system that is adapted to the fluctuating environmental conditions of the area (Figure 4.5). At any one moment an area may have a patchwork of communities in various successional stages.

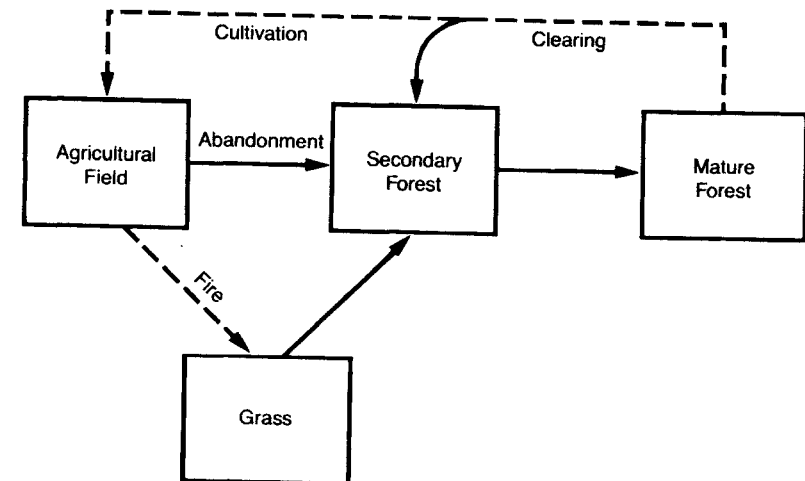


Figure 4.5. Stages of community succession in a tropical rain forest ecosystem. Solid arrows indicate natural changes; dashed arrows indicate changes induced by external disturbance.

It is important to avoid unproven generalities and stereotypes concerning tropical ecosystems. A diversity of soil, rainfall, and other environmental conditions are found in the tropics; and there is a similar variation in the plants, animals, and resulting ecosystems that have developed in those environments, as already indicated by Hutterer in Chapter 5. Some tropical forests have soils that are infertile or easily eroded and others do not. Some will support permanent agriculture; others will not. Some will quickly regenerate a forest the same as the one that was cut; others may first experience a succession to some other kind of vegetation (e.g., grassland), as described by Sajise in Chapter 8, and take many years before returning to the original forest (Figure 4.5).

MAN-MADE ECOSYSTEMS ON FOREST LANDS

The complexity outlined in the preceding pages is not unique to tropical rain forests. Although most ecosystems are considerably less complex than a rain forest, even the simplest ecosystem is overwhelmingly complex. All of the processes — the invisible movement of gases, minerals, and energy; the consumption of one organism by another, etc. — are present in all ecosystems, including agricultural ecosystems.

There are some significant differences between agricultural and forest ecosystems, however. Compared to a forest, most agricultural ecosystems are less complex and intricate in design (i.e., coadaptation of components), there is less redundancy, and most agroecosystems are less able to withstand external disturbances unless sustained by external inputs (e.g., fertilizers, pesticides, plowing). An agricultural ecosystem, such as sugarcane, rice paddy, or pasture, may be even more productive than the natural rain forest that once occupied the same land, and it is specifically designed by man to channel a much greater percentage of its production to human consumption than does a forest, but it is not self-sustaining. The soil may be too infertile for continuous crop growth unless it is fortified with fertilizers, or pest may destroy the crop unless they are held in check by pesticides.

Ecologists have used their knowledge of the structure and function of natural ecosystems to suggest how man-made ecosystems might be designed for harmony, rather than conflict, with nature. One of the major points of conflict lies in human efforts to establish and maintain artificial ecosystems that are different from the natural ecosystems they have replaced. Under such conditions there are strong natural forces to revert to the natural ecosystem by means of community succession. An example is the invasion of tropical slash-burn fields by weeds, which are the first stage in a normal succession that occurs when a patch of forest is opened up (Figure 4.5). Allowing the succession to take place (i.e., allowing a fallow that eventually leads to replacement of the field by a weedless, mature forest) is in accord with natural ecological processes like those described by Sajise in Chapter 8. It may only be possible to combat weeds without a fallow by using external

inputs such as herbicides, which are not only costly but may have undesirable side effects on the environment.

A forest fallow can also rebuild soil that has degraded under agricultural use. It may be difficult to maintain the fertility of the soil in a slash-burn field without applying significant quantities of fertilizers; and even with fertilizers, changes in soil pH or loss of soil organic matter may seriously reduce crop yields. During a forest fallow, the trees draw mineral nutrients from deep in the soil and use those minerals for the growth of their leaves. When the leaves fall to the forest floor, they replenish the mineral supply in the topsoil as they decompose. The decomposing leaves also replenish the organic matter in the topsoil — organic matter that is the basis of the soil's capacity to hold mineral nutrients and store water, sustaining crops through dry periods.

An ecological strategy for sustainable agriculture in the humid tropics should keep options open, avoiding soil degradation or other undesirable changes in the environment that may be difficult to reverse. One approach to sustainable agriculture is to structure the farm to be as similar as possible to the forest it replaced. An overstory of trees can produce litter to maintain soil organic matter and protect the soil surface from erosion, and the less bare soil there is, the less erosion there will be. The erosion in an undisturbed forest can be as little as one-hundredth the erosion with a typical field crop. The complex agricultural systems that are sometimes found in traditional human societies may be similar to forests in their structure and function, allowing them to be sustained with fewer external inputs.

An ecological perspective also permits an evaluation of the limits beyond which attempts to improve on nature are counterproductive. This has been demonstrated in North American forest management, where attempts to increase forest production by eliminating fires from "fire-adapted" forests have led to less frequent but more severe fires due to greater accumulation of litter between fires. The same thing has happened when pesticides have been used to prevent natural forest insect attacks. Pesticides have killed predators that naturally regulate insect pests, allowing the pest populations to increase to a point where they do serious damage unless expensive applications of pesticides are continued on a regular basis. Foresters have concluded it is most practical to allow minor fires and pests outbreaks to take place in a natural fashion.

In conclusion, tropical rain forests are complex ecosystems whose intricate design enables them to persist as a system. Ecological prudence suggests this design should be respected when establishing agriculture on tropical forest lands. There is mounting evidence of a trade-off between the amount of an ecosystem's energy that is channeled to human consumption and the sustainability of that ecosystem. If so, it would appear advisable to reassess the widely held view that the principal aim of agricultural development should be to attain the highest possible yields.

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CHAPTER
5**Ecology and Evolution
of Agriculture
in Southeast Asia¹**

Karl L. Hutterer

Over the past two decades, archaeological work in Southeast Asia and the western Pacific Islands, particularly New Guinea, has generated much excitement among people interested in plant domestication and the beginning of agriculture. A number of tantalizing findings have been reported: archaeological plant remains; indirect evidence of early cultivation; and traces of prehistoric field systems. The fact that these findings were made was not all that surprising in itself. After all, Southeast Asia constitutes one of the important regions of agricultural production in the world today, and it has long been understood that many of the region's crops and agricultural practices have their roots in prehistory. What was a major surprise, however, was the unexpectedly early date of many of the findings, several of them apparently indicating an early agricultural phase about eight to ten thousand years ago.

These early dates were all the more interesting as they were being announced at a time when a general reinterpretation of Southeast Asian history and prehistory was going on. Up to about 1950, it had been widely accepted that Southeast Asia was for the most part a culturally passive region

¹ A modified and somewhat expanded version of this chapter has been published in the journal *Anthropos* 78(1-2): 169-212, 1983, under the title "The Natural and Cultural History of Southeast Asian Agriculture: Ecological and Evolutionary Considerations." Reprinted by permission of the publisher.