PRODUCTIVITY AND HERBIVORY IN HIGH AND LOW DIVERSITY TROPICAL SUCCESSIONAL ECOSYSTEMS IN COSTA RICA

BY

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Abstract of Dissertation Presented to the Graduate Council of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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Chairman: Dr. John J. Ewel
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Above-ground net primary productivity (NPP), herbivory and vegetation structural characteristics were measured in high and low diversity successional and agricultural ecosystems at a wet tropical site near Turrialba, Costa Rica. Insecticide and defoliation experiments were performed to evaluate the effects of herbivory on NPP in high and low diversity ecosystems.

The four experimental ecosystems were enriched succession (natural regeneration augmented by propagule additions), natural succession (control), successional mimic (an ecosystem with investigator-controlled species composition designed to imitate natural succession), and successional monoculture (two maize crops followed by cassava). Plant species richness and leaf area index (LAI) were highest in

the enriched, high in the natural succession, intermediate in the mimic, and low in the monoculture at 1.5 yr.

Net primary productivity, estimated from biomass increments adjusted for turnover, was not related to ecosystem complexity. The NPP was highest in the most diverse (enriched) and least diverse (monoculture) systems. More than 92% of the above-ground production was lost annually through litterfall, plant mortality and herbivory. Standing dead biomass that did not fall into litter traps accounted for a significant fraction of total turnover in all ecosystems.

Herbivores consumed approximately the same amount of leaf tissue per m^2 of ecosystem in each of the three diverse systems (54-61 $cm^2\ m^{-2}$ ground day^{-1}). Consumption expressed as a percent of total leaf area was higher in the ecosystem with lower LAI (the mimic). Absolute and percent losses were lower in the monoculture than in the other ecosystems. In the less diverse systems containing cultivars, herbivory had high temporal variability. Species' herbivory rates ranged from <1 to 131 $cm^2\ m^{-2}$ leaf day^{-1} and appeared to be related to palatability, ecosystem LAI and species composition.

Herbivory stimulated NPP over a wide range of herbivory levels in both the diverse system and the monoculture. The stimulatory effect was greater, and maximum stimulation occurred at a higher herbivory level, in the diverse system.

The resilience of the diverse system, due to compensatory fluctuations in dominance of co-occurring species, has important implications for agroecosystem design.

CHAPTER I
INTRODUCTION

Complex traditional agroecosystems in the humid tropics have persisted for many years without the use of pesticides, while introduced monocultures have often been plagued by pest attacks that lead to decreased crop productivity. The magnitude of pest problems in an agroecosystem may be related to the degree of similarity between the agroecosystem and the natural system it replaces. The hypothesis is that the natural ecosystem possesses structural and functional characteristics that allow it to survive in its environment, and the more similar the agroecosystem is to the natural system, the greater is its chance for success. The objective of this study was to investigate herbivory and primary productivity in ecosystems structurally similar and dissimilar to a diverse tropical successional system.

Related Research

The Diversity-Stability Issue

In addition to the goal of maximizing production per unit of energy input, tropical agriculturists are interested in two other properties of agroecosystems: stability and

sustainability. A stable agroecosystem lacks fluctuations in productivity (or variability in yield) over time, and a sustainable agroecosystem has the ability to persist in the face of perturbations (Conway 1982). Many complex traditional agroecosystems have high sustainability and high stability, and it has been suggested that these characteristics are a function of their diversity (Soemarwoto and Soemarwoto 1979, Gliessman et al. 1981). Interest in the stabilizing effect of diversity in agroecosystems is reflected in the expressed need for development of complex agricultural systems for the humid tropics (Holdridge 1959, Dickinson 1972, Trenbath 1975, Hart 1980), and in the current agronomic emphasis on polyculture cropping systems research (Dalrymple 1971, Kass 1978).

A large body of literature on the theory of diversity-stability relationships in ecological systems bears directly on the question of agricultural diversification as a means of reducing pest problems. The traditional belief for many years among ecologists was that diverse systems were more stable than simple ones. Strong support of this view was expressed by most contributors to a symposium volume on the topic (Woodwell and Smith 1969). Subsequent work, including empirical studies and development of mathematical models (see work cited by Goodman 1975), did not support the original hypothesis. Goodman (1975) reviewed the development of the diversity-stability theory

in detail and concluded that there is no clear relationship between ecosystem diversity and stability. Empirical studies have yielded inconsistent and contradictory results, partly due to disagreement among ecologists both on the definition of the term "stability" and on appropriate criteria for measuring it.

Many empirical studies to test the relationship between diversity and stability have considered fluctuations in numbers of individuals within a single population or trophic level; fewer studies have considered the effects of diversity on ecosystem properties such as energy flow and nutrient cycling. Holling (1973) distinguished between stability (small fluctuations around an equilibrium point) and resilience (ability of a system to persist by moving between multiple equilibria). Using these definitions the spruce-fir forest of eastern Canada is an unstable system that fluctuates widely in plant and animal species composition. However, because of the instability of populations and the resulting effects on competition, regeneration and forest growth rates, this system has very high resilience (i.e., it persists).

In McNaughton's (1977) restatement of the diversity-stability hypothesis, the emphasis was on stability of ecosystem processes rather than stability of population numbers. Process stability and population stability are not necessarily related. As Margalef (1975,

page 160) stated, "A system which is highly unstable in species composition may be stable with relation to the energy flowing through it." In general, a system will tend toward the configuration of species that best processes the available energy, thus maximizing energy flow (Odum and Pinkerton 1955).

Odum (1975) proposed that the optimal diversity of a system is a function of the sources and quantities of available energies. He calculated diversity indices from empirical data on plant and animal species abundances in a variety of ecosystems. The frequency distribution of the diversity indices was bimodal. Stressed, selectively managed and subsidized ecosystems had low diversity indices; natural ecosystems where solar radiation was the primary energy source had high diversity indices.

Lugo (1978) emphasized the importance of energy drains, as well as energy sources, in determining system complexity. It is generally accepted that ecosystem complexity and efficiency of energy use are positively correlated (see Margalef 1968), and it has been hypothesized that plant diversity is positively associated with primary productivity (Connell and Orias 1964, Margalef 1968, H. T. Odum 1971). However, the development and maintenance of diversity requires energy expenditures and the complexity of an ecosystem is determined by the balance between energy inputs and energy drains (H. T. Odum 1971, Lugo 1978). For

example, very productive systems with low energy drains have high diversity (e.g., a coral reef), while very productive systems with high energy drains have low diversity (e.g., an estuary with tidal exports of organic matter).

In a natural ecosystem, high diversity of components provides many possible pathways for the flow of energy. When a high diversity system is stressed, either by a fluctuation in the energy inputs to the system or by an increase in energy drains from the system, the dominant energy pathways change, but the system may still be able to process the available energy. High diversity results in more alternative equilibrium states of the system (Holling 1973), which provide more options for maximizing energy flow under fluctuating conditions. Diversity, then, is a homeostatic mechanism operating at the ecosystem level that insures continuous energy flow through the system (Reichle et al. 1975). Species abundances change when a perturbation occurs, the decreases in some species are compensated for by increases in other species, and by this mechanism ecosystem functional properties are stabilized (McNaughton 1977). Lugo (1978) proposed that the ability of a system to respond to a perturbation depends on the dynamics of the system's energy pathways, the type and intensity of the perturbation, and the kinds and numbers of pathways altered.

Impacts of Herbivory

Herbivory stresses the ecosystem by draining energy from plant biomass. In natural ecosystems, herbivory is a normal or background stress to which the system is usually well adapted (Lugo 1978). In ecosystems that are not well adapted to herbivore stress (e.g., many agricultural systems and natural systems with introduced pests), herbivory may ultimately affect the ability of the system to persist through its impact on energy flow.

Herbivory may alter energy flow through the primary producers in two ways: (1) directly, by reducing the amount of photosynthetic tissue and by stimulating compensatory growth in remaining tissue, and (2) indirectly, by affecting structural and functional characteristics of the system, which in turn alter the primary productivity rate.

Although insects generally consume only a small fraction of the leaf tissue in a terrestrial ecosystem, the effects of herbivores are greater than simply loss of leaf area (Harper 1977, Whittaker 1979, Lubchenco and Gaines 1981). Herbivory influences ecosystem structure and function by increasing light penetration and reducing competition for nutrients, water, and light. Herbivory may accelerate nutrient cycling through increased nutrient leaching from damaged foliage and increased decomposition rates (Mattson and Addy 1975, Golley 1977, Bormann and Likens 1979, Barbour et al. 1980). Herbivores act as ecosystem regulators

through direct and indirect feedback loops to the autotrophs (Odum and Ruiz-Reyes 1970, Chew 1974, Mattson and Addy 1975, Lee and Inman 1975). The effects of herbivores on system processes may be positive or negative, depending on the characteristics and state of the system (Lugo 1978).

Direct impacts on net primary productivity. Moderate amounts of herbivory may stimulate plant productivity under certain conditions (McNaughton 1979a), and compensatory growth following defoliation has been well documented (Alcock 1962, Pearson 1965, Hodgkinson et al. 1972, Gifford and Marshal 1973, McNaughton 1976, Detling et al. 1979, Painter and Detling 1981). Many plants normally photosynthesize at less than their maximum rates. It has been suggested that the relationship between herbivory and net primary productivity (NPP) is nonmonotonic, and there is an optimum grazing level at which NPP is maximized (McNaughton 1979a). Although herbivory is usually considered a stress to the plant community, stress may accelerate processes and in some cases benefit the system (Lugo 1978). Stimulation of plant productivity by grazing is an example of a positive feedback loop within the system that amplifies energy flow (Odum 1977). Feedback may be negative rather than positive at high herbivory levels, and there is a threshold herbivory level above which plant productivity decreases (Vickery 1972, Dyer 1975, Noy-Meir 1975, Caughley 1976).

Impacts on species composition and diversity. Individual plant responses to herbivory may be positive or negative, depending on plant genetics, intensity and frequency of defoliation, the tissues affected, plant developmental stage at the time of attack, and environmental factors (McNaughton 1979a).

Herbivory may lead to a variety of physiological responses in the individual plant. These include (1) plant mortality and reduced growth (Kulman 1971); (2) alteration of plant resource partitioning (Gifford and Marshal 1973, Detling et al. 1979); (3) stimulation of compensatory growth in residual tissue (Pearson 1965, Hodgkinson et al. 1972, Dyer 1975, McNaughton 1976, 1979a, Detling et al. 1979, Painter and Detling 1981); (4) increases or decreases in plant reproductive output (Jameson 1963, Cavers 1973, Rockwood 1973, Harris 1974, Owen and Wiegert 1976, Boscher 1979, Pinter and Kalman 1979, Bentley et al. 1980, Stephenson 1981); (5) changes in plant growth patterns, such as increased branching or tillering (Oppenheimer and Lang 1969, Youngner 1972, Saunders 1978, Simberloff et al. 1978, Owen 1980); (6) increased or decreased root growth (Troughton 1960, Alcock 1962, Jameson 1963, Taylor and Bardner 1968, Dunn and Engel 1971, Whittaker 1979); (7) delay of plant senescence (Chew 1974, McNaughton 1976); (8) increased water use efficiency, due to reduced transpiration area (Daubenmire and Colwell 1942, Baker and Hunt 1961); and

(9) reduced nutritive quality of remaining leaf tissue (Schultz and Baldwin 1982).

Plant responses to herbivory reflect a complex interaction of factors. The net result of herbivory at the community level is a change in competitive advantage among species. As Whittaker (1979) pointed out, the competitive balance among species is altered by herbivory regardless of whether an individual plant is damaged or benefited. Results of numerous studies (e.g., Malone 1969, Rafes 1970, Harris 1973, McNaughton 1979b, Linhart and Whelan 1980) support the generalization that herbivory shapes the plant species composition of an ecosystem by altering the competitive balance among species. Instances of successful biological control of plant pests by introduced insects are examples of the impact that herbivory can have on plant species composition (see DeBach 1974).

By affecting competition, herbivory may regulate plant diversity in an ecosystem. It has been suggested that herbivory may maintain local species diversity by keeping plant populations at low densities and by increasing niche differentiation (Whittaker 1965, Connell 1971, Huffaker 1971, Harris 1973). Grime (1973) predicted that herbivore-susceptible species would be outcompeted at high grazing rates, herbivore-resistant species would be outcompeted at low grazing rates, and therefore highest species diversity would occur at intermediate grazing

intensities. Lubchenco and Gaines (1981) hypothesized that diversity would be a maximum at low or intermediate herbivore levels, depending on the nature of the competitive interactions between plants. Harper (1969) and Caughley and Lawton (1981) suggested that the effects of predation were determined by herbivore abundance and feeding characteristics and that herbivore activity might increase or decrease plant diversity.

Regardless of the direction of the change, the effects of herbivory-induced shifts in diversity on ecosystem processes may be important determinants of ecosystem stability. McNaughton (1977, page 516) reiterated the idea developed within the framework of diversity-stability theory that "compensatory fluctuations in the abundances of co-occurring system elements (species populations) in a variable environment can stabilize aggregate system properties." He presented empirical data from a grazing experiment in high and low diversity ecosystems that supported this idea. In the high diversity system, grazing resulted in a change in plant species diversity, but had little effect on the total plant biomass. In the low diversity system, an equal amount of grazing did not affect species diversity, but significantly reduced plant biomass. Thus high diversity provided a homeostatic mechanism that allowed functional stability (maintenance of plant biomass) in the face of a perturbation (grazing).

Diversity Effects on Herbivory

The relationship between herbivory and plant diversity is a two-way interaction. In addition to the effects of herbivory on ecosystem processes, the structural characteristics of the system also influence herbivory patterns.

It has been suggested that increased plant diversity results in decreased herbivory, and many investigators have reported fewer herbivores and/or less herbivore consumption in floristically diverse than in floristically simple systems (Burleigh et al. 1973, Root 1973, Dempster and Coaker 1974, Smith 1976, Altieri et al. 1977, Altieri et al. 1978, Bach 1980, Risch 1981). Herbivory reduction in diverse systems has been attributed to the presence of alternative hosts that divert plant pests, greater abundance and diversity of insect predators, and/or structural complexity that interferes with insect movements and makes host plants harder to find (Root 1973, Atsatt and O'Dowd 1976, Pimentel 1977).

These studies may lead to the conclusion that by increasing plant species diversity, one increases the resistance of an ecosystem to herbivore attack. However, attempts to relate ecosystem diversity to herbivory patterns have not always yielded consistent results. There is evidence that the buffered environment of a complex ecosystem may support certain pests not able to survive in a

more open monoculture, and that some pest problems may increase with ecosystem complexity (Hart 1974, van Emden 1977, Way 1977). For example, some investigators have reported fewer predaceous insects (Pimentel 1961b, Pollard 1971), lower insect predator efficiency (Price et al. 1980), and greater abundances of some herbivores (Cromartie 1975, Thompson and Price 1977) in diverse systems.

Research Questions

The primary objective of this study was to investigate net primary productivity and herbivory in high diversity and low diversity tropical successional ecosystems. The work was done as a part of a larger study designed to test the feasibility of using natural succession as a model for the development of new tropical agroecosystems. Experimental successional ecosystems that lacked, imitated, and exceeded the floristic complexity of the natural successional system provided the framework for investigating four questions: (1) Does net primary productivity differ in high and low diversity systems? (2) Do herbivore consumption rates differ in high and low diversity systems? (3) How does herbivory affect net primary productivity in high and low diversity systems? (4) Are high diversity systems more homeostatic than low diversity systems when partially defoliated?

CHAPTER II
METHODS

The Study Site

The research was carried out in the Florencia Norte Forest of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), at Turrialba, Costa Rica. The site, located at 9° 53' N, 83° 40' W, lies at the eastern edge of the central plateau of Costa Rica at an elevation of 650 m. The topography is gently undulating, and the vegetation of the area falls into the tropical premontane wet forest life zone (sensu Holdridge 1967, Tosi 1969).

Long term mean annual rainfall for the area is approximately 2700 mm, with a pronounced dry season from January through March. Mean annual rainfall for 1979-1980 (2169 mm) was somewhat lower than the long term average. Monthly rainfall amounts ranged from 14 mm in March 1980 to 460 mm in December 1980 (Fig. 1). Temperatures ranged from an average maximum of 28.4° C to an average minimum of 17.1° C, with a median temperature of 22.7° C.

The 2.4 ha study site is typical of large areas in the mid-elevation warm humid tropics that have been deforested for agricultural use. At the start of the study, the vegetation on the site consisted of 8-9 yr old second growth

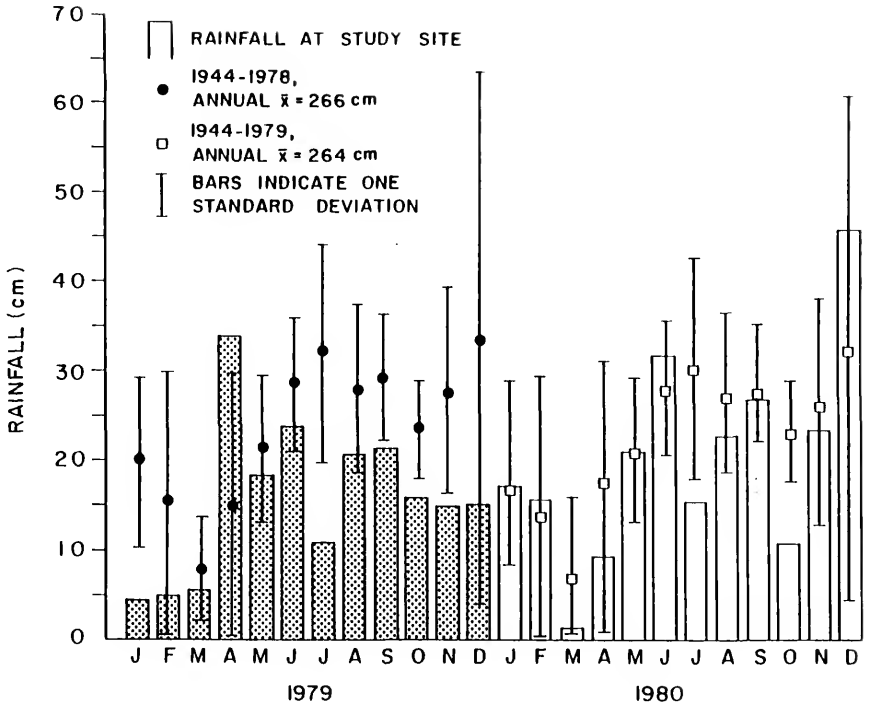


Figure 1. Monthly rainfall at the study site (1979-1980) and long term average rainfall.

interplanted with timber trees, and remnants of a 56-60 yr old secondary forest dominated by Goethalsia meiantha. The immediate study area was surrounded by diverse second growth, pasture, and experimental forestry plantings, and overlapped with some of the land where Harcombe (1977a, 1977b) did earlier studies on tropical succession.

The soil at the study site, classified as a Typic Dystrandept (Soil Conservation Service 1975), was an upland soil overlying upper Miocene or lower Pliocene rock (Harcombe 1973). This deep, freely drained soil is characterized by low bulk density, <50% base saturation, and a moderate to high cation exchange capacity.

Site Preparation

During the first week of January 1979, the vegetation was felled on six 33 x 33 m plots and several smaller plots, using machetes and a chain saw. Border strips of living vegetation at least 5 m wide were left between plots. Firewood was removed from the site, and the remaining vegetation was left on the ground through the dry season. On 22 March 1979, the plots were burned. The burn was intense and complete, and left the site with a uniform cover of white ash. The impacts of the slash and burn process on nutrient budgets, soil carbon dioxide evolution, soil seed storage, and plant growth were studied and are reported elsewhere (Ewel et al. 1981). Immediately after the burn, the four experimental manipulations were initiated.

Main Treatments

Three experimental successional ecosystems, plus a natural successional system, were studied. The experimental systems were designed to represent two types of floristically diverse successional ecosystems and one floristically simple system. Natural succession provided the baseline with which the other systems were compared. The four main treatments are described below.

Natural Succession

In this system natural regeneration began after the burn, and secondary succession was allowed to proceed with no experimental manipulations. The natural succession provided an estimate of what nature does during early tropical succession. This treatment was used as a control for comparison of structural and functional characteristics of the other three main treatments.

Mimic of Succession

In this treatment a diverse successional system was experimentally constructed and maintained. The idea was to try to imitate the structure and function of the natural successional system by substituting species morphologically similar to those found in the natural succession. The species composition of the mimic was completely investigator-controlled. Both careful observation of the

natural succession plots and prior knowledge of tropical successional trends provided guidelines for selection of species to be included in the mimic. For example, herbaceous vines (e.g., Vigna uniculata, several varieties of Phaseolus vulgaris, Cucurbita pepo and Sechium edule) imitated early successional vines in the Cucurbitaceae (e.g., Frantzia pittieri, Momordica charantia) and Leguminosae (e.g., Rhynchosia pyramidalis, Vigna vexillata). Castor bean (Ricinus communis) and papaya (Carica papaya) were substituted for fast-growing pioneer tree species (Cecropia spp. and Bocconia frutescens). Large monocots such as plantains (Musa paradisiaca) were imitations of common early succession monocots (e.g., Calathea insignis, Heliconia latispatha, and Ischnosiphon pittieri). Cultivated herbs (e.g., Capsicum sp.) replaced morphologically similar native herbs (e.g., Solanum nigrescens).

Both cultivars and non-cultivated species that were not present in the area were included in the mimic. Continuous evaluation of the mimic and regular additions of new species occurred during the 1.5 yr study period. The plots were periodically weeded to remove natural colonizers.

The mimic was a key ecosystem for testing whether it was possible to imitate succession in such a way that the productivity and homeostasis of the natural system was duplicated.

Enriched Succession

The enriched succession was a system in which the natural regeneration was supplemented by continuous inputs of propagules of many species not present in the vicinity of the study site. This was a self-design treatment in which nature controlled the selection process in an ecosystem in which the limitations of seed accessibility had been reduced. This system was used to determine whether or not the removal of some biogeographical constraints would result in an ecosystem more diverse than the natural succession, and whether the resulting ecosystem would differ structurally or functionally from the natural successional system.

Propagules of both cultivars and non-cultivars were added to the enriched succession plots at approximately bi-weekly intervals. Seeds were scattered on the ground, and stem cuttings and seedlings were planted at randomly located points within the plots. During most months, a minimum of 10,000 propagules of at least 30 species were added to each plot.

Successional Monoculture

A single species system was included in the study for comparison with the high diversity systems. A series of three monocultures was planted, with the species chosen (1) to resemble the life forms of dominant successional species

at that stage in succession, and (2) to represent important cropping systems in the area.

Maize (Zea mays var. Tuxpeno), an herbaceous monocot similar to some early successional grasses, was planted immediately after the burn (late March 1979). The first maize crop was harvested in mid-July 1979 and was followed by a second maize planting. After the second maize harvest (November 1979), cassava (Manihot esculenta var. Japonesa) was planted. Cassava is a tuber crop important throughout the tropics. Cassava was chosen for the monoculture because its woody growth form was similar to the growth form of the shrubs that were rapidly becoming dominant in the 7 mo old natural succession. The cassava was harvested in mid-September 1980 and was followed by a planting of Cordia alliodora, an important timber species. Data on the Cordia monoculture are not included in this study.

The planting procedures and management of the monoculture plots followed as closely as possible the methods used by local farmers. Maize was planted at 1.0 x 0.5 m spacing, two seeds per hole. The cassava was grown from stem cuttings planted at 1 x 1 m spacing. At plant maturity, the harvestable crop (ears or tubers) was removed from the plots, and the remaining plant material was left on the ground. All monoculture plots were periodically weeded.

Plot Layout and Variables Measured

The treatment plots were arranged in a randomized complete block design, with six replications of each of the four main treatments (Fig. 2). Each study plot measured 14 x 14 m (196 m^2) within permanent metal markers. An additional border strip approximately 1 m wide was left around each plot, making the actual plot size 16 x 16 m (256 m^2). The study plots within each replication were separated by 1 m wide access trails. Buffer strips at least 5 m wide of original, uncut vegetation were left between replications to serve as a source of seeds for the experimental plots. Specific areas within each study plot were designated for particular types of investigations, including the work reported here and the work of other researchers (Fig. 3).

Variables monitored during the 1.5 yr study period in the 4 main treatments fall into two categories: (1) vegetation structural characteristics, such as leaf area index, species composition, and vegetation height, and (2) productivity measurements. The methods employed for each type of measurement are described in detail below.

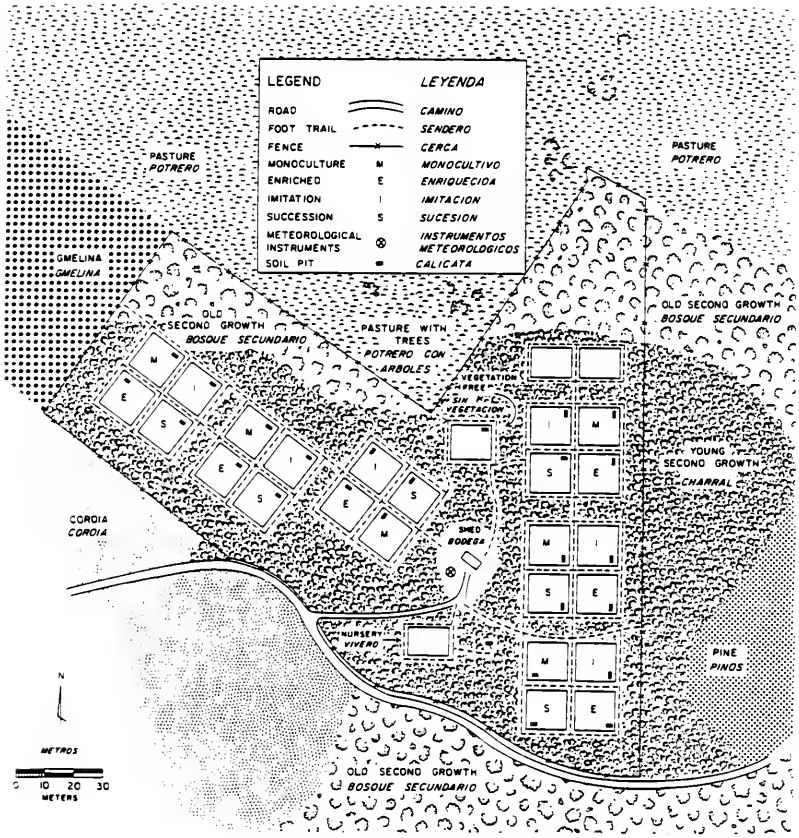


Figure 2. Map of the study site.

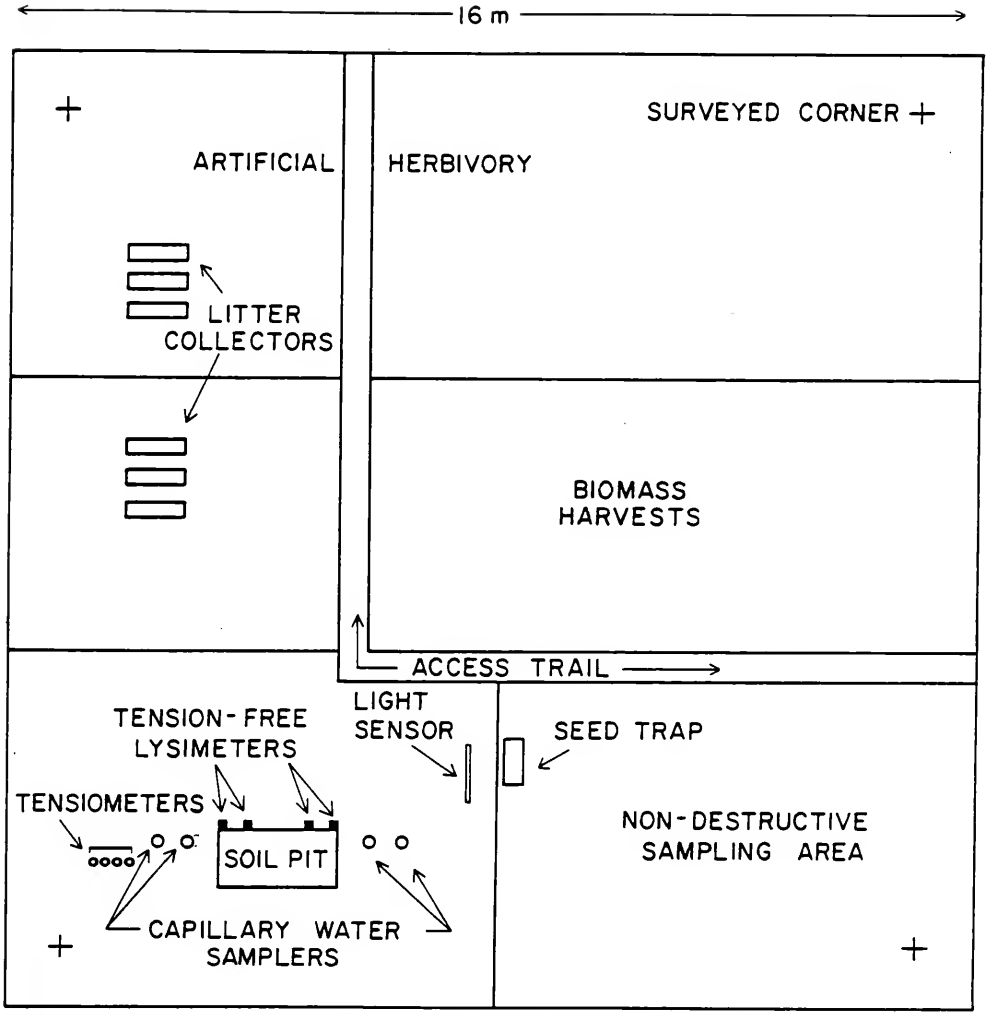


Figure 3. Diagram of study plot.

Measurements of Vegetation Structure

Leaf Area Index

Leaf area index (LAI) is defined as leaf area per unit ground area. Values are usually reported as m^2 of leaf tissue (one side of leaf) per m^2 of ground. In this study LAI was measured using a plumb-bob method similar to the method used by Benedict (1976). A thin line is lowered vertically from the top of the vegetation canopy to the ground and the number of leaves touching the line is counted. This method reduces the sampling area to a single point, and the number of leaves above a point (i.e., the number of intersections of line and leaf) is a direct measure of LAI. The intersections were recorded by species and height above the ground.

The instrument used to measure LAI was constructed from a rigid extendable metal rod. A fishing reel was connected at its base and a pulley at the tip. A thin nylon twine attached to the rod with a small weight at its end could then be easily lowered vertically through the vegetation. The twine was knotted at 25 cm intervals, and alternate intervals were painted for easy reading in the field. This instrument could be used in vegetation up to 8 m in height. In taller vegetation, it was necessary in a few cases to estimate the number of leaves above the rod.

Leaf area index measurements were made in all main plots during May 1979, July 1979, November 1979, April 1980, and

October 1980. In May 1979, 20 LAI measurements were made in each study plot of each replication. Five locations were chosen randomly in each plot, and four LAI readings were taken at each location by dropping the line vertically through the vegetation four times. For all other sample dates, 30 LAI measurements were made in each plot. Ten 1 m^2 quadrats were systematically located in each plot and permanently marked. Three LAI measurements were made in each of these quadrats on each date.

The uniform spacing of crop plants in rows created special problems in use of the plumb-bob method to measure LAI, especially in systems with very low LAI. For this reason, LAI of the maize monoculture in November 1979 was calculated using leaf biomass/leaf area regressions rather than by using the plumb-bob method.

Species data from the leaf area measurements were used to calculate LAI for individual species, and percent of total LAI was used as an estimate of relative species dominance.

Species Composition

Species inventories were done in the natural succession, enriched succession, and mimic plots during July 1979, November 1979, April 1980 and October 1980. For each plot a list was made of all flowering plants and ferns encountered in each of the ten 1 m^2 quadrats described above. From these data, diversity indices were calculated. In addition,

a complete species inventory was made in each 16 x 16 m^2 plot in October 1980. Plant specimens were identified at the National Museum of Costa Rica.

Vegetation Height

At the same time that the species composition and LAI measurements were made, the height of the tallest plant in each of the ten 1 m^2 quadrats in each plot was measured. Average canopy height for each plot was then calculated. Also, the species and height of the tallest plant in the entire 16 x 16 m^2 plot was recorded.

Productivity Measurements

Net primary productivity is one of the principal response variables that was used to compare the four experimental ecosystems. A common method for estimating net primary productivity is by using periodic biomass measurements to calculate changes in standing crop over time. However, in fast-growing tropical successional vegetation, the measurement of changes in living biomass underestimates actual net primary production because of rapid turnover of plant parts and losses to herbivores during the time intervals between harvests. Litterfall and insect consumption are two losses of net productivity that cannot be measured by biomass harvests. In this study, measurements were made of plant mortality, rates of

litterfall, and rates of herbivory, in addition to periodic measurements of above-ground living biomass. The values obtained were used to estimate above-ground net primary productivity.

Mean rates of biomass increment (g m^{-2} day^{-1}) were estimated for intervals between biomass harvests as

$$B = \frac{B(i)-B(i-1)}{t(i)-t(i-1)} \qquad \text{Eq. 1}$$

where B(i) = above-ground living biomass at harvest(i) in g/m^2, B(i-1) = above-ground living biomass at harvest(i-1) in g/m^2, and t(i)-t(i-1) = number of days between biomass harvests. These rates were plotted at the mid-points of the intervals between harvests, and the points were connected by straight lines. Linear regressions were then used to estimate daily biomass increments.

Increments of standing dead biomass (g m^{-2} day^{-1}) were estimated as

$$D = \frac{D(i)-D(i-1)}{t(i)-t(i-1)} \qquad \text{Eq. 2}$$

where D(i) = standing dead biomass at harvest(i) in g/m^2, D(i-1) = standing dead biomass at harvest(i-1) in g/m^2, and t(i)-t(i-1) = number of days between harvests. As above, the rates were plotted at the mid-points of the intervals

between harvests, the points were connected by straight lines, and linear regressions were used to estimate daily increments in standing dead biomass. The turnover rate of standing dead biomass was not known. The conservative assumption was made that turnover was negligible. Positive daily increments in the standing dead biomass category were used as estimates of daily production of standing dead biomass. If the turnover rate was high, production of standing dead and net primary productivity would both be underestimated by these methods.

Litterfall rates (g m^{-2} day^{-1}) were estimated for each ecosystem as

$$L = \frac{L(i)}{t(i)-t(i-1)} \qquad \text{Eq. 3}$$

where $L(i)$ = amount of litter collected during a 4 wk interval (g/m^2), and $t(i)-t(i-1)$ = number of days in interval. These rates were plotted at the mid-points of the intervals, the points were connected by straight lines, and linear regressions were used to estimate daily litterfall rates.

Daily herbivory rates for each ecosystem were estimated from three 1 mo sampling periods. Linear regressions were used to estimate daily herbivory rates.

Daily net primary productivity rates were calculated as

$$NPP(i) = b(i) + l(i) + h(i) + d(i) \qquad \text{Eq. 4}$$

where NPP(i) = net above-ground productivity on day(i) in g m^{-2} day^{-1}, b(i) = biomass increment on day(i) in g m^{-2} day^{-1}, l(i) = litterfall on day(i) in g m^{-2} day^{-1}, h(i) = herbivory rate on day(i) in g m^{-2} day^{-1}, and d(i) = production of standing dead biomass on day(i) in g m^{-2} day^{-1}.

Above-Ground Biomass

Immediately after the burn, randomly located subplots were marked with string and metal stakes in the area of each study plot designated for biomass harvests. Fourteen biomass harvests were made during the 1.5 yr study period. Early harvests in the natural succession, enriched succession, and mimic of succession were done at frequent intervals (approximately bi-weekly) on small (0.24 m^2) plots, and later harvests were at less frequent intervals on larger plots. Dates and plot sizes for each of the harvests were 14 May 1979, 31 May-5 June 1979, 20 June 1979, 9-10 July 1979 (0.24 m^2); 1-2 August 1979, 10-12 September 1979, 8-10 October 1979, 19-21 November 1979, 17-19 December 1979, 21-23 January 1980 (1.60 m^2); 17-19 March 1980, 19-21 May 1980, 8-11 July 1980, 28-31 October 1980 (4.00 m^2). At the time of each harvest, one randomly selected subplot was harvested in each study plot (total number of subplots harvested per treatment = 6).

It was decided that the harvest of individual plants and plant density data, rather than the harvest of vegetation in random subplots, would yield better estimates of biomass in the monoculture treatment where plants were uniformly spaced. Therefore, from one to four randomly chosen plants of the monoculture species were harvested per plot at each sampling date. Harvests of the monoculture were made at each date listed above. Additional harvests were made at crop maturity (29 October 1979 and 10-12 September 1980) and during the early growth stage of the second maize monoculture (16 August 1979). At maturity of each monoculture, samples of the harvestable crop were used to estimate economic yield.

Above-ground biomass was harvested by clipping all vegetation within subplot boundaries at ground level. All plants rooted inside the plot were included, even if parts of the plant extended outside the sample area. Likewise, all plants rooted outside the plot were excluded. Vines were clipped at the plot boundary. The vegetation from each plot was separated into four classes: leaves, stems, reproductive parts, and standing dead. Vegetation samples were weighed in the field. Subsamples of each vegetation class were taken to the laboratory, weighed to the nearest 0.1 g, dried to a constant weight at 70° C, and reweighed to obtain fresh to dry weight conversions.

Data for each vegetation component (leaves, stems, reproductive parts and standing dead) and total above-ground biomass were analyzed using a randomized complete block, fixed effects statistical model with four treatments and six blocks (replications). The biomass data did not meet the homogeneity of variance assumption of analysis of variance. Means and variances were not independent; in most cases, variance was proportional to the square of the mean. The biomass data were transformed using the following log transformation: $y=\ln(x+1)$. All analyses of variance and Duncan's multiple range tests were done on the transformed data, using the General Linear Models (GLM) program of the Statistical Analysis System (SAS). Reported means and standard deviations are of original untransformed data.

Litterfall

Three 0.25 m^2 litter collectors were located near the soil surface in each replicate of each treatment. Each collector was 1.00 x 0.25 x 0.15 m (length x width x height) and was supported approximately 2 cm above the soil surface by metal brackets. The collectors had wooden sides and fine-mesh screen bottoms for drainage. The shape and small size of the collectors allowed the successional vegetation to grow up and over the collectors rapidly.

The collectors were positioned 1 m from the access trail in the portion of each plot designated for litterfall

studies (see Plot Map, Fig. 3). Litter was collected from the baskets at 2 wk intervals throughout the 1.5 yr study period. The litter from the three collectors in each plot was combined into one composite sample, oven dried at 70° C to a constant weight, and weighed to the nearest 0.1 g.

The baskets collected both autochthonous and allocthonous litter inputs to the plots. To calculate net primary productivity of the vegetation in the plots, a measure of autochthonous litter production was needed. Allocthonous inputs were estimated from a single collector (0.25 m^2) placed near the other three collectors in each monoculture plot. For each of these 'control' baskets, leaves of the monoculture species in the basket at each sampling date were discarded. All other material in the basket was collected, dried and weighed.

Herbivory Rates

Losses of plant tissue due to herbivory were estimated by monitoring amounts of damage incurred on tagged leaves of dominant species in each treatment. It was not possible to separate losses due to plant diseases (fungal, viral, bacterial) from losses to herbivorous insects, so loss estimates include damage due to plant diseases as well as losses to herbivores.

At each of three sampling periods (October 1979, February 1980, and June 1980) the most recent LAI data were used to

select the species to be tagged. The species of each treatment were ranked from highest to lowest LAI, and those more common species that jointly accounted for at least 80 percent of the total LAI of that treatment were selected for herbivory measurements.

In the portion of the study plots designated for non-destructive sampling, five plants of each species (three in insecticide plots) were arbitrarily chosen for tagging. Usually no more than one individual of each species was tagged per replication. In a few cases, patchy distribution of a species made it necessary to tag more than one individual of that species within a single replication.

A plant stem was considered eligible for tagging if it was unbroken, unbranched, and bore at least four leaves. One eligible stem was chosen on each plant. From four to eight consecutive leaves were selected along the stem, and these individual leaves were numbered from youngest to oldest. Small plastic bands marked with yellow tape were looped around the stem at two places. Positions of leaves relative to these bands were used to identify individual leaves at the time of harvest. When the leaves were tagged, the holes present in each leaf were measured by placing a sheet of mm-ruled graph paper under the leaf and counting the uncovered squares. Brown spots on each leaf were estimated visually, and total damage (holes + brown spots) was recorded for each leaf.

The length of each leaf was measured to the nearest mm at the time of tagging. Leaf length/leaf area regressions for each species (developed from a sample of at least 50 leaves per species) were used to estimate the initial leaf area of each leaf (Table 1). For each species, the best curve fit was obtained by using a quadratic equation for all but very small leaves, and a linear equation through the origin for very small leaves. These initial leaf area estimates, together with direct measurements of leaf area at the time of harvest, were used to estimate leaf expansion during the interval. In grasses and some herbaceous species with small leaves (mature leaves <40 cm in length), leaf lengths were not measured, and leaf expansion was not estimated.

After 3 to 7 wk, the tagged leaves and all new leaves produced on the marked stems during the interval were harvested. Mortality of tagged leaves and number of new leaves were recorded for each plant. In the laboratory, the area of damage on each leaf was traced on a sheet of clear plastic and filled in using a permanent black marking pen. Two categories of damage, holes (H) and brown spots (B), were drawn separately. All missing tissue, plus damage that left only a transparent layer of leaf tissue, was recorded as holes. All other damage, including damage by leaf-mining insects, damage by rasping insects, fungal and viral damage, plus the necrotic tissue around holes, was recorded as brown spots.

Table 1. Leaf length:leaf area regression equations for common species. In the equations, x = leaf length in mm and y = leaf area in cm^2.

Species	Regression Equations	R^2
Bocconia frutescens	$x>125$: $y=0.00203x^2 + 0.303x - 47.779$ $x\leq125$: $y=0.174x$	0.96**
Borreria laevis	$x>24$: $y=0.000856x^2 + 0.0667x - 0.927$ $x\leq24$: $y=0.0469x$	0.95**
Cajanus cajan	$x>23$: $y=0.00431x^2 + 0.0475x - 1.909$ $x\leq23$: $y=0.0624x$	0.97**
Carica papaya	$x>81$: $y=0.0172x^2 - 1.837x + 56.231$ $x\leq81$: $y=0.249x$	0.92**
Clibadium aff. surinamense	$x>58$: $y=0.00440x^2 - 0.228x + 6.995$ $x\leq58$: $y=0.147x$	0.97**
Cordia inermis	$x>34$: $y=0.00318x^2 - 0.101x + 1.895$ $x\leq34$: $y=0.0624x$	0.98**
Crotalaria micans	$x>22$: $y=0.00637x^2 + 0.0803x - 3.050$ $x\leq22$: $y=0.0772x$	0.98**
Cucurbita pepo	$x>32$: $y=0.0124x^2 - 0.0163x - 6.809$ $x\leq32$: $y=0.149x$	0.99**
Canavalia sp.	$x>53$: $y=0.00473x^2 + 0.289x - 20.419$ $x\leq53$: $y=0.148x$	0.97**
Erythrina costaricensis	$x>171$: $y=0.00913x^2 - 1.061x + 82.992$ $x\leq171$: $y=0.980x$	0.95**
Frantzia pittieri	$x>77$: $y=0.0115x^2 - 0.573x + 27.339$ $x\leq77$: $y=0.661x$	0.90**
Hyptis suaveolens	$x>19$: $y=0.00361x^2 + 0.0633x - 1.042$ $x\leq19$: $y=0.0731x$	0.99**
Hyptis vilis	$x>10$: $y=0.00402x^2 - 0.0148x + 0.339$ $x\leq10$: $y=0.0591x$	0.97**
Ipomoea batata	$x>29$: $y=0.00655x^2 + 0.201x - 7.644$ $x\leq29$: $y=0.125x$	0.95**

Table 1--continued.

Species	Regression Equations	R^2
Ipomoea sp.	$x>28$: $y=0.0117x^2 - 0.341x + 4.392$ $x\leq 28$: $y=0.142x$	0.97**
Iresine diffusa	$x>30$: $y=0.00445x^2 - 0.110x + 2.373$ $x\leq 30$: $y=0.101x$	0.98**
Manihot esculenta	$x>51$: $y=0.0117x^2 - 0.784x + 25.038$ $x\leq 51$: $y=0.303x$	0.87**
Merremia tuberosa	$x>53$: $y=0.00733x^2 - 0.0228x - 10.987$ $x\leq 53$: $y=0.152x$	0.92**
Phaseolus vulgaris	$x>60$: $y=0.0135x^2 - 0.960x + 29.925$ $x\leq 60$: $y=0.344x$	0.98**
Phytolacca rivinoides	$x>31$: $y=0.00267x^2 + 0.0271x - 1.290$ $x\leq 31$: $y=0.0666x$	0.97**
Solanum jamaicense	$x>50$: $y=0.00748x^2 - 0.227x - 2.224$ $x\leq 50$: $y=0.0989x$	0.98**
Solanum torvum	$x>26$: $y=0.00352x^2 - 0.00506x - 0.522$ $x\leq 26$: $y=0.063lx$	0.98**
Solanum umbellatum	$x>50$: $y=0.00125x^2 + 0.117x - 6.52$ $x\leq 50$: $y=0.0473x$	0.98**
Vernonia patens	$x>40$: $y=0.00154x^2 + 0.221x - 8.702$ $x\leq 40$: $y=0.0610x$	0.91**
Vigna sp.	$x>47$: $y=0.00568x^2 - 0.0873 - 0.388$ $x\leq 47$: $y=0.169x$	0.92**

**$p<.01$

The leaf remnants and plastic sheets were run through a Lambda Instruments LI-COR (LI-3000) area meter, which measures the surface area of opaque surfaces to the nearest 0.01 cm^2 with an accuracy of $\pm$ 1%. In a few cases, leaves from a plant were processed as a group rather than individually.

For each leaf (or group of leaves), total damage present, D(t(f)), and gross leaf area, G(t(f)), at the time of harvest were calculated as

$$D(t(f)) = H + B \qquad \text{Eq. 5}$$

and

$$G(t(f)) = R + H \qquad \text{Eq. 6}$$

where t(f) = time of leaf harvest, H = holes present at t(f), B = brown spots present at t(f), and R = residual leaf area at t(f).

Herbivory rates (i.e., loss of leaf tissue per unit area of leaf per unit time) were calculated for each leaf of each species. Two factors contribute to the total loss due to herbivory: (1) actual consumption by herbivores and (2) loss of potential photosynthetic leaf area due to expansion of damaged areas after consumption has occurred. Since the rate of expansion of holes in a leaf is equal to the rate of expansion of the leaf (Reichle et al. 1973, Coley 1980), estimates of percent consumption are not affected by leaf

expansion during the sampling interval. Percent consumption (LOSS) was estimated for individual leaves by the following equation:

$$LOSS = \left[\frac{D(t(f))}{G(t(f))} - \frac{D(t(0))}{G(t(0))} \right] \times \frac{10000}{t(f) - t(0)} \qquad \text{Eq. 7}$$

where $D(t(i))$ = damage present at $t(i)$, $G(t(i))$ = gross leaf area at $t(i)$, $t(0)$ = time of leaf tagging, and $t(f)$ = time of leaf harvest. An absolute consumption rate was then calculated for each species by multiplying mean percent consumption of the species by LAI of the species.

The area of 50 leaves of each species was measured using the LI-COR (LI-3000) area meter. The leaves of each species were pooled, oven dried to constant weight at 70° C, and weighed. Leaf specific mass (mass per unit area of leaf) was then calculated so that herbivory rates could be expressed on a mass basis as well as on an area basis.

Three non-parametric statistics (Wilcoxon 2-sample rank sums test, Kruskal-Wallis test, and median test) were used to test for differences in herbivory rates between ecosystems for several plant species. These statistical procedures make no assumptions about the distribution of the data, but do require homogeneity of variance. The level of significance of ordinary 2-sample procedures is not preserved if the variances of the two populations differ (Pratt 1964). The robustness of the tests under departure

from the assumption varies with test used, sample size of the populations, and magnitude of departure from the assumptions. The homogeneity of variance assumption was not met by the herbivory data. In general, means and variances were proportional; large variances were associated with large means, and small variances with small means. Therefore the levels of significance associated with test results are not exact.

Estimation of Hole Expansion

For those species in which initial leaf area was estimated (using regression equations), it was possible to estimate the loss of potential photosynthetic leaf area due to expansion of the holes in leaves. The mathematical equation derived to estimate consumption and expansion is based on three assumptions: (1) the damage expansion rate equalled the leaf expansion rate; (2) the consumption rate was constant during the time interval in which herbivory was monitored; and (3) for a group of leaves on a single stem, leaf growth rate was a constant function. The validity of each of these assumptions is discussed below.

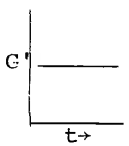
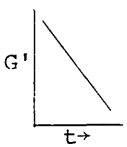
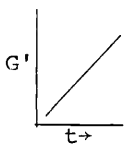
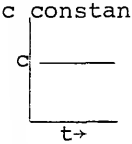
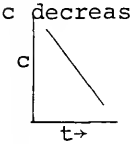
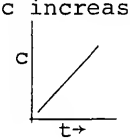
The first assumption (that hole expansion rate = leaf expansion rate) is generally assumed to be valid and has been verified experimentally by Reichle et al. (1973) for a temperate deciduous forest species (Liriodendron tulipifera) and by Coley (1980) for several tropical forest species. In

an unpublished study of a common successional species (Conostegia pittieri) in a tropical premontane wet forest at Monte Verde, Costa Rica, I found that hole expansion rate and leaf expansion rate did not differ significantly (n = 70 leaves).

Although herbivory on individual leaves does not occur at a constant rate, the rate of damage accumulation may be assumed to be constant for a population of leaves (assumption 2). Likewise, although the growth curve of an individual leaf is probably sigmoidal rather than linear, the average leaf growth rate of a population of leaves of varying ages may remain constant over time (assumption 3). Although these assumptions seem intuitively reasonable, they have not been verified experimentally.

If the assumptions are not met, bias is introduced into the estimation of the relative proportion of the total herbivory loss attributable to consumption and expansion. The results of several types of possible deviations from assumptions 2 and 3 are presented in Table 2. If consumption rate (c) and leaf growth rate (G') are both constant, then assumptions 2 and 3 are met, and the method used in this study accurately estimates percent of total damage due to consumption and expansion. If c and/or G' are increasing or decreasing functions, losses due to expansion (e) may be overestimated or underestimated by the methods used in this study.

Table 2. Comparison of estimated (e*) and actual (e) losses due to expansion, for several consumption rate (c) and leaf growth rate (G') functions; t = time.

	Case 1 (G' constant) 	Case 2 (G' decreasing) 	Case 3 (G' increasing) 
Case 1 (c constant) 	e*=e	e*>e	e*<e
Case 2 (c decreasing) 	e*<e	?	e*<e
Case 3 (c increasing) 	e*>e	e*>e	?

Using the assumptions listed above, percent consumption rate (c) and percent expansion rate (e), both in $cm^2\ m^{-2}\ day^{-1}$, were estimated for each plant by the following equations:

$$c = \frac{D(t(f)) - \left[D(t(0)) \dfrac{G(t(f))}{G(t(0))}\right]}{\dfrac{m}{n} + m \sum_{i=1}^{n-1} \dfrac{1}{n - i(1-r)}} \times \frac{10000}{G(t(f))} \qquad \text{Eq. 8}$$

$$e = \frac{D(t(f)) - D(t(0)) - (c \times m)}{m} \times \frac{10000}{G(t(f))} \qquad \text{Eq. 9}$$

where $t(0)$ = time of leaf tagging, $t(f)$ = time of leaf harvest, $m = t(f) - t(0)$ = number of days leaves were tagged, $D(t(0))$ = damaged area at $t(0)$ in cm^2, $D(t(f))$ = damaged area at $t(f)$ in cm^2, $G(t(0))$ = gross leaf area at $t(0)$ in cm^2, $G(t(f))$ = gross leaf area at $t(f)$ in cm^2, $r = G(t(0))/G(t(f))$, and n = the number of sub-intervals $(t(j-1), t(j))$ into which the time interval $(t(0), t(f))$ is divided. The derivation of Equation 8 is given in Appendix A.

In the equation above, $D(t(0))$, $D(t(f))$, $G(t(0))$, and $G(t(f))$ are totals of all tagged leaves on a given plant, excluding tagged leaves that died during the interval and

new leaves produced during the interval. Calculations of losses due to hole expansion were made using plant totals rather than individual leaf data for two reasons. (1) The precision of the regression estimates of initial leaf areas was not high enough to allow individual leaf expansion to be estimated. Although the leaf length/leaf area regressions for most species were quite good ($R^2 > 0.94$ for 19 of 25 species, Table 1), in some cases overestimates of initial leaf area led to negative leaf growth rates for individual leaves during the interval. (2) The assumption that leaf growth was a constant function is better fit by groups of leaves of varying ages than for individual leaves.

The herbivory rate calculated using plant totals is mathematically equivalent to the mean of the herbivory rates calculated for individual leaves if all of the leaves are equal in size; if damage area:leaf area is constant for all leaves (i.e., herbivory is evenly distributed among leaves); if the sums of damage area:leaf area are the same for groups of equal-sized leaves; or if total leaf areas are the same in groups of leaves with equal percent damage. None of the sufficient conditions listed for equality of the 2 methods are necessarily met by the data. Thus pooling individual leaf data for analysis may introduce a source of error. To evaluate the magnitude of the error, herbivory rates calculated from individual leaf data and from plant totals were compared for six species (Table 3). Although herbivory

Table 3. Comparison of mean consumption rates calculated from individual leaf data and from pooled leaf data for selected species.

Species	No. of Plants (n)	Rate Based on Plant Totals (cm^2/m^2 leaf/day)	Rate Based on Individual Leaf Rates (cm^2/m^2 leaf/day)	Difference $\bar{D}$ (s_D)	Value of t
Bocconia frutescens	12	11.05	9.21	1.84 (5.76)	1.10
Cajanus cajan	8	32.15	13.33	0.82 (3.91)	0.59
Carica papaya	3	2.36	2.46	-0.10 (0.29)	-0.61
Manihot esculenta	36	8.90	11.07	-2.17 (5.12)	-2.54*
Phytolacca rivinoides	24	11.62	11.39	0.23 (2.45)	0.45
Vernonia patens	13	27.33	25.61	1.72 (3.48)	1.78

*$p<.05$

rates calculated by the two methods differed considerably for some plants, the two methods yielded significantly different mean species herbivory rates for only one species (*Manihot esculenta*).

Consumption rates were estimated by an iterative process in which the time interval (t(0),t(f)) was divided into n smaller sub-intervals (t(j-1),t(j)), and consumption and expansion were calculated for each of these sub-intervals. In this method, both the expansion of damage present on the leaves at t(0) and the expansion of damage that occurred during the interval (t(0),t(f)) were excluded from the estimate of consumption. As the number of iterations (n) was increased, the precision of the estimate of c also increased. To select an appropriate value of n, consumption rates were estimated using various n values for nine plants. For each of the plants, an n value of 55 was sufficiently large to insure that the consumption rates (cm^2 $plant^{-1}$ day^{-1}) were accurate to the nearest 0.01 cm^2. For most of the sample plants, the required n value for this level of accuracy was much less than 55. On the basis of these preliminary tests, calculations of damage expansion were done with n = 55. Computer programs to calculate damage expansion were developed using the Statistical Analysis System (SAS). One program was developed for use with alternate-leaved species. A modified version of this program was used for opposite-leaved species, in which data were pooled for opposite leaf pairs.

Subtreatments

In addition to main treatment comparisons, a major objective of the study was to evaluate the effects of herbivory on net primary productivity, vegetation structure, and species composition in high and low diversity tropical successional ecosystems. To do this, comparisons were made between high diversity systems (natural succession and enriched succession) and low diversity systems (maize and cassava monocultures) at three levels of herbivory: (1) background or naturally occurring level, (2) decreased level of herbivory, and (3) increased level of herbivory.

Background Herbivory

Rates of herbivory naturally occurring in the enriched succession, the natural succession, and the monocultures were measured using the methods described earlier (Chapter II, 'Herbivory rates'). Net primary productivity and vegetation structure measurements in these treatments provided baseline data for comparison with plots experiencing artificially induced high and low levels of herbivory.

Decreased Herbivory

To compare high and low diversity systems experiencing low herbivore pressure, three auxiliary plots of the enriched succession and the monoculture were maintained at

lower than normal levels of herbivory by use of insecticides.

Each insecticide study plot was 4.5 x 14 m, with a border strip approximately 0.5 m wide around each plot. The two plots in each replication were separated by a 1 m wide access trail. The insecticide plots were separated from the main plots by strips of uncut vegetation at least 5 m wide, and were located such that other study plots would not be contaminated with insecticide residues through runoff and/or drainage. Within each plot, specific areas were designated for biomass harvests and for non-destructive sampling such as litter collection and herbivory measurements.

In all insecticide plots, above-ground plant parts were sprayed with Diazinon, a broad spectrum insecticide. Diazinon is a short-lived organophosphate with few phytotoxic effects that is effective against most sucking and chewing insects. The plots were sprayed weekly during the dry season and twice-weekly during the rainy season, using a backpack sprayer. Diazinon powder (25% active ingredient) and Pegafix (a wetting agent that increases adhesion of the insecticide to leaf surfaces) were mixed with water (1 ml Diazinon and 1.5 ml Pegafix per liter of water), and plants were sprayed until thoroughly wetted.

Aldrin, a persistent chlorinated hydrocarbon effective against root-feeding insects, was applied to the soil in the insecticide plots twice yearly at the rate of 10 kg active

ingredient per ha. Dates of Aldrin application were 31 March 1979, 1 November 1979, and 26 May 1980.

Small ditches (25 cm wide and 10 cm deep) were dug around the insecticide plots and sprinkled with 25% Aldrin powder approximately every 2 mo to prevent leaf-cutter ants (Atta cephalotes) from entering the plots. These channels were kept clear of fallen leaves and twigs that might act as passageways for ants. No leaf-cutter activity was observed in the insecticide plots.

All vegetation structure and productivity measurements made in the main treatment plots were also made in the insecticide plots. Species present in four systematically located, permanently marked 1 m^2 quadrats per plot were recorded at four sampling dates during the study period. Three LAI measurements were made in each quadrat (total number of LAI measurements per plot = 12) at each sampling date, and vegetation height was measured in each of the four quadrats at each date. Three litter collectors were placed in each plot. Litter collections, biomass harvests, and herbivory measurements were made at the same frequency and using the same methods as in the main treatments.

Increased Herbivory

To study the relative abilities of simple and complex systems to respond to high levels of insect attack, artificial defoliation experiments were performed in the

natural succession, enriched succession, and monoculture treatments.

A preliminary series of defoliations was performed in October 1979. Defoliations were done in designated 4.5 x 14 m subplots in replications 2, 5, and 6 of the enriched succession and the maize monoculture. Approximately 50% of the total leaf area on each plot was removed, by clipping (at the petiole) alternate leaves along each stem. Leaf tissue removed was weighed in the field, subsampled, and returned to the plots. Three leaf subsamples (approximately 0.5 kg each) from each plot were taken to the laboratory, weighed to the nearest 0.1 g, dried to constant weight at 70° C, and reweighed to determine fresh to dry weight conversions. Biomass harvests were made before the defoliation (May-September 1979), for 8 mo after defoliation in the enriched succession (October 1979-May 1980), and until the maize harvest (November 1979) in the monoculture.

A second defoliation study was carried out during April-June 1980 in replications 1, 2, and 3 of the natural succession and the cassava monoculture. Defoliation plots were 4.5 x 9.5 m, and defoliation techniques were the same as those used in the pilot study. In this study, a series of three defoliations was performed at 4 wk intervals. At each defoliation, approximately 50% of the total leaf area of each plot was removed.

Rate of recovery of leaf area, as measured by changes in LAI after defoliation, was the response variable used to compare the high and low diversity systems in the second defoliation study. The LAI measurements were made in each of the defoliation plots at the following times: (1) immediately before each of the three defoliations, (2) immediately after each of the three defoliations, and (3) after 2 wk of regrowth following each defoliation. The LAI measurements were made from 15 equally-spaced locations along the perimeter of each plot, five measurements per location (total per plot = 75). The LAI measurements were recorded by species and height above the ground. The non-destructive sampling areas (see diagram of study plot, Fig. 3) in replications 1, 2, and 3 of the natural succession and the cassava monoculture were used as control plots for the second defoliation experiment, and LAI was measured in the control plots on the same dates that the defoliated plots were measured (15 sampling locations x 5 measurements per location = 75 LAI measurements per control plot).

CHAPTER III
RESULTS

Vegetation Structure

Seven factors related to vegetation structure and species composition were estimated in each of the four experimental ecosystems: species richness, species evenness, overall species diversity, relative species abundance, species changes through time, leaf area index, and vertical leaf distribution. Based on these measurements, the natural succession and enriched succession were structurally very similar; the mimic, although similar in many ways to the natural succession, had several important structural differences; and the monoculture was completely dissimilar to the other ecosystems.

Species Composition

Species data from the LAI measurements were used to calculate species diversity, evenness, and rate of species turnover in the experimental ecosystems (Table 4). The number of species intersected by 180 LAI measurements was approximately equal in the natural and enriched succession at each date; fewer species were intersected in the mimic. Species richness increased during the study period in all

Table 4. Changes in number of species, diversity, and evenness in four ecosystems.

Characteristic	Vegetation Age (mo)	Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
Number of leaves intersected by 180 LAI measurements	3	734	788	321	153
	7	654	671	317	90[a]
	12	415	466	193	520[a]
	18	782	905	545	524[b]
Number of species intersected by 180 LAI measurements	3	37	35	10	1
	7	39	40	17	1
	12	36	39	15	1
	18	53	63	32	1
Number of species intersected both at 3 mo and 18 mo		26	21	6	0
Number of species gained from 3 mo to 18 mo		27	42	26	1
Number of species lost from 3 mo to 18 mo		11	14	4	1
Species diversity (H')[c]	3	1.02	1.04	0.88	0.00
	7	1.17	1.09	0.90	0.00
	12	1.15	1.04	0.58	0.00
	18	1.26	1.24	0.92	0.00
Evenness[d]	3	0.65	0.67	0.88	0.00
	7	0.73	0.68	0.73	0.00
	12	0.73	0.65	0.49	0.00
	18	0.73	0.69	0.61	0.00

Table 4--continued.

Characteristic	Vegetation Age (mo)	Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
Community similarity (C) between age 3 mo and age 18 mo[e]		0.41	0.60	0.15	0.00

[a]Not measured directly. Value estimated from leaf biomass data and leaf weight/leaf area regressions.

[b]September 1980 measurement (mature cassava).

[c]$H' = -\Sigma(n_i/N)\log(n_i/N)$, where n_i is the number of leaf intersections for species i, and N is the total number of leaves intersected (Shannon index).

[d]Evenness = H'/log S, where H' is Shannon diversity index and S is number of species.

[e]C = a(1) + a(2) +...+ a(i) +...+ a(n), where i is a species present at 3 mo and/or 18 mo, a(i) is the lesser percent LAI value for species i from the two dates, and n is the total number of species.

ecosystems except the monoculture. Species richness at 18 mo (based on a total inventory of all plots) was highest in the enriched succession (159 plant species present on 1536 m^2), followed by the natural succession (121 species), mimic of succession (82 species), and monoculture (1 species).

The Shannon diversity index (H') was calculated as a simple measure to compare overall diversity (richness and evenness) of the experimental ecosystems. An evenness index based on the Shannon index (evenness = H'/log S, where S is the number of species) was also calculated. The diversity index increased over time in the natural succession and enriched succession, but not in the mimic (Table 4). Diversity at 18 mo was higher in the natural succession and enriched succession (1.24 and 1.26 respectively) than in the mimic (0.92). Of the possible range of evenness values from 0 to 1, the values in the natural succession and enriched succession were approximately equal (from 0.65 to 0.73), with little change over time. Evenness values in the mimic were more variable (from 0.49 to 0.88).

The species composition of the natural succession and enriched succession was very similar early in succession (at 3 mo), but less similar at 18 mo. The natural succession and enriched succession had 86 species in common at 18 mo. Thirty-five of the species present in the natural succession at 18 mo were not present in the enriched succession. Seventy-three species were present in the enriched

succession but not in the natural succession, and of these at least 24 were investigator-introduced.

Some of the species differences between the natural and enriched succession may be due to random differences in seed availability of native species and to random micro-environmental differences among plots. However, at least 9% of the 264 species introduced into the enriched succession had become successfully established by the end of the study period. It was possible to increase species richness by propagule additions, and these data suggest that species richness was limited by propagule accessibility during the earliest stage of succession. This result may be a temporary phenomenon due to the stochastic nature of early succession (Webb et al. 1972, Horn 1974) and to the continuous rapid changes in vertical and horizontal plant distribution that allowed colonization by new species. Longer-term results of the study will verify whether or not the higher species richness of the enriched succession can be maintained.

To compare the degree of similarity in species composition between ecosystems, a community similarity index was calculated for each pair of ecosystems at four dates (Table 5). The index (Gleason 1920) was $C = a(1) + a(2) + \ldots + a(i) + \ldots + a(n)$, where i is a species present in at least one of the two ecosystems being compared, a(i) is the lesser percent LAI value from the two ecosystems for species

Table 5. Community similarity indices (C). Values are based on 180 LAI measurements per ecosystem on each date.

Date		Enriched Succession	Mimic of Succession	Monoculture
July 1979	Natural succession	0.66	0.00	0.00
	Enriched succession		0.01	0.00
	Mimic of succession			0.14
November 1979	Natural succession	0.68	0.00	0.00
	Enriched succession		0.06	0.00
	Mimic of succession			<0.01
April 1980	Natural succession	0.63	0.00	0.00
	Enriched succession		0.05	<0.01
	Mimic of succession			0.03
October 1980[a]	Natural succession	0.69	0.00	0.00
	Enriched succession		0.06	<0.01
	Mimic of succession			0.14

[a]September 1980 for monoculture.

i, and n is the total number of species present in the two ecosystems. C may range in value from 0 to 1. Community similarity was high between the natural succession and enriched succession. The values ranged from 0.66 to 0.69, with no significant change during the 18 mo period. Community similarity values for other pairs of ecosystems were 0 or very low, indicating little or no species overlap.

The natural succession and enriched succession were comprised of a few abundant species and many rare species Figs. 4 and 5). Most of the abundant species in the natural succession at 3 mo (July 1979) were also abundant in the enriched succession. Of the species individually accounting for $\geq$2% of total LAI in the natural succession (number of species = 9) and in the enriched succession (number of species = 9) at 3 mo, seven were common to the ecosystems (Table 6). By 18 mo (October 1980) the similarity in dominant species between the enriched succession and the natural succession had decreased. Of the 12 abundant species (those comprising $\geq$2% of total LAI) in the natural succession, only five were also abundant in the enriched succession. One of the abundant species in the enriched succession at 18 mo was an introduced species, plantain (Musa paradisiaca).

The species composition of each of the ecosystems changed during the 1.5 yr study period. The turnover of abundant species from 3 to 18 mo differed in the enriched succession

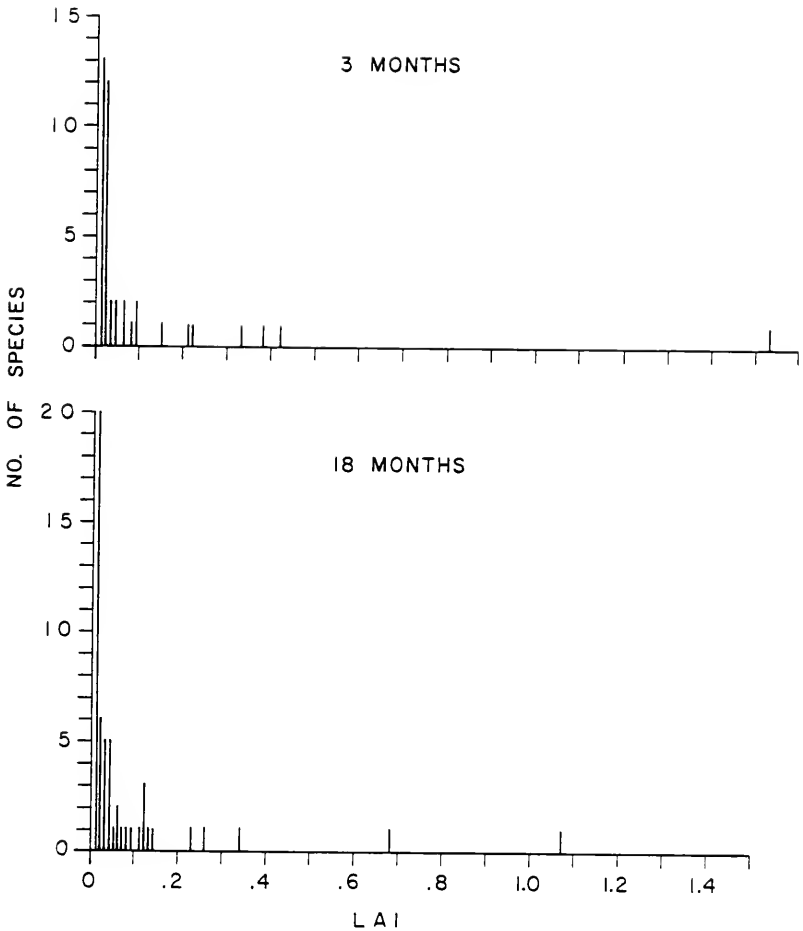


Figure 4. Number of species in the natural succession by LAI class. Values are based on 180 LAI measurements on each date.

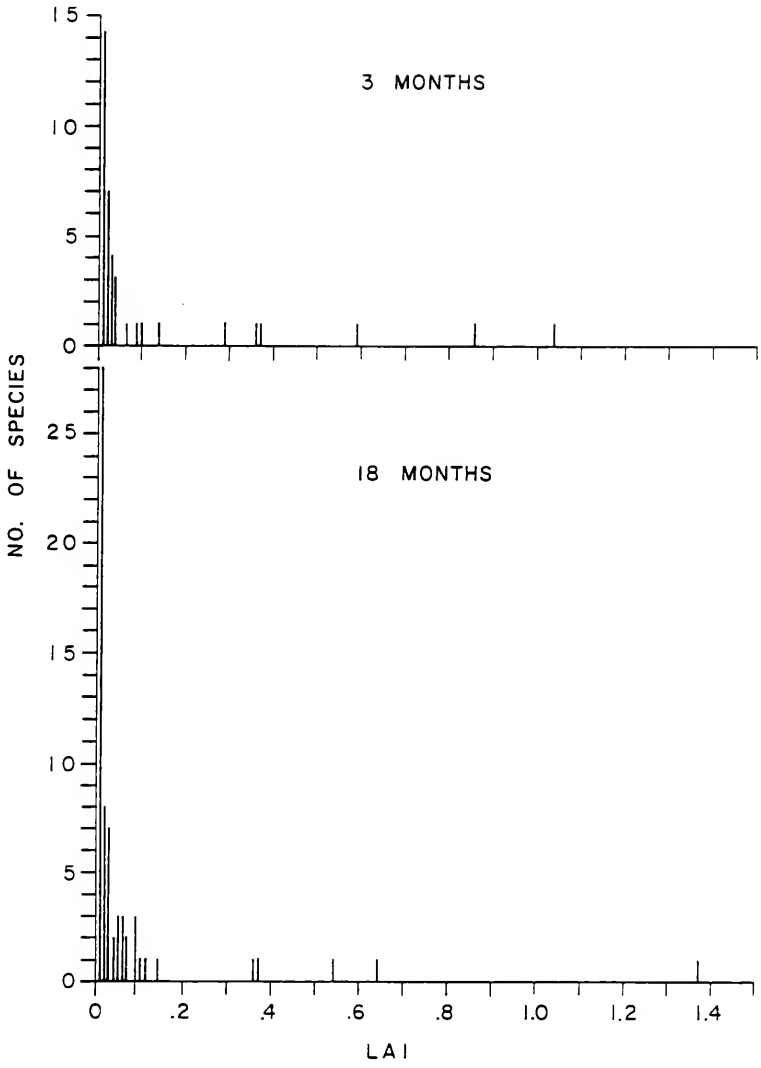


Figure 5. Number of species in the enriched succession by LAI class. Values are based on 180 LAI measurements on each date.

Table 6. Species accounting for ≥2% of LAI in four ecosystems. A dash (-) indicates that a species comprised <2% of ecosystem LAI.

Ecosystem			
Natural succession	Phytolacca rivinoides	37.5	-
	Momordica charantia	5.3	-
	Solanum nigrescens	2.3	-
	Borreria laevis	2.2	-
	Bocconia frutescens	10.4	15.7
	Clibadium aff. surinamense	9.4	7.8
	Gramineae[a]	8.2	6.0
	Panicum maximum	5.0	24.7
	Hymenachne amplexicaulis	3.7	2.8
	Trema micrantha	-	5.4
	Frantzia pittieri	-	3.3
	Acalypha macrostachya	-	3.1
	Cyperaceae[b]	-	2.7
	Panicum trichoides	-	2.7
	Vernonia patens	-	2.6
	Mikania sp.	-	2.2
Enriched succession	Phytolacca rivinoides	19.7	-
	Momordica charantia	6.7	-
	Solanum nigrescens	3.2	-
	Borreria latifolia	2.3	-
	Bocconia frutescens	13.6	10.8
	Clibadium aff. surinamense	8.2	7.2
	Gramineae[a]	8.4	12.8
	Panicum maximum	23.7	27.2
	Vernonia patens	2.2	7.3
	Ipomoea neei	-	2.9
	Musa paradisiaca	-	2.1
	Ipomoea sp.	-	2.0
Mimic of succession	Vigna sinensis	25.5	-
	Cucurbita pepo	17.4	-
	Phaseolus vulgaris	15.9	-
	Ipomoea batata	7.5	-
	Oryza sativa	5.0	-
	Cajanus cajan	4.0	-
	Zea mays	14.0	2.1
	Cymbopogon citratus	4.7	31.4
	Manihot esculenta	4.7	13.5
	Crotalaria micans	-	15.6
	Musa paradisiaca	-	3.5
	Hyptis suaveolens	-	2.9

Table 6--continued.

Ecosystem	Species	% of LAI	
		3 mo	18 mo
Monoculture	Zea mays	100.0	-
	Manihot esculenta	-	100.0

[a]Includes at least six species of grasses that were indistinguishable by vegetative parts.

[b]Includes at least four species of sedges that were indistinguishable by vegetative parts.

and the natural succession. Two woody species (Bocconia frutescens and Clibadium aff. surinamense) and two grass groups (Panicum maximum and a group of 10 grass species) were abundant in both ecosystems at 3 mo and 18 mo (Table 6). However, the enriched succession gained fewer new dominant species (Table 6), but more species overall (including all species encountered in the LAI measurements, Table 4) than did the natural succession from 3 to 18 mo. The community similarity index between the 3 mo old vegetation and 18 mo old vegetation was higher in the enriched succession (C = 0.60) than in the natural succession (C = 0.41). This is due both to the addition of fewer new dominant species and to smaller relative changes in species abundance over time in the enriched succession.

The 82 species present in the mimic plots at the time of the October 1980 species inventory represent 46% of the 178 species introduced into the mimic plots from March 1979 to October 1980. During the first 3 mo of succession, plant growth and structural development in the mimic of succession equaled or exceeded that of the natural succession. This was due primarily to the early and rapid development of herbaceous species (mainly cultivars) in the mimic. In subsequent months, development of the mimic was slower. At 18 mo, species richness and plant diversity were lower in the mimic than in the natural succession. In general, the mimic was much more similar structurally to the natural

succession than to the monoculture. The structural differences between the mimic and the natural succession indicate that (1) there was a time lag between the development of the natural succession and the development of the mimic, and/or (2) some of the species introduced into the mimic treatment, although morphologically similar to the native successional species, were not good functional mimics of the native species.

Large numbers of relatively uncommon species were present in the natural succession, but not in the mimic, at 3 mo (Figs. 4 and 6). This probably reflects the initial pattern of species introductions in the mimic by the investigators. This difference between the mimic and the natural succession elucidates an important characteristic of the natural succession that was difficult to imitate. The many rare species in the natural succession formed a pool of potentially important ecosystem components that could increase in dominance as microenvironmental factors and the competitive balance of the system changed. In managing the mimic ecosystem, anticipation of the types of species needed and introduction of such species at appropriate times to insure establishment and to maintain a pool of rare species was difficult.

Several structural characteristics of the mimic at 18 mo, including species abundance, were similar to characteristics of the natural succession and enriched succession at a much

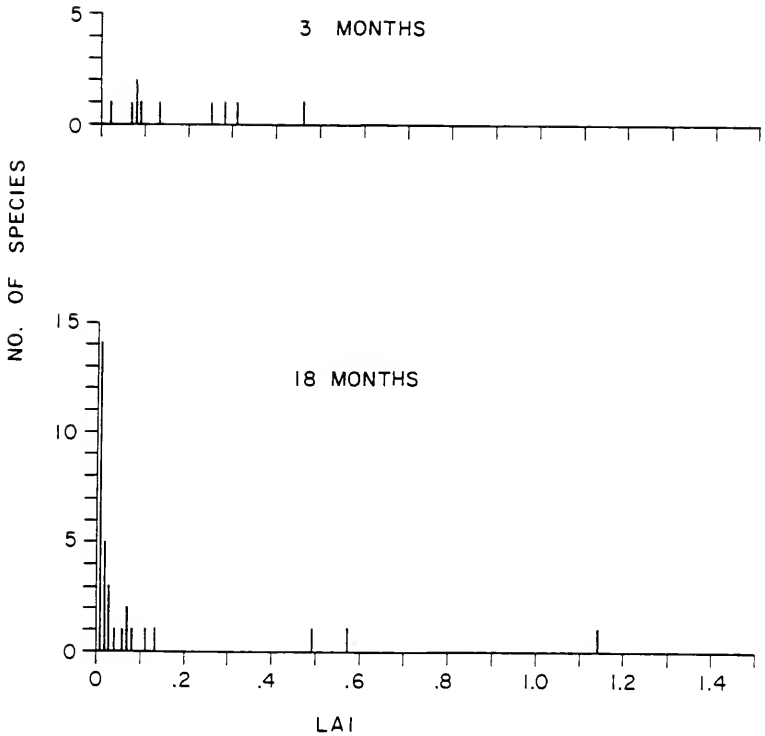


Figure 6. Number of species in the mimic of succession by LAI class. Values are based on 180 LAI measurements on each date.

earlier age (3 mo). The number of species intersected by LAI measurements in the mimic at 18 mo (32 species) is similar to the numbers intersected in the natural succession and enriched succession at 3 mo (37 and 35 species respectively). This indicates slower development of the 'investigator-controlled' treatment (the mimic) than of the 'nature-controlled' treatments (natural succession and enriched succession). For example, there was a time lag between the appearance of woody species in the natural succession and the selection and introduction of similar woody species in the mimic. It is expected that longer-term results will show convergence of structural characteristics of the mimic and natural succession.

The mimic of succession had higher turnover of species than the enriched or natural succession (Tables 4 and 6). The species composition of the 18 mo old mimic was very dissimilar to that of the 3 mo old mimic (C = 0.15). The July 1979 monoculture and the October 1980 monoculture had no species in common (C = 0.00). Changes in species composition in the monoculture were not gradual as in the other ecosystems; instead, composition changed completely as one monoculture species replaced another. If community similarity (C) is used as a measure of rate of species turnover in each ecosystem, with lower C values indicating greater changes in species composition during the first 18 mo of succession, then the systems may be ranked by

magnitude of change as follows: monoculture > mimic > natural succession > enriched succession.

Leaf Area Index

Leaf area index developed rapidly in both the natural succession and the enriched succession (Fig. 7). The LAI increased rapidly in all ecosystems during the first 2 mo, but thereafter was lower in the mimic than in the natural succession and enriched succession. Seasonal LAI fluctuations were similar in the natural succession, enriched succession, and mimic, with maximum values during the rainy season and minimum values during the dry season. Increase in LAI was rapid during the growth of the first maize monoculture (LAI = 1.22 at 2 mo), but leaf area development of the second maize crop was poor (maximum LAI = 0.5). Cassava LAI after 9 mo of growth (mean $\pm$ 1 s.d. = 2.9 $\pm$ 2.0) was not significantly different from LAI in the 7 mo old natural succession (3.7 $\pm$ 2.0). A decrease in LAI occurred during the dry season in the natural succession, enriched succession, and mimic. At 18 mo, mean LAI ($\pm$ 1 s.d.) was 4.4 $\pm$ 2.8 in the natural succession, 5.0 $\pm$ 3.4 in the enriched succession, and 3.6 $\pm$ 3.0 in the mimic.

Vertical distribution of leaf area was similar in the natural succession and enriched succession (Figs. 8 and 9), except in the lowest (0-25 cm) stratum. In this stratum near the ground LAI was consistently higher in the enriched

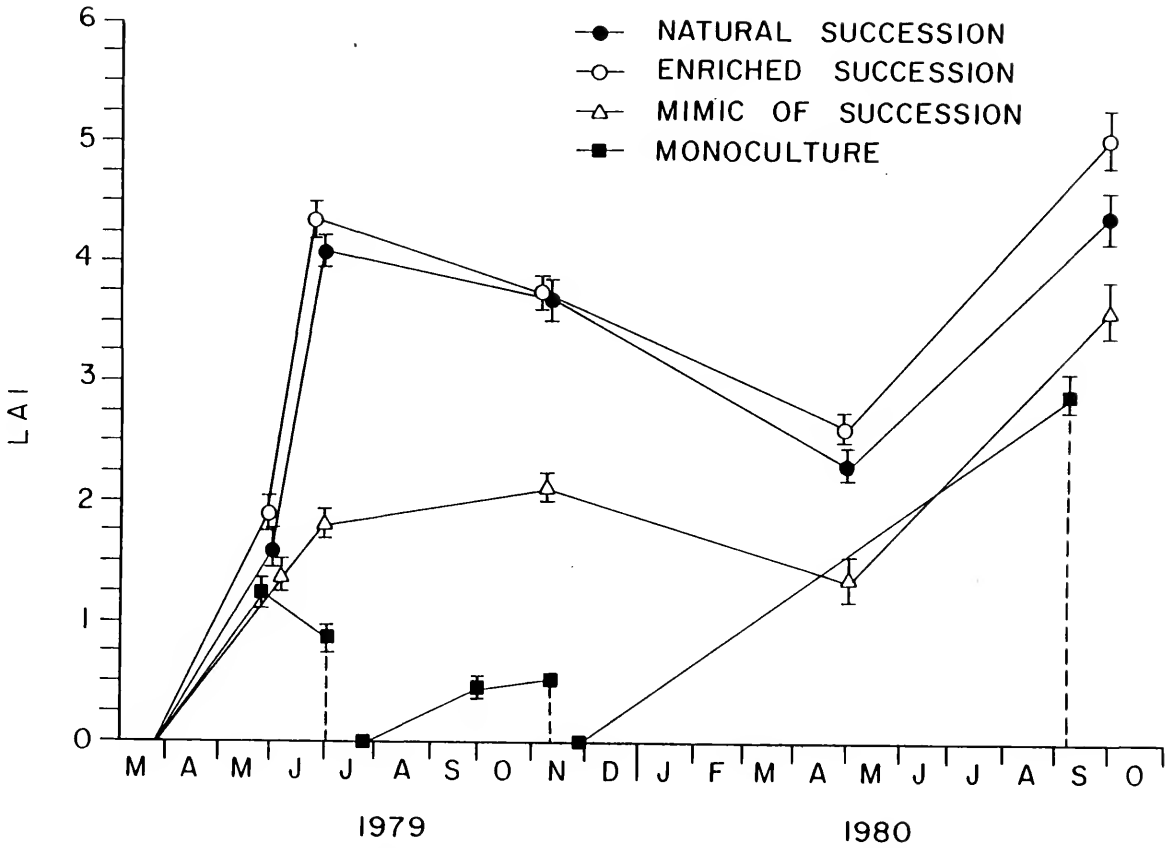


Figure 7. LAI in natural succession, enriched succession, mimic of succession, and monoculture. Values are $\bar{x} \pm 1$ s.e.

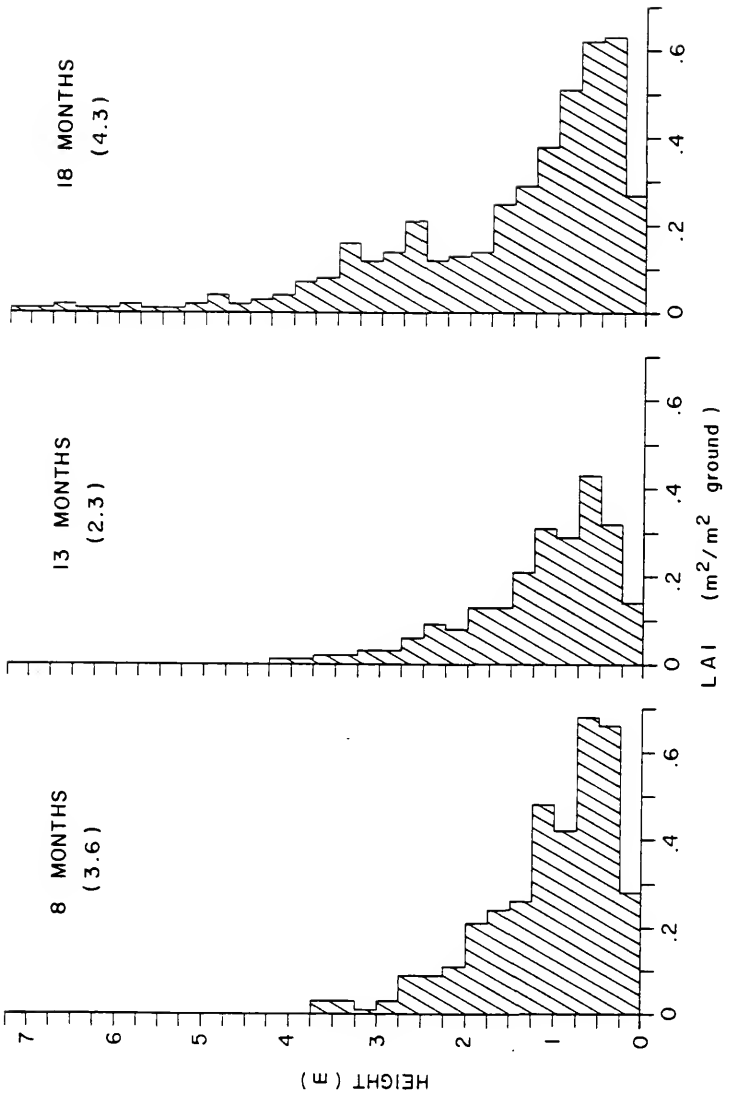


Figure 8. Vertical distribution of leaf area in the natural succession. Total LAI at each age is in parentheses.

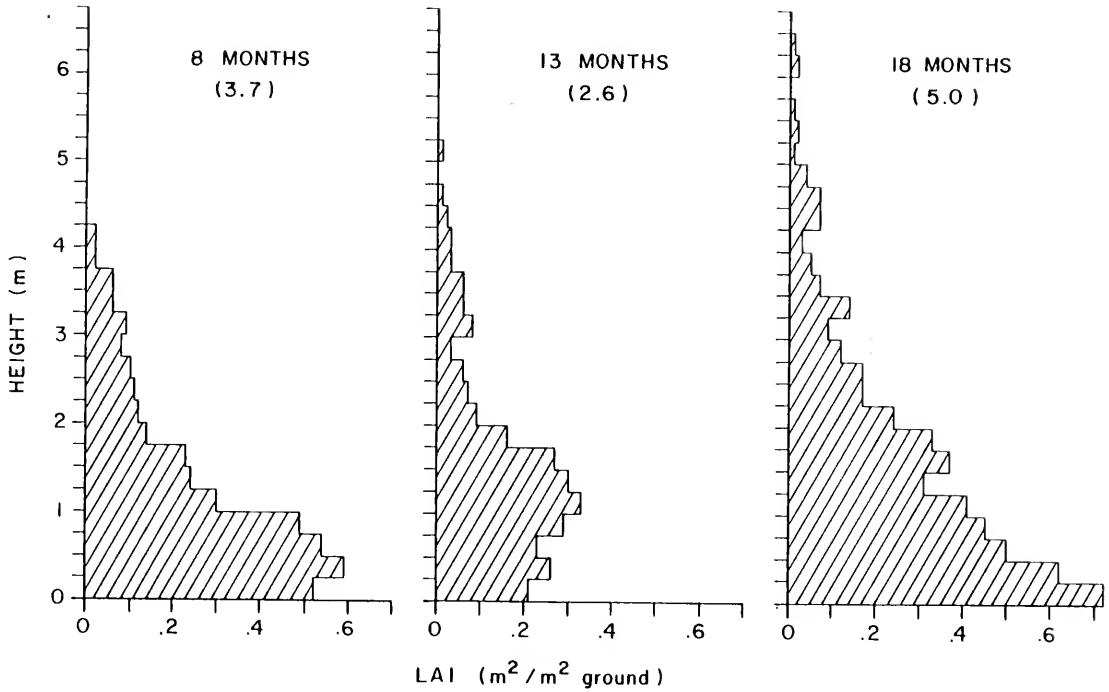


Figure 9. Vertical distribution of leaf area in the enriched succession. Total LAI at each age is in parentheses.

succession than in the natural succession. This may be due to the abundance of introduced propagules in the enriched succession, leading to increased numbers of seedlings. In the 0-25 cm stratum, 0%, 3.9%, and 6.5% of the LAI was comprised of introduced species at 8 mo, 13 mo, and 18 mo, respectively. The LAI in the mimic was concentrated <1 m from the soil surface at 8 mo and 13 mo, and leaf development higher in the canopy was patchy. By 18 mo the height of the canopy had increased in the mimic, although more than half the leaf area was still concentrated <1 m from the ground (Fig. 10). Vertical distribution of leaf area in the monoculture reflected the growth form of a single species rather than the interactions among a large array of species. In the mature cassava monoculture, leaf tissue was concentrated at 1-3 m above the ground (Fig. 11).

All ecosystems were characterized by rapid growth to an average canopy height of 3-4 m at 18 mo (Fig. 12). The natural succession and enriched succession contained some emergent plants with heights of up to 10.8 m at 18 mo (Table 7).

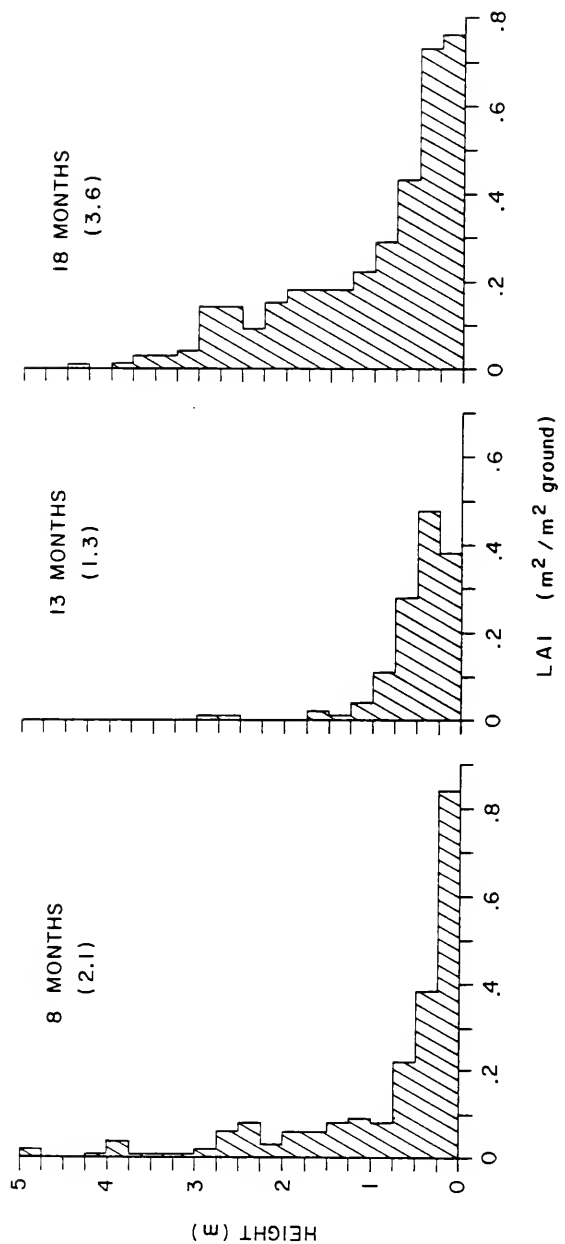


Figure 10. Vertical distribution of leaf area in the mimic of succession. Total LAI at each age is in parentheses.

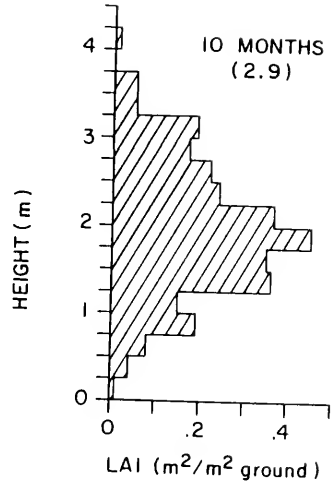


Figure 11. Vertical distribution of leaf area in the cassava monoculture. Total LAI is in parentheses.

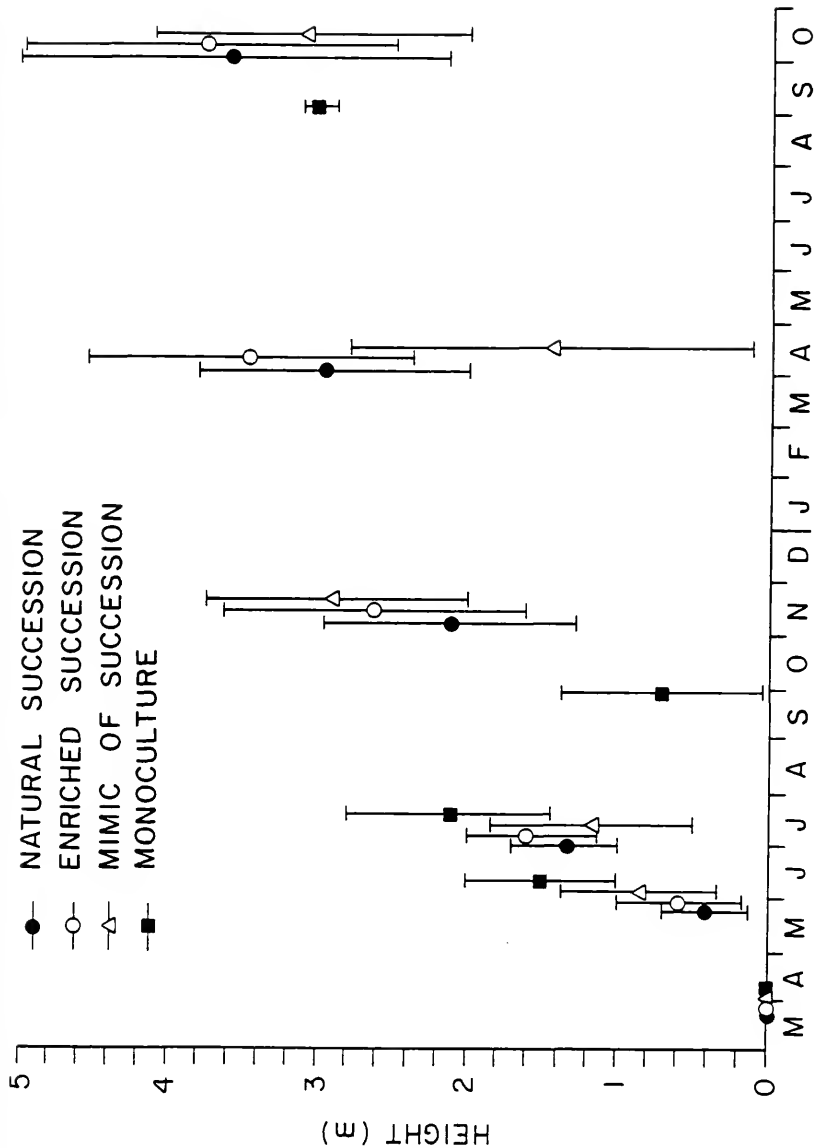


Figure 12. Vegetation height in natural succession, enriched succession, mimic of succession, and monoculture. Values are $\bar{x} \pm 1$ s.d.

Table 7. Tallest plants in natural succession, enriched succession, and mimic at 18 mo, and in cassava monoculture at 10 mo.

Ecosystem	Species	Height of tallest individual (m)
Natural succession	*Ochroma pyramidale*	10.8
	Vernonia patens	7.6
	Bocconia frutescens	5.8
Enriched succession	*Trema micrantha*	7.5
	Vernonia patens	7.0
	Musa paradisiaca	6.9
Mimic of succession	*Manihot esculenta*	5.0
	Ricinus communis	4.9
Monoculture	*Manihot esculenta*	4.2

Herbivory Rates

Mean herbivory rates varied widely among species, and among sampling dates for some species (Table 8). For most species, herbivory rates were not normally distributed. The Kolomogorov-Smirnov statistic to test the null hypothesis that the data were a random sample from a normal distribution was significant in 50 of 59 tests. Sample distributions were skewed to the right in most species studied (Fig. 13). Median losses were lower than mean losses for all species (Table 9). In three species (*Panicum trichoides*, *Erythrina costaricensis*, and *Manihot esculenta*), damage distribution was dependent on the type of ecosystem in which the species was found (Fig. 14 - Fig. 16).

Of the eight species monitored in both the natural succession and the enriched succession, one species (*Panicum trichoides*) had different herbivory rates in the two ecosystems. This species had a lower rate in the enriched succession than in the natural succession (Table 9). For the two species monitored in the enriched succession and in the mimic of succession (*Erythrina costaricensis*) and *Manihot esculenta*), both had lower herbivory rates in the enriched succession. *Manihot* also had lower rates in the monoculture than in the mimic.

Some ecosystem characteristics that may affect the herbivory rate on an individual species are species diversity, LAI, and species composition. In addition, the

Table 8. Mean herbivory losses by species and ecosystem. Losses are $\bar{x}$ (s.d.), in cm^2/m^2 leaf/day; n is number of leaves (alternate-leaved species), or number of leaf pairs (opposite-leaved species).

Species	Date	Natural Succession n	Natural Succession loss	Enriched Succession n	Enriched Succession loss	Mimic of Succession n	Mimic of Succession loss	Monoculture n	Monoculture loss
Phytolacca rivinoides	Oct. 79	37	16.5 (32.7)	21	14.4 (20.0)				
	Feb. 80	33	12.7 (24.4)	34	27.1 (46.1)				
	June 80	26	9.8 (16.8)	27	3.5 (7.1)				
Bocconia frutescens	Oct. 79	13	30.5 (24.7)	10	25.6 (20.9)				
	Feb. 80	25	11.9 (12.2)	24	15.0 (41.4)				
	June 80	14	9.2 (5.6)	13	51.0 (43.0)				
Clibadium aff. *surinamense*	Oct. 79	6	13.7 (10.4)	13	17.9 (13.8)				
	Feb. 80	17	16.0 (32.8)	14	9.2 (10.6)				
	June 80	9	13.5 (17.2)	16	16.1 (13.7)				

Table 8--continued.

Species	Date	Natural Succession n	Natural Succession loss	Enriched Succession n	Enriched Succession loss	Mimic of Succession n	Mimic of Succession loss	Monoculture n	Monoculture loss
Panicum maximum	Oct. 79	4	16.3 (7.0)	9	14.7 (13.5)				
	Feb. 80	5	6.8 (8.8)	8	12.8 (13.4)				
	June 80	9	13.0 (25.5)	9	15.5 (11.8)				
Solanum nigrescens	Oct. 79			3	8.4 (5.8)				
Cordia inermis	Feb. 80	32	6.3 (10.8)						
	June 80	30	12.5 (65.1)						
Panicum trichoides	June 80	19	21.4 (26.1)	16	3.5 (5.0)				
Gramineae[a]	Oct. 79			3	0.6 (0.5)				
	Feb. 80	9	29.7 (80.4)	6	7.6 (16.9)				
	June 80	11	36.4 (50.5)	9	13.5 (19.6)				

Table 8--continued.

Species	Date	Natural Succession n	Natural Succession loss	Enriched Succession n	Enriched Succession loss	Mimic of Succession n	Mimic of Succession loss	Monoculture n	Monoculture loss
Vernonia patens	Oct. 79			11	46.3 (31.5)				
	Feb. 80	34	24.2 (29.4)	29	34.1 (34.9)				
	June 80			20	77.9 (52.4)				
Momordica charantia	Feb. 80	6	131.4 (136.9)						
	June 80	15	15.6 (32.9)						
Cyperaceae[b]	June 80	9	21.5 (39.1)	7	10.6 (12.7)				
Solanum umbellatum	June 80	13	7.8 (5.9)						
Hymenachne amplexicaulis	Oct. 79	21	2.0 (1.1)						
	Feb. 80	5	2.3 (2.3)						
	June 80	13	11.5 (12.0)						

Table 8--continued.

Species	Date	Natural Succession n	Natural Succession loss	Enriched Succession n	Enriched Succession loss	Mimic of Succession n	Mimic of Succession loss	Monoculture n	Monoculture loss
Merremia tuberosa	Feb. 80			12	1.4 (1.6)				
	June 80			3	51.6 (43.6)				
Frantzia pittieri	Feb. 80	10	4.8 (10.3)						
	June 80	18	13.2 (15.3)						
Erythrina costaricensis	June 80			24	14.8 (20.2)	22	57.5 (40.8)		
Hyptis suaveolens	Feb. 80					16	26.2 (33.3)		
Sorghum vulgare	Feb. 80					10	5.6 (6.6)		
Phaseolus vulgaris	Oct. 79					25	44.9 (56.5)		
Zea mays	Oct. 79							14	6.2 (7.0)
Manihot esculenta	Oct. 79					26	7.3 (17.3)		

Table 8--continued.

Species	Date	Natural Succession n	Natural Succession loss	Enriched Succession n	Enriched Succession loss	Mimic of Succession n	Mimic of Succession loss	Monoculture n	Monoculture loss
Manihot esculenta	Feb. 80			17	4.0 (4.0)	24	35.7 (64.0)	68	11.5 (29.4)
	June 80					1	1.7 (-)	4	9.1 (5.4)
Cucurbita pepo	Oct. 79					4	27.7 (21.8)		
Cajanus cajan	Oct. 79					27	12.5 (29.0)		
	Feb. 80					13	62.9 (80.6)		
Cymbopogon citratus	Oct. 79					5	0.5 (0.4)		
	Feb. 80					19	1.4 (1.5)		
	June 80					15	0.9 (0.9)		
Musa paradisiaca	Oct. 79					3	1.1 (0.6)		
	Feb. 80			3	0.8 (0.7)	3	0.6 (0.4)		

Table 8--continued.

Species	Date	Natural Succession n	Natural Succession loss	Enriched Succession n	Enriched Succession loss	Mimic of Succession n	Mimic of Succession loss	Monoculture n	Monoculture loss
Musa paradisiaca	June 80			4	3.8 (2.9)				
Ipomoea batata	Oct. 79					19	28.4 (26.3)		
	Feb. 80					3	103.7 (40.7)		
Carica papaya	June 80					11	3.2 (2.5)		
Crotalaria micans	June 80					6	1.9 (1.9)		

[a]Includes at least six species of grasses that were indistinguishable by vegetative parts.

[b]Includes at least four species of sedges that were indistinguishable by vegetative parts.

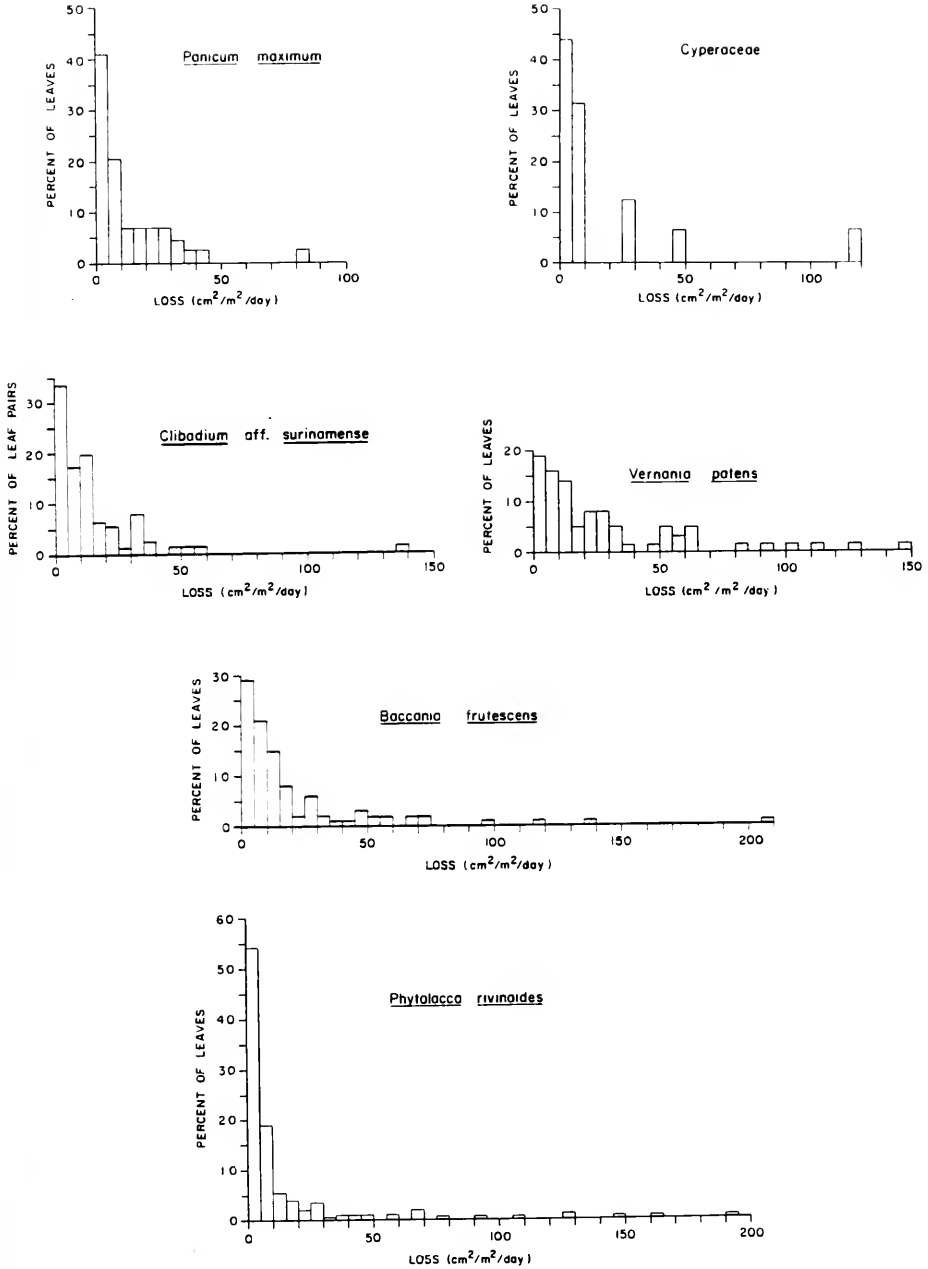


Figure 13. Distribution of loss to herbivores among leaves in six common species.

Table 9. Mean and median herbivory rates on selected species in different ecosystems. Number of leaves (n) includes samples from all dates for which treatment comparisons could be made.

Species	Ecosystem	n	Loss ($cm^2/m^2/day$) $\bar{x}$ (s.d.)	Median	p Value[a]
Bocconia frutescens	Natural succession	52	15.8 (17.2)	9.8	.70, .69, .77
	Enriched succession	47	27.2 (40.8)	10.7	
Clibadium aff. *surinamense*[b]	Natural succession	32	14.9 (25.5)	6.1	.32, .31, .72
	Enriched succession	43	14.4 (13.0)	10.8	
Cyperaceae[c]	Natural succession	9	21.5 (39.1)	5.3	.83, .79, .63
	Enriched succession	7	10.6 (12.7)	5.5	
Erythrina costaricensis	Enriched succession	24	14.9 (20.2)	7.4	<.01, <.01, <.01
	Mimic of succession	22	57.5 (40.8)	45.4	
Gramineae[d]	Natural succession	20	33.4 (63.8)	6.2	.19, .18, .05
	Enriched succession	18	9.4 (17.0)	1.6	
Manihot esculenta	Enriched succession	17	4.0 (4.0)	2.9	---, <.01, <.01
	Mimic of succession	24	35.7 (64.0)	7.1	
	Monoculture	68	11.5 (29.4)	1.3	
Panicum maximum	Natural succession	18	12.0 (18.6)	6.0	.18, .17, .54
	Enriched succession	26	14.4 (12.4)	9.1	
Panicum trichoides	Natural succession	19	21.4 (26.1)	9.5	<.01, <.01, .01
	Enriched succession	16	3.5 (5.0)	1.7	
Phytolacca rivinoides	Natural succession	96	13.4 (26.2)	4.1	.82, .82, .76
	Enriched succession	82	16.1 (33.0)	4.5	

Table 9--continued.

Species	Ecosystem	n	Loss ($cm^2/m^2/day$) $\bar{x}$ (s.d.)	Median	p Value[a]
Vernonia patens	Natural succession	34	24.2 (29.4)	11.2	.06, .06, .06
	Enriched succession	29	34.1 (34.9)	21.8	

[a]Wilcoxon 2-sample rank sums test, Kruskal-Wallis test, median test.

[b]For this species, n is number of opposite leaf pairs.

[c]Includes at least four species of sedges that were indistinguishable by vegetative parts.

[d]Includes at least six species of grasses that were indistinguishable by vegetative parts.

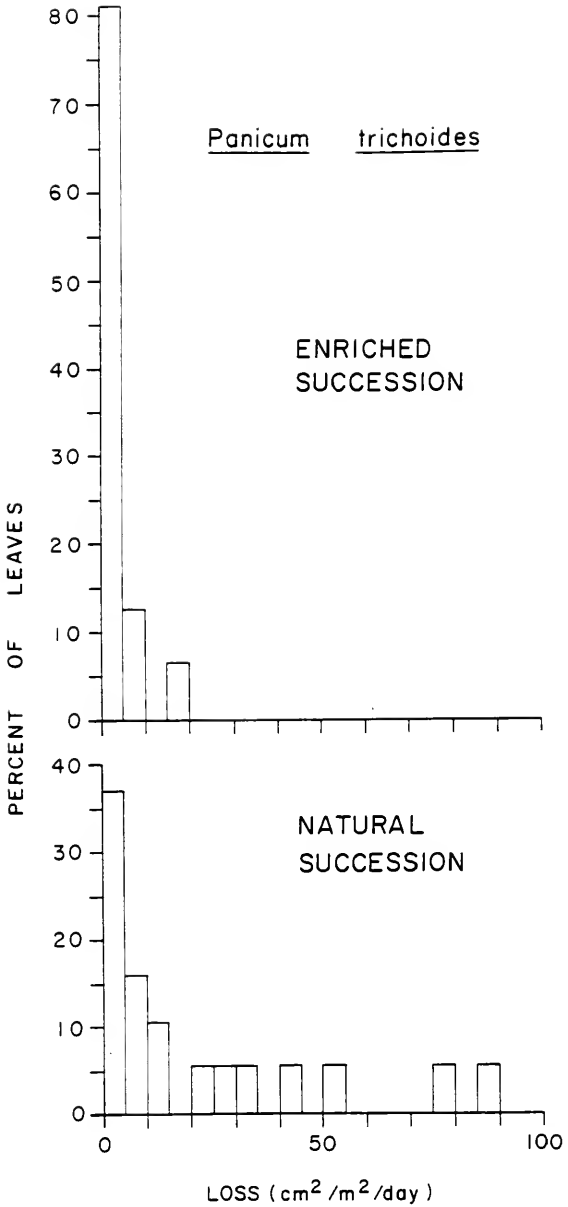


Figure 14. Loss distribution among leaves of Panicum trichoides.

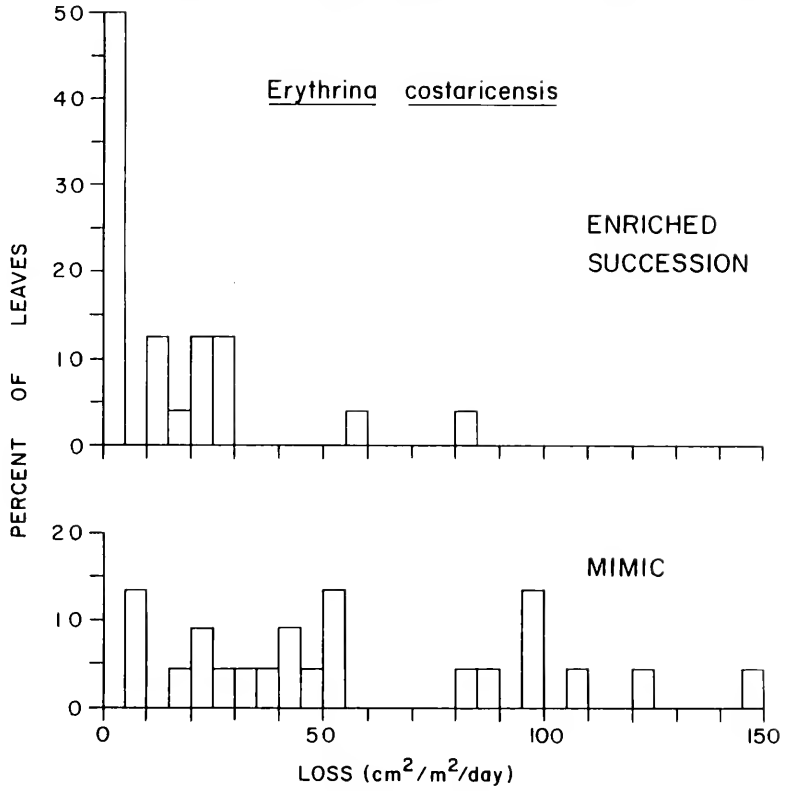


Figure 15. Loss distribution among leaves of Erythrina costaricensis.

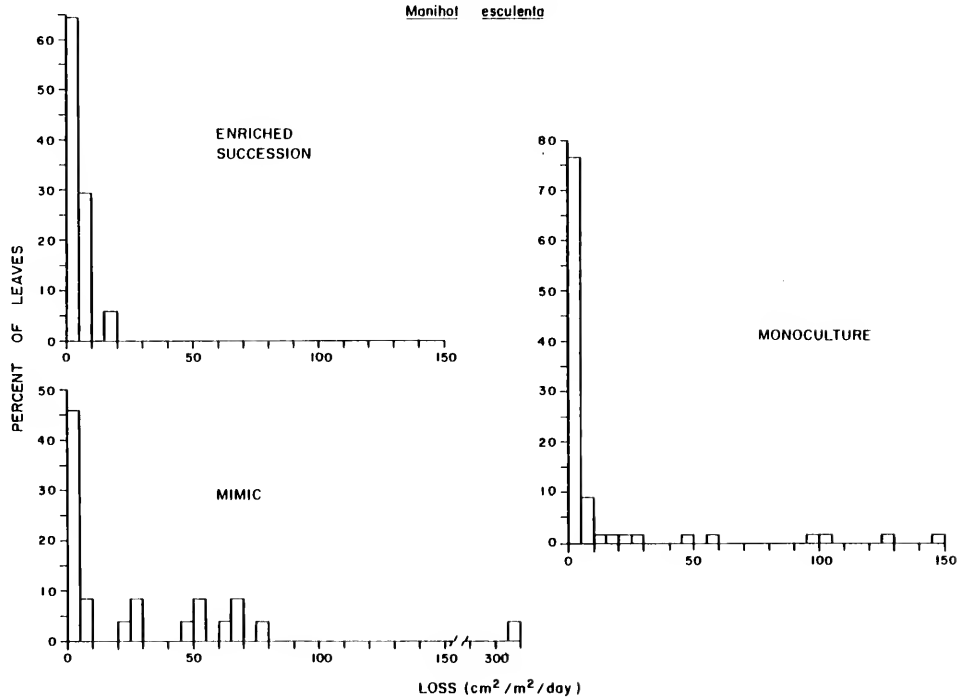


Figure 16. Loss distribution among leaves of Manihot esculenta.

abundance and spatial distribution of a particular species within the system may affect its herbivory rate. Few differences in herbivory rates between natural and enriched succession were expected, because these systems were very similar in species diversity, LAI, and species composition. Panicum trichoides had relatively low LAI in both systems (0.04 in natural succession, 0.07 in enriched succession). Thus differential plant abundance was probably not an important factor affecting herbivory rate for this species. Plant spatial distribution and/or small sample size may explain the observed difference.

Several factors may contribute to the higher herbivory rates on Erythrina in the mimic than in the enriched succession. Abundance of Erythrina was similar in the two systems. Although both systems had relatively high species diversity, the species similarity between the systems was low. In addition, the LAI of the mimic was lower than the LAI of the enriched succession. This suggests that the kinds of species that surround a given plant, as well as their abundance, may affect the herbivory rate on that plant. Manihot and Erythrina (both cultivars) had lower apparency and greater protection from herbivores when surrounded by native successional species in the enriched succession plots, than when planted in plots containing a different array of species including many cultivars.

Manihot, a relatively unpalatable species, had its highest herbivory rate in the ecosystem with intermediate species diversity and LAI (the mimic). The herbivory rate on this species was not linearly related to species diversity. This result suggests that species composition, rather than diversity per se, was an important factor influencing herbivory on Manihot.

There was no simple relationship between LAI of a species and that species' herbivory rate. However, the data indicate that in the natural succession, enriched succession and mimic, the very high rates of herbivory occurred on the less common species, and all of the very common species (LAI $\geq$ 0.5) had relatively low herbivory rates (Fig. 17). The loss rate for each species (cm^2 m^{-2} leaf day^{-1}) was multiplied by the LAI of the species to obtain the species' loss rate in cm^2 m^{-2} ground day^{-1}. Some relatively uncommon species contributed significantly to the total ecosystem loss to herbivores (Fig. 18).

The coefficient of variation (CV = s.d./mean) of herbivory rates was used to identify trends in the spatial distribution of damage among leaves and plants of several species. A large coefficient of variation (i.e., s.d. > mean) indicates high variability in herbivory rate among leaves or plants, and implies aggregation of damage, with some leaves or plants receiving very high levels of damage and others receiving very low levels. A low CV value (i.e.,

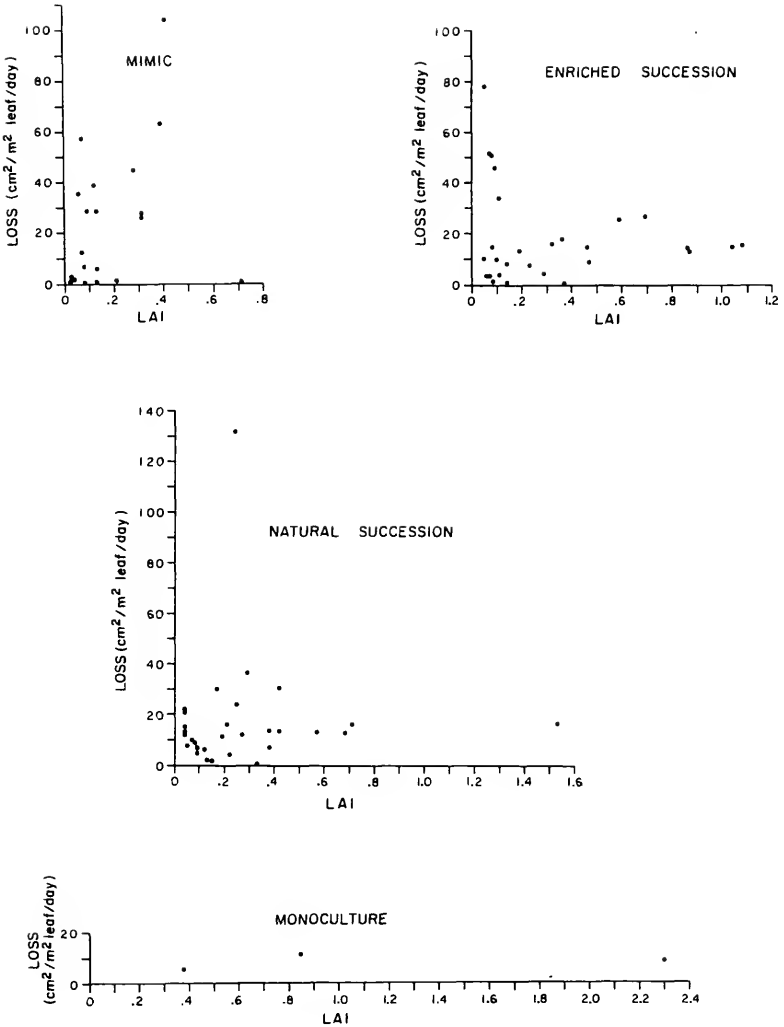


Figure 17. Losses to herbivores by LAI. Each point represents one species.

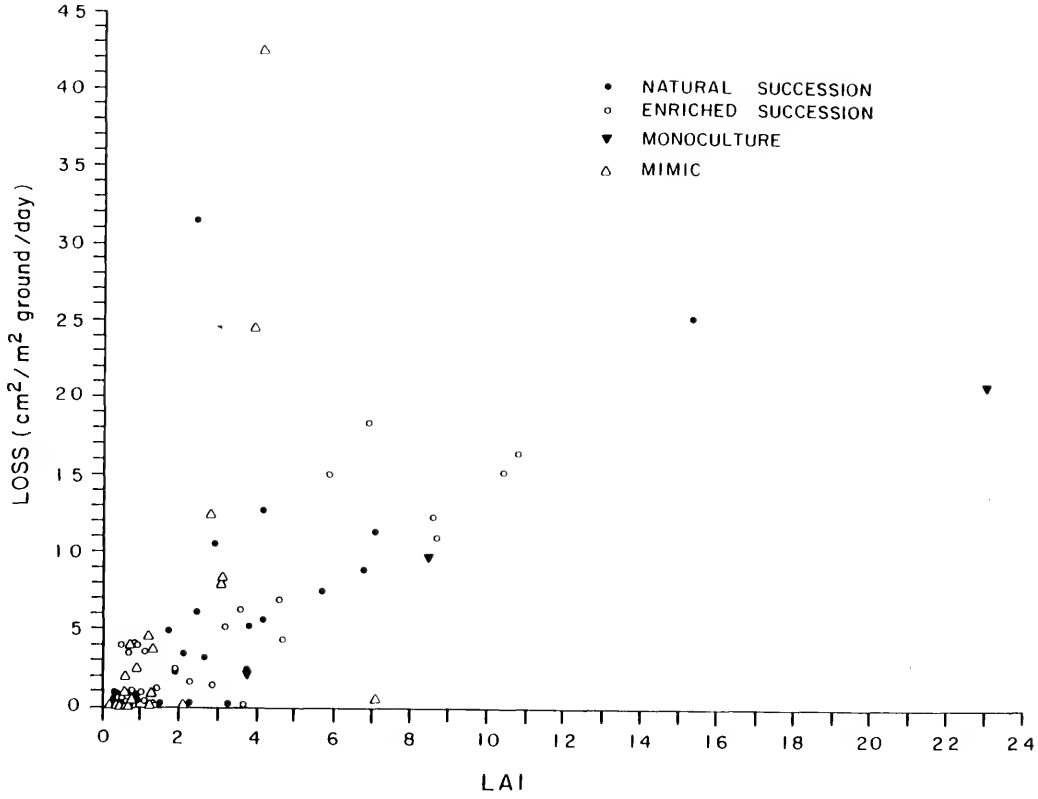


Figure 18. Herbivory rates per unit ground area by LAI. Each point represents one species.

s.d. < mean) indicates that spatial variability of damage is low and implies that damage tends to be evenly distributed among leaves or plants. The CV calculated using mean leaf herbivory rates reflects the damage distribution among leaves of a given species; the CV calculated using mean plant herbivory rates reflects the damage distribution among plants. The CV values calculated from leaf herbivory rates were higher, on the average, than the values calculated from plant herbivory rates (Table 10). This implies that leaf-to-leaf damage variability was higher than plant-to-plant variability. In other words, most damage from herbivores tended to be aggregated on a subset of the leaves of a species, but all plants of the species in the same ecosystem were equally likely to have some leaves heavily damaged by herbivores.

Both leaf-to-leaf and plant-to-plant variability were high in cassava. This result reflects the foraging pattern of one of cassava's major herbivores, the leaf-cutter ants (Atta cephalotes). These ants selected a few plants of cassava for consumption (leaving many other individuals untouched), and removed some (but not all) leaves of each selected plant almost entirely, leaving only the mid-ribs.

Young leaves and old leaves of most species were consumed at equal rates. Percent leaf expansion during the monitoring period was used as an indicator of leaf age (high percent expansion = young leaf; low percent expansion = old

Table 10. Coefficients of variation (CV) of herbivory rates by species. Coefficient of variation is calculated: (1) based on individual leaf data and (2) based on plant data.

Species	Based on Leaf Data: Number of Leaves	Based on Leaf Data: CV	Based on Plant Data: Number of Plants	Based on Plant Data: CV
Cordia inermis	62	4.89	10	2.07
Manihot esculenta	140	2.57	33	1.95
Gramineae[a]	38	2.21	9	0.81
Phytolacca rivinoides	178	2.02	27	1.53
Cajanus cajan	40	1.94	7	1.74
Momordica charantia	21	1.87	5	1.70
Hymenachne amplexicaulis	46	1.71	11	1.21
Panicum trichoides	35	1.61	10	1.27
Bocconia frutescens	99	1.46	25	1.41
Frantzia pittieri	28	1.39	6	0.68
Phaseolus vulgaris	25	1.26	5	0.81
Panicum maximum	44	1.12	13	0.76
Cymbopogon citratus	39	1.10	11	0.71
Erythrina costaricensis	46	1.08	10	0.91
Vernonia patens	94	1.01	16	0.70
Ipomoea batata	22	0.98	7	0.79

[a]Includes at least six species of grasses that were not distinguishable by vegetative parts.

leaf). Linear correlation coefficients between percent expansion and herbivory rate were non-significant for the 12 species tested. In addition to this test, the leaves of each of the 12 species were divided into two groups (leaves that expanded $\geq 10\%$ during the monitoring period, and leaves that expanded $<10\%$), and mean herbivory rates of the two groups were compared using F-tests. The herbivory rates on young (expanding) and old (not expanding) leaves were not significantly different for 10 of the 12 species. In two species (Phytolacca rivinoides and Carica papaya), herbivory rates were higher on old than on young leaves.

The LAI and herbivory rates for each species and ecosystem are summarized in Table 11. Herbivory rates on a per-leaf-area basis were multiplied by species' LAIs to obtain leaf loss rates on a per-ground-area basis. When these values were multiplied by species' specific masses (g/m^2 of leaf tissue), biomass loss rates resulted. Ecosystem herbivory rates were obtained by summing species' per-ground-area loss rates. It was assumed that losses in unsampled species equalled the weighted mean of the sampled species.

Ecosystem losses to herbivores (mean per-ground-area rates, averaged over all sampling dates) were equal in the mimic of succession (54 ± 44 cm^2 m^{-2} ground day^{-1}, natural succession (61 ± 23), and enriched succession (56 ± 9), and lower in the monoculture (11 ± 9). Variability among the

Table 11. Leaf area index, leaf specific mass, and losses to herbivores in natural succession, enriched succession, mimic of succession, and monoculture.

Ecosystem	Date	Species	LAI (m^2 Leaf/ m^2 Ground)	Percent of Total LAI
Natural succession	Oct. 79	Phytolacca rivinoides	1.53	37.5
		Bocconia frutescens	0.42	10.3
		Clibadium aff. surinamense	0.38	9.4
		Gramineae[a]	0.33	8.2
		Momordica charantia	0.22	5.3
		Panicum maximum	0.21	5.0
		Hymenachne amplexicaulis	0.15	3.7
		Borreria laevis	0.09	2.2
		Others	0.75	18.4
		Ecosystem[b]	4.08	100
	Feb. 80	Clibadium aff. surinamense	0.71	19.4
		Phytolacca rivinoides	0.68	18.7
		Panicum maximum	0.38	10.4
		Bocconia frutescens	0.27	7.3
		Vernonia patens	0.25	6.9
		Momordica charantia	0.24	6.6

Table 11--extended.

Leaf Specific Mass (g/m^2)	Herbivory Rate		
	cm^2/m^2 Leaf/ Day	cm^2/m^2 Ground/ Day	g/m^2 Ground/ Day
30.6	16.5	25.2	0.077
37.1	30.5	12.8	0.048
52.4	13.7	5.2	0.027
24.4	0.7	0.2	0.001
9.2	4.5	1.0	0.001
45.8	16.3	3.4	0.016
38.6	2.0	0.3	0.001
18.5	7.4	0.7	0.001
32.9[c]	14.7[c]	11.0	0.036
32.9	14.7	59.8	0.208
52.4	16.0	11.4	0.060
30.6	12.7	8.6	0.026
45.8	6.8	2.6	0.012
37.1	11.9	3.2	0.012
61.2	24.2	6.1	0.037
9.2	131.4	31.5	0.029

Table 11--continued.

Ecosystem	Date	Species	LAI (m^2 Leaf/ m^2 Ground)	Percent of Total LAI
Natural succession	Feb. 80	Gramineae[a]	0.17	4.7
		Hymenachne amplexicaulis	0.13	3.7
		Cordia inermis	0.12	3.4
		Frantzia pittieri	0.09	2.6
		Others	0.59	16.3
		Ecosystem[b]	3.63	100
	June 80	Panicum maximum	0.57	24.8
		Clibadium aff. surinamense	0.42	18.1
		Gramineae[a]	0.29	12.8
		Hymenachne amplexicaulis	0.19	8.4
		Bocconia frutescens	0.08	3.6
		Phytolacca rivinoides	0.07	2.9
		Solanum umbellatum	0.05	2.2
		Panicum trichoides	0.04	1.9
		Momordica charantia	0.04	1.9
		Frantzia pittieri	0.04	1.9

Table 11--extended.

Leaf Specific Mass (g/m^2)	Herbivory Rate		
	cm^2/m^2 Leaf/ Day	cm^2/m^2 Ground/ Day	g/m^2 Ground/ Day
24.4	29.7	5.0	0.012
38.6	2.3	0.3	0.001
25.8	6.3	0.8	0.002
24.5	4.8	0.4	0.001
38.6[c]	23.0[c]	13.6	0.052
38.6	23.0	83.5	0.244
45.8	13.0	7.4	0.034
52.4	13.5	5.7	0.030
24.4	36.4	10.6	0.026
38.6	11.5	2.2	0.008
37.1	9.2	0.7	0.003
30.6	9.8	0.7	0.002
38.3	7.8	0.4	0.001
30.8	21.4	0.9	0.003
9.2	15.6	0.6	0.001
24.5	13.2	0.5	0.001

Table 11--continued.

Ecosystem	Date	Species	LAI (m^2 Leaf/ m^2 Ground)	Percent of Total LAI
Natural succession	June 80	Cordia inermis	0.04	1.9
		Cyperaceae[d]	0.04	1.9
		Others	0.44	17.7
		Ecosystem[b]	2.31	100
Enriched succession	Oct. 79	Panicum maximum	1.04	23.7
		Phytolacca rivinoides	0.86	19.7
		Bocconia frutescens	0.59	13.6
		Gramineae[a]	0.37	8.4
		Clibadium aff. surinamense	0.36	8.2
		Momordica charantia	0.29	6.7
		Solanum nigrescens	0.14	3.2
		Borreria latifolia	0.10	2.3
		Vernonia patens	0.09	2.2
		Others	0.54	12.0
		Ecosystem[b]	4.38	100

Table 11--extended.

Leaf Specific Mass (g/m^2)	Herbivory Rate		
	cm^2/m^2 Leaf/ Day	cm^2/m^2 Ground/ Day	g/m^2 Ground/ Day
25.8	12.5	0.5	0.001
46.1	21.5	0.9	0.004
40.1[c]	16.6[c]	7.3	0.029
40.1	16.6	38.4	0.143
45.8	14.7	15.3	0.070
30.6	14.4	12.4	0.038
37.1	25.6	15.1	0.056
24.4	0.6	0.2	0.001
52.4	17.9	6.4	0.034
9.2	4.5	1.3	0.001
25.6	8.4	1.2	0.003
18.7	10.3	1.0	0.002
61.2	46.3	4.2	0.026
35.8[c]	14.9[c]	8.0	0.029
35.8	14.9	65.1	0.260

Table 11--continued.

Ecosystem	Date	Species	LAI (m^2 Leaf/ m^2 Ground)	Percent of Total LAI
Enriched succession	Feb. 80	Panicum maximum	0.87	23.4
		Phytolacca rivinoides	0.69	18.6
		Clibadium aff. surinamense	0.47	12.7
		Bocconia frutescens	0.46	12.4
		Gramineae[a]	0.23	6.1
		Musa paradisiaca	0.14	3.7
		Vernonia patens	0.11	2.8
		Merremia tuberosa	0.08	2.2
		Others	0.68	18.1
		Ecosystem[b]	3.73	100
Enriched succession	June 80	Panicum maximum	1.08	41.8
		Clibadium aff. surinamense	0.32	12.4
		Gramineae[a]	0.19	7.5
		Musa paradisiaca	0.11	4.1
		Erythrina costaricensis	0.08	3.2
		Bocconia frutescens	0.08	3.0

Table 11--extended.

Leaf Specific Mass (g/m^2)	Herbivory Rate		
	cm^2/m^2 Leaf/ Day	cm^2/m^2 Ground/ Day	g/m^2 Ground/ Day
45.8	12.8	11.1	0.051
30.6	27.1	18.7	0.057
52.4	9.2	4.3	0.023
37.1	15.0	6.9	0.026
24.4	7.6	1.7	0.004
81.0	0.8	0.1	0.001
61.2	34.1	3.8	0.023
54.0	1.4	0.1	0.001
42.8[c]	15.3[c]	10.4	0.045
42.8	15.3	57.1	0.231
45.8	15.5	16.7	0.077
52.4	16.1	5.2	0.027
24.4	13.5	2.6	0.006
81.0	3.8	0.4	0.003
37.5	14.8	1.2	0.004
37.1	51.0	4.1	0.015

Table 11--continued.

Ecosystem	Date	Species	LAI (m^2 Leaf/ m^2 Ground)	Percent of Total LAI
Enriched succession	June 80	Panicum trichoides	0.07	2.6
		Merremia tuberosa	0.07	2.6
		Phytolacca rivinoides	0.06	2.2
		Cyperaceae[d]	0.05	1.9
		Vernonia patens	0.05	1.9
		Others	0.43	16.8
		Ecosystem[b]	2.59	100
Mimic of succession	Oct. 79	Cucurbita pepo	0.31	17.4
		Phaseolus vulgaris	0.28	15.9
		Ipomoea batata	0.13	7.5
		Oryza sativa	0.09	5.0
		Cymbopogon citratus	0.08	4.7
		Manihot esculenta	0.08	4.7
		Cajanus cajan	0.07	4.0
		Musa paradisiaca	0.02	1.2
		Others	0.72	39.6
		Ecosystem[b]	1.78	100

Table 11--extended.

Leaf Specific Mass (g/m^2)	Herbivory Rate		
	cm^2/m^2 Leaf/ Day	cm^2/m^2 Ground/ Day	g/m^2 Ground/ Day
30.8	3.5	0.2	0.001
54.0	51.6	3.6	0.020
30.6	3.5	0.2	0.001
46.1	10.6	0.5	0.002
61.2	77.9	3.9	0.024
45.8[c]	17.9[c]	7.7	0.035
45.8	17.9	46.3	0.215
46.5	27.7	8.6	0.040
34.2	44.9	12.6	0.043
25.1	28.4	3.7	0.009
45.8	28.7	2.6	0.012
59.6	0.5	0.04	<0.001
45.4	7.3	0.6	0.003
34.7	12.5	0.9	0.003
81.0	1.1	0.02	<0.001
41.3[c]	27.3[c]	19.7	0.081
41.3	27.3	48.8	0.191

Table 11--continued.

Ecosystem	Date	Species	LAI (m^2 Leaf/ m^2 Ground)	Percent of Total LAI
Mimic of succession	Feb. 80	Ipomoea batata	0.41	19.6
		Cajanus cajan	0.39	18.5
		Hyptis suaveolens	0.31	14.6
		Cymbopogon citratus	0.21	10.1
		Musa paradisiaca	0.13	6.3
		Sorghum vulgare	0.13	6.1
		Manihot esculenta	0.06	2.6
		Others	0.46	22.2
		Ecosystem[b]	2.10	100
	June 80	Cymbopogon citratus	0.71	53.1
		Hyptis suaveolens	0.12	9.1
		Erythrina costaricensis	0.07	5.0
		Manihot esculenta	0.04	3.3
		Carica papaya	0.03	2.1
		Crotalaria micans	0.03	2.1
		Others	0.34	25.3
		Ecosystem[b]	1.34	100

Table 11--extended.

Leaf Specific Mass (g/m^2)	Herbivory Rate cm^2/m^2 Leaf/ Day	cm^2/m^2 Ground/ Day	g/m^2 Ground/ Day
25.1	103.7	42.5	0.107
34.7	62.9	24.5	0.085
31.6	26.2	8.1	0.026
59.6	1.4	0.3	0.002
81.0	0.6	0.1	0.001
49.4	5.6	0.7	0.004
45.4	35.7	2.1	0.010
40.1[c]	47.8[c]	22.0	0.088
40.1	47.8	100.3	0.323
59.6	0.9	0.6	0.004
31.6	39.0	4.7	0.015
37.5	57.5	4.0	0.015
45.4	1.7	0.1	<0.001
48.5	3.2	0.1	<0.001
26.2	1.9	0.1	<0.001
52.8[c]	9.6	3.3	0.017
52.8	9.6	12.9	0.051

Table 11--continued.

Ecosystem	Date	Species	LAI (m^2 Leaf/ m^2 Ground)	Percent of Total LAI
Monoculture	Oct. 79	*Zea mays*	0.38	100
	Feb. 80	*Manihot esculenta*	0.85	100
	June 80	*Manihot esculenta*	2.30	100

Table 11--extended.

Leaf Specific Mass (g/m^2)	Herbivory Rate		
	cm^2/m^2 Leaf/ Day	cm^2/m^2 Ground/ Day	g/m^2 Ground/ Day
53.1	6.2	2.4	0.013
45.4	11.5	9.8	0.044
45.4	9.1	20.9	0.095

[a]Includes at least six species of grasses that were indistinguishable by vegetative parts.

[b]Ecosystem values are totals (LAI, percent of total LAI, losses in cm^2/m^2 ground/day, losses in g/m^2 ground/day), and species' means weighted by LAI (leaf specific mass, losses in cm^2/m^2 leaf/day).

[c]Mean of species values weighted by LAI.

[d]Includes at least four species of sedges that were indistinguishable by vegetative parts.

three sampling dates , based on comparison of coefficients of variation, was higher in the monoculture and mimic than in the enriched succession and natural succession, possibly due to insect outbreaks on cultivars in the monoculture and mimic.

The lower rates of herbivory in the monoculture reflect characteristics of the individual species planted there. Low rates were expected on cassava, a relatively unpalatable species. Herbivory on the maize was low, perhaps because the plots were located >1 km from other agricultural experiments, in an area that had not been cultivated for many years. Although leaf loss to above-ground herbivores was low in the maize, root damage by soil herbivores was extensive, but not measured.

Losses per ground area of ecosystem were equal in the three diverse systems (natural succession, enriched succession, and mimic of succession); however, the percent of available leaf area consumed by herbivores differed among systems. For the three diverse systems, percent loss was negatively correlated with ecosystem LAI.

Consumption by herbivores ranged from 0.5 cm^2 m^{-2} leaf day^{-1} in Cymbopogon citratus, a grass in the mimic of succession, to 131 cm^2 m^{-2} leaf day^{-1} in Momordica charantia, a native vine in the natural succession. High LAI (0.41), together with high per-leaf-area herbivory rate (104 cm^2 m^{-2} leaf day^{-1}, gave Ipomoea batata the highest

per-ground-area consumption rate (42 cm^2 m^{-2} ground day^{-1}). The lowest per-ground-area rate (0.02 cm^2 m^{-2} ground day^{-1}) was in plantain (Musa paradisiaca), a species relatively uncommon in the mimic when sampled in October 1979. Biomass losses ranged from <0.001 g m^{-2} ground day^{-1} in several species to 0.107 g m^{-2} ground day^{-1} in Ipomoea batata. Herbivory rate was not correlated with leaf specific mass ($r = -0.10$ on a species-by-species basis).

Expansion of holes accounted for 6-60% of the total observed damage in the species studied (unweighted species' mean = 30%). At the ecosystem level, losses due to expansion comprised 19-43% of the total damage (Fig. 19). Percent of total loss attributable to hole expansion was lower in February 1980 than at the other two sampling periods in three ecosystems (Fig. 19). The February sampling was during the dry season, a time when leaf production and growth (and therefore leaf expansion) were low. Damage due to hole expansion, averaged over the three sampling dates, was similar in natural succession (30%), enriched succession (31%), mimic of succession (32%), and monoculture (32%).

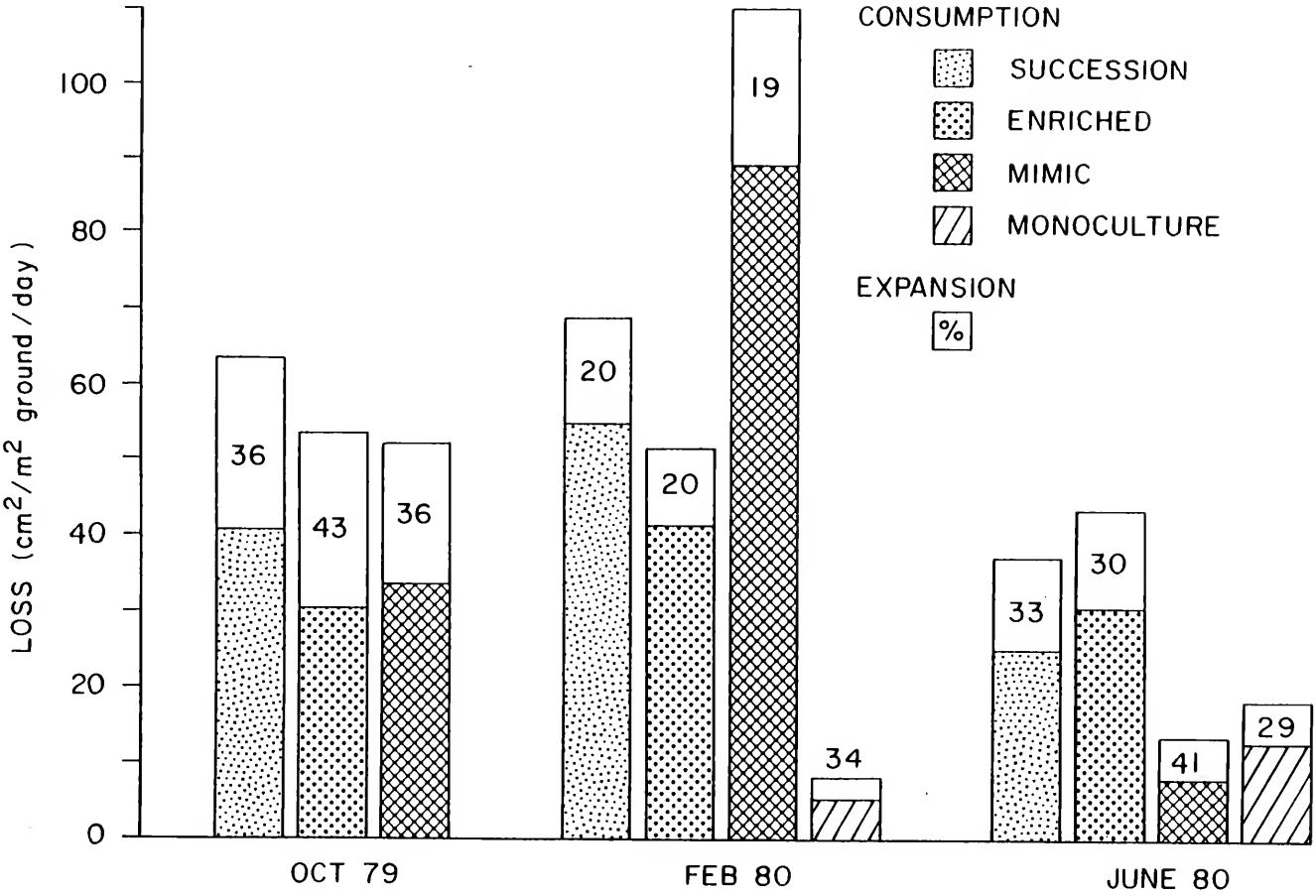


Figure 19. Proportion of total herbivory due to consumption and hole expansion.

Above-Ground Biomass

Mean biomass of each vegetation component (leaves, stems, reproductive parts, and standing dead) and total above-ground biomass (leaves + stems + reproductive parts + standing dead) are presented by treatment and harvest date in Appendix B. Values are means and standard deviations of original untransformed data.

Biomass differences are based on four-treatment analyses of variance, i.e., all four ecosystems were included in each analysis of variance (except the 28 October 1980 analyses). The vegetation in three of the four treatments (natural succession, enriched succession, and mimic) was equal-aged throughout the study. In the monoculture, three crops were consecutively planted and harvested. Therefore, after the first maize harvest the vegetation in the monoculture was younger than the vegetation in the other treatments. To compare the three equal-aged treatments (natural succession, enriched succession, and mimic), analysis of variance tests were done on these three treatments only (monoculture excluded). In 64 of 70 analysis of variance tests, the differences detected were the same in the analyses excluding the monoculture as in the analyses including the monoculture. The analyses excluding the monoculture detected more differences among the three equal-aged treatments than the analyses including the monoculture in one case, and fewer differences in five cases.

Differences among replications occurred on two dates. Total above-ground biomass was higher in replications 1 and 5 than in the other replications on 8 July 1980 ($p<.05$). Standing dead biomass was higher in replication 6 than in the other replications ($p<.05$) on 9 July 1979. Replications 1, 5, and 6 were dominated by grasses throughout the 1.5 yr study period. The differences among replications may reflect growth differences between these grasses and the dominant dicots in the other replications.

Leaf biomass (Fig. 20) increased at the same rate in all four treatments during the first 12.5 wk of growth. At 15 wk leaf biomass was highest in the maize monoculture (312 g/m^2) and lowest in the mimic (51 g/m^2). Leaf biomass of the second maize crop was low (<25 g/m^2). In the natural succession and enriched succession, leaf biomass leveled off at <500 g/m^2 after 24 wk. In the natural succession leaf biomass was maintained at this level through 83 wk, but in the enriched succession leaf biomass increased after 51 wk and was significantly high than the other treatments (1162 g/m^2) at 83 wk. High leaf biomass in the enriched succession at 83 wk was due in part to the high leaf biomass of some of the introduced species, such as plantain. Leaf biomass in the mimic fluctuated from 24 to 83 wk and was less than or equal to that in the enriched and natural succession, and greater than or equal to that in the monoculture. The cassava monoculture developed leaf biomass

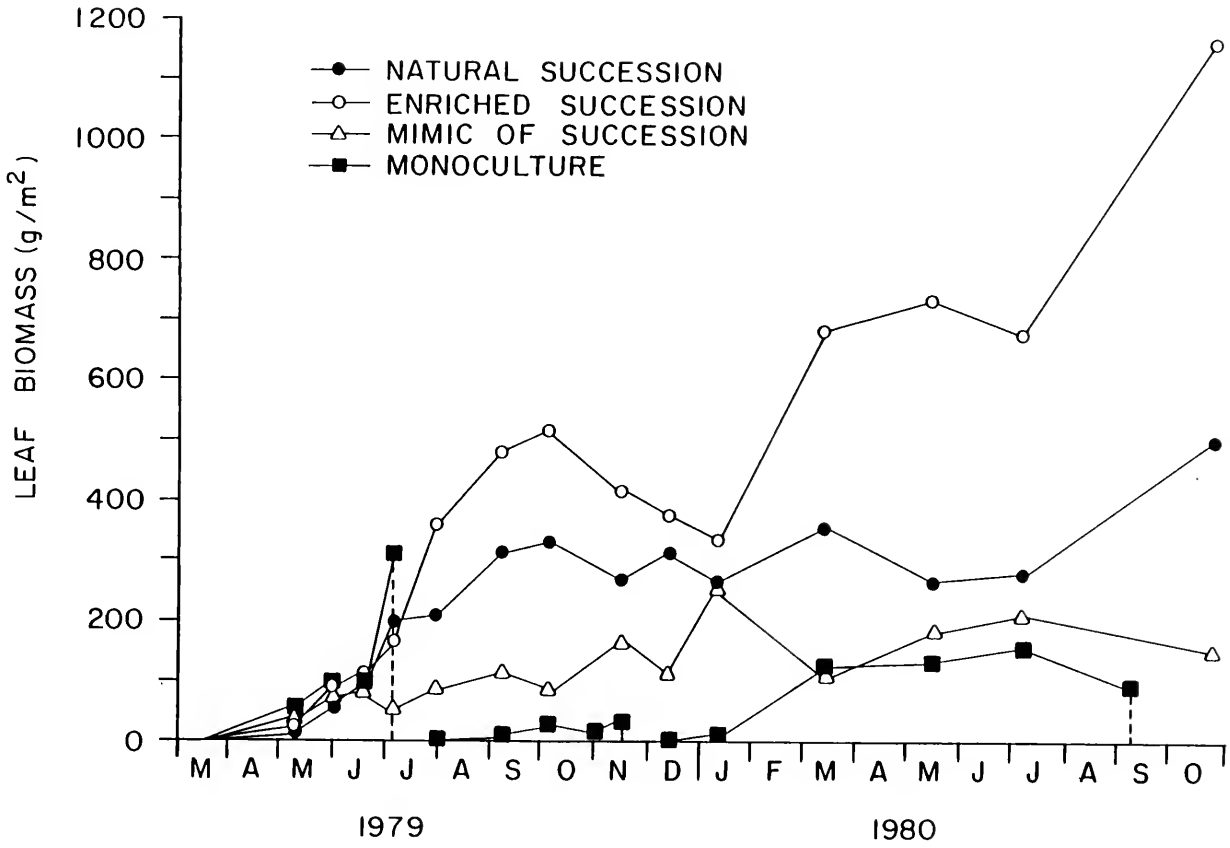


Figure 20. Leaf biomass, March 1979 - October 1980.

very rapidly, and after 16 wk of growth had leaf biomass equal to that in the older mimic treatment.

Stem biomass (Fig. 21) increased at approximately the same rate in the natural succession and enriched succession. Stem biomass in the mimic equaled that in the natural succession and enriched succession at all but three sampling dates, and was significantly lower than that in the enriched succession at 83 wk. The monoculture had higher stem biomass than the other treatments at maturity of the first maize crop (567 g/m^2 at 15 wk), but the second maize had very low stem biomass (<60 g/m^2 at harvest). Stem biomass of cassava was lower than stem biomass in the other treatments during early growth, but not at cassava maturity.

Biomass of reproductive parts (flowers and fruits) was low (<65 g/m^2) in the natural succession, enriched succession, and mimic at most sampling dates, with few significant differences among these three treatments (Fig. 22). Values were very low (<20 g/m^2) in the natural and enriched succession during the first 18.5 wk of growth and slightly higher (up to 61 g/m^2) thereafter. One exception to the low values in the mimic occurred at 18.5 wk, when the biomass of reproductive parts (255 g/m^2) was significantly higher than that in the other treatments. This peak in reproduction was due primarily to the reproductive parts of cultivars such as maize, squash, and beans. The biomass of reproductive parts in the monoculture was significantly

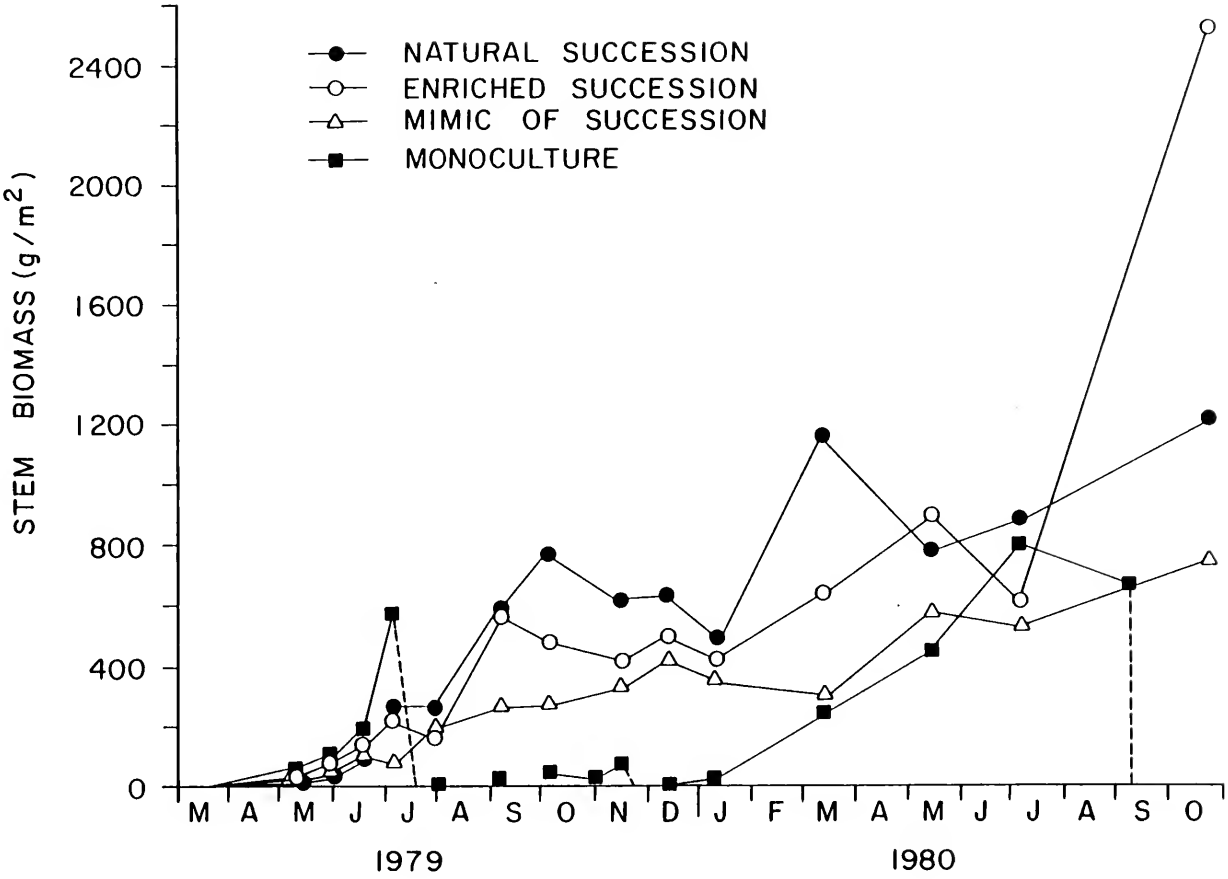


Figure 21. Stem biomass, March 1979 - October 1980.

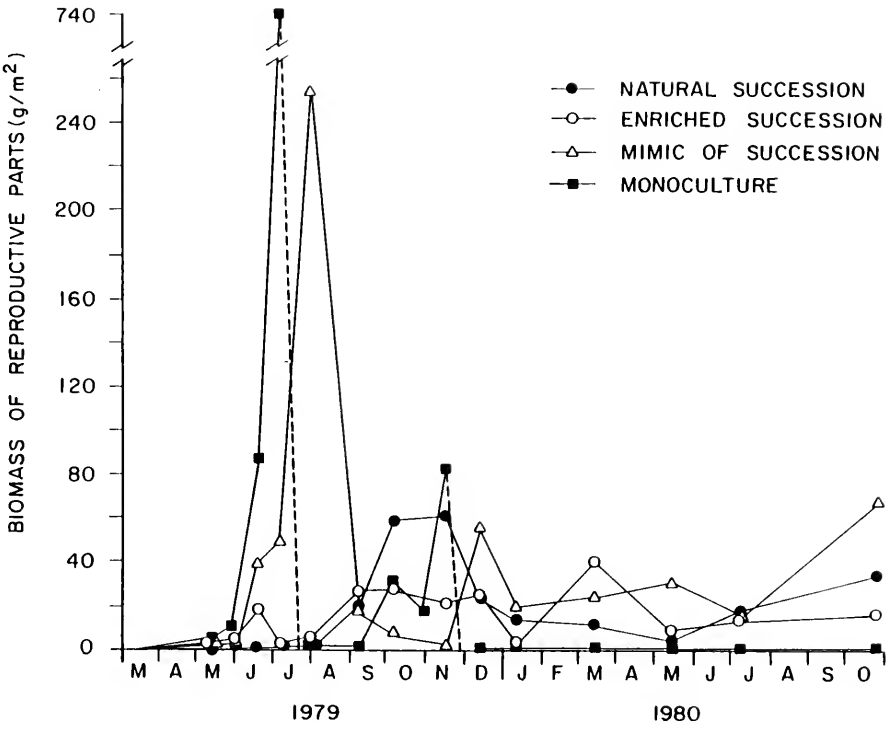


Figure 22. Biomass of reproductive parts, March 1979 - October 1980.

higher than that in other treatments at maturity of the first maize crop (740 g/m² at 15 wk) and at maturity of the second maize crop (82 g/m², 17 wk after planting). The cassava monoculture had no flowers or fruits during the first 32 wk of growth and had just begun to flower when it was harvested in September 1980.

Standing dead biomass in the natural succession and enriched succession did not differ at most sampling dates (Fig. 23). In the natural and enriched successions, standing dead biomass was <100 g/m² to 18.5 wk, and fluctuated between 200 and 400 g/m² thereafter. Standing dead biomass in the mimic was less than or equal to that in the natural and enriched successions throughout the 83 wk period. In the monoculture standing dead biomass was generally low, but was higher than in the other treatments at maturity of the first maize crop, due to dead maize leaves that remained attached to the plants.

At 83 wk total above-ground biomass was 2078 g/m² in the natural succession, 4854 g/m² in the enriched succession, and 1233 g/m² in the mimic (Fig. 24). The highest biomass value in the monoculture occurred at maturity of the first maize crop (1697 g/m² at 15 wk); the second maize crop had low total biomass (<200 g /m²), and mature cassava reached a total above-ground biomass of nearly 1000 g/m². At 83 wk, the enriched succession had higher above-ground biomass than the natural succession; at all other dates the differences

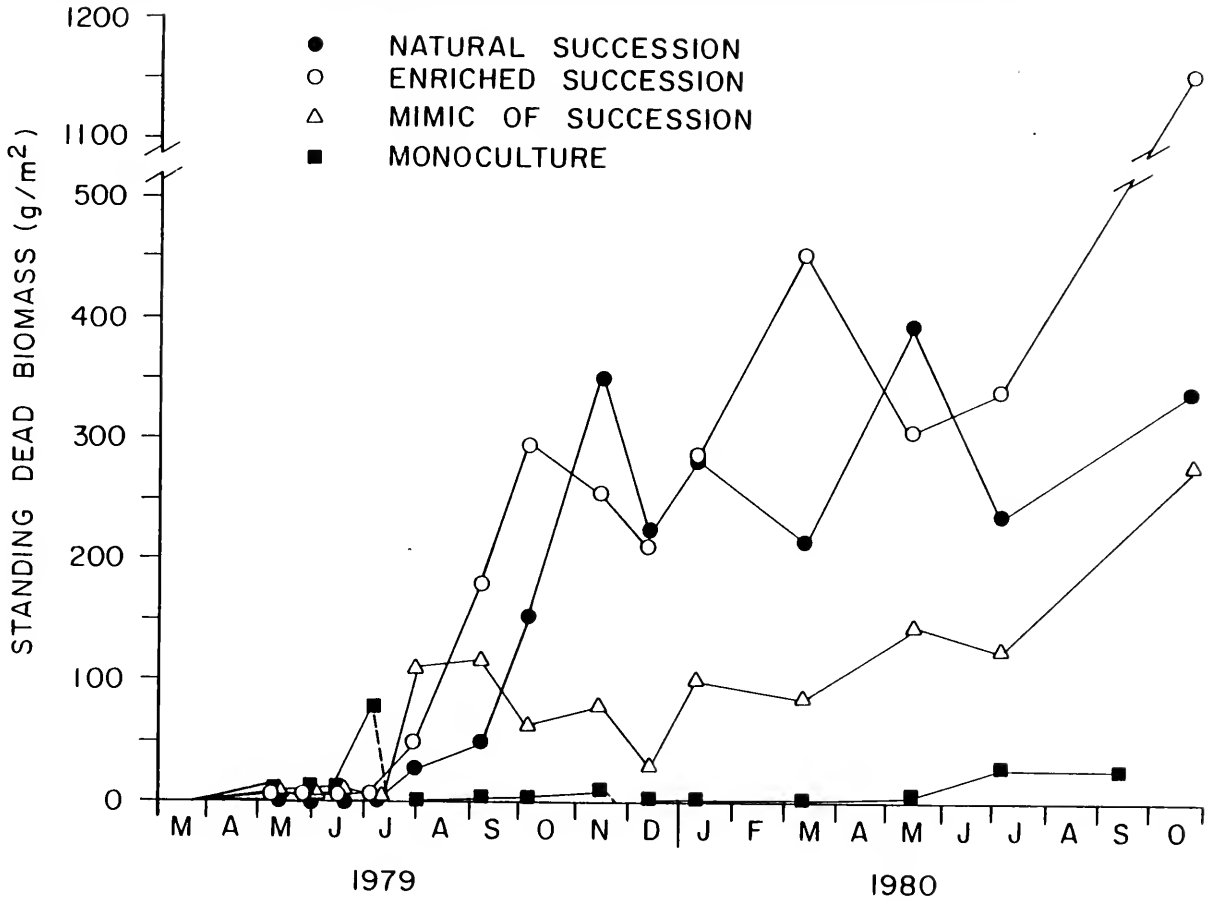


Figure 23. Standing dead biomass, March 1979 - October 1980.

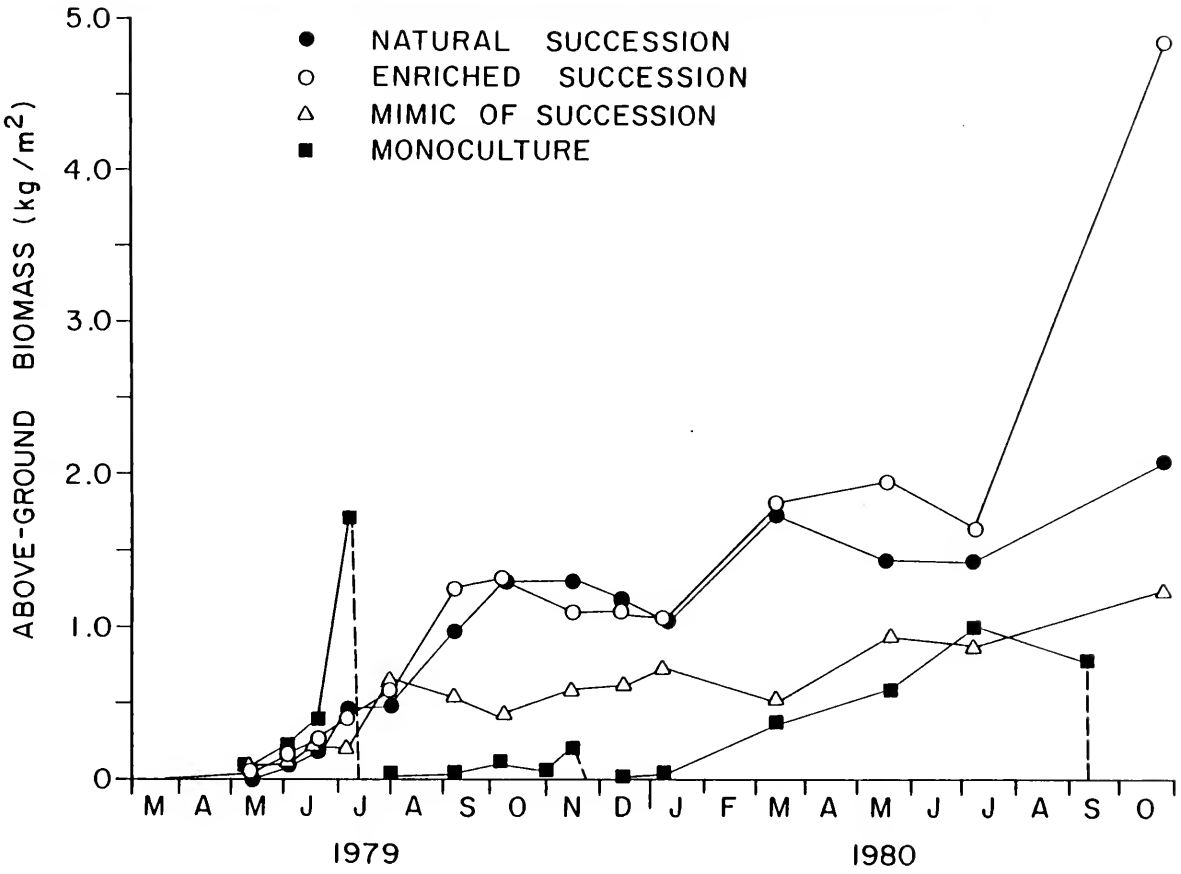


Figure 24. Total above-ground biomass, March 1979 - October 1980.

between these two treatments were not significant. Total above-ground biomass in the mimic was generally less than or equal to that of the natural succession and the enriched succession. With a few exceptions, total above-ground biomass followed the trend: enriched succession $\geq$ natural succession $\geq$ mimic of succession $\geq$ monoculture.

Total above-ground living biomass (leaves + stems + reproductive parts) in the natural succession, enriched succession, and mimic of succession increased continuously during the 1.5 yr study period, with a slight dry season decrease during January and February of 1980 (Fig. 25). The monoculture was characterized by rapid increment in above-ground living biomass during growth of the first maize crop, poor growth of the second maize crop, and rapid growth of the cassava. Total above-ground living biomass at 83 wk in the enriched succession (approximately 4 kg/m^2) was double that of the natural succession (approximately 2 kg/m^2), and total living biomass of the mimic (approximately 1 kg/m^2) was about half that of the natural succession.

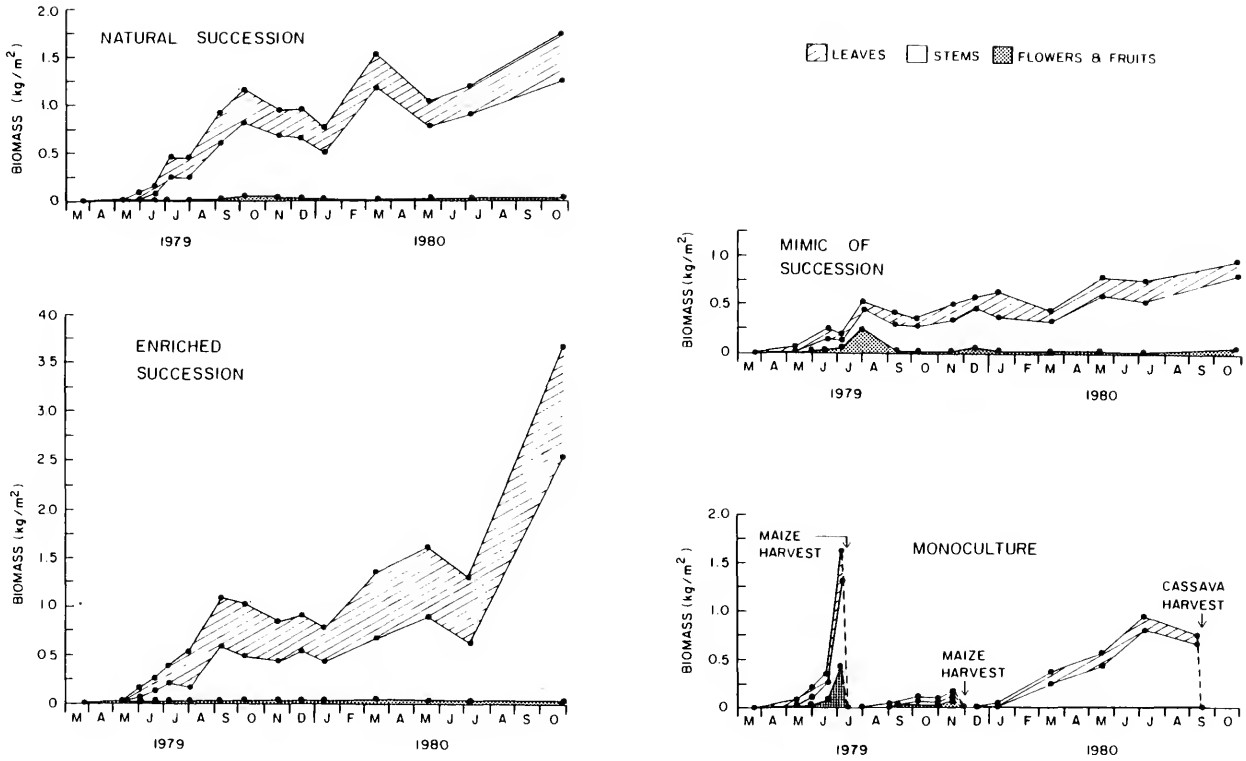


Figure 25. Above-ground living biomass, March 1979 - October 1980.

Litter

The litterfall collected in each of the plots may be divided into 2 categories: autochthonous litter (litter produced by vegetation in the plot), and allochthonous litter (litter produced by vegetation outside the plot). The total amount of litterfall (autochthonous + allochthonous) is of interest in the study of the nutrient cycling processes of the system. For calculating net primary productivity and vegetation turnover rates in each experimental ecosystem, autochthonous litterfall is the appropriate measure.

In this study, allochthonous litter accounted for 20-31% of the total litterfall (natural succession, 20%; enriched succession, 21%; mimic of succession, 26%; monoculture, 31%). This suggests that litter from the older, taller secondary forest surrounding the plots may be important as a source of nutrient inputs. The high allochthonous litter values partly reflect the small size of the experimental plots. Each replication had an area of approximately 0.12 ha and was surrounded by older secondary forest on all sides. In areas where large-scale clearing of tropical forests for cultivation has occurred, nutrient inputs from allochthonous litter would be much lower.

All litterfall comparisons among treatments are based on autochthonous litter (see Appendix B for table of means and significant differences by date). The vegetation in the

experimental ecosystems began to produce measurable amounts of litter at age 12 wk. From 12 wk to 84 wk, there were several differences in 2-wk litterfall amounts among the four treatments, with the monoculture in general producing less litter than the other treatments. Although mean monthly litterfall in the natural succession (36 $\pm$ 10 g/m^2), enriched succession (35 $\pm$ 14), mimic (26 $\pm$ 11) and monoculture (21 $\pm$ 11) did not differ statistically, the tendency was for the monoculture to produce less litter (Fig. 26). Low litterfall values were expected in the maize monoculture, because dead maize leaves commonly remain attached to the plant until they decompose. Mean litterfall in the cassava monoculture (31 $\pm$ 15 g m^{-2} mo^{-1}) was not significantly different from mean litterfall in the natural succession, enriched succession, or mimic.

At five dates (4 July 1979, 11 September 1979, 8 April 1980, 6 May 1980, and 3 June 1980), analysis of variance detected significant differences among replications. On each of these dates, litterfall was lower in replications where grasses were very common than in replications dominated by dicots.

Litterfall fluctuated over time in all treatments (Fig. 27). In the natural succession, enriched succession, and mimic, litterfall was lower during May and June of 1980 than during other months. These low values coincide with the onset of the rainy season, and may reflect a seasonal pulse

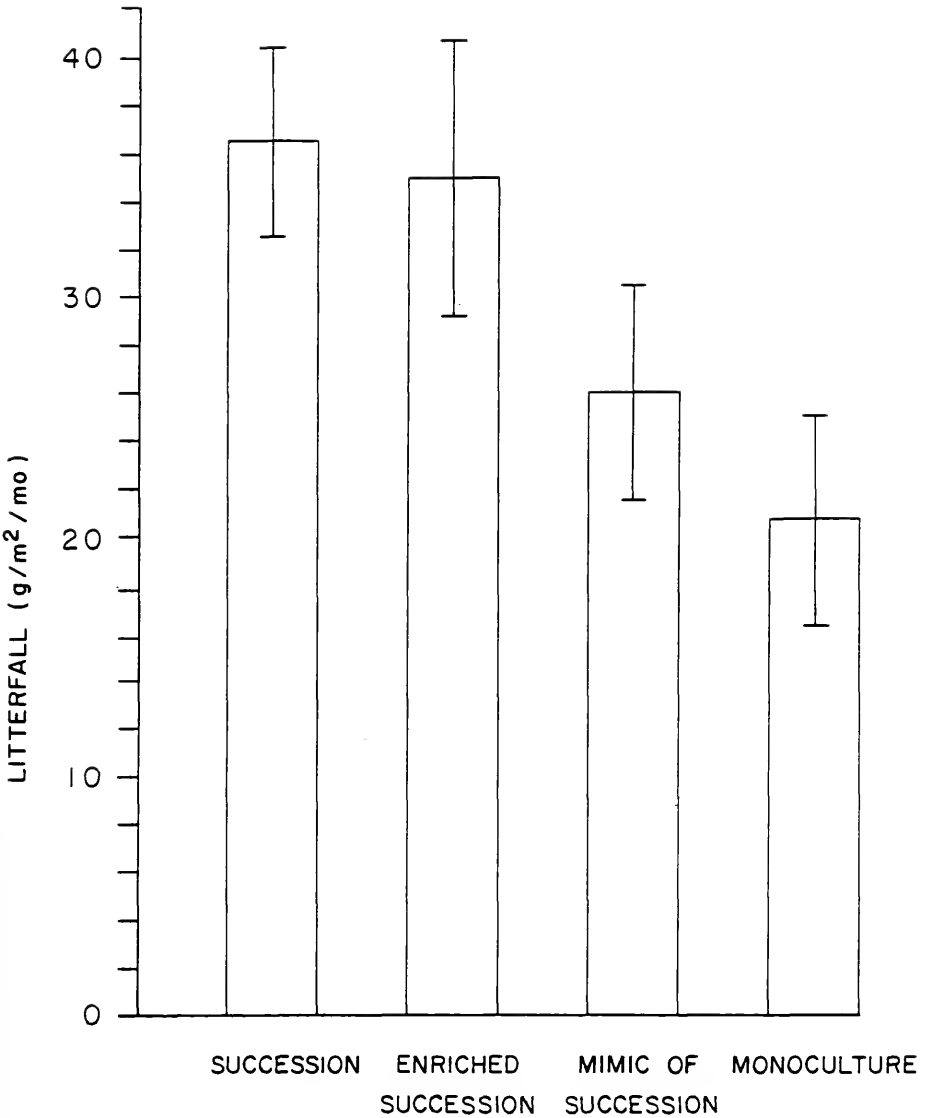


Figure 26. Monthly litterfall means in succession, enriched succession, mimic of succession, and monoculture. Confidence intervals are $\pm$ 1 s.e.

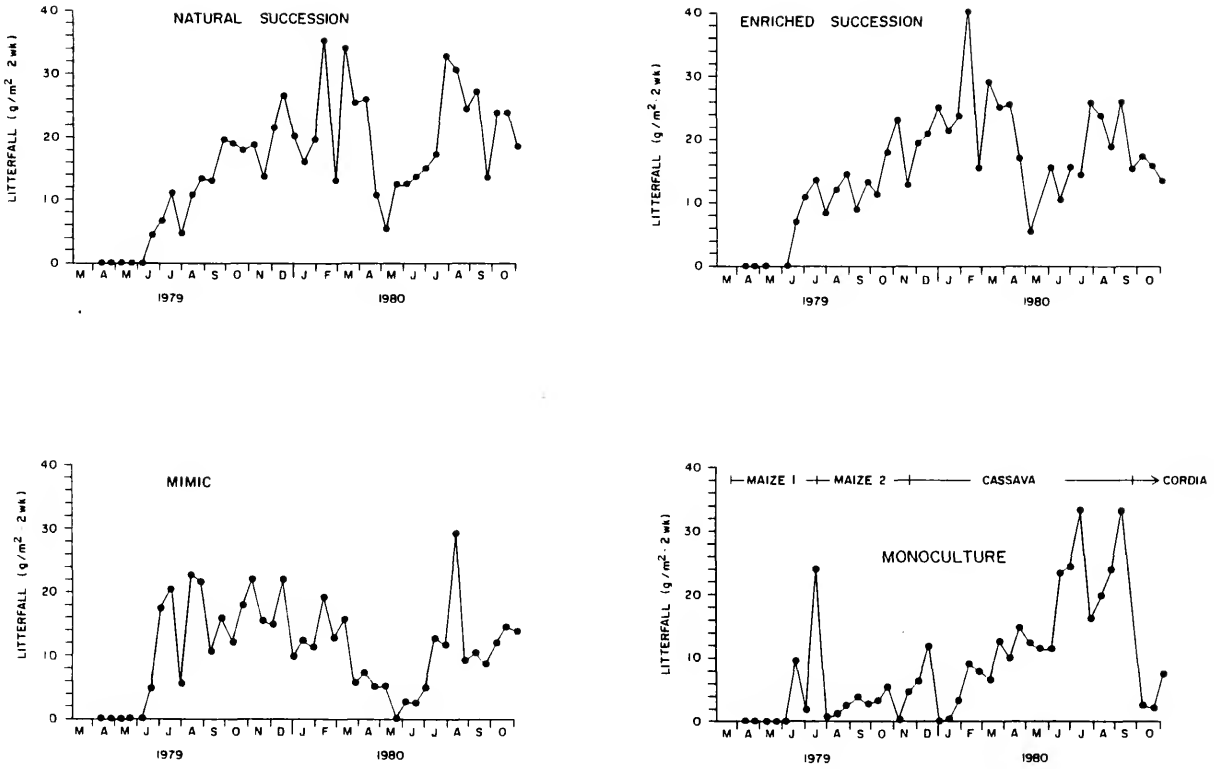


Figure 27. Litterfall in natural succession, enriched succession, mimic of succession, and monoculture, April 1979 - October 1980.

of leaf production and rapid vegetative growth, when leaf losses to litter were low.

Above-Ground Productivity

Thirty-day means of net primary productivity, above-ground living biomass, herbivory, litterfall, and production of standing dead biomass were calculated using the rate equations described in Chapter II, 'Productivity Measurements'. The curves estimated from monthly mean values and the original data points from field measurements are presented in Figs. 28 - 31. The highest net primary productivity rate was in the first maize monoculture (45 g m^{-2} day^{-1}). This high rate was maintained for <1 mo, and in general, net primary productivity was much lower in the monoculture (<10 g m^{-2} day^{-1}). Mean net productivities of the three monocultures (g m^{-2} day^{-1}) were 16.9 (first maize planting), 1.8 (second maize planting), and 4.0 (cassava).

Productivity rates were very similar in the natural succession and the enriched succession (Figs. 28 and 29), with considerable fluctuation over time. Net above-ground primary productivity values were negative for short periods of time in the natural succession, enriched succession and mimic. At least three factors may contribute to the occurrence of negative values. First, underestimation of the production of standing dead biomass by assuming negligible turnover is a source of error in the productivity

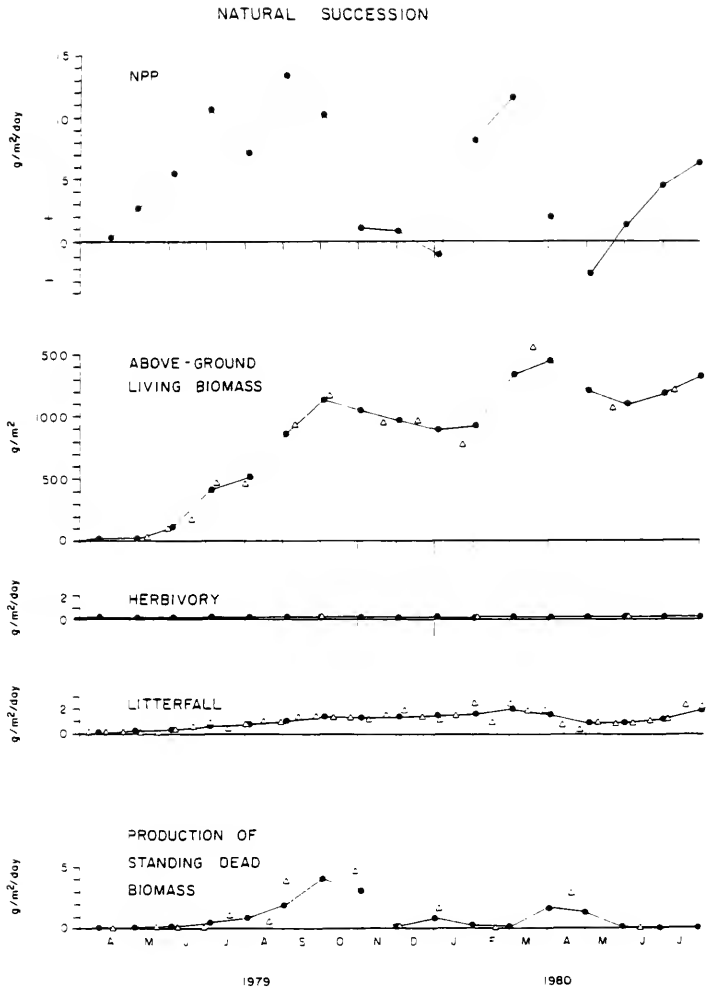


Figure 28. Net primary productivity (NPP), above-ground living biomass, herbivory, litterfall, and production of standing dead biomass in natural succession. Triangles are data from field measurements; black dots are estimated monthly means.

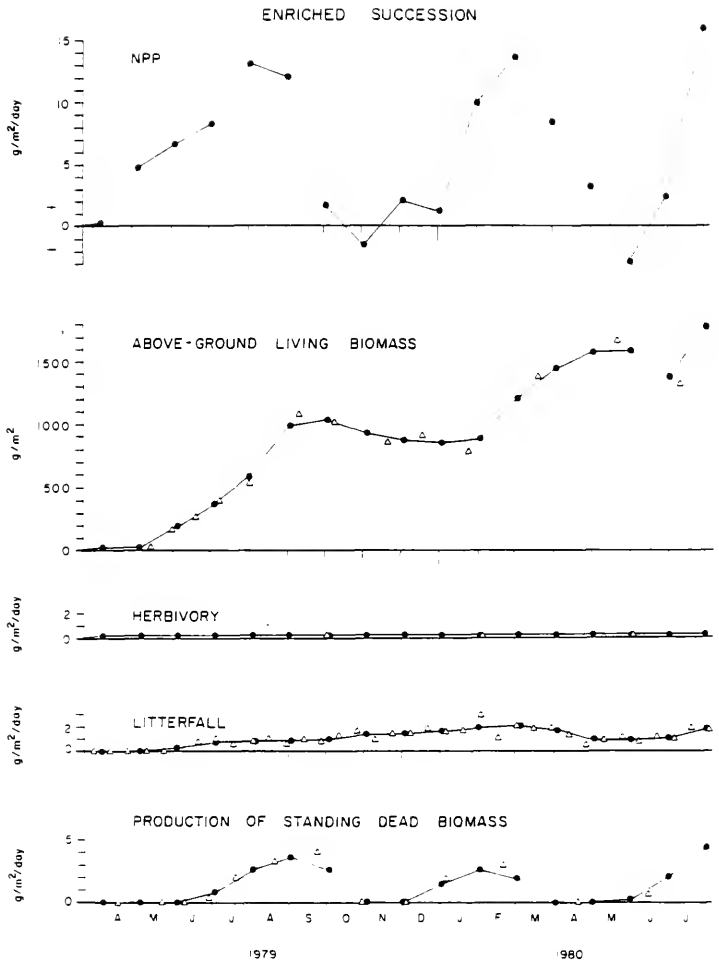


Figure 29. Net primary productivity (NPP), above-ground living biomass, herbivory, litterfall, and production of standing dead biomass in enriched succession. Triangles are data from field measurements; black dots are estimated monthly means.

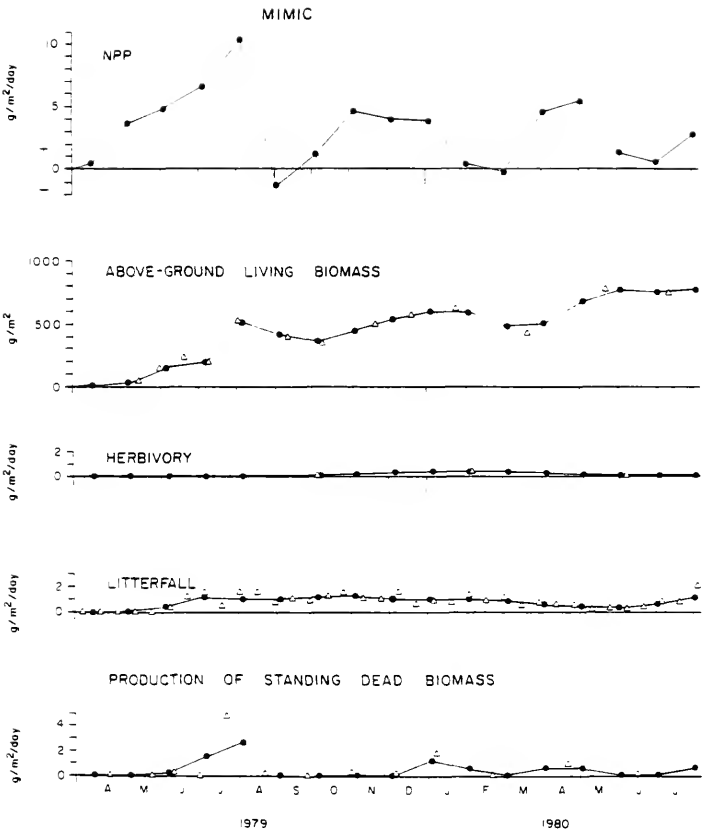


Figure 30. Net primary productivity (NPP), above-ground living biomass, herbivory, litterfall, and production of standing dead biomass in mimic of succession. Triangles are data from field measurements; black dots are estimated monthly means.

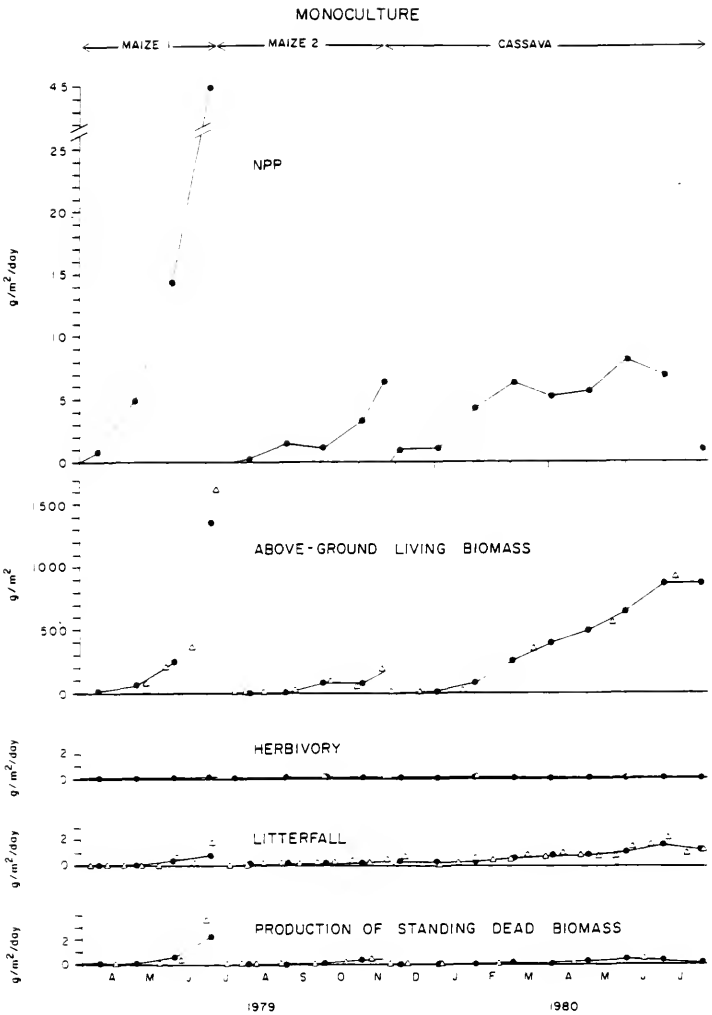


Figure 31. Net primary productivity (NPP), above-ground living biomass, herbivory, litterfall, and production of standing dead biomass in the monoculture. Triangles are data from field measurements; black dots are estimated monthly means.

calculations. The negative net primary productivity in the natural succession and enriched succession treatments during November 1979-January 1980 probably reflects the dieback of some of the early successional dominants, including Phytolacca rivinoides. Second, negative net primary productivity values may indicate periods of time during which plant respiration was higher than photosynthesis. Negative net primary productivity in the natural succession and enriched succession near the end of the dry season (April-May 1980) may be due to water stress and high plant respiration during the dry season as well as dieback of some important species. A third factor that would lead to negative net primary productivity estimates is translocation of photosynthate from above-ground to below-ground plant parts. Such translocation may have occurred during the dry season, but it was not measured.

In the mimic, seasonal fluctuations in net primary productivity were dissimilar to those in the natural succession and enriched succession. The differences probably reflect different life cycle characteristics of the dominant species in each system.

Yearly net primary productivity rates (Table 12) were highest in the enriched succession (2396 g m^{-2} yr^{-1}) and in the monoculture (2267), and lower in the natural succession (1777) and the mimic (1148). Yearly productivity rates in the natural succession, enriched succession, and mimic were

Table 12. Annual net above-ground productivity, biomass losses, and biomass accumulation in four ecosystems. Values are $g/m^2/yr$.

Ecosystem	Net Above-Ground Productivity	Biomass Losses				Net Above-Ground Biomass Accumulation
		Litterfall	Standing Dead Biomass Production	Herbivory	Harvest	
Natural succession	1777	404	302	60		1011
Enriched succession	2396	398	552	72		1374
Mimic of succession	1148	295	190	56		607
Monoculture	2267	243	89	15	1920	0

much higher than yearly losses to litterfall, standing dead, and herbivory. These systems were not in steady state, but were accumulating biomass at a rapid rate. In the monoculture, long-term biomass accumulation did not occur because of crop harvests.

In all four ecosystems, losses to litterfall and standing dead were higher than losses to herbivory. In the natural succession, for example, 40% of the net primary production was cycled through litterfall and standing dead, and only 3% through herbivory; the remaining 57% went into biomass accumulation.

Herbivores consumed <1% of the total above-ground net primary production in the monoculture, 3% in the natural succession, 3% in the enriched succession, and 5% in the mimic. Herbivores consumed 3% of the total leaf production in the monoculture, 7% in the enriched succession, 9% in the natural succession, and 12% in the mimic.

Effects of Decreased Herbivory

Rates of Herbivory in Insecticide Plots

To study the effects of reduced herbivory on community structure and function, insecticide was applied to a diverse system (the enriched succession) and a simple system (the monoculture). Herbivory rates were monitored on dominant species in the insecticide plots to determine whether or not the insecticide applications reduced damage rates.

Leaf area and herbivory rates in the enriched succession and monoculture treated with insecticide are summarized in Table 13 and Table 14. Insecticide applications to the enriched succession reduced the per-leaf-area herbivory rate by 43% in October 1979, 65% in February 1980, and 65% in June 1980 (mean reduction for all dates = 58%). Herbivory rates on species common to the insecticide plots and plots not treated with insecticide were compared using non-parametric statistical techniques (Wilcoxon 2-sample rank sums test, Kruskal-Wallis test, and median test). Because the data did not meet the homogeneity of variance assumption of these tests, the levels of significance reported are not exact (Pratt 1964).

Herbivory rates on the four species monitored in both systems (Phytolacca rivinoides, Clibadium aff. surinamense, Panicum maximum, and Erythrina costaricensis) were significantly different in the enriched succession with and without insecticide (Table 15). Rates were lower with than without insecticide for each species. The herbivory rates were not significantly different in the maize monocultures with and without insecticide. The rate in the cassava monoculture treated with insecticide was 56% lower than the rate in the cassava monoculture not treated with insecticide (Table 15).

Table 13. Leaf area index, leaf specific mass, and losses to herbivores in the enriched succession and monoculture treated with insecticide.

Ecosystem	Date	Species	LAI (m^2 Leaf/ m^2/Ground)	Percent of Total LAI
Enriched succession	Oct. 79	Clibadium aff. surinamense	0.86	20.8
		Hymenachne amplexicaulis	0.81	19.5
		Phytolacca rivinoides	0.56	13.4
		Borreria laevis	0.44	10.7
		Gramineae[a]	0.28	6.7
		Canavalia sp.	0.25	6.0
		Vigna sp.	0.08	1.3
		Solanum torvum	0.08	0.7
		Others	0.86	20.9
		Ecosystem[b]	4.22	100
	Feb. 80	Clibadium aff. surinamense	1.14	36.6
		Gramineae[a]	0.31	9.8
		Phytolacca rivinoides	0.28	8.9
		Panicum maximum	0.25	8.0
		Solanum jamaicense	0.19	6.2
		Vigna sp.	0.11	3.6
		Hyptis vilis	0.08	2.7

Table 13--extended.

Leaf Specific Mass (g/m^2)	Herbivory Rate		
	cm^2/m^2 Leaf/ Day	cm^2/m^2 Ground/ Day	g/m^2 Ground/ Day
52.4	8.8	7.6	0.040
38.6	7.6	6.2	0.024
30.6	16.5	9.2	0.028
18.5	10.9	4.8	0.009
24.4	0.1	0.03	<0.001
37.2	0.7	0.2	0.001
43.3	0.04	<0.01	<0.001
34.0	7.4	0.6	0.002
36.9[c]	8.5[c]	7.3	0.027
36.9	8.5	35.9	0.131
52.4	4.9	5.6	0.029
24.4	1.2	0.4	0.001
30.6	3.9	1.1	0.003
45.8	6.9	1.7	0.008
39.5	6.2	1.2	0.005
43.3	0.8	0.1	<0.001
23.3	6.5	0.5	0.001

Table 13--continued.

Ecosystem	Date	Species	LAI (m^2 Leaf/ m^2/Ground)	Percent of Total LAI
Enriched succession	Feb. 80	Hymenachne amplexicaulis	0.08	2.7
		Iresine diffusa	0.08	2.7
		Others	0.59	18.8
		Ecosystem[b]	3.11	100
	June 80	Clibadium aff. surinamense	0.92	26.3
		Hymenachne amplexicaulis	0.72	20.6
		Gramineae[a]	0.31	8.7
		Panicum maximum	0.31	8.7
		Canavalia sp.	0.25	7.1
		Borreria laevis	0.17	4.8
		Erythrina costaricensis	0.14	4.0
		Solanum jamaicense	0.11	3.2
		Others	0.57	16.3
		Ecosystem[b]	3.50	100
Monoculture	Oct. 79	Zea mays	1.40	100
	Feb. 80	Manihot esculenta	1.02	100
	June 80	Manihot esculenta	2.76	100

Table 13--extended.

Leaf Specific Mass (g/m^2)	Herbivory Rate		
	cm^2/m^2 Leaf/ Day	cm^2/m^2 Ground Day	g/m^2 Ground/ Day
38.6	18.0	1.4	0.006
35.6	21.4	1.7	0.006
42.6[c]	5.4[c]	3.2	0.014
42.6	5.4	16.9	0.073
52.4	6.9[d]	6.3	0.033
38.6	6.1	4.4	0.017
24.4	2.7	0.8	0.002
45.8	0.9	0.3	0.001
37.2	13.2	3.3	0.012
18.5	16.2	2.8	0.005
37.5	1.5	0.2	0.001
39.5	4.1	0.5	0.002
40.9[c]	6.3[c]	3.6	0.015
40.9	6.3	22.2	0.088
53.1	9.8	13.7	0.073
45.4	5.2	5.3	0.024
45.4	2.3	6.3	0.029

[a]Includes at least six species of grasses that were indistinguishable by vegetative parts.

Table 13--continued.

[b]Ecosystem values are totals (LAI, percent of total LAI, losses in cm^2/m^2 ground/day, losses in g/m^2 ground/day), and species' means weighted by LAI (leaf specific mass, losses in cm^2/m^2 leaf/day).

[c]Mean of species values weighted by LAI.

[d]Mean of Oct. 79 and Feb. 80 rates.

Table 14. Mean herbivory losses by species, in plots with and without insecticide treatment. Losses are $\bar{x}$ (s.d.), in cm^2/m^2 leaf/day; n is number of leaves (alternate-leaved species), or number of leaf pairs (opposite-leaved species).

Species	Date	Natural Succession n	Natural Succession loss	Enriched Succession n	Enriched Succession loss
Phytolacca rivinoides	Oct. 79	37	16.5 (32.7)	21	14.4 (20.0)
	Feb. 80	33	12.7 (24.4)	34	27.1 (46.1)
Clibadium aff. surinamense	Oct. 79	6	13.7 (10.4)	13	17.9 (13.8)
	Feb. 80	17	16.0 (32.8)	14	9.2 (10.6)
Panicum maximum	Feb. 80	5	6.8 (8.8)	8	12.8 (13.4)
	June 80	9	13.0 (25.5)	9	15.5 (11.8)
Gramineae[a]	Feb. 80	9	29.7 (80.4)	6	7.6 (16.9)
	June 80	11	36.4 (50.5)	9	13.5 (19.6)
Hymenachne amplexicaulis	Feb. 80	5	2.3 (2.3)		
	June 80	13	11.5 (12.0)		
Erythrina costaricensis	June 80			24	14.8 (20.2)
Borreria laevis	Oct. 79				
	June 80				

Table 14--extended.

Mimic of Succession		Monoculture		Enriched Succession Treated with Insecticide		Treated with Insecticide	
n	loss	n	loss	n	loss	n	loss
				15	16.5 (28.6)		
				18	3.9 (5.4)		
				11	8.8 (11.4)		
				9	4.9 (4.8)		
				3	6.9 (8.2)		
				7	0.9 (0.6)		
				9	1.2 (2.4)		
				8	2.7 (4.1)		
				4	18.0 (9.5)		
				7	6.1 (11.1)		
22	57.5 (40.8)			15	1.5 (1.2)		
				2	10.9 (5.7)		
				12	16.2 (34.0)		

Table 14--continued.

Species	Date	Natural Succession n	Natural Succession loss	Enriched Succession n	Enriched Succession loss
Canavalia sp.	Oct. 79				
	June 80				
Solanum torvum	Oct. 79				
Vigna sp.	Oct. 79				
	Feb. 79				
Solanum jamaicense	Feb. 80				
	June 80				
Hyptis vilis	Feb. 80				
Iresine diffusa	Feb. 80				
Zea mays	Oct. 79				
Manihot esculenta	Feb. 80			17	4.0 (4.0)
	June 80				

Table 14--extended.

Mimic of Succession		Monoculture		Enriched Succession Treated with Insecticide		Monoculture Treated with Insecticide	
n	loss	n	loss	n	loss	n	loss
				10	0.7 (1.1)		
				10	13.2 (26.1)		
				10	7.4 (8.7)		
				6	0.04 (0.1)		
				16	0.8 (2.6)		
				12	6.2 (5.7)		
				1	4.1 (---)		
				12	6.5 (4.6)		
				10	21.4 (51.6)		
		14	6.2 (7.0)			5	9.8 (9.1)
24	35.7 (64.0)	68	11.5 (29.4)			58	5.2 (16.1)
1	1.7 (---)	4	9.1 (5.4)			3	2.3 (0.3)

[a]Includes at least six species of grasses that were indistinguishable by vegetative parts.

Table 15. Mean and median herbivory rates on selected species in plots with and without insecticide treatment. Number of leaves (n) includes samples from all dates for which with/without insecticide comparison could be made.

Species	Not Treated with Insecticide				Treated with Insecticide				p Value[a]
	n	Loss (cm^2/m^2/day) $\bar{x}$	(s.d.)	Median	n	Loss (cm^2m^2/day) $\bar{x}$	(s.d.)	Median	
Clibadium aff. *surinamense*[b]	75	14.6	(19.2)	8.9	20	7.0	(9.0)	3.9	.02, .02, .15
Erythrina costaricensis	46	35.3	(38.1)	22.3	15	1.5	(1.2)	1.0	<.01, <.01, <.01
Manihot esculenta	72	11.3	(28.6)	1.9	61	5.0	(15.7)	0.9	.05, .05, .14
Panicum maximum	44	13.4	(15.1)	7.7	10	2.7	(4.9)	0.8	<.01, <.01, <.01
Phytolacca rivinoides	125	18.0	(33.6)	5.7	33	9.6	(20.4)	2.6	.01, .01, .08

[a]Wilcoxon 2-sample rank sums test, Kruskal-Wallis test, median test.

[b]For this species, n is number of opposite leaf pairs.

Species Composition

At 18 mo the enriched succession treated with insecticide had 81 plant species on 248 m^2, as compared to 159 species on 1536 m^2 in the enriched succession not treated with insecticide. Because the insecticide plots were smaller than the other plots, species abundance and diversity comparisons of the systems with and without insecticide were difficult. To make valid comparisons, 25 subplots were randomly selected from all subplots where species composition was monitored in the enriched succession without insecticide. Each of the subplots was 12 m^2 (3, 1x4 m strips of vegetation), equal in area and shape to the area monitored in the enriched succession with insecticide. Plant species diversity, evenness, and turnover in the enriched succession treated with insecticide were then compared to mean values from the 25 subplots in the enriched succession not treated with insecticide.

Species richness was higher in the enriched succession treated with insecticide (23 species intersected by 36 LAI measurements) than in the enriched succession not treated with insecticide (16 species) at 3 mo, but at 18 mo the values were not different (Table 16). This suggests that in the earliest stages of succession the reduction of herbivory allowed a wider variety of species to survive and compete, but increased species richness was not maintained over long periods through application of insecticide.

Table 16. Changes in number of species, diversity, and evenness in enriched succession and enriched succession treated with insecticide.

Characteristic	Vegetation Age (mo)	Without Insecticide[a]	With Insecticide[b]
Number of leaves intersected by 36 LAI measurements	3	161 (135-178)	149
	18	182 (113-258)	193
Number of species intersected by 36 LAI measurements	3	16 (11-21)	23[c]
	18	26 (19-37)	22
Number of species intersected both at 3 mo and 18 mo		8 (5-10)	11[c]
Number of species gained from 3 mo to 18 mo		18 (12-29)	11
Number of species lost from 3 mo to 18 mo		8 (6-13)	12
Species diversity (H')[d]	3	0.87 (0.60-1.05)	1.06
	18	1.03 (0.81-1.20)	1.11
Evenness[e]	3	0.71 (0.54-0.80)	0.78
	18	0.73 (0.61-0.85)	0.83
Community similarity (C) between age 3 mo and age 18 mo[f]		0.51 (0.30-0.68)	0.54

[a]Each value is the mean of measurements in 25 subplots randomly selected from the enriched succession without insecticide. Each subplot had area 12 m^2. Ranges are given in parentheses.

[b]Each value is based on measurements in 12 m^2 of ecosystem.

[c]Value is outside the 95% confidence interval for the mean in enriched succession without insecticide.

[d]$H' = -\Sigma(n_i/N)\log(n_i/N)$, where n_i is the number of leaf intersections for species i, and N is total number of leaves intersected (Shannon index).

[e]Evenness = H'/S, where H' is Shannon diversity index and S is the number of species.

Table 16--continued.

[f]$C = a(1) + a(2) +...+ a(i) +...+ a(n)$, where i is a species present at 3 mo and/or 18 mo, a(i) is the lesser percent LAI value for species i from the two dates, and n is the total number of species.

Reduction of herbivory favored some species that would not have been able to compete successfully under higher herbivore pressure. For example, six species (Solanum torvum, Gouania lupuloides, Solanum jamaicense, Vigna sp., Canavalia sp., and Ipomoea sp.) that were abundant (accounted individually for ≥2% of ecosystem LAI) in the enriched succession with insecticide were not abundant in the enriched succession without insecticide.

Although species diversity and evenness were not different in plots with and without insecticide, species composition was different at both 3 and 18 mo. At 3 mo, four of the eight abundant species in the insecticide plots were not abundant (although present) in the plots without insecticide treatment (Table 17). At 18 mo the differences were more striking; eight of the 13 abundant species in the insecticide plots were not abundant in the enriched succession without insecticide. In a complete species inventory at 18 mo, 11 species present in the enriched succession treated with insecticide (248 m^2 area) were not found in the enriched succession without insecticide (1536 m^2 area). These species included Iresine celosia, Cola nitida, Inga thibaudiana, Mollinedia costaricensis, Heliocarpus sp., Ipomoea sp., and five unidentified species.

The community similarity index, C, was used to compare rates of species turnover in the enriched succession with and without insecticide from 3 to 18 mo. Species turnover

Table 17. Species accounting for ≥2% of LAI in enriched succession without and with insecticide treatment. A dash (-) indicates that a species comprised <2% of ecosystem LAI.

Species	Age 3 mo		Age 18 mo	
	Without Insecticide	With Insecticide	Without Insecticide	With Insecticide
	% LAI		% LAI	
Phytolacca rivinoides	19.7	13.4	-	-
Solanum nigrescens	3.2	4.7	-	-
Clibadium aff. surinamense	8.2	20.8	7.2	20.2
Gramineae[a]	8.4	6.7	12.8	9.3
Momordica charantia	6.7	-	-	-
Borreria latifolia	2.3	-	-	-
Bocconia frutescens	13.6	-	10.8	-
Panicum maximum	23.7	-	27.2	16.1
Vernonia patens	2.2	-	7.3	3.1
Solanum torvum	-	2.0	-	-
Hymenachne amplexicaulis	-	19.5	-	9.3
Borreria laevis	-	12.7	-	6.2
Canavalia sp.	-	6.0	-	9.3
Ipomoea neei	-	-	2.9	-
Musa paradisiaca	-	-	2.1	-
Ipomoea sp.	-	-	2.0	3.6
Panicum trichoides	-	-	-	4.7
Gouania lupuloides	-	-	-	3.1
Vigna sp.	-	-	-	3.1
Cyperaceae[b]	-	-	-	2.6
Solanum jamaicense	-	-	-	2.6

[a]Includes at least six species of grasses that were indistinguishable by vegetative parts.

[b]Includes at least four species of sedges that were indistinguishable by vegetative parts.

was rapid, both in plots with insecticide (C=0.54) and in plots without insecticide (C=0.51). The C values for the two systems were not significantly different (Table 16), indicating that the insecticide treatment did not affect the rate of change of species composition during early succession. However, the common species early in succession in the plots treated with insecticide tended to be present in the ecosystem for a longer period of time than in plots not treated with insecticide. More species were intersected by LAI measurements at both 3 and 18 mo in the insecticide plots (11 species) than in the plots without insecticide (8 species).

Leaf Area Index

Leaf area index was higher in the monoculture treated with insecticide than in the monoculture not treated with insecticide (Fig. 32). The enriched succession had high LAI values in plots both with and without insecticide (Fig. 33). Thus naturally occurring herbivory reduced ecosystem LAI in the monoculture, but not in the diverse system. One exception to this was at the end of the dry season (May 1980), when the enriched succession with insecticide had significantly higher LAI than the enriched succession without insecticide. During the dry season in Turrialba, a period of high insect activity and low net primary productivity, losses to herbivores in the plots without

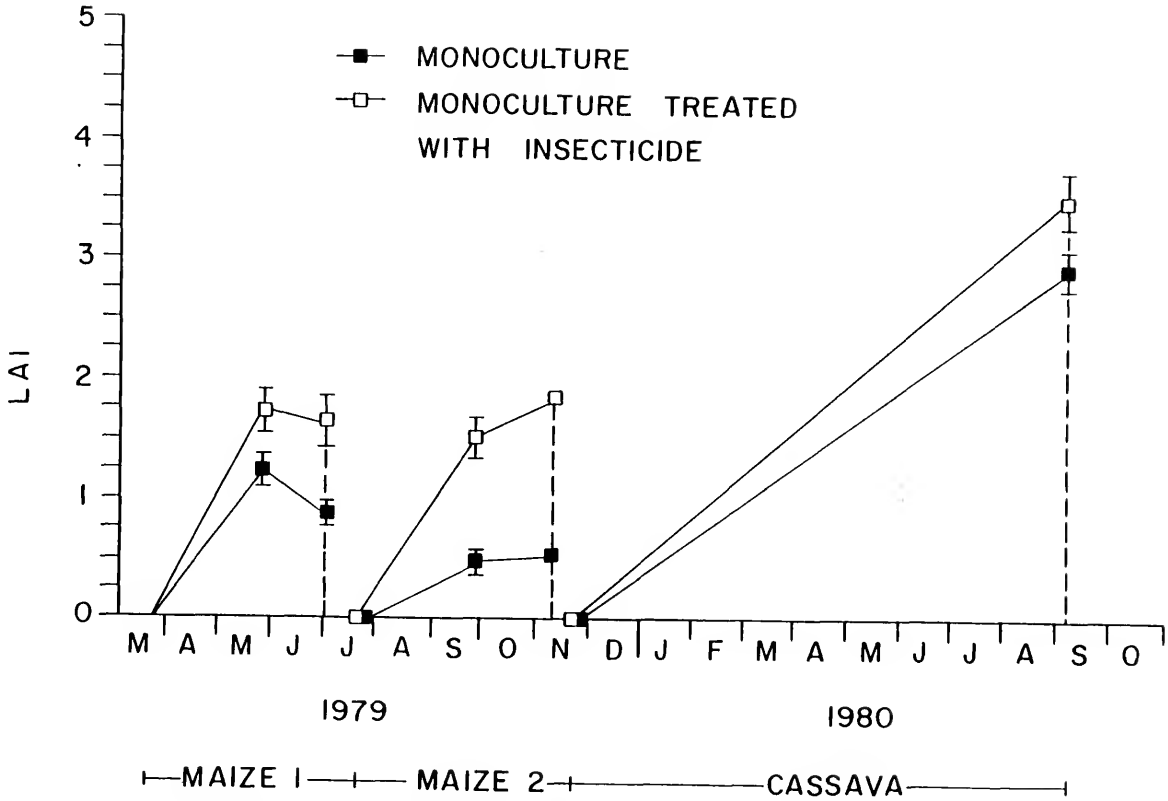


Figure 32. LAI in the monoculture with and without insecticide treatment. Values are $\bar{x} \pm 1$ s.e.

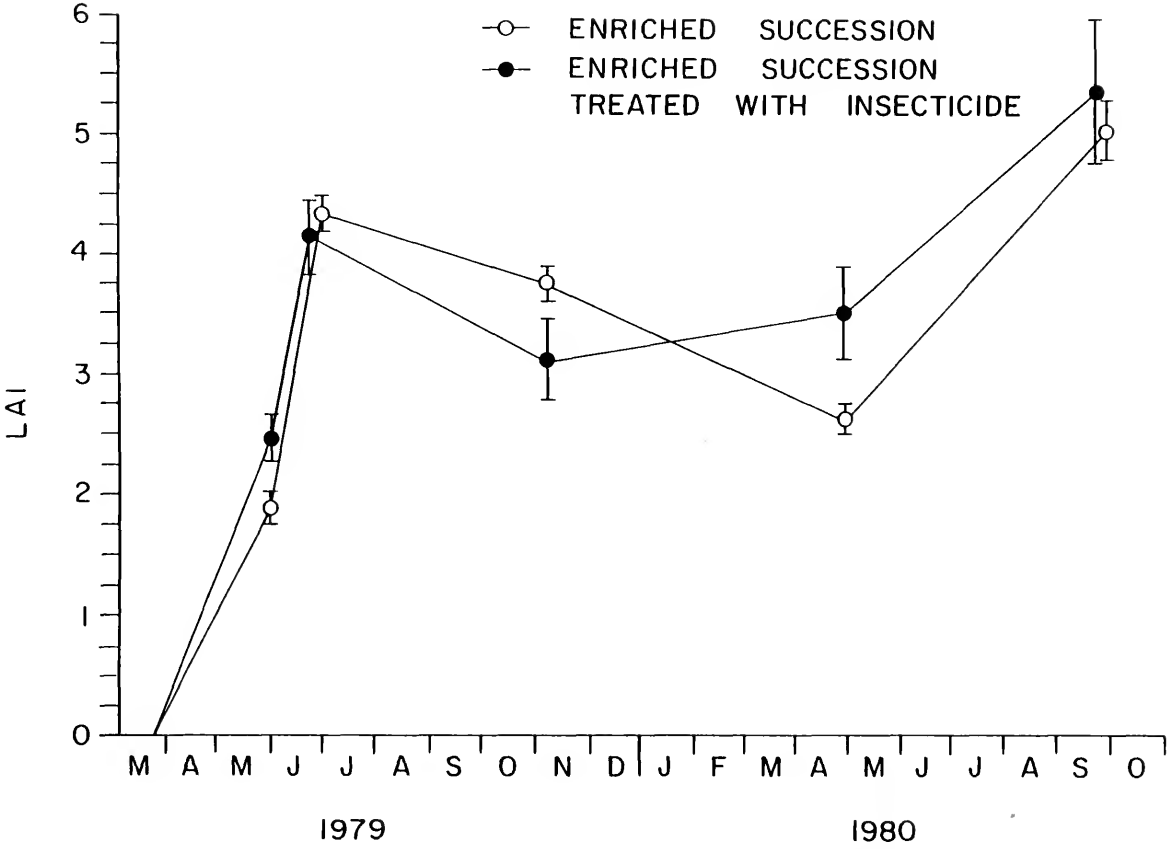


Figure 33. LAI in the enriched succession with and without insecticide treatment. Values are $\bar{x} \pm 1$ s.e.

insecticide were not offset by high leaf productivity as at other times of the year.

The enriched succession treated with insecticide had a larger concentration of leaf tissue near the top of the canopy than did the enriched succession without insecticide (Fig. 34). This may be because terminal buds and young leaves were protected from herbivory in the insecticide plots. A dry season decrease in leaf tissue near the ground occurred in the plots without insecticide (at 13 mo), but not in the plots with insecticide.

Mean canopy heights in the enriched succession with and without insecticide treatment were not significantly different at any time during the study (Table 18).

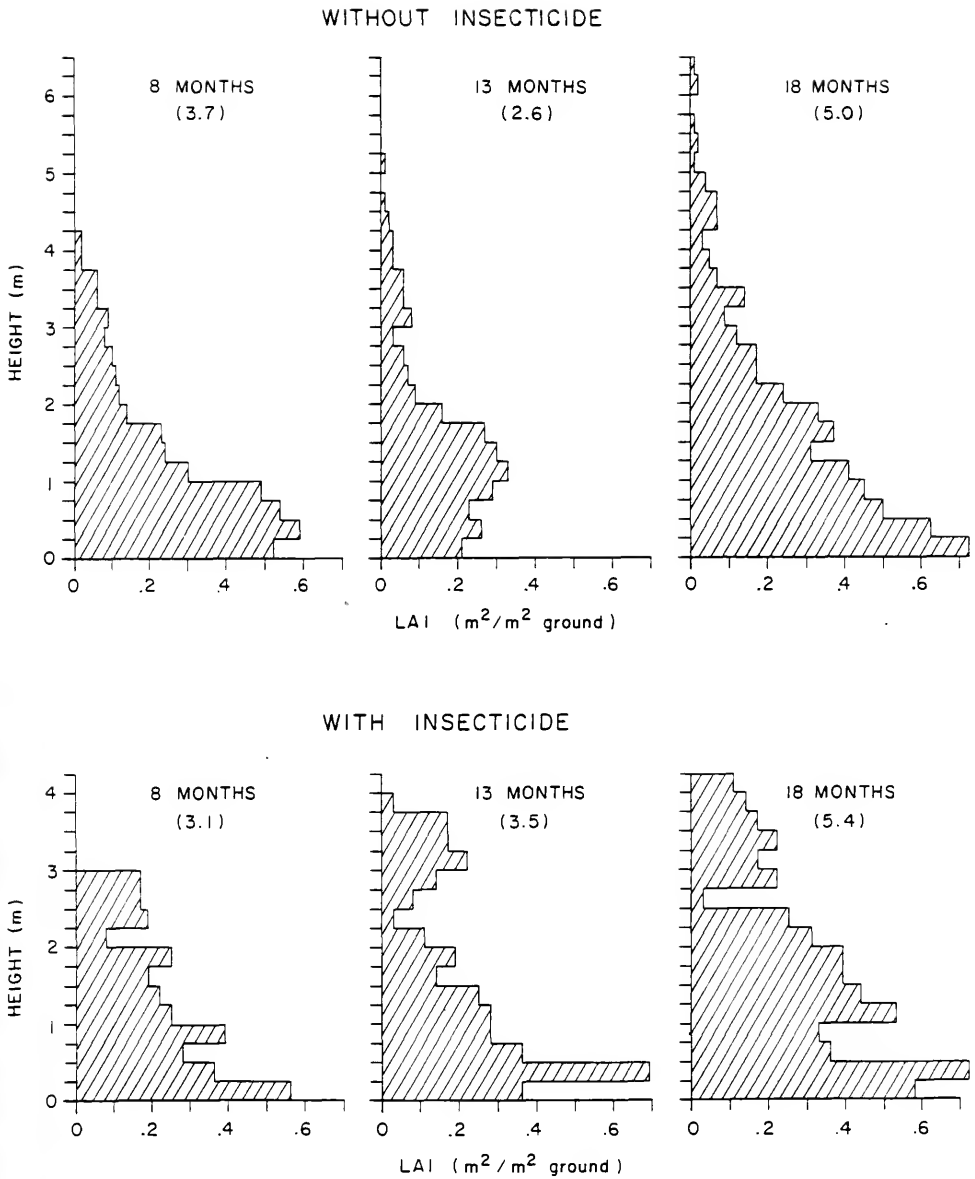


Figure 34. Vertical distribution of leaf area in the enriched succession with and without insecticide. Total LAI at each age is in parentheses.

Table 18. Mean canopy height in enriched succession with and without insecticide treatment. Values are $\bar{x} \pm$ s.d.; n=12 with insecticide, n=60 without insecticide.

Vegetation Age (mo)	Mean Canopy Height (m)	
	Enriched Succession Without Insecticide	Enriched Succession With Insecticide
3	1.6 ± 0.5	1.9 ± 0.4
7	2.6 ± 1.0	2.5 ± 0.9
12	3.5 ± 1.1	3.4 ± 0.9
18	3.7 ± 1.2	3.7 ± 1.2

Above-Ground Biomass

Above-ground biomass developed at approximately the same rate in the enriched succession and the enriched succession treated with insecticide during most of the study (Fig. 35). At 1.5 yr, however, leaf biomass and total above-ground biomass were higher in the enriched succession without insecticide than in the enriched succession with insecticide (see Appendix B for tables of biomass means). Total above-ground living biomass (leaves + stems + reproductive parts) in the enriched succession treated with insecticide was approximately 1.4 kg/m² at 1.5 yr, less than half the biomass in the enriched succession without insecticide (Fig. 36). Thus herbivores did not limit the rate of biomass accumulation in the diverse successional system. This may reflect the differences in species composition between the enriched succession and the enriched succession treated with insecticide. Some of the species competitively favored by the insecticide treatment were species that accumulated biomass at a slower rate than did the dominant species in the enriched succession without insecticide.

Above-ground biomass was similar in the monoculture plots with and without insecticide treatment for the first maize crop (Fig. 37 - 38). Maize yields from the first planting with insecticide (mean $\pm$ 1 s.d. = 2985 $\pm$ 940 kg/ha, ear fresh weight) and without insecticide (4570 $\pm$ 1606) did not differ significantly. The second planting of maize grew

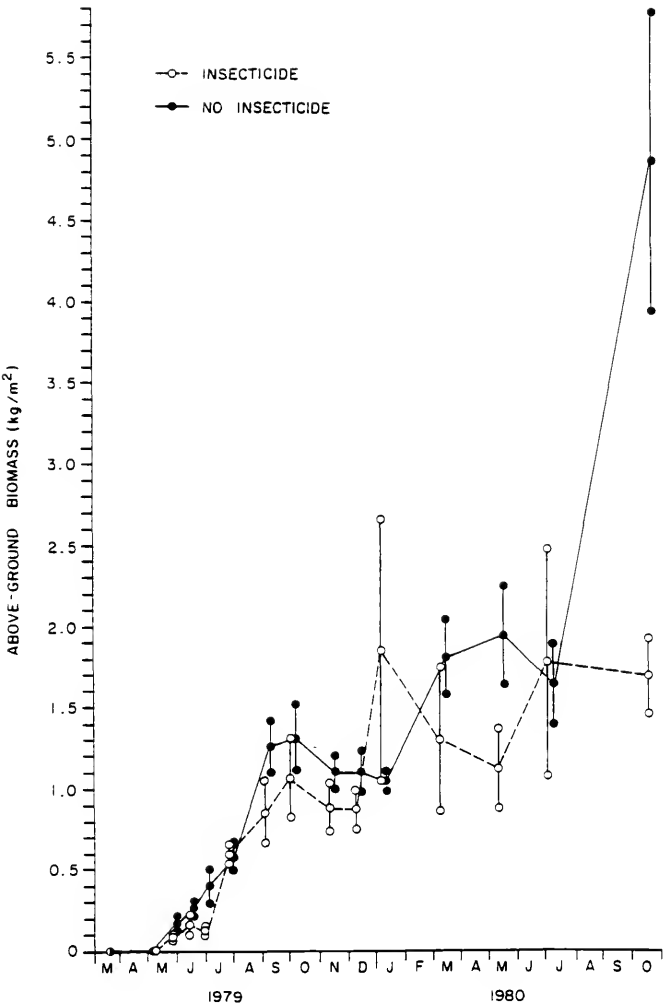


Figure 35. Total above-ground biomass in enriched succession with and without insecticide. Values are $\bar{x} \pm 1$ s.e.

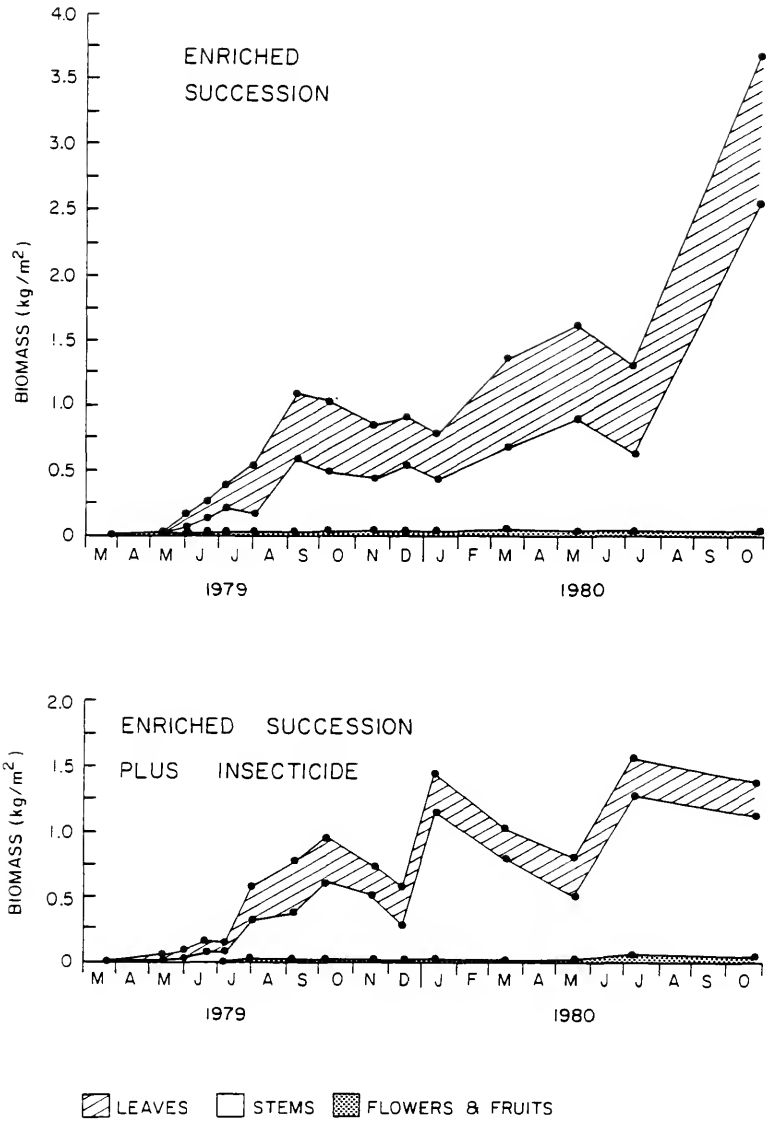


Figure 36. Above-ground living biomass by vegetation compartment in enriched succession with and without insecticide.

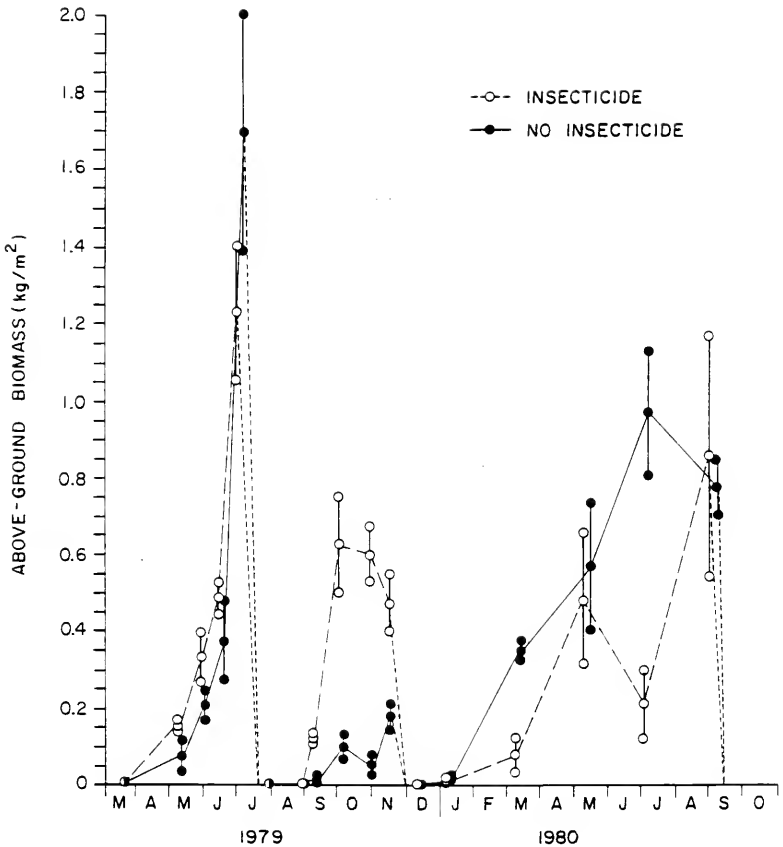


Figure 37. Total above-ground biomass in the monoculture with and without insecticide. Values are $\bar{x} \pm 1$ s.e.

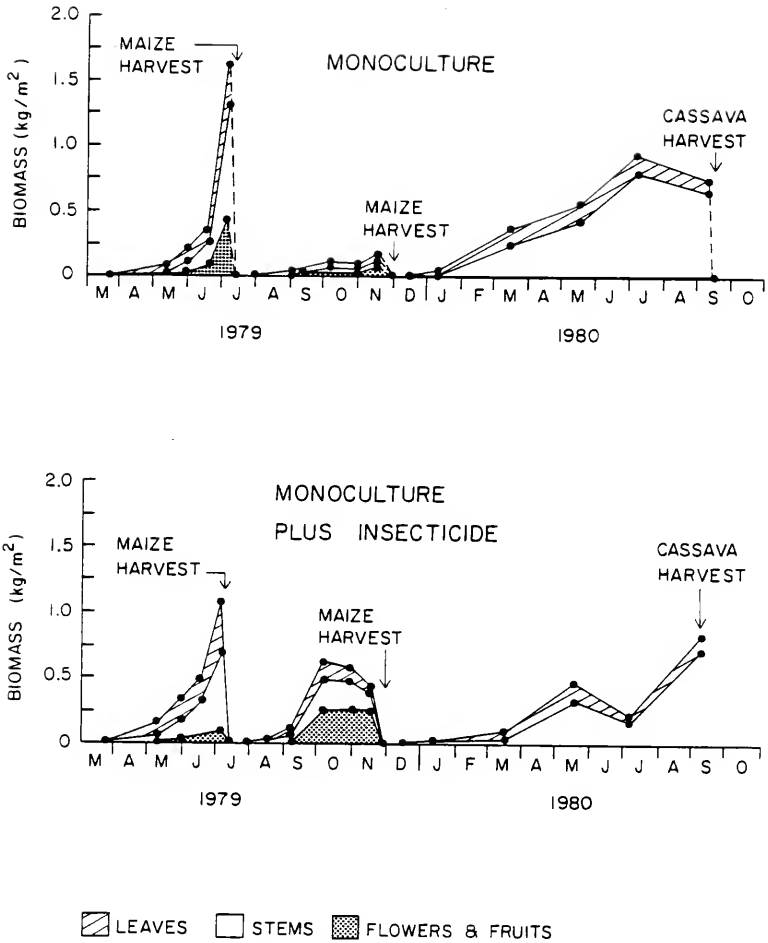


Figure 38. Above-ground living biomass by vegetation compartment in the monoculture with and without insecticide.

very poorly in the plots without insecticide. Total above-ground biomass was higher in insecticide plots from 7 wk after planting until maize harvest at 17 wk. Yield from the second maize planting was significantly higher with insecticide treatment (4390 ± 1918 kg/ha) than without insecticide treatment (1945 ± 921 kg/ha). Above-ground herbivore damage to the maize was low. The growth difference in the second maize with and without insecticide was due primarily to differences in below-ground herbivory. The first crop of maize grew equally well with and without insecticide, possibly because the experimental plots were in a newly cleared area that had not been recently cultivated. Because the plots were >1 km from the nearest cultivated maize, perhaps some agronomic soil pests did not 'find' the experimental maize and build up large populations until the second planting.

Biomass production in the cassava was approximately the same with and without insecticide application. At two dates (16 and 32 wk after planting), cassava biomass was significantly lower in plots with insecticide than in plots without insecticides (Fig. 37). Shading effects are pronounced in cassava, and the lower biomass in the cassava with insecticide may reflect delayed development due to partial shading by vegetation around the plots. At the time of harvest (42 wk), no significant differences in biomass due to insecticide application were detected. Cassava yield

(kg/ha, tuber fresh weight, mean ± 1 s.d.) did not differ significantly between plots with insecticide (8338 ± 3679) and without insecticide (10,883 ± 2642).

Litterfall

Although there were no statistically significant differences in mean monthly autochthonous litterfall between plots with and without insecticide, several trends were apparent in the data (Fig. 39). Insecticide application affected litterfall rates in the maize monocultures, but not in the cassava monoculture or the enriched succession. Higher maize biomass in the insecticide plots during growth of the second maize crop was accompanied by increased litter production. In addition, dead maize leaves remained attached to the plants and resulted in more standing dead biomass in insecticide plots. Mean monthly litterfall in the enriched succession and cassava monoculture, both with and without insecticide, ranged from 29 to 35 g/m^2, and there were no significant differences due to insecticide application.

Seasonal litterfall trends were similar in plots treated with insecticide and plots not treated with insecticide (Figs. 40 and 41). Lowest values occurred during May-June 1980, at the beginning of the rainy season. At this time of year, much dead plant material had already been shed during the dry season, and new plant growth was beginning.

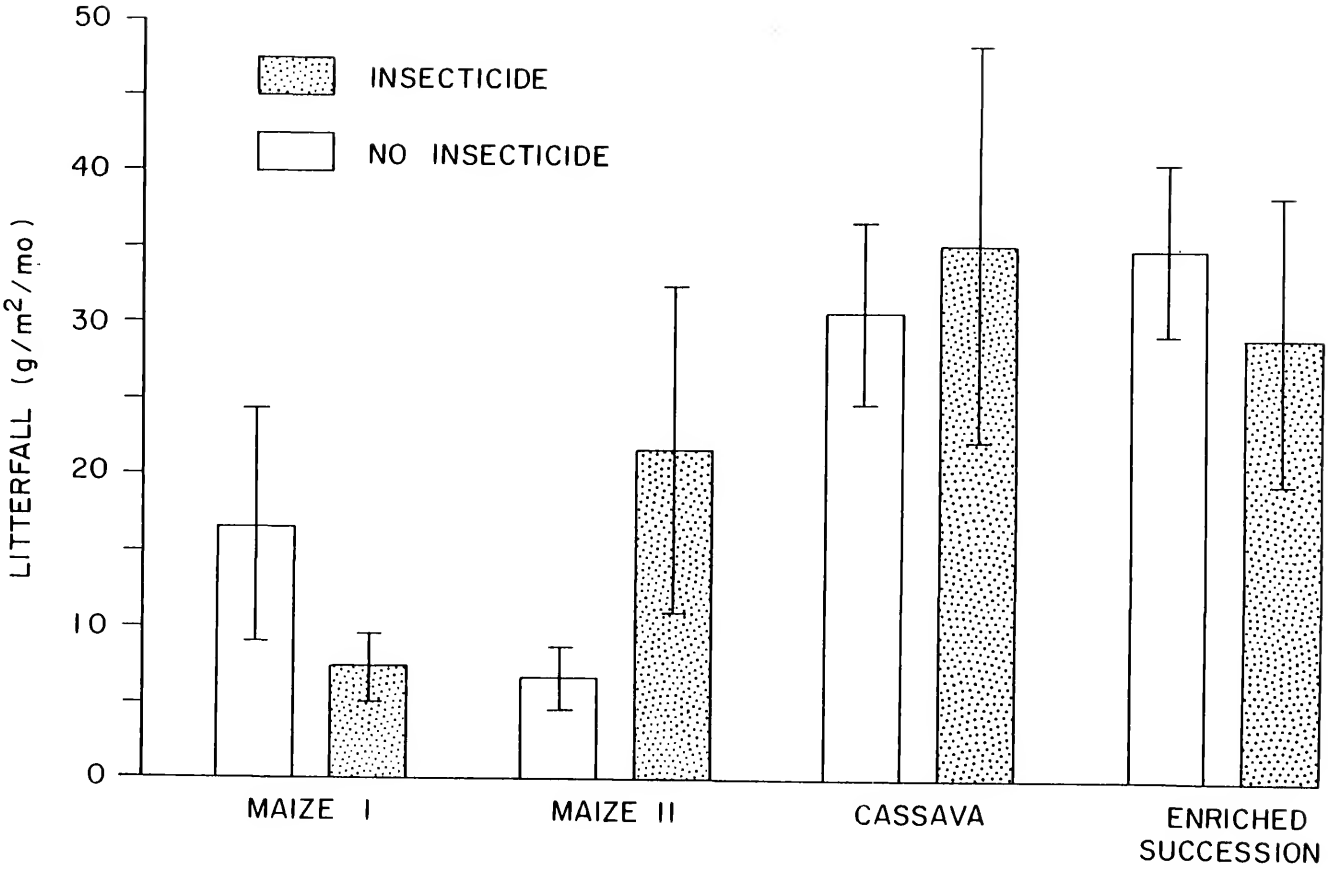


Figure 39. Monthly litterfall means in three monocultures and enriched succession, with and without insecticide. Confidence intervals are ± 1 s.e.

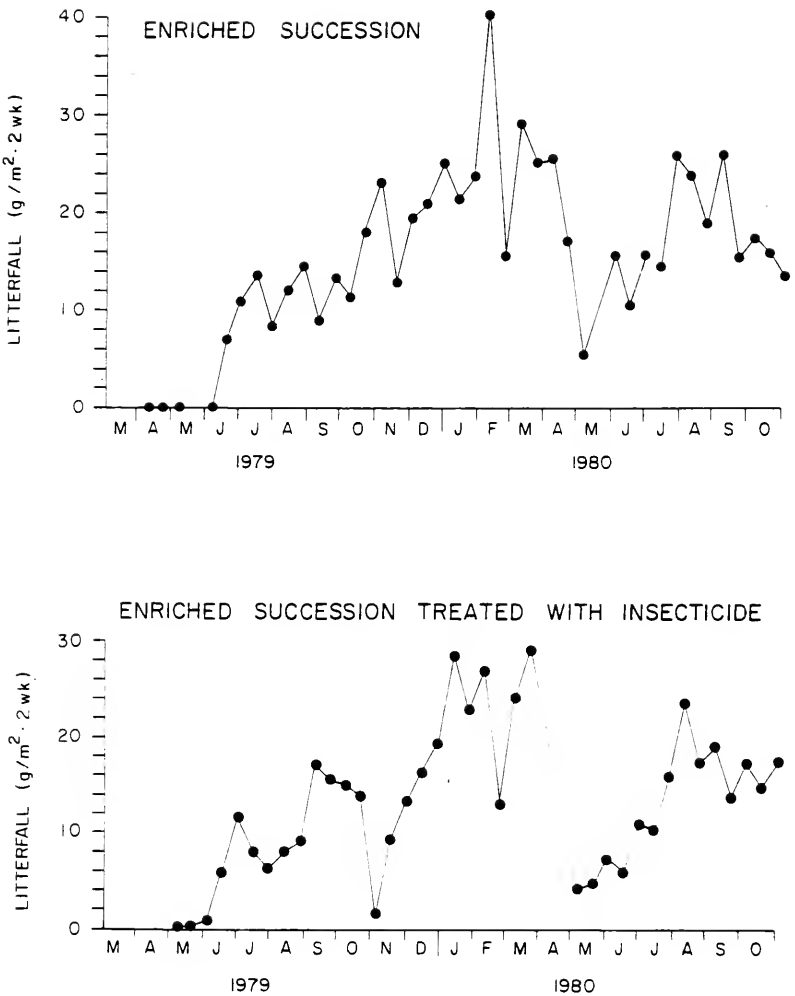
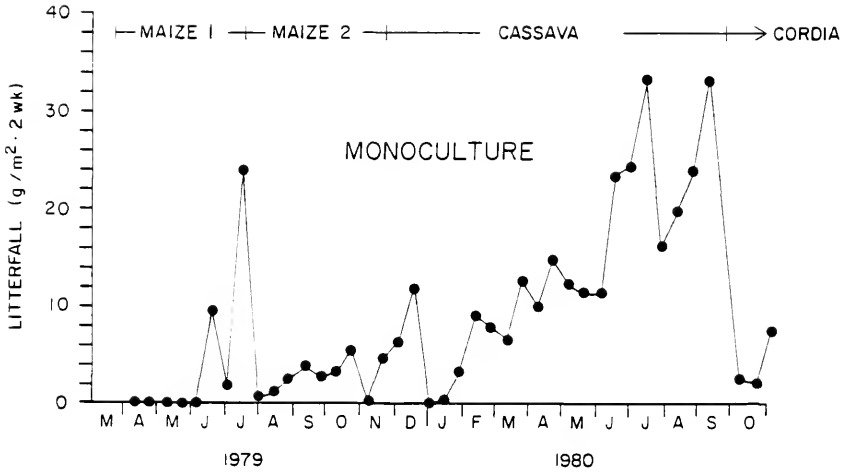


Figure 40. Litterfall in enriched succession with and without insecticide, April 1979 - October 1980.



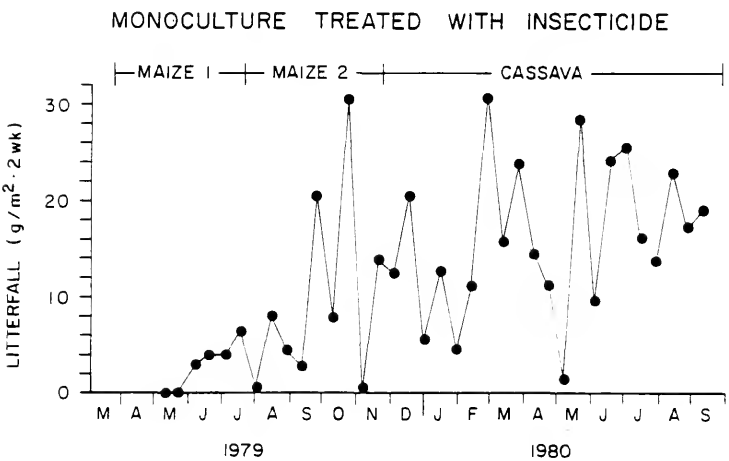


Figure 41. Litterfall in the monoculture with and without insecticide, April 1979 - October 1980.

Above-Ground Productivity

In both the enriched succession and the monoculture, annual net primary productivity rates were higher in plots not treated with insecticide than in plots treated with insecticide (Table 19). This result suggests a possible stimulation of productivity due to herbivory, and is consistent with the results of the artificial defoliation study and the work of others (e.g., Detling et al. 1979). In the enriched succession without insecticide, higher net primary productivity was accompanied by higher turnover rates (litterfall, herbivory, and production of standing dead biomass).

In the monoculture, higher net primary productivity in the plots without insecticide was not associated with higher turnover rates on an annual basis (Table 19) or for individual cultivars (Table 20). Net primary productivity was higher in plots not treated with insecticide than in plots treated with insecticide for the first maize planting and the cassava. For the second maize planting, net primary productivity was higher in plots that received insecticide (Table 20). Although above-ground insect damage on maize was not lower in the insecticide plots than in the plots without insecticide, root biomass data (C. W. Berish, unpublished data) and herbivorous nematode data indicate that below-ground herbivory was reduced substantially in the insecticide plots. The productivity differences in the

Table 19. Annual net above-ground productivity, biomass losses, and biomass accumulation in ecosystems with and without insecticide. Values are $g/m^2/yr$.

Ecosystem	Net Above-Ground Productivity	Biomass Losses				Net Above-Ground Biomass Accumulation
		Litter-fall	Standing Dead Biomass Production	Herbivory	Harvest	
Enriched succession						
Without insecticide	2396	398	552	72	0	1374
With insecticide	2039	321	316	29	0	1373
Monoculture						
Without insecticide	2267	243	89	15	1920	0
With insecticide	1956	304	150	15	1487	0

Table 20. Mean monthly above-ground productivity and plant turnover rates in three monocultures with and without insecticide. Values ($g/m^2/30$ days) were estimated from productivity model.

Monoculture	Productivity	Plant Turnover Rate			Total Plant Turnover Rate
		Litterfall	Standing Dead Biomass Production	Herbivory	
Maize (first planting)					
Without insecticide	524	9	24	0.3	33
With insecticide	373	3	50	1.9	55
Maize (second planting)					
Without insecticide	50	7	3	0.3	10
With insecticide	122	22	5	1.9	29
Cassava					
Without insecticide	123	30	3	2.0	35
With insecticide	103	35	2	0.8	38

maize with and without insecticide are probably due to the below-ground herbivory differences.

Application of insecticide to plots may affect many factors related to ecosystem function in addition to reducing herbivorous insect numbers and damage rates. Soil microorganism populations, decomposition rates, nutrient cycling rates, and insect predator and parasite populations are probably also affected by insecticide additions. Thus the results of the insecticide treatment on net primary productivity cannot be attributed entirely to reduction of herbivore pressure. Changes in other ecosystem processes due to insecticide application were not measured.

The net primary productivity curve for the enriched succession treated with insecticide (Fig. 42) was similar to the curve for the enriched succession without insecticide (Fig. 29), with high and low values occurring during approximately the same time periods in both ecosystems. Maximum production of standing dead biomass occurred at different times in the two ecosystems.

Net primary productivity curves for the monoculture with and without insecticide differed in several ways (Figs. 31 and 43). Net primary productivity rate increased more rapidly during the first few weeks of growth of the first maize crop in insecticide plots than in plots without insecticide, but the maximum daily rate was higher in the plots without insecticide (45 g m^{-2} day^{-1}) than in plots

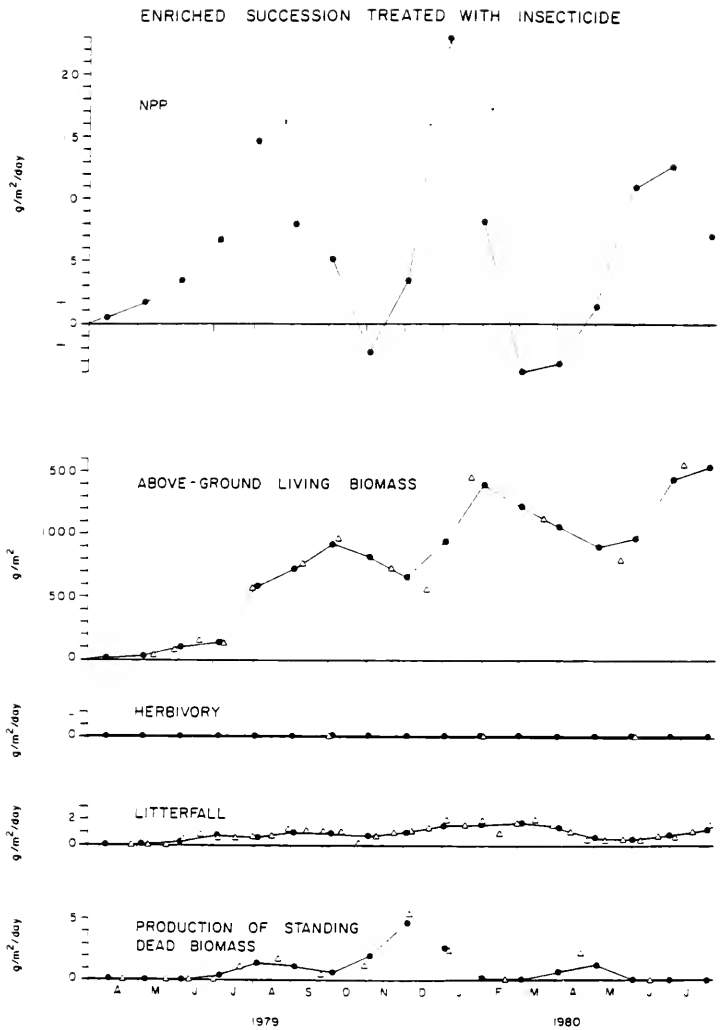


Figure 42. Net primary productivity (NPP), above-ground living biomass, herbivory, litterfall, and production of standing dead biomass in enriched succession treated with insecticide. Triangles are data from field measurements; black dots are estimated monthly means.

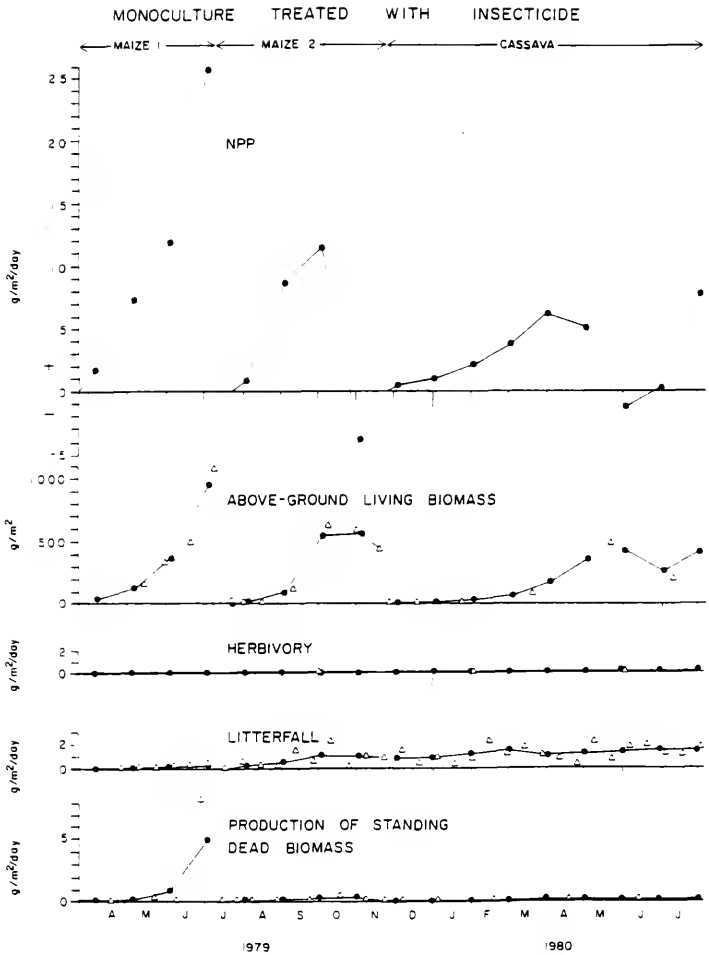


Figure 43. Net primary productivity (NPP), above-ground living biomass, herbivory, litterfall, and production of standing dead biomass in the monoculture treated with insecticide. Triangles are data from field measurements; black dots are estimated monthly means.

with insecticide (25 g m^{-2} day^{-1}). Productivity of the second maize crop was high in plots with insecticide and low in plots without insecticide. The period of low productivity in the cassava monoculture treated with insecticide may be the effect of partial shading of the cassava by plants surrounding the plots. Cassava is very sensitive to shade, and since the insecticide plots were smaller than the plots without insecticide (82.5 m^2 instead of 256 m^2), shading by surrounding vegetation was more pronounced in the insecticide plots.

Responses to Artificial Defoliation

Results of Preliminary Study

Leaf regrowth was extremely rapid in both the enriched succession and the maize monoculture after removal of approximately 50% of the leaf area of each ecosystem (Fig. 44). Although between-plot variability was high and no significant differences between defoliated and non-defoliated plots were found in this pilot study, the observed trends were interesting. In the enriched succession, leaf biomass increased rapidly in the defoliated plots at a time when leaf biomass in non-defoliated plots was decreasing. Similarly, leaf biomass did not decrease in the defoliated maize monoculture as in the non-defoliated maize. Only 6 wk after leaf removal, mean leaf biomass in the defoliated maize was almost equal to that in the

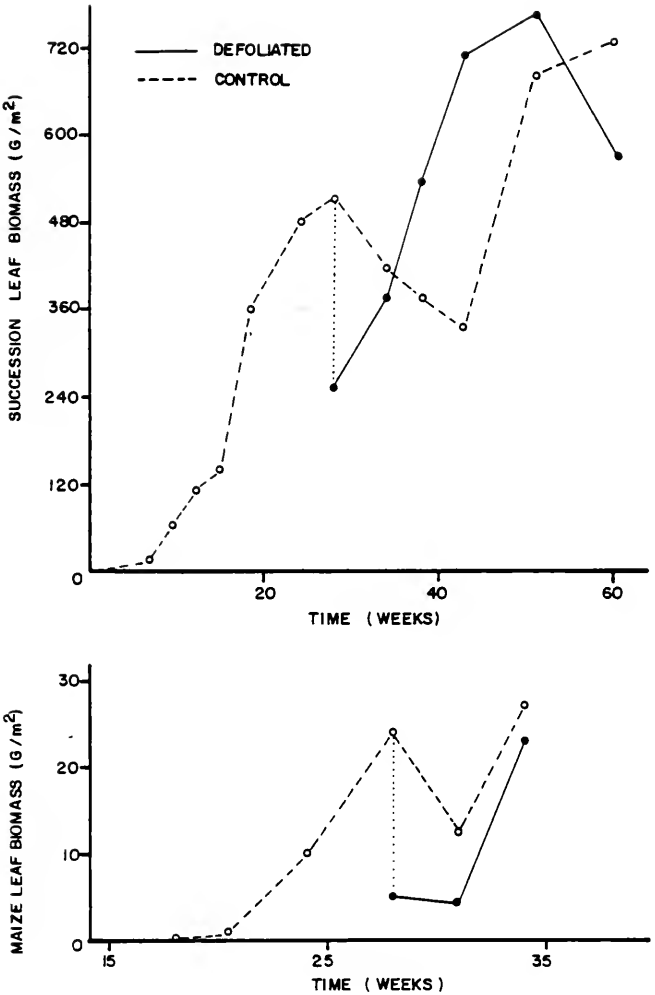


Figure 44. Leaf biomass in defoliated and non-defoliated enriched succession and maize monoculture.

non-defoliated maize. The preliminary study was done on the second planting of maize. The growth of this maize was poor because of soil pest infestations, and the effect of this additional stress on the response pattern of the maize after defoliation is not known.

Responses to Repeated Defoliation

A series of three defoliations at monthly intervals was performed in the natural succession and in the cassava monoculture. The successional vegetation was 12 mo old and the cassava was 4.5 mo old when the experiment began. Approximately 50% of the leaf area of each ecosystem was removed at each defoliation. The amount of leaf tissue removed was slightly higher than 50% for the first defoliation and slightly less than 50% for the second and third defoliations (Table 21).

Changes in leaf productivity. Production of new leaf tissue was rapid in the natural succession and in the cassava monoculture after each defoliation (Figs. 45 and 46). Leaf area index (LAI) in the defoliated cassava was not significantly different from LAI in the non-defoliated cassava at the end of 20-22 days of regrowth following the first and second defoliations (one-way analysis of variance). After the third defoliation and 19 days of regrowth, the LAI of the defoliated cassava was 28% less than the LAI of the non-defoliated cassava ($p<.01$).

Table 21. Amounts of leaf tissue removed during artificial defoliation experiments. Values are means of three replications (± s.d.).

Ecosystem	Defoliation	Leaf Tissue Removed		
		m^2 leaf/m^2 ground	g/m^2	Percent of Total Leaf Area
Natural succession	1	1.13 ± 0.19	81 ± 26	62
	2	0.92 ± 0.22	74 ± 21	43
	3	1.58 ± 0.15	108 ± 17	46
Cassava monoculture	1	1.25 ± 0.50	51 ± 22	65
	2	0.86 ± 0.38	46 ± 12	49
	3	0.99 ± 0.21	71 ± 16	47

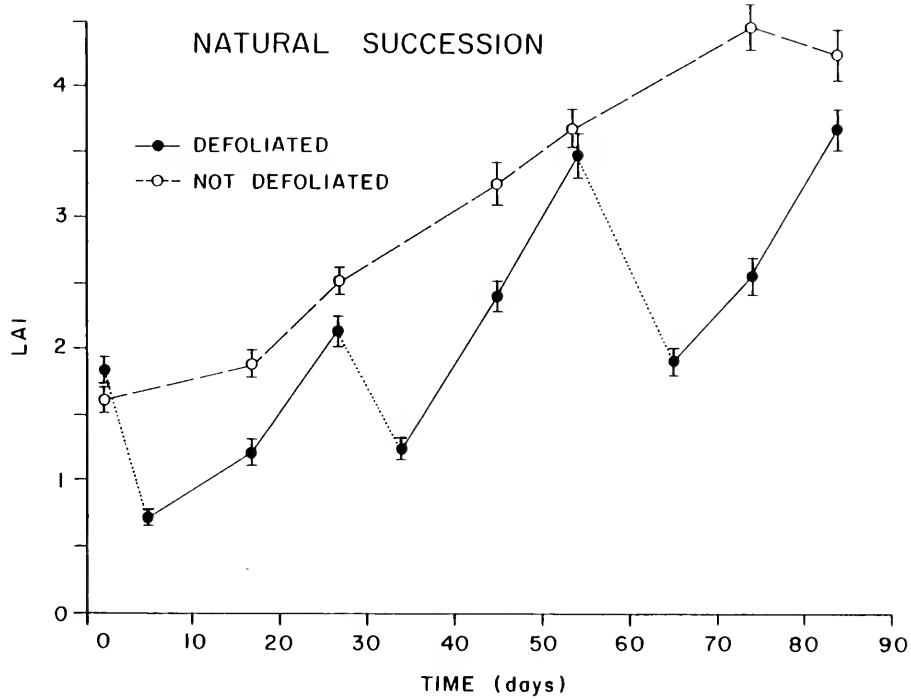


Figure 45. Leaf area index in natural succession with and without artificial defoliation. Values are $\bar{x} \pm 1$ s.e.; n = 225.

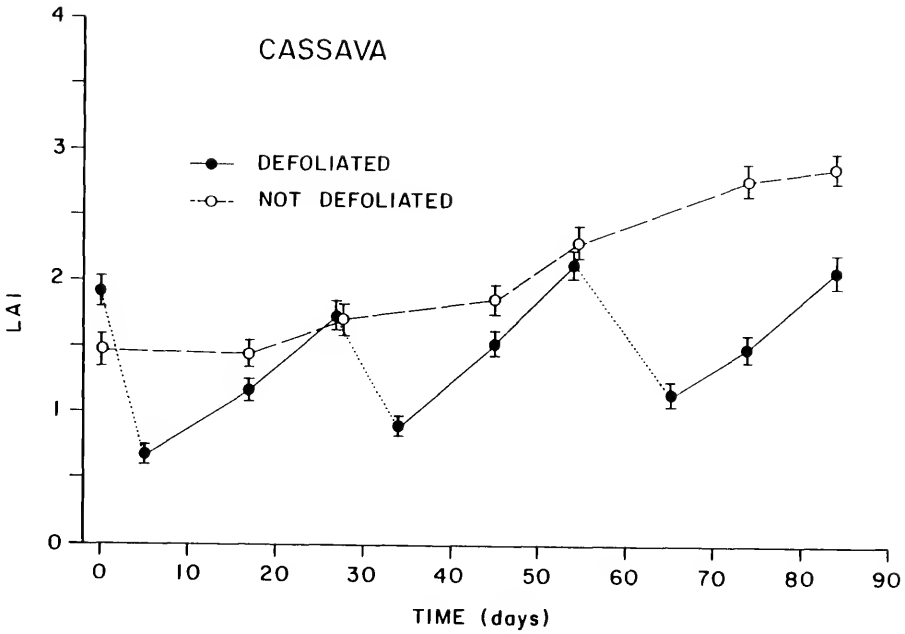


Figure 46. Leaf area index in cassava monoculture with and without artificial defoliation. Values are $\bar{x} \pm 1$ s.e.; n = 225.

The LAI in the defoliated natural succession plots was 15% less than that in the control plots after the first defoliation-regrowth period ($p<.05$), equal to that of the control plots after the second defoliation-regrowth period, and 11% less than that of control plots after the third defoliation-regrowth period ($p<.05$). It appears that the LAI in both the defoliated cassava and the defoliated succession would have reached the LAI levels in non-defoliated plots after each defoliation if the regrowth periods had been longer. Extensions of the growth curves after the third defoliation (Figs. 45 and 46) indicate that the LAI in the defoliated natural succession would equal that of the non-defoliated natural succession after 24 days of regrowth, while the LAI of the defoliated cassava would require 35 days of regrowth. Time limitations did not allow defoliation experiments with different defoliation intensities and different regrowth periods to be performed. The high defoliation level (50%) and short regrowth periods (1 mo) were chosen to simulate extreme levels of stress to the ecosystems.

The series of defoliations began at the end of the dry season (mid-April 1980). The onset of the rains approximately 15 days after the first defoliation was accompanied by increases in LAI in the non-defoliated (control) plots. Thus the LAI of the defoliated systems had to increase to levels greater than their pre-defoliation levels to 'catch up' to the non-defoliated systems.

Net rates of leaf production (increments in leaf area) were used to compare defoliated and non-defoliated ecosystems. The non-defoliated systems were growing, but the defoliated systems were growing at a faster rate. For both the cassava monoculture and the natural succession, increment in leaf area was higher in defoliated plots than in plots that were not defoliated (Fig. 47). Mean LAI increment in the defoliated natural succession was 0.091 m^2 m^{-2} ground day^{-1}, as compared to 0.032 m^2 m^{-2} ground day^{-1} in control plots. Leaf growth rates in the cassava were lower. However, defoliated cassava had higher rates (0.054 m^2 m^{-2} ground day^{-1}) than non-defoliated cassava (0.016 m^2 m^{-2} ground day^{-1}).

The data show that defoliation stimulated leaf production in both the high and low diversity systems. However, the amount of stimulation of leaf productivity differed in the two systems. To compare the amount of stimulation of leaf production in cassava and natural succession, the percent differences in leaf productivity rates between defoliated and non-defoliated plots were calculated (percent difference = $100(x-y)/y$, where x = change in LAI in defoliated plots and y = change in LAI in non-defoliated plots). In the cassava monoculture, leaf productivity was stimulated to more than five times its normal rate after the first defoliation, but the amount of stimulation was <200% after the second and third defoliations (Fig. 48). The trend was

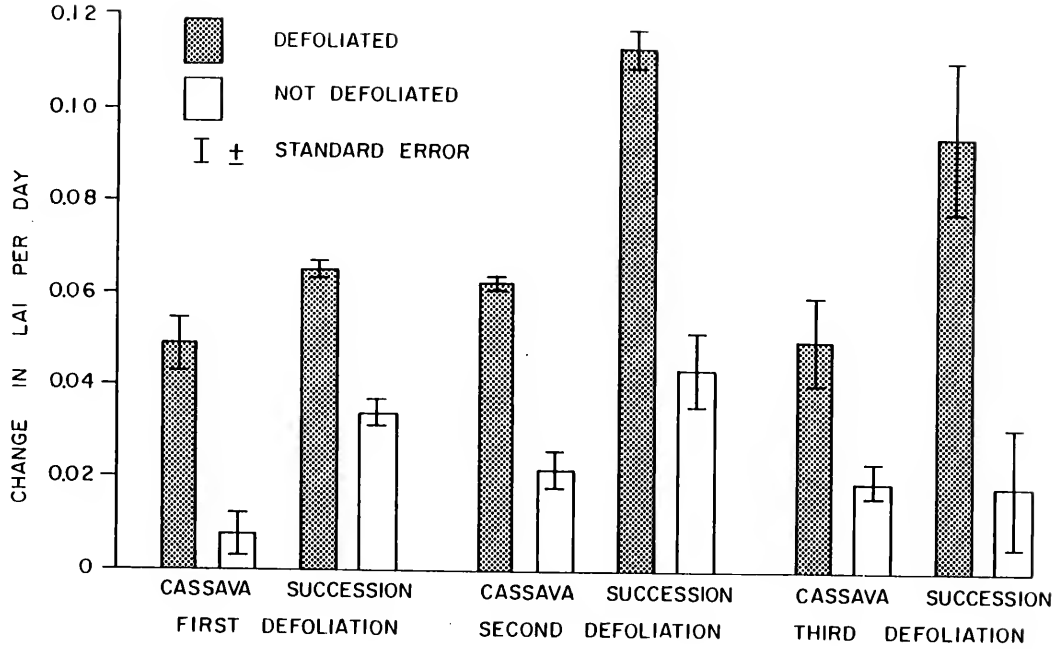


Figure 47. Production of leaf tissue in natural succession and cassava monoculture with and without artificial defoliation.

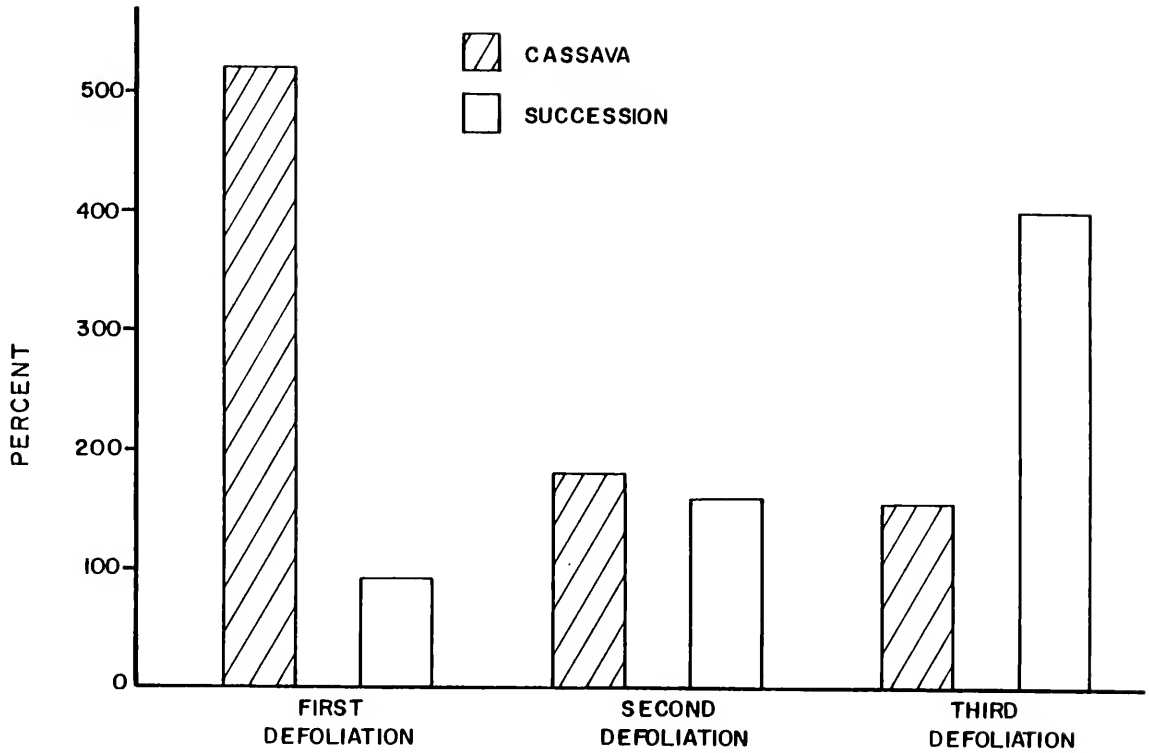


Figure 48. Stimulation of leaf productivity by defoliation. Values are percent increases in leaf production rates due to defoliation. Values are from LAI data pooled from three replications of each ecosystem.

the opposite in the natural succession: the amount of stimulation of leaf productivity increased after successive defoliations, with maximum leaf productivity four times the normal rate after the third defoliation.

Although both ecosystems responded to defoliation by increased leaf productivity, the diverse system outperformed the simple system in three ways. (1) Mean leaf productivity rates after defoliation were higher in the diverse system (0.091 $m^2\ m^{-2}$ ground day^{-1}) than in the monoculture (0.054 $m^2\ m^{-2}$ ground day^{-1}). (2) The estimated time necessary for complete recovery after the third defoliation was less in the diverse system (24 days) than in the monoculture (35 days). (3) The diverse system, but not the monoculture, continued to respond vigorously after a series of three defoliations. Percent recovery after three defoliation-1 mo regrowth periods was higher in the diverse system (89%) than in the monoculture (72%).

Changes in vegetation structure. The vertical distribution of leaves in the canopy changed after defoliation in both the natural succession and the cassava monoculture. Leaf tissue was removed equally from all layers in the canopy at each defoliation. Leaf regrowth after defoliation was not distributed evenly throughout the canopy in the natural succession or in the cassava monoculture. The natural succession was characterized by increased amounts of leaf tissue near the ground (0-1 m)

after successive defoliations (Figs. 49-51), while most of the regrowth in the cassava occurred at the tops of the plants (2-3 m above the ground).

Increases in canopy height were depressed by defoliation. The height of the defoliated cassava increased 0.75 m during the study; the height of the defoliated succession increased 0.50 m. These increases were less than those in the non-defoliated cassava and succession during the same period (1 m increase in each).

To determine whether the structural changes were due to the defoliation treatment, the changes in the defoliated plots were compared to the changes that occurred in the non-defoliated plots during the same period (Fig. 52). In the succession plots that were not defoliated, LAI increased throughout the canopy during the 3 mo study period, with the greatest increases from 0.25 m to 1.75 m above the ground. In the defoliated succession plots there was an increase in leaf area near the ground (0-1 m) and a decrase in leaf area higher in the canopy. The most striking difference between the defoliated and non-defoliated plots was the greater increase in leaf area at 0-0.25 m above the ground in the defoliated plots. This probably occurred because the defoliations opened up the canopy, more light reached the ground, and seedlings survived that would have died under the shade of the full canopy.

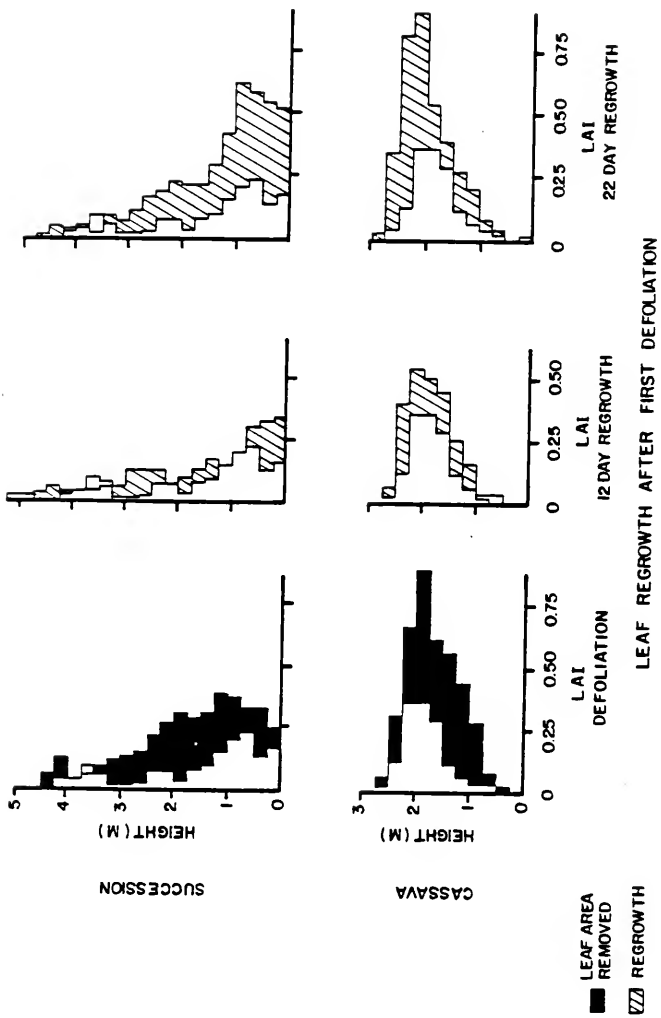


Figure 49. Leaf regrowth after first defoliation.

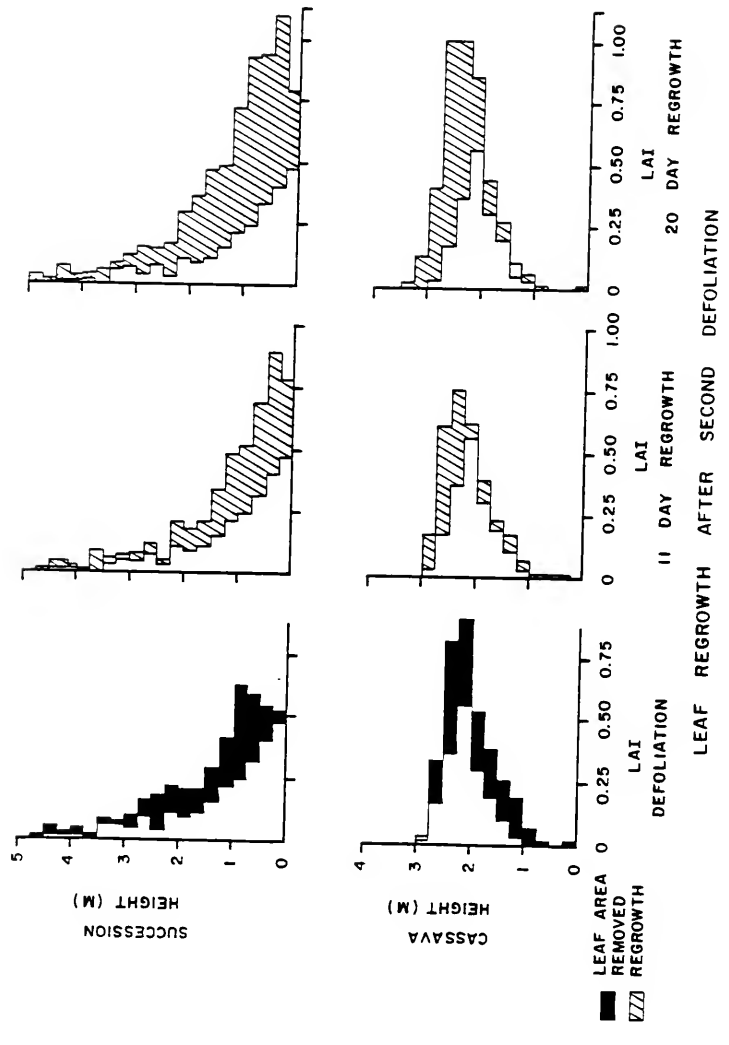


Figure 50. Leaf regrowth after second defoliation.

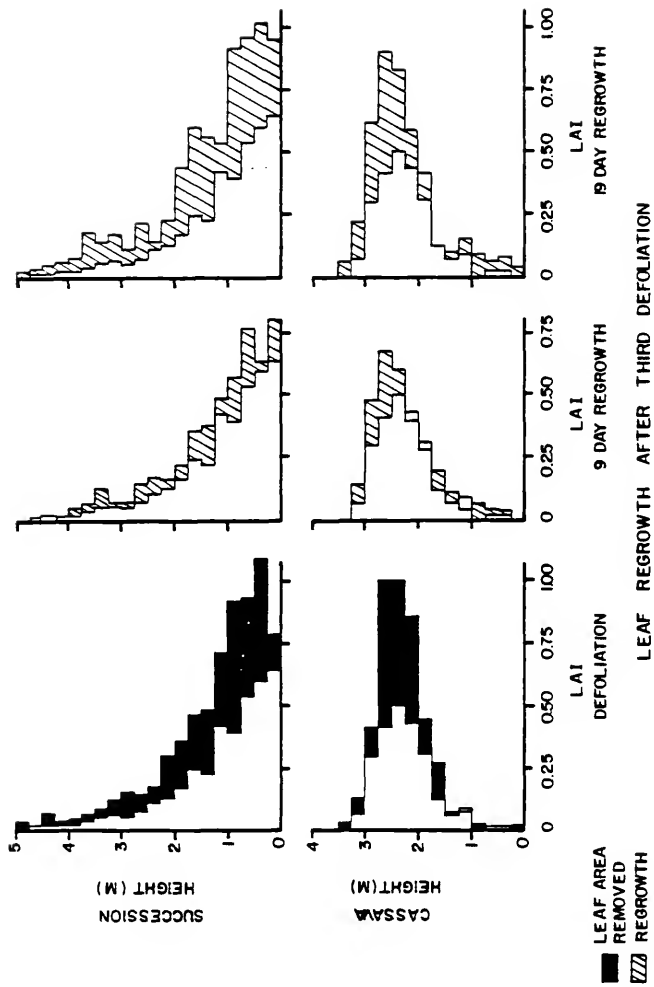


Figure 51. Leaf regrowth after third defoliation.

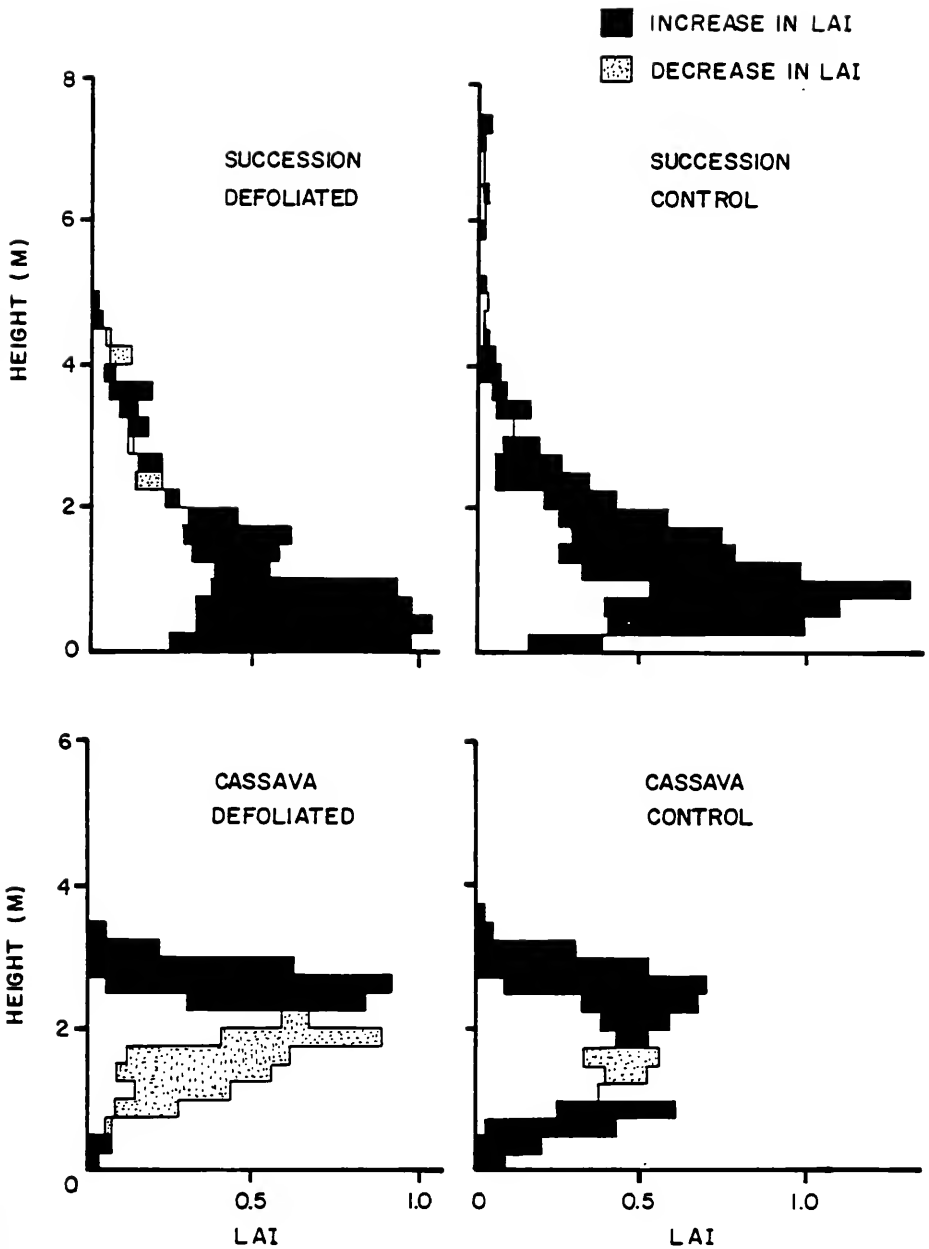


Figure 52. Changes in vegetation structure after three defoliations.

The changes in vegetation structure were quite different in the cassava monoculture. In both the defoliated and non-defoliated plots, decreases in LAI occurred from 1-2 m in the canopy, and increases occurred from 2-4 m (Fig. 52). The amount of leaf tissue lost at 1-2 m in the defoliated cassava was greater than the amount lost at the same level in the control plots. However, the data suggest that some of the leaves removed by the artificial defoliations would have been lost by the plant naturally. In both defoliated and non-defoliated cassava the lost leaves were replaced by leaves at the tips of growing shoots higher in the canopy.

Lodging of some of the cassava plants occurred in the control plots. This phenomenon was especially common in plants on slopes. The woody stems, unable to support the plant crowns, were bent to the ground by heavy rains and gusty winds. Some uprooting and stem damage occurred at the bases of the fallen plants. Resprouting and increases in leaf area occurred near the ground (Fig. 52). In the defoliated cassava, reduced leaf area made the plant crowns less vulnerable to wind and rain damage. Very little lodging occurred in defoliated plants, even on moderate slopes. This unexpected result illustrates one indirect effect of an ecosystem stress such as defoliation.

Changes in species composition. Changes in the species composition of the successional vegetation after defoliation was an expected result of the experiment. The LAI

measurements were used to rank the species in order of dominance in the ecosystem and to quantify changes in species dominance during the study. Species replacement and changes in species dominance occur rapidly in early tropical succession. Changes in species composition were occurring in the non-defoliated plots as well as in the defoliated plots. To evaluate the effect of defoliation on species composition, changes in defoliated plots were compared with changes in non-defoliated plots.

Species richness increased in both defoliated and non-defoliated plots during the 3 mo period (Table 22). However, the defoliated plots gained less new species than the non-defoliated plots, and species richness was lower in defoliated plots at the end of the experiment. In addition, species diversity (H') decreased in the defoliated plots, but not in the control plots (Table 22).

More rare species were present in the non-defoliated plots than in the defoliated plots at the beginning and end of the experiment (Fig. 53). At the end of the study, both systems were more strongly dominated by a few very common species than at the beginning of the experiment. Although increased dominance by a few species (= decreased evenness) occurred in both systems, evenness values decreased more in defoliated than in non-defoliated plots (Table 22).

Changes in LAI are listed by species in Table 23. Some species showed similar growth patterns in the defoliated and

Table 22. Changes in the number of plant species in the natural succession during 3 mo defoliation study. Values are based on 225 LAI measurements in defoliated and non-defoliated ecosystems; total area of ecosystem = 128 m^2.

Characteristic		Defoliated	Not Defoliated
Number of species	Initial	40	43
	Final	46	51
Number of species gained during 3 mo period		15	18
Number of species lost during 3 mo period		9	10
Species diversity (H')[a]	Initial	1.31	1.29
	Final	1.23	1.30
Evenness[b]	Initial	0.82	0.79
	Final	0.74	0.76

[a] $H' = -\Sigma(n_i/N)\log(n_i/N)$, where n_i is the number of leaf intersections for species i, and N is the total number of leaves intersected (Shannon index).

[b] Evenness = H'/log S, where H' is Shannon diversity index and S is number of species.

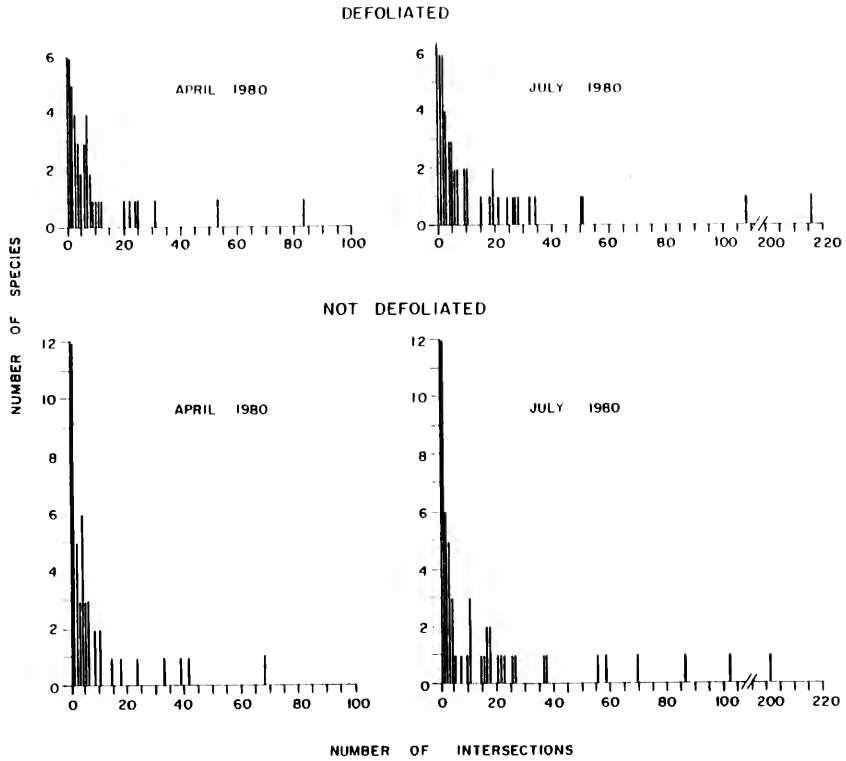


Figure 53. Species abundance in natural succession at the beginning and end of the defoliation study. Each figure is based on data from 225 LAI measurements.

Table 23. Numbers of leaf intersections in 255 LAI measurements by species, in defoliated and non-defoliated natural succession. Measurements were made at the beginning and end of the 3 mo defoliation study.

Species Number	Species Name	Number of Intersections				Significance Level[c]
		Defoliated		Not Defoliated		
		Initial	Final	Initial	Final	
14	Acalypha macrostachya	7	10	0	14	
60	Allophylus psilospermus	0	1	0	1	
61	Bidens pilosa	0	2	0	0	
2	Bocconia frutescens	31	108	17	102	Not significant
43	Borreria laevis	0	3	2	1	
39	Calathea insignis	0	5	0	4	
65	Cardiospermum grandiflorum	0	0	1	0	
56	Cecropia insignis	0	1	0	1	
24	Cestrum panamense	0	0	0	26	
1	Clibadium aff. surinamense	83	216	68	201	Not significant
29	Cordia alliodora	0	0	6	10	
8	Cordia inermis	11	28	8	55	p<.10
47	Croton panamensis	1	1	2	1	
22	Cyperaceae[a]	5	3	5	16	Not significant
30	Canavalia sp.	3	4	4	3	
53	Erechtites valerianaefolia	0	0	1	1	
20	Frantzia pittieri	8	1	23	69	p<.01
48	Goethalsia meiantha	2	2	1	0	
10	Gouania lupuloides	7	19	4	21	Not significant
16	Gramineae[b]	24	34	41	86	Not significant
31	Heliconia sp. 1	6	1	6	0	
34	Heliconia sp. 2	0	3	4	5	
49	Heliconia sp. 3	4	0	1	0	
6	Heterocondylos vitalbis	7	21	4	1	
19	Hymenachne amplexicaulis	53	50	32	58	p<.05
23	Inga edulis	5	0	6	17	
11	Ipomoea neei	12	26	4	37	p<.05
4	Ipomoea sp.	7	32	5	22	Not significant

Table 23--continued.

Species Number	Species Name	Number of Intersections				Significance Level[c]
		Defoliated		Not Defoliated		
		Initial	Final	Initial	Final	
9	Iresine diffusa	6	18	1	3	
33	Lantana trifolia	2	7	1	2	
13	Lasiacis sorghoidea	2	0	1	3	
27	Mikania sp.	4	9	3	4	
26	Momordica charantia	1	4	5	10	
32	Ochroma pyramidale	0	2	2	9	
5	Panicum maximum	6	7	0	3	
17	Panicum trichoides	20	19	10	25	$p<.10$
54	Passiflora coriaceae	0	2	0	0	
44	Passiflora vitifolia	1	0	4	0	
18	Phytolacca rivinoides	22	5	38	36	$p<.05$
50	Pothomorphe umbellata	0	4	0	0	
62	Psychotria eurycarpa	1	0	0	0	
42	Psychotria pubescens	0	0	8	0	
28	Solanum jamaicense	0	2	0	17	
25	Solanum schlechtendalium	3	9	2	7	
37	Solanum torvum	0	0	10	0	
12	Solanum umbellatum	25	51	14	20	Not significant
38	Trema micrantha	2	6	0	1	
35	Triumfetta sp.	0	0	2	10	
21	Vernonia brachiata	3	15	3	15	
3	Vernonia patens	3	24	3	16	
41	Vigna vexillata	0	6	0	2	
58	Zanthoxylum elephantiasis	0	0	0	2	
7	Unidentified sp. 1	10	27	1	3	
15	Unidentified sp. 2	9	5	0	0	
36	Unidentified sp. 3	0	10	0	2	
40	Unidentified sp. 4	8	0	1	0	
45	Unidentified sp. 5	0	3	0	2	
46	Unidentified sp. 6	4	0	1	0	

Table 23--continued.

Species Number	Species Name	Number of Intersections				Significance Level[c]
		Defoliated		Not Defoliated		
		Initial	Final	Initial	Final	
51	Unidentified sp. 7	0	0	0	4	
52	Unidentified sp. 8	0	1	0	2	
55	Unidentified sp. 9	0	0	1	1	
57	Unidentified sp. 10	2	0	0	0	
59	Unidentified sp. 11	0	1	0	1	
63	Unidentified sp. 12	0	0	1	0	
64	Unidentified sp. 13	1	0	0	0	
66	Unidentified sp. 14	0	0	0	1	
67	Unidentified sp. 15	1	0	0	0	
68	Unidentified sp. 16	0	0	0	1	
69	Unidentified sp. 17	0	0	0	1	

[a]Includes at least four species of sedges that were indistinguishable by vegetative parts.

[b]Includes at least six species of grasses that were indistinguishable by vegetative parts.

[c]H_O: The change in numbers of intersections from initial to final measurement did not differ in the defoliated and non-defoliated plots. Probabilities are from adjusted χ^2 tests with 1 degree of freedom. Blanks indicate test not performed because of small cell sizes.

non-defoliated plots. The two species that increased to high levels of dominance during the 3 mo period were the same in the defoliated and non-defoliated plots (Bocconia frutescens and Clibadium aff. surinamense). Most species whose LAI increased in the control plots also increased in LAI in the defoliated plots (Table 24). Similarly, most species whose LAI decreased in the control plots also decreased in LAI in the defoliated plots. However, five species increased in LAI in the non-defoliated plots and decreased in LAI in defoliated plots: Panicum trichoides, Cyperaceae group, Lasiacis procerrima (misidentified, but referred to in this study, as Hymenachne amplexicaulis), Inga edulis, and Frantzia pittieri. The LAI of three species (Borreria laevis, Canavalia sp., and Heterocondylos vitalbis) decreased in control plots and increased in defoliated plots. This group of eight species that showed opposite trends included common species (Panicum, Hymenachne, and Frantzia) and relatively uncommon species (the other five species), and jointly accounted for approximately 24% of total LAI in defoliated and non-defoliated plots.

Three of the above differences in growth patterns were significantly different by chi square tests (Hymenachne, $p<.05$; Frantzia, $p<.01$; Panicum, $p<.10$). For the other five species, either the differences were not significant or sample size was too small to perform the test.

Table 24. Numbers of species that increased and decreased in LAI during the 3 mo defoliation study in defoliated and non-defoliated natural succession. A "+" indicates an increase in LAI; a "-" indicates a decrease in LAI.

		Non-Defoliated Succession		
		+	-	Total
Defoliated succession	+	31	3	34
	-	5	8	13
	Total	36	11	47

In addition to species that differed in magnitude and direction of change in LAI in defoliated and non-defoliated plots, three species differed significantly in magnitude but not in direction of change. The LAI of Phytolacca rivinoides decreased more in defoliated than in non-defoliated plots, and the LAI of Ipomoea neei and Cordia inermis increased less in defoliated than in non-defoliated plots (Table 23).

Because the changes in LAI of individual species differed in direction and magnitude, the relative percent dominance of the species in the ecosystem also changed. A species can increase in percent dominance in the system because the species itself increased in leaf area, or because the other species decreased in leaf area relative to it. The changes in percent LAI of all species in the defoliated succession are ranked in Fig. 54. A few species showed large increases in percent LAI, a few showed large decreases, and many species changed little in percent LAI during the defoliation experiment. The percent changes in LAI that occurred in the defoliated plots were dissimilar to the changes that occurred in the non-defoliated plots during the same time period (Fig. 55).

The community similarity index C was used as a measure of the overall change in plant species dominance during the 3 mo defoliation study. Similarity values were equal in defoliated and non-defoliated plots (C=0.71), indicating

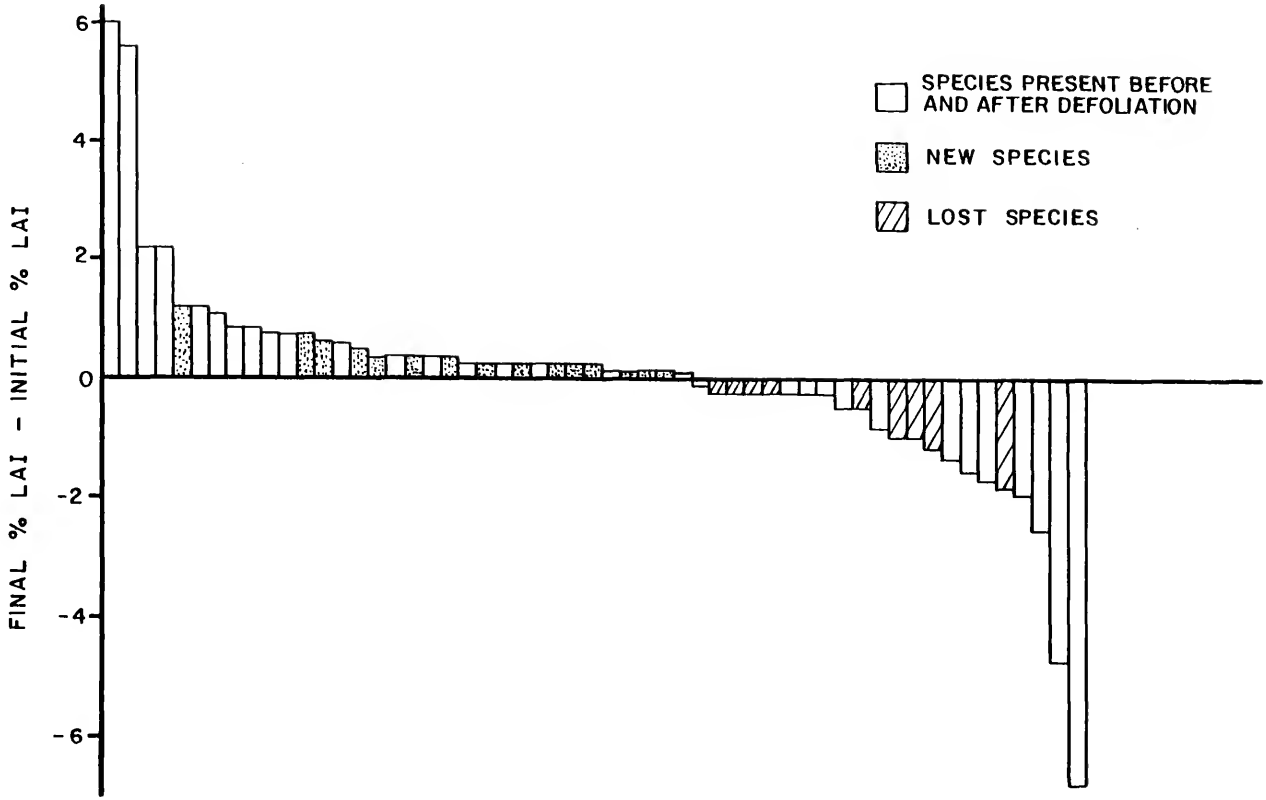


Figure 54. Changes in percent LAI in natural succession after three artificial defoliation-regrowth periods. Each vertical bar represents one species.

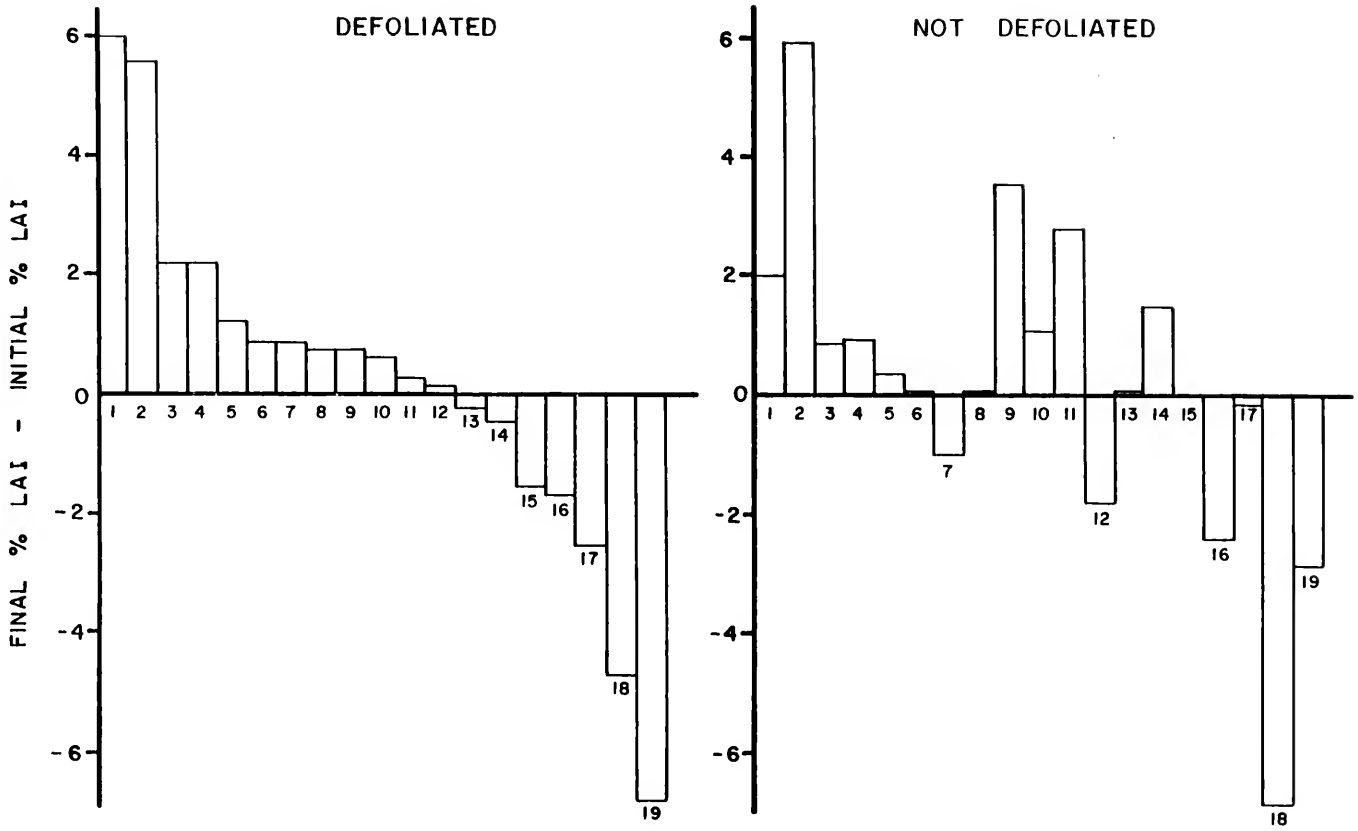


Figure 55. Changes in percent LAI for 19 common species in defoliated and non-defoliated natural succession. Each vertical bar represents one species. Species numbers correspond to numbers in Table 23.

that the overall rate of species replacement was not changed by defoliation, although the individual species involved were different.

Cassava biomass. One hypothesis was that reallocation of plant resources following defoliation and utilization of a greater proportion of the plant's energy for production of new leaf tissue would lead to decreases in the biomass of other plant compartments. The cassava data did not support this hypothesis. Mean biomass of mature cassava plants in defoliated and non-defoliated plots did not differ significantly (Table 25). In addition, the yield of cassava tubers from the defoliated plots (1219.6 $\pm$ 137.9 g/m^2 fresh weight) was not different from the yield from the non-defoliated plots (1088.3 $\pm$ 264.2).

Table 25. Cassava biomass at harvest in defoliated and non-defoliated plots. Values are $\bar{x}$(s.d.) in g/m^2 dry weight for above-ground biomass compartments, g/m^2 fresh weight for tubers. Means for above-ground compartments are based on harvest of eight plants from each of six replications in non-defoliated cassava, and eight plants from each of three replications in defoliated cassava. Tuber means are based on harvest of all plants in defoliated and non-defoliated plots.

Biomass Compartment	Mass (g/m^2) Not Defoliated	Defoliated	F
Leaves	89.3 (27.3)	97.2 (67.1)	Not significant
Stems	624.9 (128.2)	500.6 (121.4)	Not significant
Standing dead	23.5 (11.7)	15.6 (9.0)	Not significant
Edible tubers	1088.3 (264.2)	1219.6 (137.9)	Not significant

CHAPTER IV
DISCUSSION

Net Primary Productivity

Relationship Between Net Primary Productivity and Diversity

The NPP of the natural succession, enriched succession, and successional monoculture were higher than the few estimates of NPP of young tropical successional vegetation in the literature. The differences may be due to site differences or may reflect differences in methods used to estimate NPP. In this study NPP was estimated from increments in above-ground biomass, corrected for herbivory, litterfall, and plant mortality. Uhl and Murphy (1981) estimated NPP during early succession on a nutrient-poor site in Venezuela (109 g m^{-2} yr^{-1}, 1 yr succession; 1446 g m^{-2} yr^{-1}, 2 yr succession; values include root production). Their estimates were based on biomass increments, adjusted for herbivory and litterfall. Their low NPP values may be partly due to underestimation of plant turnover by infrequent biomass samples. Jordan's (1971) estimates of NPP in an irradiated tropical forest (535 g m^{-2} yr^{-1}, 3 yr succession) are not directly comparable to my data because of the nature of the disturbance on that site.

Westlake (1963) summarized NPP values for several tropical crops on fertile sites. Net production ranged from 4000 g m^{-2} yr^{-1} for rice to 9400 g m^{-2} yr^{-1} for sugarcane, with a mean of 3000 g m^{-2} yr^{-1} for tropical annual crops and 7500 g m^{-2} yr^{-1} for tropical perennial crops. These values, based on maximum biomass during the growing season, include above- and below-ground production. The NPP of the monoculture in this study was lower, partly because the crops were grown without fertilizers or pesticides. However, monoculture NPP was five times higher than the NPP reported for slash-and-burn agriculture in Venezuela (Uhl and Murphy 1981).

Excluding the monoculture, NPP was positively correlated with plant species diversity. Propagule additions provided the potential for increased diversity in the enriched succession. Species diversity was higher in the enriched than in the natural succession, and associated with increased diversity was high LAI and high NPP. These data suggest that the species added to the enriched succession allowed more complete utilization of the space and available resources. In the mimic, where diversity was limited by experimenter control of species composition, NPP was lower than in the natural succession.

The NPP of the least complex ecosystem (the monoculture) was almost as high as NPP of the enriched succession. In agricultural systems, net production is available for

harvest by humans. Therefore agricultural crops, such as the maize and cassava planted in the monoculture, are specifically selected for high NPP. Even-aged stands of a single species may be highly productive over short time intervals in an environment relatively free from inter-species competition. In most monocultures the crop is harvested at the peak of vegetative growth, before plant senescence begins. The high productivity of the monoculture in this study reflects rapid vegetative growth of a sequence of crops.

In the monoculture very high productivity (and high yield) of the first maize crop was followed by very low productivity (and low yield) of the second maize crop. Low yield stability is a problem in many monoculture systems in the tropics (Conway 1982). High yield stability has been pointed out as a desirable characteristic of complex tropical agroecosystems (Soemarwoto and Soemarwoto 1979, Conway 1982). Although yield variability was not measured in the three diverse systems, temporal variability in NPP occurred in all systems studied. Periods of low productivity in the diverse systems probably reflect mortality of dominant species and water limitations during the dry season. Although NPP measurements do not allow precise predictions of harvestable yield, the data suggest that periods of low productivity (and possibly low yield) may occur in diverse as well as in simple agroecosystems.

The diverse systems, but not the monoculture, developed permanent structure. As structure develops during succession, gross primary productivity (GPP) increases, but NPP decreases (E. P. Odum 1971). Complex agroecosystems similar to natural succession often have lower NPP and lower harvestable yield than fossil-fuel intensive monocultures. In this study, both the natural succession and the mimic of succession had lower NPP than the monoculture. The GPP (not measured) may have been higher in the diverse system than in the monoculture.

Continuous Biomass Accumulation in Diverse Systems

Equal performance in terms of production does not imply equal sustainability of simple and diverse systems. Internal dynamics of energy flow, such as rates of biomass accumulation and timing of turnover, affect sustainability and stability.

In all of the systems except the monoculture, >50% of total annual NPP went into development of permanent structure (Fig. 56). The rate of biomass accumulation during early succession was accelerated by propagule enrichment. Above-ground biomass of the enriched succession was higher than that of the natural succession at 1.5 yr, and this was due in part to the biomass of an introduced species, Musa paradisiaca. The lower biomass in the mimic of succession may reflect a time lag in development of the mimic.

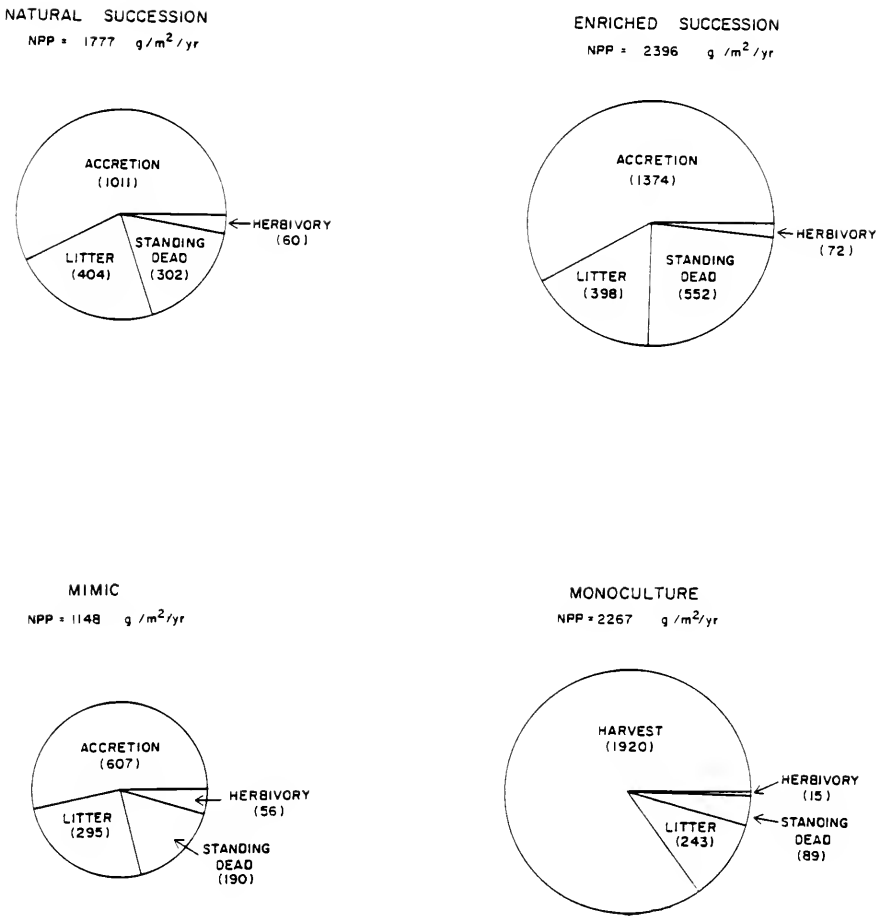


Figure 56. Biomass accretion and turnover in natural succession, enriched succession, mimic of succession, and monoculture.

Estimates of plant biomass in early tropical succession are more numerous than estimates of productivity. Above-ground biomass estimates in the natural succession and enriched succession were high compared to literature values from other sites (Table 26). The Turrialba site was on relatively nutrient-rich volcanic soil. Also, nutrient availability was high after the initial slash-and-burn site preparation (Ewel et al. 1981). Above-ground biomass in the natural succession at 12 mo (1522 g/m^2) was higher than the above-ground biomass at 12 mo (1113 g/m^2) reported by Harcombe (1973) on the same site. These differences may reflect effects of the burn (Harcombe's plots were not burned) and year-to-year rainfall differences at the site.

Continuous biomass accumulation is a key characteristic that distinguished the three diverse ecosystems from the monoculture. In the monoculture, living biomass was cut at each harvest. The soil, left without a protective vegetative cover, was vulnerable to erosion and nutrient leaching. In the diverse successional systems, the permanent structure of the systems buffered microenvironmental fluctuations and allowed the development of complex biological interactions that may enhance sustainability.

Table 26. Above-ground living biomass in several tropical young successional ecosystems.

Age (yr)	Location	Annual Rainfall (mm)	Above-Ground Living Biomass (g/m^2)	Reference
0.8	Guatemala	1970	388-1441	Tergas and Popenoe 1971
1	Venezuela	3500	56	Uhl and Murphy 1981
1	Guatemala	2000	836	Snedaker 1970
1	Guatemala	2000	874	Tergas 1965
1	Costa Rica	2700	1113	Harcombe 1973
1	Puerto Rico	880	459	Ewel 1971
1	Costa Rica	2300	135	"
1	Costa Rica	1800	951	"
1	Puerto Rico	3600	634	"
1	Costa Rica	4800	1159	"
1.5	Costa Rica (natural succession)	2700	1740	This study
1.5	Costa Rica (enriched succession)	2700	3701	"
1.5	Costa Rica (mimic of succession)	2700	954	"
2	Venezuela	3500	966	Uhl and Murphy 1981

Table 26--continued.

Age (yr)	Location	Annual Rainfall (mm)	Above-Ground Living Biomass (g/m^2)	Reference
2	Colombia	4000	1585	Golley et al. 1975a
2	Panama	2000	1298	Ewel 1971
2	Guatemala	2000	1419	Snedaker 1970
2	Belgian Congo	1800	1092	Bartholomew et al. 1953
2	Panama	2000	1302	Golley et al. 1975b

Continuous Biomass Turnover in Diverse Systems

The proportion of NPP that went into development of permanent structure was approximately equal (53-57%) in the three diverse systems (Fig. 56); the remaining fraction of the annual production (43-47%) was cycled through litterfall, plant mortality and herbivory. A much smaller fraction (15%) of the total annual production in the monoculture turned over during crop growth. If crop harvest is included as turnover, annual turnover in the monoculture was 100%.

An important difference between the monoculture and the diverse systems was in the timing of the turnover. Litterfall, plant mortality and herbivory were fairly constant and continuous in the diverse systems. In the monoculture, low biomass turnover during the growth of each crop was followed by high turnover at crop harvest. The conversion of living to dead biomass was a pulse that left the monoculture free of living vegetation at each harvest and possibly susceptible to rapid nutrient leaching from dead plant material.

Importance of Standing Dead Biomass

Litterfall rates in all systems studied were within the range of values reported for other young tropical successions and were lower than values for older successions and mature tropical forests (Table 27).

Table 27. Annual litterfall rates in several tropical successional and mature forests.

	Litterfall ($g/m^2/yr$)	Reference
Tropical Succession		
1 yr succession (Guatemala)	460	Ewel 1976
1 yr dipterocarp forest (Philippines)	200	Kellman 1970
1.5 yr wet forest succession (Costa Rica)	404	This study
1.5 yr enriched succession (Costa Rica)	398	"
1.5 yr mimic of succession (Costa Rica)	295	"
1.5 yr successional monoculture (Costa Rica)	243	"
3 yr succession (Guatemala)	580	Ewel 1976
4 yr succession (Guatemala)	610	"
5 yr succession (Guatemala)	650	"
6 yr succession (Guatemala)	800	"
5-7 yr bush fallow (Nigeria)	855	Swift et al. 1981
7 yr succession (Philippines)	700-1280	Kellman 1970
9 yr succession (Guatemala)	800	Ewel 1976
14 yr succession (Guatemala)	1000	"
19 yr succession (Philippines)	760-1220	Kellman 1970
21-27 yr succession (Philippines)	720-1250	"
Tropical Mature Forests		
Montane rain forest (Jamaica)	604[a]	Tanner 1980
Lowland rain forest (Brazil)	730[b]	Klinge and Rodrigues 1968

Table 27--continued.

	Litterfall ($g/m^2/yr$)	Reference
Tropical Mature Forests		
Lowland *Mora excelsa* forest (Trinidad)	690[b,c]	Cornforth 1970
Lower montane rain forest (Puerto Rico)	478[c]	Wiegert 1970
Lower montane rain forest (New Guinea)	722-793	Edwards 1977
Terra firme forest (Brazil)	990	Klinge 1977
Varzea (seasonally flooded) forest (Brazil)	900	"
Igapo (water-logged) forest (Brazil)	780	"
Equatorial forests[d]	550-1530	Bray and Gorham 1964
Tropical wet forest (Colombia)	874-1202	Folster *et al.* 1976
Tropical premontane wet forest (Panama)	1048	Golley *et al.* 1975b

[a]Mean of 4 forest sites.

[b]Value from summary in Tanner 1980.

[c]Leaf litter only.

[d]Includes mature and secondary forest and 25-30 yr old tree plantations.

To account for plant turnover in estimates of NPP, litterfall during a time interval is often added to the biomass increment for the interval. However, rates based on biomass changes plus litterfall underestimate true NPP rates in ecosystems where there is a significant amount of standing dead biomass. Plant mortality was an important pathway for vegetation turnover in the three diverse systems studied (Fig. 56). Standing dead biomass production, estimated from changes in standing dead biomass over time, included all plants and plant parts that died and remained above the ground. Standing dead biomass was comprised mainly of standing dead stems (of Phytolacca and maize, for example), fallen branches, and fallen leaves trapped before they reached the ground. Standing dead biomass production accounted for >30% of annual plant turnover in the three diverse systems. Excluding the standing dead biomass component from the productivity calculations would reduce the estimates of NPP by >15% in the diverse systems.

Litterfall rates have also been used to estimate gross nutrient cycling rates in mature tropical forests (Golley 1975). This method fails to account for standing dead biomass. Standing dead matter decomposes above the ground, without contact with soil, roots or mycorrhizae. If the decomposition rate of standing dead biomass differs from the decomposition rate of organic material on the ground, significant amounts of standing dead biomass may have

important implications in ecosystem nutrient cycling processes.

Herbivory

Low Herbivory Rates

In all four experimental ecosystems, herbivory was a less important pathway for cycling of organic material than were litterfall and plant mortality. Only 0.7 to 5% of the annual NPP was consumed by insects. Estimates of consumption by herbivores in other tropical and temperate ecosystems range from 0.3% of NPP in slash-and-burn agriculture in Venezuela to 38.3% of NPP in a short grass area of the Serengeti (Table 28). The highest rates reported were in grasslands with large herbivores (Andrews et al. 1974, Sinclair 1975) and temperate old fields (Odum et al. 1962, Van Hook 1971, Boring et al. 1981). The lowest rates were in a Liriodendron forest in Tennessee (Reichle et al. 1973), a tropical palm savannah (Lamotte 1975), and tropical slash-and-burn agriculture (Uhl and Murphy 1981).

Methods for estimating herbivory rates and productivity rates varied widely among studies. This accounts for some of the differences in percent consumption reported in the literature. Herbivory rates are often difficult to estimate precisely because herbivory is extremely variable both temporally and spatially (Janzen 1981).

Table 28. Above-ground net primary productivity (NPP), consumption by herbivores, and percent of NPP consumed in several tropical and temperate ecosystems.

	Above-Ground NPP ($g/m^2/yr$)	Consumption by Herbivores ($g/m^2/yr$)	Percent of NPP Consumed	Reference
TROPICAL SUCCESSIONAL ECOSYSTEMS				
1 yr wet forest succession (Venezuela)	109[a]	3	2.8	Uhl and Murphy 1981
2 yr wet forest succession (Venezuela)	1446[a]	20	1.4	"
1.5 yr wet forest succession (Costa Rica)	1777	60	3.4	This study
1.5 yr enriched succession (Costa Rica)	2396	72	3.0	"
1.5 yr mimic of succession (Costa Rica)	1148	56	4.9	"
1.5 yr wet forest succession (Costa Rica)	1777	34[f]	1.9	Blanton 1982
1.5 yr enriched succession (Costa Rica)	2396	30[f]	1.2	"

Table 28--continued.

	Above-Ground NPP ($g/m^2/yr$)	Consumption by Herbivores ($g/m^2/yr$)	Percent of NPP Consumed	Reference
TROPICAL SUCCESSIONAL ECOSYSTEMS				
1.5 yr mimic of succession (Costa Rica)	1148	78[f]	6.8	Blanton 1982
TROPICAL AGRICULTURAL ECOSYSTEMS				
Monoculture--2 maize plantings followed by cassava (Costa Rica)	2267	15	0.7	This study
Cassava monoculture before harvest (Costa Rica)	1484	99[f]	6.7	Blanton 1982
Cassava monoculture before, during, and after harvest (Costa Rica)	1484	76[f]	5.1	"
First yr shifting cultivation	400	1.6[b]	0.4	Uhl and Murphy 1981
Second yr shifting cultivation	483	1.4[b]	0.3	"

Table 28--continued.

	Above-Ground NPP ($g/m^2/yr$)	Consumption by Herbivores ($g/m^2/yr$)	Percent of NPP Consumed	Reference
TROPICAL MATURE ECOSYSTEMS				
Moist serpentine forest (Puerto Rico)		55		Benedict 1976
Dry limestone forest (Puerto Rico)		23	3.0-6.5	"
Elfin woodland (Puerto Rico)		16		"
Serengeti grassland (Tanzania)[c]				
Long grass area	598	165	27.6	Sinclair 1975
Short grass area	470	180	38.3	"
Kopjes area	598	86	14.4	"
Palm savannah (Ivory Coast)	2000	14	0.7	Lamotte 1975
TEMPERATE SUCCESSIONAL ECOSYSTEMS				
1-7 yr old fields (South Carolina)[d]	310	41	13.2	Odum et al. 1962
30 yr old field (Michigan)	345	5	1.4	Wiegert and Evans 1967
4-5 yr grassland (Tennessee)	319	31	9.7	Van Hook 1971

Table 28--continued.

	Above-Ground NPP ($g/m^2/yr$)	Consumption by Herbivores ($g/m^2/yr$)	Percent of NPP Consumed	Reference
TEMPERATE SUCCESSIONAL ECOSYSTEMS				
Lespedeza stand (South Carolina)	638	6	0.9	Menhinick 1967
1 yr hardwood forest succession (North Carolina)	196	23	11.7	Boring et al. 1981
TEMPERATE MATURE ECOSYSTEMS				
Spartina alterniflora salt marsh (Georgia)[d]	1565	144	9.2	Teal 1962
Shortgrass prairie (Colorado)[d]				
Ungrazed by cattle	140	3	2.1	Andrews et al. 1974
Lightly grazed by cattle	240	14	5.8	"
Heavily grazed by cattle	182	28	15.4	"
Liriodendron forest (Tennessee)	1333	9	0.7	Reichle et al. 1973 Reichle & Crossley 1967

Table 28--continued.

	Above-Ground NPP ($g/m^2/yr$)	Consumption by Herbivores ($g/m^2/yr$)	Percent of NPP Consumed	Reference
TEMPERATE MATURE ECOSYSTEMS				
Acer-Fagus forests (Ontario)	1222	22	1.5-2.5	Bray 1964
Hardwood forest (North Carolina)	876	36	4.1	Boring et al. 1981
Deciduous oak woodland (Poland)	549[e]	42	7.7	Petrusewicz and Grodzinski 1975
Oak-pine forest, late successional (New York)	1171	32	2.7	Woodwell and Whittaker 1967

[a]Includes root production.

[b]Includes only consumption of cassava leaves.

[c]Values summarized by Pfeiffer and Wiegert (1981) were converted using the caloric conversion factor for grass (4.137 Kcal/g dry weight) employed by Sinclair (1975).

Table 28--continued.

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[d]Values summarized by Pfeiffer and Wiegert (1981) were converted assuming 4 Kcal/g dry weight.

[e]Portion of NPP available as food to herbivores.

[f]Consumption by Atta leaf-cutting ants only.

The herbivory rate measured in the monoculture may underestimate the true rate because of the sampling techniques used. Monocultures are characterized by pest outbreaks in which much damage is very localized and concentrated over a short time interval (Pimentel 1961b). Such outbreaks may be missed completely by non-continuous monitoring of randomly selected plants. Field observation confirmed that above-ground damage rates in the maize monoculture were actually quite low. In the cassava monoculture, true herbivory rates were probably higher than the rates reported here.

Leaf-cutter ants (Atta cephalotes) were the principal herbivore in the cassava monoculture. Because Atta's foraging activity was intense and concentrated on a few plants, monitoring herbivory rates on a small number of cassava plants missed most of the Atta damage. In a study of leaf-cutter ants (Atta cephalotes) at the same site, Blanton (1982) found that the ants removed an average of 88 cm^2 leaf m^{-2} ground day^{-1} in the cassava monoculture. Blanton's values, obtained by monitoring activity on leaf-cutter trails, are more than four times the values I obtained by measuring damage rates on randomly selected plants.

In the diverse systems, individuals of all dominant plant species were tagged. The number of plants (and total leaf area) monitored for damage was much greater in the diverse

systems than in the monoculture. Larger sample size reduced the underestimation problem due to non-random foraging by some herbivores, and the herbivory rates measured in the diverse systems are better estimates of true loss rates.

Absolute Losses and Diversity Not Correlated

Herbivory rate was calculated as an absolute amount of leaf tissue consumed per unit area of ecosystem per unit time and as a percent of total leaf area consumed per unit time.

Absolute consumption rate was not related to ecosystem diversity (Fig. 57). The three high diversity systems incurred approximately equal amounts of damage (54-61 cm^2 m^{-2} ground day^{-1}); the monoculture incurred less damage. If Blanton's (1982) herbivory rates for the cassava monoculture are used, absolute consumption rates in the monoculture were slightly greater than in the diverse systems. These data indicate that herbivores consumed approximately the same amount of leaf tissue per unit of ground area, regardless of system diversity.

These data do not support the dogma that diverse systems receive less damage from herbivores than do simple systems. The timing of herbivory may make the damage more apparent in low diversity systems. In this study, herbivory was much more variable temporally in the less diverse systems. High concentrations of insect attack occurred during short time

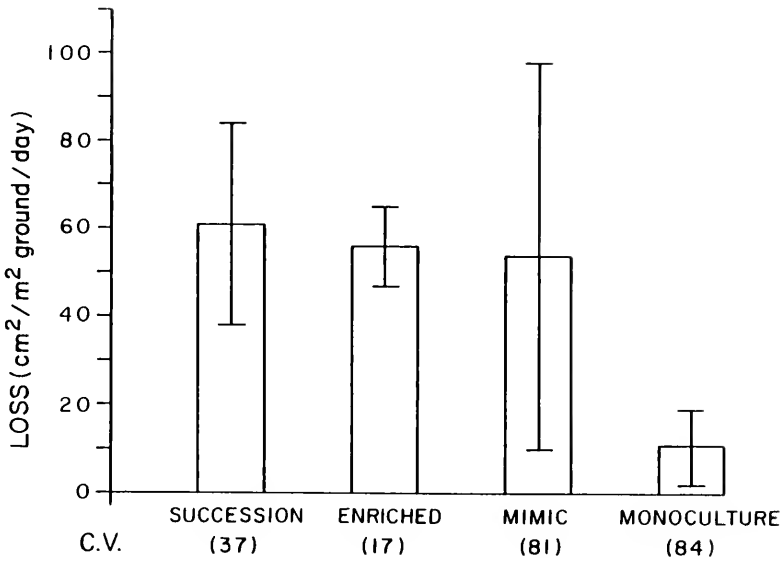

Figure 57. Losses to herbivores per ground area of ecosystem. C.V. is coefficient of variation.

intervals. In the diverse systems herbivory occurred at a more constant rate, so damage was less noticeable.

Percent Losses Correlated with LAI

The mimic ecosystem had lower LAI than the other two diverse systems. Although absolute losses did not differ, percent losses to herbivores were higher in the mimic than in the enriched succession and natural succession (Fig. 58). Using my data, percent losses were low in the monoculture; if Blanton's (1982) values are used, percent consumption in the monoculture was at least as great as in the mimic. Herbivory had most impact on the systems with least leaf area.

It has been suggested that diversity per se is not the factor that controls herbivory in an ecosystem, and that herbivory patterns are better explained by examining ecosystem structural properties that influence insect behavior (Feeny 1974, van Emden and Williams 1974, Murdoch 1975, Root 1975). Leaf area index is a structural property affecting herbivory that is often, but not always, correlated with system diversity. Diverse systems may maintain higher LAI than simple systems because many species with different growth forms are able to utilize the available space in the ecosystem more fully than can a single species (Trenbath 1974). However, LAI is not always correlated with diversity; monocultures, as well as diverse systems, may have high LAI (Ewel et al. 1982).

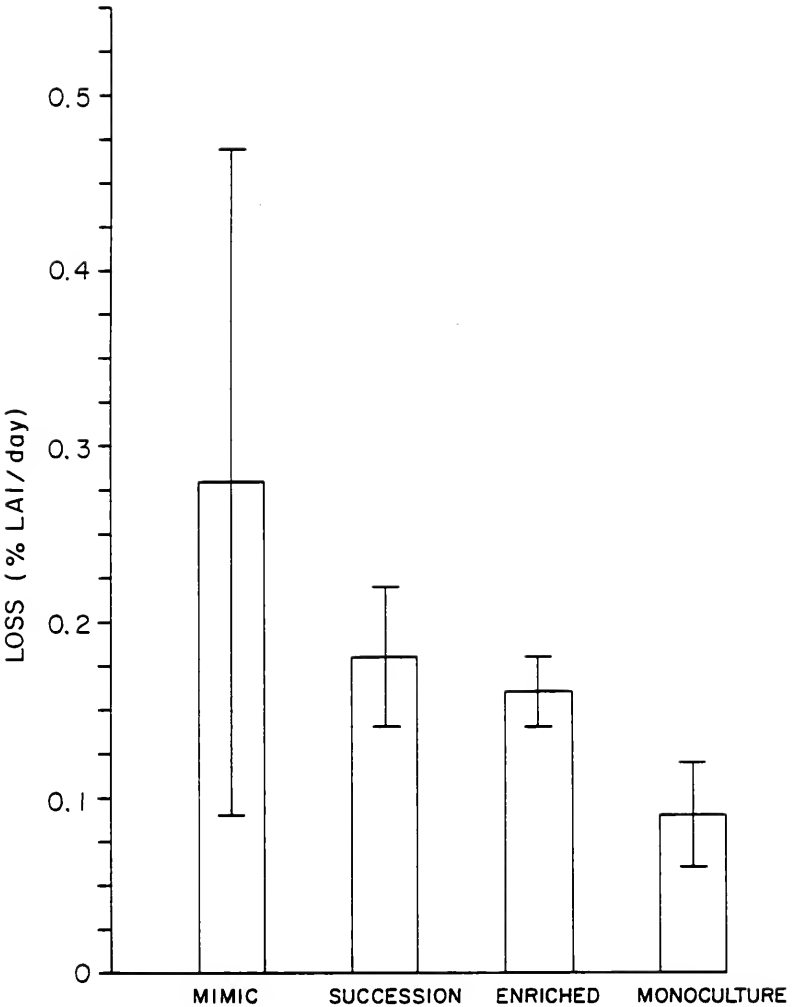

Figure 58. Percent of total LAI lost to herbivores in four ecosystems. Values are $\bar{x} \pm 1$ s.d.; n = 3 sampling dates.

In this study plant diversity and LAI were positively correlated. The systems without investigator-controlled diversity developed both high diversity and high LAI. In the systems where diversity was investigator-controlled, LAI was lower (Table 29). The high diversity, high LAI systems had lower percent losses to herbivores than the low diversity, low LAI systems. Because the effects of diversity and LAI were confounded, it was not possible to separate the single effects of these two factors.

Although both host plant density and overall ecosystem LAI are recognized to be important factors that affect herbivory patterns (Pimentel 1961a, Root 1975, Bach 1980, Rauscher 1981, Solomon 1981), few researchers have attempted to separate density effects from diversity effects (e.g., Rauscher 1981, Risch 1981, Bach 1980, Benedict 1982). Bach (1980) found that plant density had no effect on herbivory and that the difference in beetle abundance on cucumbers in monoculture and polyculture was a function of plant diversity. Pimentel (1961a) found more herbivores per unit leaf area in dispersed and sparse plantings of Brassica species, but more herbivores on a per unit ground area in dense plantings. Solomon (1981) reported that horsenettle plants at low density had more moth larvae per plant than plants at high density, but the numbers of larvae per unit ground area did not differ. Risch (1981) reported equal numbers of herbivorous insects in monocultures and

Table 29. Diversity, leaf area index (LAI), percent herbivory and net primary productivity (NPP) in four experimental ecosystems.

Ecosystem	Diversity	LAI	Percent herbivory	NPP
Enriched succession	Highest	Highest	Medium	High
Natural succession	High	High	Medium	Medium
Mimic of succession	Medium	Medium	High	Low
Monoculture	Low	Low	Low	High

dicultures of corn and sweet potato, but because plant density was higher in the dicultures, the numbers of insects per unit leaf area were lower in the dicultures. Ewel et al. (1982) found that herbivore consumption was a nearly constant proportion (2-10%) of the leaf area present rather than a constant amount per unit ground area. Those data were based on amounts rather than rates of damage and are not directly comparable to the results of this study.

The results of this and most other studies suggest that LAI affects herbivory rates. This may be due to physical interference with insect movement patterns and reduced apparency of host plants in structurally complex systems (Root 1973, Atsatt and O'Dowd 1976, Pimentel 1977). To minimize the impact of herbivory on the ecosystem, maintenance of high LAI is an important design consideration for high diversity agroecosystems.

Effects of Plant Species Composition

Diverse systems have certain characteristics (such as microhabitat complexity, diversity of plant herbivore defenses and high LAI) that affect herbivory patterns. However, two equally diverse systems containing different plant species may have very different herbivory rates. The particular species that are found together in an ecosystem and their relative abundances have an important influence on herbivory patterns.

Ecosystem herbivory rates reflect characteristics of the component species that comprise the system. Monocultures may have high or low herbivory rates, depending on characteristics of the single plant species in the system. For example, palatable species in monospecific stands have higher herbivory rates than unpalatable species in monospecific stands (Ewel, Brown and Ojima, unpublished data).

Similarly, diverse systems may have different herbivory rates because of differences in plant species composition. For instance, the median species herbivory rate was much higher in the mimic of succession (23.5 $cm^2\ m^{-2}$ leaf day^{-1}) than in the natural succession (12.9). On a species-by-species basis, the species in the mimic incurred higher herbivory rates than the species in the natural succession. This is partially due to the high palatabilities of many of the cultivars introduced into the mimic plots.

In the natural succession, the enriched succession, and the mimic, very high herbivory rates occurred only on species with LAI <0.5, while very abundant species (LAI $\geq$ 0.5) incurred lower than average rates. The same trend has been reported in other studies of herbivory in successional and agricultural systems, in which the more apparent, relatively abundant species in the ecosystem were the least consumed (Reader and Southwood 1981, Ewel et al. 1982). Low

herbivory rates may partially expain the dominance of some species in the diverse ecosystems.

The mimic had only one species with LAI $\geq$ 0.5 (*Cymbopogon citratus*). With respect to herbivory patterns, the paucity in the mimic ecosystem of abundant species with low herbivory rates was a major difference between the mimic and the natural succession. Such species help tc maintain high LAI in the ecosystem and reduce the apparency of more palatable species in the system. The data suggest that unpalatable species may be essential components of stable, complex aqroecosystems.

Tahvanainen and Root's (1972) hypothesis that a plant species may have increased resistance to herbivore attack through association with other species is probably valid in naturally diverse ecosystems where the abundant species are the less consumed species. However, my data suggest that the degree of associational resistance gained by a species in the system is determined by the relative consumption rates of the species in the ecosystem. In some cases, the associatien may be negative instead of positive. A relatively unpalatable species may experience 'associational susceptibility' to insects rather than 'associational resistance.'

For example, cassava (a species with a low herbivory rate) incurred more damage from herbivores in the mimic system, surrounded by an array of heavily consumed species,

than in the enriched succesion or in the monoculture. In the enriched succession, the cassava plants were surrounded by many little-consumed successional species; in the monoculture, each cassava plant was surrounded by little-consumed cassava plants.

Similar results have been reported by others. Bach (1980) found more beetles on corn when grown in a polyculture with cucumbers (a heavily consumed species), than when grown in monoculture. Risch (1981) observed that numbers of beetles were lower in polycultures containing at least one non-host species, and higher in polycultures containing all host species. In an unpublished study by Ewel, Brown and Ojima, palatable species were consumed less in a diverse successional ecosystem than when grown in a monoculture, but unpalatable species were consumed more in the diverse ecosystem than in monoculture.

Another species (Erythrina costaricensis) was damaged less in the enriched succession than in the mimic. In addition to the different range of consumption rates for species in the mimic and in the enriched succession, the enriched succession was more floristically diverse and had higher LAI than the mimic. All of these factors may have influenced the herbivory rate on Erythrina.

The data suggest that to build associational resistance rather than associational susceptibility into an agroecosystem, the plant species must be very carefully

selected. Species that are relatively unpalatablae to herbivores are important in providing associational protection to the herbivore-susceptible species in the system.

Plant Herbivore Defenses

Diverse ecosystems contain both palatable and unpalatable species, with a wide range of chemical and physical herbivore defenses. In this study, mean species herbivory rates varied by more than two orders of magnitude in the natural succession (0.7 to 131.4 cm^2 m^{-2} leaf day^{-1}), enriched succession (0.6 to 77.9), and mimic of succession (0.5 to 103.7). Other investigators have reported herbivory rates that ranged widely among tropical pioneer and persistent species (Coley 1980) and among species in three subtropical and one warm temperate forest (Benedict 1976).

Although herbivore defenses were not measured in this study, the wide range of herbivory rates suggests that herbivore defenses varied among successional species and among successional mimic species. The diversity of secondary compounds in successional herbaceous species is high (Feeny 1976). Small amounts of toxic compounds, i.e. 'qualitative' chemical defenses, are common in successional species (Feeny 1974). Low herbivory rates on some species in the diverse ecosystems may have been due to the presence of chemical defenses, the presence of physical defenses, or

'associational resistance'. Chemical and physical defenses are intrinsic properties of a plant species; 'associational resistance', the resistance of a species to herbivore attack due to characteristics of the species around it, is an ecosystem attribute (Tahvanainen and Root 1972, Atsatt and O'Dowd 1976). Associated plants may function as insectary plants that maintain predator and parasite populations; as insect repellants with spines, toxins, or olfactory deterrents; or as attractant plants that serve as alternative prey for herbivores (Atsatt and O'Dowd 1976).

Structural Complexity

Floristically diverse systems are generally more complex in structure than are floristically simple systems. The diverse successional systems in this study contained species with many different growth forms, including herbaceous dicots, grasses, erect woody plants, and climbing vines. Because of the variety of growth forms, the diverse systems had a more even vertical and horizontal distribution of leaf tissue than did the monoculture. Greater variety in plant physiognomy leads to a diversity of microhabitats in the ecosystem (Pimentel 1961a, Dempster 1969, Dempster and Coaker 1974, Smith 1976, Bach 1980), and these 'enemies' may keep herbivore populations at low levels (Root 1973). In addition, the structure of diverse vegetation may create physical barriers that affect insect movements and make host

plants harder to find (Root 1973, Rauscher 1981, Risch 1981, Solomon 1981).

Herbivory, Diversity and Energy Flow

Many studies of herbivory have considered responses of single plants or species to increased or decreased herbivory (e.g., see review by Jameson 1963). This study differs in that entire ecosystems were manipulated under field conditions. Herbivory was experimentally controlled by use of insecticides and artificial defoliation, and responses to increased and decreased herbivory were monitored. Vegetation structure, species composition and net primary productivity were affected by changes in herbivory, and responses differed in high and low diversity systems.

Interpretation of the results must consider the design of the experiments. The insecticide experiment was a long-term study (1.5 yr); the defoliation experiment was a short-term study (3 mo). The application of insecticide affected all types of herbivory, including damage from stem borers, piercing insects and root herbivores; in the defoliation experiment, only one type of herbivory, removal of leaf tissue, was simulated.

Herbivory rates on all species were increased or decreased nondifferentially, imitating the effects of generalist herbivore activity. The results have practical implications for agricultural systems where insect pests are

generalists. The results are not comparable to theoretical predictions based on the assumption that changes in herbivore intensity have different effects on palatable and unpalatable species.

Energy Flow Model

The model in Fig. 59 shows some of the energy flows that affect the relationships among plant productivity, plant species richness, and herbivory in an ecosystem.

This study involved manipulation of plant species richness in several successional ecosystems. Investigator control of propagules and the size of the species pool that determined the richness of the ecosystem varied among the four ecosystems. In the natural succession, no manipulations were imposed; the species richness of this system was determined by naturally occurring seed inputs from outside the system, plus reproduction of plants in the system. In the enriched succession, these two sources of propagules were supplemented by artificial seeding of additional species. In the mimic system, artificial seeding of many species, outside seed sources, and reproduction in the system provided propagules. However, in this system only the artificially seeded species were allowed to grow and reproduce; all other species were weeded out. The monoculture was seeded with a single species, and other species were removed by weeding.

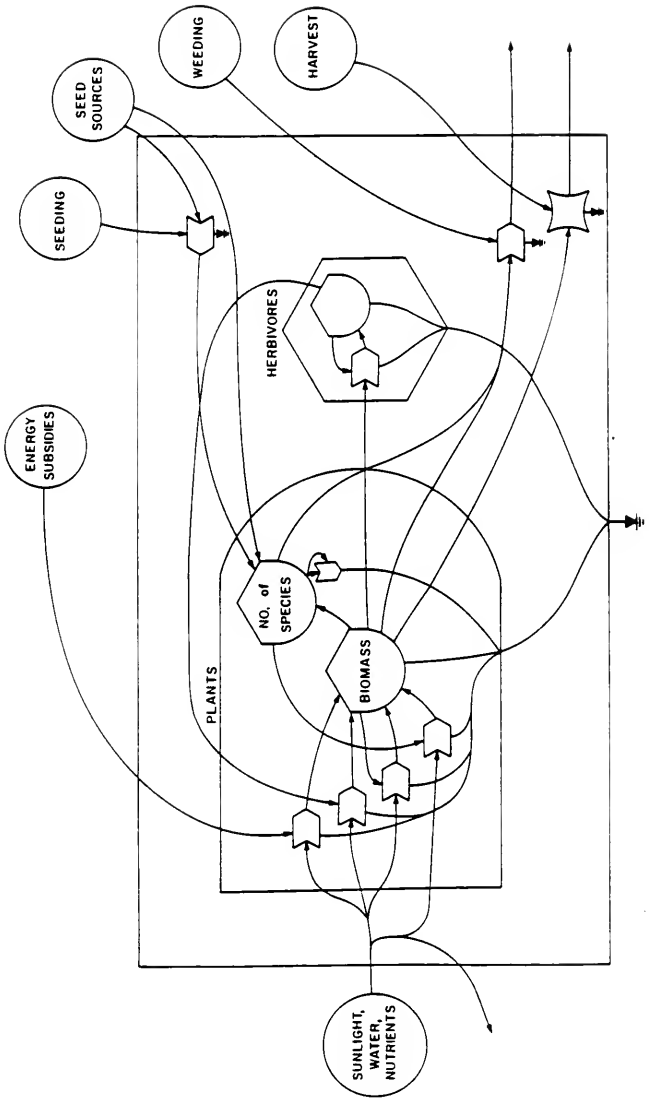

Figure 59. Energy flow model.

How might these differences in availability of propagules affect the primary productivity of the systems? If the energy available to the system is not used completely by the species present, additional propagules provide a pool of species that may be able to utilize the energy more fully, because they have different growth forms and growth requirements.

Herbivory stimulates primary productivity; however, the amount of stimulation is influenced by level of herbivory and plant diversity of the system (see Chapter IV, 'Resilience of High and Low Diversity Ecosystems'). When plant biomass is lost to herbivores, the system may respond in at least two ways. First, plant growth may be altered by a variety of physiological mechanisms (see Chapter I, 'Impacts on species composition and diversity'), including stimulation of photosynthesis in residual leaf tissue. Second, changes in species composition may result from compensatory interactions among co-occurring species and from addition of new species to the system (when seed sources are present). The process is one of adjustment in species and numbers, and the result is a new complement of species utilizing the energy available to the system.

In the monoculture, plant species richness was tightly controlled; the fluctuations in species composition that contributed to the high resilience of the diverse system were not allowed. Although productivity of residual plants

was stimulated in the monoculture as well as in the diverse systems, overall stimulation in the monoculture was less (see Chapter IV, 'Resilience of High and Low Diversity Ecosystems'). Thus, productivity in the monoculture was primarily a function of the growth rate of the species and outside energy subsidies. Outside subsidies were low, but information that went into planting (e.g., propagule selection, spacing, timing) may be considered an energy subsidy. Fossil-fuel based subsidies are often very important in modern agriculture; this flow is often so large that high net productivity of the agroecosystem is maintained regardless of other processes occurring in the system.

The monoculture had overall NPP almost as great as the NPP of the most diverse system studied (the enriched succession). From the model, one might predict that productivity of a monoculture without energy subsidies would be less than productivity of a diverse system because it lacks the compensatory mechanism provided by diversity. Three factors help to explain the high monoculture productivity.

First, the species planted in monoculture (maize and cassava) had high growth rates and low losses to herbivores. Second, the monoculture was a subsidized system in the sense that the species were carefully selected, planted in rows, and maintained under conditions favorable for rapid growth

(i.e., kept free of competition from other species by weeding). Third, the monoculture, but not the other ecosystems, was periodically harvested. Because the plants were harvested at maturity, the senescence stage of the life cycle (a period of low NPP) was bypassed.

Although overall productivity of the monoculture was high, NPP varied widely among plantings. In the first maize planting, losses to herbivores were low; NPP was high. In the second maize planting, losses to soil herbivores (not measured in this study) were apparently quite high; NPP was low. The NPP was high, however, in the second maize monoculture treated with insecticide (i.e., when the system was subsidized).

Many factors determine the size of the herbivore population, and the details of this are not shown in the model. As a result of other processes (not shown), herbivore populations fluctuate and the rate of herbivore consumption varys temporally. Although the data from this study did not indicate that diverse systems lost less biomass to herbivores than simple systems, the simple system showed more temporal variability in losses. Higher variability both in herbivory rates and in NPP in the monoculture are key characteristics that distinguish it from the diverse systems.

One flow that is not shown in the model is a possible effect of herbivory on plant diversity. Some researchers

have reported reductions in species richness of marine organisms after predator removal (Paine 1971) and reductions in plant diversity after herbivore exclusion (Harper 1969). Others have reported increases in plant diversity after applications of insecticide (Malone 1969, Shure 1971). The results from this study concerning changes in plant diversity due to herbivory are inconclusive. The experiments were not designed specifically to test the hypothesis that herbivory causes changes in diversity. Although the data from both the insecticide experiment (decreased herbivory) and the defoliation experiment (increased herbivory) suggest that plant diversity may decrease as herbivory increases, the indication is not strong. For example, in the defoliation study species richness increased in both defoliated and non-defoliated plots. However, species richness increased less in defoliated plots. It is unclear whether this result should be interpreted as a positive or a negative effect of high herbivory on diversity.

Thus, the model diagrammatically summarizes important relationships (among plant production, herbivory, seed sources, and energy subsidies) that are suggested by the data. Although it does not demonstrate the complex interactions between plant species richness and herbivory, it is consistent with findings on ecosystem resilience, the topic of the next section.

Resilience of High and Low Diversity Ecosystems

It has been proposed that stability has two component parts: resistance, or the lack of fluctuations after a perturbation, and resilience, the ability to return to an equilibrium point after perturbation. This definition of stability implicitly assumes that a system is fluctuating around a single equilibrium point.

Holling (1973) approached the problem of stability by recognizing that more than one equilibrium point may exist in many systems. He defined a stable system as one with small fluctuations and rapid response to a state of equilibrium after perturbation, and a resilient system as one able to adapt to perturbations by moving among multiple equilibria. Holling pointed out that increasing the stability of a system (e.g., using insecticides to reduce insect population fluctuations) might in fact decrease the resilience of the system. Resilience is a measure of the functional stability of relationships between populations or state variables in the system (Holling 1973).

Are diverse systems more resilient than simple systems? Few researchers have addressed this question directly. In this study the effects of a perturbation (herbivory) on an ecosystem process (NPP) in a diverse and a simple system were investigated. Fig. 60 summarizes the results and is based on data from the insecticide experiment (reduced herbivory), routine measurements of herbivory (background

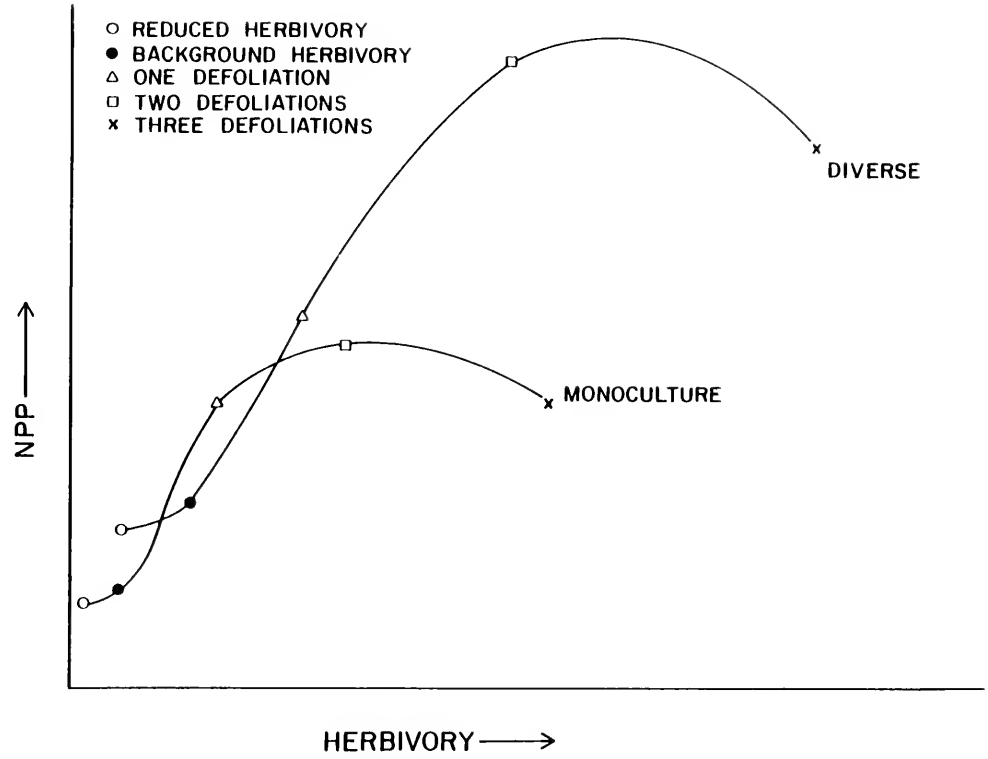

Figure 60. Net primary productivity (NPP) in a diverse ecosystem and a monoculture at different levels of herbivory.

levels), and the three defoliations (increased herbivory). Quantitative comparisons were not possible because the units and time scale for measurement of NPP and herbivory differed among experiments. However, the figure was derived from data and does show qualitative relationships between the variables and between ecosystems.

Herbivory (abscissa) is based on absolute amounts, rather than percent, of leaf tissue consumed. Because LAI and leaf specific mass were higher in the diverse system than in the monoculture, each 50% defoliation removed more grams of leaf tissue from the diverse system. This is reflected in Fig. 60 as higher herbivory at one, two, and three defoliations in the diverse system than in the monoculture.

Background (naturally occurring) herbivory was higher in the diverse system than in the monoculture. When herbivory was reduced by insecticide in the diverse system, herbivory was still as high as background herbivory in the monoculture. This result does not support the idea that high diversity systems incur less damage from herbivores than do low diversity systems. Monoculture herbivory in Fig. 60 includes data only from the cassava monoculture (maize monoculture excluded). Cassava leaves contain cyanogenic glycosides and are relatively unpalatable to most leaf-feeding insects (although not to leaf-cutter ants; see Blanton 1982). This intrinsic resistance to herbivores may be one reason for the widespread cultivation of cassava in

many tropical areas. It is likely that herbivory would have been different had other species been planted in monoculture. Also, the true herbivory rate on cassava may have been higher than the value reported here (see Chapter IV, 'Low Herbivory Rates'), but was probably not significantly greater than the rate in the diverse system.

If diverse systems incur as much damage from herbivores as do simple systems, why do polycultures appear to have an advantage over monocultures with respect to herbivory? The answer may be in the different responses of diverse and simple systems to herbivore attack. In this study the responses of diverse and simple systems to herbivory (summarized in Fig. 60) were similar in one respect and differed in two respects.

In both systems herbivory stimulated NPP over a wide range of herbivory levels. At the highest herbivory level (three 50% defoliations), more than five times the annual background loss to herbivores was artificially removed. Even this high herbivory level stimulated NPP in both the simple and diverse systems.

Compensatory growth following grazing has been reported for a wide variety of plant species (see summary of previous work in Chapter I), and several researchers have suggested a nonmonotonic productivity response to grazing (Vickery 1972, Dyer 1975, Noy-Meir 1975, Caughley 1976, McNaughton 1979a). The results of this study suggest that the nonmonotonic form

of the NPP response curve may be appropriate for plant communities comprised of many species as well as for single species. In both systems there was an herbivory level at which maximum stimulation occurred, and at higher herbivory the stimulatory effect decreased (Fig. 60).

The NPP response to herbivory in the high and low diversity systems differed in two ways. First, over most of the herbivory range studied, and particularly at high herbivory levels, the stimulatory effect on NPP was greater in the diverse system. Given equal herbivory, NPP was higher in the diverse system than in the monoculture, except over a narrow range of low herbivory rates. At these low rates the monoculture had higher NPP than the diverse system. The implication for agriculture is that a polyculture may be better able to maintain high NPP than a monoculture under heavy herbivore pressure, but at low herbivory levels a monoculture may perform equally well.

Second, maximum stimulation of NPP occurred at a higher herbivory level in the diverse system than in the monoculture. If the two curves in Fig. 60 are extrapolated to the right by drawing straight lines through the last two points on each curve, the monoculture curve reaches the abscissa at a lower herbivory level than does the curve for the diverse system. Although the exact shape of these curves is not known, the data suggest that the stimulatory effect of herbivory on NPP spans a much wider range of

herbivory levels in the diverse than in the simple system. A high herbivory level that has a negative effect on NPP in a monoculture may produce a positive response in a diverse system.

Positive response to a wide range of herbivory levels in the diverse system indicates high resilience. Holling (1973) proposed that diverse systems should be more resilient than simple systems for the following reason. A system with many species has many equilibrium points, each with its own domain of attraction. Although fluctuations in population numbers will move the diverse system from one domain of attraction to another, system function will be maintained and the system will persist. McNaughton (1977) gave examples of empirical studies in which fluctuations in the species composition of diverse systems had a stabilizing effect on ecosystem processes. Shifts in diversity are common responses to perturbations such as insecticide application and nutrient enrichment (see, for example, Shure 1971, Harcombe 1977a).

In this study both increased and reduced herbivory levels in the diverse system resulted in changes in the dominant plant species. The wide positive response range to herbivory in the diverse system was probably due to compensatory interactions among the co-occurring species. Changes in species dominance favored those species best able to respond to the perturbation. Species varied in their

responses to herbivory, depending on timing and intensity of the herbivory relative to the life cycle of the plant. However, because many complements of species could utilize equally well the available space and resources, positive response occurred over a wide range of herbivory levels. The diverse system was able to maintain energy flow through the system (NPP) by species substitutions, but the monoculture was limited by the regrowth capacity of a single species.

For example, the effect of herbivory on vertical distribution of leaf tissue differed in the diverse ecosystem and the monoculture. Defoliation allowed greater light penetration through the canopy. In the diverse system the result was increased growth of understory plants and an increase in leaf area near the ground. After defoliation of the cassava monoculture, leaf tissue developed at the top of the canopy rather than near the ground. This reflected the growth form of the cassava and the lack of understory plants (due to weeding) to take advantage of increased light transmission.

High resilience of diverse ecosystems may have important implications for the design of agroecosystems. Although diverse agroecosystems and monocultures may incur equal amounts of damage from herbivores, the wider range of response to herbivory in diverse systems makes them more sustainable. High resilience of complex agroecosystems that

imitate succession translates into a reduction of the risk of total crop loss by the farmer. As in the natural system, compensatory species substitutions may occur in complex agroecosystems. In agroecosystems these substitutions are controlled by management, but the principle is the same: compensatory effects result in maintenance of energy flow through the system. Because minimizing risk is often more important to a subsistence farmer than maximizing yield (Barlett 1980), incorporating resilience into agroecosystems by crop diversification is a critical design consideration.

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APPENDIX A

CALCULATION OF HERBIVORY RATES

Equation 8 (Methods, "Estimation of Hole Expansion") was derived by Dr. Ronald E. Harrell (Department of Mathematics, Allegheny College, Meadville, PA) and Becky J. Brown, as follows.

Let (t_o,t_f) be the time interval over which herbivory was monitored on a group of leaves. Let (t_o,t_f) be divided into n equal sub-intervals such that $\Delta t = t_j - t_{j-1}$, $j = 1,\ldots,n$.

The damage present on the group of leaves at t_1 may be expressed as

$$D(t_1) = D(t_o) + c\Delta t + \frac{D(t_o)}{G(t_o)}\left(G'\Delta t\right)$$

$$= c\Delta t + D(t_o)\left[1 + \frac{G'\Delta t}{G(t_o)}\right] \qquad (1)$$

where c = rate of consumption by herbivores,

$G(t_i)$ = gross leaf area at t_i, and

G' = average leaf growth rate = $\dfrac{G(t_f) - G(t_o)}{n\Delta t}$

Similarly,

$$D(t_2) = D(t_1) + c\Delta t + \frac{D(t_1)}{G(t_1)}\left(G'\Delta t\right) \tag{2}$$

$$= c\Delta t + D(t_1)\left[1 + \frac{G'\Delta t}{G(t_1)}\right]$$

$$= c\Delta t + \left[c\Delta t + D(t_o)\left(1 + \frac{G'\Delta t}{G(t_o)}\right)\right]\left[1 + \frac{G'\Delta t}{G(t_1)}\right]$$

$$= c\Delta t + c\Delta t\left(1 + \frac{G'\Delta t}{G(t_1)}\right) + D(t_o)\left(1 + \frac{G'\Delta t}{G(t_o)}\right)\left(1 + \frac{G'\Delta t}{G(t_1)}\right)$$

and

$$D(t_f) = c\Delta t\left[1 + \left(1 + \frac{G'\Delta t}{G(t_{n-1})}\right) + \left(1 + \frac{G'\Delta t}{G(t_{n-2})}\right)\left(1 + \frac{G'\Delta t}{G(t_{n-1})}\right) + \ldots + \left(1 + \frac{G'\Delta t}{G(t_1)}\right)\cdots\left(1 + \frac{G'\Delta t}{G(t_{n-1})}\right)\right] + D(t_o)\left(1 + \frac{G'\Delta t}{G(t_o)}\right)\cdots\left(1 + \frac{G'\Delta t}{G(t_{n-1})}\right)$$

$$D(t_f) = c\Delta t \left[1 + \sum_{i=1}^{n-1} \prod_{j=n-i}^{n-1} \left(1 + \frac{G'\Delta t}{G(t_j)} \right) \right] + D(t_o) \prod_{j=0}^{n-1} \left(1 + \frac{G'\Delta t}{G(t_j)} \right) \tag{3}$$

Solving for c,

$$c = \frac{D(t_f) - D(t_o) \prod_{j=0}^{n-1} \left(1 + \frac{G'\Delta t}{G(t_j)} \right)}{\Delta t \left[1 + \sum_{i-1}^{n-1} \prod_{j=n-i}^{n-1} \left(1 + \frac{G'\Delta t}{G(t_j)} \right) \right]} \tag{4}$$

Let $G(t_o) = rG(t_f)$, for some r such that $0 \leq r \leq 1$. Then,

$$1 + \frac{G'\Delta t}{G(t_j)} = 1 + \frac{\frac{(G(t_f) - G(t_o))\ (\Delta t)}{n\Delta t}}{G(t_o) + \frac{G(t_f) - G(t_o)}{n\Delta t} \left(j\Delta t \right)} = 1 + \frac{G(t_f) - rG(t_f)}{(n-j)G(t_o) + jG(t_f)} \tag{5}$$

$$= 1 + \frac{1 - r}{(n-j)\ r + j} = 1 + \frac{1 - r}{nr + j(1-r)}$$

and

$$\prod_{j+n-i}^{n-1}\left(1 + \frac{G'\Delta t}{G(t_j)}\right) = \prod_{j=n-i}^{n-1}\left(1 + \frac{1 - r}{nr + j(1-r)}\right)$$

$$= \left(1 + \frac{1 - r}{nr + (n-i)(1-r)}\right)\left(1 + \frac{1 - r}{nr + (n-i+1)(1-r)}\right) \cdots \left(1 + \frac{1 - r}{nr + (n-1)(1-r)}\right)$$

$$= \left(1 + \frac{1 - r}{n - i(1-r)}\right)\left(1 + \frac{1 - r}{n - (i-1)(1-r)}\right) \cdots \left(1 + \frac{1 - r}{n - (1-r)}\right)$$

$$= \left(\frac{n - (i-1)(1-r)}{n - i(1-r)}\right)\left(\frac{n - (i-2)(1-r)}{n - (i-1)(1-r)}\right) \cdots \left(\frac{n}{n - (1-r)}\right)$$

$$= \frac{n}{n - i(1-r)} \qquad (6)$$

When i = n,

$$\prod_{j=0}^{n-1} \left(1 + \frac{G'\Delta t}{G(t_j)}\right) = \frac{n}{n - n(1-r)} = \frac{1}{r} = \frac{G(t_f)}{G(t_o)} \tag{7}$$

Let $m = t_f - t_o = n\Delta t$. (8)

By substitution of (6), (7), and (8) in equation (4),

$$c = \frac{D(t_f) - D(t_o)\,\dfrac{G(t_f)}{G(t_o)}}{\dfrac{m}{n} + m \sum_{i=1}^{n-1} \dfrac{1}{n - i(1-r)}} \tag{9}$$

APPENDIX B

BIOMASS AND LITTERFALL MEANS

Table 30. Leaf biomass in natural succession, enriched succession, mimic of succession, and monoculture. Mass values are $\bar{x}$ (s.d.); n = 6. At each date, means followed by the same letter are not significantly different at the .05 level.

Date	Vegetation Age: Natural, Enriched, Mimic (wks)	Vegetation Age: Monoculture (wks (crop))	Dry Mass (g/m^2): Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
14 May 79	7.0	7.0 (1st maize)	9.6^{A} (11.1)	13.0^{A} (15.4)	27.8^{A} (30.5)	50.4^{A} (66.0)
31 May 79	9.5	9.5 (1st maize)	58.6^{A} (37.3)	85.4^{A} (39.8)	78.7^{A} (51.1)	92.0^{A} (34.0)
20 June 79	12.5	12.5 (1st maize)	89.8^{A} (28.4)	108.1^{A} (51.7)	86.2^{A} (55.8)	99.4^{A} (59.1)
9 July 79	15.0	15.0 (1st maize)	195.8^{A} (97.9)	165.7^{A} (105.8)	50.6^{B} (32.3)	311.8^{A} (149.0)
1 August 79	18.5	1.0 (2nd maize)	206.3^{A} (121.8)	357.4^{A} (218.9)	83.4^{B} (49.0)	0.2^{C} (0.1)
16 August 79[a]		3.5 (2nd maize)				0.8 (0.3)
10 September 79	24.0	7.0 (2nd maize)	311.9^{A} (201.9)	480.8^{A} (367.4)	114.6^{B} (161.8)	9.8^{C} (7.8)
8 October 79	28.0	11.0 (2nd maize)	330.9^{A} (270.8)	516.2^{A} (519.9)	78.8^{B} (110.7)	24.1^{B} (16.7)
29 October 79[a]		14.0 (2nd maize)				12.3 (15.4)

Table 30--continued.

Date	Vegetation Age: Natural, Enriched, Mimic (wks)	Vegetation Age: Monoculture (wks) (crop)	Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
19 November 79	34.0	17.0 (2nd maize)	265.3^{AB} (154.4)	416.8^{A} (303.2)	165.9^{B} (193.4)	27.2^{C} (20.0)
17 December 79	38.0	3.0 (cassava)	308.3^{A} (173.5)	373.9^{A} (218.8)	112.0^{B} (40.8)	0.0^{C} (0.0)
21 January 80	43.0	8.0 (cassava)	262.2^{A} (117.7)	334.3^{A} (167.9)	251.4^{A} (272.8)	11.6^{B} (4.4)
17 March 80	51.0	16.0 (cassava)	348.5^{A} (130.2)	682.5^{A} (491.9)	107.5^{B} (83.0)	123.9^{B} (16.9)
19 May 80	60.0	25.0 (cassava)	258.9^{B} (149.5)	730.8^{A} (548.9)	176.1^{B} (140.4)	131.1^{B} (75.2)
8 July 80	67.0	32.0 (cassava)	276.8^{AB} (76.6)	673.3^{A} (548.9)	206.6^{BC} (154.1)	153.0^{C} (118.5)
13 September 80[a]		42.0 (cassava)				89.3 (27.3)
28 October 80	83.0		494.4^{B} (259.2)	1162.2^{A} (510.1)	144.4^{C} (70.8)	

[a]Monoculture only harvested.

Table 31. Stem biomass in natural succession, enriched succession, mimic of succession, and monoculture. Mass values are $\bar{x}$ (s.d.); n = 6. At each date, means followed by the same letter are not significantly different at the .05 level.

Date	Vegetation Age: Natural, Enriched, Mimic (wks)	Vegetation Age: Monoculture (wks (crop))	Dry Mass (g/m^2): Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
14 May 79	7.0	7.0 (1st maize)	1.8^{A} (2.6)	4.2^{A} (5.7)	13.0^{A} (15.9)	23.1^{A} (31.6)
31 May 79	9.5	9.5 (1st maize)	29.4^{B} (22.1)	71.2^{AB} (77.7)	64.0^{AB} (47.1)	102.9^{A} (59.9)
20 June 79	12.5	12.5 (1st maize)	73.9^{A} (34.3)	128.3^{A} (89.2)	105.0^{A} (59.1)	181.4^{A} (119.7)
9 July 79	15.0	15.0 (1st maize)	259.2^{B} (110.6)	215.8^{B} (178.5)	78.5^{C} (50.5)	567.1^{A} (175.2)
1 August 79	18.5	1.0 (2nd maize)	249.9^{A} (90.3)	164.3^{A} (147.5)	189.8^{A} (149.2)	0.0^{B} (0.0)
16 August 79[a]		3.5 (2nd maize)				0.0 (0.0)
10 September 79	24.0	7.0 (2nd maize)	588.9^{A} (237.1)	562.8^{A} (208.6)	263.5^{B} (449.6)	5.6^{C} (4.9)
8 October 79	28.0	11.0 (2nd maize)	765.8^{A} (698.5)	472.9^{A} (278.8)	269.8^{A} (510.1)	43.5^{A} (32.4)
29 October 79[a]		14.0 (2nd maize)				22.1 (28.8)

Table 31--continued.

Date	Vegetation Age: Natural, Enriched, Mimic (wks)	Vegetation Age: Monoculture (wks) (crop)	Dry Mass (g/m^2): Natural Succession	Dry Mass (g/m^2): Enriched Succession	Dry Mass (g/m^2): Mimic of Succession	Dry Mass (g/m^2): Monoculture
19 November 79	34.0	17.0 (2nd maize)	611.8^{A} (326.0)	405.4^{A} (238.9)	331.6^{A} (465.3)	59.9^{A} (41.9)
17 December 79	38.0	3.0 (cassava)	621.6^{A} (264.7)	492.2^{A} (333.3)	408.4^{A} (426.6)	0.0^{B} (0.0)
21 January 80	43.0	8.0 (cassava)	479.3^{A} (133.1)	418.8^{A} (249.4)	350.8^{A} (322.2)	8.9^{B} (5.4)
17 March 80	51.0	16.0 (cassava)	1161.6^{A} (939.6)	632.6^{A} (649.2)	294.9^{A} (207.9)	228.9^{A} (38.6)
19 May 80	60.0	25.0 (cassava)	774.0^{A} (460.3)	894.4^{A} (598.4)	571.4^{A} (667.5)	436.1^{A} (330.3)
8 July 80	67.0	32.0 (cassava)	880.7^{A} (394.1)	605.0^{A} (502.3)	520.5^{A} (328.6)	787.8^{A} (277.0)
13 September 80[a]		42.0 (cassava)				662.7 (136.8)
28 October 80	83.0		1211.6^{AB} (921.7)	2522.4^{A} (1869.8)	743.8^{B} (759.1)	

[a]Monoculture only harvested.

Table 32. Biomass of reproductive parts in natural succession, enriched succession, mimic of succession, and monoculture. Mass values are $\bar{x}$ (s.d.); n = 6. At each date, means followed by the same letter are not significantly different at the .05 level.

Date	Vegetation Age: Natural, Enriched, Mimic (wks)	Vegetation Age: Monoculture (wks) (crop)	Dry Mass (g/m^2): Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
14 May 79	7.0	7.0 (1st maize)	0.2^{A} (0.5)	0.0^{A} (0.0)	0.0^{A} (0.0)	0.0^{A} (0.0)
31 May 79	9.5	9.5 (1st maize)	0.0^{B} (0.1)	5.0^{B} (12.1)	2.7^{B} (3.3)	11.1^{A} (8.3)
20 June 79	12.5	12.5 (1st maize)	0.7^{C} (1.7)	18.3^{BC} (30.9)	39.1^{AB} (20.0)	86.7^{A} (73.9)
9 July 79	15.0	15.0 (1st maize)	1.2^{C} (2.9)	3.2^{C} (3.6)	50.4^{B} (30.3)	739.7^{A} (510.3)
1 August 79	18.5	1.0 (2nd maize)	1.0^{BC} (1.5)	5.8^{B} (7.3)	254.5^{A} (260.3)	0.0^{C} (0.0)
16 August 79[a]		3.5 (2nd maize)				0.0 (0.0)
10 September 79	24.0	7.0 (2nd maize)	21.2^{A} (20.3)	27.1^{A} (16.3)	19.5^{A} (37.7)	0.0^{B} (0.0)
8 October 79	28.0	11.0 (2nd maize)	58.0^{A} (59.3)	27.5^{A} (17.6)	8.1^{A} (13.1)	31.1^{A} (34.4)
29 October 79[a]		14.0 (2nd maize)				18.5 (22.1)

Table 32--continued.

Date	Vegetation Age: Natural, Enriched, Mimic wks	Vegetation Age: Monoculture wks (crop)	Dry Mass (g/m^2): Natural Succession	Dry Mass (g/m^2): Enriched Succession	Dry Mass (g/m^2): Mimic of Succession	Dry Mass (g/m^2): Monoculture
19 November 79	34.0	17.0 (2nd maize)	61.3^{AB} (51.3)	21.0^{BC} (32.0)	2.3^{C} (2.3)	81.6^{A} (47.5)
17 December 79	38.0	3.0 (cassava)	23.0^{A} (17.3)	24.2^{A} (25.0)	56.3^{A} (74.6)	0.0^{B} (0.0)
21 January 80	43.0	8.0 (cassava)	14.5^{AB} (15.5)	4.2^{BC} (5.8)	19.7^{A} (20.2)	0.0^{C} (0.0)
17 March 80	51.0	16.0 (cassava)	11.7^{A} (11.4)	40.4^{A} (76.2)	24.5^{A} (18.0)	0.0^{B} (0.0)
19 May 80	60.0	25.0 (cassava)	4.6^{AB} (5.1)	8.9^{AB} (18.0)	29.9^{A} (56.4)	0.0^{B} (0.0)
8 July 80	67.0	32.0 (cassava)	18.2^{A} (10.8)	13.9^{AB} (17.5)	14.7^{B} (32.5)	0.0^{C} (0.0)
13 September 80[a]		42.0 (cassava)				0.2 (0.3)
28 October 80	83.0		33.9^{A} (67.6)	16.3^{A} (26.1)	65.9^{A} (94.8)	

[a]Monoculture only harvested.

Table 33. Standing dead biomass in natural succession, enriched succession, mimic of succession, and monoculture. Mass values are $\bar{x}$ (s.d.); n = 6. At each date, means followed by the same letter are not significantly different at the .05 level.

Date	Vegetation Age: Natural, Enriched, Mimic wks	Vegetation Age: Monoculture wks (crop)	Dry Mass (g/m^2): Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
14 May 79	7.0	7.0 (1st maize)	0.0^{A} (0.0)	0.0^{A} (0.0)	0.0^{A} (0.0)	0.0^{A} (0.0)
31 May 79	9.5	9.5 (1st maize)	0.0^{B} (0.0)	0.0^{B} (0.0)	1.5^{AB} (3.3)	1.7^{A} (1.7)
20 June 79	12.5	12.5 (1st maize)	0.0^{B} (0.0)	0.0^{B} (0.0)	8.1^{B} (19.9)	10.2^{A} (9.9)
9 July 79	15.0	15.0 (1st maize)	1.7^{B} (4.2)	6.5^{B} (16.0)	0.1^{B} (0.3)	78.8^{A} (26.4)
1 August 79	18.5	1.0 (2nd maize)	26.2^{A} (15.0)	52.0^{A} (41.5)	111.5^{A} (118.2)	0.0^{B} (0.0)
16 August 79[a]		3.5 (2nd maize)				0.0 (0.0)
10 September 79	24.0	7.0 (2nd maize)	47.0^{A} (27.6)	180.6A (181.7)	117.3^{A} (106.7)	0.4^{B} (0.4)
8 October 79	28.0	11.0 (2nd maize)	153.4^{AB} (131.1)	295.2^{A} (255.6)	64.4^{B} (47.5)	1.3^{C} (0.8)

Table 33--continued.

Date	Vegetation Age: Natural, Enriched, Mimic wks	Vegetation Age: Monoculture wks (crop)	Dry Mass (g/m^2): Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
29 October 79[a]		14.0 (2nd maize)				1.4 (2.0)
19 November 79	34.0	17.0 (2nd maize)	352.8^{A} (236.9)	255.6^{A} (129.5)	78.2^{B} (20.6)	11.1^{C} (13.5)
17 December 79	38.0	3.0 (cassava)	224.4^{A} (77.2)	216.9^{A} (107.7)	30.6^{B} (13.7)	0.0^{C} (0.0)
21 January 80	43.0	8.0 (cassava)	281.8^{A} (112.5)	284.3^{A} (209.5)	98.1^{B} (71.5)	0.0^{C} (0.0)
17 March 80	51.0	16.0 (cassava)	215.1^{A} (89.1)	453.3^{A} (490.3)	86.2^{B} (53.1)	0.0^{C} (0.0)
19 May 80	60.0	25.0 (cassava)	393.8^{A} (85.7)	307.6^{A} (114.8)	144.6^{B} (111.6)	4.5^{C} (3.3)
8 July 80	67.0	32.0 (cassava)	235.7^{A} (118.6)	340.8^{A} (268.4)	125.6^{A} (64.5)	28.5^{B} (18.6)
13 September 80[a]		42.0 (cassava)				23.6 (11.7)
28 October 80	83.0		338.6^{AB} (180.0)	1153.4^{A} (1038.6)	278.6^{B} (416.2)	

[a]Monoculture only harvested.

Table 34. Total above-ground biomass (leaves + stems + reproductive parts + standing dead) in natural succession, enriched succession, mimic of succession, and monoculture. Mass values are $\bar{x}$ (s.d.); n = 6. At each date, means followed by the same letter are not significantly different at the .05 level.

Date	Vegetative Age: Natural, Enriched, Mimic wks	Vegetative Age: Monoculture wks (crop)	Dry Mass (g/m^2): Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
14 May 79	7.0	7.0 (1st maize)	11.7^{A} (14.1)	17.2^{A} (21.0)	40.8^{A} (46.4)	73.5^{A} (97.4)
31 May 79	9.5	9.5 (1st maize)	88.1^{B} (59.1)	161.6^{AB} (123.7)	147.0^{AB} (102.5)	207.7^{A} (98.7)
20 June 79	12.5	12.5 (1st maize)	164.4^{A} (54.6)	254.8^{A} (130.8)	238.5^{A} (142.2)	377.7^{A} (247.7)
9 July 79	15.0	15.0 (1st maize)	458.0^{B} (199.4)	391.3^{B} (269.1)	179.5^{C} (86.8)	1697.4^{A} (756.3)
1 August 79	18.5	1.0 (2nd maize)	483.5^{A} (156.8)	579.5^{A} (218.1)	639.2^{A} (384.9)	0.2^{B} (0.1)
16 August 79[a]		3.5 (2nd maize)				0.8 (0.3)
10 September 79	24.0	7.0 (2nd maize)	969.0^{A} (419.8)	1251.4^{A} (391.5)	514.9^{B} (591.7)	15.8^{C} (12.7)
8 October 79	28.0	11.0 (2nd maize)	1308.0^{A} (715.2)	1311.8^{A} (506.2)	421.1^{B} (659.0)	100.0^{B} (78.2)
29 October 79[a]		14.0 (2nd maize)				54.2 (63.5)

Table 34--continued.

Date	Vegetation Age: Natural, Enriched, Mimic (wks)	Vegetation Age: Monoculture (wks (crop))	Dry Mass (g/m^2): Natural Succession	Dry Mass (g/m^2): Enriched Succession	Dry Mass (g/m^2): Mimic of Succession	Dry Mass (g/m^2): Monoculture
19 November 79	34.0	17.0 (2nd maize)	1291.2^{A} (245.4)	1098.7^{A} (261.8)	578.0^{B} (666.6)	179.7^{C} (85.7)
17 December 79	38.0	3.0 (cassava)	1177.4^{A} (322.7)	1107.2^{A} (329.3)	607.4^{B} (485.7)	0.0^{C} (0.0)
21 January 80	43.0	8.0 (cassava)	1037.8^{A} (270.8)	1041.6^{A} (160.2)	720.0^{A} (592.2)	20.5^{B} (9.8)
17 March 80	51.0	16.0 (cassava)	1736.9^{A} (1031.0)	1808.7^{A} (561.8)	513.1^{B} (123.7)	352.8^{B} (51.7)
19 May 80	60.0	25.0 (cassava)	1431.4^{AB} (442.2)	1941.8^{A} (732.6)	922.0^{BC} (946.5)	571.8^{C} (405.0)
8 July 80	67.0	32.0 (cassava)	1411.5^{AB} (547.2)	1633.0^{A} (599.5)	867.5^{C} (421.5)	969.3^{BC} (389.4)
13 September 80[a]		42.0 (cassava)				775.8 (168.4)
28 October 80	83.0		2078.5^{B} (1033.4)	4854.4^{A} (2250.4)	1232.8^{C} (892.6)	

[a]Monoculture only harvested.

Table 35. Above-ground biomass, enriched succession treated with insecticide. Mass values are $\bar{x}$(s.d.); n=3.

Date	Vegetation Age (wks)	Dry Mass (g/m^2) Leaves	Stems	Reproductive Parts	Standing Dead	Total
14 May 79	7.0	25.7 (24.6)	8.6 (14.9)	0.0 (0.0)	0.0 (0.0)	34.3 (38.0)
31 May 79	9.5	48.2 (19.5)	29.5 (13.3)	0.0 (0.0)	0.0 (0.0)	77.7 (32.7)
20 June 79	12.5	85.6 (48.3)	78.2 (52.7)	0.8 (1.4)	0.0 (0.0)	164.6 (100.1)
9 July 79	15.0	50.8[a] (18.8)	78.2 (43.3)	0.0[a] (0.0)	0.0 (0.0)	129.0[a] (61.9)
1 August 79	18.5	249.7	312.7	10.7	26.3	599.4
10 September 79	24.0	382.1 (219.0)	348.9 (155.1)	29.3 (17.4)	95.7 (67.7)	855.9 (338.5)
8 October 79	28.0	343.4 (194.5)	595.0 (469.4)	19.5 (3.9)	108.0 (62.9)	1066.0 (422.8)
19 November 79	34.0	196.6 (25.6)	520.4 (336.0)	10.2 (6.9)	155.8 (81.4)	882.9 (262.0)
17 December 79	38.0	280.5 (121.1)	262.8 (173.5)	15.1 (18.6)	313.4 (44.2)	871.8 (207.7)
21 January 80	43.0	263.2 (299.7)	1160.8 (1374.7)	25.9 (36.1)	400.6 (316.1)	1850.6 (1394.3)

Table 35--continued.

Date	Vegetation Age (wks)	Dry Mass (g/m^2) Leaves	Stems	Reproductive Parts	Standing Dead	Total
17 March 80	51.0	317.2 (116.1)	798.3 (691.4)	3.4 (2.5)	182.4 (44.0)	1301.4 (765.0)
19 May 80	60.0	281.1 (120.8)	501.3 (177.5)	13.0 (11.8)	327.6 (308.6)	1123.0 (423.8)
8 July 80	67.0	277.3 (260.8)	1225.0 (804.1)	61.1 (57.5)	211.3 (92.7)	1774.7 (1204.5)
28 October 80	83.0	261.5[a] (123.3)	1096.7 (604.1)	25.9 (21.4)	307.3 (110.0)	1691.4[a] (399.5)

[a]Significantly less than enriched succession without insecticide at the .05 level.

Table 36. Above-ground biomass, monocultures treated with insecticide. Mass values are $\bar{x}$(s.d.); n=3.

Date	Vegetation Age wks (crop)	Dry Mass (g/m^2) Leaves	Stems	Reproductive Parts	Standing Dead	Total
14 May 79	7.0 (1st maize)	98.3 (14.8)	50.8 (21.8)	0.0 (0.0)	0.0 (0.0)	149.2 (36.6)
31 May 79	9.5 (1st maize)	152.5 (26.2)	158.0 (64.1)	17.8 (17.5)	5.1 (1.5)	333.5 (109.2)
20 June 79	12.5 (1st maize)	157.4 (8.3)	256.5 (44.5)	66.4 (30.9)	3.1 (0.1)	483.5 (83.9)
9 July 79	15.0 (1st maize)	384.4 (190.6)	593.2 (114.5)	92.1 (29.8)	159.2[a] (32.1)	1229.0 (302.8)
1 August 79	1.0 (2nd maize)	0.2 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.1)
16 August 79	3.5 (2nd maize)	1.5 (0.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.5 (0.9)
10 September 79	7.0 (2nd maize)	65.0[a] (8.4)	50.9[a] (10.0)	0.0 (0.0)	3.1[a] (1.8)	119.0[a] (20.2)
8 October 79	11.0 (2nd maize)	124.1[a] (14.6)	248.2[a] (29.1)	251.1[a] (172.7)	3.7 (6.5)	627.1[a] (218.6)
29 October 79	14.0 (2nd maize)	102.2[a] (27.2)	222.9[a] (96.3)	260.8[a] (183.1)	16.0[a] (5.1)	602.0[a] (122.8)

Table 36--continued.

Date	Vegetation Age wks (crop)	Dry Mass (g/m^2) Leaves	Stems	Reproductive Parts	Standing Dead	Total
19 November 79	17.0 (2nd maize)	19.8 (18.1)	149.5 (74.4)	258.8 (64.3)	46.8[a] (18.6)	474.8[a] (128.6)
17 December 79	3.0 (cassava)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
21 January 80	8.0 (cassava)	7.2 (2.2)	4.5 (1.6)	0.0 (0.0)	0.0 (0.0)	11.7 (3.7)
17 March 80	16.0 (cassava)	31.7[b] (27.7)	46.3[b] (53.6)	0.0 (0.0)	0.0 (0.0)	78.0[b] (81.3)
19 May 80	25.0 (cassava)	138.0 (75.7)	343.4 (217.5)	0.0 (0.0)	2.0 (0.5)	483.4 (293.5)
8 July 80	32.0 (cassava)	23.1[b] (22.5)	179.9[b] (152.1)	0.0 (0.0)	10.3 (15.3)	213.3[b] (156.5)
13 September 80	42.0 (cassava)	133.7 (94.4)	704.8 (437.0)	0.2 (0.3)	15.0 (8.6)	853.7 (538.9)

[a]Significantly greater than monoculture without insecticide at the .05 level.

[b]Significantly less than monoculture without insecticide at the .05 level.

Table 37. Litterfall in natural succession, enriched succession, mimic of succession, and monoculture. Values are mean dry weight; n=6. At each date, means followed by the same letter are not significantly different at the .05 level.

Date	Vegetation Age: Natural, Enriched, Mimic wks	Vegetation Age: Monoculture wks (crop)	Litterfall ($g/m^2/2$ wk): Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
10 April 79	2	2 (1st maize)	0.0^{A}	0.0^{A}	0.0^{A}	0.0^{A}
24 April 79	4	4 (1st maize)	0.0^{A}	0.0^{A}	0.0^{A}	0.0^{A}
9 May 79	6	6 (1st maize)	0.0^{A}	0.0^{A}	0.0^{A}	0.0^{A}
22 May 79	8	8 (1st maize)	0.0^{A}	0.0^{A}	0.0^{A}	0.0^{A}
6 June 79	10	10 (1st maize)	0.0^{A}	0.0^{A}	0.0^{A}	0.0^{A}
21 June 79	12	12 (1st maize)	4.5^{A}	6.8^{A}	5.6^{A}	10.2^{A}
4 July 79	14	14 (1st maize)	6.9^{BC}	10.8^{AB}	17.5^{A}	2.6^{C}
17 July 79	16	16 (1st maize)	11.2^{A}	13.7^{A}	21.0^{A}	25.6^{A}
31 July 79	18	1 (2nd maize)	4.8^{A}	8.2^{A}	6.2^{A}	1.5^{A}
14 August 79	20	3 (2nd maize)	10.8^{AB}	12.0^{AB}	22.9^{A}	1.5^{B}

Table 37--continued.

Date	Vegetation Age: Natural, Enriched, Mimic wks	Vegetation Age: Monoculture wks (crop)	Litterfall ($g/m^2/2$ wk): Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
28 August 79	22	5 (2nd maize)	13.5^{A}	14.5^{A}	21.7^{A}	3.0^{A}
11 September 79	24	7 (2nd maize)	13.2^{A}	8.8^{AB}	10.6^{A}	4.5^{B}
25 September 79	26	9 (2nd maize)	19.7^{A}	13.4^{A}	15.9^{A}	2.7^{B}
9 October 79	28	11 (2nd maize)	19.0^{A}	11.1^{B}	12.2^{B}	3.9^{C}
24 October 79	30	13 (2nd maize)	18.0^{A}	18.0^{A}	18.0^{A}	5.8^{B}
6 November 79	32	15 (2nd maize)	18.7^{A}	23.1^{A}	22.3^{A}	0.0^{B}
20 November 79	34	17 (2nd maize)	13.8^{A}	12.8^{A}	15.5^{A}	4.6^{A}
4 December 79	36	1 (cassava)	21.4^{A}	19.3^{A}	14.9^{AB}	6.6^{B}
18 December 79	38	3 (cassava)	26.8^{A}	20.5^{A}	22.3^{A}	11.8^{A}
2 January 80	40	5 (cassava)	20.0^{A}	25.1^{A}	9.9^{AB}	1.3^{B}

Table 37--continued.

Date	Vegetation Age: Natural, Enriched, Mimic wks	Vegetation Age: Monoculture wks (crop)	Litterfall (g/m^2/2 wk): Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
15 January 80	42	7 (cassava)	16.2^{A}	21.3^{A}	12.4^{AB}	1.2^{B}
30 January 80	44	9 (cassava)	20.0^{AB}	23.8^{A}	11.2^{BC}	4.0^{C}
12 February 80	46	11 (cassava)	35.5^{A}	40.3^{A}	19.3^{B}	9.2^{B}
26 February 80	48	13 (cassava)	13.3^{A}	15.5^{A}	12.6^{A}	8.2^{A}
11 March 80	50	15 (cassava)	34.4^{A}	29.6^{A}	15.8^{A}	8.5^{A}
25 March 80	52	17 (cassava)	25.5^{A}	25.0^{A}	6.5^{B}	12.7^{AB}
8 April 80	54	19 (cassava)	27.0^{A}	26.4^{A}	9.6^{B}	11.4^{B}
22 April 80	56	21 (cassava)	11.2^{A}	18.4^{A}	9.1^{A}	15.4^{A}
6 May 80	58	23 (cassava)	6.3^{A}	6.8^{A}	9.0^{A}	13.4^{A}
19 May 80	60	25 (cassava)	14.0^{A}	12.4^{A}	2.9^{A}	11.3^{A}

Table 37--continued.

Date	Vegetation Age: Natural, Enriched, Mimic wks	Vegetation Age: Monoculture wks (crop)	Litterfall ($g/m^2/2$ wk): Natural Succession	Enriched Succession	Mimic of Succession	Monoculture
3 June 80	62	27 (cassava)	12.6^{A}	15.9^{A}	4.3^{A}	11.6^{A}
17 June 80	64	29 (cassava)	13.7^{AB}	10.4^{B}	3.6^{B}	23.3^{A}
1 July 80	66	31 (cassava)	15.1^{AB}	16.2^{AB}	5.5^{B}	24.6^{A}
15 July 80	68	33 (cassava)	17.2^{B}	14.7^{B}	12.8^{B}	33.4^{A}
29 July 80	70	35 (cassava)	33.0^{A}	26.0^{AB}	11.8^{B}	16.1^{B}
12 August 80	72	37 (cassava)	30.7^{A}	23.9^{A}	29.4^{A}	19.7^{A}
26 August 80	74	39 (cassava)	24.4^{A}	18.7^{A}	9.3^{A}	24.0^{A}
9 September 80	76	41 (cassava)	27.3^{A}	26.1^{A}	10.5^{B}	33.1^{A}
23 September 80	78	43 (cassava)	13.5^{A}	15.2^{A}	8.8^{A}	0.0^{B}
8 October 80	80	1 (Cordia)	23.6^{A}	17.4^{AB}	12.2^{BC}	2.7^{C}

Table 37--continued.

Date	Vegetation Age: Natural, Enriched, Mimic wks	Vegetation Age: Monoculture wks (crop)	Litterfall ($g/m^2/2$ wk): Natural Succession	Litterfall ($g/m^2/2$ wk): Enriched Succession	Litterfall ($g/m^2/2$ wk): Mimic of Succession	Litterfall ($g/m^2/2$ wk): Monoculture
21 October 80	82	3 (Cordia)	23.7^{A}	15.9^{A}	14.7^{A}	2.6^{B}
4 November 80	84	5 (Cordia)	18.3^{A}	13.6^{A}	13.9^{A}	7.7A

BIOGRAPHICAL SKETCH

Becky Jean Brown was born in Texas in 1948 and raised in Texas and Georgia. She received a B.S. in mathematics education from the University of Georgia in 1970 and an M.S. in statistics and biometry from Emory University in 1974. In January 1983, she will assume the position of assistant professor at the University of Wisconsin-Madison, Institute for Environmental Studies/Department of Botany.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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December 1982

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