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STUDIES OF FOREST, AGRICULTURAL, AND
SUCCESSIONAL ENVIRONMENTS IN THE
UPPER RIO NEGRO REGION OF THE AMAZON BASIN

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Christopher Uhl

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Peter G. Murphy
Major professor

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STUDIES OF FOREST, AGRICULTURAL, AND SUCCESSIONAL ENVIRONMENTS IN THE UPPER RIO NEGRO REGION OF THE AMAZON BASIN

By

Christopher Uhl

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ABSTRACT

STUDIES OF FOREST, AGRICULTURAL, AND SUCCESSIONAL ENVIRONMENTS IN THE UPPER RIO NEGRO REGION OF THE AMAZON BASIN

By

Christopher Uhl

Investigations of forest, agricultural, and successional environments were conducted near the town of San Carlos de Rio Negro in the Amazon Basin of Venezuela (lat 1.56 N., long 67.03 W).

The forest environment was characterized through studies of species composition, vegetation structure, and regeneration. Three mature tierra firme (i.e. never flooded) forest sites, ranging in size from 0.5 to one hectare, were surveyed. When compared to most other wet tropical tierra firme forests, the San Carlos forest sites had higher densities of trees in the smaller size classes and a lower basal area per hectare.

There was an average of 75 tree species per site. Most species were rare, having importance values of less than one. The few relatively common species were well represented in all diameter size classes indicating that the sites studied were floristically stable. Gaps were common in the forest and their occurrence is probably beneficial to a persistent sapling and seedling pool.

An analysis of the energetics of the local farming system [i.e. slash and burn cultivation of yuca (*Manihot esculenta*, Crantz.)] and a comparison of productivity between farm crops and secondary vegetation was conducted. Yuca root production was 1.46 metric tons dry weight per hectare in the first year of farm site use but declined to 1.0 metric

tons per hectare in the second year. Local farmers maintain a ratio of energy output to energy input of 13.9 to one, (measured as the caloric content of the farm site yield vs. calories expended in farming activities).

The productivity of secondary vegetation in a cut and burn plot was 109 grams dry weight per m^2 in the first year of succession and 1446 grams dry weight per m^2 in the second year.

Changes in vegetation structure, species composition, and species dominance were studied over the first 22 months of succession after the cutting and burning of several mature tierra firme forest sites. Only 0.58 individuals per m^2 were present four months after burning. The density of secondary woody plants, forbs, and grasses increased sharply from the fourth to the tenth month of succession. There was less change in plant density between the tenth and twenty-second month, but a large change in vegetation height occurred during this time. By 22 months a loose canopy of Cecropia spp. was present at 5 m height.

To explain the observed succession, additional field investigations were undertaken. Many of the forest tree species had the ability to sprout when cut. However, burning killed sprouts present on the study sites. Burning also significantly reduced the size of the seed pool. Nevertheless, the first secondary woody colonizers established from seed pool seeds which survived the burn. The first forb and grass colonizers established from seeds dispersed onto the site after the disturbance. The common secondary woody species had bat or bird dispersed seeds. Many forbs and grasses had wind dispersed seeds. Population densities were low during the first months of succession because of the low numbers of propagules present and because low rainfall during this time was

not favorable for seedling germination or establishment. There was a rapid increase in population size after about the fourth month of succession because the early colonizers had begun to produce, and disperse locally, large numbers of seeds by that time. There were six distinct microhabitat types present on the post-burn sites. Most species tested showed distinct microhabitat preferences.

This dissertation is dedicated to Nan

ACKNOWLEDGEMENTS

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were the resident ecologists in San Carlos.

Thanks are likewise extended to Juan Moreno, Getulio Gomez, Pablo Livino, Jose Maquirino and Manuel Silva, the men who worked in the field with me at various times. Their patience with my faltering Spanish and their willingness to help in all tasks, no matter how tedious or bizarre, allowed me to accomplish far more than I would have alone. Special thanks go to Pedro Maquirino, whose overall-field competence, intelligence, and dependability made his help particularly valuable.

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GENERAL INTRODUCTION

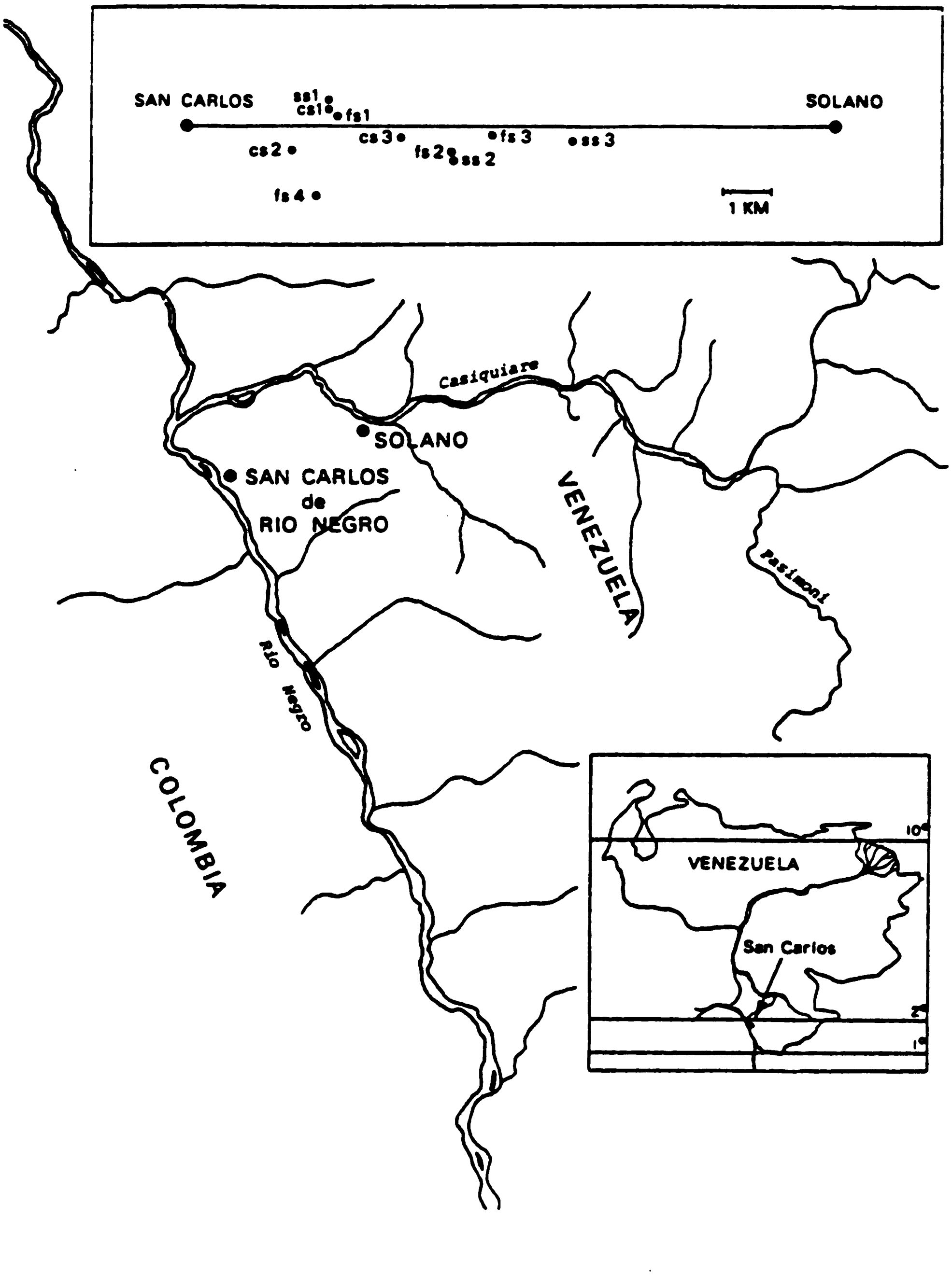
Organization

Since 1974 an international team of scientists has been investigating tropical rain forest structure and function in the upper Rio Negro region of the Amazon Basin (Medina *et al*., 1977). The study is a Man and the Biosphere I Pilot Project under the MAB classification "Ecological effects of increasing human activities in tropical and subtropical forest ecosystems." The project is headquartered at the Instituto Venezolano de Investigaciones Cientificas (IVIC) in Caracas, Venezuela. My participation in this project was sponsored through a National Science Foundation grant written by Drs. F. Golley and C. Jordan entitled "Nutrient dynamics of a tropical rain forest and changes in the nutrient cycle due to cutting and burning".

Field Site Location and Climate

The field site is situated in the Venezuelan state of Amazonas about four kilometers east of the village of San Carlos de Rio Negro, close to the confluence of the Guainia and Casiquiare rivers (lat 1.56 N., long 67.03 W) (Figure 1). San Carlos is 119 m above sea level. The state of Amazonas is one of the most sparsely populated regions of the world, having fewer than 0.05 inhabitants per km^2 (Anon., 1973). Human settlements occur mainly along waterways. Most residents of San Carlos are of Indian descent.

Figure 1. A map of Venezuela (bottom inset) with an enlargement of the San Carlos de Rio Negro region. The top inset shows the locations of the study sites relative to each other and to the town of San Carlos. Forest sites are abbreviated FS, succession sites SS, and conuco (i.e. farm) sites CS.


SAN CARLOS
SOLANO
ss1
cs1
fs1
cs3
fs3
ss3
cs2
fs2
ss2
fs4
1 KM
Casiquiare
SOLANO
SAN CARLOS de RIO NEGRO
VENEZUELA
Pasimoni
Rio Negro
COLOMBIA
VENEZUELA
San Carlos
10°
2°
1°

The climate of the region is equatorial with a 26° C mean daily temperature. The average annual rainfall is 3500 mm with all months usually receiving in excess of 100 mm of rain. There are distinct seasonal trends in rainfall abundance; the driest months occur between November and February (Heuveldop, 1977). The local people concentrate most of their farming and fishing activities in the drier months.

Geology and Soils

The configuration of the Amazon Basin dates back to the paleozoic era (Putzer, 1968 cited in Herrera, 1978). The present day basin is delimited by the Guiana shield on the north, the Brazilian shield on the south and the Andes on the west. Since the paleozoic, the basin has been filling in with sediments eroded from the surrounding higher terrain. The soils of the San Carlos region were derived from nearby sandstone shields in Guiana (Fittkau *et al.*, 1975). The lack of recent geologic activity, the leaching effects of the continually hot wet climate, and the lack of bedrock exposure through erosion over the generally undisturbed flat to rolling landscape has resulted in an extremely oligotrophic environment. (Jordan and Herrera, 1979).

In the San Carlos region the terrain consists of a system of rolling hills, some rising as much as 50 m above the mean river level (Herrera, 1977). The higher areas are referred to as "tierra firme" (i.e., never flooded). Granite batholiths (inselbergs) and flat topped sandstone "tepuis" are the sole orographic features over this vast rolling plain. The tierra firme soils are oxisols containing a moderately developed A horizon overlying lateritic gravel and clay. The soil surface in the tierra firme areas is covered by a mat of fine roots which varies in thickness from 5 to 40 cm. Thirty-seven percent of the total root biomass and fifty-eight percent of the feeder root biomass occurs in this root mat (Stark and Spratt, 1977). The presence of most of the feeder roots above the soil surface (even though the soil is well drained) emphasizes the oligotrophic nature of the environment. Water draining from these tierra firme sites is clear.

Between the tierra firme sites are lower areas with soils composed of sandy quartz. These soils have a well developed B_h horizon at one meter depth and have been classified as spodosols (Klinge and Herrera, 1977). The upper 30 cm of these soils consists of humus in various stages of decomposition. Water draining from these lowland areas is stained a yellowish brown, the same color as the Rio Negro. The color results from the low exchange capacity of the spodosols which permits cations and decomposing organic matter in the form of humic acids to become dissolved in the soil water and move into the nearby streams (Medina *et al.*, 1977). Areas of limited extent have soils which are distinct from the tierra firme oxisols and lowland site spodosol soils.

Research Goals

My research has focused on three distinct aspects of tropical ecology: 1) the composition, structure, and regeneration of the tierra firme forests; 2) the productivity of agricultural and successional sites; and 3) the dynamics of early succession after man-induced disturbances. Multiple sites were used for each of these studies. The sites were designated as Forest, Conuco (i.e. farm) and Succession Sites 1, 2, 3, etc. Figure 1 contains a map showing the location of the study sites relative to each other and to the town of San Carlos de Rio Negro. All the sites were within two kilometers of a dirt road running between the towns of San Carlos and Solano. I conducted my research during four three-month stays (occurring at approximately nine month intervals) in the San Carlos region of the Rio Negro during the period from September 1975 to December 1978.

The common goal of the U.S. scientists participating in this project has been to measure nutrient cycles in the forest, agricultural, and early successional environments of the San Carlos region of the Rio Negro. My research provides information needed to elucidate nutrient cycling rates. For example, in my forest study I collected data on the density and size of the forest trees which were used by Dr. C. Jordan and myself (Jordan and Uhl, 1978) to determine the standing crop biomass of the tierra firme forest (a parameter that must be quantified to determine the standing crop of nutrients). My studies on succession dynamics and agricultural energetics have provided data on standing crop biomass, litter production, and insect herbivory, all of which were necessary to evaluate the role of successional communities and crop plants in nutrient cycling. My research was conducted on plots where Dr. R. Herrera concurrently followed changes in soil fertility over time and Dr. C. Jordan monitored changes in the nutrient content of precipitation, leached soil water, and stream flow. By pooling our data we have been able to determine rates of nutrient cycling for forest, farm, and successional tierra firme ecosystems.

While my research has contributed information necessary to the quantification of nutrient cycles, it went beyond this immediate project goal and addressed questions of fundamental importance regarding tropical forest composition and regeneration, shifting cultivation energetics, and early succession dynamics.

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PART I

FOREST COMPOSITION, STRUCTURE, AND REGENERATION

INTRODUCTION

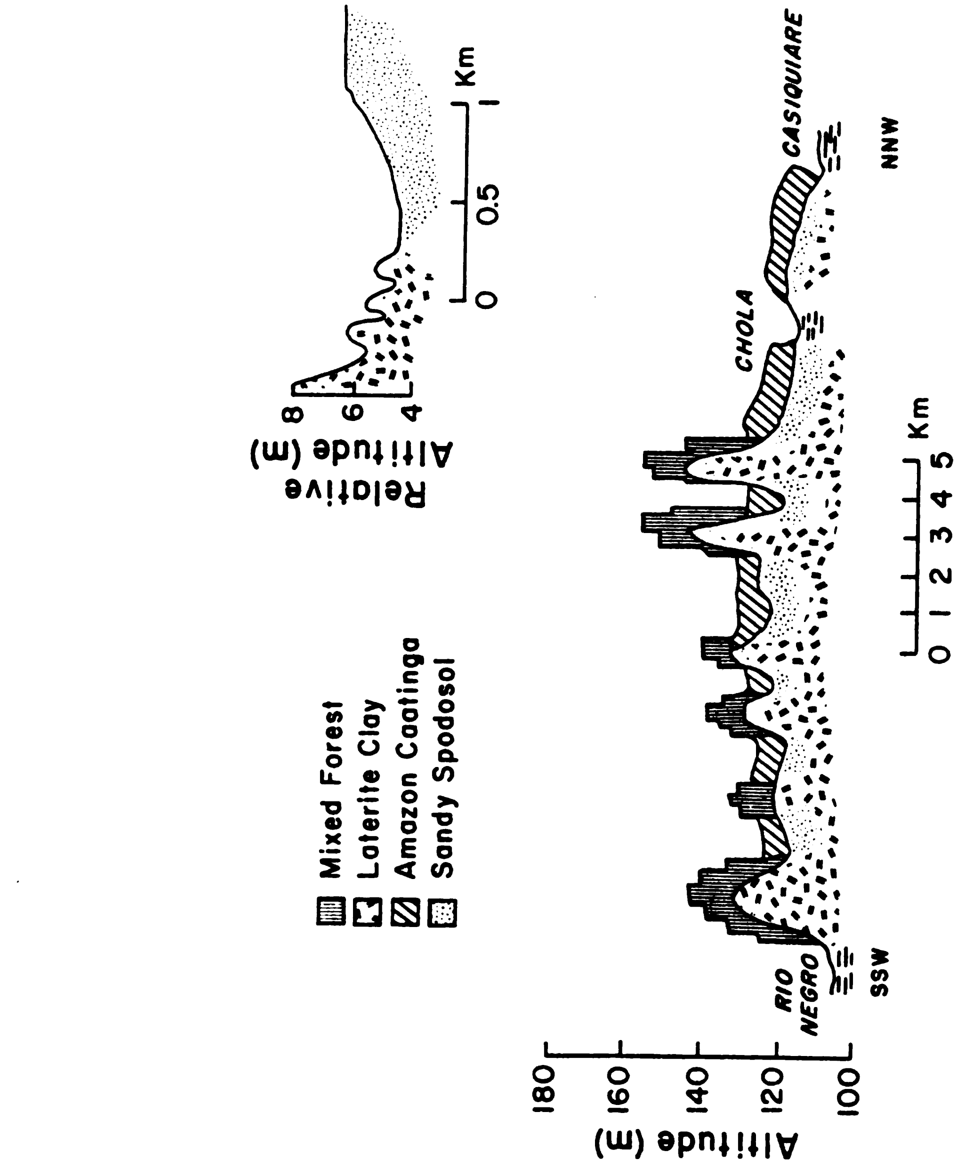
The vegetation types of Amazonia were systematically described by Ducke and Black (1953) and more recently by Prance (1978). Prance detailed eight principle vegetation types: forest on tierra firme (i.e., never flooded), forest on inundated sites, savanna on tierra firme, savanna on inundated sites, campina (i.e., low vegetation on white sands), montane vegetation, littoral vegetation, and river beach vegetation. Surveys of Amazonia by the Brazilian Projecto RADAM, a radar survey of the entire Amazon basin, and by LANDSAT photographs are providing much needed data on the extent and distribution of these vegetation types. Tierra firme forest, the subject of this study, is by far the most common vegetation type, covering approximately 85% of the Amazonia (Prance, 1978).

Some of the more common tree families in Amazonia are the Leguminosae, Rosaceae, Lecythidaceae, Moraceae, Annonaceae, Burseraceae, Lauraceae, Myristacaceae, Vochysiaceae, Olacaceae, Linaceae, Dichapetalaceae, Tiliaceae and Palmae (Ducke and Black, 1953). There are still many unclassified plant species. In some areas more than one percent of the collections made may prove to be new species (Goodland and Irwin, 1975). Prance (1972) recently monographed the Chrysobalanaceae plant family and found 22 new species from Amazonia. The central and northeastern portions of Amazonia are recorded to be considerably richer in species than are the eastern and western outreaches. The northern area of the basin including the Rio Negro region is considered to be the most species rich and to have the largest number of endemic species (Brünig and Klinge, 1975). Continental drift and Pleistocene climate changes have been invoked to explain floristic differences within Amazonia (Prance, 1978), but soil can also exert influences on species composition (Fittkau *et al*., 1975).

Brünig and Klinge (1975) provide an excellent review of the numerous forest inventories that have been conducted in Amazonia. Most of these studies estimate merchantable timber volume only, but a few investigators have examined tierra firme forest structure in detail (Takeuchi, 1961; Rodrigues, 1963). In addition, several workers have examined species richness and abundance patterns in Amazonian tierra firme forest (Black *et al*., 1950; Pires *et al*., 1953; Cain *et al*., 1956).

Several vegetation types are found in the rolling topography characteristic of the San Carlos region. A topographic profile depicting the edaphic conditions and related vegetation types is shown in Figure 1. The higher tierra firme areas are covered by a mixed forest with a canopy height at 25 to 30 meters. The soils are oxisols. The low areas between these hills contain soils composed of sandy quartz. Altimetric transect studies conducted by Herrera (1977) showed these valleys to be slightly dome-shaped with Amazon caatinga vegetation (sensu Klinge *et al*., 1977), dominated by *Micrandra spruceana*, occurring on the wettest sites and low savanna-like vegetation (known as "bana") present on the more elevated, better drained domes. A third vegetation type occurs in the lowland sites in areas where the terrain is dissected by deep water holes and small streams. The soil here consists of mixed kaolinite clays and is related to the tierra firme soils. *Eperua purpurea* is a strong dominant on these sites. Brünig *et al*. (1977) have detailed the

Figure 1. An altimetric transect between the Rio Negro and the Casiquiare river showing maximum river level for 1976. The inset at the right upper corner shows a tracing of the microrelief in the lowland area. (Figure used with the permission of Herrera).


Mixed Forest
Laterite Clay
Amazon Caatinga
Sandy Spodosol
Relative Altitude (m)
8
6
4
0
0.5
1
Km
Altitude (m)
180
160
140
120
100
RIO NEGRO
SSW
CHOLA
CASIQUIARE
NNW
0 1 2 3 4 5
Km

composition and structure of these three lowland vegetation types.

The purpose of this study was to characterize the composition and structure of the tierra firme forest in the San Carlos region. In addition, I investigated certain aspects of forest regeneration in this forest type.

METHODS

Four tierra firme sites comprising a total area of 2.5 ha were chosen for study (See Figure 1, General Introduction for location of sites). Sites 1, 2, and 3 showed no evidence of recent disturbance and were used for the study of mature forest composition, structure, and regeneration. Site 1 was 1 ha in size and located approximately 4 km east of the town of San Carlos. Studies of nutrient cycling, forest productivity, and forest meteorology have been conducted on this site by other project participants. Sites 2 and 3 were each 0.5 ha in size and were located, respectively, 6 and 7 km east of San Carlos. These three sites were similar in elevation (approximately 100 masl), slope (less than 5°), and soil type (oxisols). According to local inhabitants these sites had never been disturbed by man. Site 4 had been cleared and then farmed for several years approximately 60 years previously. This site was located approximately 1.5 km south of Site 1. Structural characteristics were compared between this old secondary site and the three mature forest sites.

In each site all trees 10 cm or more in dbh were mapped and identified either by the local common name or assigned a number. The diameter of each tree was measured. Estimates of tree heights and crown dimensions were made by eye with periodic checks on relatively exposed trees using a Haga altimeter. Those trees between 5 and 10 cm dbh were identified, mapped, and measured in three 10 x 100 m transects in Site 1; and trees 1 to 5 cm dbh were similarly surveyed in two 5 x 100 m transects in this site.

Initially, I relied heavily on local woodsmen who identified the more common species based on leaf type, trunk shape, presence of latex or other sap, and various characteristics of the inner and outer bark including odor, thickness, color, and texture. Every time a new species was encountered in the transects, a specimen was collected, dried, and placed in a reference collection. I used this reference collection to verify any questionable identifications provided by the woodsmen. Generally their determinations were accurate, although several species were sometimes lumped together under one designation. By constantly collecting specimens and comparing these collections with the reference collection, I was usually able to uncover inconsistencies and make distinctions between similar species.

Additional collections of each species were sent to the Venezuelan National Herbarium in Caracas for drying and storage. Unfortunately, I was only able to find fertile specimens of about one-fourth of the tree species present in the study sites. Because it is exceedingly difficult to make identifications of sterile plants from a poorly known flora, the help of Ronald Liesner from the Missouri Botanical Garden was enlisted to collect fertile specimens of tierra firme forest trees and to provide species determinations. Identification of collected specimens is currently under way at Missouri.

In addition to the study of tierra firme forest composition and structure, the following three aspects of forest regeneration were investigated in Site 1: (1) regeneration of common tree species, evaluated through an analysis of size-class distributions; (2) the extent of three forest phases (gap, building, and mature) (Whitmore, 1975), determined by mapping these phases to scale; and (3) mortality and establishment in forest floor seedling communities, investigated through the use of 10 1 m^2 permanent plots. In each of these plots all individuals were mapped, identified, and measured for height. These plots were periodically resurveyed over a three-year period.

RESULTS AND DISCUSSION

Composition and Structure of Mature Forest

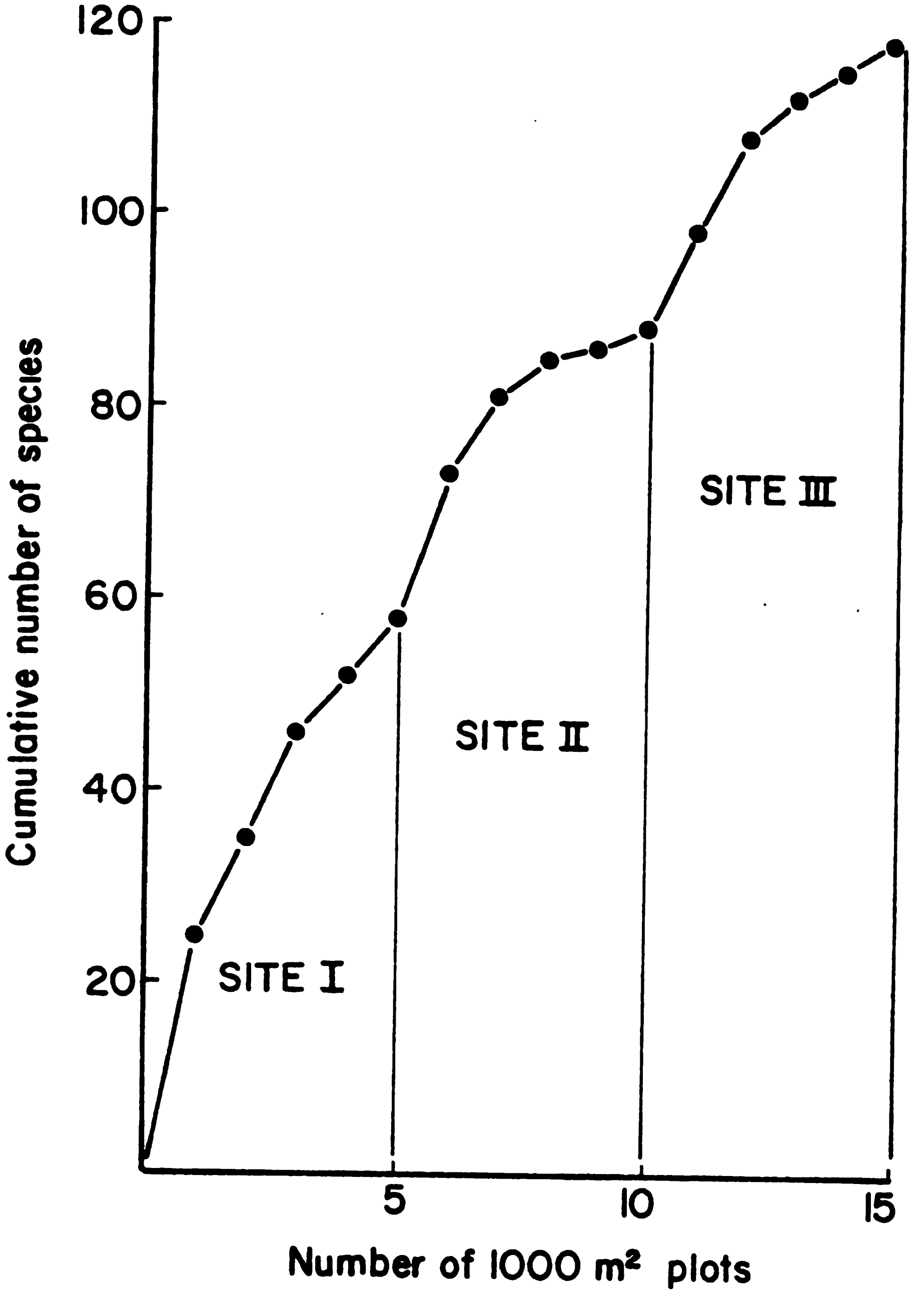
The diversity of tree species

The high tree species diversity of Amazonian forests is well known (Black *et al*., 1950; Pires *et al*., 1953; Cain *et al*., 1956; Takeuchi, 1961; Rodrigues, 1963; Prance *et al*., 1976). At San Carlos 83 species of trees 10 cm or more in dbh were present in Site 1, 79 in Site 2, and 63 in Site 3. Most species were represented by fewer than four individuals per ha (Appendix Table 1). Several integrative indices have been devised which are sensitive to both species richness and species abundance. Two of these, the Simpson's index and the Shannon-Wiener index were calculated for the San Carlos sites (Appendix Table 2).

Figure 2 shows that there was a sharp increase in cumulative species number each time a new site was surveyed. Hence, many of the species encountered were only found in one of the three sites. This suggests that species in this forest may be clumped in their distribution. In accord with this, Hubbell (1979) found that most tree species in a Costa Rican dry forest were, in fact, clumped in their distribution.

In an effort to compare the species richness of the San Carlos tierra firme forest with studies using both larger and smaller plots, I considered the suggestion of Cain and Castro (1959) that communities can be compared with regard to the number of species per unit area if the data are illustrated in semi-log fashion. These authors speculated that

Figure 2. The relationship between cumulative number of species and area for three 0.5 ha tierra firme plots several kilometers apart.


120
100
80
60
40
20
Cumulative number of species
SITE I
SITE II
SITE III
5
10
15
Number of 1000 m² plots

a straight line relationship might exist for species number vs. log area for all communities. If so, direct comparisons between communities could be accomplished by comparing line slopes or more simply by comparing species number/log area values. Figure 3 shows such a semi-log plot for Site 1, San Carlos. Given the size of the area sampled, the points do not describe a straight line. A similar graph presented by Brünig for several forest types in Sarawak and Borneo likewise shows a non-linear relationship (Brünig, 1973). If most Amazonian tierra firme tree species are clumped in their distribution (rather than hyper-dispersed), then very large minimum survey areas (e.g. 10 km^2) may be necessary for intersite comparisons of species richness based on species number/log area values.

Importance values for tree species

The high species diversity values for the San Carlos tierra firme forest (Appendix Table 2) suggest the absence of numerical dominance by any tree species. A more realistic assessment of the extent of dominance from the structural standpoint, however, may be achieved with an index that incorporates measures of basal area and extent of spatial distribution, as well as population size. In this regard, Curtis and McIntosh (1951) proposed that the "importance" of a population in the community of which it is a component can be expressed as the sum of its relative density, relative dominance, and relative frequency. Importance values were first used in the characterization of tropical vegetation by Cain *et al*. (1956). I computed importance values for all species in each site. Results for Site 1 are shown in Figure 4. Eighteen species comprise 79.3 percent of the total importance value in this

Figure 3. The relationship between species number and log area for Site 1. Area is expressed as m^2.

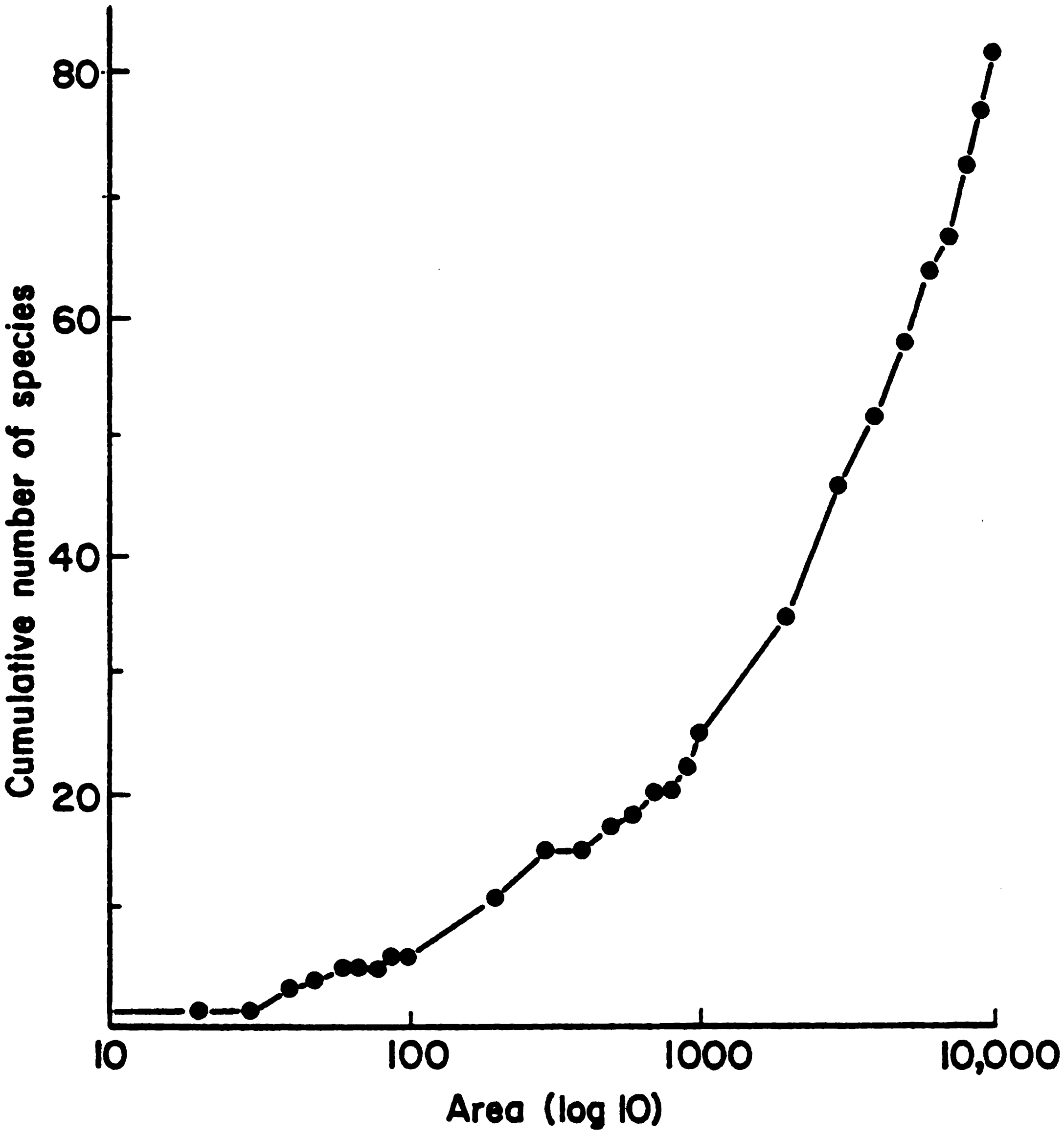
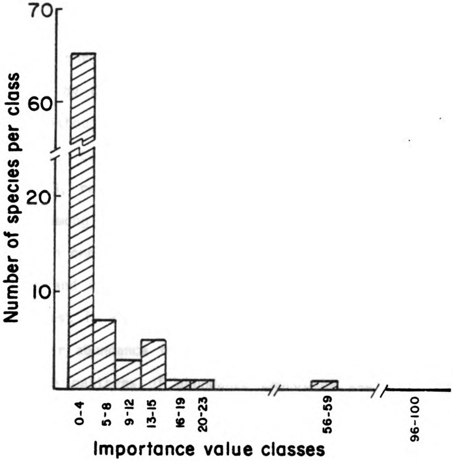

80
60
40
20
Cumulative number of species
10
100
1000
10,000
Area (log 10)

Figure 4. The number of species in Site 1 occurring in a series of importance value classes. Only trees 10 cm or more in dbh were considered.


70
60
20
10
Number of species per class
0-4
5-8
9-12
13-15
16-19
20-23
56-59
96-100
Importance value classes

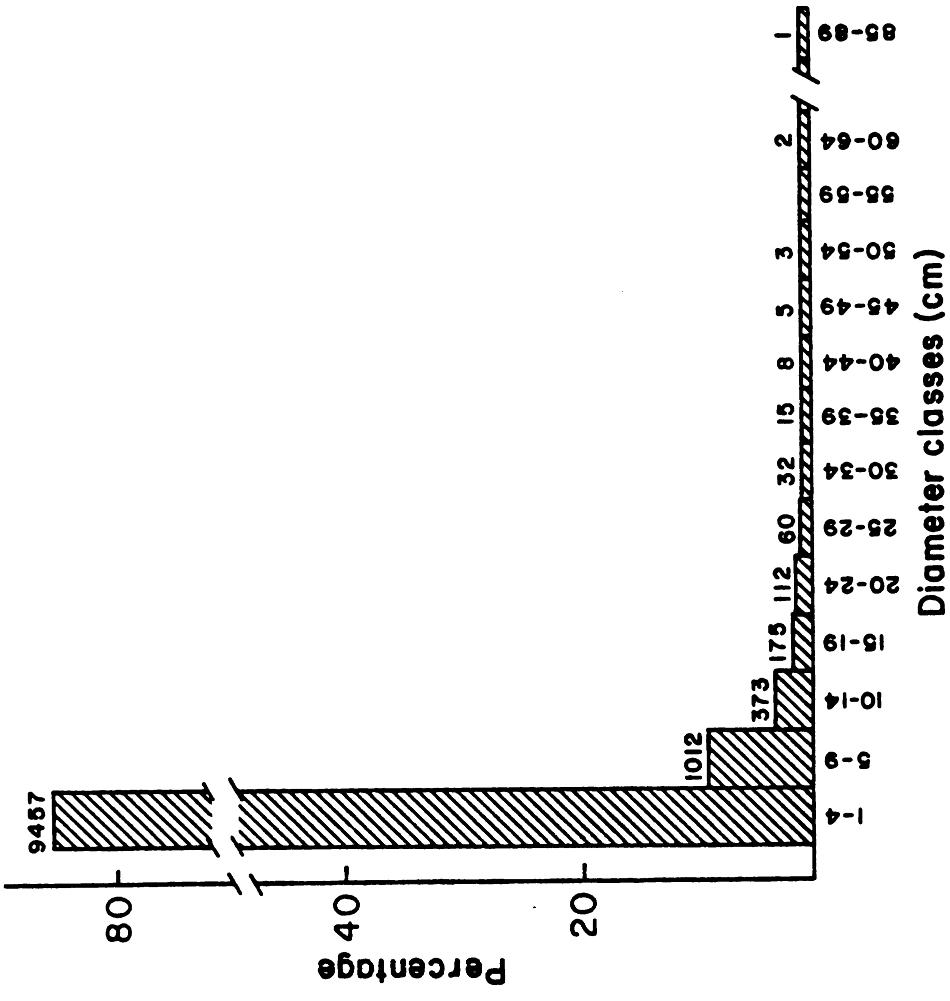
site. The remaining 20.7 percent of the importance value is shared among 65 species all having importance values of less than 1.7 percent. Expressed in more general terms, three-quarters of the species present in Site 1 constitute only one-fifth of the total importance value. Similar trends were seen in Sites 2 and 3.

The highest importance value (as percentage of total) in Site 1 was 19.1 percent for Licania sp. This appears to be an unusually high value for Amazonian tierra firme forest. The highest importance values for Sites 2 and 3 were 11.6 percent and 10.2 percent, respectively. These lower values are more in accord with the importance value high of 7.8 percent reported by Cain et al. (1956) for a tierra firme forest in Belem, Para. Although Licania sp. had an importance value of 19.1 percent in Site 1, its importance value was 11.6 percent and 6.1 percent in Sites 2 and 3, respectively. Differences in importance values of this magnitude among sites were common and reflect the fact that a species common on one tierra firme site may be rare or even absent in another. Pires and Prance (1977) and Prance et al. (1976) working on tierra firme forest in Brazil also found that tree species varied considerably in their abundance from place to place within their range of dispersion. Such patterns of abundance cannot be explained until we understand how tropical tree populations are distributed in space. Current studies by Hubbell in Panama are addressing this question.

Density and basal area

Figure 5 shows the distributions of trees in different diameter classes for San Carlos, Site 1. There is a high density of stems 15 cm in diameter at breast height (dbh) and a paucity of trees more than 50 cm dbh. Forest tree density in tropical lowland regions varies

Figure 5. The percentage of the total number of Site 1 trees, 1 cm or more in dbh, occurring in a series of five cm diameter classes.


Percentage
80
40
20
9457
1012
373
175
112
60
32
15
8
5
3
2
1
1-4
5-9
10-14
15-19
20-24
25-29
30-34
35-39
40-44
45-49
50-54
55-59
60-64
85-89
Diameter classes (cm)

considerably (Table 1). Reported values range from 347 stems ha^{-1} in British Guiana (Fanshawe, 1954) to over 800 stems ha^{-1} in Armenia Vieja, Ecuador (Grubb *et al.*, 1963) for trees 10 cm or more in dbh; and from 187 stems ha^{-1} in Belem (Pires *et al.*, 1953) to 466 stems ha^{-1} in Armenia Vieja (Grubb *et al.*, 1963) for trees 20 cm or more in dbh. Density of trees 10 to 20 cm dbh is considerably higher for the San Carlos sites than for other lowland tropical forests (Table 1). When trees 20 cm or more in dbh are considered, the San Carlos values are typical of those reported in other rain forest studies; however, when density for trees 40 cm or more in dbh is examined, the San Carlos values are lower than other reported values. The striking difference in density between large and small trees is also evident in the ratio of trees 10 cm or more in dbh to trees 20 cm or more in dbh (Table 1). I am not aware of any other study of lowland tropical tierra firme forest which reports ratios as high as these found in the three San Carlos study sites.

The mean basal area for the three San Carlos forest sites was 27.8 m^2 ha^{-1} for trees 10 cm or more in dbh. This figure is somewhat lower than the 33.2 m^2 value reported for the tierra firme forest in the Manaus region of Brazil (Takeuchi, 1961) and considerably less than the 40-60 m^2 values reported by Holdridge (1972) for lowland wet forest sites in Costa Rica. The low San Carlos basal area values are reflected in the low tierra firme forest biomass of 391 mt ha^{-1} (Jordan and Uhl, 1978).

Density and basal area as a function of A horizon depth

The thickness of the sandy A horizon overlying the heavy clay horizon varied from 3 to over 100 cm within Sites 1, 2, and 3. The

Table 1. Forest tree density by size classes for lowland tierra firme sites at San Carlos and elsewhere.

	Density of Stems per Hectare				
Location(a) Source	A ≥ 10 cm dbh	B ≥ 10 ≤ 20 cm dbh	C ≥ 20 cm dbh	D ≥ 40 cm dbh	Size Class A / Size Class C
San Carlos, Site 1	786	548	238	19	3.30
San Carlos, Site 2	774	542	232	30	3.34
San Carlos, Site 3	670	444	226	46	2.96
San Carlos, mean	743	511	232	32	3.20
Belem, Black *et al.*, 1950	423	228	195	n.d.	2.17
Belem, Pires *et al.*, 1953	448	236	187	n.d.	2.26
Belem, Cain *et al.*, 1956	594	n.d.(b)	n.d.	n.d.	n.d.
Manaus, Takeuchi, 1961(c)	677	n.d.	n.d.	n.d.	n.d.
Ecuador, Armenia Vieja	869	403	466	n.d.	1.86
Ecuador, other tierra firme sites Grubb *et al.*, 1963(d)	723	376	347	n.d.	2.08
Costa Rica, Siquirres	597	n.d.	n.d.	n.d.	n.d.
Costa Rica, Osa Holdridge, 1972	521	n.d.	n.d.	n.d.	n.d.

Table 1. (Continued)

Location Source	Density of Stems per Hectare				Size Class A / Size Class C
	A ≥ 10 cm dbh	B ≥ 10 ≤ 20 cm dbh	C ≥ 20 cm dbh	D ≥ 40 cm dbh	
Uganda, Eggeling, 1947^(e)^	459	249	210	61	2.19
New Guinea, Paijmans, 1970	575	353	222	n.d.	2.59
Nigeria, Richards, 1939	523	294	229	46	2.28
British Guiana, Fanshawe, 1954	347	n.d.	n.d.	n.d.	n.d.

(a) Unless otherwise specified, data represent one site.
(b) n.d. indicates that no data were available.
(c) Mean of three plots.
(d) Mean of four plots.
(e) Mean of two plots.

density of large trees appeared to be related to differences in A horizon thickness. I checked for a relationship between A horizon thickness and four elements of forest structure: basal area m^{-2} for trees with a dbh of more than 10 cm, number of trees with a dbh of more than 20 cm, number of trees more than 20 m tall, and number of trees 1-5 cm dbh.[1]

Plots (100 m^2) having the thickest A horizon layer (more than 25 cm thick) had a mean basal area significantly greater (at the 0.05 level) than plots (100 m^2) with the shallowest (between 5 and 15 cm thick) A horizon depth (t = 3.45, d.f. = 18). The density of trees with a dbh of more than 20 cm was also significantly greater (at the 0.05 level) in the plots with the thicker A horizon (t = 3.26, d.f. = 18). There was no significant difference in the density of small stems or in the density of trees more than 20 m tall between plot groupings.

Thus, differences in density of large diameter trees and basal area are associated with A horizon thickness and these differences can be detected on the scale of 100 m^2 plots. The lack of an association between the density of trees 1-5 cm dbh and A horizon depth indicates that variations in A horizon thickness do not differentially affect seedling establishment or the survivorship or pole-sized trees. The failure to find an association between A horizon depth and the density of trees more than 20 m tall was at first surprising, because the density of trees more than 20 cm dbh is associated with A horizon thickness.

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[1] The thickness of the mineral soil was measured at 344 evenly distributed points within Site 1 with a thin metal rod that was inserted into the soil until the lateritic gravel was reached. Basal area, diameter, and height of trees were measured in ten 100 m^2 plots in the locations having the thickest layer of mineral soil and likewise in ten 100 m^2 plots in the locations having the thinnest layer of mineral soil. A t-test was then used to check for differences in these four structural elements between each group of ten plots.

However, many of the trees in the sites studied are more than 20 m tall but have a dbh of less than 20 cm. It may be that trees more than 20 m tall on thin soils have very slow growth rates giving them a high probability of falling over or being knocked over before reaching 20 cm dbh.

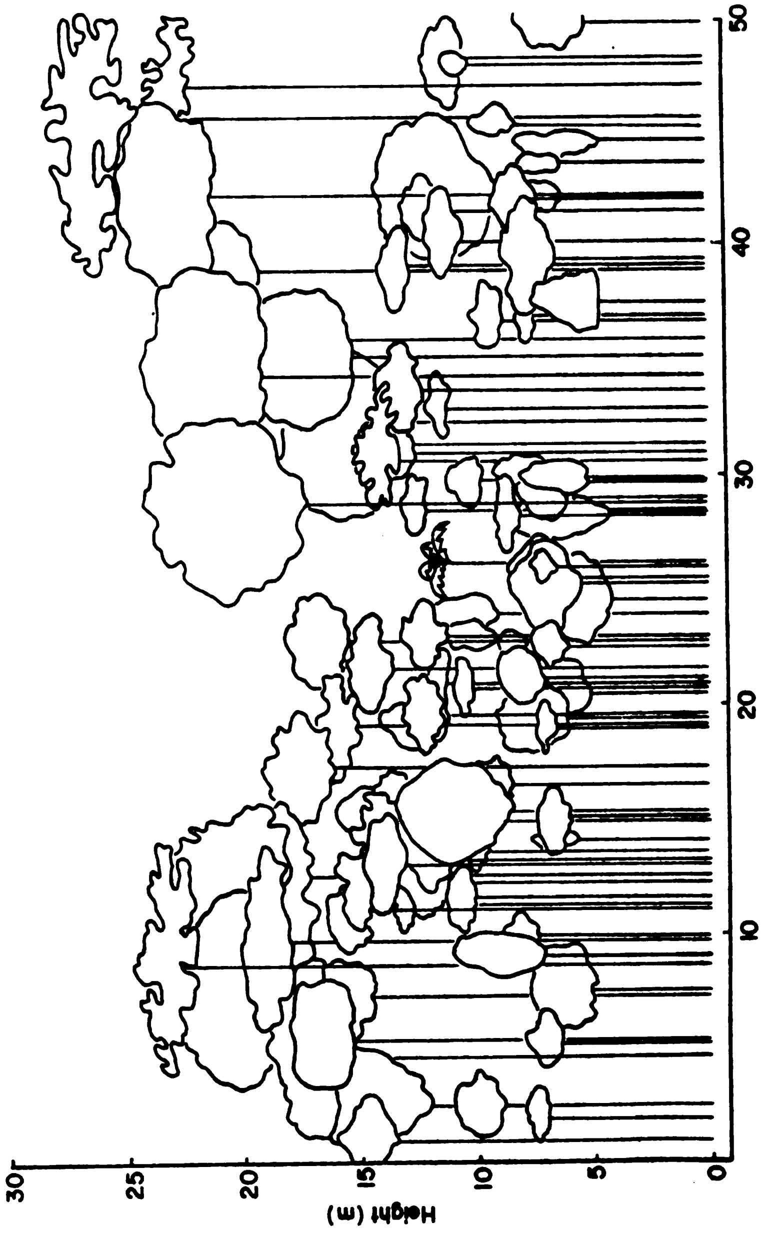
Vertical structure

The most common approach in studying the vertical structure of lowland tropical rain forests has been to construct profile diagrams. By illustrating vegetational features that are difficult to describe in words or numbers, profile diagrams serve as a useful tool in the study and comparison of tropical forest communities. To illustrate the vertical structure of the San Carlos tierra firme forest, a standard type (Davis and Richards, 1933) and an idealized type (Holdridge, 1970) of profile diagram were constructed.

The Davis and Richards type of diagram is a scale drawing of a 50 x 7.6 m strip of forest based on measurements of the position, height, diameter, and crown dimensions of the constituent trees. This type of diagram has the disadvantage of being quite subjective in that individual workers rarely choose the same area as being the most representative of the forest type under investigation. Hence, no two diagrams from the same forest will be identical.

Figure 6 is a profile diagram for the San Carlos tierra firme forest. Trees range to 30 m in height. The majority of the smaller trees depicted in this diagram are not mature and with time will become part of the upper canopy. Some portions of the diagram show distinct layering (e.g. between the 40 and 50 horizontal marks). In other portions of the diagram no layering is evident (e.g. between the 1 and 30

Figure 6. A profile diagram of the tierra firme forest, San Carlos de Rio Negro. The diagram represents a strip of forest 50 m long by 7.6 m wide. Only trees over 7.6 m tall are depicted.

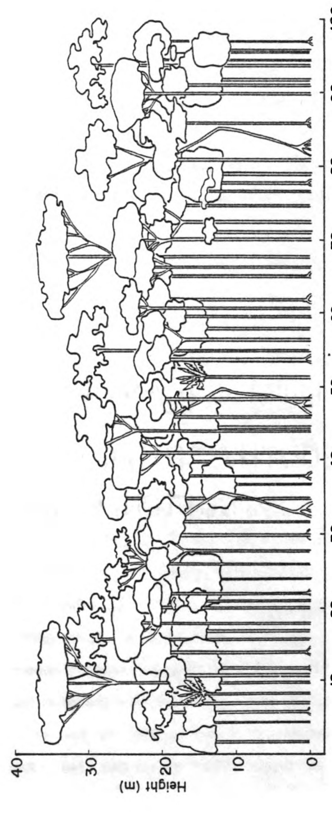

Height (m)
0
5
10
15
20
25
30
Distance (m)
0
10
20
30
40
50

horizontal marks). It is clear that even within this 50 m strip of forest, vertical structure differs from point to point primarily due to regeneration patterns and species specific differences in the height of mature individuals.

The second type of profile diagram constructed was the idealized profile diagram of Holdridge (1970). The idealized profile attempts to represent the total mature structure which has been attained and toward which any immature portions of the forest are developing. Mature individuals are represented in proportion to their density. The resultant diagram is an abstract representation which eliminates the subjectivity of the standard profile. An idealized profile diagram for Site 1 is shown in Figure 7. Although the forest tree species differ in their mature heights, the differences are continuous (i.e., mature-height species clustering or strata are not apparent). In theory, species stratification could result from groups of species whose average mature heights are different enough to form distinct strata with discontinuities between them. However, there is no convincing evidence from tropical rain forest studies for this type of stratification (Grubb _et al._, 1963); nor does this study provide support for species stratification.

The stratification of individuals based on total height or canopy height is more controversial and has been frequently addressed in studies of vertical structure. Some workers have presented evidence for the existence of strata in some stands (Grubb _et al._, 1963, Bimbino site), while others have found no evidence for their existence (Schulz, 1960; Paijmans, 1970). In this study, two approaches were employed to test for the existence of stratification of individuals. First, the percentage of foliage-free space at 1 m vertical intervals was estimated using

Figure 7. An idealized profile diagram of the San Carlos de Rio Negro tierra firme forest based on ten 0.1 ha plots.


Height (m)
0
10
20
30
40
Distance (m)
10
20
30
40
50
60
70
80
90
100

the Davis and Richards type profile diagram in Figure 6. Results of this analysis are illustrated in histogram form, Figure 8. As a second test of stratification, midcrown height was calculated for all trees more than 10 cm dbh in Site 1 and the number of trees in one meter mid-crown height classes was determined. Results are illustrated in histogram form in Figure 9. The interpretation of these figures requires a subjective judgment as to whether a peak in the histogram really represents a stratum. Furthermore, as Grubb et al. (1963) pointed out, wide height classes will tend to obscure strata while narrow ones will produce more. I have used both 1 and 3 m height intervals for both histograms, and peaks or hollows are not apparent in either case. Although both histograms suggest that strata do not exist on a hectare scale, layering is present on a smaller scale. The occurrence of gaps results in a flush of growth from previously suppressed sapling populations. If heights of these gap scale strata vary throughout the forest, the distribution of heights shown in Figure 9 would be expected.

A summary index of forest composition and structure

Information on species richness can be combined with data on density, basal area, and height into a single quantitative expression using Holdridge's complexity index (Holdridge, 1972). In examining tabulated data from several study sites in Costa Rica, Holdridge noted that these four vegetation parameters could be combined multiplicatively to produce a numerical value which agreed with his subjective impression of vegetation physiognomy. The use of indices based on combined characters is not without precedent. Goff and Cottam (1967) suggested that vegetation parameters such as height, basal area, and density could be combined in a variety of ways to form meaningful indices.

Figure 8. The percentage of open or non-canopy space at 1 m vertical intervals in a 7.6 x 50 m strip of forest in Site 1.

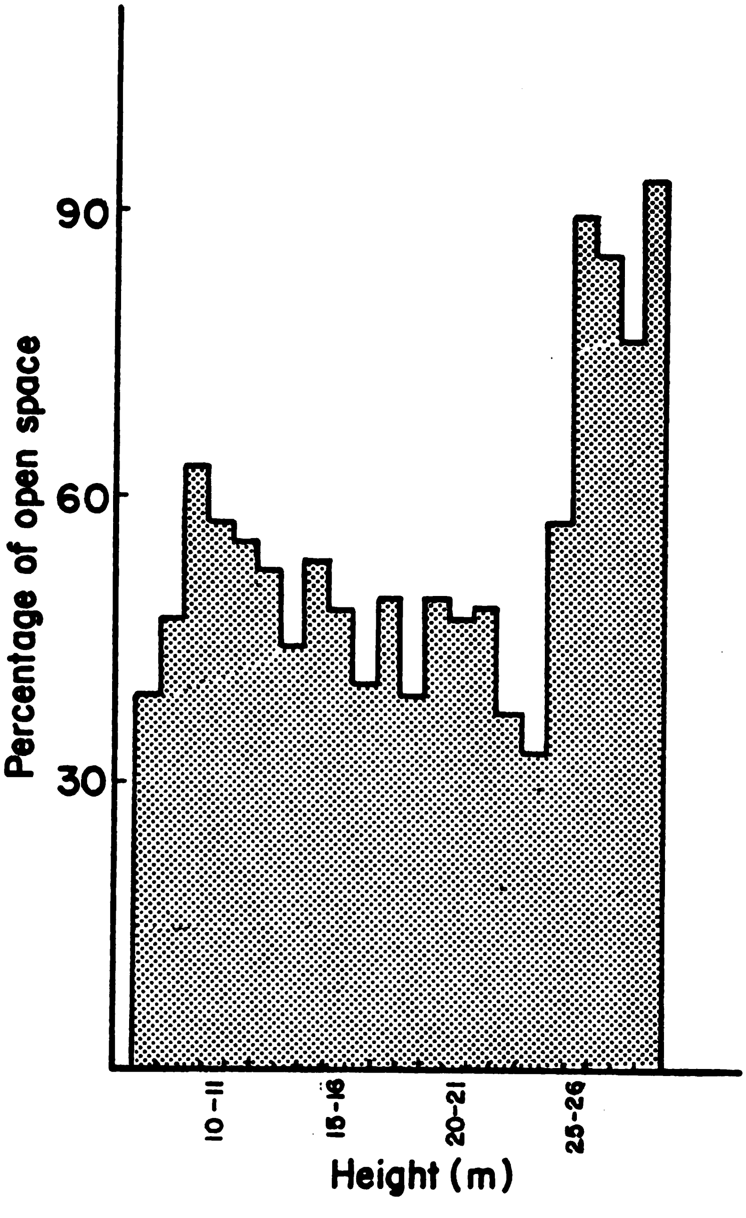
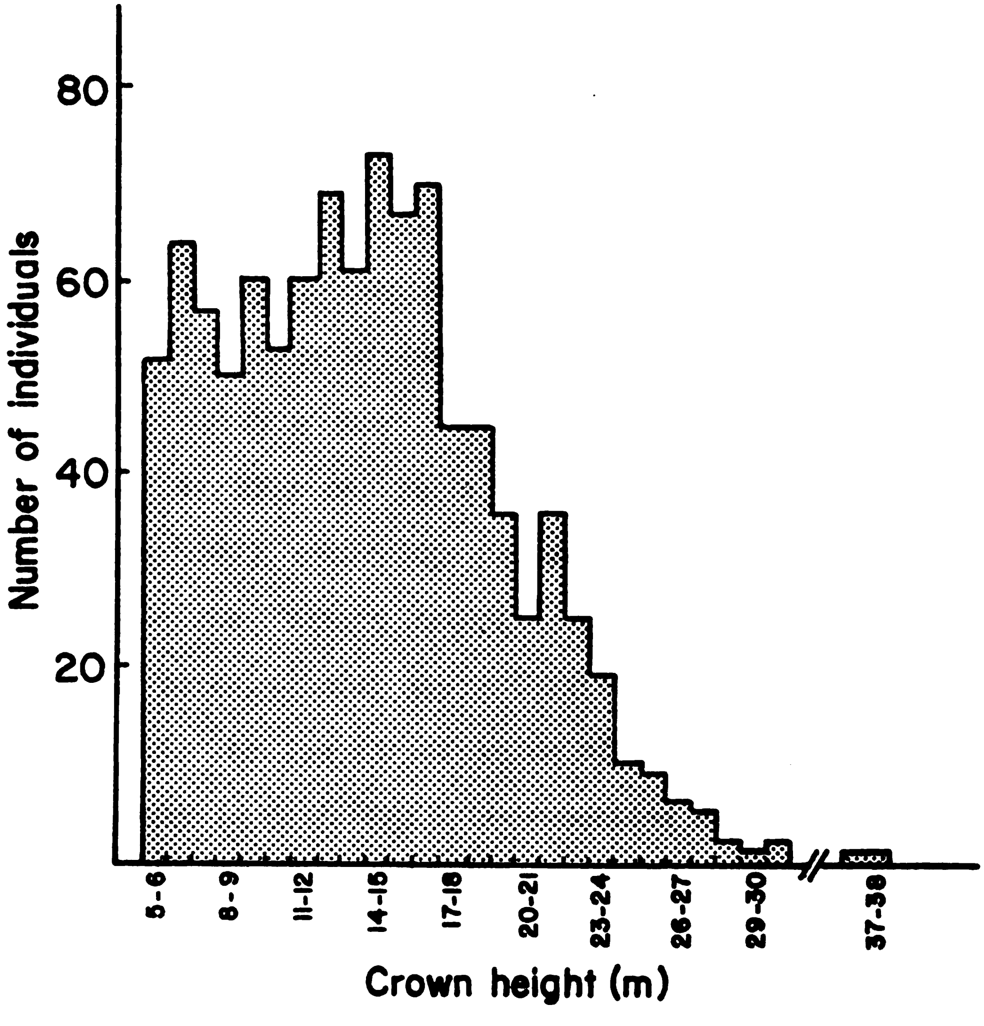

Percentage of open space
90
60
30
10–11
15–16
20–21
25–26
Height (m)

Figure 9. The distribution of mid-crown heights for trees 10 cm or more in dbh in Site 1. Mid-crown height = tree height - (crown depth/2).


80
60
40
20
Number of individuals
5-6
8-9
11-12
14-15
17-18
20-21
23-24
26-27
29-30
37-38
Crown height (m)

The complexity index and the component values thereof are shown for the San Carlos forest and three other tropical tierra firme forests in Table 2. The mean complexity index value of 197.3 (based on twenty 10 x 100 m plots) for the three San Carlos sites is only 55 percent to 58 percent of the values reported by Holdridge (1972) for Costa Rican tierra firme rain forest and 75 percent of the value derived from the data of Takeuchi for Manaus (1961). Costa Rican forests have higher complexity index values than the San Carlos forest because they are taller and have a greater basal area per m^2, whereas the main component contributing to a higher complexity index value for the Manaus tierra firme forest is the number of species.

San Carlos, with a mean annual temperature of 26°C and a mean yearly rainfall of 3500 mm, falls into Holdridge's moist forest life zone (Holdridge, 1972). Holdridge proposed 270 as a standard complexity index value for the "mature natural moist forest life zone on well drained upland sites without any excessively favorable or restrictive growth factors." The San Carlos value of 197.3 is considerably below this (more similar to Holdridge's lower montane wet forest values). The infertile tierra firme soils of San Carlos (Herrera _et al_., 1978) may constitute a "restrictive growth factor" and thereby account for the low San Carlos complexity index value.

As previously noted, the complexity index components (i.e. species number, density, basal area, and height) were quite variable both within and between sites. Holdridge (1972) recommended that at least three 0.1 ha plots be used to calculate the mean value of each complexity index component. To determine if three 0.1 ha plots were sufficient to give a reliable complexity index estimate for the San Carlos forest, four sets

Table 2. Complexity index and the component values thereof for the San Carlos forest and other tierra firme sites.

Location	Height	Basal Area	Density	Species Number	Complexity Index
San Carlos (Sites 1, 2, 3)	31.3	2.85	72.9	31.1	197.3
Manaus, Brazil Takeuchi, 1961	33.0(a)	3.32(a)	65(a)	38.0(b)	270.6
Siquirres, Costa Rica Holdridge, 1972	43.0	4.38	59.7	31.5	354.2
Osa, Costa Rica Holdridge, 1972	54.0	4.19	52.1	31.4	370.1

(a) Computed from dispersal table; Takeuchi, page 13, 1961.

(b) Computed from species area curve; Takeuchi, page 3, 1961.

of three 0.1 ha plots were analyzed in Site 1. Plot sets chosen for analysis were separated by ten meter wide strips with the first plot randomly selected. Mean complexity index values (for the four sets of plots) ranged from 92.5 to 199.8, s = 44.04 [$(64.0 \leq 150.3 \leq 236.6)$ = 95% confidence interval]. Given this variability for complexity index means based on three 0.1 ha plots, it is apparent that reports of the Holdridge complexity index should include a measure of variability.

The successional status of the forest under study

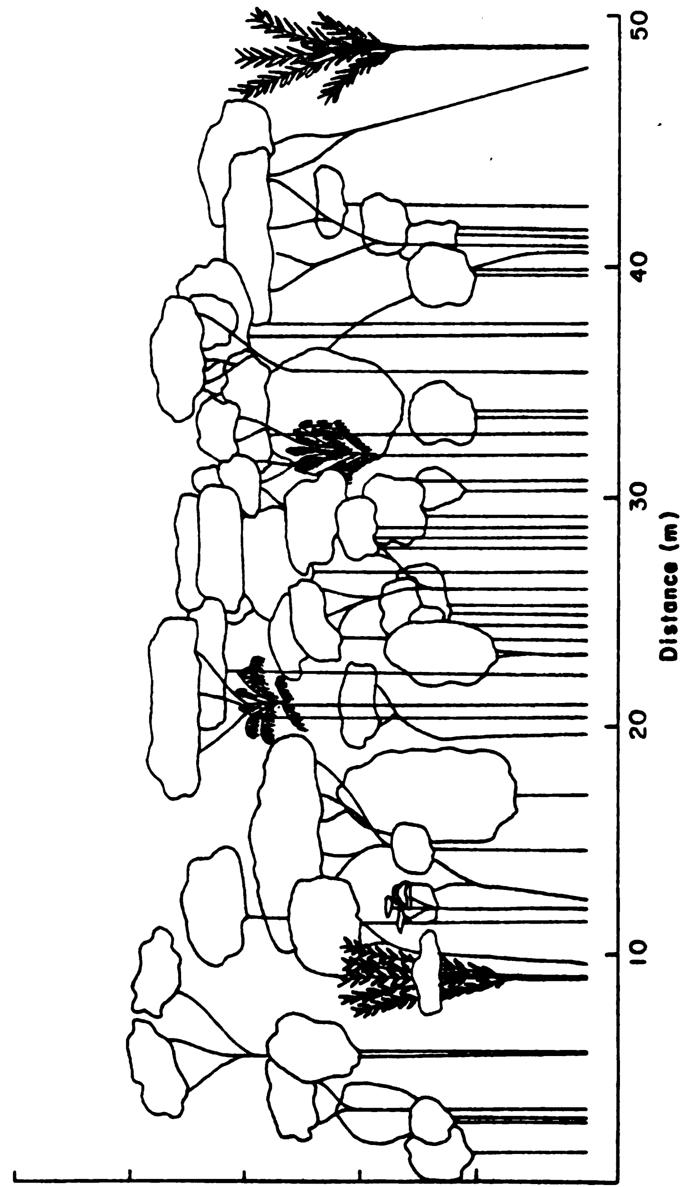
Throughout this study I have referred to the tierra firme forest on Sites 1, 2, and 3 as "mature." Yet, the high density of stems in the smaller size classes, the low basal area per hectare, and the low canopy height of these forest sites, as compared to literature values for lowland tropical forest structural features, may suggest that the sites studied are late secondary forest still in the building phase of development. To compare the three tierra firme study sites with secondary forest, I visited 17 abandoned agricultural sites along the Rio Negro with Manuel de Silva and Pedro de Silva, serving as guides. Both are old men who have lived in the San Carlos region all their lives. Most sites consisted of a deteriorated dwelling surrounded by a mosaic of abandoned agricultural plots of different ages ranging from ten years old to more than 60 years old. The sites more than 60 years old were distinguishable because: 1) the canopy was lower; 2) trees of higher diameter classes were absent or when present were of fast growing, soft-wooded species; and 3) fruit trees which were planted at the time of clearing had grown to be canopy trees. An old abandoned site which was typical of the others in structural development was chosen for further study and designated as Site 4. One of the guides recalled his relatives having cleared this site when he was a young boy. On this basis, the site was estimated to be about 60 years old. The soils of this site were similar to those of Sites 1, 2, and 3.

Site 4 (0.5 ha) had 68 species of trees 10 cm or more in dbh. Sites 2 and 3 (each also 0.5 ha) had 79 and 63 species of trees present, respectively. Hence, there may be no difference in tree species diversity between late secondary sites and the older undisturbed forest sites at San Carlos (Appendix Table 2). Knight (1975) reached a similar conclusion from his studies of old and very old secondary sites in Panama.

The Site 4 canopy was at 20 m with many stems loosely packed in the understory space (Figure 10). In contrast, the profile of Site 1 (Figure 6) shows a canopy height at about 25 m with some evidence of local stratification under the tallest trees. The mean height for trees 10 cm or more in dbh was 13.9 m in Site 4 vs 17.2 m in Site 1. The smaller stature of Site 4 is also reflected in the low basal area value for this site (Table 3).

The density of both small and large diameter trees was greater in Site 1 than Site 4 (Table 3). It is possible that the more closed, even canopy of the 60 year old site inhibits understory growth, whereas the more broken canopy of the older forest (i.e., Site 1) allows greater light penetration and therefore a denser understory. A second factor of importance may be that forest understory species are slow to colonize disturbed sites. In accord with this idea, an estimated 25.1 percent of the 1-4 cm diameter stems in Site 1 belonged to understory species (i.e., never growing to more than 5 m in height or 5 cm dbh). Only 3 percent of the Site 4 1-4 cm dbh stems were of understory species.

Figure 10. A profile diagram of a 60 year old second growth forest, San Carlos de Rio Negro. The diagram represents a strip of forest 50 m long by 7.6 m wide. Only trees over 7.6 m high are depicted.



60 YEARS

Table 3. Structural characteristics of a 60 year old abandoned farm site and a mature forest site (i.e., Site 1).

Characteristic	60 Years	Mature
Mean height for trees ≥ 10 cm dbh	13.9	17.2
Basal area per ha of trees ≥ 1 cm dbh	19.0	34.3
Density per ha of trees 1-4 cm dbh	2,816	9,457
Density per ha of trees 5-9 cm dbh	553	1,012
Density per ha of trees ≥ 10 cm dbh	518	786

Only one of the 17 old secondary sites I visited was indistinguishable from the surrounding tall forest. One of my guides recalled visiting this site 50 years earlier. At that time, the remains of a long abandoned village were barely evident among the forest regrowth. I estimated the site to be 150 to 200 years old. Based on the study of Site 4 and my travels in the region, I am satisfied that Sites 1, 2, and 3 represent the mature phase of forest development for this region.

The question as to why the San Carlos forest is comparatively low in stature and basal area when compared to other tropical rain forests of the world still deserves attention. The central Amazon basin is a region of very infertile soils (Herrera *et al.*, 1978). Grime (1979) has suggested that under conditions where mineral elements are scarce, natural selection has led to the evolution of plant species which make low demands upon the nutrient stocks of the soil. These species are, in turn, reduced in stature and in potential growth rate. I have already discussed the reduced stature of the San Carlos forest, and results from five years of tierra firme forest tree growth monitoring (Murphy and Jordan, unpublished data) show that dry matter production is also low in this forest (i.e., about 1 mm diameter growth per year for trees more than 10 cm dbh). Hence, I hypothesize that the small stature of the forest is a reflection of the oligotrophic conditions of the central Amazon basin.

Regeneration within Mature Forest

Seedling dynamics

Seedlings are abundant in the tierra firme forest and have high initial survivorship. I defined seedlings as plants less than one cm in dbh but more than two cm tall. The mean density of seedlings in November 1976, based on a survey of 52 randomly located 1 m^2 plots in Site 1, was 15.2 m^{-2} (s = 10.1, range 8 to 82). Hence, the estimated number of seedlings per ha is 152,000. The distribution of seedlings in four height classes is shown in Table 4. The difference in seedling number between two size classes can be interpreted as the probability of a seedling surviving from the smaller to the larger size class. For example, the probability of a seedling surviving from the $\geq$ 2 cm < 25 cm size class to the $\geq$ 150 cm size class is 9 percent (Table 4).

I followed survivorship and mortality of tree seedlings through time by conducting four surveys at roughly one year intervals on ten permanent 1 m^2 plots located by random methods in Site 1 (Table 5). Mean annual survivorship of marked tree seedlings was 89.3 percent. Most mortality (96 percent of total) occurred in the 2-25 cm height group. Nevertheless, the mean annual percentage of individuals surviving in this height group over the three year study period was 83 percent. The mean annual percentage survivorship for individuals greater than 25 cm tall was 99 percent. However, it appears that an estimated 85 percent of the individuals 25 cm or more in height die before reaching a height of 150 cm (Table 4). This suggests that many years are necessary to grow from a height of 25 cm to a height of 150 cm.

The height growth of tree seedlings was, in fact, very slow based

Table 4. The height distribution of seedlings based on the survey of 52 one m^2 plots in Site 1.

	$\geq$ 2 cm < 25 cm	$\geq$ 25 cm < 50 cm	$\geq$ 50 cm < 150 cm	$\geq$ 150 cm
Total individuals	393	229	135	34
Mean per m^2	7.6	4.4	2.6	0.65
Standard deviation	9.5	2.2	1.9	0.89

Table 5. Summary of the changes in seedling numbers over a three year period in 10 permanent 1 m^2 plots located in Site 1.

Time of Surveys	Total Density	Density $\geq$ 2 cm < 25 cm tall	Deaths	Establishments	$\frac{\text{Establishment}}{\text{Mortality}}$
12/75	144	84	--	--	--
2/77	136	78	16	8	0.5
11/77	162	104	12	38	3.17
12/78	157	99	19	14	0.74

on a one year growth study of 15 tree seedlings between 10 and 20 cm tall and having less than ten leaves. The mean annual stem elongation was 1.57 cm (range 0.5 to 3.5). The mean number of new leaves produced over the one year study period was 1.53 (range 1 to 4), while the mean number of leaves lost was 0.86 (range 0 to 3).

The high annual seedling survivorship, low rates of seedling establishment (Table 5), and the slow seedling growth rates suggest a persistent ground layer community. Temporal stability of forest floor vegetation in the tropics has been noted by other authors. Went (1973) found 12.2 five to ten year old seedling per m^2 in the Amazonian forest near Manaus. In this regard, it may be instructive to think of tropical rain forests as containing a seedling and sapling pool lying in wait for long periods of time until disturbances favor their growth.

Gap and building phases

The most common disturbance that provides favorable conditions for the growth of this seedling and sapling pool is the creation of gaps. Poore (1968), working in central Malaya, found that 9.9 percent of the rain forest there was in the gap phase.[2] Hartshorn (1978) found 5.05 (mean of four plots) of the La Selva, Costa Rica forest to be in the gap phase. I mapped the portions of Site 1 in the gap, building, and mature phases of development; using this map (Figure 11), I determined that 4.8 percent of the San Carlos forest was in the gap phase and 18.4 percent was in the building phase of development. Knowing the proportion of an

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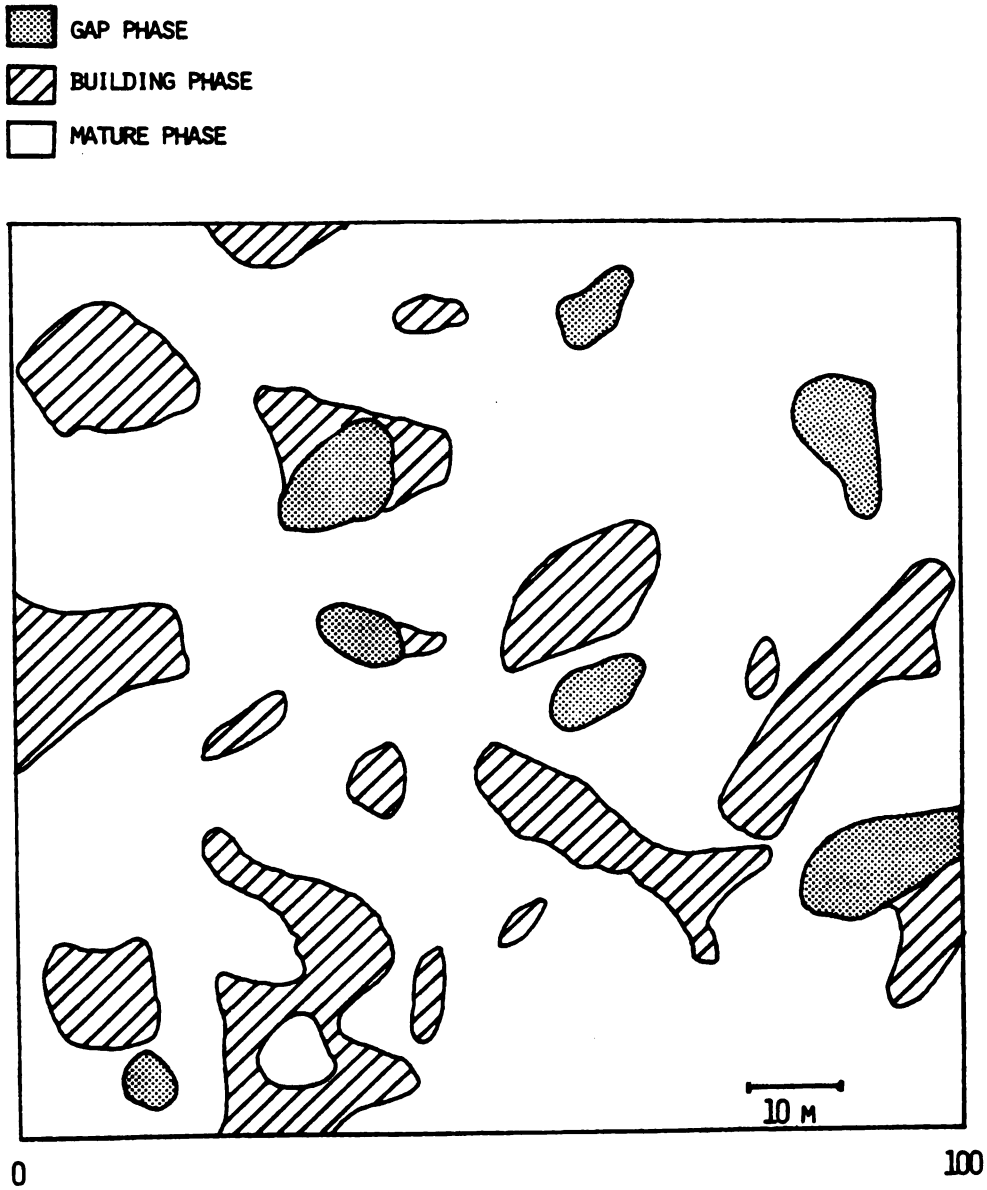
[2] Gap phase is any opening in the forest canopy with seedlings and saplings not exceeding 2.7 m tall. Building phase consists of juvenile trees of pole size, but no large trees. The mature phase of the forest has large trees, poles and seedlings intermixed (Whitmore, 1975).

Figure 11. A map of Site 1 showing the locations of the gap, building, and mature forest phases.


GAP PHASE
BUILDING PHASE
MATURE PHASE
10 M
0
100

area in gap phase, it is possible to calculate the forest turnover time. Gap phase persists for about five years in the San Carlos forest. Hence, the turnover time for San Carlos forest is approximately 104 years (100/4.8 x 5 = 104.1). This is comparable to Hartshorn's (1978) calculated turnover time of 118 ± 27 years for the La Selva forest in Costa Rica.

Size class distribution of important tree species

As the turnover time for the San Carlos tierra firme forest appears to be quite short, (i.e. approximately 100 years), it was of interest to know if the species composition would change in the future. Several tropical forest studies have shown the floristic composition of the upper canopy stratum to be different from that of the seedling and sapling strata (Watson, 1937; Aubreville, 1938; Richards, 1939; Jones, 1945). To explain this phenomenon, Aubreville (1938) proposed that the floristic composition of a given area of forest is changing continually, but in a cyclical fashion with groups of species succeeding each other periodically. Support for Aubreville's idea has come mainly from studies in the old world tropics. I analyzed the size class distributions of the common tree species in the San Carlos tierra firme forest (Site 1) to evaluate the applicability of Aubreville's ideas to this forest.

Eighteen tree species comprised 79.3 percent of the total importance value for Site 1 (Figure 4). At maturity all of these species have diameters in excess of 20 cm and yet 13 of the 18 species had more than one-half of their individuals in the 1-5 cm dbh class. Because all transects used to sample trees less than 10 cm dbh were located in non-gapped forest, these 13 species appear to be able to regenerate in the shaded understory or at least to persist there for a long time. Furthermore, the representation of each of these species in almost all diameter classes up to 30 cm suggests a temporal continuum of regeneration.

Three of the 18 most common species in Site 1 had few or no representatives in the smaller size classes. Most of the individuals of these three species were in the 15-25 cm dbh size class. Although I lack information on the floristic composition of gaps, this type of distribution (i.e. skewed towards the larger size classes), is commonly interpreted to mean that the species in question requires gaps in order to regenerate (Schultz, 1960). The remaining two species had size class distributions which were difficult to interpret because of small sample size.

Given that 72 percent of the 18 most common Site 1 tree species were regenerating on site, the abundance pattern of the common tree species will not change appreciably over time on this site. Although this contradicts Aubreville's ideas, it is in accord with the findings of Davis and Richards (1933) for British Guianan mixed forest and with results reported by Schulz (1960) for Surinam. Richards (1952) suggested that African forests which appear to have cyclic regeneration may actually be early seral stages. Again, the evidence suggests that in spite of its overall small stature, the San Carlos tierra firme forest may well be representative of one of the region's natural climax vegetation types.

SUMMARY

Composition, structure, and regeneration were investigated in the tierra firme rain forest of the San Carlos region of the Rio Negro. Species richness of this forest was comparable to other lowland tierra firme forests. Eighty-three tree species 10 cm or more in dbh were found in one 1-ha site. The species area curve appeared to level off slightly as 0.1 ha plots were grouped within sites, but when 0.1 ha plots from additional nearby tierra firme sites were added, the cumulative number of species increased sharply, suggesting that species in this forest may be clumped in their spatial distribution. Species abundance patterns were similar to other tropical areas, most species being quite rare. The island-like nature of tierra firme sites in the forest landscape offers a unique study opportunity for investigations of plant distribution and evolution.

Structural differences were also noted between and within sites. The density and basal area of trees more than 20 cm dbh were greater in locations with a thick A horizon than in locations with a thin A horizon.

When compared structurally to other lowland tierra firme forests described in the literature, the San Carlos forest:

(1) has a higher number of trees 10 cm or more in dbh, but a smaller number of trees 40 cm or more in dbh;

(2) has a basal area value 84 percent that of the tierra firme forest near Manaus, and considerably lower than most other lowland tierra firme forests where values are known;

(3) is similar in height (averaging 17.3 m for trees more than 10 cm dbh) to tierra firme forest in the Manaus area but is less

tall than lowland forests in other areas where data are available;

(4) is similar in vertical structure to other tierra firme forests, showing no evidence of stratification of mature species height (idealized profile diagram) nor any evidence of stratification of individuals; and

(5) has a mean Holdridge Complexity Index of 197.3 which is considerably lower than predicted for lowland rain forest without restrictive growth factors.

Although the San Carlos forest has relatively high density values for small trees more than 10 cm dbh and relatively low basal area values, this forest is clearly different in vertical structure, canopy height, density, and basal area from old secondary sites, and on this basis is considered to be representative of mature forest for the San Carlos de Rio Negro region. The small stature of this forest is thought to be a reflection of the oligotrophic conditions of the central Amazon Basin.

The high seedling survivorship (83 percent mean annual survivorship over a three year period for seedlings 2 to 25 cm tall), low rates of seedling establishment, and slow seedling growth rates suggest a persistent forest floor seedling community. Gaps are common in the forest and their occurrence is probably beneficial to the persistent seedling and sapling pool. Most of the important tree species were well represented in all diameter size classes indicating that the sites studied are floristically stable.

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Appendix Table 1. The percentage of total species present in a geometric series of abundance classes for San Carlos, Site 1, and other lowland tropical tierra firme sites.

	Abundance Classes									
Location	1	2-3	4-8	9-16	17-32	33-64	65-128	129-264	Total Species	Total Area
San Carlos	45.8	16.9	13.2	8.4	9.6	3.6	---	1.2	83	1 ha
Belem Black *et al.*, 1950	37.9	34.5	13.8	5.7	4.6	3.4	---	---	87	1 ha
Castanhal Pires *et al.*, 1953	39.8	26.8	20.4	9.3	2.8	0.9	---	---	108	1 ha
Mucambo Cain *et al.*, 1956	43.8	24.2	15.7	9.1	3.9	2.0	1.3	---	153	2 ha

Appendix Table 2. Diversity index values for trees $\geq$ 10 cm dbh in Sites 1, 2, 3, and 4.

Site Designation	Size	Number of Species	Number of Individuals	Simpson's Index(a)	Shannon-Wiener Index(b)			$\frac{\text{No. Individuals}}{\text{No. Species}}$
					H	Hmax	E	
Site 1	1 ha	83	744	.92	4.8	6.4	.75	9.0
Site 2	0.5 ha	79	387	.96	5.4	6.3	.86	4.9
Site 3	0.5 ha	63	335	.96	5.3	6.0	.89	5.2
Site 4	0.5 ha	68	259	.93	5.0	6.1	.82	3.8

(a) $D = 1 - \Sigma(P_i)^2$ where P_i = proportion of individuals of species i in the community.

(b) $H = 3.3219\ (\log_{10} N - \frac{1}{N} \Sigma\, n_i \log_{10} n_i)$ where: N = the total number of individuals of all species; n_i = the number of individuals of the i^{th} species; and 3.3219 = a conversion factor from $\log_{10}$ to $\log_2$.

$H_{max} = \log_2 S$ where S = the number of species in the community.

$E = H/_{Hmax}$

PART II

PRODUCTIVITY OF AGRICULTURAL AND SUCCESSIONAL SITES

INTRODUCTION

Inhabitants of the Rio Negro region of the Amazon Basin farm by shifting cultivation. The essential characteristics of shifting cultivation are that an area of forest is cut, burned, and farmed for several years without tilling the soil and then allowed to revert to forest before being cleared to farm again.

A typical shifting cultivation cycle in the San Carlos region of Amazonia begins with the cutting of a one-half to two hectare patch of mature tierra firme (i.e., never flooded) forest. The small trees and lianas are cut with machete while the larger trees are felled with an axe. Cutting occurs in September and October (i.e., at the beginning of the dry season). The cut vegetation is left to dry for several months and then burned. Burning causes carbon, nitrogen, and sulfur to be volatilized as oxides. The remaining nutrients are added to the soil as carbonates (e.g., $CaCO_3$, KCO_3) or as phosphates and silicates (Nye and Greenland, 1960). Soon after burning, yuca (_Manihot_ _esculenta_, Crantz) is planted at a density of one to three stem stocks per m^2 throughout the clearing known locally as a "conuco." Yuca roots are ready for harvest about one year after planting. Yuca harvesting goes on continually after the first year, a 100 to 300 m^2 area being harvested every one to two weeks. The harvested areas are replanted to yuca immediately. By 18 months the conuco consists of a mosaic of small plots containing yuca in varying stages of development. Approximately 20 percent of the conuco has crops such as pineapple, plantain, banana, cashew, sugar cane, yams, potatoes, or beans planted in combination with yuca.

Frequently the conuco is abandoned after the second yuca crop because of declining crop production. On better soils conuco use continues for a third cropping period. When it becomes apparent to the cultivator that the plot will only produce one more yuca crop, he cuts a new section of mature tierra firme forest. Sometimes the new plot is immediately adjacent to the plot being abandoned. Occasionally old (i.e., more than 60 years old) second growth stands are chosen for farming, but the low population density of this region precludes the necessity of cropping fallowed land at the present time.

This method of agriculture is common throughout the lowland tropics, occurring on a wide array of soil types and practiced by people of widely varying cultures (Nye and Greenland, 1960). Shifting cultivation practices have been the focus of numerous studies. A bibliography by Conklin (1963) lists over 1300 titles related to all facets of shifting cultivation. In addition to ecologists, the study of shifting cultivation has attracted geographers (Watters, 1960) and anthropologists (Leach, 1959) who have been interested in the cultural aspects of the phenomenon. Nye and Greenland (1960) and UNESCO (1978) provide reviews of the shifting cultivation literature.

Three detailed studies of shifting cultivation have been conducted in Venezuela. Watters (1971) working in Northwest Venezuela, investigated the technological, sociological, and economic aspects of shifting cultivation and made recommendations for stabilizing and improving conditions of rural land use. His report includes information on farm size, labor inputs, and crop yields. Jolly _et_ _al_. (1961; cited by Petriceks, 1968) conducted a similar study on small farm sites in

Northeast Venezuela.

Petriceks (1968), in a study encompassing northern and central Venezuela, focused on land tenure practices, kinds of crops planted, yields, population movement, education of farmers, income distribution, and timber exploitation. These three studies provide an excellent overview of shifting cultivation in all areas of Venezuela except the state of Amazonas where no farm sites were examined.

The first part of this paper is devoted to an energetic analysis of shifting cultivation as it is practiced in the San Carlos de Rio Negro region of Amazonia. I compare the energetic returns in the form of food output with the human energy input necessary to raise this food. The energetic efficiency values presented in this paper provide one standard by which land-use planners, agronomists, and others can judge the merits of alternative farming schemes proposed for Amazonia.

The second part of this paper compares conuco crop productivity with early successional vegetation productivity. It has been suggested that the rates of net primary production attained by natural plant communities may be indicative of the rates that can be achieved through innovative agricultural systems (Gomez-Pompa *et al.*, 1973). If this is true, and if the San Carlos conuco crops are significantly less productive than the natural vegetation, there would be a basis for attempting to design more productive agricultural systems using the structural and life-form dominance patterns of the natural vegetation as a model. The relevance of such a scheme for the San Carlos region of the Amazon Basin is discussed.

METHODS

Time and Energy Expenditure in Yuca Crop Production

I timed conuco field activities and yuca root processing activities in several conucos in the San Carlos vicinity. Field activities were broken down into the following 10 categories: cutting of small stems by machete, felling of large trees by axe, burning, post-burn clearing, yuca stem gathering, stem cutting, stem planting, weeding, crop harvesting, and transportation. Each activity was measured on at least two occasions, and all activity times were expressed on a hectare basis. Yuca root processing activities were divided into seven steps: peeling, grating, squeezing, sifting, fire building, baking, and transportation. Activity times for each of these activities were measured by monitoring the yuca root preparation process from beginning to end over two separate three-day periods.

I estimated the human energy expended in these conuco field and root processing activities by separating the activities according to their difficulty into light, intermediate, demanding, and very damanding work groupings. I used calorie expenditure values of 50 kcal per 45.4 kg human body weight per hour for light work, 100 kcal per 45.4 kg per hour for intermediate work, 150 kcal per 45.4 kg per hour for demanding work, and 250 kcal per 45.4 kg per hour for very demanding work. These values agree with figures supplied by Rose (1938) for work ranging from light (e.g., washing dishes) to heavy (e.g., sawing wood). Men do most of the field work while women do most of the root processing. I estimated that the average adult male weighed 59 kg (basal metabolism approximately 60 kcal per hour) and the average adult female weighed 54 kg (basal metabolism approximately 55 kcal per hour). Basal metabolism values are from Carpenter (1948). Using these values, I was able to estimate the total amount of human energy necessary to farm a one hectare conuco and the energy expended in processing a given quantity of yuca roots.

Yuca root productivity per hectare for a two-crop cycle of conuco use was estimated based on measurements taken in experimental plots (see yuca production). Knowing the energetic content (in kcal) of the yuca root production, I was able to compare the energetic returns in the form of food with the total work energy input necessary to secure that food, and thereby evaluate the energetic efficiency of the indigenous farming system.[1]

Conuco Productivity

A 60 x 120 m section of mature tierra firme forest was cut in September 1976 and burned in December 1976. This site was used to compare the productivity of the native crop plants with the productivity of the naturally colonizing early successional vegetation for the two year period following burning. The agricultural plot, designated Conuco Site 1 (see Figure 1, General Introduction, for location), was 30 x 50 m

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[1] Generally, conucos are farmed actively for two to three years (i.e., the time necessary to produce two yuca crops). Yuca is by far the most important crop in all conucos of the San Carlos region; 93 percent of the edible crop production in Conuco Site 1 was yuca. Because other crops represent a minor portion of the total crop production, they were not considered in the energetic analysis.

in size and occupied the southern half of the burned site.

All conuco work was performed by local workers who were paid for their assistance. Juan Moreno, an experienced local farmer, was employed to supervise the cutting, burning, planting, weeding, and harvesting operations to ensure that each conformed with local practices. This approach allowed ready access to the conuco for measurements and experimentation, while ensuring that the site was being operated in a traditional manner.

Yuca (Manihot esculenta), pineapple (Ananas sativas), plantain (Musu sp.) and cashew (Anacardium occidentale) were planted in this site starting in January 1977. Productivity was measured differently for each of these four crops.

Yuca production

Yuca production was estimated through measurements of standing crop biomass, litter production, and herbivory by chewing insects. Standing crop biomass was determined by weighing the above ground (i.e., non-edible) biomass and the below ground (i.e., edible) biomass of all yuca plants ready for harvest during the study period.[2] Subsamples of leaves, stems, and roots were taken for dry weight determination.

Yuca leaf litter production was estimated by counting leaf scars on 50 randomly located plants at each harvest period. Leaf litter samples

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[2] Large roots were separated from roots less than 1 cm diameter for 50 randomly located yuca plants. The ratio of these two root fractions was determined to allow for the estimation of fine root biomass which the farmers do not bother to remove in the general root harvest. In addition, the above ground portions of each of these 50 plants were separated into leaf and stem fractions and weighed. Subsamples were taken for dry weight determination. This leaf to stem dry weight ratio was used to estimate the leaf and stem fractions of all subsequently harvested yuca plants.

were taken to determine the mean dry weight per leaf. The number of plants being harvested and the length of the cropping period were then used to estimate yuca leaf litter production. Yuca branch litter production was estimated prior to each harvest by gathering all downed yuca branches in two 1 x 30 m permanent transects. The collected branch litter was dried and weighed.

Yuca production lost to chewing insects was measured by removing the bottom-most leaf (i.e., the oldest leaf) from 75 randomly selected yuca plants at the end of years one and two. The leaves were traced, and the leaf area and area eaten were determined using planimetry. Traced leaf blades were weighed to determine their area to weight relationship. This information was combined with estimates of the total number of leaves produced per year to determine yuca production losses to chewing insects.

Yuca production was investigated in two additional one year old conucos designated as Conuco Sites 2 and 3 (see Figure 1, General Introduction) to determine if the production values in Conuco Site 1 were representative of other nearby conucos. Both of these conucos were planted for the first time concurrently with Conuco Site 1. The diameter and stem length of all yuca individuals in 30 one m^2 plots were measured in each of these two conucos and in Conuco Site 1 at the end of the first year. Root production was then estimated using a regression equation.

All yuca production data were expressed on an annual basis to permit comparison with succession site data and on a crop basis to allow for an analysis of agricultural energetics.

Pineapple production[3]

Pineapple fruit production was measured by harvesting and weighing all ripe pineapples at weekly intervals. Periodic subsamples were taken for dry weight determination. Pineapples were occasionally eaten by frugivores. Production losses to frugivores were estimated by multiplying the mean weight for non-damaged fruits by the total number of fruits with frugivore damage.

Twenty marked pineapple plants were checked every two weeks for litter production. All dead leaves or dead parts of leaves were collected, oven dried, and weighed. These data were used to estimate the rate of litter production.

At the end of year two the number of pineapple plants in the conuco was counted and each plant was categorized as pre-fruit-bearing, fruit-bearing, or post-fruit-bearing. Five individuals typical of each of these categories were harvested, separated into fruit, leaf, stem, and root portions, and weighed. Sub-samples were taken for dry weight determination. The total density of pineapple plants in each of these three stages and the average weight of a plant in each stage were combined with the fruit harvest and litter collection data to estimate pineapple plant production for the two year period. The proportion of the two year pineapple plant production occurring in year one was estimated to be one-third of the estimated two-year standing crop (since pineapple plants were only present for six months of year one) plus the

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[3] Local farmers introduce pineapple, plantain, and cashew plants into their conucos throughout the first year of conuco farming. The relative proportions and overall density of these fruit plants are dictated in large part by the availability of plants from neighboring conucos. All fruit plantings were introduced into Conuco Site 1 approximately six months after the burn.

litter production during year one minus the estimated pineapple plantlet input weight.

Plantain production

No plantain fruits were produced during the two year study period. Plantain generally begins to fruit in the second or third year of conuco use and continues fruiting after the conuco has been abandoned. The diameter and height of all plantain plants present at the end of two years were measured. Several plantain plants were then harvested outside of Conuco Site 1 and used to establish regressions between diameter^2 x height and below ground biomass, and diameter^2 x height and above ground biomass. These regression equations were then used to estimate the plantain standing crop biomass in Conuco Site 1. To measure plantain litter production, 10 marked plantain plants were surveyed every two weeks, and all dead leaves or dead leaf parts were removed, oven dried, and weighed. The regression estimate of standing crop biomass together with the litter production measurements were used to estimate plantain production for the two-year period. The proportion of the total two-year plantain production occurring in year one was approximated in the same manner as described for pineapple.

Cashew production

Several of the 11 cashew trees present in Conuco Site 1 were beginning to flower at the end of two years but none had produced fruit.

Leaf standing crop at two years and leaf litter production up to two years were estimated by counting the number of leaves and leaf scars on all cashew trees present in the site at two years. Weight per leaf was determined by harvesting, oven drying, and weighing 50 cashew leaves. The total length of brown (i.e., old, 1.5 to 4 cm diameter) and green (i.e., young, 0.3 to 1.5 cm diameter) stems per plant at two years together with the weight per cm of each stem type was used to estimate the total two year stem production per plant. Root weight, as a percentage of above ground weight, was determined by destructive sampling outside of the study plot. The proportion of the two year cashew production occurring in year one was approximated in the same manner as described for pineapple.

Weed production

Weeds are common in conucos, particularly after the first year. The harvest method was used to estimate weed production. Twenty-seven 1 x 1.5 m plots were randomly located in Conuco Site 1 ten months after burning. Light weeding which occurred prior to the establishment of these plots was not measured. All non-crop plants in these 27 plots were removed at 10, 16, and 21 months. The harvested plants (i.e., weeds) in each plot were placed in one of five groups: forbs, grasses, secondary woody species, forest tree species, and lianas. The plants in each of these groups were divided into root, stem, and leaf parts. The plant material thus divided was bagged, oven dried, and weighed. This method slightly underestimated weed production because a few forbs and grasses had fruited and begun to decompose by the time the weedings occurred.

Secondary Site Productivity

Secondary site productivity was measured in Succession Site 1. This site was immediately adjacent to Conuco Site 1 (see Figure 1, General Introduction). Measurements of standing crop biomass, litter production, and leaf herbivory by chewing insects were used to determine the productivity of this site.

Standing crop biomass at year one was measured by harvesting all plants present in 25 one m^2 plots. Plants in each plot were grouped as forbs, grasses, secondary woody plants, forest trees established by sprouting, forest trees established from seed, and lianas. The plant groups present in each plot were then divided into leaf, stem, and root tissue and bagged, oven dried, and weighed. Year two biomass was measured in the same manner for all plants, except those individuals, two meters or more tall, in the genus Cecropia. The root and stem standing crop of these larger Cecropia was estimated by the regression of diameter^2 x height on root weight and on stem weight for 13 Cecropia individuals harvested outside of the study site. Cecropia leaves of these harvested plants were placed in three size classes, and the mean weight of leaves in each size class was determined. Then, the stem diameter, height, and number of leaves in each leaf size class were measured for all Cecropia, two meters or more tall, in nine 5 x 5 m plots located in three transects placed in the center of Succession Site 1. The standing crop of the Cecropia individuals present in the nine plots was estimated using the regression and leaf-size-class weight relations.

Litter production for the first 10 months of succession was estimated by counting leaf scars on all plants present in 25 randomly chosen one m^2 plots in Succession Site 1. Plants of the same species as those encountered in the survey plots or of the same general type, in the case of forest trees and lianas, were located outside of Succession Site 1.

Twenty-five lower leaves (about to fall) were taken from each plant species and from each plant type for dry weight determination.[4] This procedure provided an estimate of mean dry weight per leaf of each plant species and plant type which was then used to calculate litter production for the first 10 months of succession.

Litter production in Succession Site 1, after 10 months, was measured by harvesting 16 randomly located 2 x 2 m permanent plots at weekly intervals. Litter collected from each plot was bagged, oven dried, and weighed.

The amount of leaf material removed by chewing insects was estimated by removing the bottom-most leaf from 30 to 40 plants of the herbaceous, secondary woody, primary tree, and liana plant groupings at the end of years one and two. The total leaf area and area eaten were measured by planimetry for each plant group. Petioles were removed and the leaf blades dried and weighed to determine area to weight relationships for each plant group. The litter collections at 11, 16, and 23 months, were separated into leaves of herbaceous, secondary woody, primary tree, and liana species and the percentage of the total leaf litter contributed by each of these plant groups was calculated. The estimates of the total leaf litter production for years one and two, the percentage of the total leaf litter belonging to each of the four plant groupings, the amount eaten by chewing insects for each of the plant groupings, and the leaf area to weight relationship for each plant grouping were used to determine the dry weight of the collected leaf

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[4] Leaves of forest tree species were generally similar in size, belonging to the mesophyll size class of Raunkiaer (1934). Leaves of lianas were more variable in size and shape, but most were also in the mesophyll size class.

litter which had been removed by chewing insects prior to leaf fall.

The percentage of the standing crop leaf biomass removed by chewing insects for years one and two was considered to be equal to the percentage removed by chewing insects from the bottom-most leaves in each of the plant groupings based on the assumption that leaves are only vulnerable to insect attack during the phase of leaf expansion [see Nicholson, Paterson, and Curie (1970) and Rhoades and Cates (1976) for support of this contention].

RESULTS AND DISCUSSION

Time and Energy Expenditure in Yuca Crop Production

Table 1 shows the time spent, the relative difficulty, and the estimated energy expended in conuco field activities undertaken during a two crop cycle of conuco use. The activities are listed in the chronologic order of their occurrence. Forest cutting accounts for 8.0 percent of the total human energy devoted to farming (i.e., to both field activities and root processing activities). The understory tree species and saplings of canopy species are cut with a machete. Three experienced conuco farmers, working for 11 hours each, machete-cleared 11,979 m^2 or 363 m^2 per man-hour. At this rate, 28 man-hours are necessary to clear one hectare by machete. Generally, trees more than 10 cm in diameter are cut by axe. The intermediate sized trees (i.e., 10 to 40 cm diameter) are only partially cut. The large trees are then completely felled. As the large trees fall, they carry down with them the partially cut trees. Four adult males required 243 hours to axe-fell 2.47 hectares of mature forest. Thus, the men cleared 102 m^2 per hour or one hectare in 98 hours.

The cut slash is left to dry for several months. The burn occurs in December or January, the driest period of the year, and is immediately preceded by four to five consecutive rainless days. Using a torch fashioned from tree bark, several farmers start numerous small fires along one side of the clearing and then walk through the clearing to the

Table 1. The time spent, the relative difficulty, and the estimated energy expenditure in conuco field activities during a two crop cycle of conuco-use.

Activity	Time (hours per hectare)	Kcal (per hectare)	Kcal (% of Total)	Difficulty
Cutting of small stems with machete	28	10,777	3	very demanding
Cutting of large trees with axe	98	37,719	11	very demanding
Burning	6	2,309	1	very demanding
Post-burn clearing	50	19,244	6	very demanding
Yuca stem gathering and transport	40	10,197	3	demanding
Yuca stem cutting and planting	83	21,160	7	demanding
First crop weeding	66	16,826	5	demanding
First crop harvest	160	40,789	13	demanding
Site cleaning in preparation for second crop	125	31,867	10	demanding
Second planting	83	21,160	7	demanding
Second weeding	66	16,826	5	demanding
Third weeding	66	16,826	5	demanding
Second crop harvest	160	40,789	13	demanding
Transportation	193	36,661	11	intermediate
TOTAL	1224	323,150		

other side, igniting slash as they go. These small blazes converge and the whole clearing burns powerfully for 10 to 15 minutes. The fire never advances more than a few meters into the surrounding forest, however. Six man-hours are required to burn one hectare. The work is demanding, but because of its short duration, accounts for only 0.4% of the total human energy input to farming.

After the site is burned, yuca stem stocks must be gathered from surrounding conucos and transported to the site. Conucos are usually within 10 minutes walking distance of each other, and farmers are generally willing to give away stem stocks of harvested plants. I estimated that 4800 yuca stems (i.e., the number of stems necessary to plant one hectare at a density of 2.4 stem stocks per m^2) could be gathered, bundled into groups of 100, and transported to a new conuco in 40 hours. This estimate provides 30 minutes to gather and bundle 100 stems with 20 minutes for transport. Based on this time estimate and the demanding nature of the work, 1.7 percent of the total conuco energy input is devoted to this activity.

Once yuca stems are on the site, they must be cut and planted. The time necessary to cut yuca stems into 20-30 cm stem stocks and insert these into the soil was measured by timing an experienced farmer engaged in these activities. Fourteen stem stocks were cut per minute. To plant the stem stocks, a hole is made in the ground using a stick with a pointed end, and the stocks are inserted into this hole. An average of 7.4 stem stocks were planted per minute. On this basis 83 man-hours are required to cut yuca stems and plant one hectare at a density of 2.4

stem stocks per m^2.[5] These activities account for 7.0 percent of the total human energy input to farming.

A considerable amount of work goes into site cleaning and weeding in a two crop conuco cycle. After the burn, time must be spent cutting, piling, and reburning any remaining small slash. The time devoted to this activity (i.e., post-burn clearing) varies, but if the site burns poorly, 100 or more hours per hectare may be required to render it clean enough for planting. Based on my observations, I have assigned 50 hours per hectare as an average amount of time devoted to this activity. About eight months after the site has been cleaned and planted, the first weeding is done. As the life of the conuco is prolonged, weeding occurs with increasing frequency. Weeds are removed by their roots where possible, and the work is demanding. I measured the time it took farmers to weed measured areas of their conucos on two occasions, and found that they weeded approximately 152 m^2 per hour. At this rate, 66 hours are needed to weed one hectare. A thorough weeding combined with trash burning occurs at each yuca harvest. I observed and timed this activity in Conuco Site 1 and in a nearby conuco. Approximately 80 m^2 were cleared per hour; hence, an estimated 125 hours are required to clean one hectare after a yuca harvest. Based on these time estimates for the various conuco cleaning and weeding activities and the difficulty of these activities, they consume an estimated 16.7 percent of the total conuco energy input.

Once the yuca plants are large enough to remove, harvesting of 100

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[5] Density is usually 1 to 3 individuals per m^2 at the first yuca planting when stem stocks must be transported to the site from varying distances, and 2 to 3 individuals per m^2 for subsequent crops when stem stocks are readily available on the site.

to 300 m^2 sections of conuco occurs every few weeks until the site is abandoned. The plants are removed from the soil by first tugging gently at the base of the stem until the roots are loosened and then pulling firmly. The roots are broken from the base of the stem by hand. The main stems and branches are then broken into 1.5 to two m sections and stacked. A portion of these stems supplies the stem stocks for the next yuca planting. The remaining stems are either given away or rot in place. Labor devoted to the harvesting process accounts for 13.4 percent of the total energy input for a two crop cycle of conuco use.

Foot travel to and from conucos depends on conuco location relative to dwelling location and on work day length. Most conucos were 1/2 to 1 hour walking distance from San Carlos. On this basis, the average conuco was considered to be 3/4 hours away from the family dwelling. The amount of time a man works in his conuco on a given day varies but is usually from 5 to 10 hours. I regarded eight hours as an average day's work and divided the total field hours worked during a two crop cycle of conuco use by eight to estimate the number of trips taken to the conuco. This number (128.9) was then multiplied by the number of hours necessary to walk to and from this hypothetical conuco (i.e., 1.5) to arrive at an estimated 193 hours spent in transportation. Implements and produce are usually carried on these trips. Walking with light loads requires intermediate amounts of energy (i.e., approximately 100 kcal per 45.4 kg human body weight per hour). Given these time and energy estimates, 6.1 percent of the total conuco energy input occurs as transportation to and from the conuco to do field work.

Table 1 shows that 1224 hours are devoted to conuco field activities during a two crop conuco cycle. This field time input corresponds to an estimated 323,150 kcal or an energy input of 264 kcal per work hour.

After the yuca roots are harvested, many hours of work are required to transform them into a palatable form.[6] This is accomplished by peeling, grating, and soaking the roots. This procedure provides a favorable environment for linase, a naturally occurring enzyme in the yuca roots, to break down a glucoside in the roots to glucose, acetate, and hydrocyanic acid. The soaking material is then squeezed to remove the water soluble hydrocyanic acid.

Table 2 shows the estimated time spent processing an amount of yuca roots equal to that produced by the first two yuca crops on Conuco Site 1. This table divides root processing into seven activities and shows the estimated energy expenditure and difficulty for each activity.

Yuca roots are peeled by scraping the skin off with a dull knife. This is light, but time-consuming work; it comprises an estimated 15.6 percent of the total conuco energy input.[7]

After peeling, the tubers are rendered into a gruel by rubbing them vigorously on a grating board. This moderately demanding work comprises an estimated 9.0 percent of the total energy input to farming. After soaking, the ground roots are squeezed dry and sifted. These operations account for 2.6 percent of the total conuco energy input.

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[6] Bitter yuca is much more common than sweet yuca (a variety of bitter yuca) in the San Carlos area conucos. When questioned, the farmers indicated that the bitter yuca stores better in the soil and is less fed-upon by insects and rodents than sweet yuca. These advantages may outweigh the greater efficiency of preparing sweet yuca for consumption.

[7] Approximately one-half of the harvested roots are soaked for two to three days before peeling. The skins of these soaked roots are readily removed by hand. Some fermentation takes place during soaking. This fermentation may lead to protein enrichment, although the local people maintain that soaking is done only to improve the flavor of the processed yuca.

Table 2. The time spent, the relative difficulty, and the energy expended in processing 7175 kilograms of yuca roots (7175 kilograms is the estimated yuca yield per ha over a two crop cycle of conuco-use).

Activity	Time (hours)	Kcal (per hectare)	Kcal (% of Total)	Difficulty
Root peeling	825	94,439	33	light
Root grating	233	54,385	19	demanding
Root squeezing	72	8,242	3	light
Sifting	66	7,551	3	light
Fire building and tending	143	16,369	6	light
Baking and frying	239	27,359	10	light
Transportation	432	74,969	26	intermediate
TOTAL	2,010	283,314		

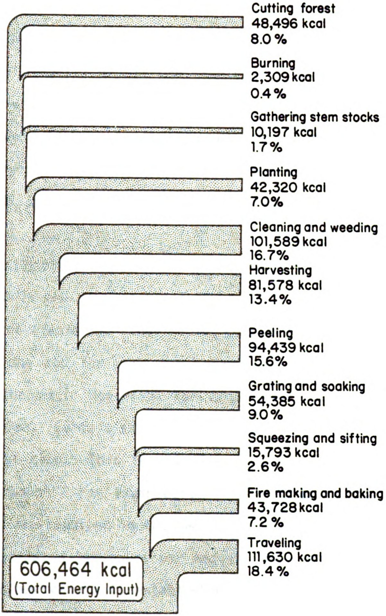
The sifted material is sometimes formed into large flat cakes, 50 cm in diameter and 1 cm thick, called "casabe," which are baked over an open fire for several minutes. Alternatively, the sifted material may be stir-fried for 20 to 30 minutes, producing a dry granular cereal called "manioco." Fire building and cooking account for 2.7 percent and 4.5 percent of the total conuco energy input, respectively.

Travel to and from the conuco for yuca processing occurs every one to two weeks. Approximately 100 kilograms of yuca roots are processed at one time. I estimated that yuca was processed 72 times based on the fact that the wet weight yield of the two yuca crops produced in Conuco Site 1 was 717.5 grams per m^2 or approximately 7175 kg per ha. Each processing requires two round-trips (1.5 hours each) by two adult women. On this basis, 432 hours are devoted to travel for root processing in a two crop cycle. Expressed in energetic terms, 12.4 percent of the total conuco energy input goes to this activity.

Figure 1 summarizes the human energy inputs to yuca crop production for a two crop cycle of conuco use in the San Carlos area. An estimated 606,464 kcal are devoted to field work and root processing activities. Slightly more energy (53 percent) is spent in field work than in root processing (47 percent). Harvesting and weeding are the field activities demanding the most energy; in combination they account for 30 percent of the total conuco energy input. The peeling and grating of yuca roots are the most energy consuming processing activities, accounting for an estimated 25 percent of the total human energy input to conuco agriculture.

Total wet weight yuca root production in Conuco Site 1 for both crops was approximately 7,175 kilograms per hectare (to be discussed

Figure 1. A summary of the human energy inputs to yuca crop production for a one ha site over a two crop cycle of conuco-use.


Cutting forest
48,496 kcal
8.0 %
Burning
2,309 kcal
0.4 %
Gathering stem stocks
10,197 kcal
1.7 %
Planting
42,320 kcal
7.0%
Cleaning and weeding
101,589 kcal
16.7%
Harvesting
81,578 kcal
13.4%
Peeling
94,439 kcal
15.6%
Grating and soaking
54,385 kcal
9.0 %
Squeezing and sifting
15,793 kcal
2.6%
Fire making and baking
43,728 kcal
7.2 %
Traveling
111,630 kcal
18.4 %
606,464 kcal
(Total Energy Input)

more fully in the next section). Based on a literature value (Montaldo, 1977), the total energy content of this yield is estimated to be 8,406,345 kcal. A total of 3234 hours was spent in conuco field and root processing activities over the two crop cycle. The estimated energy yield per man hour of work was 2602 kcal (Table 3). Hence, a man farming in San Carlos can satisfy his caloric needs with one hour of work a day. A family of six can receive its caloric needs if the husband and wife each farm for approximately two hours a day. Should the family decide to produce yuca in excess of its needs, it can sell the surplus manioco in increments of 12 kilograms for 30 Bolivars (US $7.50). Approximately 18 hours of labor would be necessary to produce these 12 kilograms.

The ratio of total energy output in the form of food to total energy input in the form of human labor for a two crop conuco use cycle is 13.9 to one (Table 3). This ratio, computed for crop one separately, is 14.8 to one and for crop two separately is 12.6 to one (Appendix Table 1). The ratio decreased for crop two because of a decrease in yuca production. Farmers sometimes abandon their conucos after harvesting the first crop. This is not always a wise strategy from an energetics standpoint. For example, post-harvest cleaning, planting, and two weedings are required in the second cropping period of conuco operation. An estimated 340 hours per hectare are needed for these activities. If a new conuco is established instead, the time necessary for cutting, burning, post-burn clearing, stem stock gathering and transport, planting, and one weeding will be 371 hours per ha. Hence, establishing a new conuco will require 31 more field hours; this extra work input may not be compensated for by higher production in the new site.

Table 3. A summary of human energy inputs and yuca crop energy outputs for a two crop cycle of conuco use.

Parameter	Unit of Measurement	Kcal
Total wet weight root production	7175 kg/ha	8,406,345[(a)]
Total field labor spent in food production	1224 hours	323,150
Total processing labor spent in food production	2010 hours	283,314
Manioco yield per man hour work	691 grams[(b)]	2,602
Ratio of energy out (i.e., yuca yield caloric content) to energy in (i.e., human energy inputs)	13.9 to 1.0	

(a) Calculated as follows:
7,175 x 1000 = 7,175,000 grams yuca roots
7,175,000 x 0.3116 = 2,235,730 grams dry weight of manioco
2,235,730 x 3.76 = 8,406,345 kcal.
One gram dry weight of yuca has 3.76 kcal (Montaldo, 1977).

(b) Calculated as follows:
.3116 x 7175 = 2235.7 kg dry weight of manioco produced
1224 + 2010 = 3234 hours spent in field and processing work
2235.7/3234 = 0.691 kilograms of manioco produced per hour human energy input

If the decision is between clearing a new site after the second yuca harvest or continuing to farm the same site for a third cropping period, the energetically correct choice is almost always to abandon, because yuca yields decline markedly and increased time must be spent weeding in the third cropping period.

Some native cultivators, however, take pride in being able to farm a site for three or even four cropping periods, even though they sacrifice labor efficiency in doing so. There may be benefits in extending the period of conuco use. For example, many kinds of fruit trees can be planted, given a longer cropping period. Conuco fruits may be the main source of some essential minerals or vitamins for the local inhabitants. In addition, longer cropping periods may maximize long term yuca production per land parcel, thus maximizing the percentage of the surrounding land in mature forest at any one time. Maintaining a high percentage of the surrounding land in primary forest may reduce disease, improve hunting, allow ready access to necessary fibers, or accomplish other desired ends. An alternative explanation is that farmers who maintain conucos for more than two cropping periods prefer to do light work (e.g., weeding) for long periods of time rather than heavy work (e.g., forest clearing) for short periods of time. They may maintain this preference even though doing the heavy work would require less overall labor energy input.

Several other studies have focused on the energetics of shifting cultivation. Watters (1971) measured the total field labor inputs at four conuco sites in northern Venezuela. Between 65 and 86 days per year were required to do all tasks in the annual cycle for a one hectare conuco. The San Carlos estimate of 64 conuco field work days per ha per crop (see Table 1) is in accord with Watters' findings. Norman (1978) using data from Clark and Haswell (1970) gathered in Africa found energy output to input ratios ranging from 7 to 37 (unweighted average 18.5) for cereal crops and from 9 to 54 (unweighted average 29.5) for non-cereal crops. Carneiro (1961) estimated that 9,880,000 kcal of yuca roots were produced per ha per crop by the Kuikuru Indians of central Brazil. This is more than two times the energy content of the San Carlos yuca crop yield. Carneiro did not detail the labor inputs necessary to achieve this yield, but he did comment that Kuikuru men only work two hours per day in the field. This suggests that the Kuikuru farming system also has high energy output to input ratios. Finally, Rappaport (1971) reported that the ratio of crop energy output to work energy input was 16.5 to one for shifting cultivators in New Guinea. Although similar to the San Carlos ratio of 13.9 to one, the energy outputs and inputs in Rappaport's study were nearly three times greater than those for San Carlos. Infertile soils are the probable cause of the comparatively low crop yields in the San Carlos region.

The high energetic efficiency at the expense of economic efficiency characteristic of shifting cultivation systems is in sharp contrast to mechanized agriculture in developed regions. Pimentel _et_ _al_. (1973) investigated energy outputs and inputs involved in corn production in the United States. Twenty-two hours of human labor were required to grow one hectare of corn in 1970. In contrast, approximately 516 hours of field labor per hectare are necessary per year in San Carlos. However, after determining the energy inputs in the form of machinery, gasoline, fertilizer, seeds, irrigation, herbicides, drying, electricity, and transportation, Pimentel _et_ _al_. estimated that the ratio of kilocalories food produced to kilocalories energy input was 2.82 to one. Most of the energy input was in the form of gasoline and fertilizer, neither of which are used in the San Carlos conucos. Human labor inputs can be reduced to a minimum in the United States because labor saving energy inputs are presently inexpensive there. However, in Amazonia, annual incomes are very low and labor saving inputs are very expensive. Given these conditions, labor-intensive systems of land use are the most sensible for this region.

Gross *et al*. (1979), in their study of the agriculture and market participation of four Brazilian Indian societies, found that the degree of participation in the external market economy by the Indian groups was related to their difficulty in making a living from slash and burn agriculture. The San Carlos area farmers must spend 384 hours to produce one million kilocalories of food. Indian groups with efficiencies in this range had become active in the market economy in the Gross *et al*. study. Wage labor and occasional construction of handicrafts are the principal ways San Carlos residents are involved in the market economy. The local people readily suspend their agricultural activities when offered outside employment. However, in the case of the San Carlos region, it is not the degradation of the habitat per se that prompts the movement from shifting cultivation to market activities (as Gross *et al*. suggest), but rather the extremely low fertility soils and low faunal numbers (i.e., the habitat is "degraded" to begin with) that prompts one to seek money as a means of improving his living conditions. When money is available, the residents normally buy guns, machetes, boats, outboard motors, and chickens (i.e., all protein related purchases).

Conuco Productivity

Table 4 summarizes yuca, pineapple, plantain, and cashew production in Conuco Site 1 for years one and two.

Yuca production

Nineteen percent of the total yuca production was leaf material. Most of these leaves (72 percent) had fallen as litter prior to yuca root harvest. Leaf production losses due to herbivory by chewing insects accounted for less than 3 percent of the total leaf production (Table 5). Cutting *et al*. (1959) suggested that one reason conucos are abandoned is because of the buildup of insect pests. The percentage of yuca leaf blade eaten on Conuco Site 1 was 2.14 percent at year one and 2.20 percent at year two (Table 5). The low damage by chewing insects and the lack of a difference between years one and two indicates that this component of the herbivore population probably does not reduce the longevity of conucos in the San Carlos region.

Stems comprised 51 percent of the dry weight yuca production over the two year period. Stem litter was estimated at 1.6 and 3.4 grams per m^2 for years one and two, respectively. Yuca roots made up the remaining 30 percent of the total yuca production. The dry weight yuca root production was 146.5 and 100.6 grams per m^2 in years one and two, respectively. A small fraction of the total root production (9.4 percent) was composed of fine roots too small to be processed for consumption.

Table 6 compares yuca root production in Conuco Site 1 with yuca root production in two nearby conucos (i.e., Conuco Sites 2 and 3) at the time of the first yuca crop harvest. Appendix Table 2 contains the regression equation used to estimate root production in Conuco Sites 2

Table 4. A summary of crop and weed productivity (grams dry weight per m^2 per year) in Conuco Site 1 for years one and two.

		Production Year 1	 Year 2
YUCA:	Leaves[(a)]	92.8	82.1
	Stems[(b)]	241.2	234.6
	Roots (large)[(c)]	146.5	100.6
	Roots (fine)	14.5	11.1
	Total	495.0	428.4
PINEAPPLE:	Leaves and stems	36.2	74.0
	Roots	0.5	1.0
	Fruits[(d)]	---	18.6
	Total	36.7	93.6
PLANTAIN:	Leaves	0.3	0.5
	Stems[(e)]	-1.8	1.9
	Roots	0.6	1.2
	Total	-0.9	3.6
CASHEW:	Leaves	1.0	2.1
	Stems	0.4	1.1
	Roots	0.2	0.6
	Total	1.6	3.8
TOTAL CROP PRODUCTION		532.4	529.4
TOTAL EDIBLE HARVEST (Yield)		146.5	119.2
WEED PRODUCTION		30.0	67.9
TOTAL CROP AND WEED PRODUCTION		562.4	597.3

(a) Leaf weights include litter production for each crop. Leaf weights of yuca include an estimate due to loss by chewing insects. Leaf weights of pineapple include the leafy tops of the fruits.

(b) All year one crop stem weights are corrected by subtracting the weight of the plantings used in establishing the plants. Stem weights of yuca include stem litter production.

(c) Roots must be processed before eating. In root processing the bark and large fibers are removed. The processed root yield is 135.3 and 92.8 grams dry weight per m^2 for years one and two respectively.

(d) Pineapple fruit weight includes an estimate of the standing crop fruit weight at two years and an estimate of fruit weight lost to frugivores.

(e) High mortality of plantlet inputs caused a negative value.

Table 5. Values for the measurements taken in the estimation of yuca leaf herbivory by chewing insects.

	Year One	Year Two
Grams total leaf production per m^2	91.2	78.7
Grams total leaf blade production per m^2	74.8	64.5
Grams total leaf petiole production per m^2	16.4	14.1
Percentage of leaf blade eaten	2.14	2.20
Grams leaf blade eaten per m^2	1.6	1.4

Table 6. A comparison of yuca root production for the first crop in three San Carlos conucos. Values are based on the survey of 30 1 x 1 m plots in each site.

	Conuco Site 1	Conuco Site 2	Conuco Site 3
Yuca density per m^2	1.5	1.8	0.8
Mean root dry weight per m^2 (grams)	170.6	177.4	98.2
Mean root dry weight per plant (grams)	115.3	100.5	116.4

and 3. The density of plants was slightly higher in Conuco Site 2 than in Site 1, but the mean dry root weight per m^2 was almost identical in these two sites. Conuco Site 3 had an unusually low density of yuca plants because the farmer had trouble securing sufficient stem stocks to plant. Nevertheless, the mean dry root weight per plant was estimated to be within two grams of that measured for Conuco Site 1. Although this is a limited sample, it appears that the first year yuca production value for Conuco Site 1 is similar to yuca production values for other conucos in the San Carlos area.

The wet weight yuca production values in Conuco Site 1 were 4.31 metric tons (m.t.) and 2.81 m.t. per ha for years one and two, respectively. Doku (1969) reported that yuca yields range from 11 to 34 m.t. per ha in Ghana. The average yield of yuca in Brazil is 12.7 m.t. per ha (Normanha, 1970). Petriceks (1968) estimated the average yuca yield to be seven m.t. per ha for northern Venezuela. The world average yuca production has been recently estimated to be 8.4 m.t. per ha (Kay, 1973). Kay indicates, however, that production can drop to three m.t. per ha on poor soils. The extreme infertility of the San Carlos soils (Herrera _et_ _al_., 1978) probably explains the low yuca production for this region.

Pineapple production

There were 0.21 pineapple plants per m^2 in Conuco Site 1 at two years. Table 4 summarizes pineapple production. The pineapple plantlet input was 26.3 grams dry weight per m^2. Leaf and stem production for the two year period was 85 percent of the total plant production. Leaf litter comprised 16 percent of the total leaf and stem production.

Estimated yearly root production was negligible, but these figures are undoubtedly underestimates of the true root production. Plant harvesting occurred during a dry spell and roots were poorly developed; I have observed that pineapple roots are well developed during rainy times of the year. Fifty-one percent of the pineapple plants had either produced fruit or were bearing fruit at the end of two years. The average wet weight per fruit, without the leafy top, was 1028 grams; the average dry weight per fruit was 180 grams. The total pineapple fruit production, not including the leafy tops, was 18.6 grams dry weight per m^2. Of this fruit production, an estimated 2.1 grams per m^2 was lost to rodents.

Plantain production

Seven plantain plants were present in Conuco Site 1 at the end of year two, giving a density of one plant per 214 m^2. Most of these individuals had produced additional stems vegetatively. Stem inputs were 2.71 grams dry weight per m^2. Because 53 percent of the stem plantings died, the input biomass exceeded the estimated year one production. By two years some of the plantain plants had reached three meters in height, but none had begun flowering. The estimated production of plantains for year two was 3.6 grams per m^2.

Cashew production

There were nine cashew plants present in Conuco Site 1 at the end of year two, or one plant per 167 m^2. Six individuals died in the first year. Plantlet inputs were 0.14 grams dry weight per m^2. Production was estimated at 1.6 and 3.8 grams dry weight per m^2 for years one and two, respectively (Table 4). No fruits were produced during the two-year study period, although several plants were flowering at the end of year two.

Weed production

Table 7 summarizes the weed biomass harvested at 10, 16, and 21 months in Conuco Site 1. Weeds comprised 5.6 percent of the total crop plant production in year one and 12.8 percent of the total crop plant production in year two.[8] Grasses and forbs increased in biomass and density after the first weeding, whereas secondary woody species, forest woody species, and lianas all declined in biomass and density with each successive weeding. Forbs and grasses are favored by weeding because they produce many wind dispersed seeds within a few months of colonization (i.e., their life cycles are shorter than the interval between weedings). In contrast to forbs and grasses, secondary woody species are weeded out before they can produce seeds locally. After several weedings the seed pool which gives rise to the secondary woody colonizers is exhausted, and the rate of long distance seed dispersal is apparently not adequate to allow continual regeneration of these groups.

Total production

The total dry weight production of crop plants was 532.4 grams per m^2 for year one and 529.4 grams per m^2 for year two (Table 4). Of this production, 146.5 grams per m^2 was the yield of edible crop in year one and 119.2 grams per m^2 was edible crop yield in year two. Year one yield was composed exclusively of yuca roots. Yuca roots made up 84

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[8] Year one weed production (Table 4) was calculated as the sum of the ten month weed harvest and one-third of the 10 to 16 month harvest; year two weed production was computed as the sum of the 21 month weed harvest, one-half of the 21 to 27 month weed harvest, and two-thirds of the 10 to 16 month weed harvest.

Table 7. The mean dry weight biomass of weedy species harvested from 27 permanent 1 x 1.5 m plots for the period 0-10 months, 11-16 months, and 17-21 months.

	Grams Dry Weight per m^2		
	0-10 months	11-16 months	17-21 months
Forbs	4.30	27.23	18.93
Grasses	0.41	9.32	8.74
Secondary woody species	5.83	3.22	1.42
Forest woody species	0.86	0.64	0.43
Lianas	4.40	2.11	0.61
TOTAL	15.80	42.52	30.13

percent of the year two yield, pineapple fruits accounting for the remaining 16 percent of the yield. There was a 19 percent decline in overall yield and a 32 percent decline in yuca yield between years one and two. A second year decline in yield is common in tropical agriculture. Tondeur (1956), working in the Belgian Congo, reported a 33 percent decline in yuca yield between the first and second crop. Popenoe (1957), in Guatemala, reported that maize yields of the second crop are often reduced to one-half those of the first crop.

Among those factors thought to cause tropical farm site yields to decline over time are: 1) herbivores; 2) weeds; 3) erosion; 4) decomposition of the organic material covering the soil; and 5) deterioration of the physical and nutrient status of the soil.

The impact of sucking insect herbivores was assessed at San Carlos using radioactive tracers (Montagnini, 1980). Her results indicate that the overall impact of this group is minor. I found no increase in the amount of yuca leaf production removed by chewing insects from year one to year two (Table 5). Hence, herbivory by insects does not appear to be an important causal factor in the second year decline of conuco yields in the San Carlos region.

Several authors have associated weeds with declining yields (Joachim and Kandiah, 1944; Watters, 1958). Kang (cited in UNESCO, 1978), working in Nigeria, demonstrated experimentally that loss of soil fertility and weed competition contributed almost equally to the decline of maize yields over time, following clearing. In San Carlos, the presence of weeds did not appear to cause reduced crop yields (provided weeding was done regularly). Total weed production for the two year period was only 9 percent of total crop production.

There is little apparent erosion during the first year of conuco use in San Carlos because a root mat shields the soil surface from the impact of rain. By the second year, however, much of the root mat has decomposed and erosion is apparent. In some areas of two year old conucos two to three cm of soil are washed away, but one also sees many areas in these conucos where eroded soil has accumulated (e.g., on the upslope side of logs). Given the abundance of slash in conucos, it is probable that most eroded soil remains within the confines of the site.

Combined with erosion effects are possible changes in soil surface organic matter, soil structure, and soil fertility. The root mat covering the soil varies in thickness from 5 to 30 cm when conucos are first planted. This root mat represents a source of readily decomposable organic matter which supplies nutrients for crop growth. After two years most of this root mat has decomposed exposing the infertile soil. Declines in conuco productivity parallel root mat decomposition. In contrast, only slight changes in soil structure and soil fertility occur over the first two years of conuco use, and therefore these factors are not thought to be important in causing reduced yields in the San Carlos region (C. Jordan, personal communication). Hence, it appears that the loss of the root mat is the most important factor causing declining crop yields in the San Carlos region. Aside from supplying nutrients, the root mat protects the soil from erosion and inhibits the establishment of weeds (see Part III of this thesis).

Succession Site Productivity

The productivity of Succession Site 1 was determined through measurements of standing crop biomass, litter production, and leaf herbivory by chewing insects. Table 8 summarizes the standing crop biomass of this site at the end of one and two years. The standing crop biomass after two years was 1175.3 grams dry weight per m^2, an amount more than 17 times greater than the year one value of 65.7 grams per m^2. All plant groups increased in biomass from year one to year two. The greatest increase was in the secondary woody plant grouping (i.e., Cecropia spp. and all other secondary woody plants) which comprised 33 percent of the total dry weight biomass after one year and 88 percent of the total dry weight biomass after two years.

The percentage of the Succession Site 1 biomass in leaves and stems changed from year one to year two (Table 8). Leaves comprised 48 percent of the total year one harvested biomass but only 23 percent of the year two harvested biomass, whereas stems increased from 36 percent of the year one to 59 percent of the year two harvested biomass. Thus the leaf and stem components of the successional vegetation do not increase at uniform rates. Ewel (1971), working in second growth stands in Panama, reported similar trends.

Table 9 compares the San Carlos standing crop biomass at one and two years with values reported in other lowland tropical succession studies. The year one San Carlos standing crop value is much lower than the one year values from Guatemala. However, the Guatemalan sites were agricultural fallows which had probably accumulated an abundant seed pool before abandonment. The standing crop biomass value reported by Jordan (1971) for an irradiated montane forest site in Puerto Rico is also greater at one year than the San Carlos value. The two year San Carlos standing crop biomass figure of 1175 grams dry weight per m^2 is more similar to literature values (Table 9).

Table 8. A summary of the standing crop biomass (grams dry weight per m^2) for Succession Site 1 at one and two years following the burn.

		Grams Dry Weight per m^2			
Plant Grouping	Plant Part	Year 1	% of Total	Year 2	% of Total
Forbs	Leaves and stems	8.4	12.8	7.9	0.7
	Roots	2.2	3.3	7.5	0.6
Grasses	Leaves and stems	2.4	3.6	18.6	1.6
	Roots	0.5	0.8	4.2	0.4
Forest trees from sprouts	Leaves	5.7	8.6	18.8	1.6
	Stems	8.4	12.8	23.9	2.0
Forest trees from seed	Leaves	0.5	0.8	1.1	0.1
	Stems	0.3	0.5	1.3	0.1
	Roots	0.05	0.07	0.2	.02
Secondary trees, *Cecropia* spp.	Leaves	8.7	13.2	172.6	14.7
	Stems	4.0	6.1	563.8	48.0
	Roots	2.2	3.3	177.9	15.1
Secondary woody trees, other	Leaves	3.1	4.7	34.2	2.9
	Stems	1.9	2.9	75.8	6.4
	Roots	1.5	2.3	14.1	1.2
Lianas	Leaves	8.8	13.4	19.3	1.6
	Stems	3.9	5.9	28.9	2.5
	Roots	3.2	4.9	5.2	0.4
Total Biomass		65.7		1175.3	
Leaves, % of total			48.0		23.0
Stems, % of total			36.0		59.0
Roots, % of total			15.0		18.0

Table 9. The standing crop biomass of one and two year old succession sites at San Carlos de Rio Negro and elsewhere in the lowland tropics.

Site Location	Grams Dry Weight per m^2 One Year	Grams Dry Weight per m^2 Two Year
San Carlos, Site 1	66	1175
Columbia, N.W.(a) (Golley *et al.*, 1975)	--	1585
Guatemala (Snedaker, 1970)(a)	836	1419
Guatemala (Tergas, 1965)	1165	--
Panama, Site 1	--	1602
Site 2 (Ewel, 1971)	--	1460
Puerto Rico (Jordan, 1971)	242	761
Africa, Congo (Bartholomew, 1953)	--	1786

(a) Only above ground biomass was harvested in these studies.

Dry weight litter production in Succession Site 1 was 39.5 grams per m^2 in year one and 317.2 grams per m^2 in year two. Leaves comprised 98.1 percent of the total litter production over the two year study period; the remaining 1.9 percent was stem litter. Ewel (1968) estimated litter production at 460 grams dry weight per m^2 for the first year on a post-agricultural site in Guatemala, and Kellman (1970), on a post-agricultural site in the Philippines, estimated litter production at 204 grams dry weight per m^2. Reports of litter production for the second year of succession are not available in the literature to my knowledge.

An estimated 1.7 and 10.3 grams dry weight per m^2 of leaf litter production were lost to chewing insects in years one and two, respectively (Appendix Table 3), while a calculated 1.7 (year one) and 9.3 (year two) grams dry weight per m^2 of the harvested standing crop leaf biomass were lost to chewing insects. Adding the leaf herbivory losses from the leaf litter and leaf standing crop fractions, an estimated 3.4 grams dry weight per m^2 were removed from Succession Site 1 by chewing insects in year one and 19.6 grams dry weight per m^2 were removed in year two. These estimates considered separately represent 4.8 percent and 3.3 percent of the total leaf production for years one and two, respectively. None of the four plant groupings had more than eight percent of their total leaf area eaten in either year (Appendix Table 3), but four-fold differences in percentage eaten occurred between some of the plant groupings indicating that specific plant life forms may be fed on differentially by chewing insects.

Summing the yearly estimates of standing crop biomass, litter production, and herbivory by chewing insects gave an estimate of net production (Table 10). Year one net production was 108.6 grams dry weight per m^2; production for year two was 1446.4 grams dry weight per m^2 or 3.96 grams dry weight per m^2 per day. These productivity values are underestimates because root turnover of plants establishing from seed, root production of sprouts, leaf and stem production losses to sucking insects, and root production losses to herbivores were not measured. The measurement of these parameters poses many problems and has seldom been attempted.

The ratio of net primary productivity to ecosystem respiration is probably below one in both years one and two because of the decomposition of large amounts of partially burned logs and stumps from the forest previously occupying the site. By about the tenth year most of this wood has decomposed and the site begins to accumulate biomass.

There have been no other studies in the lowland tropics, to my knowledge, which estimate the productivity of secondary vegetation after a cutting and burning treatment. Early succession productivity values are available from the temperate zone, but large differences in the length of the growing season and the nature of the pre-fallow disturbance make interlatitudinal comparisons difficult to interpret. Odum (1960) investigated early successional vegetation in Georgia, USA, and found that production in the first year was about 500 grams dry weight per m^2 and declined in subsequent years to about 300 grams dry weight per m^2. He attributed the high production value for year one to the presence of residual fertilizer. In contrast to Odum's findings, production in San Carlos was much higher in the second year of succession than in the first year. Several factors are important in explaining the low year one San Carlos production value: 1) the burn kills most tree

Table 10. A summary of production for years one and two in Succession Site 1.

	Production (grams dry weight per m^2)	
	Year One	Year Two
Standing living biomass	65.7	1175.3
Litter production	39.5	317.2
Herbivory loss(a)	3.4	19.6
Production, each year separately	108.6	1446.4(b)
Production, both years together	1555.0(c)	

(a)Only herbivory by chewing insects was estimated.

(b)Production for year two is equal to total production for both years minus year one production.

(c)Production for both years together is equal to: year two standing biomass + litter production for both years + herbivory losses for both years.

sprouts, thereby eliminating sprouting as an avenue for quick recovery; 2) several relatively dry months usually follow burning making it difficult for seedlings to establish; 3) seed pools are significantly depleted by the burn; and 4) the burn leaves behind a mosaic of surface types, many of which are not suitable for seedling establishment. Each of these factors is discussed in detail in Part III of this thesis.

Table 11 compares the production of Succession Site 1 vegetation with Conuco Site 1 crop plant production during years one and two. The conuco was far more productive than the succession site in year one (532 vs. 109 grams dry weight per m^2). However, in the second year this trend was reversed, the succession site producing 1446 grams dry weight per m^2 vs. 529 grams dry weight per m^2 for the conuco. In fact, the succession site production for year two alone was greater than the combined years one and two production in the conuco.

A consideration of leaf area index (LAI), leaf production, and leaf retention time helps to explain the difference in productivity between the conuco and the succession site (Table 12). Crop LAI during most of the two year study period was well below one. The yuca leaf area index at one year (i.e., just prior to harvest) was 0.62. This value is probably close to the maximum leaf area cover attainable by yuca on this site. Leaf area index for the other three crop plants was estimated at 0.083 at year one and 0.38 at year two. Leaf area index in the succession site was also less than one during the first year, but increased to 2.79 by the end of year two, giving the secondary vegetation a greater leaf surface available for photosynthesis than the conuco crops during much of the second year. In accord with this, the total leaf production in the succession site over the two-year period was 648 grams dry weight

Table 11. A comparison of year one and year two production between Succession Site 1 and Conuco Site 1.

	Production (grams dry weight per m^2)			
	Succession Site 1		Conuco Site 1	
	Year 1	Year 2	Year 1	Year 2
Production, each year separately	109	1446	532	529
Production, both years together	1555		1061	

Table 12. A comparison of leaf cover and leaf production in Succession Site 1 and Conuco Site 1 over the two year study period.

	Conuco Crops	Secondary Vegetation
Leaf area index	1.0[a]	2.79
Total leaf production over years one and two (grams dry weight per m^2), all crops	289.1	648
Leaf production as a % of total production, all crops	27	42
% of total leaf production measured as standing crop leaves	28[b]	45

[a] This represents the maximum LAI during the two year study period.

[b] Only yuca is considered in this estimate.

per m^2 vs. 289.1 grams dry weight per m^2 for the conuco crops. These values represent 42 percent of the total primary production in the succession site and 27 percent of the total crop plant production in the conuco site. In addition to producing more leaves, the succession site vegetation retained its leaves longer. Forty-five percent of the total succession leaf production was measured as standing crop leaves, while only 28 percent of the yuca crop leaf production represented standing crop leaves. Hence, three interrelated factors explain, at least in part, why the secondary vegetation was more productive than the conuco crops over the two year study period. These factors are: 1) high LAI values in the succession site in year two compared to the conuco; 2) a greater percentage of total production devoted to leaves in the succession site; and 3) longer leaf retention time for the secondary vegetation.

Prospects for Increased Yields

The results of this comparative productivity study suggest that agricultural production in the San Carlos region could be increased. The use of legumes, dry mulching, and crop breeding in a planting scheme which resembles the natural succession in structure and life form dominance offers, in my opinion, the best hope for increasing yields.

Legumes are little used in the San Carlos area. However, the cowpea, lima bean, and winged bean all do well in the wet tropics (Greenland, 1975) and their presence supplies nitrogen to the soil. Experiments done at Turrialba, Costa Rica (North Carolina State University, 1973) on the intercropping of beans with yuca showed that yuca presence did not negatively effect bean yields. Similar experiments should be conducted in the San Carlos area.

The use of dry mulching, likewise, offers promise for the San Carlos region. Rockwood and Lal (1974), working in Nigeria, found that using crop residues as mulch on traditional no-tillage farm plots increased maize yields by as much as 50 percent when compared with plowed plots. The use of a mulch of harvested yuca stems and forest tree leaves could reduce erosion, maintain soil aggregates, conserve soil nutrients, and reduce the establishment of weeds.

Crop breeding programs also could have a substantial effect on agricultural productivity in the San Carlos area. Magoon (1970) reported that inter-varietal hybridization greatly increased yuca yields in India. Many varieties of yuca are present in the San Carlos area, and some farmers have a good knowledge of varietal differences. Hence, the potential for cooperative work between breeders and knowledgeable farmers is good.

The natural succession provides a model for the construction of sustained-yield agro-ecosystems which use legumes, dry mulching, and specially bred crop plants. Sakae Oti, working in Brazil, has designed a farming scheme where all plants present from the earliest successional stage to the well developed forest are of economic value (described in Sioli, 1973). Ewel (1979) is currently developing this concept in Costa Rica by building agro-ecosystems which imitate the structure and function of natural regrowth. The life form dominance patterns of early successional vegetation in San Carlos could, and to some extent already does, serve as a model for agriculture. During the first year of succession, forbs, grasses, secondary woody species, lianas, and primary forest trees are present in one stratum and each contributes about equally to the standing crop biomass of the site (Table 8). To parallel this, conucos can first be planted with forb species (e.g., beans, pineapple), grass species (e.g., upland rice, corn, sugar cane), secondary woody species (e.g., yuca, cashew, papaya), liana species (e.g., yams, sweet potatoes), and primary forest tree species (e.g., brazil nuts, rosewood). The optimal density and pattern of plantings can be determined experimentally. By year two the fast growing woody crops form one or more additional strata above the ground layer just as secondary woody species do in two year old succession sites. Later, the primary forest tree analogs can assume dominance. This approach to tropical agriculture, by maintaining a continual crop cover, reduces the amount of nutrient loss by leaching, while providing crop yields over extended periods of time.

The theme of efficiency underlies both the energetic and productivity results presented in this study. The San Carlos conuco farmers receive an energetic return on work energy inputs of 13.9 to one; farming for one hour a day supplies their food energy needs. Introduced farming systems which do not achieve this ratio of return are inferior in energetic efficiency to the native system.

Plant nutrients represent a finite resource and agronomic systems should, likewise, be evaluated with respect to the efficiency of their nutrient use (i.e., the degree to which the nutrient capital present within a system is retained within the boundaries of that system over time). In tropical forests, most of the nutrient capital is in biomass (Kira and Shidei, 1967). If large areas of forest are cut, burned, and used intensively for many years, most of the nutrients will be lost. Many hundreds of years may be required to rebuild this nutrient capital.

In contrast, the natural successional vegetation conserves available nutrients and re-establishes mechanisms to cycle them (Ewel, 1979). Agricultural systems which mimic the natural successional systems in structure and life form dominance may be able to quickly take up a large portion of the nutrients from the cut forest and cycle these nutrients internally.

A land ethic based on the efficiency of resource use, whether the resource be energy or nutrients, will ultimately improve the quality of life in the San Carlos area, as well as assure the conservation of rain forest resources in this oligotrophic region of the Amazon Basin.

SUMMARY

An analysis of the energetics of conuco agriculture (i.e., shifting cultivation) and a comparison of productivity between conuco crops and secondary vegetation were undertaken in the Rio Negro region of the Amazon basin.

Although relatively unproductive, conuco agriculture is much more energy efficient than mechanized agriculture. The ratio of energy output in the form of processed food to energy input in the form of human labor was 13.9 to one for a two crop conuco-use cycle. Slightly more energy was devoted to field activities than to processing activities. The field activities demanding the most energy were harvesting and weeding; in combination they accounted for 30 percent of the total conuco energy input. The peeling and grating of yuca roots were the most energy consuming processing activities accounting for an estimated 24 percent of the total conuco energy input. The return per unit kilocalorie work input decreased for the second cropping period because yields declined and increasing time was spent in weeding.

Conucos in the San Carlos area are planted predominantly in yuca (*Manihot esculenta*, Crantz.). Yuca wet weight production was 4.31 m.t. per ha in year one and declined to 2.81 m.t. per ha in the second year of conuco use. The infertile soils of the region are probably the major reason for these low yields. No increase in damage by chewing insects was noted from year one to year two.

The standing crop biomass of the one year old San Carlos succession site vegetation was much lower than other reported values; however, biomass increased greatly in the second year and was similar to literature values for two year old tropical regrowth sites. Leaf herbivory of the secondary vegetation by chewing insects was low in both years, but may differ among plant life forms.

The conuco crops were more productive than the adjacent succession site vegetation during the first year after cutting and burning, but in the second year the secondary vegetation was more than two times as productive as the conuco crops. This year two difference in production is probably due to the higher leaf area index values, the greater resource allocation to leaves, and the longer leaf retention time of the secondary vegetation.

Attempts to increase crop yields should seek both to preserve the extremely favorable food energy output to work energy input ratios characteristic of the native farming system and to minimize the loss of accumulated nutrient capital present on the site after burning.

Farm practices which imitate the structure and life form dominance patterns characteristic of early successional vegetation merit attention. Planting the crop equivalents of forbs, grasses, secondary woody species, lianas, and primary forest species in a man-devised agricultural succession, combined with an increased emphasis on legumes, dry mulching, and crop breeding may represent the best hope for raising agricultural yields in this region.

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APPENDIX TABLES

Appendix Table 1. Human labor input and yuca output for crops one and two of a two crop conuco cycle.

Activity	Energy Inputs and Outputs Crop One of Two Crop Cycle (kcal)	Crop Two of Two Crop Cycle (kcal)
Cutting and burning	70,049	0
Field work	88,972	127,468
Travel (for field work)	19,132	17,529
Processing	130,060	78,285
Travel (for processing)	46,800	28,169
Total energy inputs	355,013	251,451
Yuca production energy output	5,247,668	3,158,677
Energy out:Energy in	14.8:1	12.6:1

Appendix Table 2. Regression equations and coefficients of determination used for the estimation of standing crop biomass for crop plants and for *Cecropia* spp.

Plant	Relationship	Equation	r^2
Yuca	Dia^2 x stem length vs. root wgt.	$y = .11x + 79$	.80
Yuca	Stem length vs. stem wgt.	$y = .84x + 17.8$	.88
Yuca	Leaf number vs. leaf wgt.	$y = .66x + 10.5$	.78
Plantain	Dia^2 x height vs. stem wgt.	$y = 49.3x + 1071.6$	.98
Plantain	Dia^2 x height vs. leaf wgt.	$y = 2.6x + 69.7$	.98
Plantain	Dia^2 x height vs. below-ground wgt.	$y = 22.6x + 950.3$	.97
Cecropia spp.	Dia^2 x height vs. stem wgt.	$y = .39x + 245.1$	.94
Cecropia spp.	Dia^2 x height vs. root wgt.	$y = .12x - 4.1$	.89

Appendix Table 3. Summary of the data used in estimating chewing insect herbivory losses from the leaf litter fraction of leaf production in Succession Site 1.

Plant Grouping	% of Total Litter Fall		% of Total Leaf Area Missing		Grams Dry Weight per m^2 Eaten[(a)]	
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
Secondary herbaceous	11.7	4.5	5.3	8.0	0.3	1.2
Secondary woody	79.7	82.5	3.9	2.5	1.3	6.6
Forest trees	1.0	8.0	6.1	8.0	0.0	2.2
Lianas	6.7	5.0	4.2	2.0	0.1	0.3
					1.7	10.3

(a) To illustrate how these estimates were made, I have detailed the calculation steps used in computing the year one secondary herbaceous leaf litter production loss to chewing insects.

$0.117 \times 39.6 = 4.63$ gr/m^2 = estimated herbaceous litter production in year one

$1.0 - .053 = .947$ = fraction of 1 that was left uneaten

$4.63/.947 - 4.63 = 0.26$ gr/m^2 removed by chewing insects

PART III

EARLY SUCCESSION STUDIES

INTRODUCTION

The lack of detailed succession studies in the lowland tropics and the importance of such studies was pointed out by Richards (1952) and more recently by Whitmore (1975). Many tropical succession studies have focused on species listings and general descriptions of different successional stages (Kenoyer, 1929; Stevenson, 1929; Holdridge et al., 1947; Fosberg, 1950; Grieg-Smith, 1952; Allen, 1956). Several recent investigators (Budowski, 1961; Blum, 1968; Kellman, 1970; Snedaker, 1970) have attempted to piece together succession in tropical lowland areas by looking at different-aged stands at one point in time. This approach assumes that the age of a site is the most important determinant of site floristics and structure, but this may not be the case. For example, Kellman (1970), working in the Philippines, found that above ground biomass varied by as much as five times in successional plots of the same age but with different histories of agricultural use prior to abandonment.

A second approach to the study of succession is to initiate specific types of disturbances and then to study the subsequent recovery through time using permanent plots. Symington (1933), working in Malaysia, was the first to use this experimental-type approach in studies of tropical succession. Using this method, the investigator can evaluate the effects of different factors (i.e., the treatments used) on succession. The importance of such factors as the type of disturbance, the size of the disturbance, the duration of the disturbance, and the seasonal occurrence of disturbance can be evaluated using this approach. Other factors such as the flora in the vicinity of the disturbance, the species specific dispersal characteristics of this flora, and the type and abundance of seed dispersal vectors available in the vicinity of the disturbance are more difficult to handle experimentally but certainly merit study as their influence on succession may be great.

In this study I have combined a structural and floristic description of early succession after cutting and burning in the San Carlos de Rio Negro region of the Amazon Basin with experiments designed to elucidate the factors which control this succession. To explain the observed succession, answers to seven questions were sought. The questions were:

1. Do cut forest trees have the ability to sprout?
2. What effect does burning after cutting have on sprouts and on seed pools?
3. Do the first secondary colonizers after the burn originate from wind dispersed seeds or seed pool seeds?
4. What are the dispersal strategies employed by secondary species?
5. Why are population densities so low during the first months of succession?
6. Why do population densities increase rapidly after about the fourth month of succession?
7. Can the spatial distribution of species colonizing early succession sites be related to any physical factors?

Detailed field observations and experiments were used to answer each of these questions.

I specifically chose to investigate the succession after forest cutting and burning because almost all man-induced disturbances in the Amazon Basin involve forest cutting and burning.

METHODS

Three tierra firme sites, designated as Succession Sites 1, 2, and 3 were used in this study. Figure 1 (General Introduction) gives the locations of these sites relative to the town of San Carlos de Rio Negro. The vegetation on these three sites prior to cutting was mature forest. Forest cutting in the Rio Negro region usually occurs at the beginning of the relatively dry months; burning occurs about three months after cutting. Succession Sites 1 and 2 were cut in September 1976 and burned in December 1976; Succession Site 3 was cut in August 1978 and burned in November 1978. The three sites were similar in size (0.25 ha) and slope (less than 5°).

Vegetation Development

Structural changes in the early successional vegetation in Succession Site 1 were depicted using profile diagrams. All plants present in a 1 x 20 m permanent transect were mapped, measured, and drawn to scale at 3, 10, and 22 months following the burning of this site.

Changes in plant density, species number, and species dominance were studied in Succession Sites 1 and 2 using 27 1 x 1.5 m randomly located plots in each site. Each plot was surveyed at 4, 10, 16, and 22 months. In the first survey period, all established plants (defined to be greater than 5 cm tall) were identified (by scientific name where possible), measured for height, mapped, and marked with plastic toothpicks. At each subsequent survey period all new establishments were identified, measured, and marked and all mortality of previously marked individuals was recorded.

Vegetation Development Explained

Sprouting of cut trees

The effect of a cutting treatment on succession was investigated in Succession Site 3 using 19 one m^2 permanent plots. Nine plots were located in areas of heavy slash cover; five plots in areas of moderate slash cover; and the remaining five plots in areas of light slash cover. This partitioning was in accord with the nature of slash distribution. One week before the site was burned all individuals that had established since the forest was cut (i.e., three months previously) were counted, classified as sprouts or seedlings, and tagged in each of these 19 plots.

Effects of burning on sprouts and seed pools

Peak burn temperatures were measured in each of the 19 one m^2 permanent vegetation study plots in Succession Site 3 using 10 temperature sensitive lacquers (Tempilaq, Omega Engineering, Inc., Stamford, Connecticut), having distinct melting points ranging from 38 to 593°C. These lacquers were painted on asbestos boards. Each board was set vertically with approximately 10 cm in the soil and 20 cm protruding above the soil surface.

The effect of differences in peak burn temperature on post-burn sprout and seedling establishment was investigated by resurveying the 19 one m^2 permanent vegetation study plots in Succession Site 3 three months after the burn. All pre-burn sprouts and seedlings (i.e., marked) and new sprouts and seedlings in these plots were recorded.

The effect of burning on seed pools in Site 3 was evaluated by comparing the number of seed germinations in soil samples taken from the burned site and the non-burned mature forest adjacent to the site. Each sample was 20 x 20 x 5 cm deep. One half (i.e., 10) of the burn site samples were located in areas which had experienced high burn temperatures; the other half were located in areas which were only lightly burned. All samples were spread on vermiculite or sterilized sand and set 1.7 m above the ground in a sunny location on large tables. Trays were watered daily. Contamination by wind and animal-borne seeds was checked through surveys of five trays, containing soil which had been oven dried at 250°C for five hours, placed among the sample trays under study. Trays were surveyed for new germinations three times a week for two months, after which time the soil in each tray was turned over and mixed. Surveys continued until no further germinations were found. Seedlings were identified whenever possible.

Seed source of the first colonizers after burning

To evaluate the relative contribution of the seed pool surviving the burn vs. post-burn seed dispersal in the establishment of plant cover, six sets of 2 x 2 m paired plots were established in Succession Site 3 immediately after the burn. Methyl-bromide was applied to one plot in each pair to kill the seed pool. All plots were covered with moderate amounts of slash to simulate the post-burn slash cover of the area. A survey of plant density and composition was made in all plots four months after the treatments were initiated. The degree of difference in recovery between plots not receiving the methyl-bromide treatment and those receiving it was regarded as a measure of the importance of the seed pool in recovery. To check that methyl-bromide effectively exterminated the seed pool, potted seeds of seven of the more common succession species, representing all successional life forms, were subjected to the methyl-bromide treatment. Seeds of these same seven species, not exposed to methyl-bromide, were planted in pots containing methyl-bromide treated soil to verify that the treated soil would not negatively affect the germination and establishment of post-treatment dispersed seeds.

Dispersal strategies of secondary species

The time necessary for plants to colonize cut and burn succession sites and the species composition of these sites is influenced by the dispersal strategies of the surrounding flora. These strategies were studied through observations of adaptations for mechanical dispersal in fruits and seeds and through vector capture studies. Bats were mist netted on two consecutive evenings using seven nets in the vicinity of Succession Site 1. Birds were mist netted on two consecutive mornings in the same location where bat netting occurred. Seeds in the feces of the bat and bird species caught in the nets were germinated and identified.

Low population densities during the first months of succession

The effect of short droughts (defined as two or more days without rain) on seed germination and seedling establishment was studied in Succession Site 1 using 17 randomly located 1 x 1.5 m plots. All new seedlings in these 17 plots were marked at approximately monthly intervals using plastic, color-coded toothpicks beginning 10 months after the burning of this site and continuing until the twenty-third month of succession. Attempts were made to correlate monthly rainfall totals with the number of new germinations present in each monthly survey and with seedling mortality and seedling establishment.

Rapid population increase after the fourth month of succession

Germination and establishment of seeds produced within the succession site (rather than of seeds dispersed from afar) was thought to account for the rapid population increase after the fourth month of succession. To evaluate the magnitude of short distance (i.e., within-site) seed dispersal vs. long distance (i.e., intersite) seed dispersal, 30 seed traps, each with an area of 154 cm^2, were placed in Succession Site 1 sixteen months after the burning of this site. Succession Site 1 had a complete cover of vegetation at that time. The traps were set at 2 m intervals along two transects. Thirty seed traps were simultaneously placed in a nearby freshly burned site (i.e., no vegetation present). The difference in seed numbers caught in seed traps in these two sites provided a measure of the relative importance of local vs. long distance seed dispersal.

Microhabitat preferences of secondary species

Successful establishment from seed frequently depends on the physical characteristics of the microhabitat in which the seed lands. In the San Carlos region, root mat, charred wood, and bare soil are the principal surfaces available for colonization after burning. These three surface types are sometimes in combination with slash giving a total of six post-burn microhabitats (i.e., root mat, charred wood, bare soil, root mat with slash, charred wood with slash, and bare soil with slash). The percentage cover of the root mat, charred wood, and bare soil surfaces and of slash was estimated in each of the 27 permanent vegetation study plots located in Succession Site 1. Preferential colonization of these microhabitat types by the natural flora was measured by constructing the six microhabitats in blocks in Succession Site 2. Each treatment block was located non-randomly in areas with root mat present. The root mat was removed for the two exposed soil and two charred-wood treatments. Freshly made charcoal (charcoal was used instead of charred wood to avoid seed contamination) was crushed to roughly 1 cm square chunks and placed in a 2 cm thick layer in the charred wood (hereafter referred to as charcoal) treatment. Seven 30 cm long by 3 cm diameter poles were placed in each of the three treatments receiving slash in each block. Fifteen blocks were constructed in this manner with each treatment type 30 x 30 cm in size. Two months after initiating this experiment, the height and identification of all establishments in each treatment type were recorded. Results were analyzed using a two-way analysis of variance.

To determine microhabitat preferences at the species level, seeds of seven of the more common secondary species (one grass, two forb, and four secondary woody species) were broadcast on additional sets of blocks containing these six microhabitat types. Five to seven blocks were used for each of the seven species tested. Approximately 300 seeds were placed in each treatment type within each block. Seeds were counted or measured volumetrically to ensure that uniform numbers were broadcast. The height and number of establishments in each treatment were recorded at roughly one month intervals for two to four months after the experiments were initiated.

Physical characteristics which often affect seedling establishment were also investigated in the six treatment types. Measurements of surface and soil temperature were taken at hourly intervals from 8:00 AM to 5:00 PM in each microhabitat type on three rainless days. Soil evaporation was measured by removing plugs of soil (with adjacent root mat or charcoal when present) from each treatment type and placing each plug in an aluminum container. The soil in each can was wetted to field capacity, weighed, and replaced in the field. At dusk the cans were collected and reweighed. Subtracting evening weight from morning weight gave soil water evaporation for the day for each of the microhabitats. This procedure was repeated on three consecutive days.

RESULTS AND DISCUSSION

Vegetation Development

Vegetation structure

Figure 1 shows three profile diagrams representing the plants present at 3, 10, and 22 months in a permanent 1 x 20 m transect located in Succession Site 1. These three profiles are typical of the sequence of structural development seen throughout Succession Site 1 and in other cut and burn sites in the San Carlos area. Density was low at three months but had increased sharply by the 10 month survey. There was little change in density between the 10 and 22 month surveys. However, a large change in vegetation height occurred between these survey periods. By 22 months a loose canopy of *Cecropia* was present, and vegetation cover had increased from the 10 month value of 20 to 70 percent. Boerboom (1974) reported a similar development of vegetation structure on well drained soils after cutting and burning in Surinam.

Density

Figure 2 illustrates the changes in density in different groupings of plant species over the first 22 months of succession in Succession Site 1. The first colonizers appeared five weeks after the burn. The total plant density at four months was 0.58 individuals per m^2. All of these plants were less than 25 cm tall. Forest tree species accounted for 41 percent of all individuals present at this time. By 10 months herbaceous and woody secondary species had increased rapidly relative to forest tree species and accounted for 74 percent of the total

Figure 1. Three profile diagrams representing the plants present at 3, 10, and 22 months in a permanent 1 x 20 m transect located in Succession Site 1. Only individuals more than 5 cm tall are illustrated.

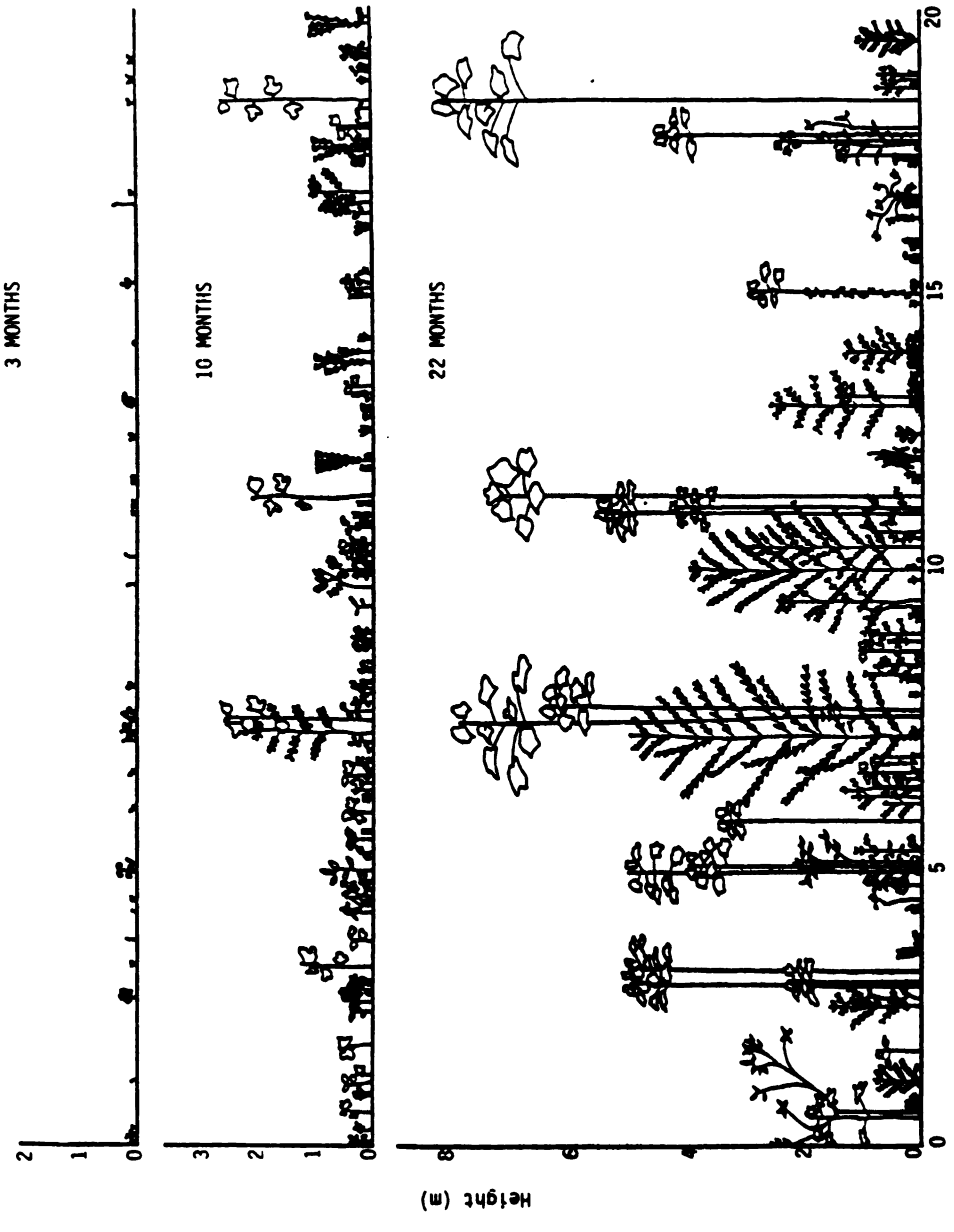
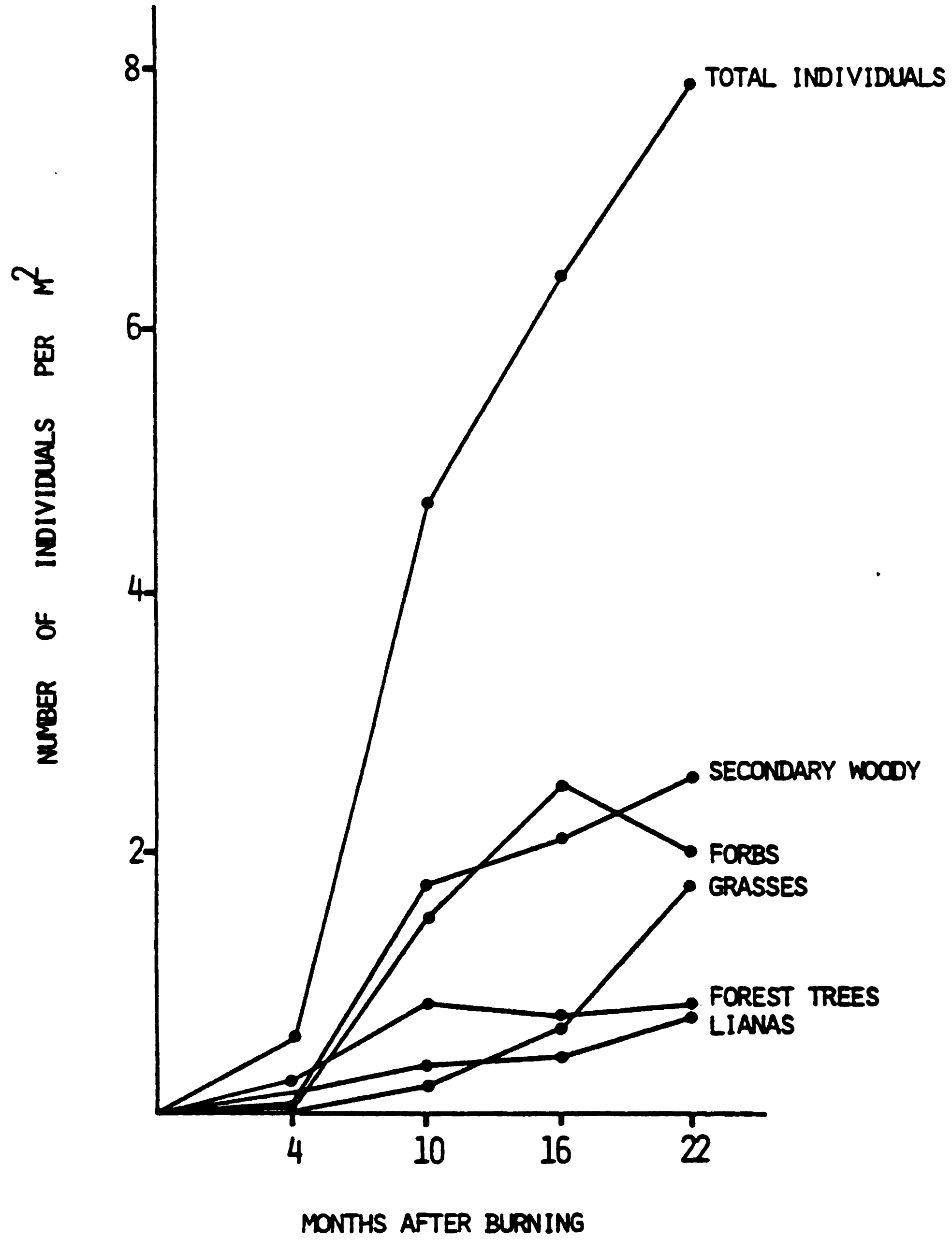

3 MONTHS
10 MONTHS
22 MONTHS
Height (m)
Distance (m)
0
1
2
3
4
6
8
5
10
15
20

Figure 2. The changes in density, for five plant groupings considered separately, and for all individuals together, over the first 22 months of succession following burning in Succession Site 1. Only individuals more than 5 cm tall were considered as established.


8
6
4
2
NUMBER OF INDIVIDUALS PER M^2
4
10
16
22
MONTHS AFTER BURNING
TOTAL INDIVIDUALS
SECONDARY WOODY
FORBS
GRASSES
FOREST TREES
LIANAS

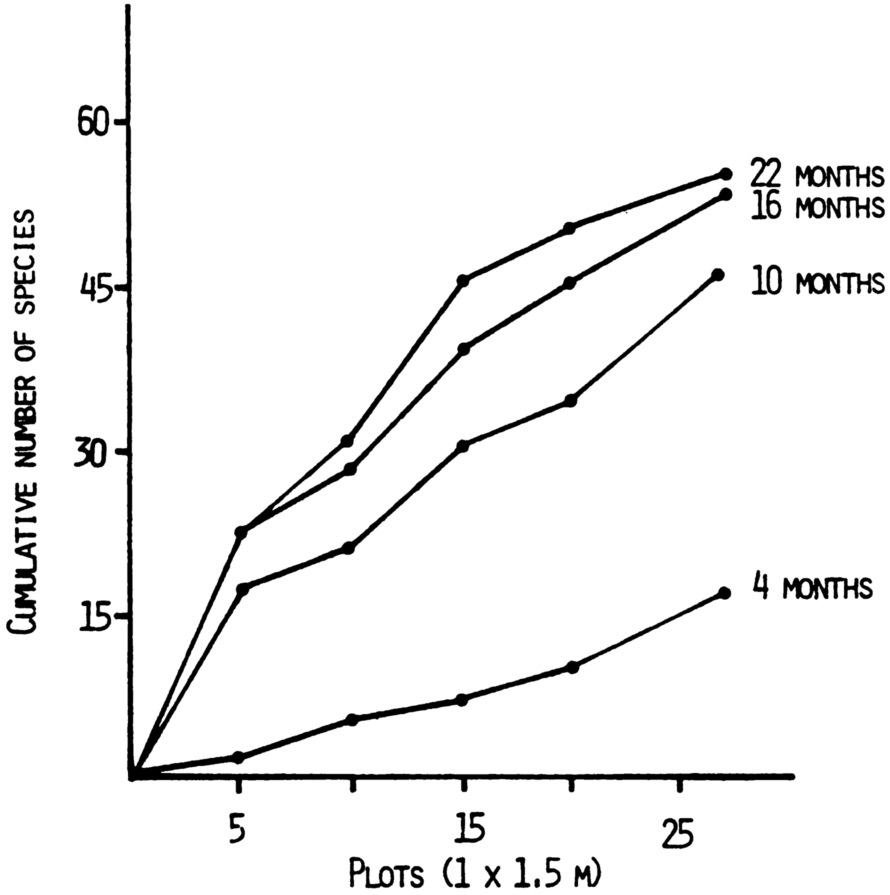
individuals present. The increase in total density after 10 months was slower. Forbs increased until 16 months and then decreased, while grass and secondary woody species numbers continued to increase throughout the study period. There was a total of 7.88 individuals per m^2 at 22 months with secondary species (i.e., forbs, grasses, and secondary woody plants) comprising 80 percent of all individuals. Forest tree species accounted for only 10 percent of the total individuals present at 22 months. The detailed results of these density surveys are presented in Appendix Table 1.

Similar to Succession Site 1, the density at four months in Site 2 was low (i.e., 0.35 individuals per m^2). The density increased to 9.33 individuals per m^2 at 10 months primarily because of heavy colonization by the monocarpic herbaceous composite, Eupatorium cerasifolium. By 16 months most individuals of this species had fruited and died causing a drop in total density to 3.81 individuals per m^2. Trends in the other plant groupings were similar to those recorded in Succession Site 1 (see Appendix Table 2). Other sites that I have observed show a pattern of density change similar to that described for Succession Site 1, although variation in detail such as that described for Succession Site 2 does occur.

Species richness

Species area curves (Figure 3), based on the survey of the 27 1 x 1.5 m vegetation survey plots in Succession Site 1, were constructed four times over the 22 month study period. At four months the species area curve had a low slope but did not appear to be leveling off. Seventy-one percent of the species sampled at that time were forest tree

Figure 3. Species area curves for Succession Site 1 at 4, 10, 16, and 22 months following the burning of this site. Only individuals more than 5 cm tall were considered.



Cumulative number of species
60
45
30
15
5
15
25
Plots (1 x 1.5 m)
22 months
16 months
10 months
4 months

or liana species. Because of the high diversity of the forest flora this curve would probably have continued with its positive slope through many more sample plots. The 10, 16, and 22 month curves increased sharply for the first five plots sampled and more gradually as the remaining plots were considered. Appendix Table 3 summarizes the changes in species number with time in each of six plant groupings (i.e., forbs, grasses, secondary woody, lianas, forest trees from sprouts, and forest trees from seed). All groupings show the same trend of increasing rapidly in species number up to 10 months and slowly thereafter. The sharp increase in total species number between the four and ten month survey parallels the abrupt increase in total plant density recorded for this time period (Figure 2).

Once a species was encountered in a survey, it generally appeared in subsequent surveys. For example, of the 46 species present in the 10 month survey, 40 were still present at 22 months. Five of the six species not present were of forest species represented by only one individual in the 10 month survey. Hence, the early successional flora (i.e., up to two years) may be best regarded as one unit or association rather than a series of associations which replace one another. Figure 4 indicates that most of the early successional flora in Succession Site 1 had been sampled by 22 months.

Species dominance

At the 10 month survey, one-half of the 46 species present in the 27 vegetation study plots (i.e., a combined area of $40.5m^2$) in Succession Site 1 were represented by only one individual (Table 1). Only four species had more than eight individuals present. Eupatorium cerasifolium, a herbaceous composite, was the only species with more

Figure 4. The change in the total number of species and in the number of newly encountered species for Succession Site 1 at 4, 10, 16, and 22 months following the burning of this site. Results are based on repeated surveys of 27 1 x 1.5 m permanent plots.

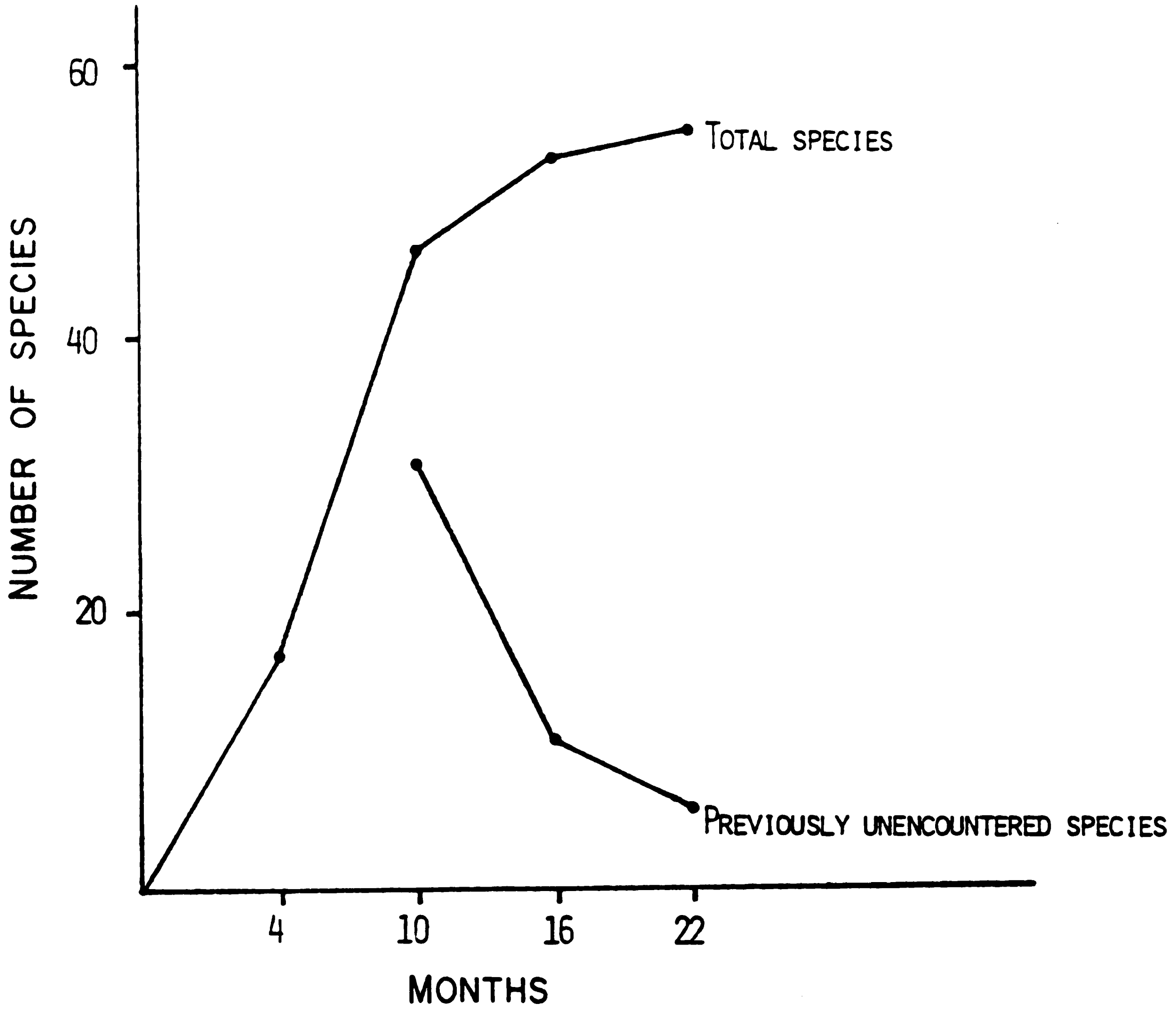

NUMBER OF SPECIES
60
40
20
TOTAL SPECIES
PREVIOUSLY UNENCOUNTERED SPECIES
4
10
16
22
MONTHS

Table 1. The number of species present in a series of abundance classes in five plant groupings. The abundance classes refer to the number of individuals, of a given species, present in the 27 Succession Site 1 vegetation survey plots (i.e., a total area of 40.5 m^2). Values are for surveys conducted 10 and 22 months after the burning of this site. Only individuals more than 5 cm tall were considered.

	Number of Species					
Abundance Classes (number of individuals)	Forbs	Grasses	Secondary Woody	Lianas	Forest Trees	Total
(a) 10 Months						
1	4	2	4	4	9	23
2-4	1	2	4	5	5	17
5-8			1	1		2
9-16	1		2			3
17-32	1					1
(b) 22 Months						
1	3	2	5	2	11	23
2-4	3		3	6	5	17
5-8	1	2	3	2		8
9-16	1	2	1			4
17-32			2			2
33-64	1					1

than 16 individuals present in the 40.5 m^2 sample area. Lack of numerical dominance was particularly evident among grasses and primary forest trees, no species having more than four individuals present.

At 22 months, many species (i.e., 42 percent) were still represented by only one individual in the sample plots (Table 1). All liana and forest tree species had less than nine individuals present at that time. Other plant groupings showed evidence of numerical dominance, however. For example, Eupatorium cerasifolium had more than one individual present per m^2. Two grass species each had more than nine individuals present in the 40.5 m^2 sample area. The secondary woody genera Cecropia and Solanum had also increased in density. Viewed in terms of biomass, Cecropia spp. was the overwhelmingly dominant genus at 22 months, accounting for approximately 78 percent of the total Site 1 living phytomass (see Part II, Table 8). The gradual increase in Cecropia spp. dominance over the first 22 months of succession was accompanied by an increase in species richness within the site. This finding suggests that the clear dominance of Cecropia spp. at 22 months did not affect species packing (given the 0.25 ha scale used in this study). If this is true, it would not conform to Grimes' (1979) conclusion that increasing dominance is associated with decreasing species richness.

Throughout the lowland American tropics, succession after burning or short fallows appears to lead quickly to a stage dominated by secondary woody species, frequently in the genus Cecropia. Kenoyer (1929), working on Barro Colorado Island in the Panama Canal Zone, noted that grasses, sedges, and herbs dominated the first months of succession followed by large-leaved monocots at one year and secondary woody species in the genera Cecropia, Trema, Ochroma, and Cordia at two years.

Snedaker (1970) noted the frequent occurrence of monodominant stands of *Heliconia* spp. and *Calathea* spp. in one year old fallows in Guatemala. These monocultures were generally overtopped by rapidly growing softwoods such as *Cecropia* spp. and *Cochlospermum* spp. in the second year of succession.

Many investigations in temperate areas have also described the first stages of succession after forest fires (Skutch, 1929; McMinn, 1951; Lynton, 1955; Lutz, 1956; Cremer and Mount, 1965). Bryophytes, ferns, herbs, and woody sprouts are the most commonly reported dominant vegetation elements in these studies. Hence, with the exception of bryophytes, which are infrequent, all the floristic elements of temperate postburn succession are conspicuous in the San Carlos recovery.

Questions Posed by the Results of the Vegetation Development Study

To fully understand the factors which control succession in the upper Rio Negro region of the Amazon basin, I found it necessary to buttress my descriptive studies of succession with further field observations and experiments. Answers to the following seven questions were sought:

1. Do cut forest trees have the ability to sprout?
2. What effect does burning after cutting have on sprouts and on seed pools?
3. Do the first secondary colonizers after the burn originate from wind dispersal seeds or seed pool seeds?
4. What are the dispersal strategies employed by secondary species?

5. Why are population densities so low during the first months of succession?

6. Why do population densities increase rapidly after about the fourth month of succession?

7. Can the spatial distribution of species colonizing early succession sites be related to any physical factors?

Vegetation Development Explained

Sprouting of cut trees

The importance of stump and root sprouting in recovery following the cutting of tropical forests has frequently been mentioned (Ducke and Black, 1953; Emerson, 1953; Sarukhan, 1964; Jordan, 1969; Snedaker, 1970). Sprouting is the most common means of regeneration after forest cutting in the San Carlos region as well. Succession Site 3 had 7.3 individuals present per m^2 three months after the mature forest occupying this site was cut. Eighty-seven percent of these individuals were of sprout origin (Table 2). Forest ground layer herbs and tree seedlings (probably present but not damaged during cutting) comprised the remaining 13 percent (i.e., 18 plants) of the individuals present in the plots. No secondary plants were encountered, indicating that cutting may inhibit their establishment. Succession Sites 1 and 2 were also dominated by tree sprouts three months after forest cutting.

In most cases, it was easy to distinguish sprouts from seed-established individuals once the plant was excavated because sprouts usually retained evidence of scar tissue where the stem had been cut by machete, as well as a characteristic stem curvature below the scar tissue where a lateral bud had grown around the cut region of the stem.

Table 2. The number of sprouts and seedlings present in 19 1 m^2 plots in Succession Site 3 three months after the mature forest occupying this site was cut.

	Sprouts	Seedlings
Total Individuals	121	18
Mean per m^2	6.37	0.95
Percentage of Total	87	13

Two additional cut-only tierra firme sites, one and two years old, were observed in the San Carlos vicinity. Tree sprouts were the dominate component of the vegetation in both of these sites. The two year site had regenerated to a height of 5 to 6 meters.

Hence, in answer to the first question posed, cutting of the forest in this region stimulates sprouting. This proclivity toward sprouting by forest trees simplifies the succession after cutting. There is only one seral stage; tree sprouts dominate the early months of succession and simply grow larger.

Effects of burning on sprouts and seed pools

Succession after the burning of a cut forest is distinct from the characteristic succession following cutting, suggesting that burning is very important in influencing succession. The burns in the San Carlos region can be very hot. The temperature reached at a given distance above or below ground in Succession Site 3 was projected to be midway between the temperature sensitivities of the pair of lacquers, one of which melted and the other of which did not melt. On this basis, the approximated mean peak burn temperature was 392°C at 7.5 cm above ground (range 148° to 593°C; s.d. = 157.0); 138° at the soil surface (range 76° to 310°C; s.d. = 62.4); and 100°C at one cm below the soil surface (range 48° to 199°C; s.d. = 44.6). The wide ranges and high standard deviations at each of these measurement points indicates that burn effects on cut sites are not spatially uniform. In accord with this, burn measurements in areas of light slash cover had surface temperatures ranging from 76° to 124°C. Surface temperatures in areas of heavy slash cover ranged from 226° to 310°C.

Literature reports of peak temperatures for slash burns differ greatly because the investigated fires have occurred under varied weather conditions and with different quantities and qualities of fuel. Brinkmann and Vieira (1971), measuring the burn temperatures of a cut second growth forest in the Manaus region of Brazil, reported surface temperatures ranging from 100° to 150°C and below ground temperatures (at 2 cm depth) ranging from 95° to 125°C. Hotter burns have been recorded in the temperate zone. For example, Isaac and Hopkins (1937) recorded temperatures of 1005°C above the forest floor and 320°C at 2.5 cm below the soil surface in coniferous forest slash fires.

There was no apparent correlation (all correlation coefficients were less than 0.3) between burn peak temperatures at 10 to 20 cm above ground, or 0 to 1 cm below ground (as measured in the 19 one m^2 vegetation study plots) and sprout or seedling density in these plots. Temperatures in all of the 19 plots may have been high enough to kill sprouts. Plant tissue is damaged or killed when subjected to temperatures in excess of 54°C for several minutes (Hare, 1961). All the Succession Site 3 burn measurement plots experienced temperatures greater than 124°C at 20 cm above the ground. Indeed, of the 121 sprouts present in the 19 one m^2 vegetation survey plots (Table 2), only one survived the burn. Furthermore, very few new sprout establishments (i.e., 0.63 per m^2) were present four months after burning. Hence, the burn effectively eliminated sprouting as a quick means of recovery.

The reason for the absence of any apparent correlation between burn intensity and the density of colonizers establishing from seed was difficult to understand, but investigations on the effects of burning on seed pool mortality provided some insights to this question. The mean number of germinations per soil sample from lightly burned areas in Succession Site 3 was 7.3 ($n = 10$) vs. a mean of 5.3 ($n = 10$) germinations per sample for areas which were heavily burned in this site. This difference was not significant ($t = 0.69$). A possible explanation for this result (and for the lack of a correlation between burn intensity and seedling establishment) is that the threshold temperatures beyond which seed mortality occurs (i.e., below 100°C for the seven most common secondary species in the San Carlos area; Uhl, unpublished data) were reached throughout Succession Site 3 at the soil surface, but that this threshold was not reached for buried seeds in either lightly or heavily burned areas. In accord with this, 14 of the 19 burn measurement plots had temperatures in excess of 124° at the soil surface, but only 2 of the 19 plots reached temperatures as high as 124°C at 1.5 cm below the soil surface.

Table 3 summarizes the seed pool germination results from Succession Site 3 and from the tierra firme forest adjacent to this site. The forest was regarded as a control from which the effects of burning on seed pools could be evaluated. There was a significant difference ($t = 7.37$; $\alpha = 0.001$) between the tierra firme forest seed pool and the postburn Succession Site 3 seed pool (samples from lightly burned and intensively burned plots pooled) indicating that burning does deplete seed pools.

Succession Site 3, sampled immediately after the burn, had an estimated germinable seed pool of 157 seeds per m^2 . Twenty-two percent of the seedlings did not grow to an identifiable stage. Cecropia spp. seedlings were the most frequent, comprising 78 percent of all identified individuals. Only two forest trees (Ficus sp.) and one herb

Table 3. A comparison between the post-burn seed pool in Succession Site 3 and the seed pool of the tierra firme forest adjacent to this site.

	Post-Burn Site	Forest Site
Number of samples	20	17
Mean number of germinations per sample(a)	6.3	30.1
Mean number of germinations per m^2	157	752
Percentage of total germinations growing to an identifiable stage	78	71
Percentage of total identified germinations, forest species	4	4
Total number of forest species	1	1
Percentage of total identified germinations, secondary species	96	96
Percentage of total identified germinations, *Cecropia* spp.	78	90
Total number of secondary species	7	6

(a) Only two contaminations (i.e., 0.4 per sample) occurred in the control trays during the three month observation period.

(Euphorbiaceae) were present. The remaining individuals belonged to six species of secondary woody plants and one species of liana.

The tierra firme forest had an estimated germinable seed pool of 752 seeds per m^2, Table 3. Cecropia spp. comprised 90 percent of all identified germinations. Four percent of the identified germinations were of forest trees, all of one species. The remaining individuals belonged to four species of secondary woody plants, three species of lianas, and one forb species. Guevara and Gomez-Pompa (1972) found 175 to 689 germinable seeds per m^2 in lowland primary forest in Veracruz, Mexico. Most of these seeds, likewise, were of secondary species. And Keay (1960), working in Nigeria, found approximately 100 germinable seeds per m^2 in forest soils there. Eighty-four percent of the germinations in Keay's study were of secondary species; 15 percent were herbs and lianas and only 1 percent were forest trees.

Hence, in answer to the second question posed regarding burn effects on early succession, burns in the San Carlos area can be very hot, reaching above ground temperatures in excess of 593°C and soil temperatures (at one cm depth) in excess of 173°C. Most pre-burn sprouts are killed by the burn, and sprout establishment is low after the burn. Seed pools, likewise, are significantly reduced by burning.

Seed source of the first colonizers after burning

Seed pool germination studies (Table 3) showed that, although burning reduces the size of the seed pool, there is still a substantial germinable seed pool (i.e., approximately 157 seeds per m^2) present following burning. The results from the methyl-bromide seed pool extermination experiment indicate that this seed pool is important in the post-burn establishment of some plant species.

A mean of 4.0 woody individuals (i.e., 1.0 plant per m^2) had established from seed four months after the burn in the non-methyl-bromide plots vs. 0.2 (i.e., 0.05 plants per m^2) in the methyl-bromide plots. This difference was significant at the 0.05 level (paired t statistic = 3.0; d.f. = 5). Fifty-seven percent of these woody establishments were in the genus Cecropia; the remaining individuals were of other secondary woody species and of forest species. Hence, it appears likely that the first woody colonizers of cut and burn disturbances in this region originate from seed pool seeds.

Grasses were present in both treatment types after four months. Means of 6.0 and 2.2 grass individuals per treatment plot were recorded in the methyl-bromide and the non-methyl-bromide treatments, respectively. This difference was not statistically significant (paired t = 0.57; d.f. = 5) providing evidence that grasses rely on post-burn seed dispersal for their initial establishment of site populations rather than on seeds present in the seed pool. This conclusion is supported by the forest seed pool germination study (Table 3) in which no grass establishments were recorded. Forbs did not establish in either treatment suggesting that they, too, are dependent on post-burn dispersal. Controls verified that seeds were killed by methyl-bromide and that seeds would germinate and grow in methyl-bromide treated soil.

These results provide an answer to the third question posed by providing evidence that post-burn dispersal is an important seed source for the initial establishment of forbs and grasses, but that the first secondary and primary woody colonizers of cut and burned sites in this region originate from seeds present in the seed pool.

Dispersal strategies of secondary species

Although most seeds produced by secondary plants appear to remain close to the parent plant, the wide distributions of many tropical weedy species indicate that means of long distance (i.e., inter-site) dispersal also exist for secondary plants (Kellman and Adams, 1970).

Many of the common forb and grass species in the San Carlos region post-burn succession have wind-dispersed seeds. In contrast, the common secondary woody species have berries (e.g., *Vismia* spp., *Solanum* spp., and *Clidemia* spp.) or multiple fruits (e.g., *Cecropia* spp.) and rely on animal vectors for dispersal. Without the aid of vectors, these fruits fall to the ground below the parent plant. Three species of bats, *Vampyros helleri*, *Artibeus* sp. and a species in the Sturniratildae were mist netted and found through feces germination tests to be transporting copious seeds of *Cecropia ficifolia* while one bat species, *Grollia perspicillata* was transporting seeds of *Vismia lauriformis*. Five species of birds were also mist netted. The three most common species in the nets (i.e., represented by 4 to 10 individuals each) were transporting hundreds of seeds of *Solanum stramonifolium* and *Clidemia sericea*. Based on this limited survey, it appears that the four dominant secondary woody plant species (i.e., in terms of numbers and biomass) rely on bats or birds for dispersal.

The role of bats and birds in the dispersal of secondary plants was noted by Beard (1945) in his successional studies on St. Vincent Island in the West Indies. More recently, Vasquez-Yanes *et al*. (1975) stressed the importance of bats in seed dispersal in the humid tropics, and Trejo (1976), studying seed dispersal in 106 frugivorous bird species in Mexico, found most bird species to be dispersing seeds of secondary species.

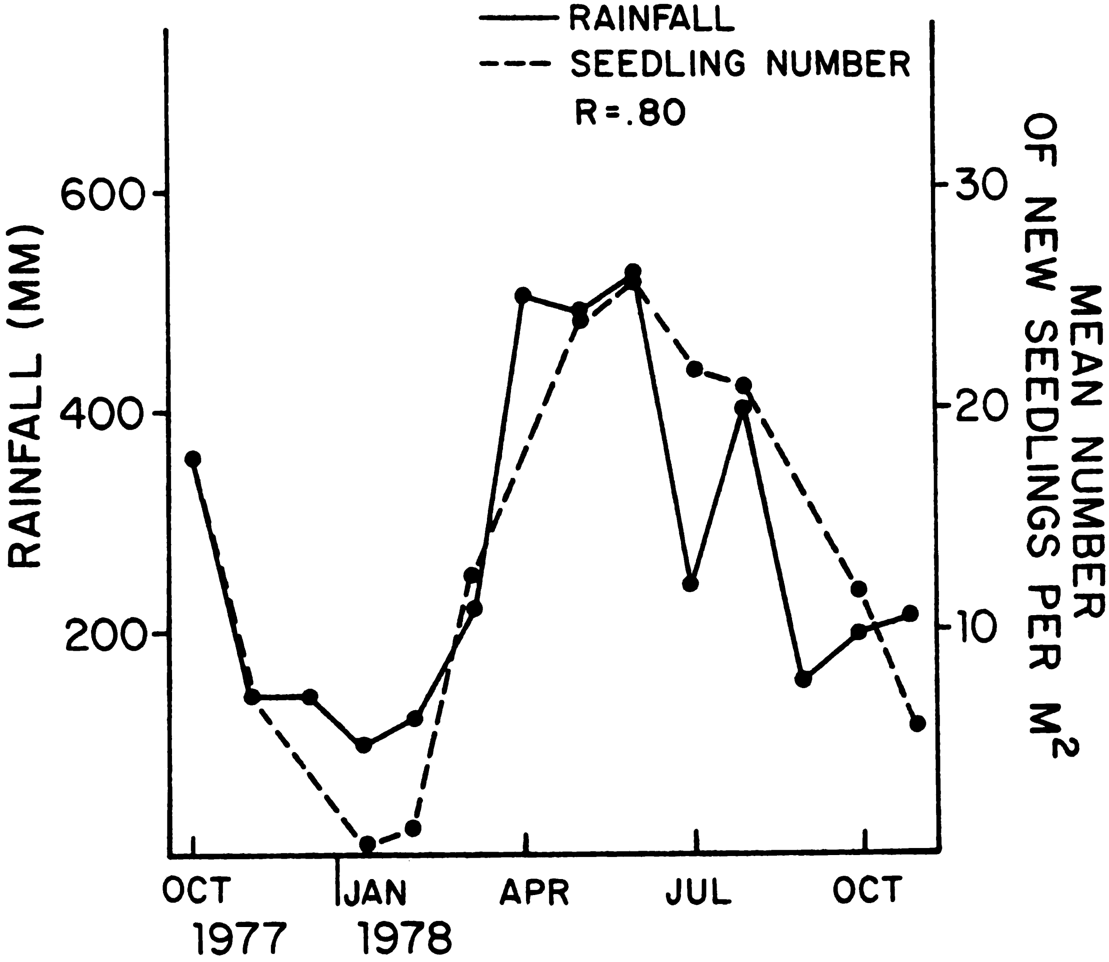
In answer to the fourth question posed, effective means of between site seed movement (e.g., mechanical or with the aid of animal vectors) appear to be incorporated into the seed dispersal strategies of most secondary species of the San Carlos region.

Low population densities during the first months of succession

Monthly rainfall is generally greater than 100 mm for all months in the San Carlos region, but a relatively dry season occurs from about October to March of each year. This period of lower rainfall is also a time of low seed germination and low seedling establishment in early successional sites. Figure 5 illustrates monthly rainfall simultaneous with the mean number of new germinations present in monthly surveys of 17 1 x 1.5 m plots in Succession Site 1 for the period from 10 to 23 months following the burning of this site. A total of 4,332 germinations were marked during this 13 month survey. The lowest number of germinations (0.31 m^2) and the lowest rainfall (101 mm) were in January 1978. The rainfall high, 524 mm, was for the month of June at which time the mean number of new germinations present (26.5 per m^2) also peaked. The correlation coefficient between monthly rainfall and the mean number of germinations present in monthly surveys for the 13 month period was .80.

Lower numbers of germinations during the drier months resulted in lower numbers of establishments at that time. In the four month period from December 1977 through March 1978 (i.e., the 12th to the 16th month of succession), seven individuals became established in the 17 plots under survey. A total of 593 mm of rain fell during this four month period. In contrast, 1763 mm of rain fell in the next four months and

Figure 5. Monthly rainfall simultaneous with the mean number of new germinations present in monthly surveys of 17 1 x 1.5 m plots in Succession Site 1 for the period from 10 to 23 months following the burning of this site.


RAINFALL
SEEDLING NUMBER
R=.80
RAINFALL (MM)
600
400
200
MEAN NUMBER OF NEW SEEDLINGS PER M²
30
20
10
OCT
JAN
APR
JUL
OCT
1977
1978

25 individuals established. The monthly rainfall for this eight month period was positively correlated with the number of seedlings marked each month which subsequently established (r = .87).

As these results indicate, seedling mortality can be reduced artificially by watering. In a separate experiment, 75 naturally colonizing seedlings in open, bare soil plots were watered and surveyed daily for 14 days and compared to 75 control seedlings (i.e., non-watered). Mortality from desiccation was 25 percent in the non-watered plots vs. 5 percent in the watered plots (significant at the 0.05 level, paired t-test).

These results provide an answer to the fifth question posed by showing that periods of relatively low rainfall reduce the rate of seed germination and seedling survivorship in cut and burn sites. Aside from the period of reduced rainfall from the 12th to the 16th month of succession in Succession Site 1, rainfall was also relatively low during the first three months of succession in this site (and in Succession Site 2 and 3 as well). The relatively low rainfall coincident with the first months of succession, in part, explains the slow initial colonization of these sites.

Rapid population increase after the fourth month of succession

The initial succession site colonizers, regardless of origin, are at very low densities during the first months of succession after burning (Figure 2). The first forb and grass colonizers on Succession Site 1 flowered and fruited from the fourth to the sixth month after burning, thereby supplying seeds locally which gave rise to comparatively dense populations of forbs and grasses. These second populations grew more slowly, flowering and fruiting toward the end of the first year of succession. Most of the seeds produced by these plants landed below the parent plant. Many of these seeds germinated but few individuals matured. Some individuals of Eupatorium cerasifolium persisted as seedlings for up to five months before dying. The few individuals that did mature from this third generation fruited at about 16 to 20 months. Further establishment of forbs and grasses after this time was restricted to exposed locations.

A similar pattern was observed in Succession Site 1 for secondary woody species. It was only after the sparsely distributed early colonizers began to flower and fruit (i.e., at about 10 months) that high population densities of secondary woody species' seedlings were recorded for this site. The magnitude of within-site seed dispersal as compared to between-site seed dispersal is reflected in the results of the seed trap study. No seeds were dispersed on to the seed traps in the freshly burned (non-vegetated) site over the two week sample period; whereas 91 seeds were captured in the seed traps placed in the 16 month old succession site indicating that approximately 197 seeds per m^2 were dispersed within this site over the two week sample period. Hence, in answer to the sixth question posed, my results, based on field observations and a limited seed trapping survey, indicate that within-site seed dispersal is important in explaining the rapid increase in population size observed after the fourth month of succession.

Microhabitat preferences of secondary species

Root mat, charred wood, and bare soil surfaces and these three surface types combined with slash comprise the principal microhabitats available for plant colonization in cut and burn succession sites in the San Carlos region. Root mat surfaces (i.e., a 5 to 30 cm thick mesh of

0.1 to 2 mm diameter roots produced by the forest trees previously occupying the site) can comprise up to 80 percent of the total surface cover in lightly burned sites. Mineral soil overlain with charred wood occurs in areas where burns are intense and large slash abundant. Bare soil surfaces occur where the root mat is thin and dry enough to burn completely. The percentage of bare soil surface increases with time because the root mat decomposes exposing the bare soil, and the charred wood is washed away in heavy rains leaving bare soil below. In the later stages of succession the root mat is reformed over the bare soil surface.

The mean percentage cover of slash and of these three surface types, as estimated in the 27 1 x 1.5 m vegetation study plots in Succession Site 1 at 10 months, were quite similar (Table 4). All three surface types and slash are clumped in distribution (Table 4). Slash clumping is the result of the felling technique practiced by local farmers whereby the toppling of large trees is used to sweep over tens of partially cut smaller trees. This procedure produces large concentrations of slash (e.g., 100 to 900 m^2) in some areas with essentially open area in between. Burning is most intense in areas of high slash concentration. These areas also have the highest charred wood surface cover and log cover after burning.

Plants establishing from seed in the 27 plots were also clumped in their distribution ($s^2/x = 3.9$, $t = 10.2^{***}$). The number of seed established plants was weakly correlated with both percent charred wood surface cover ($r = .40$) and percent slash cover ($r = .51$). Establishment was not correlated with percent root mat surface ($r = .10$) and was

Table 4. The manner of distribution of root mat, charred wood, bare soil, and slash at 10 months after burning in Succession Site 1. Values are based on the survey of 27 1 x 1.5 m plots.

	Mean (%)	s^2	$s^2/\bar{x}$	t	Distribution
Root mat surface	38.9	1104.5	28.4	99.7***(a)	clumped
Charred wood surface	27.8	473.7	17.0	57.8***	clumped
Bare soil surface	26.7(b)	726.9	27.2	94.6***	clumped
Slash cover	36.2	387.7	10.7	34.6***	clumped

(a) ***indicates $p < .001$.

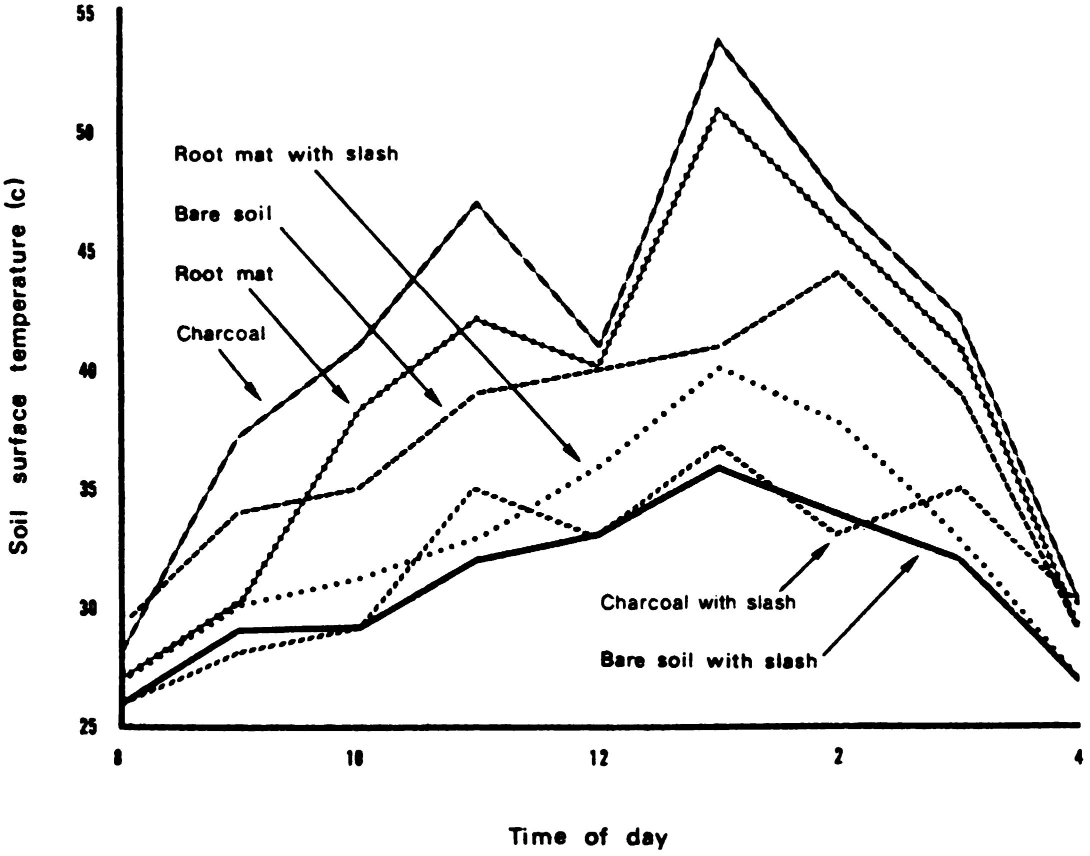
(b) The sum of the three surface cover types does not equal 100% because in some plots slash was lying directly on the ground precluding estimation of surface type.

somewhat negatively correlated with percent bare soil surface (r = -.41). Based on these distribution and correlation analyses, it appeared that locations with charred wood and slash were favored sites for establishment.

I was able to determine, in more definitive terms, the microhabitat preferences of colonizing species and the physical characteristics of the microhabitats available for colonization by constructing multiple sets of the six post-burn microhabitat types and then measuring their physical differences and the rate at which they were colonized.

With regard to physical factors, these six microhabitats differ markedly in their temperature and evaporation characteristics. Figure 6 shows the changes in surface temperature for each of the microhabitats during a typical day having a maximum air temperature of 33°C. Surface temperatures increased until 1:00 to 3:00 PM in all microhabitats and then declined steadily. The charcoal surface heated most rapidly and reached the highest temperature for any microhabitat (i.e. 54°C). The bare soil surface, a cream colored sand, was heated less than the charcoal and root mat surfaces. Accordingly, reflected light from the bare soil surface, measured in luxes, was 7.6 percent of open site light on an overcast day vs. 3.9 percent and 2.4 percent of open site light, respectively, for the root mat and charcoal surfaces. Slash presence shaded the soil surface thereby reducing surface temperatures. Light was reduced to 33 percent of open site light among the nested wood poles in the three slash treatments. The bare soil surface had the lowest temperature of the slash treatments with the root mat and charcoal slash surfaces loosely grouped at slightly higher temperatures.

Figure 6. The changes in soil surface temperature over an eight hour period in each of six microhabitat types.


Soil surface temperature (c)
55
50
45
40
35
30
25
Root mat with slash
Bare soil
Root mat
Charcoal
Charcoal with slash
Bare soil with slash
8
10
12
2
4
Time of day

Soil temperature differences (2 cm depth) were more muted for the six microhabitats, but again the three slash and the three non-slash treatments were clusterd (Figure 7). The soil temperatures of the charcoal and root mat microhabitats were slightly lower than the soil temperatures for the bare soil microhabitat; these surfaces apparently insulate the soil from direct solar radiation. No clear differences in soil temperature were present among the three surfaces with slash.

Soil evaporation (Figure 8) was greatest from the bare soil microhabitat followed by the root mat surface type and then the charcoal surface type; this order was repeated in these three microhabitat types with slash present. All but the charcoal vs. bare soil with slash and the root mat with slash vs. charcoal with slash treatment comparisons were found to be significantly different from each other at the 0.05 level [Duncan's multiple range test (DMR)] based on a two-way ANOVA. There is a close correspondence between the soil evaporation ranking by treatment type and the soil temperature ranking. Appendix Table 4 provides a summary of the physical characteristics of the six microhabitat types.

The existence of clear differences in temperature and soil evaporation among the six microhabitats suggested that differences in germination and establishment would occur for seeds dispersed on to these microhabitat types. Figure 9 shows the results of the natural colonization of these six microhabitat types over a three month period based on the survey of 15 six treatment blocks. The charcoal surface with slash had a significantly greater number of establishments ($p < 0.05$, DMR) than the other treatments, and the root mat with slash treatment had significantly more establishments ($p < 0.05$, DMR) than the three

Figure 7. The changes in soil temperature (2 cm depth) over an eight hour period in each of six microhabitat types.

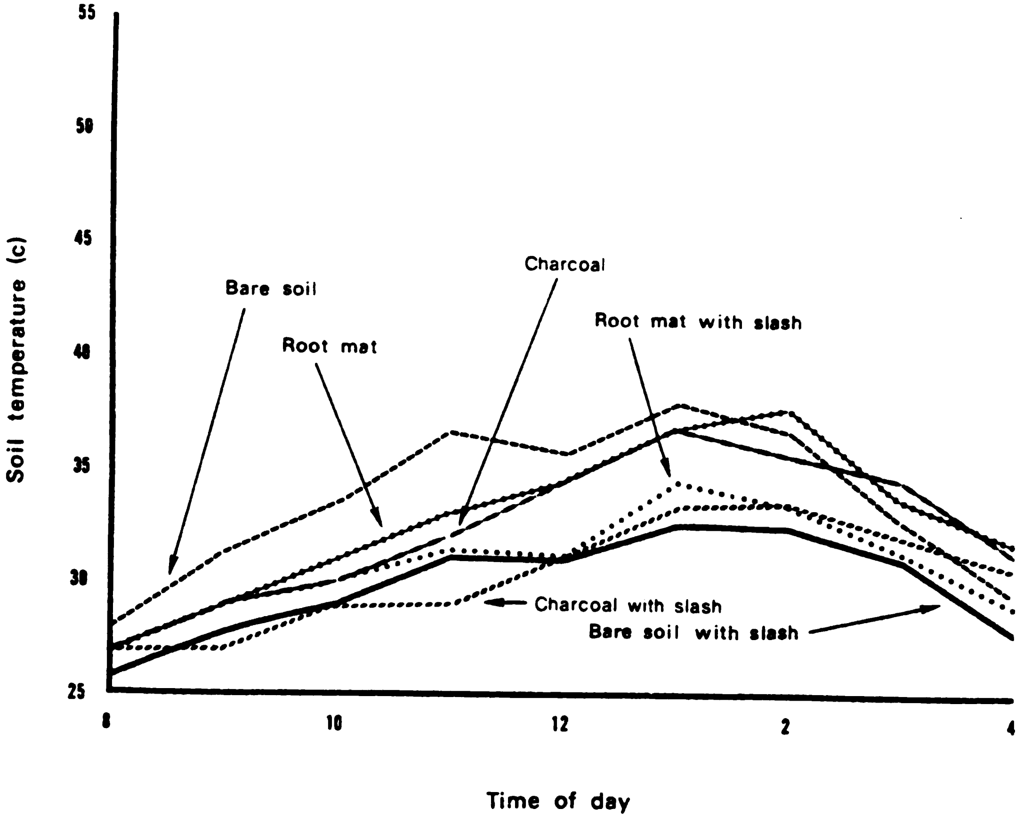

Soil temperature (c)
55
50
45
40
35
30
25
8
10
12
2
4
Time of day
Bare soil
Root mat
Charcoal
Root mat with slash
Charcoal with slash
Bare soil with slash

Figure 8. The mean amount of water lost over an eight hour daylight period from five evaporation containers placed in each of six microhabitat types.

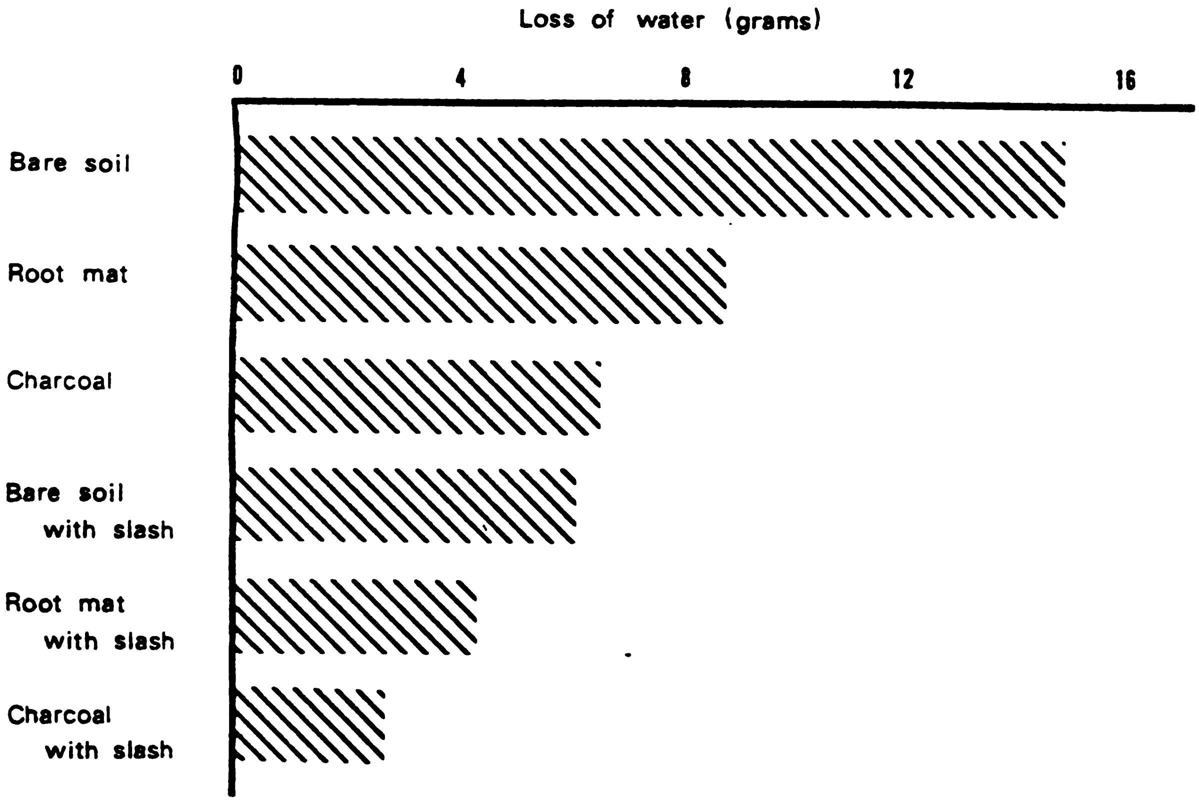
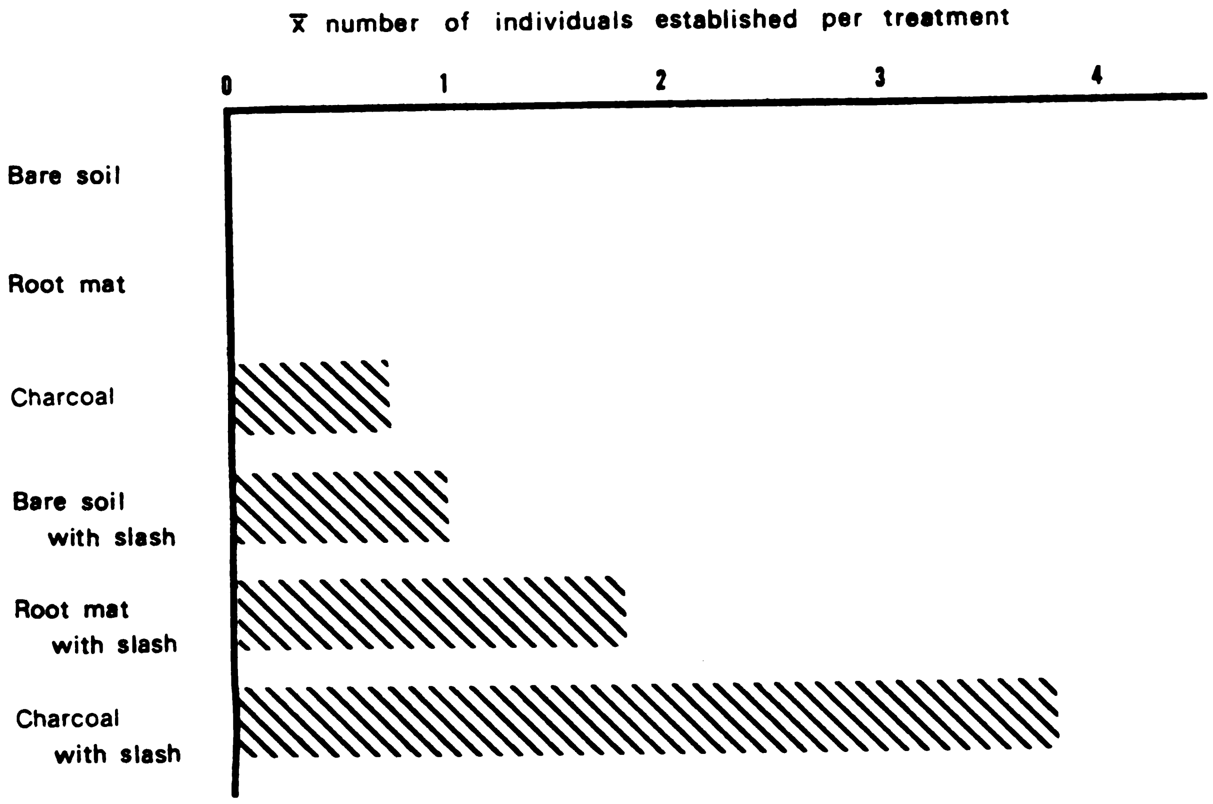

Loss of water (grams)
0
4
8
12
16
Bare soil
Root mat
Charcoal
Bare soil with slash
Root mat with slash
Charcoal with slash

Figure 9. The mean number of individuals establishing from seed over a four month period in each of six microhabitat types.

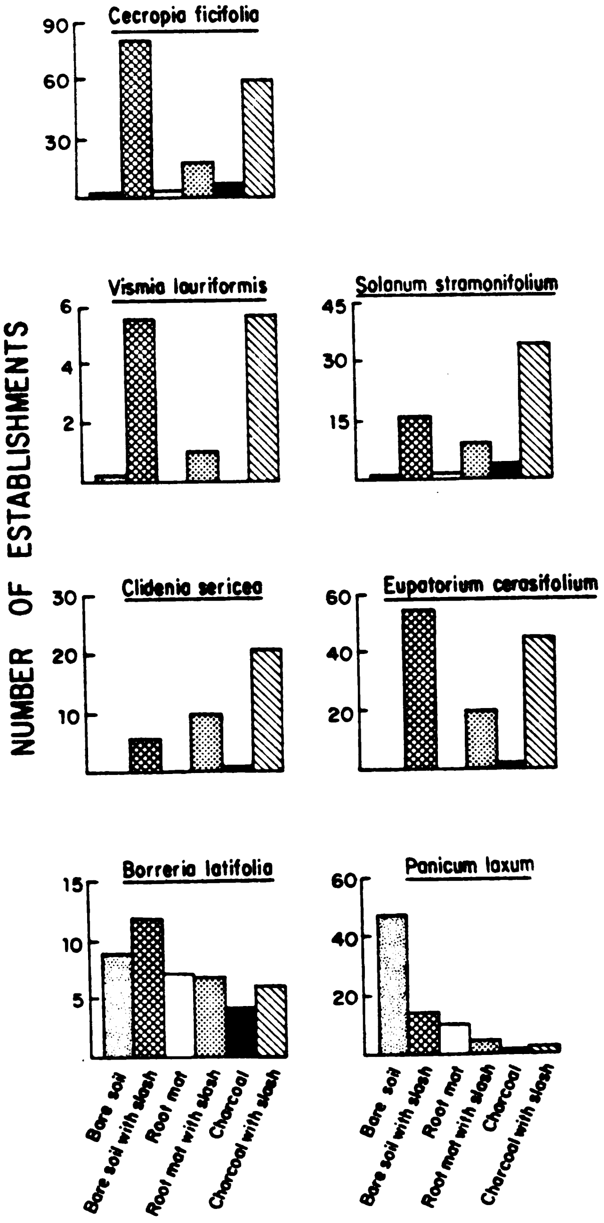

$\bar{x}$ number of individuals established per treatment
0
1
2
3
4
Bare soil
Root mat
Charcoal
Bare soil with slash
Root mat with slash
Charcoal with slash

non-slash treatments. The examination of Figures 8 and 9 simultaneously suggests that evaporation and establishment are inversely related. Where evaporation was greatest (i.e., bare soil and root mat treatments), establishment was lowest. These results, then, provide experimental evidence that the distribution of plants in early succession sites could be strongly influenced by the distribution of surface types.

The results of this microhabitat colonization experiment did not necessarily reflect the microhabitat preferences of all secondary species in the region, because only three secondary species colonized the treatment blocks during the experiment. More detailed information on species microhabitat preferences was gained by placing seeds of secondary species directly on the six microhabitat types and then checking for establishment differences. Seven of the more common secondary species were tested in this way for their microhabitat establishment preferences. Figure 10 illustrates microhabitat differences in establishment for each species.

The four secondary woody species: *Cecropia ficifolia*, *Vismia lauriformis*, *Solanum stramonifolium*, and *Clidemia sericea* and the forb, *Eupatorium cerasifolium* had their highest establishment in the slash treatments (Figure 10). *C. ficifolia* had significantly greater ($p < 0.05$, DMR) establishment in the bare soil with slash and charcoal with slash treatments than in all other treatments. V. *lauriformis*, like *C. ficifolia*, had its greatest establishment in the bare soil with slash and charcoal with slash treatment (significantly greater $p < 0.1$ DMR than in all other treatments except the root mat with slash treatment). *S. stramonifolium* had significantly greater establishment ($p < 0.05$, DMR) in the charcoal with slash treatment than in all other treatments

Figure 10. The mean number of establishments in each of six microhabitat types for seven common early successional species. An equal number of seeds (from 300 to 600 depending upon the species) were broadcast in each microhabitat type. From five to seven replicates were used for each species.


NUMBER OF ESTABLISHMENTS
Cecropia ficifolia
90
60
30
Vismia lauriformis
6
4
2
Solanum stramonifolium
45
30
15
Clidenia sericea
30
20
10
Eupatorium cerasifolium
60
40
20
Borreria latifolia
15
10
5
Panicum laxum
60
40
20
Bare soil
Bare soil with slash
Root mat
Root mat with slash
Charcoal
Charcoal with slash
Bare soil
Bare soil with slash
Root mat
Root mat with slash
Charcoal
Charcoal with slash

except the bare soil with slash treatment. *C. sericea*, likewise, showed it highest establishment in the charcoal with slash treatment, having significantly greater establishment ($p < 0.05$, DMR) there than in all other treatments except the root mat with slash treatment. The forb, *E. cerasifolium*, had its best establishment ($p < 0.1$, DMR) in the bare soil with slash and charcoal with slash treatments.

In contrast to these species, the grass, *Panicum laxum*, showed a clear preference for the bare soil microhabitat, having significantly greater establishment there ($p < 0.01$, DMR) than in all other treatments (Figure 10). Very few individuals of this species established in the three slash treatments.

The second forb species tested, *Borreria latifolia*, showed the least microhabitat preference of all species tested (Figure 10); no significant differences between treatments were detectable at the 0.1 level (DMR) for this species.

Other investigators have found species distributions to be correlated with microhabitat distributions [e.g., Bratton (1976) in temperate deciduous forest herbs and Grime (1979) in temperate pastures on shallow soils over fissured limestone]. Ultimately, there were differences in the number of establishments in the six microhabitat types for a given species because of differential germination of seeds and/or differential mortality of seedlings. Differences in germination among the field treatments used may have resulted from different frequencies of favorable germination microsites. The moisture, temperature, and surface roughness of the six treatments were different, and these factors probably determined the number of safe germination sites. Harper and Benton (1966), in an experiment where they placed seeds of three species on sinter plates with water under different tensions, showed that seed germination, for the species tested, was related to the percentage of the total seed surface area in contact with the sinter plate and the evaporating power of the atmosphere. Differences in seed surface area for the species used in the San Carlos experiment are reflected in differences in seed weight for these species which sometimes exceeded an order of magnitude (Table 5).

Once seeds germinate, their establishment differs depending on the microhabitat they are in. For example, establishment was very low in the root mat treatment for all species tested. Seeds entrapped in the root mat may germinate several cm above the soil surface under favorable moisture conditions but die before the hypocotyl penetrates the soil below. Those seeds that sift through the root mat and germinate in contact with the soil may not have sufficient starch reserves to grow through the root mat to the lighted environment above. It is also possible that germination or growth inhibitors are present in the dead roots comprising the root mat. Ooyama (1954) found that extracts of unburned litter inhibited germination and seedling growth for some tree species.

The seven species tested also had low establishment in exposed charcoal microhabitats, but establishment was generally high on the charcoal surface with slash. Charcoal acts to increase surface temperature, but reduces soil temperature and evaporation. Charcoal can also increase soil pH (Tyron, 1948). I frequently noted wilted and dried seedlings in the charcoal treatments. The establishments that do occur in this treatment probably result from seeds landing in moist microsites, germinating, and then growing quickly during relatively cool wet

Table 5. Factors related to germination and establishment in seven common secondary species occurring after cut and burn disturbances.

Species	Factor	
	Dry Weight (mg) per Seed (n = 160)	Hypocotyl Length (cm) before Cotyledon Emergence (n = 15)
Cecropia ficifolia	0.5	0.9
Vismia lauriformis	--[(a)]	0.7
Solanum stramonifolium	1.0	4.1
Clidemia sericea	0.05	0.2
Borreria latifolia	0.7	2.6
Eupatorium cerasifolium	0.05	0.2
Panicum laxum	0.1	0.5

(a)Data not available.

periods.

Establishment was high in the bare soil with slash microhabitat for all secondary species tested presumably because the short hypocotyls of these species can enter the soil directly while receiving protection from direct solar radiation. Establishment was low in the exposed bare soil microhabitat for all species tested except the grass, P. laxum. The extremely wet period (there was rain on 21 consecutive days following the broadcasting on the grass seeds) during which this experiment was conducted probably influenced the outcome. Seeds of this same grass species were re-broadcast in each of the six microhabitat types during drier weather with almost the opposite results. At this time, there were over 100 establishments in the bare soil with slash treatment and only three establishments in the exposed bare soil treatment; establishments were also higher in the charcoal with slash treatment than in the charcoal treatment. No establishments occurred in the root mat treatments. Heat probably promotes germination in this species. During rainy periods the wet slash microsites may be too cool for establishment. During drier periods, however, these slash microsites are warmer, yet moist, and stimulate germination. Hence, during rainy periods some species may be able to colonize exposed microhabitats where they are unable to establish during drier periods.

I hypothesized that species with heavier seeds (larger endosperm) and long hypocotyl lengths before cotyledon emergence would be at an advantage in the exposed microhabitats, and that species with lighter seeds and shorter hypocotyles would be restricted to the slash microhabitats. The two species with the lightest seeds and shortest hypocotyles (C. sericea and E. cerasifolium) were largely restricted to the slash microhabitat as predicted (Table 5). However, _S_. _stramonifolium_, the species with the heaviest seeds and longest hypocotyles, did poorly in the exposed microhabitats. _B_. _latifolia_ (the species with the second heaviest seeds) had good establishment in these non-slash plots. _B_. _latifolia_ seedlings which were germinated in petri plates appeared to have contractile roots. This attribute may contribute to the success of this species in the exposed microhabitats.

The seventh question that I sought to answer in this investigation was: can the spatial distribution of species colonizing early succession sites be related to any physical factors? The results of these experiments strongly indicate that, given ample seeds, the distribution of secondary species after a cut and burn disturbance is predictable from a knowledge of the microhabitat distribution within the site. Of the three surface types, the bare soil was the most preferred and the root mat the least preferred for establishment. Secondary woody species had their highest establishment in the slash microhabitats; whereas the grass species studied established best in the exposed microhabitats. One of the forb species tested showed no microhabitat preference and the other forb studied established best in the slash microhabitats. A knowledge of seed germination triggers, seed weight, and seedling morphology (e.g., hypocotyl length) may help in predicting which microhabitat a species may best be able to colonize. It is further suggested that microhabitat preferences may differ for some species depending on whether dispersal onto a given microhabitat occurs during a rainy or a dry period.

SUMMARY

Vegetation Development

An investigation of changes in vegetation structure, plant density, and species richness was conducted during the first 22 months of succession after the cutting and burning of mature tierra firme forest sites in the Rio Negro region of the Amazon Basin. Very few plants established during the first four months after burning. The density of secondary woody plants, grasses, and forbs increased sharply from the fourth to the tenth month following burning. There was less change in plant density between the tenth and twenty-second month, but a large change in vegetation height occurred during this time. By the 22nd month of succession a loose canopy of *Cecropia* was present, light at two meters above the ground had been reduced to 26 percent of full sunlight, and the percentage vegetation cover had increased from the ten month value of 20 percent to 70 percent.

Species number increased rapidly from the fourth to the tenth month. Once a species was encountered in a survey it was generally present in subsequent surveys. By 22 months, most of the early successional flora present in the site under study had been sampled using 27 1 x 1.5 m permanent plots. This early successional flora is perhaps best regarded as a single association.

Species dominance was not apparent during the first year of succession, only one species having more than 16 individuals present in a 40.5 m^2 sample area (i.e., 27 plots), but by 22 months *Cecropia* spp. was the dominant genus on the sites (accounting for 78 percent of the total living phytomass in Site 1). The clear dominance of Cecropia at 22 months did not affect species packing on the 0.25 ha scale used in this study.

Vegetation Development Explained

Many tree species of the tierra firme forest are stimulated to sprout when they are cut. Hence, after the forest is cut there is a quick, single seral stage return to forest via sprouting.

Burning after cutting changes the nature of succession dramatically. Burn temperatures are high enough to kill most sprouts and to reduce, significantly, the size of the seed pool. The first secondary woody colonizers after burning were shown to arise from seed pool seeds, while the first forb and grass colonizers arose from seeds dispersed onto the site after the burn. The common secondary woody species had bat and bird dispersed seeds while many grass and forb species had seeds with adaptations for wind dispersal.

Population densities were low during the first months of succession because of the low number of propagules present and because relatively low rainfall during this period reduced the rate of seed germination and seedling survival. Population numbers increased sharply after the fourth month of succession because many of the initial colonizers began to set seed locally at this time.

There were six distinct microhabitat types present on post-burn sites. These microhabitat types were different from each other in soil temperature and soil evaporation. Most species tested showed clear microhabitat preferences. Hence, the actual spatial distribution of species within secondary sites was somewhat predictable from a knowledge of the distribution of these microhabitat types.

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APPENDIX TABLES

Appendix Table 1. The number of individuals per m^2 in five plant groupings at 4, 10, 16, and 22 months following the burning of Succession Site 1. Only individuals more than 5 cm tall were considered.

Plant Grouping	4 Months	Number of Individuals per m^2		22 Months
		10 Months	16 Months	
Forbs	0.06	1.49	2.45	2.00
Grasses	0.00	0.20	0.64	1.75
Secondary woody	0.10	1.75	2.10	2.57
Lianas	0.18	0.37	0.47	0.74
Forest trees	0.24	0.83	0.74	0.82
TOTAL	0.58	4.64	6.40	7.88

Appendix Table 2. The number of individuals per m^2 in five plant groupings at 4, 10, 16, and 22 months following the burning of Succession Site 2. Only individuals more than 5 cm tall were considered.

		Number of Individuals per m^2		
Plant Grouping	4 Months	10 Months	16 Months	22 Months
Forbs	0.02	6.77	1.85	1.41
Grasses	0.02	0.07	0.07	0.24
Secondary woody	0.00	0.96	0.75	1.81
Lianas	0.11	0.47	0.55	0.48
Forest trees	0.20	1.06	0.59	0.80
TOTAL	0.35	9.33	3.81	4.74

Appendix Table 3. The change in species number in six plant groupings over the first 22 months of succession after a cutting and burning disturbance. Results are based on the survey of 27 1 x 1.5 m permanent plots located in Succession Site 1. Values in parentheses represent the number of species in each life form not encountered in previous surveys. Only individuals more than 5 cm tall were considered.

		Number of Species		
Plant Grouping	4 Months	10 Months	16 Months	22 Months
Forbs	2	7 (5)	10 (3)	9 (1)
Grasses	0	4 (4)	6 (2)	6 (1)
Secondary woody	3	11 (8)	13 (2)	14 (1)
Lianas	7	10 (3)	10 (1)	10 (0)
Forest trees (established by sprouting)	5	12 (9)	12 (3)	14 (3)
Forest trees (established from seed)	0	2 (2)	2 (0)	2 (0)
TOTAL	17	46 (31)	53 (11)	55 (6)

Appendix Table 4. A physical characterization of the six principal microhabitat types present after the cutting and burning of tierra firme sites in the San Carlos region.

	Microhabitat Types					
Measurements Taken	Bare Soil	Bare Soil and Slash	Root Mat	Root Mat and Slash	Charcoal	Charcoal and Slash
Mean daylight surface temperature(a)	36.7	30.9	38.2	32.8	40.8	31.8
Mean daylight sub-surface temperature	33.5	29.8	32.7	30.6	32.2	30.2
Evaporation per cm^2 of surface (gr)(b)	0.16	0.06	0.07	0.04	0.07	0.03
Direct light (as % of full sunlight)	100.0	33.0	100.0	33.0	100.0	33.0
Reflected light (as % of direct light)	7.6	--	3.9	--	2.4	--

(a) Values for both surface and subsurface temperatures are based on one day's measurement

(b) Values are based on measurements for a one day period (8:00 a.m. to 5:00 p.m.). Each microhabitat had five replicates.

EPILOGUE

This thesis has focused on forest, agricultural, and successional environments in the upper Rio Negro region of the Amazon Basin in Venezuela. Each study could be extended to provide a fuller understanding of the tropical environments investigated.

The description of forest composition and structure (Part I) gave a static view of the tierra firme forest with a suggestion of processes provided by seedling establishment and mortality studies, gap mapping, and size-class distribution analysis. A full understanding of the tree population dynamics of the Amazonian forests can only be achieved through long-term studies of large permanent plots. In addition, detailed investigations of dormancy, seed germination requirements, seedling growth requirements, breeding systems, and dispersal mechanisms need to be undertaken for the dominant species in Amazon forest communities. Very little is known of the ecology of these species. No doubt, there are many different ecological strategies which provide solutions to the problems posed by a rain forest existence. Finally, we need to begin studying below ground forest structure and function. Certainly many of the approaches used to characterize forest structure above ground could be modified for use in describing below ground forest structure. Root morphospecies can often be distinguished on the basis of color, branching, bark, and exudate. It is important for our understanding of forest functioning to know the rooting depth of trees, the degree of root species packing, and the amount (if any) of root stratification.

Parts II and III of this thesis focused on disturbed environments, both farming and successional. The Food and Agricultural Organization (FAO) of the United Nations estimates that about 40 percent of the tropical forests of the world have been destroyed in the last 150 years. There may be only small patches of this once massive belt of forest left by the end of this century. Meanwhile, populations continue to increase very rapidly in tropical countries. The annual increase in population size for Latin America is 2.7 percent; this is the highest growth rate for any major geographic area. Yet the volume of food production in Latin America is barely keeping ahead of population growth. As their population increases, South American countries are looking increasingly to the Amazon Basin as a source of crop and grazing land. Already Brazil has embarked on an ambitious program to resettle farmers from more arid regions into Amazonia.

Before attempts are made to farm Amazonia on a large scale, the native agricultural system should be studied in detail. The indigenous farmers have a broad knowledge of farming based on generations of natural experimentation. Agronomist and land-use planners have much to learn from these native farmers.

Much applied research on a local scale is also needed. In the entire Amazon Basin (one-half the size of the United States) there are only ten experimental stations, some with only one researcher with as much as a high school education. Yet there is a great diversity of ecosystem types in the Amazon Basin. Annually flooded varzea forest occupies 1-2 percent of Amazonia. Flooding results in the deposition of nutrient-rich silt while eliminating pests and weeds. With the use of dikes and annual crops, these areas offer high agricultural potential. In addition, isolated areas of high soil fertility are scattered among the senile oxisols and could be farmed intensively. There are also islands of savanna within the forest which could be effectively used for cattle grazing. Perhaps the best potential for development lies with the waterways. There are 20,000 miles of navigable rivers present in Amazonia and approximately 2,000 fish species present (the world's richest fish fauna). Improved fishing techniques and fish culture could probably multiply fish production several fold.

The area with the least potential for profitable agricultural development is the tierra firme forest on nutrient-poor soils. However, the vast extent of this forest type demands that ways of use also be investigated. The killing of large non-economic trees in situ will increase the growth of species desirable for their fruit, latex, resin, oils, pharmaceuticals, etc. Canopy harvesting for tree species rich in protein should also be investigated.

We need to operate from the premise that the continued clearing of Amazonian forests is inevitable as long as the environmental consequences of forest clearing are unclear. Hence, we need to design our research along applied lines. Studies of the effects of forest clearing on local climate should receive high priority. Succession studies should include investigations of the effects of small vs. large scale disturbance and bulldozer scraping on recovery. Life history studies of secondary species should be emphasized as much as studies of primary forest species. Through an understanding of the biology of the important species will emerge an understanding of observed processes.

The International Amazon Project at San Carlos de Rio Negro is providing one example of how basic research with an emphasis on application could help to shape developmental policy. Workers with a wide range of expertise have investigated the structure and function of the natural forest ecosystem and then measured the effects of disturbance on ecosystem functioning. The results are providing planners with a concrete indication of the effects of human disturbance in the Rio Negro region. Attention now needs to be focused on ways in which this environment can be used without being irreparably destroyed.

By restricting themselves to esoteric questions, biologists surrender all power that they might have to temper development or to ensure that development be pursued wisely. Presenting government decision makers with a list of 50 rare species, some of which are biologically interesting or aesthetically pleasing, will have no effect on a policy maker in a country struggling under the burden of rapid population growth, food and energy shortages, and runaway inflation. If, on the other hand, decision makers are provided with information on the ecological consequences of different development plans, they can use this information in land-use policy decisions. At the very least our obligation is to supply relevant facts, not emotional entreaties.