To the Graduate Council:

I am submitting herewith a dissertation written by Juan Guillermo Saldarriaga entitled "Forest Succession in the Upper Rio Negro of Colombia and Venezuela." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

Herman H. Shugart, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Vice Provost
and Dean of The Graduate School

FOREST SUCCESSION IN THE UPPER RIO NEGRO OF COLOMBIA AND VENEZUELA

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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Juan Guillermo Saldarriaga

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ABSTRACT

Woody vegetation from 23 forest stands along the Upper Rio Negro of Venezuela and Colombia was sampled in 1982. Stands were selected from the tierra firme forests to represent a chronosequence of succession following "slash-and-burn" agricultural practices. The objectives of this study were to examine the hypothesis that the Amazon forest has been largely undisturbed since the Pleistocene, to quantify vegetation development during different stages of succession following agricultural development, and to determine the time required for a successional stand to become a mature forest.

The ubiquitousness of charcoal in the tierra firme forest indicated the presence of fire associated with extreme dry periods and human disturbances. Charcoal amounts ranged from 3 to 24 t/ha, and the dates of charcoal from radiocarbon determinations ranged from approximately 6200 years before present (B.P.) to the present. Several sample dates coincide with dry phases recorded during the Holocene for central Amazonia. Ceramic shards were found at several sites, and thermoluminescence analyses indicated that their age ranged from 3750 to 460 years B.P. The substantiated age of the charcoal and shards confirms that the region has been subjected to fire and human disturbances.

Changes in species composition, vegetation structure, and woody biomass were studied on 19 abandoned farms and four mature forest stands. The number of tree species per stand ranged from 33 to 96 in

900-m^2 plots. On 2.1 ha of cumulative stand area, $\sim$ 290 tree species $\geq$ 1 cm dbh were identified.

The distribution of stems by size class showed that 76 to 95% of the trees are within 1 to 5 cm dbh. Trees $\geq$ 40 cm dbh were found only in stands 40 years and older, representing < 1% of the total stems. Basal area ranged from 11.12 m^2/ha for a 10-year-old stand to 36.95 m^2/ha for a mature forest.

Living and dead biomass for the trees and their components was determined by regression equations developed from measurements of harvested trees. Total living aboveground and belowground biomass ranged from 51 t/ha for a 10-year-old stand to 336 t/ha for a mature forest. Belowground biomass ranged from 7.4 t/ha for a 10-year-old stand to 64 t/ha for a mature forest. Belowground root biomass was greater in mature forests than in any successional stands.

The rate of recovery of floristic composition, structure, and biomass following disturbance is relatively slow. Aboveground dead biomass remained high 14 years after the forest was disturbed by the agricultural practices. The lowest dead biomass is reached 20 years after abandonment, and the largest values are found in mature forests. Data analysis of 80-year-old stands showed that the species composition approached that of a mature forest. Approximately 140 to 200 years was required for an abandoned farm to attain the basal area and biomass values comparable to those of a mature forest. The results of this study indicate that recovery is five to seven times longer in the Upper Rio Negro than it is in other tropical areas in South America.

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CHAPTER 1

BACKGROUND AND OBJECTIVES

INTRODUCTION

Tropical forests cover approximately 12 million square kilometers of the earth of which 57% are in Tropical America (Technologies to Sustain Tropical Forest Resources 1984). These areas are being logged or converted to agriculture, forest plantations, pasture, etc., at a rate of 70,000 to 200,000 square kilometers per year (FAO/UNEP 1981, National Academy of Science 1980). Most disturbed areas are abandoned after 1 to 8 years and begin the process of regeneration. The rate of succession depends on the intensity of past use, the size of the area affected, and the soil characteristics of the original system.

This research focuses on forest succession following slash-and-burn agriculture in parts of the tropical rain forest of the Amazon Basin. The research area is located along the Upper Rio Negro near San Carlos, Venezuela, and San Felipe, Colombia. Each year many 0.5- to 2-ha forested areas are cut, burned, and cropped for 2 to 4 years and then abandoned for more than 10 years. This land represents a large area of rain forests being used for shifting cultivation (swidden agriculture). The work described in the following chapters documents the succession of forest vegetation in these cultivated plots, called "conucos" while being cultivated and "rastrojos" (fallows) after abandonment. The research that will be discussed is particularly relevant, since shifting cultivation is one of the major

agricultural systems of the world, involving more than 140 million people (National Academy of Sciences 1980).

Succession in tropical rain forests has been explained according to concepts introduced by Clements (1916). Theoretically, given sufficient time after disturbance, a fallow develops the structure, function, and complexity of a mature forest (Margalef 1963, Odum 1969, Harris 1972). This generalization has emerged in the scientific literature in part from the lack of studies that adequately address the temporal scale of successional sequences. Most successional work has been based on descriptions of changes in floristic composition and structure in early stages of species colonization (Greig-Smith 1952, Ross 1954, Richards 1955, Budowski 1961, Blum 1968, Snedaker 1970). There has been little work directed toward making biomass estimations (Bartholomew et al. 1953, Greenland and Kowal 1960, Scott 1977), and only recently have a few contributions emphasized forest dynamics (Hartshorn 1978, Ewel 1980, Whitmore 1978, Crow 1980). This lack of information on forest succession in tropical regions emphasizes the need to focus on the changes in diversity, structure, and biomass of the rain forests. By utilizing the chronosequence technique, 23 stands ranging from recently abandoned fallows to mature forests were studied to obtain details regarding the processes occurring during succession in a tropical rain forest.

Traditional farming in the Amazon Basin consists of clear-felling and burning of tierra firme (never flooded) forests to produce the conucos that are used to grow food crops for 2 to 4 years. Study sites ranged from recently disturbed areas to mature tierra firme (MTF)

stands where charcoal, floristic composition, structure, and biomass studies were conducted. The age of the fallows was provided by local inhabitants, and ^{14}C data from charcoal pieces found in the soil of mature forests clarified the disturbance history of these once thought "undisturbed" forests. Sites were distributed in an area within a radius of 30 km of the towns of San Felipe, Colombia, and San Carlos, Venezuela. The field work was conducted from September 1982 to July 1983.

The study area is remote from major population centers. Its dominant vegetation is rain forest which is subject to localized slash-and-burn agriculture. Hence, the forests are a mosaic of successional and mature forest stands with many abandoned farm sites of known history.

RESEARCH OBJECTIVES

To study forest succession on a tierra firme forest following slash-and-burn agricultural practices, the following objectives were considered:

1. Examine the disturbance history of the Amazon forests since the Pleistocene.
2. Quantify different stages of succession following agricultural abandonment.
3. Determine the time required for an abandoned agricultural site to become a mature forest.

This dissertation begins with a literature review (Chapter 2) concerning the history of the Amazon forest in the Upper Rio Negro region (URN) of Colombia and Venezuela. Chapter 3 documents charcoal

as evidence of fire in the tierra firme forests since the Pleistocene. Charcoal amounts, distribution in the soil profile, and dates are presented. Chapter 4 describes changes in tree species diversity through succession and gives detailed accounts of the forest's structural characteristics: diameter and height distribution, tree density, leaf area, and tree damage. Chapter 5 provides a description of the distribution of aboveground and belowground living biomass, dead biomass, the accumulation process of aboveground living biomass, and the time required for a successional site to attain the biomass of a mature forest. Chapter 6 is the concluding section, summarizing the main points discussed in the preceding four chapters.

This research provides an integrated description of succession, offering a more secure base from which to examine important ecological problems such as the rate of recovery of tropical forest vegetation, living and dead biomass accumulation, the global carbon budget, changes in tree species diversity, and the stability of tropical rain forests.

SITE SELECTION AND PLOT ESTABLISHMENT

The research sites, near the confluence of the Casiquiare River and the Rio Negro, are at 119 m in elevation and are located at 1°56'N latitude, 67°03'W longitude (Figure 1.1). Climate in this region is equatorial with 3565 mm of annual rainfall (Heuveldop 1980). Rainfall is reduced between October and March, with the two driest months being January and February. However, each month receives an average of more than 200 mm of rainfall. The wettest period is May, June, and July, with each month averaging more than 400 mm.

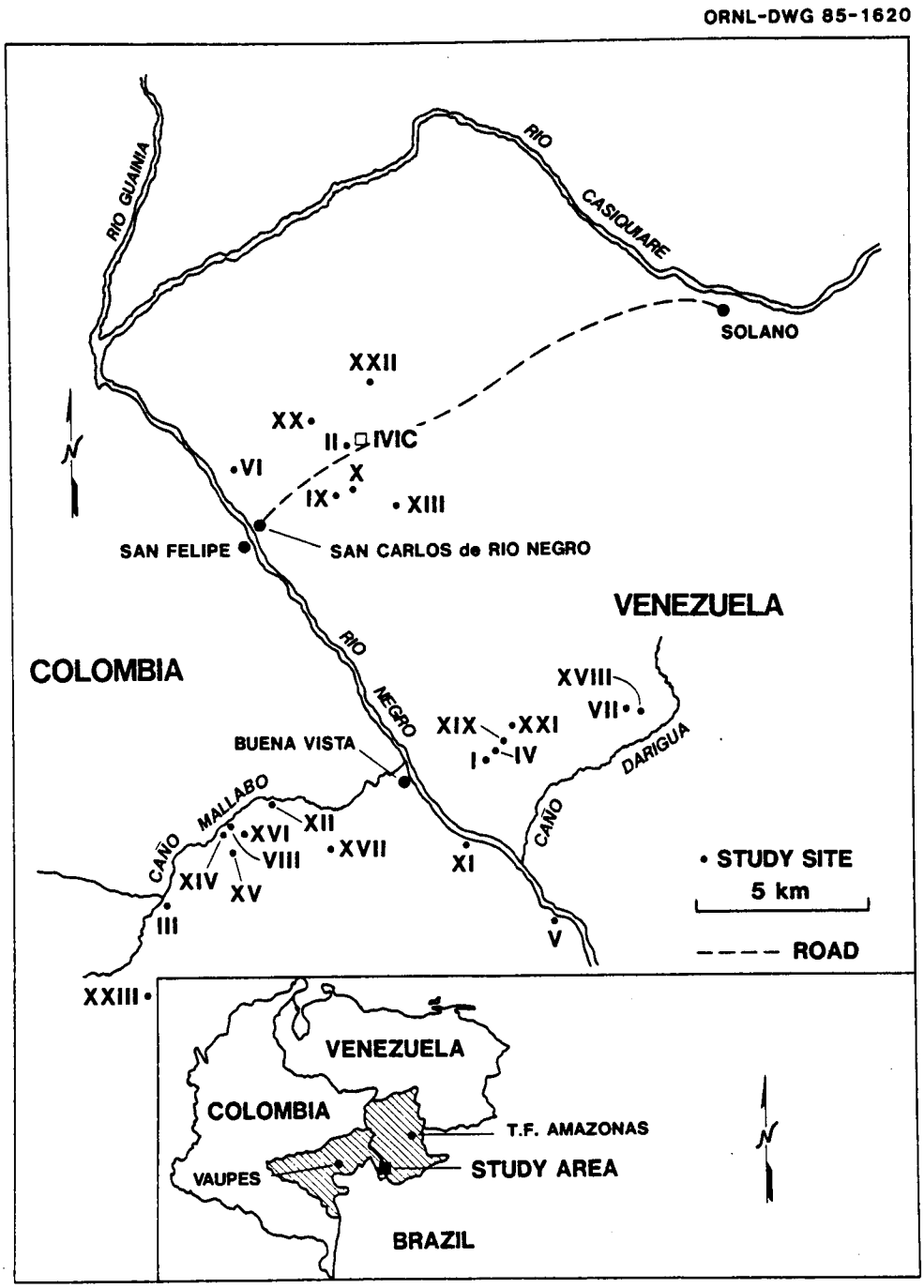

Figure 1.1. Map showing location of the study area, the selected stands, and the Instituto Venezolano de Investigaciones Cientificas (IVIC) in the Upper Rio Negro region of Colombia and Venezuela. Each Roman numeral corresponds to a stand.

Vegetation is classified as tropical, moist forest (Ewel and Madriz 1968) on a landscape that is generally flat with smooth, rolling hills rising 25 to 50 m above the river. There are three main vegetation types. "Tierra firme" forests occur on the sides and top of the hills and cover about 30% of the land area (Bennacchio 1981). This forest is the only one cut and burned for agricultural purposes (Uhl and Murphy 1981). "Caatinga" is a nonflooded forest which occurs on white-sand Spodosols, and "igapo" is a seasonally flooded forest.

Soils of the region are thought to have been derived from nearby sandstone shields in Brazil and Guiana (Fittkau et al. 1975). Intense weathering and leaching throughout much of geological history has resulted in extremely oligotrophic soils (Jordan 1980). Oxisols and Ultisols represent 74.9% of the soil in the Amazon Basin; in contrast, Spodosols represent 2.2%. Soil samples were collected and analyzed for the 23 stands; the results are presented in Table 1.1. Oxisols occur on top of hills and are well drained. They are composed of plinthitic material (laterite) which contains abundant ferric concentrations, forming an irregular cover over the sand and clay horizon. Ultisols are found at intermediate elevations and have good to poor drainage. They do not have spodic or oxic horizons. Spodosols are found on low elevations, where waterlogging is a common characteristic, and have a spodic horizon at about 1-m depth (Klinge and Herrera 1983).

Ninety-six sites distributed over an area within a radius of 30 km of the towns of San Felipe, Colombia, and San Carlos, Venezuela, were visited, and 23 sites were selected from these for intensive vegetation and soil analyses. Locations of the selected sites are shown in

Table 1.1

Physical characteristics of soils in the Upper Rio Negro region of Colombia and Venezuela.

Stand	Years since disturbance	Soil type	Horizon	Depth (cm)	Munsell code	Color	Clay (%) (< 0.002 mm)	Silt (%) (0.002-0.05 mm)	Sand (%) (0.05-2 mm)
I	9	Ultisol	A11	0-15	10 YR 3/3	Dark brown	4.5	8.7	87.8
			A12	15-30	10 YR 2/2	Very dark brown	6.0	10.0	84.0
			A3	30-52	10 YR 3/5	Dark yellowish brown	14.6	7.2	78.2
			B2	52-100	10 YR 6/6	Brownish yellow	16.0	5.8	78.2
II	11	Oxisol	A11	0-11	10 YR 3/1	Very dark gray	2.0	8.0	90.0
			A12	11-50	10 YR 3/1	Very dark gray	4.5	10.0	85.5
			B1	50-80	10 YR 4/5	Dark yellowish brown	11.9	6.0	82.1
			B2	80-100	10 YR 5/6	Yellowish brown	16.8	5.0	78.2
III	12	Oxisol	A11	0-13	10 YR 2/2	Very dark brown	6.0	7.0	87.0
			A12	13-55	7.5 YR 3/2	Dark brown	12.2	12.7	75.1
			A3	55-72	7.5 YR 4/4	Dark brown	27.4	10.5	62.1
			B2	72-100	5 YR 5/5	Yellowish red	29.9	8.1	62.0
IV	14	Ultisol	A11	0-10	10 YR 3/1	Very dark gray	6.0	1.7	92.3
			A12	10-25	10 YR 2/1	Black	6.5	8.7	84.8
			A3	25-45	10 YR 4/1	Dark gray	11.0	8.7	80.3
			B2	45-100	10 YR 6/4	Light yellowish brown	17.0	5.6	77.4
V	20	Oxisol	A11	0-15	5 YR 3/1	Very dark gray	12.4	18.0	69.6
			A12	15-25	5 YR 2.5/2	Dark reddish brown	18.0	12.0	70.0
			B1	25-83	5 YR 4/5	Yellowish red	24.9	11.6	63.5
			B2	83-100	5 YR 5/5	Yellowish red	28.9	12.5	58.6
VI	20	Ultisol	A11	0-11	10 YR 2/1	Black	5.2	5.4	89.4
			A12	11-38	10 YR 2/1	Black	9.9	9.0	81.1
			B1	38-71	10 YR 6/4	Light yellowish brown	19.8	4.0	76.2
			B2	71-100	10 YR 7/5	Yellow	21.8	2.0	76.2

Table 1.1 (continued)

Stand	Years since disturbance	Soil type	Horizon	Depth (cm)	Munsell code	Color	Clay (%) (< 0.002 mm)	Silt (%) (0.002-0.05 mm)	Sand (%) (0.05-2 mm)
VII	20	Oxisol	A11	0-12	7.5 YR 3/2	Dark brown	12.0	10.0	78.0
			A12	12-52	7.5 YR 3/2	Dark brown	19.2	12.8	68.0
			A3	52-61	7.5 YR 4/4	Dark brown	36.0	8.0	56.0
			B2	61-100	7.5 YR 6/5	Reddish yellow	35.80	5.5	58.7
VIII	20	Ultisol	A11	0-12	10 YR 3/1	Very dark brown	4.0	6.0	90.0
			A12	12-50	10 YR 3/3	Dark brown	13.4	9.3	77.3
			A3	50-70	10 YR 4/4	Dark yellowish brown	18.4	6.2	75.4
			B2	70-100	10 YR 6/6	Brownish yellow	22.5	7.0	70.5
IX	30	Ultisol	A11	0-12	10 YR 3/2	Very dark grayish brown	4.8	6.0	89.2
			A12	12-31	10 YR 3/1	Very dark gray	7.2	9.9	82.9
			A3	31-45	10 YR 4/1	Dark gray	17.4	10.0	72.6
			B2	45-100	10 YR 8/4	Very pale brown	20.5	7.3	72.2
X	35	Ultisol	A11	0-10	2.5 YR 3/0	Very dark gray	6.0	11.0	83.0
			A12	10-30	2.5 YR 4/2	Dark grayish brown	9.0	9.0	82.0
			A3	30-50	2.5 YR 6/3	Light yellowish brown	16.4	6.5	77.1
			B2	50-100	2.5 YR 8/2	White	22.1	6.5	71.4
XI	35	Ultisol	A11	0-9	10 YR 2/2	Very dark brown	6.4	3.7	89.9
			A12	9-35	10 YR 2/2	Very dark brown	9.4	10.0	80.6
			A3	35-54	10 YR 4/2	Dark grayish brown	14.7	9.4	75.9
			B2	54-100	10 YR 7/6	Yellow	20.2	5.9	73.9
XII	40	Ultisol	A11	0-10	10 YR 2/1	Black	0.8	2.8	96.4
			A12	10-40	10 YR 2/1	Black	3.9	7.3	88.8
			B11	40-70	10 YR 4/2	Dark grayish brown	14.6	8.7	76.7
			B2	70-100	10 YR 8/4	Very pale brown	23.8	4.9	71.3
XIII	60	Ultisol	A11	0-5	10 YR 2/2	Very dark brown	2.8	8.0	89.2
			A12	5-55	10 YR 2/1	Black	4.6	10.0	85.4
			B11	55-68	10 YR 4/4	Dark yellowish brown	12.8	4.4	82.8
			B2	68-100	10 YR 6/6	Brownish yellow	21.3	6.0	73.7

Table 1.1 (continued)

Stand	Years since disturbance	Soil type	Horizon	Depth (cm)	Munsell code	Color	Clay (%) (< 0.002 mm)	Silt (%) (0.002-0.05 mm)	Sand (%) (0.05-2 mm)
XIV	60	Ultisol	A11	0-10	10 YR 3/2	Very dark grayish brown	6.8	5.9	87.3
			A12	10-50	10 YR 4/1	Dark gray	16.73	10.4	72.8
			B11	50-60	10 YR 5/2	Grayish brown	25.8	7.4	66.8
			B12	60-100	7.5 YR 7/5	Reddish yellow	31.2	7.7	61.1
XV	60	Ultisol	A11	0-11	10 YR 3/2	Very dark grayish brown	2.0	8.0	90.0
			A12	11-48	10 YR 2/0	Black	5.7	7.9	86.4
			B1	48-72	10 YR 3/5	Dark yellowish brown	12.8	9.9	77.3
			B2	72-100	10 YR 6/5	Brownish yellow	21.8	8.9	69.3
XVI	80	Ultisol	A11	0-10	10 YR 2/2	Very dark brown	1.0	2.0	97.0
			A12	10-50	10 YR 2/1	Black	3.7	8.3	88.0
			A3	50-70	10 YR 3/2	Very dark grayish brown	14.0	7.0	79.0
			B2	70-100	10 YR 6/6	Brownish yellow	19.0	7.0	74.0
XVII	80	Ultisol	A11	0-10	2.5 YR 2/0	Black	6.4	5.1	88.5
			A12	10-40	2.5 YR 2/0	Black	8.1	8.1	83.8
			A3	40-90	10 YR 6/1	Gray	14.8	5.3	79.9
			B2	90-100	2.5 YR 8/2	White	26.4	8.8	64.8
XVIII	80	Oxisol	A11	0-13	10 YR 3/2	Very dark grayish brown	6.8	14.0	79.2
			A12	13-71	10 YR 3/2	Very dark grayish brown	23.8	10.7	65.5
			B1	71-80	10 YR 4/4	Dark yellowish brown	33.4	10.0	56.6
			B2	80-100	10 YR 6/6	Brownish yellow	37.4	7.0	55.6
XIX	80			NA*	NA	NA	NA	NA	NA
XX	MTF	Ultisol	A11	0-10	10 YR 3/2	Very dark grayish brown	6.2	7.0	86.8
			A12	10-33	10 YR 2/1	Black	7.2	8.5	84.3
			A3	33-69	2.5 YR 5/2	Grayish brown	10.3	9.5	80.2
			B2	69-100	10 YR 7/5	Yellow	18.2	5.0	76.8

Table 1.1 (continued)

Stand	Years since disturbance	Soil type	Horizon	Depth (cm)	Munsell code	Color	Clay (%) (< 0.002 mm)	Silt (%) (0.002-0.05 mm)	Sand (%) (0.05-2 mm)
XXI	MTF	Ultisol	A11	0-6	10 YR 2/1	Black	3.2	4.0	92.8
			A12	6-45	10 YR 3/1	Very dark gray	5.3	15.0	79.7
			A3	45-62	10 YR 4/2	Dark grayish brown	10.0	10.0	80.0
			B2	62-100	2.5 YR 7/3	Pale yellow	13.6	6.7	79.7
XXII	MTF	Ultisol	A11	0-10	10 YR 4/2	Dark grayish brown	4.0	4.0	92.0
			A12	10-30	10 YR 4/1	Dark gray	8.8	10.4	80.8
			A3	30-40	10 YR 7/1	Light gray	14.8	8.8	76.4
			B2	40-100	10 YR 8/1	White	17.6	6.6	75.8
XXIII	MTF	Oxisol	A11	0-16	10 YR 3/4	Dark yellowish brown	5.3	10.7	84.0
			A12	16-43	10 YR 4/4	Dark yellowish brown	7.6	13.4	79.0
			B1	43-70	10 YR 5/5	Yellowish brown	15.3	8.7	76.0
			B2	70-100	10 YR 6/6	Brownish yellow	22.5	8.0	69.5

*NA = data not available.

Figure 1.1. The sites were those with the most complete information of past history and with similar intensity of land use, types of soils, and topography, and of a size large enough to allow the establishment of several plots for the vegetation survey. Sites very close to towns or main paths were excluded, so that human disturbance since abandonment would be minimized.

The ages of fallows older than 30 years were established by interviewing long-time residents of the region and by taking into account historic events of recognizable importance, e.g., the rubber boom, the migration of the people from San Carlos to the interior of the forest during the government of Funes, and the immigration and settlement of Europeans after World War II. These events had a significant enough impact on the lives of the people to remain in their memories. Dates of such events were used to estimate or verify the ages of the fallows. Abandoned farms less than 30 years old belong to people living in San Carlos. These people provided details concerning the planted crops and the frequency and intensity of use of the sites. The sites with contradictory information were rejected. Most of the sites visited were owned by informants or their relatives.

Once sites were selected, they were classified by "time since last disturbance" and grouped into six age categories: 9 to 14 years (n = 4), 20 years (n = 4), 30 to 40 years (n = 4), 55 to 60 years (n = 3), 75 to 85 years (n = 4), and mature tierra firme forest (n = 4). In this study a mature tierra firme forest is one probably undisturbed in the past by man. This forest has tall canopy trees from larger diameter classes, and these trees have relatively slow growth rates.

Buttressed trees are generally found on these stands, but they are rarely abundant.

Plot size was determined according to the size of the trees. Three plots (10 x 30 m = 0.03 ha) per site were established at all sites. In all plots, individuals with a dbh $\geq$ 1 cm and 2 m in height were recorded. In addition, at each site trees with a dbh of < 1 cm and between 1 and 2 m in height were counted by species in three plots of 152 m^2. The plots were distributed over the stand to encompass a representation of vegetation structure. The first plot was located near the edge of the fallow. The edge of the site is usually the first abandoned area and generally has the largest and most diverse species composition. The second plot was established in the center where dead trees might be found, and the living trees show the slowest growth and least diversity. The third plot was established between the first and second. A fourth plot was established at two sites (XII and XVII) that were unique for having a community dominated by only one or two species, respectively. An additional plot (50 x 50 m = 0.25 ha) was established in sites older than 20 years to measure trees $\geq$ 10 cm dbh.

CHAPTER 2

HISTORY

INTRODUCTION

Geologic and climatic forces are often considered to be the main disruptive agents in the Amazon forest. Several episodes of aridity in tropical lands occurred between 21,000 and 13,000 years before present (B.P.), and as a result the forest was fragmented into scattered areas or refuges (Van Der Hammen 1972, 1974; Vuilleumier 1971). The last such dry period was 13,000 years B.P. While it is frequently assumed that the Amazon forest has been virtually undisturbed from 13,000 B.P. until the recent past, there is increasing evidence to suggest otherwise.

This review examines the generally held belief that the Amazon forest has been largely undisturbed during a major part of the post-Pleistocene by looking at climatic changes and human history in Amazonia during the last 6000 years. The discussion will focus on the Upper Rio Negro (URN) area of Venezuela and Colombia.

CLIMATIC CHANGES IN THE AMAZON BASIN

Palynological evidence obtained from northern Rondonia (Brazil) and from the Colombian Eastern Cordillera suggests that the mean Holocene continental temperature may have dropped 4 to 5°C relative to the present, and the climate may have been considerably drier (Van der Hammen 1972, 1974). This condition allowed open grass savannas to develop on areas now covered by continuous tropical rain forest. Bigarella (1971) postulated episodic dry periods between 4500 and

2500 years B.P. in southern Brazil. Haffer (1974) places the last severe arid period between 4000 and 2500 years B.P.

Recent studies of Holocene sediments from five sites in Central Amazonia and the Roraima Territory suggest that climatic changes in the Amazon Basin may have been frequent during the late Holocene (Absy 1982). Dry periods were reported at one site after 4000 years B.P. and at three sites between 2700 and 2000 years B.P. A minor drier phase was also found at one site at 1500 years B.P., with a drier phase at two sites around 700 years B.P. These were followed by a minor dry period around 400 years B.P. Observations by Williams (1979) suggest that water levels were low on the Kassikaityu and Upper Essequivo Rivers in Guyana during various arid periods in the Holocene. Similar arid conditions in Amazonia have been documented by Absy (1982).

Present day observations illustrate the magnitude of temporal and spatial variation in rainfall. For example, the town of San Fernando de Atabapo in the North Central Amazon Basin has an average annual rainfall of 2900 mm, with three consecutive dry months averaging $\leq$ 100 mm of precipitation (Clark 1983). In contrast, the town of San Carlos de Rio Negro located 260 km to the south has a mean annual precipitation of 3500 mm, and each month has more than 200 mm (Heuveldop 1980). Even at San Carlos, two periods of 20 and 23 consecutive days without rain occurred in 1980 and 1983. Tavera-Acosta (1954) mentions "extreme dry periods" at San Carlos in 1910 and 1911. Another dramatic example of drought in lowland rain forests occurred in the East Kalimantan Province in Borneo where there was a period of more than 6 months without rain in 1983. This indicates that tropical rain

forests may experience infrequent climatic stress sufficiently intense to produce a moderate to severe disturbance in vegetation.

INDIGENOUS POPULATION BEFORE THE ARRIVAL OF EUROPEANS

Archaeological information from the Amazon Basin is scarce with reports from only a few isolated sites (Megger and Evans 1957, Myers 1973). One reason is that this region is inaccessible, inhospitable, and large. A second reason is that Amazon Indian cultures left behind no artifacts other than ceramic pot shards. A final hindrance in studying the prehistory of this area is the vast disruption of the Indian culture by the first Europeans. Many Indian tribes disappeared, while others lost their indigenous customs, modes of life, houses, and language making it difficult to reconstruct the past (Wallace 1969).

Lathrap's work, "Culture Ecology or Cultural History," hypothesizes that around 4000 years B.P., members of the Proto-Arawak culture were concentrated on the floodplain of the Central Amazon near the present city of Manaus. These agricultural groups in this area were successful, and as their population increased, there was heavy demand on the land of the floodplain, causing many Indian groups to look for other available areas of alluvial lands. To obtain suitable locations, some of them moved to areas of alluvial soils such as in the Upper Rio Negro (Lathrap 1970).

Estimation of the Ameridian population size before the arrival of Europeans is very controversial. The first records of inhabitants were made by the missionaries who arrived in Brazil in 1549 (Beckerman 1979). Such records usually indicated only the number of people baptized or the number that were living in established missions.

Nevertheless, their accounts provide some information on the size of the Indian population at the arrival of the first Europeans.

Also, an historical account yielding an estimate of the Indian population was made by Friar Gaspar de Carvajal who recorded the trip of Francisco de Orellana along the Amazon river in late 1541 (Figure 2.1). This is the first narrative describing the Indian population on the floodplains of the Amazon River. He discussed crops, sources of protein, distribution of villages, customs, and degree of Indian development. According to the description, the distribution of the population was irregular. In the first 400 leagues (a league is an unstandardized measure of distance about 2.4 to 5.0 miles), Indian villages were small and few in number. The single exception was the village of Aparia the Lesser. Beyond this point, the size and number of villages increased. An example was Machiparo, which surprised the conquistadors with its quantity of available food. According to Carvajal's account, "Food was in such great abundance that there was enough to feed an expeditionary force of one thousand men for one year" (Medina 1970). The Spaniards were very impressed by the large number of inhabitants in this area. Carvajal's account stated, "... which in the opinion of all extended for more than eighty leagues, for it was all of one tongue, these (eighty leagues) being all inhabited ... and there was one settlement that stretched for five leagues without there intervening any space from house to house along the river ... but, judged from its (apparent wealth of natural) resources and its (general) appearance, it must be the most populous that has been seen" (Medina 1970).

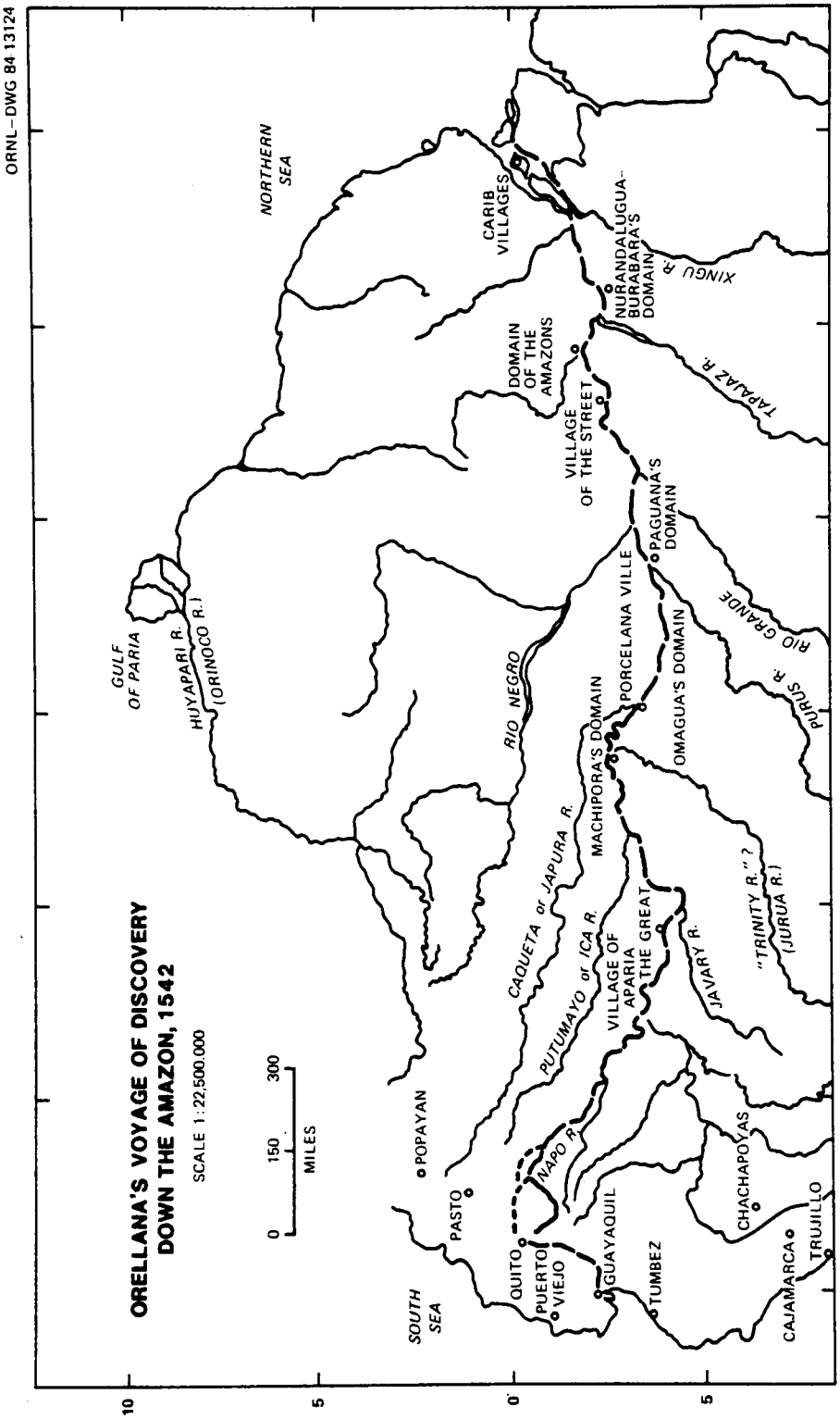

Figure 2.1. Map showing the route of Orellana's voyage down the Amazon in 1541. Based on the Oviedo and Medina versions of Carvajal's account (from Medina 1970).

After Machiparo, Carvajal observed another city of similar size, the Omagua, which spread along more than one hundred leagues of river bank (Medina 1970). Carvajal said, "the villages were so numerous and so large and because there were so many inhabitants the captain did not wish to make port" (Medina 1970). Another example was the place called, by the Spaniards, the Province of San Juan, which covered more than one hundred and fifty leagues. For the rest of the trip, Carvajal continued monitoring the presence of large and small villages. In spite of the fact that they stopped in small villages to avoid fights, they found a considerable amount of maize, yuca, fish, and fruits. In many of these places, they found roads that went into the interior of the country (Medina 1970). In the Province of the Gibbets Indians (Picotas), which extended down the river seventy leagues, they found roads made by hand with forest trees at each side of the road (Medina 1970). In other villages, they found a great quantity of maize in hampers which were buried in ashes for protection from weevils (Medina 1970). They also found many wild animals used as meat resources, such as crocodiles, manatees, parrots, turtles, turkeys, ducks, fish, birds, monkeys, and tapirs.

Another reason to suspect that the Amazon Basin population prior to European contact was larger than at present is the documentation of about five epidemics recorded 15 years after the Jesuits arrived in Brazil in 1549 (Beckerman 1979). In other records there are examples of virulent and highly communicable diseases, such as smallpox, malaria, and yellow fever, introduced by Europeans and by African

slaves, that decimated the lower Amazon in 1621 and upper Amazon in 1651 (Meggers 1971).

Estimates of the native population in the Amazon Basin vary widely (Table 2.1). The figures were obtained by "educated guess" (Moran 1974) or estimates without explanation (Murphy and Murphy 1974). Rosenblat (1945) made his estimates based on colonial records and guess.

Table 2.1. Estimates of the Amazon Basin population at the arrival of the first Europeans.

Author	Date	Number of inhabitants
E. Moran	1974	500,000
A. Rosenblat	1945	1,400,000 (Brazil only)
J. Steward	1949	1,500,000 (Brazil only)
Y. and R. Murphy	1974	1,500,000 (Brazil only)
J. Hemming	1978	2,400,000 (Brazil only)
E. Galvao	1967	2,000,000 (Brazil only)
W. M. Denevan	1976	6,800,000
J. Rondon*	1951	10,000,000

*In Comas (1951, cited by Denevan 1976).

The first systematic estimate of Amazonian population was made by Steward (1949). He estimated 1,500,000 people for Brazil only. With his method Steward judged the size of each group by calculating the area the group occupied and estimating the density of habitation. His population density estimates ranged over areas of 0.07 to 0.60 km^2. Estimation of the Indian population of the Rio Negro region for the year 1500 was made by Hemming (1978). He estimated 177,000 inhabitants for this region including the Isana and Vaupes Rivers. In his work he

followed the same basic method of Steward, but Hemming gave more importance to clues from chronicle reports and the soil fertility of each region.

Denevan (1976) examined the main "habitats" in Amazonia and the subsistence patterns of each in relation to resources, estimating the possible native population density of each. He distinguishes seven main areas on the basis of soil and wildlife resources in order of decreasing population density: (1) floodplain, (2) Brazilian Coast, (3) lowland savanna, (4) upland forest, (5) upland savanna, (6) lowland forest, and (7) uninhabitable. The number of people range from 0.1 to 28.0 per square kilometer.

EFFECTS OF EUROPEAN SETTLEMENT ON AMAZON POPULATIONS IN THE RIO NEGRO

Slavery

In the seventeenth century, the main center of operation for Europeans was the Central Amazon floodplain where French, English, Dutch, and Portuguese settlements began to proliferate. When political rivalry among these groups increased, each recruited thousands of Indians to defend its territories. At the end, the Portuguese controlled the area and few natives remained (Meggers 1971).

After the decimation of the indigenous population in this area, the Portuguese began, in the late 1600's, to conduct slave raids in the Upper Rio Negro (Meggers 1971). The upper Orinoco and the Rio Negro were the two main routes by which the slave trade was made. Trade in the Rio Negro was dominated by the Portuguese from Para and by the Manau Indians who lived on the middle Rio Negro and traded Indian

slaves to the Portuguese (Wright 1981). In the 1720's, the Portuguese declared war against the Manau and later against the Maiapena tribe. As a result, the Manau and Maiapena Indians were either eliminated or pushed away from the banks of the Rio Negro. The Manau people were the most numerous, powerful, prosperous, and enterprising people of the middle Rio Negro Valley until the 1730's (Wright 1981).

Enslavement continued against the other tribes on the banks of the Rio Negro. This period is characterized by massacres of thousands of Indians and by the relocation of whole societies (Wright 1981). Sweet (1974) said that, "nothing in the documents for this period gives cause to doubt that a minimum of 1000 slaves a year were brought to Para during this decade as before (a figure which makes no account of the perhaps equal numbers resettled by means of Jesuit, Carmelite and Mercedarian "descimentos" from upriver missions to their aldeas on the lower valley)." This rate was maintained from 1690 to 1730, during the ruthless government operated "tropas de rescate" on the Rio Negro. A conservative estimate of slaves taken from the URN between 1740 and 1750 was about 20,000 (Wright 1981). By the 1760's entire tribes which had been prominent in the URN region were gone (Wright 1981).

Colonial Government, the Rubber Boom (1860-1910), and Funes (1913-1921)

Between the 1750's and the 1800's, there was the introduction of a permanent colonial government that forced natives to participate in programs of economic development and Christianity. The main characteristics of this period were the recruitment of Indians by means of "descents", which consisted of persuading the Indians to descend the rivers from the headwaters and settle permanently on the Rio Negro, and

to accept European government (Wright 1981). With this program the Indians were relocated in new villages on the Rio Negro, which were selected primarily on the basis of military advantage. By 1760 six Spanish settlements had been established; the first in the upper Orinoco, called San Fernando de Atabapo. Two other important settlements were San Carlos and Don Francisco Solano, located on the URN and Casiquiare. In the 1760's, all Indians in the URN had to accept the direct and continuous presence of the military, whose main purpose was to persuade the native populations to descend to the Rio Negro villages (Wright 1981). Furthermore, in the 1760's through the 1780's, various epidemics plagued the Rio Negro with devastating effects on the population. Many Indians fled from villages to the forests, and the population in all Spanish territories decreased in number. Exceptions were San Carlos, San Francisco Solano, San Felipe, and San Miguel, which accounted for about one-third of the entire population in the Capuchino territory from the upper Orinoco to its headwaters (Wright 1981).

Colonial programs began to fail because a substantial labor force was needed to maintain the crops and conduct military expeditions (Wright 1981). By the onset of the 1800's, the process of colonization in the Rio Negro slowed, allowing the few Indians that were still alive to return to their traditional homelands and rebuild their societies. In 1850 the Portuguese and Spanish failed to revive their programs of colonization, which included forced resettlement of Indians, compulsory labor programs, and missionation (Wright 1981).

Major economic transformations occurred during the "rubber boom" in the Amazon region around 1850. However, these changes did not reach the URN until the late 1860's and early 1870's. The most important trading posts in the Rio Negro were Thomar, Barcellos, San Gabriel, and San Carlos. At the beginning of the 1900's, most of the adult male Indians of the Baniwa, Bare, and Tucano were working in the exploitation of Hevea spp. (rubber tree) as far away as the lower Rio Negro (Wright 1981). The annual production around San Carlos approached 150 tons per year with a labor force of approximately 2000 (Tavera-Acosta 1954).

Another important event in the URN was the political movement organized by Tomas Funes. For a period of eight years, he established a dictatorial regional government characterized by murder and terror in the Venezuelan-Amazon territory (Alamo 1979). During this time, many villages and towns were abandoned, and their inhabitants fled into the forests. Many of the old stands, called "rastrojos" (abandoned agricultural sites), that are found today in San Carlos are the result of the activities at that time.

MAN AS AGENT OF DISTURBANCE

Slash-and-Burn Agriculture in the Past

A slash-and-burn agricultural system was developed by inhabitants of tropical forests thousands of years ago. In the Amazon Basin it was, and still is, the most important form of subsistence, and most of the farming tribes use this method (Lowie 1963). The traditional method of agriculture practiced by the first inhabitants of this region

was characterized by three main tasks: (1) cut and burn secondary vegetation or mature forests to produce a clearing; (2) farm for a period of two to five years, depending upon fertility of the soil and the care of the owner; and (3) abandonment of the site when productivity dropped (Lathrap 1970; Metraux 1963; Meggers 1971; Levi-Strauss 1963; Wallace 1969).

Lowie (1963) indicated that some Indian tribes completely changed their habits because of the disruptive impacts produced by conquistadors. Two examples are the Guayaki and the Mura tribes, who abandoned cultivation and have subsisted by hunting native animals and harvesting natural plants since the Conquest. The opposite occurred with a few tribes, such as the Shiriana, the Guaharibo, and the Macu of the Rio Negro, who formerly did not farm but have adopted farming from their neighbors.

In the Rio Negro area, the primary cultivars were root crops. Seed crops were secondary, but virtually all tribes grew several varieties of maize (Lowie 1963). Sauer (1963) and Lowie (1963) present a list of the main crops used by the Indians in the Amazon Basin. Those found in the Rio Negro included manioc (Manihot esculenta), maize (Zea mays), pijiguao (Bacteris gasipaes), and beans (Phaseolus spp.).

The Amazon Basin in the last six millenia has been exposed to two consecutive and distinct types of human use. The first corresponds to a stage of near-equilibrium between inhabitants and the environment. It existed before Europeans arrived, and during this time the Amazon Basin was primarily modified by climatic and topographic factors. Human utilization resulted from adaptations to the natural conditions

of this system. After domestication of a few plants around 5000 to 3000 B.P. (Lathrap 1970; Meggers 1971, 1982; Roosevelt 1980), man changed his life-style to a more sedentary way of life but one that was still adapted to the environmental conditions of the area.

The second type of human use of the Amazon corresponded to cultural changes and alteration of the environment in order to satisfy European needs. This began 450 years ago, extended to the present, and has been characterized by drastic cultural changes and degradation of the environment. Utilization of resources changed from limited personal use to uncontrolled harvesting and large-scale efforts to develop the region, beginning with the extraction of products such as sarsaparrilla (Petroselinum saturum) and brazil-wood (Dalbergia spp.) in the 1500's (Dean 1983).

Other examples of changes in agricultural habits of the Indians can be observed from the historical descriptions presented by Wright (1981), based on documents from the end of the 1700's. For instance, the Royal Expedition organized by Spain, from the late 1750's until the mid-1780's, introduced livestock and crops to the Upper Orinoco and URN. Livestock included cattle and horses, and the crops included indigo, cacao, fruit trees, and other legumes. The total export of indigo was over 1400 arrobas ($\sim$ 22 tons) in 10 years (Wright 1981). Manioc was produced in quantities that allowed exportation. The two main centers of manioc production were Lamalonga, which produced thirteen tons in the year 1785-86, and the area between Santa Izabel and San Gabriel. Manioc was the most important product of the URN for a century (Wright 1981).

Present Slash-and-Burn Agriculture

Traditional shifting cultivation continues to be used in the URN. The areas used in this system are called "conucos," and they are generally found adjacent to the Rio Negro in the tierra firme forests (nonflooded land). Clearing begins with cutting of the trees, which is done from September through December and burning occurs whenever there is an extended rainless period from January to the end of March. Manioc stem segments are carried to the sites, and planting begins after the rainy season starts. This is done between remaining standing tree stems and fallen logs. The soil is rarely cultivated and is weeded by hand. Bitter manioc is usually planted, but sometimes sweet manioc is used. Maize is planted in small plots (2 to 4 m^2) throughout the site where there are accumulations of ashes and charcoal that may enhance fertility. Crops such as mapuey (Dioscorea spp.) and yam (Ipomoea spp.) are planted around the edges. During the first year, crops such as bananas and plantains (Musa spp.), pineapple (Anana spp.), aji (Capsicum spp.), and tupiro (Solanum spp.) are planted in small areas scattered throughout the field. Close to the farm shelter, fruit trees such as guama (Inga spp.), cashew (Anacardium occidentale), limon (Citrus spp.), manaca (Euterpe spp.), cumare (Astrocaryum spp.), copoasu (Theobroma spp.), Yuri (Poraqueiba sericea), avocado (Persea americana), temare (Sapotaceae), pijiguao (Bacteris gasipaes), and medicinal plants are established.

Conuco (farm) sizes range from 0.5 to 2 ha, although the old people in San Carlos say that 3 ha was a common size among family groups. Conucos are generally round to elliptical in shape and are

cultivated for 2 to 4 years before being abandoned for 10 to 60 or more years before reuse.

The system of multiple cropping was a characteristic of the traditional system used by the old people, while criollos (non-natives) grow only a few species in their conucos. The difference between groups illustrates the gradual shift in the agricultural system from Amazonian to European traditions.

Current Subsistence Activities

In the small villages of the region, the majority of the settlers still maintain subsistence levels of existence with fishing, hunting, and farming. Annually, during a period of three months, they exploit forest products such as chiquichique palm (Leopoldina piasaba). On the Colombian side of the Rio Negro, more than 50% of the adult male population works at this activity. In the larger towns of San Carlos and Maroa on the Venezuelan side, many families have government jobs, and only a few of them continue to depend upon traditional activities (Clark and Uhl 1985).

Better economic and social conditions in Venezuela result in an influx of money which affects the social conditions of the region. Small villages on the Colombian side have originated as a result of better conditions on the Venezuelan side. This population consists of merchants, adventurers from the interior of the country, native people from the area, as well as Indians and Caboclos (descendants of Indians and whites) from Brazil. Such people have been accelerating the alteration of the ecosystem begun 400 years ago by the Europeans. Alterations are also being made by Indians and non-natives, whose

attitudes and behavior were developed in a different environmental context than were those of the original Indian inhabitants. These alterations generate new social conditions that are often incompatible with the local ecosystems.

SUMMARY

Although tropical rain forests are commonly thought to have experienced little climatic change, substantial evidence indicates these forests have been subjected to infrequent periods of climatic stress during the past 6000 years. Data from the late Holocene document dry periods from several sites in the Amazon Basin. Palynological studies show that these events have exerted an effect on past vegetation structure and composition. Man has been present in the Amazon Basin during the last 6000 years. For the first few thousand years, the Indian population was scattered. With shifting agricultural methods, the Indians probably lived in equilibrium with environmental conditions of the area. After the arrival of Europeans, settlements became concentrated, and utilization of resources changed from a limited use of maintaining the natives, to large scale consumption and exportation of some resources. In recent time, forest cutting has become more frequent and clustered in some areas of the basin such as Central Amazonia.

CHAPTER 3

CHARCOAL IN SOIL

INTRODUCTION

The Amazon region has been regarded as a highly stable area throughout most of the Quaternary (Darlington 1957; Richards 1952, 1973; Schwabe 1969; Walter 1971). However, studies in the last 20 years indicates that this region was affected by several dry episodes during the Pleistocene (Damuth and Fairbridge 1970, Van der Hammen 1974). The nature and effect of climatic changes during this period probably had an influence on the species diversification of the region; an assumption which is born out by studies on forest birds, lizards, and flora (Haffer 1974, Vanzolini and Williams 1970, Vuilleumier 1971, Prance 1973).

The notion of Amazon forest stability is also challenged by the presence of charcoal in soils of three forest types in the Upper Rio Negro [tierra firme, nonflooded forest on Oxisols and Ultisols; igapo, seasonally flooded; caatinga, nonflooded forest on white-sand Spodosols (Klinge et al. 1977, Herrera 1977)]. This chapter documents the presence of charcoal in the soils of the URN region of Colombia and Venezuela. Charcoal presence indicates that the presently moist tropical forest is possibly less stable than previously thought. In this chapter, charcoal amounts, its distribution in the soil profile, and the radiocarbon dates are presented. The effects of fire disturbance on forest vegetation is also discussed.

METHODS

Charcoal Sampling

Charcoal was sampled by two methods at 84 locations on both sides of the Rio Negro in an area of approximately 200 km^2 around San Carlos. Charcoal was collected from 4 or 5 soil pits (50 x 50 x 100 cm) from seven stands (5 fallows and 2 mature forests). Charcoal was also collected from soil cores from 13 locations, the seven stands mentioned above, five additional ones, and one caatinga forest (Figure 3.1). The soil cores, 8 cm in diameter, were taken to a depth of 70 cm at 35-m intervals along transects. All samples were separated into 10-cm layers; the charcoal was removed by hand with the aid of a 0.5-mm-mesh seive, oven dried at 90°C and weighed.

Radiocarbon Dates

Charcoal samples from different depths were ^{14}C-dated by the benzene method at Beta Analytic, Inc., Coral Gables, Florida. Samples not large enough for laboratory analyses were pooled with other samples at the same depth from different pits at the same site. The rootlets were removed from the samples, and a hot acid wash was used to eliminate carbonates. The samples were rinsed to neutrality, soaked in hot alkali to remove humic acids, and washed again in acid with a final rinsing to neutrality.

Shards were submitted to Alfa Analytic, Inc., Coral Gables, Florida for thermoluminescence dating. The outer 2 mm of the shard surface was removed prior to dissaggregation. A standard treatment was used to eliminate light-bleached minerals. Multiple settings in

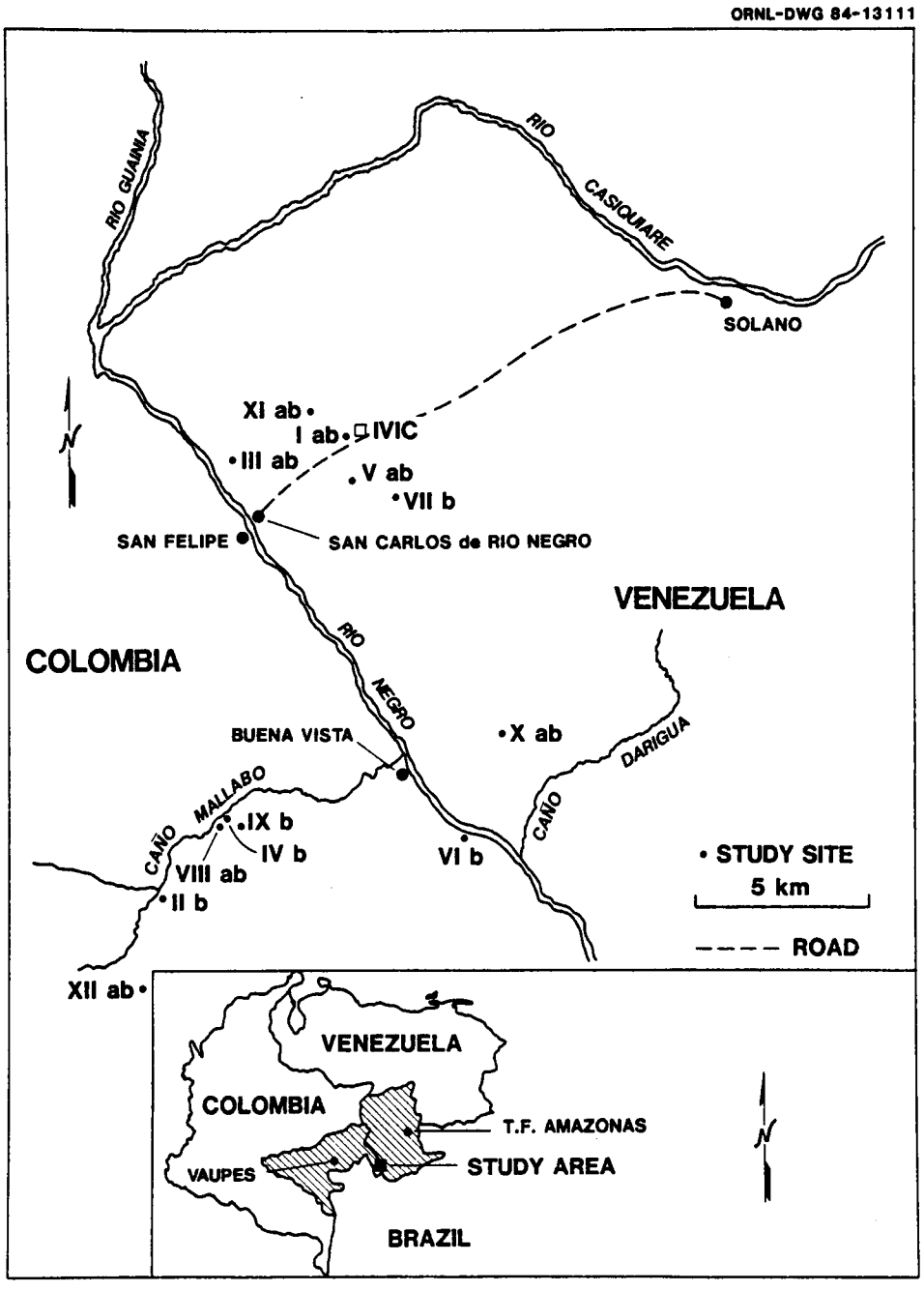

Figure 3.1. Map with locations of the study areas, the station of the Instituto Venezolano de Investigaciones Cientificas (IVIC), and a caatinga site (CA) in the Upper Rio Negro region of Colombia and Venezuela. Each Roman numeral corresponds to a stand. Letters designate type of sampling, a = pits, b = cores.

acetone were made for separation of the 2 to 8 micron grain fraction, and dating was determined by the fine-grain technique.

RESULTS

Charcoal was found in 14 of 15 mature forest (MTF) stands and in each of the 69 rastrojos. In the transects from caatinga to tierra firme, charcoal was only found in the ecotone of each forest type. Ceramic pot shards were found between a depth of 30 to 80 cm in two stands, III and VIII. Charcoal in the soil shows a very uneven distribution with depth. It is mixed with soil particles without spatial arrangements. Distribution by depth shows that 86 to 99% of the charcoal is found in the upper 50 cm of tierra firme soils (Table 3.1). Charcoal abundance generally increases from surface to 20 cm and in some cases to 30 or 40 cm (Table 3.1, 3.2). Both sampling methods generally gave similar charcoal estimates.

The size of charcoal particles varied between 0.7 and 2 cm^3 in the top 30 to 50 cm. At 50 cm, charcoal pieces are generally less than 0.5 cm^3. Charcoal weight shows no relationship with the age of the vegetation. Lowest values were found in two mature forest stands (Table 3.2) when core samples were taken.

Charcoal samples were collected from three mature forests and five fallows of different ages. Charcoal age in the first 10 cm in the three mature forests varied between 250 $\pm$ 60 and 350 $\pm$ 70 years before present (B.P.). The age of the charcoal found at 10 to 20 cm (Table 3.3) varied between 400 $\pm$ 80 and 640 $\pm$ 50 years B.P. Charcoal age in the mature forest at stand XII varied between 350 $\pm$ 70 and 3080 $\pm$ 1120 years B.P. The oldest date was 6260 $\pm$ 110 years B.P., found on

Table 3.1

Distribution of charcoal in metric tons/ha by depth. Values are means from 4 pits (50 x 50 x 100 cm) per stand (except stands I, VIII, and XI with 5 pits). Standard deviations are in parentheses.

Stand	Years since disturbance	Depth (cm)					Total	
		0-10	10-20	20-30	30-40	40-50	0-50 cm	0-100 cm
I	11	2.76 (2.49)	2.56 (1.83)	3.78 (2.526)	2.14 (1.05)	1.56 (1.420)	12.83 (7.49)	13.41 (7.42)
III	20	2.43 (0.86)	5.12 (2.77)	5.18 (1.11)	3.91 (2.85)	1.69 (1.08)	18.35 (5.71)	21.37 (9.49)
V	35	5.56 (3.57)	5.79 (3.63)	5.31 (6.87)	0.49 (0.65)	0.21 (0.17)	17.37 (9.04)	17.70 (9.13)
VIII	60	0.61 (0.33)	2.02 (1.43)	1.13 (0.57)	1.80 (0.86)	0.56 (0.44)	6.14 (1.52)	6.68 (1.77)
X	80	4.40 (3.41)	5.60 (1.99)	3.36 (0.20)	0.38 (0.18)	0.09 (0.06)	13.84 (3.51)	13.92 (3.53)
XI	200	0.24 (0.11)	3.91 (1.42)	5.21 (3.25)	1.17 (0.47)	0.15 (0.13)	10.71 (4.00)	10.83 (4.03)
XII	200	0.31 (0.46)	0.61 (0.58)	1.64 (0.64)	0.99 (0.46)	0.20 (0.03)	3.76 (0.909)	*

*Samples were collected only to 50-cm soil depth.

Table 3.2

Distribution of charcoal in metric tons/ha by depth. Values are means from 8 cores (8-cm diameter) per stand. Standard deviations are in parentheses.

Stand	Years since disturbance	Depth (cm)					Total
		0-10	10-20	20-30	30-40	40-50	
I	11	2.50 (2.03)	5.69 (5.46)	1.64 (1.42)	1.18 (1.32)	0.46 (0.33)	11.47
II	12	2.60 (2.73)	1.48 (1.47)	3.39 (3.46)	1.25 (0.96)	0.67 (0.53)	9.39
III	20	8.45 (8.38)	5.05 (4.91)	4.56 (3.23)	3.59 (1.93)	2.83 (1.90)	24.48
IV	20	1.14 (1.35)	2.00 (2.53)	2.40 (1.71)	6.63 (12.64)	1.91 (1.75)	14.08
V	35	5.83 (8.84)	7.73 (11.05)	1.46 (2.39)	0.45 (0.72)	0.31 (0.35)	15.78
VI	35	3.20 (2.04)	3.30 (2.50)	4.93 (3.93)	4.28 (3.26)	2.20 (2.57)	17.91
VII	60	1.50 (1.41)	3.88 (2.62)	6.88 (7.19)	1.51 (1.32)	1.30 (1.67)	15.07
VIII	60	2.15 (2.68)	1.73 (1.38)	2.95 (3.02)	2.04 (2.30)	0.94 (0.65)	9.81
IX	80	2.51 (2.34)	3.43 (1.91)	4.90 (2.64)	3.13 (2.33)	1.54 (1.26)	15.51
X	80	4.15 (2.47)	3.35 (2.31)	2.45 (2.20)	1.38 (1.41)	0.62 (0.92)	11.95
XI	200	1.06 (0.9)	3.95 (1.36)	2.65 (2.07)	1.53 (2.07)	0.09 (0.08)	9.28
XII	200	0.46 (0.25)	1.18 (1.03)	0.70 (0.32)	0.51 (0.48)	0.26 (0.13)	3.11

Table 3.3

Radiocarbon dates (years B.P. ± S.D.) of soil charcoal from rastrojos and mature forest stands in the Upper Rio Negro region of Colombia and Venezuela.

Depth (cm)	Stands							
	Mature Forests			Rastrojos				
	XII	XI	IVIC†	X	VIII	V	III	I
0-10	350 ± 70	250 ± 50	250 ± 60	††	*	*	*	*
10-20	500 ± 50	640 ± 50	400 ± 80	280 ± 50	††	480 ± 50	*	*
20-30	1540 ± 80	1560 ± 60	*	910 ± 50	530 ± 50	670 ± 50	*	*
30-40	1320 ± 60**	1700 ± 60	*	2460 ± 90	740 ± 50	1100 ± 50	*	*
40-50	1290 ± 80**	1180 ± 90**	*	950 ± 60**	1040 ± 50	920 ± 90	*	*
50-60	*	1220 ± 80**	*	*	1170 ± 50	1100 ± 90	*	*
60-70	3080 ± 1120	1260 ± 80**	*	*	1230 ± 90	6260 ± 110	1430 ± 60	1240 ± 50
70-80	*	*	*	*	*	*	2070 ± 80	1410 ± 80

†Sanford et al. 1985.

††Modern.

*Not recorded.

**Pooled samples.

stand V at 60 to 70 cm (Table 3.3). Three stands, III, X, XII, had dates over 2000 years B.P., and four of eight stands showed dates from 1400 to 1600 years B.P. (Table 3.3). Dates were generally older with depth, except in six cases where the ages at lower depths were younger.

Ceramic pot shards were found at stands III and VIII. Stand III had shards at 30 to 80 cm. At the other stand, they were found at 40 to 50 cm. Two shard pieces from stand VIII were thermoluminescence dated. The oldest one was 3750 years B.P., ± 20% (S.D.), and the most recent was 460 ± 20% (S.D.).

DISCUSSION

Charcoal is unevenly distributed in the soil profile, and there is a high variation in charcoal weights among samples at the same depth as indicated by the standard deviations (Table 3.1, 3.2). Charcoal in the uppermost 10 cm of soil is less abundant than in the next 10- to 20-cm layers. This means that charcoal may have washed out, filling depressions on the forest floor. High charcoal weight (16.20 t/ha, S.D. = 9.40) was found in five pits of tierra firme and caatinga with slopes of 5 to 20%. This may indicate that charcoal is removed from tierra firme (high elevations) to caatinga (low elevations). However, it does not mean that low elevation forests such as caatinga and igapo are not themselves susceptible to wildfire or human occupancy. Examples of charcoal and ceramic pot shards in caatinga forests near Manaus are evidence that this type of forest was also occupied by pre-Columbian Indians. The dates of shards and charcoal from the caatinga sites ranged between 750 ± 80 and 1150 ± 41 years B.P. (Prance and Schubart 1977, 1978).

Distribution of charcoal dates by depth did not present an apparent pattern. For example, at 20- to 30-cm depths the charcoal date was 1560 ± 60 years B.P. at stand XI, 910 ± 50 years B.P. at stand X, 530 ± 50 years B.P. at stand VIII, and 670 ± 50 years B.P. at stand V. These data show that the rate at which charcoal moves to lower soil depths varies among sites, depending on the topography, soil texture, macroinvertebrates, and stratigraphy at each site. For example, the charcoal found at stand XII at 20 to 30 cm has a date of 1540 ± 80 years B.P. In contrast, the same date is found at 70 to 80 cm at stand I and at 60 to 70 cm at stand III.

Pooled samples from different pits at the same depth at several stands (X, XI, XII) were sometimes younger than samples from the upper layers. This may be attributed to the stratigraphic variation of the soils at each site, or the introduction of statistical "noise" when the samples are mixed, or soil perturbations by animals, man, and uprooted trees.

Charcoal is often found in mature forests of the URN region far from the main river. Earlier researchers in the San Carlos project (Klinge et al. 1977, Stark and Spratt 1977, and Herrera 1979) were impressed by the frequency with which charcoal was found in soil profiles. More systematic sampling in areas more distant from San Carlos, such as Guanabano (50 km southeast of San Carlos near the Brazilian border), have confirmed the presence of abundant charcoal in tierra firme forests and in some caatingas and igapo forests (Sanford et al. 1985). A thorough assessment of charcoal abundance,

distribution, and associated soil types within the Amazon Basin is lacking.

Palynological data indicates that relatively dry periods occurred in central Amazonia during the Holocene (Absy 1982). Similar results were found using ^{14}C dates and pollen analysis from the Amazon area, the inland savannas, and the lower Magdalena Valley in South America (Van der Hammen 1982). The most significant dry phases recorded in the mentioned areas are between 4200 and 3500 years B.P., 2700 or 2400 and 2000 years B.P., 1500 years B.P., 1200 years B.P., and 700 and 400 years B.P. (Absy 1982, Van der Hammen 1982). Some of these dry phases may be related to climatic change marked by sea level changes during the last 5 millennia (Fairbridge 1976) and episodic dry periods between 4500 and 2500 years B.P. in the southern part of Brazil (Bigarella 1971).

The present study shows radiocarbon dates corresponding to those dry phases already mentioned by Absy (1982) and Van der Hammen (1982). Two stands, III and X, have ^{14}C dates around 2400 and 2000 years B.P.; four stands, I, III, XI, and XII, have radiocarbon dates between 1400 and 1600 years B.P.; five stands, I, V, VIII, XI, and XII have dates ranging from 1100 to 1200 years B.P.; four stands, V, VIII, XI, and XII have ^{14}C dates between 400 and 500 years B.P. This indicates that under unusually dry climatic periods, fire may have destroyed large areas of forest vegetation previously believed to be resistant to burning.

In the present century, there are reports of unusually short dry periods in the URN region. For example, Tavera-Acosta (1954) mentions

"extreme dry periods" at San Carlos in 1910 and 1911. Similar reports exist from informants from the URN area who indicated that the forests were burned during dry periods occurring in the 1940's. Another unusually dry year in this region was the drought of 1958; in northeast Brazil the rainfall ranged from 20 to 90% of the normal amount (Rose 1980). The most recent droughts in the San Carlos area were two periods of 20 and 23 consecutive days without rain in 1980 and 1983, respectively. During these dry periods, two fires occurred near San Carlos on an 8-ha low igapo forest (seasonally flooded), and on a 12-ha hilltop or "cerro" forest (Uhl and Clark 1983). The occurrence of dry periods may be one possible explanation for the amounts and extent of charcoal on well developed tierra firme, caatinga, and igapo forests. Extreme dry years seem to occur in the tropical rain forest producing devastating effects such as the one observed in the East Kalimatan, Borneo in 1983. In this region, fire destroyed 3.5 x 10^6 ha of forests (Webster 1984). These examples show that extreme weather conditions may occur in "stable ecosystems" in the wet tropics and make them susceptible to fire disturbances.

Some anthropologists consider the Amazon Basin to have had the lowest pre-Columbian aboriginal population density of any major region in the New World (Steward and Faron 1959, Moran 1974, Murphy and Murphy 1974). Historical documents and evidence concerning the population size of Amazonia indicate that there are many reasons to suspect that the initial Amazon Basin population was larger in pre-Columbian times than at present (Medina 1970, Beckerman 1979, Denevan 1976, Sweet 1974, Wright 1981).

Anthrosols, "Indian black earths with pot shards," have been reported throughout the Basin suggesting that precontact, indigenous populations were large and sedentary (Smith 1980, Von Hildebrand 1976, Eden et al. 1984). Around San Carlos and in the Casiquiare region, there are anthrosols with ceramic shards (Sternberg cited by Klinge et al. 1977, Sanford et al. 1985). Furthermore, in this study ceramic shards were found at two stands. The oldest piece, 3750 $\pm$ 20% (S.D.) years B.P., seems to be the oldest ceramic pot shard reported in the interior of the Amazon. The oldest radiocarbon date for an anthrosol is 2400 $\pm$ 75 years B.P. from Paredao near Manaus (Hilbert 1968, cited by Eden et al. 1984).

The amounts, extent, and dates of charcoal found in the well-developed tierra firme forests of the URN may be explained by the agricultural system of shifting cultivation used in the area. This agricultural system was developed by the inhabitants of tropical forests thousands of years ago (Lathrap 1970), and in the Amazon Basin it continues to be the most important form of subsistence farming (Lowie 1963). The area covered with tierra firme forests (farmable forest) in the URN is about 30% (Bennacchio 1981), which means agricultural land in this area is scarce. This explains the presence of charcoal on almost all tierra firme areas bordering major rivers and streams of the URN, where the human population has been concentrated for more than 3 millenia. This illustrates that charcoal in this area may also correspond to human occupation as a result of large populations or the cumulative effect of long term or occasional, sedentary Indian populations. Areas remote from population centers

need to be explored for charcoal presence, and additional charcoal samples need to be dated in order to provide more detailed information concerning the origin of charcoal in this area.

Radiocarbon dates from the three tierra firme forests indicate that they have burned twice in the last 600 years (Table 3.3, page 35). The differences in basal area and biomass among these three mature forests appear to be related to time since burning. The dates represent the accumulated age of the woody tissues at the time of the fire. The dates indicate that stand XII was burned for the last time 350 $\pm$ 70 years B.P. (Table 3.3, page 35). Its basal area varied between 36.95 and 40.75 m^2/ha (Table 4.5, page 58), and biomass ranged between 271.20 and 325.77 t/ha (Table 4.3, page 55). In contrast, stands XI and IVIC had the last fire disturbance 250 years ago (Table 3.3, page 35). Their basal areas ranged from 19.10 to 36.21 m^2/ha, respectively, and biomass varied between 134.62 and 263.60 t/ha, respectively. The differences in basal area and biomass may be attributed to the number of years since the last severe disturbance in each stand as suggested by radiocarbon dates of charcoal in each forest.

SUMMARY

Charcoal was found in most of the tierra firme forests surveyed in the URN. Its distribution in soil is very uneven with large variations in amounts among depths at the same site. Nevertheless, 90% of the charcoal in the top meter of soil is found in the upper 50 cm. Charcoal weight ranges from 3 to 24 t/ha.

Dates of charcoal from radiocarbon determinations varied between present time and 6260 years B.P. Dry phases recorded during the Holocene in other locations in South America and Central Amazonia coincide with several of the charcoal dates found in the URN.

Ceramic pot shards were found at two stands. Thermoluminescence analysis indicates that the age of two of the ceramic pieces are 460 and 3750 years B.P. The 3750 date is the oldest reported for any artifact from interior Amazonia.

Charcoal presence in the moist, tropical forests of the URN indicates that this region has been subjected to fire disturbance as a result of extreme dry periods, human disturbances, or interaction of both climate and humans. The charcoal dates suggest the occurrence of fire in this forest for the last 3000 years.

CHAPTER 4

DIVERSITY AND STRUCTURE

INTRODUCTION

Amazonia covers approximately 6 million square kilometers and is the largest area of tropical forests on earth. Large tracts of Amazon forests have been cut in the last 50 years to make way for pasture and crops (National Academy of Sciences 1980). Such deforestation of extensive areas covered by forests is leading to the disappearance of countless plant and animal species which may represent a genetic resource of inestimable value. Moreover, this widespread deforestation is hindering research of processes and mechanisms of succession following natural or anthropogenic disturbances.

In temperate areas, several investigators have tried to explain succession. Classical concepts of plant succession (Clements 1916, Weaver and Clements 1937) assume that following disturbance, an orderly process of successional patterns occurs. More recent work (Egler 1954, Drury and Nisbet 1973, Bormann and Likens 1981, Peet and Christensen 1980) suggests that at early stages of succession all plants, including those that are dominant in later stages, are present, and the change in species composition is a thinning process. Several researchers (Boerboom 1974, Swaine and Hall 1983) have observed similar patterns in early stages of succession on tropical sites, but this study documents a different conclusion.

Some studies have documented ecosystem recovery in terms of floristic and structural composition after the use of shifting

cultivation (Uhl et al. 1981, Uhl and Jordan 1984). An extensive description of changes in species composition and structure on successional vegetation has been made, mainly in Central America (Budowski 1961, Blum 1968, Knight 1975). Recently, an autoecological study of several tree species was conducted in Costa Rica (Herwitz 1981). Several studies have been conducted on mature forests of Amazonia primarily from a structural (Takeuchi 1961) and phytosociological standpoint (Black et al. 1950, Pires et al. 1953, Cain et al. 1956).

The objectives of this chapter are: (1) to document changes in species diversity and floristic composition through time following slash-and-burn agriculture; (2) to describe the changes in structure through time; and (3) to determine the time required for abandoned farms to attain a basal area which approximates that of a mature forest.

METHODS

Species Identification

Species identification was made by local woodmen who have been working with the San Carlos project for the last 7 years. Tree identification was based on stem shape, leaf type and texture, color and odor of the bark and wood, and presence of latex or other types of sap. A reference collection was organized with specimens taken at each site and common names assigned. Generally, classification of the species was accurate, but in some cases several species were classified under one name. Clarification was accomplished by comparison with the reference collection. For new species, common names were assigned and

used for future identification. The collected specimens were sent for identification to Howard Clark at the Institute of Ecology, University of Georgia, and to Marcano Verty, Universidad de los Andes, Merida, Venezuela.

Species Diversity

Differences in species diversity among fallows of different ages were examined to determine the changes of species richness and abundance through time. The following determinations were made separately for all trees having a dbh > 1 cm and for those with a dbh $\geq$ 10 cm: (1) total number of species; (2) species-area curve; (3) Simpson's index of dominance in the community,

$$D = 1 - \Sigma_{i=1}^{S} (P)_i^2 ,$$

where P_i = proportion of individuals of the i^{th} species in the community, and S is the number of species in the sample (Simpson 1949); (4) Shannon-Wiener index of general diversity,

$$H = - \Sigma_{i=1}^{S} P_i \log_2 P_i,$$

where P_i and S are the same as above; and (5) the importance value (IV) index (Curtis and McIntosh 1951). The relative importance value (RIV) was calculated for each species by dividing the IV of each species by the total IV of all species in the stand.

Structure

Various measurements were taken of the individual trees in each stand. Diameter was measured at 130 cm or above buttresses,

whichever was lower. Total height and height to the base of the crown were measured with a 10-m pole or estimated by eye and periodic checks with an Haga altimeter. The height to the base of the crown was measured at the first line branch or stem fork, whichever was lower. Crown maximum and minimum diameter was appraised by eye with periodic checkings done by stretching a surveyor's tape between points directly below the edges of the crown.

A two-dimensional profile diagram was constructed for two successional stands, 11 and 40 years old, and an MTF (Richards 1952). Features used for this representation were total height, height to the first branch or fork, and maximum and minimum diameter of the crowns. In three, 10- x 30-m, plots within each stand, all trees $\geq$ 10 cm dbh that had visibly damaged crowns were counted. Standing dead trees with a dbh $\geq$ 10 cm were recorded in one, 50- x 50-m plot.

Leaf samples from each of 44 trees were collected and pressed. They were oven dried, weighed, and their surface area calculated by using a LI-COR area meter model LI-3100. Linear regressions were developed to estimate leaf area based on leaf dry weight. The general model has the following form:

$$Y = a + b X \quad ,$$

where Y is the leaf area of the whole tree, and X is the leaf weight. Separate regressions were developed for palms, Heliconia spp., and all other tree species. Leaf area calculations for stands were made by placing the trees into one of the three groups mentioned above. Leaf area by group was summed for each stand and expressed in m^2/ha.

RESULTS

Species Diversity Changes Through Time

Among the trees $\geq$ 1 cm dbh on the 2.1 ha of cumulative plot area, approximately 290 tree species were identified; 141 species had a dbh $\geq$ 10 cm (Table 4.1). The species number increases from 10-year-old fallows to MTF, e.g., 33 to 96 species were found when considering trees $\geq$ 1 cm in contrast to 5 to 30 species for trees $\geq$ 10 cm dbh. The ratio, number stems/number species, drops more sharply for trees $\geq$ 1 cm than for those $\geq$ 10 cm dbh when considering young and old stands. For example, when including the smaller size class, a mean of 11 stems/species was found in the 10-year-old stands, and a mean of 5 stems/species was found for MTF stands. When trees $\geq$ 10 cm dbh are considered, the number of stems/species show small differences between young and MTF stands, i.e., the mean for 10-year-old stands is 4 compared to 2 for the MTF.

Diversity (H) ranges from 3.32 to 5.90 for the successional stands (Table 4.1). In MTF, it varies between 4.75 and 5.45. The data show little if any trend. The Simpson index indicates that dominance is high for the 10-year-old stands, declines somewhat at 20 years, and remains more or less constant thereafter. The ratio, E, of H and H_{max} (Brower and Zar 1984) indicates a relatively high degree of species eveness. Figure 4.1 shows that there was a sharp increase in cumulative species number each time a new stand was surveyed.

Table 4.1

Stand density, number of species, ratio for number of stems/number of species, and diversity index values. Values are totals calculated from three, 10- x 30-m, plots.

Stand	Years since disturbance	No. of stems		No. of species		No. stems/no. species		Diversity index (stems ≥ 10 cm)			
		dbh ≥ 1 cm	dbh ≥ 10 cm	dbh ≥ 1 cm	dbh ≥ 10 cm	dbh ≥ 1 cm	dbh ≥ 10 cm	Simpson's index	Shannon-Wiener H	H_{max}	Index* E
I	9	621	21	50	5	12.42	4.20	0.89	3.86	5.64	0.68
II	11	458	17	33	8	13.88	2.12	0.85	3.32	5.04	0.66
III	12	485	58	43	15	11.28	3.87	0.90	4.10	5.42	0.76
IV	14	472	27	56	7	8.43	3.86	0.94	4.63	5.81	0.80
V	20	649	54	65	15	9.98	3.60	0.94	4.84	6.02	0.80
VI	20	953	25	76	17	12.54	1.47	0.94	5.01	6.24	0.80
VII	20	498	38	50	11	4.98	3.45	0.93	4.49	5.64	0.79
VIII	20	458	49	63	24	7.27	2.04	0.89	4.38	5.97	0.73
IX	30	629	29	77	13	8.17	2.23	0.96	5.18	6.27	0.83
X	35	389	49	68	19	5.72	2.58	0.94	4.98	6.08	0.82
XI	35	450	53	70	18	6.43	2.94	0.96	5.30	6.12	0.87
XII	40	487	63	75	16	6.49	3.93	0.96	5.38	6.22	0.86
XIII	60	221	32	62	13	3.56	2.46	0.96	5.25	5.95	0.88
XIV	60	285	43	70	25	4.07	1.72	0.94	4.89	6.12	0.80
XV	60	267	44	66	23	4.04	1.91	0.95	5.09	6.04	0.84
XVI	80	323	54	72	17	4.49	3.18	0.95	5.18	6.16	0.84
XVII	80	471	74	73	25	6.45	2.96	0.96	4.94	5.98	0.83
XVIII	80	287	58	60	30	4.78	1.83	0.94	5.90	6.58	0.89
XIX	80	354	50	79	22	4.48	2.27	0.97	5.02	6.04	0.83
XX	MTF	272	51	75	30	3.63	1.70	0.96	5.30	6.23	0.85
XXI	MTF	394	55	66	14	5.97	3.93	0.95	5.45	6.30	0.86
XXII	MTF	478	51	96	28	4.45	1.82	0.97	4.75	5.91	0.81
XXIII	MTF	264	48	63	23	4.19	2.09	0.95	5.25	6.19	0.85

*$H_{max} = \log_2 S$; where S = number of species in the site, and $E = H/H_{max}$.

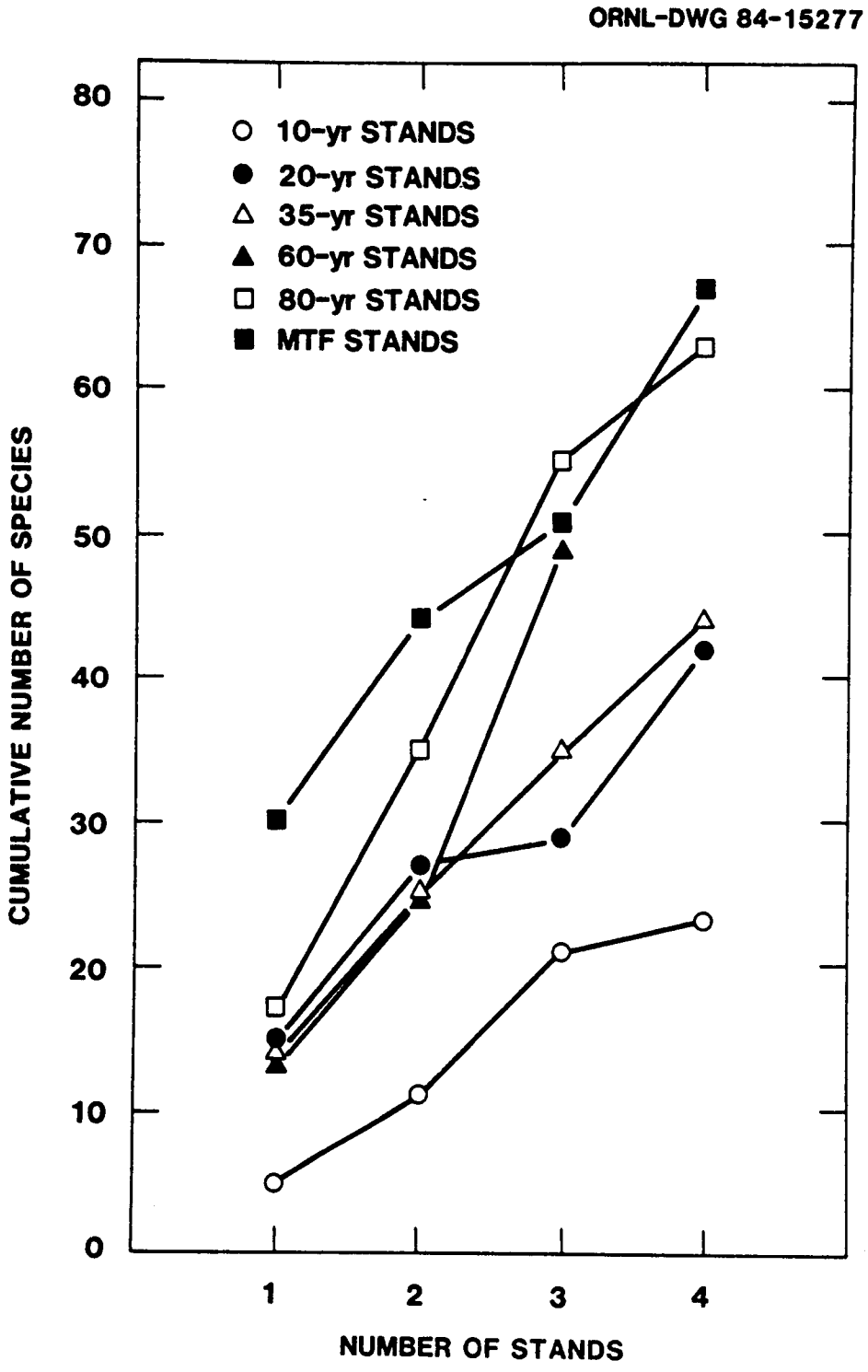

Figure 4.1. Relationship between cumulative number of species for stands of similar age in the Upper Rio Negro region of Colombia and Venezuela.

Species Dominance

The species are grouped according to their relative importance value (RIV). In the 10-year-old stands, two to five species comprise 60% of the RIV (Appendix Table A.1). Two species, Vismia japurensis and Bellucia grossularioides, have the highest RIV in three of the four 10-year-old stands. Both species together comprise approximately 60% of the number of stems and basal area of the stands. The remaining RIV is shared by three to 12 species depending upon the stand.

In 20-year-old successional stands, four to eight species comprise 60% of the RIV (Appendix Table A.2). Different species are dominant in each stand, and their RIV ranges from 11.41 for Inga sp. to 21.14 for Vochysia sp.; Vismia japurensis and Vismia lauriformis, two species from early stages of succession, are still among the dominant species on two of the four stands.

The RIV for the four, 30- to 40-year-old stands are presented in Appendix Table A.3. Humeria balsamifera and Eperua purpurea are the dominant species in density and basal area in three of the four stands. Humeria balsamifera comprises almost 40% of the RIV in stand XII. Other species (e.g., Bellucia grossularioides and Vismia japurensis) persist from earlier stages of succession. Four to six species constitute 60% of the RIV.

The RIV for 60-year-old stands ranges from 13.97 to 35.90 for the dominant species (Appendix Table A.4). The species with the highest RIVs are Eperua purpurea, Goupia glabra, and Vochysia obscura. The most visibly dominant species was Eperua purpurea, which represents 31%

of the number of stems and 58% of the basal area of stand XIII. Three to 10 species comprise 60% of the RIVs in the 60-year-old stands.

The dominant species in 80-year-old stands are presented in Appendix Table A.5. The RIVs of the most dominant species range from 13.40 to 22.68. Three species, Bellucia grossularioides, Alcornea sp., and Protium sp., were among the dominant ones found in three of the four stands. Seven to 11 species comprise 60% of the RIV.

The RIVs for the MTF species are shown in Appendix Table A.6. Five to 12 species comprise 60% of the RIVs. The higher RIVs vary from 10.58 to 21.74. Two species, Eperua purpurea and Swartzia schomburgkii, have values over 18% for number of stems and basal area in stands XXI and XXII, respectively.

Other Forest Characteristics

Most of the species of the mature forests and successional stands have well-formed, slender, and cylindrical stems. Some species attain a combination of buttress and root mass reaching more than 3 m up the trunk, e.g., Monopterix sp. and some palm species have prop roots. A few species grow buttresses between 0.50 and 1 m tall, e.g., Conceveiba guianensis and Micrandra sprucei.

Thirty to 40% of the individuals sampled in the mature forests produced a white to yellowish latex, a reddish sap, resins, or oils. These substances were found in Sapotaceae, Moraceae, Clusiaseae, Mimosaceae, Myristicaceae, Caesalpinaceae, Apocynaceae, and Fabaceae.

Wood samples of the dominant species were collected for density measurements. The wood was weighed, oven dried at 106°C, weighed again, and the density calculated and expressed as the relationship of

dry weight to volume. The density of dry wood increases from young stands to mature forests (Table 4.2). Mean values range from 0.50 g/cm^3 in stand III, 12 years old, to 0.66 g/cm^3 in stand XXIII, an MTF. One exception is stand XI that has a mean density of 0.63 g/cm^3. A possible explanation of its high density is the dominance of several species such as Humeria balsamifera, Bellucia grossularoides, and Goupia glabra which have a wood density between 0.60 and 0.67 g/cm^3.

Sprouting is more common in young secondary forests than in mature forests. Numbers range from 22 to 4516 sprouts/ha (Figure 4.2). Number of sprouts increases toward the 10- to 35-year-old classes and declines toward old secondary and mature forests. The exception was stand XIX which had 1644 sprouts/ha and 150 wind-damaged trees.

Tree Density by DBH and Height

Table 4.3 shows the distribution of stems by diameter class for the 23 stands. The total number of stems for trees with dbh < 1 cm and height > 1 m ranges from 8,799 to 21,942/ha, and for those trees with dbh $\geq$ 1 and height $\geq$ 2 m, the range is from 4,913 to 11,988/ha. The highest concentration of trees was found among the two smallest dbh classes (dbh $\leq$ 1 and 1 $\leq$ dbh < 5 cm). The total number of stems including sprouts in these two classes ranged from 6,776 to 20,180 (Table 4.3) representing 76 to 95% of the total number of stems on each stand.

The number of stems in the two smallest dbh classes represents 61 to 85% of the total with a maximum of 10,200 stems/ha in stand VI (Table 4.3). The number of stems in the 5- to 20-cm diameter class is

Table 4.2

Mean density of wood (oven dry) by stand.

Stand	Years since disturbance	Wood density (g/cm^3)
I	9	0.52
II	11	0.54
III	12	0.50
IV	14	0.59
V	20	0.54
VI	20	0.55
VII	20	0.53
VIII	20	0.54
IX	30	0.58
X	35	0.63
XI	35	0.58
XII	40	0.65
XIII	60	0.66
XIV	60	0.57
XV	60	0.58
XVI	80	0.57
XVII	80	0.60
XVIII	80	0.59
XIX	80	0.61
XX	MTF	0.67
XXI	MTF	0.65
XXII	MTF	0.64
XXIII	MTF	0.66

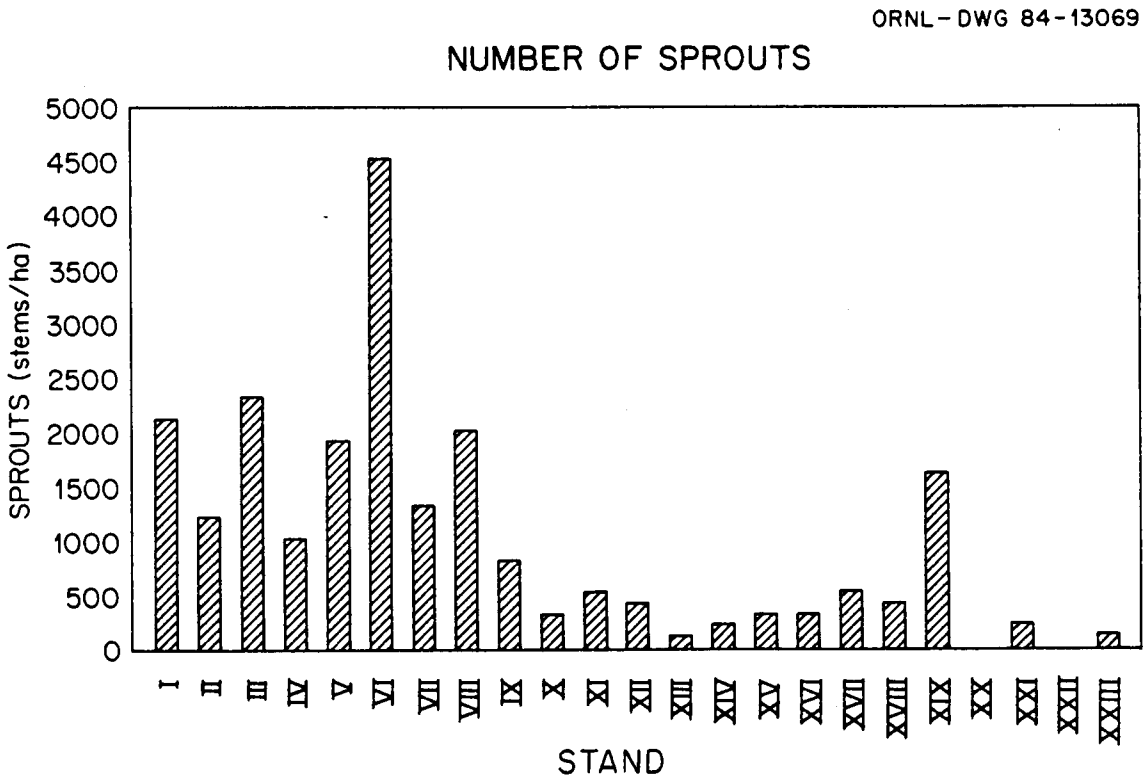

Figure 4.2. Number of sprouts in successional and mature forest stands in the Upper Rio Negro region of Colombia and Venezuela.

Table 4.3

Number of stems (by dbh) per ha. Values are totals of three plots (10 x 30 m) per stand except for XII and XVII which have four plots.

Stand	Years since disturbance	dbh class (cm)							Total	Total
		< 1	1 to < 5	5 to < 20	20 to < 40	40 to < 60	60 to < 90	≥ 90	≥ 1	all classes
I	9	2872	5144	1811	0	0	0	0	6955	9827
II	11	3354	3556	1889	0	0	0	0	5445	8799
III	12	5942	4111	1844	33	0	0	0	5988	11930
IV	14	5547	3544	1711	11	0	0	0	5266	10813
V	20	4977	5755	1645	33	0	0	0	7433	12410
VI	20	9954	10200	1788	0	0	0	0	11988	21942
VII	20	3420	3356	2145	44	0	0	0	5545	8965
VIII	20	6928	3767	1489	100	0	0	0	5356	12284
IX	30	8463	5722	1499	11	0	0	0	7232	15695
X	35	8134	6324	1302	121	0	0	0	7747	15881
XI	35	6687	6158	2056	78	0	0	0	8292	14979
XII	40	13600	6580	883	225	8	0	0	7696	21296
XIII	60	5393	3181	1566	155	11	0	0	4913	10306
XIV	60	5878	4684	800	165	66	0	0	5715	11593
XV	60	8354	4565	745	189	22	0	0	5521	13875
XVI	80	7126	4922	1233	155	11	0	0	6321	13447
XVII	80	6594	5528	1258	167	16	0	0	6969	13563
XVIII	80	4889	3971	1133	223	0	0	0	5327	10216
XIX	80	7411	5944	967	233	0	0	0	7144	14555
XX	MTF	8090	6158	1200	166	11	11	0	7546	15636
XXI	MTF	8485	6539	1133	121	55	11	0	7859	16344
XXII	MTF	9976	7751	1167	166	33	0	11	9128	19104
XXIII	MTF	5328	4660	945	99	44	0	11	5759	11087

large for the young stands, declining in number toward the MTF (Table 4.3). For trees 20 to 40 cm dbh, stems were concentrated in the old second-growth and MTF with fewer stems in most of the 20-year-old or younger stands (Table 4.3). Considering all stands, stems in the 40- to 60-cm dbh range are most prevalent in the older stands. These trees were present in 40-year-old and older stands with the exception of two of the 80-year-old stands (Table 4.3). Trees with dbh $\geq$ 60 cm were found only in the four MTF stands. Several trees in stand XXIII were more than 150 cm dbh, the largest being 213 cm dbh.

The number of stems was also grouped by height and placed in six height classes (Table 4.4). Stems < 1 cm dbh and 1 to 2 m in height represent 29 to 64% of the total number of stems. These values reach 48 to 82% of the total density for trees less than 4 m in height (Table 4.4). Trees $\geq$ 17 m in height were absent in six of the stands younger than 40 years. Trees taller than 26 m were missing in most of the successional stands except in stands XIV and XVII, 60 and 80 years old, respectively, but they were present in all MTF (Table 4.4).

Basal Area of Living Trees

Basal area was grouped into six dbh classes. Total basal area varied from 11.12 to 36.95 m^2/ha (Table 4.5). There were significant differences ($P \leq 0.05$) in total basal area between the means of MTF and successional stands (Appendix Table A.7). There were also differences between 60- and 80-year-old and the 10- and 20-year-old stands.

Basal area of trees smaller than 5 cm dbh ranged from 1.56 to 5.20 m^2/ha (Table 4.5). Significant differences ($P \leq 0.05$) were

Table 4.4

Number of stems ≥ 1 m in height per ha. Values are totals of three plots (10 x 30 m) per stand except for XII and XVII which have four plots.

Stand	Years since disturbance	Height classes (m)						
		1 to < 2	2 to < 4	4 to < 9	9 to < 17	17 to < 26	≥ 26	Total
I	9	2872	1833	4789	333	0	0	9827
II	11	3354	1012	2833	1600	0	0	8799
III	12	5942	1755	2900	1300	33	0	11930
IV	14	5547	1611	2911	744	0	0	10813
V	20	4977	2556	3600	1266	11	0	12410
VI	20	9954	4955	5933	1100	0	0	21942
VII	20	3420	1267	2767	1489	22	0	8965
VIII	20	6928	1589	2844	889	34	0	12284
IX	30	8463	3089	3200	943	0	0	15695
X	35	8134	3876	2871	1000	0	0	15881
XI	35	6687	3827	3281	1082	102	0	14979
XII	40	13600	3967	2837	651	241	0	21296
XIII	60	5393	2278	1688	747	200	0	10306
XIV	60	5878	2911	2027	522	244	11	11593
XV	60	8354	3028	1815	611	67	0	13875
XVI	80	7126	3420	1795	906	200	0	13447
XVII	80	6594	3358	2510	684	392	25	13563
XVIII	80	4889	2091	2258	711	267	0	10216
XIX	80	7411	3700	2600	700	144	0	14555
XX	MTF	8090	3683	2853	711	288	11	15636
XXI	MTF	8484	4016	2754	790	211	89	16344
XXII	MTF	9976	4445	3513	793	255	122	19104
XXIII	MTF	5328	3338	1517	727	133	44	11087

Table 4.5

Forest tree basal area (m^2/ha) by dbh classes (cm). Values are totals of three, 10- x 30-m, plots for all size trees and one, 50- x 50-m, plot for trees ≥ 10 cm dbh.

Stand	Years since disturbance	dbh class (cm)							
		1 to < 5	5 to < 20	20 to < 40	40 to < 60	60 to < 90	≥ 90	Total	Total (50- x 50-m plot)
I	9	3.34	7.83	0.00	0.00	0.00	0.00	11.17	NR*
II	11	2.35	9.17	0.00	0.00	0.00	0.00	11.52	NR
III	12	2.50	13.63	1.18	0.00	0.00	0.00	17.31	NR
IV	14	2.17	8.58	0.37	0.00	0.00	0.00	11.12	NR
V	20	3.44	12.69	1.37	0.00	0.00	0.00	17.49	NR
VI	20	5.20	9.25	0.00	0.00	0.00	0.00	14.45	NR
VII	20	2.17	12.98	1.91	0.00	0.00	0.00	17.06	NR
VIII	20	2.38	10.63	5.69	0.00	0.00	0.00	18.70	NR
IX	30	2.84	8.46	0.40	0.00	0.00	0.00	11.71	8.33
X	35	2.54	10.78	6.29	0.00	0.00	0.00	19.62	12.61
XI	35	3.01	13.88	3.18	0.00	0.00	0.00	20.07	8.97
XII	40	2.63	7.51	11.73	1.11	0.00	0.00	22.97	14.84
XIII	60	1.56	6.15	8.43	1.55	0.00	0.00	17.68	21.91
XIV	60	2.32	5.91	12.23	10.58	0.00	0.00	31.03	22.00
XV	60	2.06	6.33	11.71	4.64	0.00	0.00	24.74	23.23
XVI	80	2.19	9.66	8.30	2.16	0.00	0.00	22.34	18.61
XVII	80	2.21	10.76	10.31	3.16	0.00	0.00	26.45	25.71
XVIII	80	1.97	8.61	13.34	0.00	0.00	0.00	23.91	19.59
XIX	80	2.90	7.62	12.68	0.00	0.00	0.00	23.21	18.24
XX	MTF	2.59	10.05	10.63	2.96	4.22	0.00	30.44	31.98
XXI	MTF	2.99	9.52	8.60	11.21	3.30	0.00	35.62	26.66
XXII	MTF	3.05	9.49	10.04	4.90	0.00	8.73	36.21	19.10
XXIII	MTF	2.05	8.21	6.26	7.48	0.00	12.95	36.95	40.75

*NR = not recorded.

only found between the means of 60- and 20-year-old stands (Appendix Table A.7).

Trees 5 to 20 cm dbh have high basal area among some of the stands younger than 40 years and low values among the 60-year-old group. Basal area for this size category ranges from 5.91 to 13.88 m^2/ha (Table 4.5) and represents 55 to 79% of the total basal area of stands younger than 40 years. There were significant differences ($P \leq 0.05$) between the means of the 60-year-old stands and the other stands including the MTF (Appendix Table A.7).

Trees 20 to 40 cm dbh are concentrated in the older successional stands and MTF. The basal area values range between 0 and 13.34 m^2/ha (Table 4.5) which represents 37 to 55% of the total basal area for 60- and 80-year-old successional stands and 17 to 35% for those of the MTF. There were significant differences ($P \leq 0.05$) between the basal area values of stands 60 and 80 years old and those 35 years old and younger (Appendix Table A.7).

Basal area of trees 40 to 60 cm dbh ranged from 0 to 11.21 m^2/ha (Table 4.5). Trees in this size category represent 10 to 34% of the total basal area on 60-year-old and MTF stands. Trees with a dbh larger than 60 cm were only recorded in the MTF. Their values ranged from 3.30 to 12.95 m^2/ha (Table 4.5) and represent from 9 to 35% of the total basal area.

Total basal area of standing dead trees ranges from 0.41 to 4.50 m^2/ha with the largest values in the 80-year-old stands and one MTF (XXI). Basal area values for dead trees of 1.54 and 1.58 m^2/ha were found among trees 40 to 60 cm dbh on stand XIII and XVII, 60 and

80 years old, respectively. Stand XXI, a mature forest, has a standing dead tree basal area of 2.15 m^2/ha when considering trees 20 to 40 cm dbh.

Basal area values for all stands were fit to a linear and a logarithmic regression to estimate the time required for an abandoned farm to gain similar values of an MTF (Figure 4.3). Results, using both regressions, are as follows:

$$Y = 12.47 + 0.16\ X$$
$$(n = 19,\ r^2 = 0.60,\ P < 0.0001,\ CV = 19.21\%);\ \text{and}$$
$$\ln Y = 1.75 + 0.34\ \ln X$$
$$(n = 19,\ r^2 = 0.65,\ P < 0.0001,\ CV = 6.46\%)\ ,$$

where Y is the mean basal area in m^2/ha, and X is age in years (Appendix Table A.7). By solving for X with the above regression coefficients, where Y is equal to 34.80 m^2/ha (mean basal area of four MTF), the time required for the basal area of a successional forest to attain the basal area of an MTF is 140 years using the linear model and 199 years using the logarithmic model.

Tree Height and Diameter

Figure 4.4 depicts a sigmoid relationship between tree height and dbh. According to the data, a tree with a smaller dbh reaches the canopy and may reach the plateau of the curve with a dbh of 30 to 40 cm.

Several regressions were used to determine the best estimator of tree height as a function of dbh. The most satisfactory result was obtained using a regression equation of the following form:

$$H = 2.95 + 1.43\ D - 0.02\ D^2\ ,$$

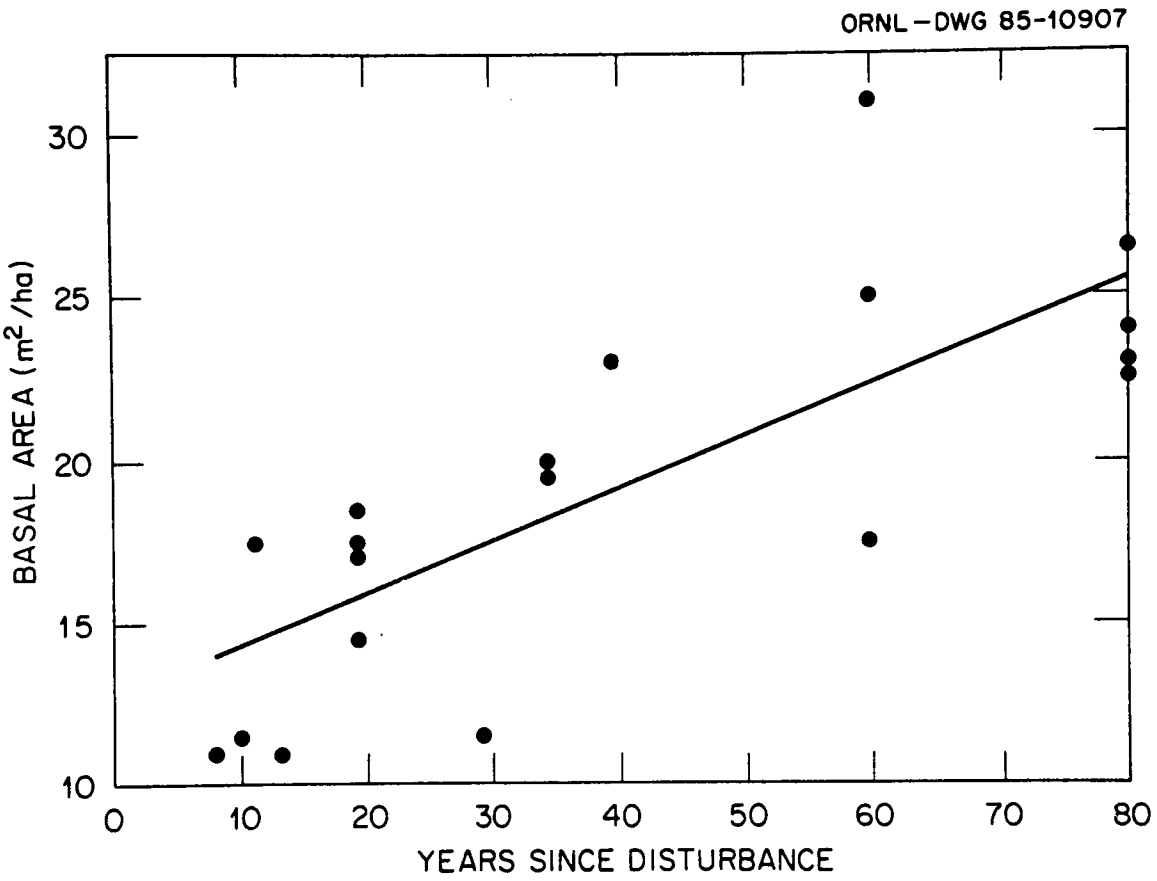

Figure 4.3. Relationship between basal area (m^2) and time (years since disturbance) in the Upper Rio Negro region of Colombia and Venezuela.

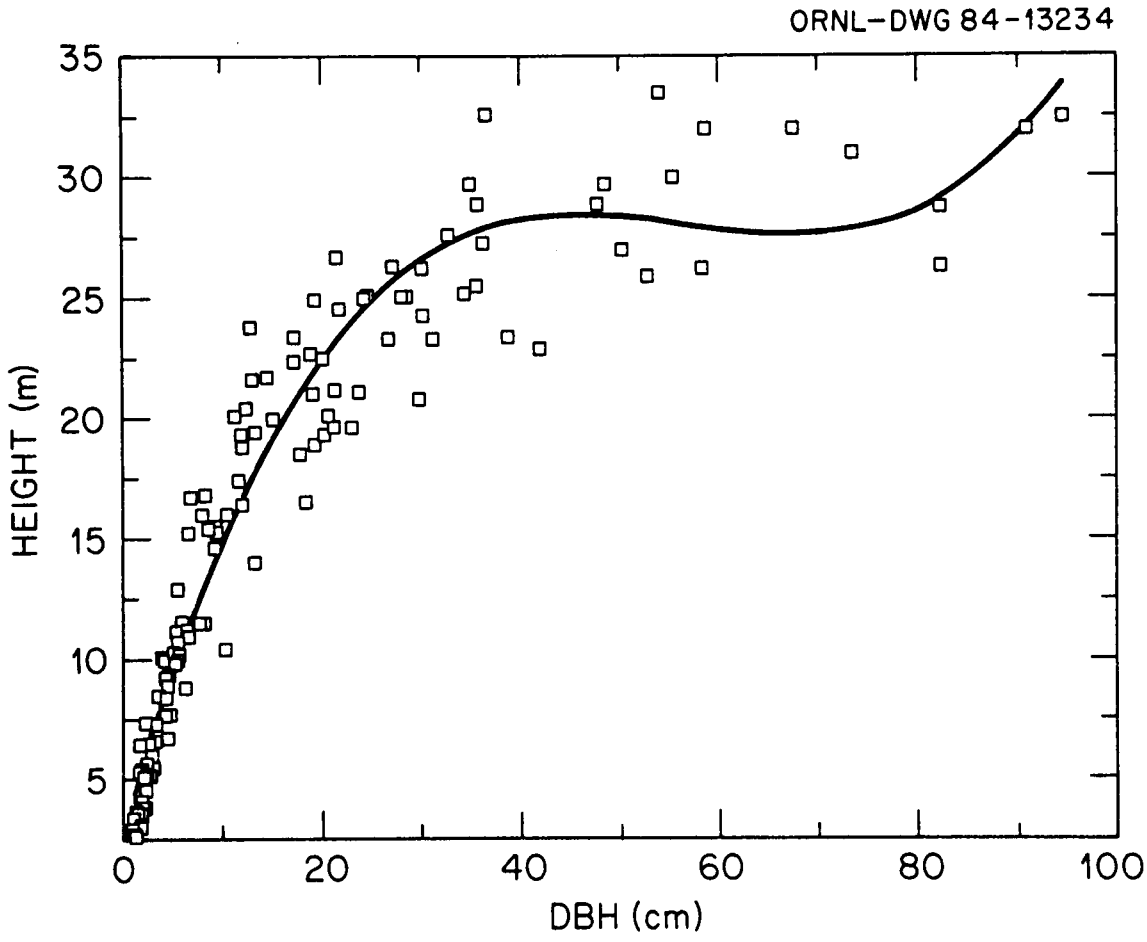

Figure 4.4. Relationship between height and dbh of trees in the Upper Rio Negro region of Colombia and Venezuela. The regression equation is $H = 2.95 + 1.43\ D - 0.02\ D^2$, where H = height (m) and D = dbh (cm). The regression was statistically significant ($P < 0.0001$).

with n = 131, r^2 = 0.92, P < 0.0001, CV = 24.06%, maximum dbh = 94 cm, and minimum dbh = 1 cm, where H is tree height and D is dbh. There is closer agreement between the observed heights and the predicted values, generated by the model, for diameters $\leq$ 60 cm than for larger trees.

Stratification

Figure 4.5a depicts the profile of an 11-year-old stand. The trees at the left are adjacent to an MTF. They are 10 to 13 m tall, and 6 to 12 cm dbh. Toward the middle of the stand, trees are 6 to 9 m tall and 5 to 10 cm dbh with several standing dead trees. At the right, trees are 8 to 10 m tall and 6 to 12 cm dbh. The shallow depression in the middle of the diagram reveals the apparent effect of more intense land use. The stand has one layer with tree crowns lying principally between 5 and 12 m with some palm and Heliconia spp. crowns between 3 and 6 m.

Figure 4.5b depicts a 40-year-old stand. The forest has two distinguishable layers. The upper layer is formed by a regular canopy approximately 14 to 19 m in height. Several trees have broad crowns as a result of multiple stem sprouts. The second layer is 9 to 14 m in height.

Figure 4.5c represents the profile of an MTF. The upper stratum is formed by a scattering of large trees reaching 35 m in height and 120 to 213 cm dbh with irregularly shaped crowns lying in the 18- to 35-m stratum. Below this layer are a few trees 10 to 14 m tall with conic crowns. To the left of the tallest trees, there is a gap and a mixture of trees with heights varying from 10 to 25 m. Below 9 m,

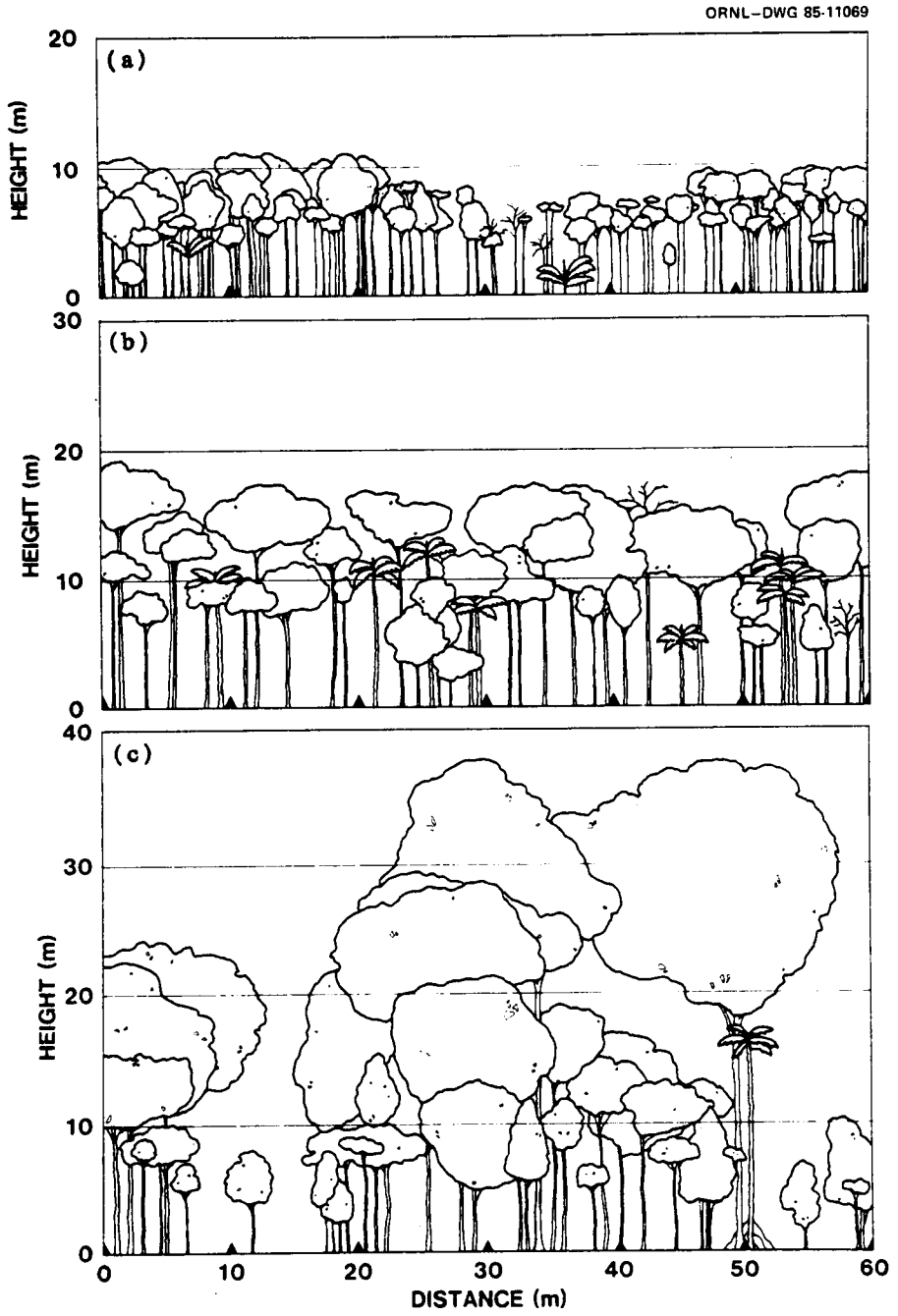

Figure 4.5. Profiles of three tierra firme forests in the Upper Rio Negro region of Colombia and Venezuela. The diagram represents a strip 7.6 x 60 m; (a) forest 11 years old; (b) forest 40 years old; (c) mature forest.

there are several trees with small round and conic shapes without a layered pattern.

Leaf Area Index (LAI)

Leaf area was estimated by using three allometric regressions; one for Heliconia spp., one for palms, and one for all other tree species (Table 4.6). Leaf area index varies from 4.93 to 7.66 m^2/m^2 for successional stands and from 6.90 to 7.88 m^2/m^2 for MTF (Table 4.7).

Table 4.6

Regression equations used for calculations of leaf area index (Y = leaf area and X = leaf biomass).

Type of tree	Equation	r^2	CV (%)	n
Heliconia spp.	Y = 0.141 + 3.330 X	0.99	4.60	10
Palms	Y = 6.535 + 3.387 X	0.98	13.19	18
Other tree species	Y = 10.202 + 6.151 X	0.94	32.69	80

Damaged and Dead Trees

The number of trees with broken crowns varied from 0 to 150/ha. The highest numbers, 131 and 150, were found in stands XVII and XIX, respectively (Appendix Table A.8). In the MTF the number of damaged trees ranged from 12 to 43. Standing dead trees were found in the successional stands as well as in the MTF. The largest numbers were detected in stands 80 years old (Appendix Table A.8). Mature forests have 20 to 44 dead trees.

Table 4.7

Leaf area index (LAI) of three tree species groups.

Stand	Years since disturbance	LAI (m^2/m^2)			
		Palms	*Heliconia* spp.	Other tree species	Total
I	9	0.68	0.00	5.25	5.93
II	11	0.83	0.00	4.69	5.52
III	12	0.65	0.03	5.75	6.43
IV	14	0.75	0.00	4.67	5.42
V	20	1.63	0.09	5.63	7.35
VI	20	0.82	0.01	6.78	7.66
VII	20	1.73	0.39	4.12	6.24
VIII	20	0.90	0.00	5.52	6.42
IX	30	0.66	0.00	5.18	5.84
X	35	0.87	0.00	5.95	6.82
XI	35	1.16	0.20	6.03	7.39
XII	40	0.90	0.00	5.50	6.40
XIII	60	0.98	0.00	3.95	4.93
XIV	60	0.80	0.00	5.46	6.26
XV	60	0.82	0.00	4.89	5.71
XVI	80	1.10	0.01	5.17	6.28
XVII	80	1.07	0.00	5.56	6.63
XVIII	80	1.24	0.00	4.67	5.91
XIX	80	0.78	0.00	5.92	6.70
XX	MTF	0.92	0.00	6.54	7.46
XXI	MTF	0.74	0.00	7.04	7.78
XXII	MTF	1.07	0.00	6.81	7.88
XXIII	MTF	0.72	0.00	6.18	6.90

DISCUSSION

The number of species increases from early successional stands to MTF with the most rapid increase in the first 10 years. Then, the species number remains relatively constant toward MTF. Similar results were reported by Knight (1975) on Barro Colorado Island. His study indicated a rapid increase in species richness during the first 10 to 15 years. However, he suggested that the number of species may continue increasing very slowly after 50 to 60 years. Uhl and Jordan (1984) studied succession on a cut and burned area in the URN and reported that 56 tree species occurred at five years. Their species number is higher than three of the 10-year-old stands in this study but is similar to the number found in stand IV. The lower numbers in the present study can be explained by the use of the land for agriculture for four years while Uhl and Jordan's plots were cut and burned and allowed to succeed.

In the URN, 67 tree species $\geq$ 10 cm dbh were encountered in an area of 3600 m^2. This value is low compared to other studies in Amazonia taking into account trees of the same size. For example, Black et al. (1950) reported 79 and 87 species on two, 1-ha, plots; Pires et al. (1953) reported 179 species on a 3.5-ha plot; Prance et al. (1976) found 179 species > 15 cm dbh and 235 species > 5 cm dbh in 1 ha. The last figure represents the highest value recorded for a neotropical lowland forest.

The species area curves (Figure 4.1, page 49) show that a considerable number of additional species will be found for each older

age category sampled. The accumulated number of species of trees > 10 cm dbh is 141 for the URN.

The average Shannon-Wiener diversity values in the URN range from 3.98 to 5.19 for four 10-year-old and four MTF stands, respectively (Table 4.1, page 48). These values present small differences from those reported by Knight (1975) and close to values calculated by Uhl and Murphy (1981). Knight's values for seven young and five old forest stands on Barro Colorado Island, Panama, ranged from 4.4 to 5.4, respectively; Uhl and Murphy (1981) reported 5.17 for three mature forests near the study area. The Simpson index in the study area varies from 0.90 to 0.96 which is very close to the values of 0.92 and 0.95 reported by Knight, and Uhl and Murphy.

Traditional shifting cultivation involves the clearing of small, isolated plots and converting the forests into cultivated land. Not only is the original vegetation destroyed, but the site is subjected to continued perturbation by fire, cropping, and weeding.

Several works in temperate areas (Egler 1954, Drury and Nisbet 1973, Horn 1976, Heinselman 1981) suggest that long-lived, primary forest species establish together with pioneer species. The species dominants in the later stages are the result of a prolonged thinning process taking into account differential growth and survival of each individual.

In this study the number of primary tree species (dbh $\geq$ 1 cm) on 10-year-old stands is less than one-half of the total found in the mature forests. Primary tree species increases with the age of the stand. Species recruited as pioneers die during the first 20 years.

Later, new species enter as gaps are produced by tree falls. The species composition and dominance at each stand seems to be determined randomly. The species composition of the mature forest depends on a small fraction of primary species able to survive from early stages of succession and on the introduction of many primary tree species at later stages of succession.

Once the stand is abandoned for agricultural use, several species that are aggressive colonizers and have competitive ability cover the ground. Uhl (1982a) reported that farms which are abandoned are covered by forbs, herbs, grasses, and some successional woody plants within 4 months. Other woody species that are dispersed by birds and small mammals begin colonizing the area. A few trees from the original forests may produce shoots, sprouting from stems and roots (Ducke and Black 1953, Snedaker 1970, Uhl et al. 1981), and the surrounding forest serves as a seed source to promote regeneration. Five years later, 10 to 20 woody species may occupy one abandoned area (Uhl 1983).

In the present study, 87 species were found (dbh $\geq$ 1 cm) among the four, 10-year-old, stands. Each stand had from 33 to 56 species (Table 4.1, page 48). After 30 to 40 years, species such as Humeria balsamifera, Epeura purpurea, Vochysia sp., and Goupia glabra began to increase in number and basal area (Appendix Table A.3). At this stage the early successional species are replaced by groups of other fast growing and more persistent species such as Vochysia sp., Alcornea sp. and Jacaranda copaia. These species can attain 40 cm dbh and 25 m height at 30 years. These species will become dominant in the number

of stems and basal area for the next 50 years and in some cases may continue to be important in the MTF.

Major floristic changes take place on 40- to 80-year-old stands. Species such as Conceveiba guianensis, Goupia glabra, Vochysia obscura, Vochysia sp., and Alcornea sp. are dominant in basal area and biomass. The most important changes at this stage are senescence of previously dominant species, tree falls, and reduction of the importance value of the early dominant species. Dominance is then attained by some of the MTF species (Eperua purpurea, Swartzia schomburgkii, Micrandra sprucei, Monopterix sp., and Licania sp.). The intensity of disturbance produced by the replacement of the dominant trees determines which species next occupy the fallow. In the study area there are stands that demonstrate the variation in time required for the introduction of mature forest species. Stand XIV is an example of the replacement of canopy dominants without producing dramatic changes in the structure of the forest. In this stand, dead trees and tree falls are absent. This implies the stand is approaching the composition of mature stages. Absence of gaps in this stand could be attributed to the fact that the dominant species in the canopy have not reached senesence.

In contrast, 60- to 80-year-old stands have high concentrations of dead biomass, dead trees (Appendix Table A.8), tree falls, and species from earlier stages of succession. These findings indicate extensive alterations in the structure and composition of the forests and may delay the introduction of species from mature forests.

Mature forests are characterized by a large number of tree species. There were 155 tree species with dbh $\geq$ 1 cm found among the

four MTF. According to the assessment of dominance measured by the IV, no single species expresses dominance for these MTF. However, the IV for trees $\geq$ 10 cm dbh shows that some species are co-dominants. For example, Eperua purpurea and Protium sp. together represent 49% of the number of stems and 48% of the basal area on stand XXI. High values were also found for Swartzia schomburgkii and a leguminoseae on stand XXIII (Appendix Table A.6). Similar results were found by Uhl and Murphy (1981) in one tierra firme forest in the same region where Licania sp. reached an importance value of 19.1. In general, the data suggest that the IV decreases from succession to MTF because of the increase in the number of species from successional to MTF.

Differences in IVs among dominant species were common in the successional fallows as well as MTF stands. Species that are common in one stand can be rare or absent in another of the same age. This implies that chance events related to dispersal and establishment may largely determine which species are present on a given stand. Uhl and Murphy (1981) and Prance et al. (1976) working in two tierra firme forests in Amazonia found similar patterns of species distribution.

The secondary and mature forest vegetation of the URN is characterized by numerous small trees. The distribution of the number of stems by dbh class is represented by a reversed J-shaped curve, often with trees missing in the large size classes. Tree density by dbh and height classes is very similar in all stands. Most of the trees (80% or more) do not reach 5 cm dbh or 9 m in height; less than 3% have a dbh greater than 20 cm and are taller than 17 m. The main

difference between dbh and height is that more trees reach the canopy than trees attaining the larger dbh classes (> 60 cm dbh).

Stands that are older than 40 years have similar numbers of canopy trees in the 17- to 26-m height range. However, canopy dominants (> 26 m height) are more numerous in MTF stands. Height of the trees seems to indicate that the trees gain greater elongation with small dbh, i.e., a tree with only 5 cm dbh is $\sim$ 12 m tall and with 30 cm dbh is $\sim$ 27 m tall. Several species (Licania spp., Eschweilera sp., Protium sp., Ocotea sp., Xilopia spruceana and others) reach the canopy with 25 or 33% of their maximum dbh.

Similar stem distribution by dbh was observed in La Selva, Costa Rica (Hartshorn 1978). More than 14% of the trees there attain at least 40 cm dbh compared to less than 1% in the URN. Hartshorn (1978) attributed the low stem density in one large dbh class to the high frequency of natural tree falls which prevents most trees from attaining large diameters.

In the URN the large number of small individuals (up to 11,000 trees/ha < 5 cm dbh) in all stages of succession is a result of species strategies for survival in a dynamic ecosystem that is caused by low soil nutrient availability. Trees appear to germinate, establish, and then remain as seedlings and saplings for a comparatively long period of time. The establishment of new individuals depends upon the dynamics of replacement in the upper strata and the ability of seedlings and saplings to survive under limited conditions. Canopy positions are attained by either those trees that can grow fast for short periods of time and can take

advantage of disturbance or those trees that grow slowly over long periods of time and are not affected by natural disturbance.

Among mature forests in lowland regions of the Amazon Basin, the distribution of stems by dbh class varies considerably. Uhl and Murphy (1981) reported large tree density for trees > 10 cm dbh; Black et al. (1950), Pires et al. (1953) and Takeuchi (1961) found trees with 10 to 20 cm dbh at a low density and trees > 40 cm dbh with high density values (Table 4.8). Tree density in the Amazon forests compared with that of Ecuador shows low numbers mainly among trees > 20 cm dbh. The Ecuadorian forests of Armenia Vieja contains up to 40% more stems through all size classes than the URN forests. Density differences among these forests apparently reflect variability due to soils, structure, microrelief, and frequency of disturbance. Table 4.8 shows that the ratio between diameter classes, A (dbh $\geq$ 10 cm) and B (dbh $\geq$ 20 cm), was generally larger for the URN than for the other forests in Central Amazon, Ecuador, and British Guiana.

The number of trees > 10 cm dbh in successional and MTF stands in the URN shows an increase in density toward the old successional and mature forest stands with high variability in the large size classes (dbh $\geq$ 40 cm). The ratio of small versus large trees was high for 10-year-old stands, 15.27, and low for older stands and MTF, 2.20 and 3.16, respectively (Table 4.8). Late successional stands have a lower ratio value than the MTF because of the presence of more trees 20 to 40 cm dbh in the successional stands than in the MTF.

The mean basal area in the URN ranged from 12.78 m^2/ha (S.E. = 1.51) in 10-year-old stands to 34.80 m^2/ha (S.E. = 1.48) in the MTF

Table 4.8

Forest tree density by size class for tropical lowland and tierra firme forests at several sites in the Amazon Basin and elsewhere. Numbers in parentheses are one standard error.

Site	Altitude (m)	Years since disturbance	Stems/ha (dbh in cm)				
			A dbh ≥ 10	10 ≤ dbh ≤ 20	B dbh ≥ 20	dbh ≥ 40	A/B
URN	120	10	336 (127)	325 (119)	22 (10)	0	15.27
URN	120	20	467 (109)	423 (74)	44 (23)	0	10.61
URN	120	35	476 (65)	365 (52)	111 (51)	2 (2)	4.28
URN	120	60	447 (40)	244 (22)	203 (21)	33 (18)	2.20
URN	120	80	594 (18)	329 (30)	201 (18)	7 (5)	2.95
URN	120	MTF	585 (18)	400 (8)	185 (12)	47 (12)	3.16
San Carlos* Uhl and Murphy 1981	120	60	518	NA+	NA	NA	NA
San Carlos Uhl and Murphy 1981	120	MTF	743	511	232	32	3.20
Tefe* Black et al. 1950	95	MTF	NA	NA	220	NA	NA
Belem* Black et al. 1950	< 30	MTF	443	228	195	NA	2.29
Belem* Pires et al. 1953	< 30	MTF	423	236	187	58	2.26
Belem* Cain et al. 1956	< 30	MTF	585	NA	NA	NA	NA
Manaus** Takeuchi 1961	< 60	MTF	540	290	250	64	2.16
Shinguipino[1] Grubb et al. 1963	< 400	MLF	592	NA	291	NA	2.04
Araki[1] Grubb et al. 1963	< 400	MLF	667	NA	280	NA	2.38
Bimbino[1] Grubb et al. 1963	< 400	MLF	796	NA	366	NA	2.18
Armenia Vieja[1] Grubb et al. 1963	< 400	MLF	882	NA	473	NA	1.86
British Guiana[1] Davis & Richard (1933-1934)	< 30	MLF	461	NA	247	NA	1.87

*Data represent one stand.

+NA = data not available.

**Mean of three plots in one stand.

[1]The figures were recalculated from a 10,000 ft^2 plot.

MLF = mature lowland forest.

(Table 4.5, page 58). The variability of basal area within the same stand increased when a 0.25-ha plot was measured. Basal area of MTF ranged from 19.10 to 40.75 m^2/ha in four, 0.25-ha, plots. In contrast, basal area in 12, 0.03-ha, plots ranged from 30.44 to 36.95 m^2/ha. The mean MTF value of 34.8 m^2/ha is similar to the 34.28 m^2 reported by Jordan and Uhl (1978) for another tierra firme stand in the area, and considerably less than the 40- to 60-m^2 values for lowland wet forests found in Costa Rica (Holdridge 1972).

The height frequency distribution of trees on successional stands and MTF did not show a pattern that implies the presence of canopy strata. The highest number of stems occurs from 2 to 4 m in height (Table 4.4, page 57). The number of stems gradually declines from 4 to 9 m in height and falls steeply after 9 m, with the sharpest decline among trees greater than 17 m in height. Similar results were found by Davis and Richards (1933, 1934) on Moraballi Creek, British Guiana. The results obtained using profile diagrams show better stratification in the two successional stands than in MTF. They show one stratum at early stages of succession, a 10-year-old stand, two strata in a stand 40 years old, and no strata in the MTF. The MTF has trees of different heights but with no indication that the forest is uniformly layered. This means that the number of strata increases from an early stage of succession to some point in succession where the trees still have similar heights and homogeneous species composition. In MTF, the presence of strata depends on the rate of recruitment, growth, mortality, and the probability of natural disturbances.

Estimates of leaf area index (LAI) obtained in other tropical forests range widely, e.g., from 3 in Costa Rica (Stephens and Waggoner 1970), 5.2 in San Carlos (Jordan and Uhl 1978), 6 to 7 in Puerto Rico (Odum et al. 1963, Jordan 1969), 6.9 in the lower Rio Negro (Williams et al. 1972), and 12 in Thailand (Kira et al. 1967). In the URN, the variation in the LAI is related to the differences in estimated leaf weight. Jordan's leaf weight value was 8.02 t/ha (Jordan and Uhl 1978). In this study, leaf weight ranged from 8.59 to 10.67 t/ha.

Gap frequency, number of dead trees and stem sprouts, and basal area of standing dead trees indicate that natural disturbances are common events in the URN. These disturbances produce small and large scale differences in the structure of the forests and may help explain differences in structure within and among stands of the same age. On a small scale, an unbalanced picture of the forest might emerge. For example, a wind storm may throw several hectares of an MTF, or a secondary forest 60 to 80-years-old can contain many senescing canopy dominants. On a large scale, the forest is a mosaic of different-aged patches and structural characteristics with high variability among stands depending on soils, microrelief, species composition, and disturbance dynamics.

The data indicate that natural disturbances play a dominant role in determining the structure of the URN forests. The size-class distribution of stems in the MTF stands shows a reversed J-shaped curve with the majority of trees in small size classes. The distribution of living biomass by dbh shows that some dbh classes are missing. Large trees (40 to 90 cm dbh) were uncommon among the four MTF (Chapter 5).

Gaps were frequent in the study sites and the four MTF showed several gaps from 0.06 to 0.25 ha. The presence of gaps is probably the primary reason for the biomass difference between the 0.03- and 0.25-ha plots in stand XXII. Until recently, little attention has been given to the effects and frequency of gaps since the visible damage does not persist for more than 10 years (Poore 1968).

Other works in the URN report the presence of tree damage and gaps in the forests. For example a 0.41-ha area of MTF was hit by wind and 80% of the trees > 20 cm dbh were uprooted (Uhl 1982b). Eight gaps from 0.20 to 0.60 ha were found in several MTF and caatinga forests during 1984 (Kate Clark 1983). Uhl (1982b) reported mechanical damage as an important cause of tree mortality in San Carlos. Uhl also reported two dead trees $\geq$ 20 cm dbh/ha/year (based on a 5-year study in a 1-ha forest). Wind damage could be a strong disruptive force in the Amazon forests. Thunderstorms with high wind speeds occur commonly in this area. Komarek (1964) cited 60 storm days for the URN in 1963.

The fast turnover rate for trees in the URN forests is a mechanism for sustaining a forest on nutrient-poor soils. The frequent death of trees with the subsequent, rapid decomposition is an important factor in nutrient availability in these forests. The turnover rate explains part of the basal area variability among and within stands and the structural characteristics of this forest marked by a high density of small trees and few larger ones.

SUMMARY

Approximately 290 tree species $\geq$ 1 cm dbh and 141 tree species $\geq$ 10 cm dbh at 23 stands were encountered. The tree diversity ranged

from 33 to 96 species in 900-m^2 plots. The Shannon-Wiener index of general diversity showed an increase in species diversity from 10-year-old stands to MTF. The opposite occurred with species dominance expressed by the Simpson index which indicates high species dominance at early stages of succession and a reduction through the MTF.

The distribution of stems by size class shows that from 76 to 95% of the trees are within 1 to 5 cm dbh in the URN. Trees $\geq$ 40 cm are only found in stands 40 years and older and always represent less than 1% of the total stems.

Basal area ranges from 11.12 m^2/ha for a 10-year-old stand to 36.95 m^2/ha in an MTF. Basal area of standing dead trees increases from 10-year-old stands toward MTF. The largest values were found on the 80-year-old stands and MTF. Approximately 140 to 200 years are required for an abandoned farm to attain the basal area of an MTF. The leaf area index increases from 5.93 m^2/m^2 at 10-year-old successional stands to 7.88 m^2/m^2 for an MTF.

Small areas disturbed by slash-and-burn agriculture recover their original species composition, but the time required is more than 80 years, depending upon the intensity and frequency of disturbance in the area. Gap frequency, number of dead trees, stem snaps, and broken crowns indicate that natural disturbances are common events in the URN and have an important role in the structure of the forests. The dynamics of the forests result in differences in structural characteristics of the stands and are a mechanism for making nutrients available to a system that is nutrient poor.

CHAPTER 5

BIOMASS

INTRODUCTION

In temperate areas, ecologists studying biomass dynamics have constructed chronosequences from stands of different ages on similar sites (Ovington 1957, Switzer et al. 1966). Recently, this method has been used by Cooper (1980) in northern Michigan to document 70 years of change in biomass and productivity patterns of a bigtooth aspen (Populus gradidentata) forest, and by Peet (1980) who used a series of stands to monitor forest biomass dynamics for 50 years in the mountain regions of Colorado and the Piedmont of North Carolina.

Few studies documenting ecosystem recovery after the use of slash-and-burn agriculture have been conducted in Amazonia (Fearnside 1980, Uhl 1982a, Uhl and Jordan 1984). However, a considerable amount of work on ecosystem recovery has been done in Central America (Blum 1968, Budowski 1961, Ewel 1971, Harcombe 1977, Snedaker 1970). Most of this research has been done on the process of ecosystem degradation and recovery following human disturbance. Bartholomew et al. (1953) estimated wood biomass of four fallows (2, 5, 8, and 17 to 18 years old) in the Belgian Congo. Similar work was done by Greenland and Kowal (1960) in Ghana on a fallow approximately 50 years old. In tropical America, Scott (1977, 1978) estimated the biomass of three successional sites (3, 10, and 25 to 30 years old) and determined the recovery time required for a fallow in the Gran Pajonal, Peru. Other studies have concentrated on early stages of succession, e.g., Snedaker

(1970) in Guatemala and Ewel (1971) in five successional areas in Central America.

The objectives of this chapter are threefold: (1) to provide data on living (aboveground and belowground) and dead biomass of tierra firme forests (MTF) in the Amazon Basin; (2) to determine the time required for a successional stand to reach a biomass equivalent of an MTF; and (3) to describe the accumulation of aboveground living biomass. The study utilizes plot chronosequences in analyzing biomass accumulation and provides the longest known record of successional development for the Amazon region.

METHODS

Aboveground Biomass

Trees were cut and weighed to develop regression equations for estimating biomass of all trees measured in each stand. These trees were randomly selected to include all size classes and species. Forty-four trees, 10 to 127 cm diameter at breast height of 1.3 m (dbh), were selected in areas of secondary and primary forests. Twenty-eight trees were harvested from either 80-year-old fallows or MTF and 16 trees were harvested from 10- to 35-year-old fallows. In addition, 18 palms, 10 Heliconia spp. and 54 small trees (1 < dbh < 10 cm) were taken from either young fallows (< 30 years) or MTF. Biomass data collected by Jordan (unpublished, 1977) were added to these data to increase the number of species and trees greater than 40 cm dbh.

Measurements of 126 selected trees were taken prior to harvest. Diameter was measured at 130 cm dbh or above buttress, whichever was

lower. Crown maximum and minimum diameters were measured by stretching a surveyor tape between two points directly below the edge of the crown. After the tree was felled, four height measurements were made: (1) from the ground to stump top, (2) from the butt to the first branch, (3) from the first branch to the base of the crown, and (4) from the base of the crown to the top of the crown. Trees were then sectioned into stem, branches (limbs with diameters > 1.5 cm), twigs (branches smaller than 1.5 cm diameter) and leaves. Each section of a tree was weighed using a hanging scale. The stump was cut at ground level, weighed, and added to the weight of the stem. Stem weights of large trees were calculated using volume and wood density. Biomass for trees less than 2 m tall and non-woody plants was not estimated because of their small contribution to total biomass. Samples of the stem, branches, twigs, and leaves were collected from each tree, immediately weighed, and packed for later dry weight and leaf area determinations. Trees, $1 \leq$ dbh < 5 cm, were divided into wood and foliage for weight and moisture determinations.

Barkless cross section samples (2 to 3 cm thick) of stems greater than 5 cm diameter and branches greater than 30 cm in diameter were traced on acetate, and the areas calculated. The volumes of the discs were estimated using these areas and their thickness. The relationship of dry weight and disc volume was used to estimate specific wood density.

Estimates of aboveground biomass were based on the weight measurements made on individual trees (i.e., stem, branches, twigs, and leaves), dbh, total height, length of crown, length to the first

branch, diameter of the crown, volume of the crown, area of the crown, and wood density.

Regressions were developed to estimate whole tree and component biomass (leaves, twigs, branches, and stems). Most regressions are logarithmic, but a few are linear. The general logarithmic model has the following form:

$$\ln Y = a + b \ln X_1 + c \ln X_2 + d \ln X_3 ;$$

where Y is the biomass of the whole tree or a component, X_1 is dbh, X_2 is total height, and X_3 is wood density per species. The linear equation has the following form:

$$Y = a + b X_1 + c X_2 ;$$

where Y is the biomass of the whole tree and X_1 and X_2 represent dbh and total height.

Biomass calculations for each stand were made by placing trees into three classes based on dbh, and using regression equations to estimate component and whole-tree biomass. Total biomass by size categories ($1 \leq$ dbh < 5 cm, $5 \leq$ dbh < 20 cm, dbh ≥ 20 cm) was summed for each stand and expressed as metric tons per hectare (t/ha). Total stand biomass estimates were obtained by summing the biomass values for all size categories. Contributions of tree components to total aboveground biomass were calculated.

For estimation of aboveground living and belowground root biomass, logarithmic transformations of the different components were used because of the wide range in the size of the individuals. Logarithmic transformations may cause systematic errors (Crow 1971, Baskerville 1972, Beauchamp and Olson 1973) because of the differences between

logarithmic and arithmetic means. However according to Jordan and Uhl (1978) and Whittaker and Marks (1975), corrections are unlikely to improve the estimates, and for this study, the logarithmic regressions were not adjusted.

Aboveground biomass obtained in three, 0.03-ha, plots was used to estimate total biomass because 0.03-ha plots were established at all stands, and trees $\geq$ 1 cm dbh were sampled. In contrast, 0.25-ha plots were located only on stands older than 20 years, and trees $\geq$ 10 cm dbh were sampled. Both size plots are used for biomass comparisons.

Aboveground Dead Biomass

Two components of aboveground dead biomass were surveyed. First, standing dead trees were sampled in a plot (0.25 ha) in stands older than 20 years. DBH was recorded for trees $\geq$ 10 cm. Dead biomass was estimated using the regression equation as follows:

$$\ln Y = a + b \ln X \quad ;$$

where Y is biomass of the standing dead tree and X is its dbh. Twenty-two trees $\geq$ 10 cm dbh were sampled to develop the regression equation. All dead branches and stems with diameters larger than 5 cm, lying on the forest floor, were weighed from three plots (2 x 60 m) per stand. When boles were too heavy, volume estimates were made based on length and diameter measurements. Several wood samples were collected from standing and lying dead logs to determine wood density and moisture content.

Belowground Root Biomass

Root biomass was sampled from four pits (50 x 50 x 100 cm) distributed throughout the stand at six of the study sites representing the full range of age classes. Pit locations were marked with a 0.5- x 0.5-m metal frame. Litter was removed, and all roots on the soil surface were collected and separated into size classes. Soil was then removed in 10-cm layers. The roots were separated from the soil by hand at each 10-cm depth, cleaned, weighed, and dried at 90°C to constant weight.

Belowground root biomass for each stand was estimated by correlating basal area of trees (dbh $\geq$ 1 cm and height $\geq$ 2 m in 5- x 5-m and 10- x 10-m plots) with the amount of root biomass found in the pits. Regression equations were developed to estimate belowground root biomass for stands where roots were not sampled. The equations express mean total dry root biomass at 10-cm depth intervals as a function of mean basal area for each stand. The total was determined by summing the root biomass values between the surface of the soil to 70 cm depth. The general equation has the following form:

$$\ln Y = a + b \ln X ;$$

where Y is the mean belowground root biomass at the respective depth and X is the mean basal area of the trees.

RESULTS

Aboveground Biomass

The aboveground biomass for individual trees and their components is presented in Table 5.1. The decision to use three equations was

Table 5.1

Regression equations used for calculation of aboveground biomass

Size category (cm)	Component Y	X_1	X_2	X_3	Equation*	r^2	CV(%)	N
Trees	Tree	D^2	H		$Y = -0.292 + 0.369\ X_1 - 0.087\ X_2$	0.93	27.58	49
$1 \leq DBH < 5$	Stem	D^2	H		$Y = -0.912 + 0.209\ X_1 + 0.156\ X_2$	0.89	33.54	49
	Twigs & leaves	D^2	H		$Y = 0.620 + 0.159\ X_1 - 0.243\ X_2$	0.63	91.37	49
Trees	Tree	D^2	H	d	$\ln Y = -1.981 + 1.047 \ln X_1 + 0.572 \ln X_2 + 0.931 \ln X_3$	0.92	5.84	39
$5 \leq DBH < 20$	Stem	D^2	H	d	$\ln Y = -5.961 + 1.074 \ln X_1 + 1.656 \ln X_2 + 0.566 \ln X_3$	0.94	6.19	22
	Branches	D^2	H	d	$\ln Y = 0.043 + 1.352 \ln X_1 - 0.576 \ln X_2 + 4.588 \ln X_3$	0.88	23.87	18
	Leaves	D^2	H	d	$\ln Y = -1.981 + 1.049 \ln X_1 - 0.584 \ln X_2 + 0.550 \ln X_3$	0.56	45.85	39
	Twigs	D^2	H	d	$Y = -15.363 + 0.125\ X_1 - 1.5983\ X_2 + 66.318\ X_3$	0.82	48.63	20
Trees	Tree	D^2	H	d	$\ln Y = -1.086 + 0.876 \ln X_1 + 0.604 \ln X_2 + 0.871 \ln X_3$	0.93	4.09	43
$DBH \geq 20$	Stem	D^2	H	d	$\ln Y = -8.298 + 0.536 \ln X_1 + 3.336 \ln X_2 + 0.459 \ln X_3$	0.95	4.94	22
	Branches	D^2	H	d	$\ln Y = 5.558 + 1.285 \ln X_1 - 2.720 \ln X_2 + 1.551 \ln X_3$	0.93	7.12	20
	Twigs	D^2	H	d	$\ln Y = -1.439 + 0.424 \ln X_1 + 0.740 \ln X_2 + 0.586 \ln X_3$	0.47	15.79	34
	Leaves	D^2	H	d	$\ln Y = -4.111 + 0.605 \ln X_1 + 0.848 \ln X_2 + 0.438 \ln X_3$	0.48	28.21	43
Palms	All plant	$1/D^2$	H		$\ln Y = -6.3789 - 0.877 \ln X_1 + 2.151 \ln X_2$	0.89	13.17	19
(all	Stem	D	H		$\ln Y = -8.170 + 1.248 \ln X_1 + 3.182 \ln X_2$	0.92	15.80	19
individuals)	Leaves	D	H		$\ln Y = -5.332 + 2.623 \ln X_1 + 0.303 \ln X_2$	0.76	26.45	19
Heliconia spp	All plant	D	H		$\ln Y = 5.502 + 1.481 \ln X_1 + 2.000 \ln X_2$	0.96	16.55	10
(all	Stem	D^2H			$\ln Y = -7.630 + 1.451 \ln X_1$	0.88	53.01	10
individuals)	Leaves	D	H		$\ln Y = -3.956 + 1.923 \ln X_1 + 0.288 \ln X_2$	0.78	118.85	10

*Y = biomass component (kg), D = diameter (cm) at 130 cm aboveground (DBH), H = height (m), d = density of wood (g/cm^3), CV = coefficient of variation, and N = number of individuals. All regressions were statistically significant ($P < 0.0001$) except *Heliconia* spp. ($P < 0.004$).

based on the best estimates among biomass values obtained directly in the field, and those obtained by allometric regressions (Table 5.2).

Expressions of goodness of fit of the allometric regressions are given by the "coefficient of determination" (r^2) and the "coefficient of variation" or "relative errors of estimate" (CV). The best regressions were obtained for whole trees and stems of trees with a dbh $\geq$ 20 cm. These regressions have an $r^2 > 0.95$ and a CV < 8%. The other models for trees, $1 \leq$ dbh < 5 cm, and leaves and twigs yielded expressions of goodness of fit ($0.47 \leq r^2 \leq 0.93$) and a CV between 15.79 and 91.37%. The regressions for palms and Heliconia spp. show highly significant coefficients of determination ($0.78 \leq r^2 \leq 0.96$) and moderate to high coefficients of variation ($13.17\% \leq CV \leq 118.85\%$).

Estimation of leaves, branches, and twigs presents a variety of problems. Total height, dbh, and wood density were not the most useful independent variables. The CV were large, $\geq$ 25%, and the r^2 accounted, in several cases, for less than 60% of the variation of biomass components as a function of stem size (Table 5.1).

Stands were classified into six age groups. The first group represents the four youngest stands, 9 to 14 years old. Biomass values for all size classes varied from 43.91 to 81.76 t/ha (Table 5.3). The highest value was found among trees 5 to 10 cm dbh, and the total distribution of biomass across the dbh classes varied between 2.5 to 37.5 t/ha (Appendix Figure B.1).

For the four, 20-year-old stands, trees are distributed between 1 and 40 cm dbh, with the main contribution of biomass from trees between

Table 5.2

Percent deviation of actual biomass weights from predicted values

Component	Tree compartment				
	Whole (%)	Stem (%)	Branch (%)	Twig (%)	Leaves (%)
All trees	10	11	19	-13	-17
Trees 1 $\leq$ DBH < 5 cm	-2	1	NR	NR	5*
Trees 5 $\leq$ DBH < 20 cm	-4	-2	-3	-19	-13
Trees DBH $\geq$ 20 cm	-1	8	1	16	2
Palms	-38	-16	NR	NR	-21
Heliconia spp.	3	5	NR	NR	-9

* = foliage.

NR = not recorded.

Table 5.3

Biomass estimated from single (i.e., whole tree) and separate allometric equations for leaf, twig, branch, and stem biomass.

Stand	Years since disturbance	Aboveground biomass (t/ha)				RBD1 (%)	RBD2 (%)	RBD3 (%)	RBD4 (%)	Biomass (t/ha)			
		Whole tree 1*	Tree components 1**	Whole tree 2+	Tree component 2++					Belowground	Total living(1)	Dead	Total (living + dead)
I	9	43.91	44.83	NR	NR	-2	NR	NR	NR	7.45	51.36	31.22	82.58
II	11	52.91	51.47	NR	NR	3	NR	NR	NR	7.88	60.79	22.47	83.26
III	12	81.76	77.48	NR	NR	5	NR	NR	NR	16.42	98.18	2.64	100.82
IV	14	53.38	55.63	NR	NR	-4	NR	NR	NR	7.40	60.78	15.23	76.01
V	20	83.31	86.27	NR	NR	-4	NR	NR	NR	16.75	100.06	0.70	100.76
VI	20	61.48	63.19	NR	NR	-3	NR	NR	NR	11.86	73.34	1.63	74.97
VII	20	63.85	63.12	NR	NR	1	NR	NR	NR	16.02	79.87	0.83	80.70
VIII	20	97.63	102.39	NR	NR	-5	NR	NR	NR	18.88	116.51	1.01	117.52
IX	30	53.80	58.83	55.02	58.61	-9	-2	0	-7	8.11	61.91	9.01	70.92
X	35	109.33	139.27	84.41	94.31	-27	23	32	-12	20.59	129.92	8.51	138.43
XI	35	107.99	117.94	61.09	78.68	-9	43	33	-29	21.49	129.48	1.03	130.51
XII	40	159.40	171.73	107.61	105.63	-8	32	38	2	27.36	186.76	5.69	192.45
XIII	60	116.22	106.04	171.88	152.00	9	-48	-43	12	17.07	133.29	32.40	165.69
XIV	60	197.40	178.24	155.74	145.28	10	21	18	7	47.09	244.49	2.74	247.23
XV	60	137.87	152.55	144.49	140.20	-11	-5	8	3	31.30	169.17	34.18	203.35
XVI	80	134.08	127.50	113.32	134.53	5	15	-6	-19	26.03	160.11	8.23	168.34
XVII	80	177.59	166.70	188.61	169.44	6	-6	-2	10	35.50	213.09	7.60	220.69
XVIII	80	144.21	129.76	122.81	111.73	10	15	14	9	29.43	173.64	40.40	214.04
XIX	80	141.93	155.60	134.63	129.85	-10	5	17	4	27.89	169.82	10.03	179.85
XX	MTF	223.19	212.22	219.08	215.54	5	2	-2	2	45.48	268.67	8.18	276.85
XXI	MTF	262.09	233.47	204.41	181.84	11	22	22	11	60.38	322.35	53.03	375.50
XXII	MTF	263.60	245.73	134.62	133.55	7	49	46	1	62.20	325.80	15.12	340.92
XXIII	MTF	271.20	243.12	325.77	291.37	10	-20	-20	11	64.50	335.70	14.61	350.31

*Whole tree 1 = aboveground biomass values obtained from three allometric equations (Table 5.1) according to the DBH of trees (i.e., 1 cm ≤ DBH < 5 cm and taller than 2 m, 5 cm ≤ DBH < 20 cm, DBH ≥ 20 cm) in three, 10- x 30-m, plots (stands XII and XVII have four plots).

**Tree components 1 = aboveground biomass values obtained from allometric equations (Table 5.1) for leaf, twig, branch and stem according to the DBH of trees (i.e., 1 cm ≤ DBH < 5 cm and taller than 2 m, 5 cm ≤ DBH < 20 cm, DBH ≥ 20 cm) in three, 10- x 30-m, plots (stands XII and XVII have four plots).

+Whole tree 2 = same as whole tree 1 but for trees ≥ 10 cm DBH in one, 50- x 50-m, plot.

++Tree component 2 = same as tree component 1 but for trees ≥ 10 cm DBH and in one, 50- x 50-m, plot.

RBD1 = % difference between whole tree 1 and tree component 1 relative to whole tree 1 biomass.

RBD2 = % difference between whole tree 1 and whole tree 2 relative to whole tree 1 biomass.

RBD3 = % difference between tree component 1 and tree component 2 relative to tree component 1 biomass.

RBD4 = % difference between whole tree 2 and tree component 2 relative to whole tree 2 biomass.

NR = not recorded.

(1) Total living = whole tree 1 + belowground.

1 and 20 cm dbh (Appendix Figure B.2). The total aboveground living biomass for all stands in this group ranges from 61.48 to 97.63 t/ha (Table 5.3). Stands VI and VII, which have the lowest biomass values, have larger numbers of stems in the smaller dbh classes, with biomass concentrated in trees no greater than 10 cm dbh. Stands V and VIII, which have the highest biomass values, have a bell-shaped biomass distribution with maximum values for trees 10 and 20 cm dbh. The differences between stands with low and high biomass may be attributed to differences in the intense use of the land. Stands VI and VII have been used for agriculture twice in the last 40 years.

The third group consists of four, 30- to 40-year-old, stands. It has the largest variation in biomass among trees of similar age, i.e., from 53.80 to 159.40 t/ha (Table 5.3). Trees were distributed between 1 and 40 cm dbh, and biomass values ranged from 5 to 37.5 t/ha among dbh classes (Appendix Figure B.3). Biomass is greater in the smaller dbh sizes for stand IX and approached a normal distribution for the other stands.

Three stands, 60 years old, had noticeable differences in biomass among plots of the same size, possibly due to canopy gaps. Estimated biomass ranged from 116.22 t/ha to 197.40 t/ha (Table 5.3). Values of 144.49 to 171.88 t/ha were obtained for the larger plots (0.25 ha). The trees were distributed between 1 and 60 cm dbh. Biomass varied by size class between 5 and 50 t/ha (Appendix Figure B.4). Stands XIII and XV contained two and five tree-fall gaps, respectively, in the 0.25-ha plots.

The biomass values for four, 80-year-old, stands (Appendix Figure B.5) are relatively consistent varying from 134.08 to 177.59 t/ha. Greater variation among stands was seen for the 0.25-ha plots with biomass values from 113.32 to 188.61 t/ha (Table 5.3). The trees were distributed between 1 and 55 cm dbh with maximum biomass in the 10 to 35 cm size classes. Biomass distribution by size class was from 5 to 35 t/ha. Biomass distribution in the 80-year-old stands showed missing trees in the larger dbh classes, and two of the stands had missing trees between 30 and 45 cm dbh (Appendix Figure B.5).

The last group is formed by four MTF ($\sim$ 200 years). Biomass values were very similar across stands and among plots of different sizes. The single exception is stand XXII which has almost 50% less biomass in the 0.25-ha plot (Table 5.3). Forest biomass ranged from 223.19 to 271.20 t/ha (Table 5.3). The distribution of trees by size class shows an absence of individuals in the upper intermediate range of 40 to 90 cm dbh (Appendix Figure B.6). Biomass values varied between 7 and 103 t/ha per size class with the highest values for trees $\geq$ 90 cm dbh.

Aboveground Biomass Estimates Using Different Allometric Regressions and Plot Sizes

Several comparisons were made to estimate the variability of aboveground biomass according to plot size and regression type. Data were obtained from two plot sizes. The smaller plots were 10 x 30 m (0.03 ha). Three of these plots were sampled at each stand while an additional 50- x 50-m (0.25 ha) plot was sampled at stands older than 20 years. Comparisons were made between biomass values found from a

single whole tree regression equation and the sum of separate tree component regressions, among plots of the same size and combinations of the two plot sizes (Table 5.3).

Percentage differences between biomass estimates for the whole tree and tree components were low for the 0.03-ha plots. When single, separate equations were used, the percentage difference between whole tree 1 and tree component 1 in relation to whole tree 1 biomass (RBD1, Table 5.3) for all stands was $\pm$ 11%, with the exception of stand X where the biomass was underestimated by 27%. Relative differences for the 0.25-ha plot, RBD4, is $\pm$ 12% with the exception of stands XVI and XI where biomass was underestimated by 19 and 29%, respectively. However, the relative differences, RBD2 and RBD3, ranged between $\pm$ 48%.

Leaf Biomass

Leaf biomass ranged from 5.76 to 10.73 t/ha (Table 5.4), similar to successional sites and mature forests in other areas of the tropics (Folster et al. 1976, Klinge et al. 1975, Scott 1977). The percentage of the total biomass represented by leaf biomass declines in a reversed J shape during succession (Figure 5.1a). The highest values, 8 to 13%, occurred among stands younger than 30 years and dropped to 5% for stands 60 to 80 years old and from 2.8 to 3.5% in the MTF (Table 5.4).

Twig Biomass

Twig biomass ranged from 9.96 to 16.73 t/ha for stands no older than 20 years, 11.03 to 20.61 t/ha for stands 30 to 80 years old, and 19.19 to 22.57 t/ha in MTF (Table 5.4). Percent of total biomass represented by twigs declines in a reversed J shape from 21% in younger

Table 5.4

Components of aboveground biomass for successional stands and mature forests. Values are from trees ≥ 1 cm dbh in three plots (10 x 30 m) per stand; the exceptions are stands XII and XVII which have four plots. each tree component is estimated from separate allometric equations (Table 5.1). Percentage of each tree component is calculated relative to total living biomass.

		Aboveground biomass (t/ha)										
Stand	Years since disturbance	leaf	% leaf*	twig	% twig*	branch	% branch*	stem	% stem*	Total above-ground based on tree components	Belowground root	Total living
I	9	6.96	13.31	11.22	21.46	8.88	16.99	17.75	33.95	44.83	7.45	52.28
II	11	6.50	10.95	11.44	19.28	12.34	20.79	21.18	35.69	51.47	7.88	59.35
III	12	7.84	8.35	16.49	17.56	16.02	17.06	37.11	39.52	77.48	16.42	93.90
IV	14	6.24	9.90	13.30	21.10	15.22	24.15	20.85	33.08	55.63	7.40	63.03
V	20	10.73	10.42	16.73	16.24	20.24	19.65	38.55	37.42	86.27	16.75	103.02
VI	20	9.93	13.23	12.43	16.56	13.31	17.73	27.51	36.66	63.19	11.86	75.05
VII	20	9.45	11.94	9.96	12.59	15.20	19.21	28.50	36.01	63.12	16.02	79.14
VIII	20	8.12	6.70	17.22	14.20	40.15	33.11	36.89	30.42	102.39	18.88	121.27
IX	30	6.80	10.16	13.71	20.48	17.37	25.95	20.95	31.30	58.83	8.11	66.94
X	35	8.69	5.44	20.61	12.89	75.40	47.17	34.56	21.62	139.27	20.59	159.86
XI	35	10.29	7.38	18.93	13.58	41.36	29.67	47.34	33.95	117.94	21.49	139.43
XII	40	8.01	4.02	17.45	8.76	89.88	45.15	56.38	28.32	171.73	27.36	199.09
XIII	60	5.76	4.68	11.03	8.96	46.11	37.45	43.12	35.03	106.04	17.07	123.11
XIV	60	7.67	3.40	16.11	7.15	76.61	34.00	77.85	34.55	178.24	47.09	225.33
XV	60	6.82	3.71	13.66	7.43	92.45	50.29	39.62	21.55	152.55	31.30	183.85
XVI	80	8.16	5.31	15.92	10.37	42.42	27.63	60.99	39.73	127.50	26.03	153.53
XVII	80	8.63	4.27	17.83	8.82	48.01	23.74	92.21	45.60	166.70	35.50	202.20
XVIII	80	7.73	4.86	13.79	8.66	49.90	31.35	58.32	36.64	129.76	29.43	159.19
XIX	80	8.41	4.58	16.80	9.16	80.93	44.11	49.45	26.95	155.60	27.89	183.49
XX	MTF	9.82	3.81	22.57	8.76	72.86	28.27	106.95	41.50	212.22	45.48	257.70
XXI	MTF	10.05	3.42	21.93	7.46	75.79	25.79	125.69	42.77	233.47	60.38	293.85
XXII	MTF	10.67	3.47	19.58	6.36	70.68	22.95	144.79	47.02	245.73	62.20	307.93
XXIII	MTF	8.59	2.79	19.19	6.24	85.14	27.68	130.18	42.32	243.12	64.50	307.62

*Percentage of total living biomass.

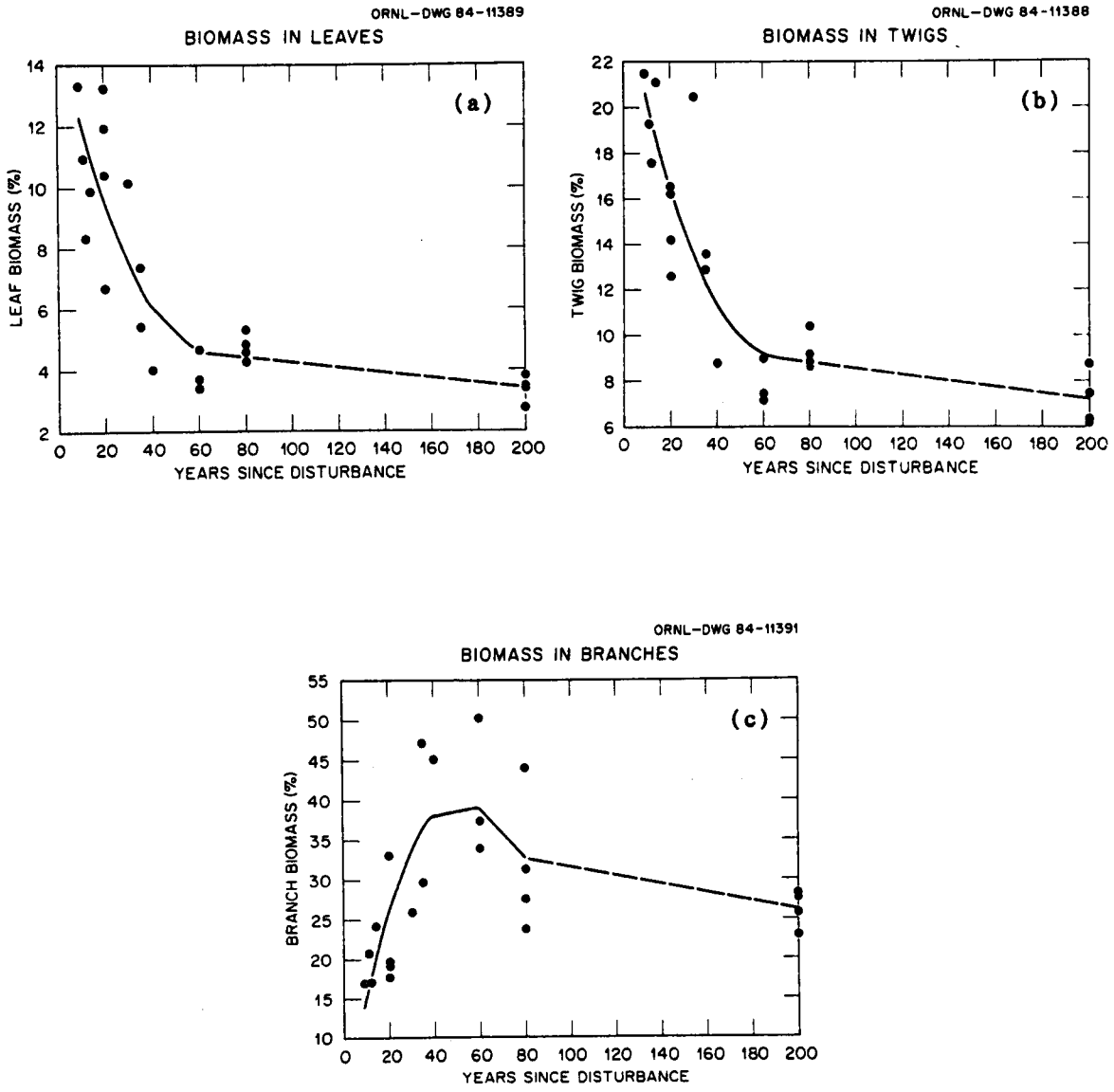

Figure 5.1. Relationship between leaf, twig, and branch biomass percentages and years since disturbance in the Upper Rio Negro region of Colombia and Venezuela. The equations are as follows: (a) leaf = 15.19 - 0.35 age + 0.003 age^2 - 1.06E-5 age^3; (b) twig = 24.94 - 0.53 age + 0.005 age^2 - 1.58E-5 age^3; and (c) branch = 0.14 + 1.71 age - 0.02 age^2 + 7.03E-5 age^3. The three regression equations are statistically significant ($P < 0.001$).

stands to 6% in MTF (Figure 5.1b). This pattern is similar to that of the leaf biomass although the values are higher. The results indicate that as age increases, stands become more uniform in twig biomass.

Branch Biomass

Stands 10 to 20 years old had 8.88 to 40.15 t/ha, stands 30 to 80 years old had 17.37 to 92.45 t/ha, and the MTF had 72.86 to 85.14 t/ha of branch biomass (Table 5.4). The relative contribution of branch to total biomass increased until 40 to 60 years and then decreased for MTF (Fig. 5.1c). Percentage of branch biomass for successional stands 10 to 80 years old ranged between 16.99 and 50.29%, and MTF varied from 22.95 to 28.27% (Table 5.4). These values indicated that trees have more branches during late successional stages.

Stem Biomass

Stem biomass ranged from 17.75 to 38.55 t/ha for the first 20 years, 20.95 to 56.38 t/ha for stands 30 to 40 years old, and 49.45 to 144.79 t/ha for stands 80 years old and MTF (Table 5.4). The percentage of stem biomass relative to the total was opposite from branch biomass, indicating that in successional stages with open spaces the trees have more branches and large crowns with smaller proportions of stem biomass than those of MTF (Fig. 5.2a). The relative contribution of stems and branches to total biomass increases to a peak at 60 years, then declines through MTF (Fig. 5.2b). Values of branch and stem biomass together varied from 26.63 to 215.47 t/ha, representing between 51 and 70% of the total aboveground biomass.

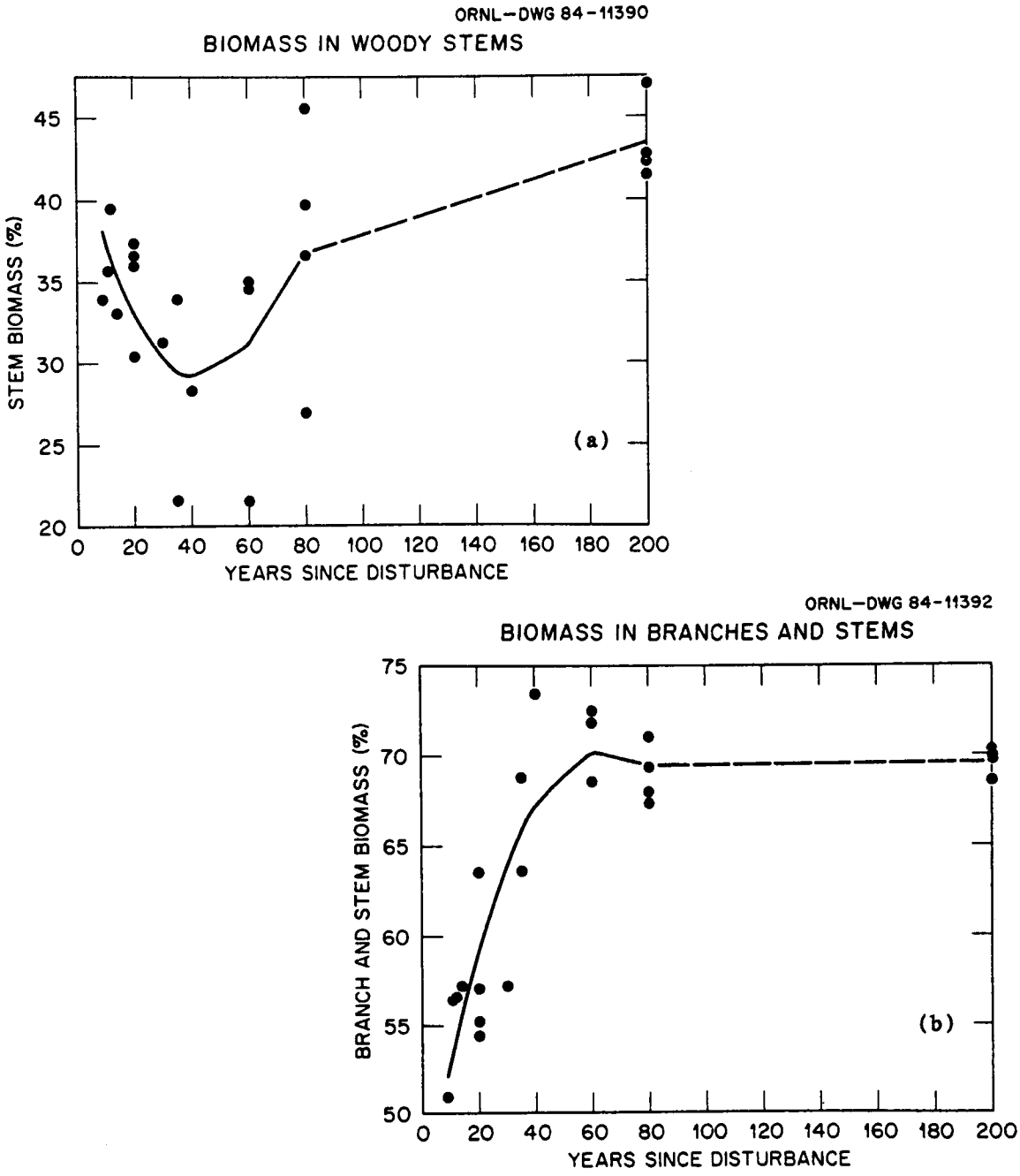

Figure 5.2. Relationship between woody stem and branch and stem biomass percentages and years since disturbance in the Upper Rio Negro region of Colombia and Venezuela. The equations are as follows: (a) woody stem = 44.33 - 0.79 age + 0.01 age^2 - 3.97E-5 age^3; and (b) branch and stem = 44.49 + 0.92 age - 0.01 age^2 + 3.05E-5 age^3. The two regression equations are statistically significant ($P < 0.03$).

Aboveground Biomass Recovery

Aboveground living biomass data from the URN were fitted to a linear and logarithmic regression equation to estimate the time required for an abandoned farm site to reach the mean biomass characteristics of an MTF (Figure 5.3). Results, using both regressions, are as follows:

$$Y = 48.73 + 1.43\ X$$

$(n = 19,\ r^2 = 0.67,\ P < 0.0001,\ CV = 25.50\%)$; and

$$\ln Y = 2.71 + 0.54\ \ln X$$

$(n = 19,\ r^2 = 0.74,\ P < 0.0001,\ CV = 5.29\%)$,

where Y is the aboveground living biomass in t/ha, and X is age in years. By solving for X where Y is the mean aboveground biomass of 255 t/ha for MTF, the time required for the biomass of a successional forest to reach the biomass of an MTF is 144 years using the linear model and 189 years using the logarithmic model.

Aboveground Dead Biomass

The regression equation used to estimate dead biomass is as follows:

$$\ln Y = -1.80 + 2.00\ \ln X\ ;$$

($r^2 = 0.82,\ P < 0.0001,\ CV = 14.95\%,\ n = 22$), where Y is dead biomass (kg) and X is dbh (cm). Dead biomass increased through succession, varying between 0.70 and 53.03 t/ha (Table 5.3, page 88). Lowest dead biomass values were found in stands that had been subjected to slash-and-burn agriculture within the last 50 years. Dead biomass is low on these younger stands because the soft-wooded species that dominant the early stages of succession decay quickly.

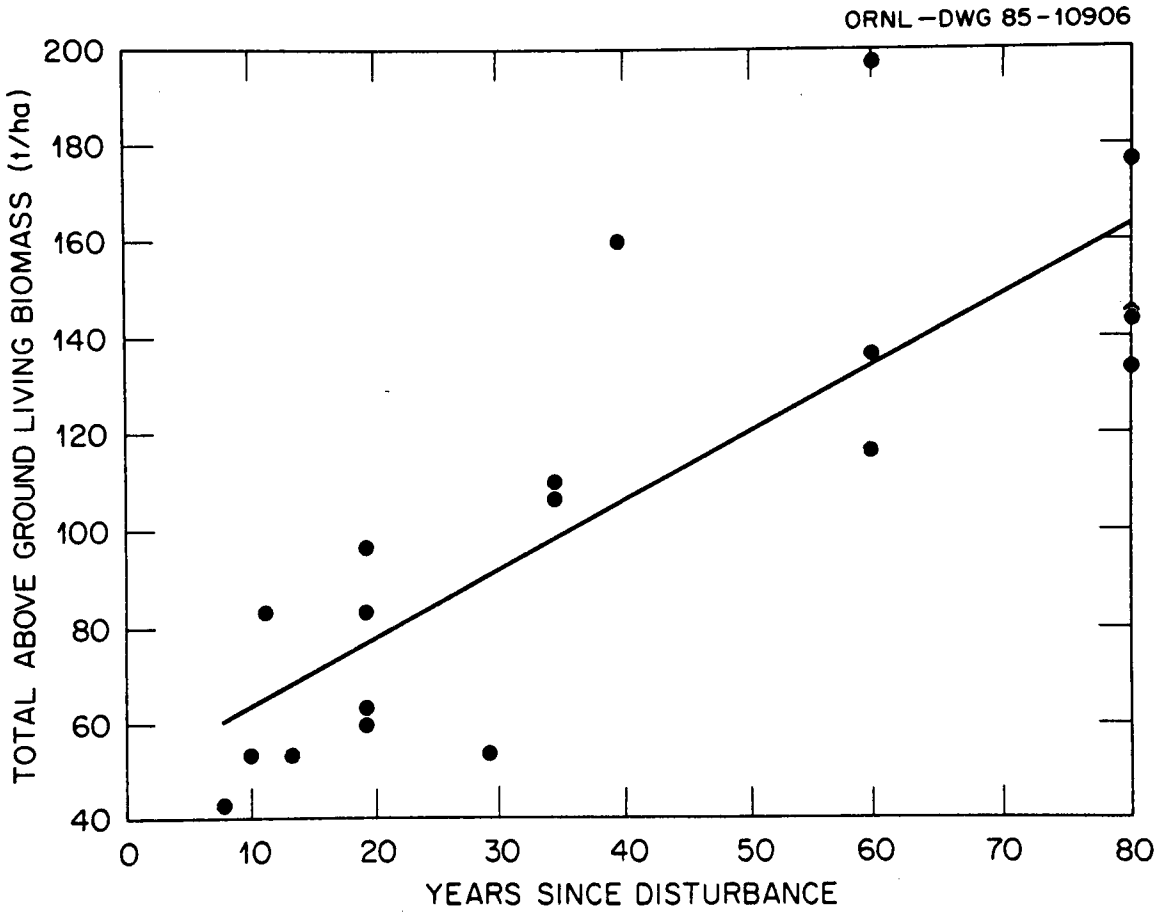

Figure 5.3. Relationship between total aboveground living biomass (t/ha) and time (years since disturbance) in the Upper Rio Negro region of Colombia and Venezuela.

In the 10-year-old stands, dead biomass ranged from 2.64 to 31.22 t/ha (Table 5.3, page 88). Approximately 95% of the totals came from trees of the former forests which had not yet fully decomposed. The 20-year-old stands had the least dead biomass of all age classes and consisted of dead trees from early successional stages. Dead biomass values ranged from 0.70 to 1.63 t/ha (Table 5.3, page 88). Such low values probably have resulted from decomposition of the wood during the 20 years since clearing and loss of woody material during burning.

Dead biomass values in the 30- to 40-year-old stands ranged from 1.03 to 9.01 t/ha (Table 5.3, page 88). More than 80% of the dead woody material came from successional trees. Stand IX illustrates the impact of intense use of a site during shifting cultivation. It had the largest amount of dead biomass and the least aboveground living biomass. Most of the dead biomass lying on the floor was from successional vegetation. Few late successional or primary forest species were present. An even more dramatic example of how intensive human use can slow succession occurred in an area 3000 m away from stand IX where the organic matter was removed to control weeds and establish crops. Fourteen years later, only a few trees were present with maximum heights between 3 and 4 m.

Dead biomass values for the 60-year-old stands ranged from 2.74 to 34.18 t/ha (Table 5.3, page 88). Stand XIV had the least dead biomass while stand XV had the highest of its age class. Both stands located in the same area showed a major difference in the number of standing

dead trees 50 to 60 cm dbh. There were also several dead trees greater than 50 cm dbh in stand XIII.

Four, 80-year-old, stands yielded dead biomass values from 7.60 to 40.40 t/ha (Table 5.3, page 88). Dead trees were in the larger size classes (40 to 70 cm dbh), and their presence in some cases may explain missing size classes.

There was a large variation in dead biomass of MTF with values ranging from 8.18 to 53.03 t/ha (Table 5.3, page 88). At stand XXI approximately half of the total dead biomass consisted of logs between 80 and 130 cm diameter. In stand XXII, there were several logs lying on the forest floor with diameters larger than 80 cm in the 0.25-ha plot, indicating a high value for the stand, but they were not sampled. Stand XX shows a low biomass value because it only includes dead biomass lying on the floor and not standing dead biomass.

Belowground Root Biomass

Root biomass data from six stands were used to develop regression equations for estimating root biomass for the 23 stands (Table 5.5, Figure 5.4). The best regressions were based on basal area obtained from 10- x 10-m plots centered on the 50- x 50- x 100-cm pits where root biomass was sampled. The correlation coefficient ranged from 0.50 to 0.90, and the coefficients of variations were 8.47% to 35.41% (Table 5.5). The regressions for surface root mat and the first 10 cm account for 50 to 63% of the variation with the coefficient of variation at 17.95% and 35.41%, respectively.

Other allometric regressions were used to predict belowground root biomass between 10- and 70-cm depth. These models have similar slopes,

Table 5.5

Regression equations used for calculating belowground root biomass.

X	Y	Equations	r^2	CV(%)
$\overline{B}$	$\overline{W}$(1) (surface)	ln Y = -2.516 + 1.375 ln X	0.50	35.41
$\overline{B}$	$\overline{W}$(2) (10 cm)	ln Y = -1.802 + 1.431 ln X	0.63	17.95
$\overline{B}$	$\overline{W}$(3) (20 cm)	ln Y = -2.695 + 1.852 ln X	0.89	9.15
$\overline{B}$	$\overline{W}$(4) (30 cm)	ln Y = -2.642 + 1.863 ln X	0.90	8.47
$\overline{B}$	$\overline{W}$(5) (40 cm)	ln Y = -2.518 + 1.839 ln X	0.89	8.67
$\overline{B}$	$\overline{W}$(6) (50 cm)	ln Y = 2.422 + 1.817 ln X	0.88	8.66
$\overline{B}$	$\overline{W}$(7) (60 cm)	ln Y = -2.354 + 1.80 ln X	0.88	8.74
$\overline{B}$	$\overline{W}$(8) (70 cm)	ln Y = -2.343 + 1.80 ln X	0.88	8.76

$\overline{B}$ = mean basal area (four, 0.01-ha, plots for six stands).

$\overline{W}$ = mean belowground root biomass, four pits per stand, samples from surface to 70 cm depth (shown in parentheses).

CV = coefficient of variation.

All regressions are statistically significant ($P < 0.01$).

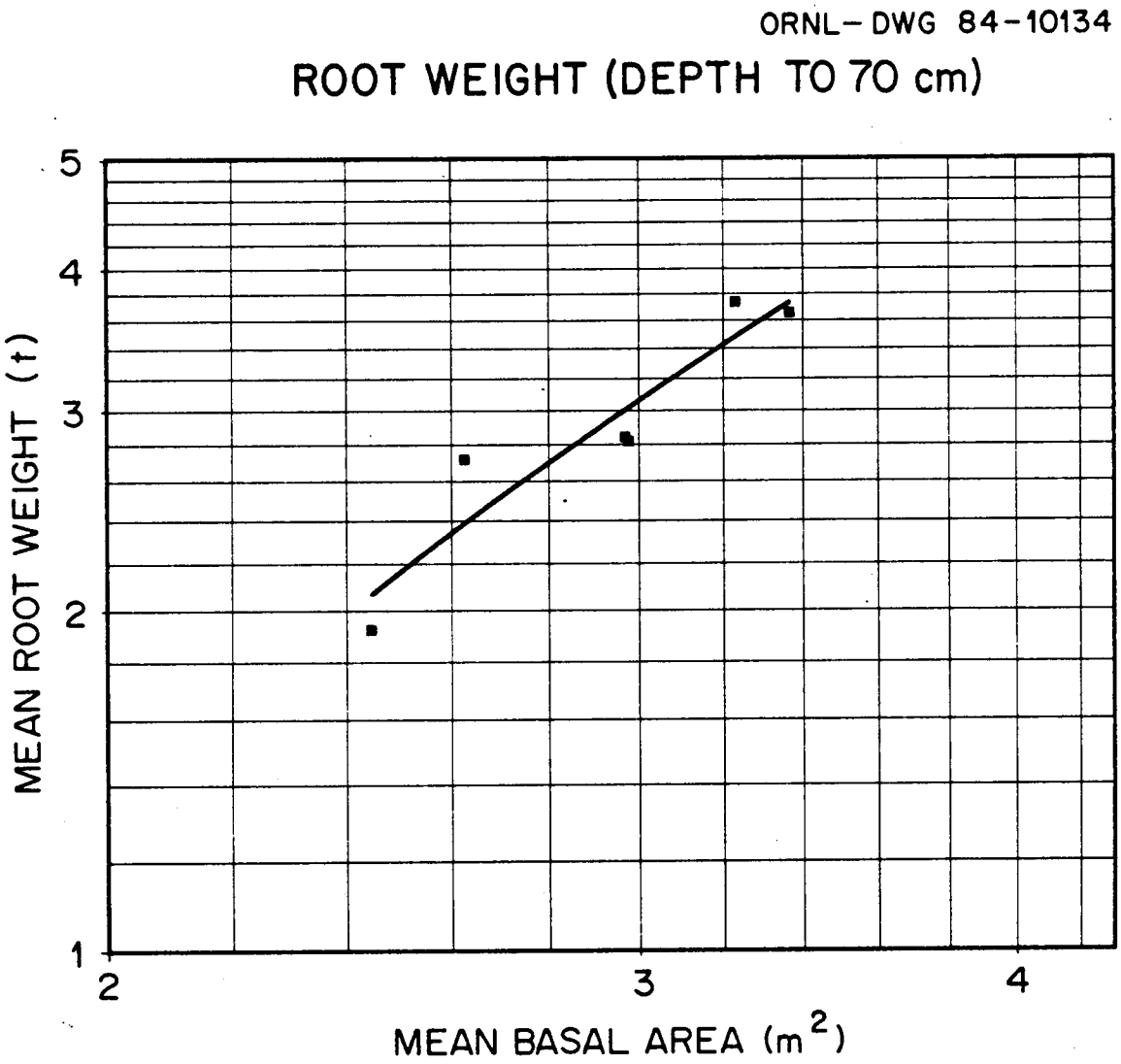

Figure 5.4. Relationship between total root weight and basal area in the Upper Rio Negro region of Colombia and Venezuela.

low coefficients of variation (8.47% to 9.15%), and a coefficient of determination from 0.88 to 0.90.

Root biomass values obtained in the field varied from 6.88 to 38.66 t/ha for an 11-year-old and an MTF stand, respectively (Table 5.6). A successional stand, 60 years old, had the highest value, 42.01 t/ha (Table 5.6).

For five of the six stands where data were collected, the regression equations overestimated total root biomass by 13 to 39%; one stand, VI, was underestimated by 27%. Estimations by the regression models to a 70-cm depth varied from 7.45 to 64.50 t/ha, for a 9-year-old stand and MTF, respectively (Table 5.6). At the surface, the values ranged from 2.23 to 11.55 t/ha. Root biomass decreased with depth except for the MTF stands which had the greatest values at their 10- to 20-cm depths.

The proportion of total root biomass to a 30-cm depth ranged from 86 to 78% for 10- and 20-year-old stands, 93 and 94% for 30- to 80-year-old stands, and 85% for MTF (Table 5.7). The ratio of belowground root biomass to aboveground biomass showed some variability, ranging from 0.14 to 0.25 (Table 5.6). There is no apparent trend of belowground to aboveground biomass between successional stages and MTF.

Root biomass was divided into diameter classes (< 1, 1 to < 3, 3 to < 6, 6 to < 10, 10 to < 20, 20 to < 40 and ≥ 40 mm) (Table 5.7). Fine roots (< 1 mm) were concentrated on the surface of soil and decreased with depth. The proportion of roots, < 6 mm diameter between the surface and the 30-cm depth, varied between 18 and

Table 5.6

Estimated belowground root biomass for successional stands and mature forests (values in parentheses indicate actual field data).

Stand	Years since disturbance	Mean belowground root biomass (t/ha)					Belowground root biomass/ aboveground biomass
		Surface (1)	0-10 cm (2)	10-20 cm (3)	20-30 cm (4)	Surface to 70 cm (5)	
I	9	2.23	2.98	0.69	0.50	7.45	0.17
II	11	2.32 (2.45)	3.12 (1.99)	0.80 (0.89)	0.53 (0.54)	7.88 (6.88)	0.15
III	12	4.07	5.69	3.53	1.18	16.42	0.20
IV	14	2.21	2.98	0.68	0.50	7.40	0.14
V	20	4.13	5.78	3.64	1.22	16.75	0.20
VI	20	3.17 (2.86)	4.36 (6.03)	1.98 (2.37)	0.83 (1.13)	11.86 (15.16)	0.19
VII	20	3.99	5.57	3.38	1.15	16.02	0.25
VIII	20	4.52	6.37	4.43	1.39	18.88	0.19
IX	30	2.37	3.20	0.86	0.56	8.11	0.15
X	35	4.83 (3.88)	6.83 (5.71)	5.08 (5.03)	1.53 (0.89)	20.59 (16.75)	0.19
XI	35	4.99	7.07	5.43	1.60	21.49	0.20
XII	40	6.00	8.92	7.81	2.09	27.36	0.17
XIII	60	4.19	5.87	3.76	1.24	17.07	0.15
XIV	60	9.09 (16.64)	13.41 (14.45)	16.68 (5.60)	3.80 (2.21)	47.09 (42.01)	0.24
XV	60	6.65	9.62	9.49	2.42	31.30	0.23
XVI	80	5.78	8.28	7.26	1.98	26.03	0.19
XVII	80	7.32	10.66	11.33	2.78	35.50	0.20
XVIII	80	6.35	9.15	8.68	2.26	29.43	0.20
XIX	80	6.09 (4.18)	8.75 (7.64)	8.03 (3.39)	2.14 (0.99)	27.89 (17.19)	0.20
XX	MTF	8.85 (4.77)	13.04 (7.89)	15.92 (15.62)	3.64 (4.42)	45.48 (38.66)	0.20
XXI	MTF	10.98	16.42	23.18	4.98	60.38	0.23
XXII	MTF	11.23	16.83	24.08	4.90	62.20	0.24
XXIII	MTF	11.55	17.33	25.24	5.36	64.50	0.24

(1) Estimated by equation $\overline{W}(1)$ (Table 5.5).

(2) Estimated by equation $\overline{W}(2)-\overline{W}(1)$ (Table 5.5).

(3) Estimated by equation $\overline{W}(3)-\overline{W}(2)$ (Table 5.5).

(4) Estimated by equation $\overline{W}(4)-\overline{W}(3)$ (Table 5.5).

(5) Estimated by equation $\overline{W}(8)$ (Table 5.5).

Table 5.7

Root biomass (t/ha) for successional stands and mature forests. Numbers are means with one standard error, n = 4. Values in parentheses indicate percentage of total biomass within a specified diameter class.

Stand	Years since disturbance	Depth (cm)	Root diameter classes (mm)							
			< 1	1 to < 3	3 to < 6	6 to < 10	10 to < 20	20 to < 40	≥ 40	Total
II	11	Surf	0.651 ± 0.15	0.263 ± 0.02	0.059 ± 0.02	0.153 ± 0.13	1.325 ± 0.75	0.00 ± 0.0	0.00 ± 0.0	2.451
		0-10	0.424 ± 0.09	0.328 ± 0.06	0.535 ± 0.24	0.403 ± 0.30	0.300 ± 0.30	0.00 ± 0.0	0.00 ± 0.0	1.990
		10-20	0.345 ± 0.08	0.200 ± 0.05	0.120 ± 0.08	0.231 ± 0.23	0.00 ± 0.00	0.00 ± 0.0	0.00 ± 0.0	0.896
		20-30	0.241 ± 0.06	0.137 ± 0.04	0.077 ± 0.02	0.090 ± 0.09	0.00 ± 0.00	0.00 ± 0.0	0.00 ± 0.0	0.545
		Total to 30	1.661 (83)	0.928 (76)	0.791 (84)	0.877 (83)	1.625 (100)	0.00	0.00	5.882 (86)
		Total to 70	2.001 ± 0.31	1.217 ± 0.19	0.940 ± 0.37	1.062 ± 0.73	1.625 ± 1.04	0.00 ± 0.0	0.00 ± 0.0	6.845
VI	20	Surf	0.968 ± 0.22	0.562 ± 0.18	0.825 ± 0.34	0.346 ± 0.24	0.167 ± 0.16	0.00 ± 0.0	0.00 ± 0.0	2.868
		0-10	0.680 ± 0.19	0.760 ± 0.21	1.398 ± 0.23	1.779 ± 0.23	0.859 ± 0.77	0.562 ± 0.56	0.00 ± 0.0	6.038
		10-20	0.526 ± 0.12	0.493 ± 0.07	0.518 ± 0.19	0.725 ± 0.31	0.109 ± 0.10	0.00 ± 0.0	0.00 ± 0.0	2.371
		20-30	0.374 ± 0.15	0.283 ± 0.05	0.358 ± 0.13	0.083 ± 0.04	0.041 ± 0.03	0.00 ± 0.0	0.00 ± 0.0	1.139
		Total to 30	2.548 (72)	2.098 (75)	3.099 (83)	2.933 (87)	1.176 (100)	0.562 (100)		12.416 (78)
		Total to 70	3.533 ± 0.60	2.785 ± 0.35	3.740 ± 0.68	3.370 ± 0.61	1.176 ± 0.90	0.562 ± 0.56	0.00 ± 0.0	15.846
X	35	Surf	1.349 ± 0.40	0.773 ± 0.06	0.922 ± 0.30	0.405 ± 0.25	0.438 ± 0.26	0.00 ± 0.00	0.00 ± 0.0	3.887
		0-10	1.368 ± 0.44	0.945 ± 0.17	0.746 ± 0.10	1.108 ± 0.31	0.664 ± 0.38	0.880 ± 0.88	0.00 ± 0.0	5.711
		10-20	0.529 ± 0.17	0.516 ± 0.11	0.794 ± 0.22	0.474 ± 0.14	1.304 ± 0.79	1.414 ± 1.23	0.00 ± 0.0	5.031
		20-30	0.270 ± 0.10	0.257 ± 0.07	0.245 ± 0.09	0.127 ± 0.05	0.00 ± 0.00	0.00 ± 0.0	0.00 ± 0.0	0.899
		Total to 30	3.516 (91)	2.491 (82)	2.707 (89)	2.114 (100)	2.406 (100)	2.294 (100)	0.00	15.528 (93)
		Total to 70	3.869 ± 1.08	3.042 ± 0.36	3.032 ± 0.36	2.114 ± 0.16	2.406 ± 1.36	2.294 ± 1.20	0.00 ± 0.0	16.757
XV	60	Surf	1.207 ± 0.20	0.948 ± 0.28	0.688 ± 0.09	0.835 ± 0.18	1.043 ± 0.63	0.316 ± 0.31	11.611 ± 8.54	16.648
		0-10	0.681 ± 0.06	0.842 ± 0.04	0.683 ± 0.14	2.177 ± 0.33	1.520 ± 0.86	1.878 ± 1.63	6.674 ± 5.60	14.455
		10-20	0.359 ± 0.04	0.468 ± 0.11	0.478 ± 0.03	0.907 ± 0.24	1.724 ± 0.34	0.940 ± 0.69	0.726 ± 0.72	5.602
		20-30	0.195 ± 0.03	0.168 ± 0.05	0.261 ± 0.06	0.381 ± 0.22	0.371 ± 0.37	0.00 ± 0.0	0.843 ± 0.84	2.219
		Total to 30	2.442 (88)	2.426 (84)	2.110 (80)	4.300 (85)	4.658 (95)	3.134 (94)	19.854 (97)	38.924 (93)
		Total to 70	2.782 ± 0.27	2.894 ± 0.43	2.641 ± 0.32	5.050 ± 0.57	4.888 ± 1.18	3.321 ± 1.73	20.437 ± 8.70	42.013
XIX	80	Surf	0.547 ± 0.17	0.599 ± 0.12	0.704 ± 0.10	0.912 ± 0.29	0.728 ± 0.43	0.698 ± 0.69	0.00 ± 0.0	4.188
		0-10	0.644 ± 0.15	0.634 ± 0.14	1.053 ± 0.25	1.242 ± 0.43	2.451 ± 1.01	0.143 ± 0.14	1.478 ± 1.47	7.645
		10-20	0.537 ± 0.11	0.473 ± 0.05	0.413 ± 0.10	0.685 ± 0.33	1.288 ± 0.62	0.00 ± 0.0	0.00 ± 0.0	3.396
		20-30	0.143 ± 0.04	0.272 ± 0.04	0.241 ± 0.06	0.026 ± 0.02	0.310 ± 0.17	0.00 ± 0.0	0.00 ± 0.0	0.992
		Total to 30	1.871 (88)	1.978 (84)	2.411 (88)	2.865 (100)	4.777 (99)	0.841 (100)	1.478 (100)	16.221 (94)
		Total to 70	2.129 ± 0.24	2.347 ± 0.20	2.738 ± 0.41	2.865 ± 0.41	4.800 ± 1.38	0.841 ± 0.84	1.478 ± 1.47	17.198
XX	MTF	Surf	1.440 ± 0.36	1.031 ± 0.17	0.751 ± 0.15	0.465 ± 0.17	0.482 ± 0.38	0.606 ± 0.60	0.00 ± 0.0	4.775
		0-10	0.515 ± 0.13	0.653 ± 0.12	1.125 ± 0.27	1.431 ± 0.51	2.177 ± 0.52	1.994 ± 0.82	0.00 ± 0.0	7.895
		10-20	0.401 ± 0.10	0.487 ± 0.09	0.691 ± 0.14	1.086 ± 0.36	2.001 ± 0.67	2.197 ± 1.51	8.765 ± 8.76	15.628
		20-30	0.588 ± 0.12	0.449 ± 0.11	0.820 ± 0.31	1.173 ± 0.47	1.040 ± 0.51	0.353 ± 0.28	0.00 ± 0.0	4.423
		Total to 30	2.944 (72)	2.620 (71)	3.387 (71)	4.155 (87)	5.700 (82)	5.150 (93)	8.765 (100)	32.721 (85)
		Total to 70	4.083 ± 0.43	3.700 ± 0.28	4.794 ± 0.68	4.801 ± 1.15	6.993 ± 0.71	5.530 ± 2.49	8.765 ± 8.76	38.666

62% of the total root biomass, with the highest values in stand VI. The percent of root biomass > 20 mm varied from 0 to 59% of the total with the lowest values for 9- and 20-year-old stands and the highest for 60-year-old and MTF stands.

Mean Biomass by Age Class

The mean aboveground living biomass for the six age groups ranged from 58 (S.E. = 8.21) to 255 (S.E. = 10.79) t/ha (Table 5.8). Successional stands, 10 to 80 years old, had 23 to 59% of the aboveground biomass of MTF. The mean aboveground biomass of mature forests was significantly greater ($P \leq 0.05$) than those found in the successional stands (Table 5.8). Among successional stands, significant differences occurred between 60- to 80-year-old stands and 10- to 20-year-old stands.

The mean belowground root biomass varied from 10 (S.E. = 2.21) to 58 (S.E. = 4.30) t/ha (Table 5.8). Successional stands had 17 to 55% of the belowground biomass when compared with MTF. The mean aboveground dead biomass for 10-year-old stands to MTF had 18 (S.E. = 6.04) to 23 (S.E. = 10.20) t/ha with low values of 1 and 6 t/ha in 20- and 35-year-old stands (Table 5.8). There were no significant differences ($P \leq 0.05$) in aboveground dead biomass among MTF and successional stands (Table 5.8).

The sum of total living and dead biomass ranged from 86 (S.E. = 5.30) to 336 (S.E. = 21) t/ha for 10-year-old to MTF stands (Table 5.8). Total mean biomass for 10- to 80-year-old stands corresponded to 26 and 62% for that of an MTF. There were significant differences ($P \leq 0.05$) among successional stands and MTF. There were

Table 5.8

Biomass changes through time. Numbers are means with one standard error, n = 4, except age class 60 with n = 3. Statistics were calculated using one way ANOVA and Duncan's multiple range test. Means designated with the same letter (in parentheses) were not significantly different at the $P \leq 0.05$ level.

Biomass type	Years since disturbance	Mean biomass (t/ha)	S.E.	% of MTF biomass
Aboveground	10	57.99 (D)	8.21	22.74
	20	76.56 (CD)	8.55	30.02
	35	107.63 (BC)	21.56	42.20
	60	150.49 (B)	24.27	59.01
	80	149.45 (B)	9.62	58.60
	200	255.02 (A)	10.79	100.00
Belowground*	10	9.78 (D)	2.21	16.82
	20	15.87 (D)	1.47	27.30
	35	19.38 (CD)	4.04	33.33
	60	31.82 (B)	8.66	51.10
	80	29.71 (BC)	2.05	54.73
	200	58.14 (A)	4.30	100.00
Total living	10	67.77 (D)	10.36	21.64
	20	92.43 (CD)	9.83	29.52
	35	127.01 (BC)	25.52	40.56
	60	182.31 (B)	32.76	58.22
	80	179.16 (B)	11.65	57.21
	200	313.16 (A)	15.09	100.00
Aboveground dead	10	17.89 (A)	6.043	
	20	1.05 (A)	0.202	
	35	6.06 (A)	1.828	
	60	23.10 (A)	10.196	
	80	16.49 (A)	7.990	
	200	22.73 (A)	10.221	
Total biomass	10	85.66 (C)	5.29	25.50
	20	93.48 (C)	9.72	27.83
	35	133.07 (C)	24.86	39.62
	60	205.41 (B)	23.56	61.15
	80	195.65 (B)	12.72	58.25
	200	335.89 (A)	20.99	100.00

*Root biomass is estimated from regression equations.

also differences between 60- to 80-year-old stands and 10- to 20-year-old stands.

The proportion of total biomass represented by aboveground living biomass ranged from 53.17 to 83.08%. The percentage of belowground and dead from total biomass varied from 9.02 to 19.85% and from 0.69 to 37.81%, respectively.

DISCUSSION

The results for standing biomass were obtained using allometric regressions specific to size class and based on dbh, height, and species-wood density. Biomass for whole trees, stems, and branches was overestimated by 10 to 19% from the value obtained in the field when a single regression was used for all size classes. However, the estimate of total biomass was within 4% when trees were grouped into three dbh categories. Twig and leaf biomass was underestimated by 13 and 17%, when the general regression was used; the regression for trees 5 to 20 cm dbh underestimated these components by 19 and 13%, respectively (Table 5.2, page 87). Leaves and branches were overestimated by 12 and 11%, respectively, when a regression for trees greater than 20 cm dbh was used.

Biomass estimations by whole-plot-harvesting produced high variability, suggesting that several replicate plots should be harvested (UNESCO 1978). However, biomass estimates from harvested plots are frequently used to assess the amount of biomass on successional stands (Brown 1980, Lugo and Brown 1982). Biomass variability by harvesting whole plots has been calculated for many studies. In Panama, Golley et al. (1976) assessed the biomass of a

4-year-old successional stand by harvesting three, 3- x 3-m, plots. The mean biomass was 4940 g/m^2 and the standard error was 7110. Similarly high variability was found in Thailand by Ogawa et al. (1965) who examined the variation of biomass by clear-felling four, 10- x 10-m, plots. The mean and standard error for stems and branches together were 3.95 t/ha and 3.28, respectively. A fundamental problem of whole-plot-harvesting is determining the number of plots required to sample forest biomass adequately. For example, Hozumi et al. (1969) estimated that over 300, 2- x 2-m, plots would be required for estimating biomass at the 95% confidence level. In the present study, regressions for biomass of the whole tree and tree components using diameter, height, and wood density as independent variables allowed the estimation of biomass.

There were differences as high as $\pm$ 48% in aboveground biomass values between plots of different sizes (0.03 and 0.25 ha) within the same stand (Table 5.3, page 88). Similar results appeared in other rain forest studies where regressions were used. Ogawa et al. (1965) reported differences as much as 20% among biomass values on several plots of the same size in Thailand. Folster et al. (1976) presented differences of 53% among mature forest stands in Colombia. Biomass differences reflect variability in the forests related to the size of plots sampled and the sampling method. These differences can also be attributed to the variability in soils, species composition, microrelief, and disturbances.

Wood density values for the species in the URN vary from 0.26 to 0.80 g/cm^3 dry weight. The weighted mean for wood density based on

biomass contribution of the species per stand for all trees > 1 cm varied from 0.50 g/cm^3 for the 10-year-old stands to 0.67 g/cm^3 for the MTF (Chapter 2). These wood density values are close to the range reported by Chudnoff (1980) of 0.57 to 0.62 g/cm^3 for other tropical forests. Omitting wood density as an independent variable in the biomass regression equation will result in differences in the estimated values of biomass. Early successional forests, dominated by fast-growing species with low wood density, have relatively high stand volumes but may show low biomass values when wood density is considered.

Biomass of crown components has been estimated by allometric regressions based on stem diameter and total tree height (Kira 1978, Ogawa et al. 1965, Jordan and Uhl 1978, Folster et al. 1976). The estimation of crown biomass as a function of dbh and height has low reliability (Whittaker and Woodwell 1968, Unesco 1978, Madgwick and Krek 1980). A reason for this discrepancy is that dbh and height increase during the life of the tree, whereas leaf and branch biomass fluctuates from year to year according to the position of the tree in the forest. Several allometric regressions were tried, but the biomass estimates were not included in the total biomass results because crown dimensions (area and volume of the crown) were not recorded for all trees. The addition of crown cross-sectional area or volume as an independent variable gave the best results with an increase in the r^2 value from 0.47 to 0.82.

Mean leaf biomass reached a value of 6.88 (S.E. = 0.35) t/ha in 10-year-old stands. Leaf weight shows little variation, remaining relatively constant among successional stands and attaining a mean

value of 9.78 (S.E. = 0.43) t/ha in MTF. Similar results were reported in other tropical rain forests with values between 7 and 10 t/ha (Aubreville 1938, Ogawa et al. 1965, Golley et al. 1969, Klinge et al. 1975). A possible explanation for the small variation in leaf biomass between successional stages and MTF is made by Monsi and Saeki (1953) who suggest that leaf amounts in a plant community are largely determined by incident light intensity and efficiency of light extinction. The relative proportion of leaf and twig biomass was high in the early stages of succession, declining toward the mature forest. This indicates that foliage remains relatively constant in relation to total aboveground biomass.

Calculated branch biomass was higher than stem biomass for several stands between 40 and 80 years old. In these stands, canopy trees grow without competition for space, thus developing large crowns. This is especially true for trees with several sprouts. The opposite occured in the mature forests where the trees compete to reach the canopy and develop relatively small crown biomass compared to bole biomass. The relative proportion of branch to total aboveground biomass in the MTF varied between 25.79 to 28.27% and 70 to 85 t/ha (Table 5.4, page 92). These values are higher than those reported in Colombia (14% and 23.6 t/ha; Folster et al. 1976) and similar to those from Brazil (20% and 101 t/ha; Klinge et al. 1975). Stem biomass values in MTF ranged from 106.95 to 144.79 t/ha, representing low values compared to other tropical rain forests (134 to 360 t/ha; Aubreville 1938, Ogawa et al. 1965, Klinge et al. 1975, Folster et al. 1976).

The mean total aboveground and belowground living biomass for the four MTF is 313 t/ha (Table 5.8) and is similar to the value of 309 t/ha reported by Uhl and Jordan (1984) for San Carlos. Other studies concerning living biomass of tropical forests around the world report both higher and lower values compared to those found in this study. Golley et al. (1969) estimated biomass from 284.13 to 380.23 t/ha for a tropical moist forest in Panama. Ogawa et al. (1961, 1965) showed values from 200 to 350 t/ha for the northwest highlands forest and 326 to 404 t/ha for a forest in the reserve of Khao Chong. However, in the Pasoh forest of Malaysia, Kato et al. (1974, cited in Jordan and Uhl 1978) estimated values of 475 and 664 t/ha for two plots. Klinge et al. (1975) reported 989.9 t/ha (fresh weight $\sim$ 450 t/ha dry weight) near Manaus, Brazil, while in the Magdalena Valley, Colombia, Folster et al. (1976) reported aboveground biomass for three plots between 171.89 and 325.81 t/ha. Extensive studies across the Amazon basin along transects covering an area of 15.05 ha indicated that approximately 50% of the area surveyed had aboveground biomass values less than 200 to 220 t/ha (Brown 1980).

The data on aboveground dead biomass by age category indicate that: (1) a mean of 17.89 t/ha (S.E. = 6.04, Table 5.8) from the former forest still remains on fallows 10 years after abandonment; (2) the mean declines to a value of about 1.05 t/ha (S.E. = 0.20) on 20-year-old stands; (3) an increase begins at 20 years and reaches 23.10 t/ha (S.E. = 10.19) in 60-year-old stands; (4) after 60 years the value varies; and (5) the occurrence of stochastic events, such as storms, may topple large trees, thus adding large amounts of previously

living biomass to the dead biomass compartment. Examples of large amounts of aboveground dead biomass with values between 32.40 and 53.03 t/ha were found in URN in 60-year-old successional stands and MTF (Table 5.3, page 88).

Some studies show high values of dead biomass for tropical successional sites; 17.40 and 71.96 t/ha in 18 and 50 year secondary forest in Yangambi, Belgian Congo, and Kade forest, Ghana, respectively (Bartholomew et al. 1953, Greenland and Kowal 1960). Other workers report lower values. For example, Golley et al. (1969) estimated 14.64 t/ha in a Panamanian forest, Klinge et al. (1975) reported 25.8 t/ha for a forest in Central Amazonia, Jordan and Uhl (1978) reported values ranging from 1.83 to 8.31 t/ha for four MTF in the San Carlos area.

Total belowground root biomass, to a depth of 70 cm, was greater in MTF than in successional stands. The mean belowground root biomass ranged from 9.78 to 29.71 t/ha for 10- and 80-year-old stands, respectively, and 58.14 t/ha for MTF (Table 5.8, page 106). Belowground biomass for stand XIII was probably underestimated by the regression because of the low basal area values for the 0.03-ha plots. These low basal area estimates are the result of recent tree falls, and if the basal area of the 0.25-ha plot is considered its root biomass would be 30 to 40 t/ha instead of 17 t/ha.

A mean root biomass of 58.14 t/ha is shown for the four MTF (Table 5.8, page 106). This value is greater than the range of 0.40 to 32.80 t/ha reported for other tropical forests (Santantonio et al. 1977). However, this value is close to that of 56 t/ha reported by

Stark and Spratt (1977) for an MTF forest plot near San Carlos. The root biomass values for successional sites in the URN are low compared to those for el Gran Pajonal, Peru, where Scott (1977) showed 45.0, 59.8, 84.6 t/ha for 10- 17- and 32- to 37-year-old stands, respectively.

In all URN stands, fine roots were concentrated in the upper 10-cm layer and decreased with depth. The proportion of total fine roots found to a 30-cm depth was higher for all successional stands than for the MTF, while the biomass of large diameter roots was greater in stands older than 40 years. Total fine root biomass to a depth of 30 cm in successional stands ranged from 56% to 83% of that for a mature forest. The exception was stand X, which was 19% greater. Fine root biomass, to a depth of 70 cm, was between 49 and 95% of that for a mature forest. Temperate studies have reported decreasing amounts of fine roots with soil depth (Fogel and Hunt 1979, McQueen 1968, 1973). These results indicate that in an environment poor in nutrients, the fine roots not only cover the first 30 cm of soil in early stages of succession, but they continue penetrating to deeper layers and developing an extensive system that provides nutrients to trees.

Large roots (diameter > 40 mm) were absent in the first 40 years of succession. In older stands, they represent between 9 and 50% of total belowground biomass to a 30-cm depth in the soil. The proportion of total belowground root biomass in the upper 30 cm ranged from 78 to 94% (Table 5.7, page 104). This shallow system renders the forest more susceptible to wind and storm effects.

Aboveground living biomass in the URN accumulated at a slower rate in some successional stands than in other tropical rain forests.

Table 5.8, page 106, shows the mean total living biomass with values of 67.77 t/ha (S.E. = 10.36), 127.01 t/ha (S.E. = 25.52) and 179.16 t/ha (S.E. = 11.65) for 10- 35- and 80-year-old successional stands, respectively. These values are equivalent to 22, 41 and 57%, respectively, of total aboveground living biomass of an MTF.

Studies of aboveground biomass recovery on abandoned tropical fallows have estimated that 30 to 40 years are required to attain a biomass equivalent to that of a mature forest (Snedaker 1970, Lugo et al. 1974, Scott 1977). The present study indicates a longer time is required for a stand to attain biomass values of a mature forest. One reason for this difference is that the URN region soils are poor in nutrients compared to those in many other tropical areas. Comparisons between nutrients in soils from URN and Costa Rica show 10- to 130-fold differences in available cations (K, Ca, Mg), and four to five times more carbon and total nitrogen (Hardy 1961, cited by Harcombe 1977, Uhl and Jordan 1984). Also, evidence from this study indicates that some methods described in the literature, for estimating biomass values, are biased toward a shorter time required for biomass accumulation. For example, data from fallows less than 10 years old were fitted to a regression equation to determine recovery time (Snedaker 1970); biomass estimations were based on only 14 trees with small dbh sizes (2 to 10 cm) and heavy weights (i.e., a tree 10 cm dbh weights 200 kg dry weight) (Scott 1977); biomass values were obtained by harvesting less than three plots, producing a relatively high biomass value (Bartholomew et al. 1953, Greenland and Kowal 1960); age-biomass

correlations included data suggesting biomass overestimations were used (Lugo et al. 1974).

This study is based on a chronosequence of stands of different ages that have been used in slash-and-burn agriculture. The time of abandonment of the farms imposed an even-aged condition that allowed temporal ordering of the studied stands. Biomass accumulation occurs in the following way. The first stage is equivalent to the "reorganization" phase of Bormann and Likens (1981); a rapid cover of the site by forest vegetation, herbs, and grasses. Living aboveground biomass increases from 9.64 t/ha at 1 to 2 years (Uhl et al. 1982) to 57.99 t/ha (S.E. = 8.21) (Table 5.8, page 106) at 9 to 14 years. Individual trees can reach 20 cm dbh, 13 to 16 m height, and 70 kg dry weight during this period. Dead biomass declines from 97 t/ha (S.E. = 10.4) at 3 to 4 years to 17.89 t/ha (S.E. = 6.04) (Table 5.8, page 106) at 9 to 14 years. Trunks from the previous forests account for more than 95% of the dead biomass. In the first 5 years, dead biomass was greater than the net accumulation of living biomass.

The second successional stage corresponds to the "aggradation" phase of Bormann and Likens (1981). It occurs on fallows abandoned for 15 to 80 years. Canopy dominants in the best sites may reach 90 cm dbh, 30 m height, and dry weight up to 4 tons. Aboveground living biomass averaged 108 t/ha (S.E. = 21.56) and 149 t/ha (S.E. = 9.62) (Table 5.8, page 106) in 35- and 80-year-old stands, respectively. During this phase, dead biomass showed high variability with the lowest value, 1.05 t/ha (S.E. = 0.20), at 20 years. After this, dead biomass increased to a peak; 23 t/ha (S.E. = 10.19) at 60 years and remained

relatively constant until 80 years. Tree-fall gaps begin to appear at 20 years forming openings of 100 m^2 on stands 20 to 40 years old. In stands 60 to 80 years old, tree falls are the result of windthrow and the senescene of species of secondary stages that are canopy dominants such as Alcornea spp., and Vochysia sp. The end of the "aggradation" phase may occur between 60 to 80 years according to the following characteristics: species diversity attains the highest diversity value (Chapter 4) at this age, forest structure begins to resemble mature forest (Chapter 4), and aboveground living biomass is 50 to 60% of the value reached for an MTF.

The third stage is called "steady state" of Bormann and Likens (1981). Mature forests are composed of the largest trees, 60 to 220 cm dbh, 30 to 40 m tall, with dry weights of individual trees approaching 11 tons. These trees represent less than 1% of the number of stems $\geq$ 1 cm dbh. Their basal area ranges from 4 to 13 m^2/ha (10 to 35% of total basal area of the stand) (Chapter 4), and their aboveground biomass varies from 50 to 103 t/ha (22 to 38% of the total biomass of the stand). Dead aboveground biomass shows high variability among different size plots ranging from 8 to 53 t/ha (Table 5.3, page 88).

In addition to senescence, suppression, disease, and damage by animals, wind and fire have not been considered important agents in the dynamics of species composition, structure, and biomass of Amazonian forests. Uhl (1982b) mentions an example of small-scale damage by episodic wind storms in the URN forests. Kate Clark (1983) found 12 gaps ranging from 0.4 to 1.0 ha that were formed during a storm in 1984, and Sandford et al. (1985) documents the presence of fire in this

area in the past. Other evidence such as a reversed J-shaped curve for stem density, i.e., very low numbers of large trees (Chapter 4), and missing biomass values for larger dbh categories (Figure B.5, B.6) suggest that forest disturbance occurs regularly and severely in the study region. Komarek (1964) reports 60 to 200 thunderstorm days per year for the Amazon Basin including the URN region. Nevertheless, it is possible that winds are not strong enough to destroy large forest areas as hurricanes or cyclones do in other parts of the world. However, wind frequency over long periods of time may transform the mature forests to successional stands.

The tierra firme forests of the URN appear stable and undisturbed to human perception because of size, structure, and luxurious vegetation. In reality, this forest is a mosaic of stands of different ages and growth rates resulting from natural and anthropogenic disturbances. Observed changes in living aboveground biomass accumulation during succession in the URN cannot be explained clearly in terms of the logistic model offered by Odum (1969), the shifting mosaic model showed by Bormann and Likens (1981), or the time lag model presented by Peet (1980). After the agricultural field is abandoned, aboveground biomass accumulates steadily to a plateau at 60 to 80 years. At this time a period of disruption and replacement occurs when canopy-dominant secondary species begin dying. These species are replaced by others from mature stages. The rate of replacement depends on the species composition. Major changes occur when many dominant trees senesce at the same time, giving an opening to species found at earlier stages of succession. Replacement of canopy dominants in

stands with species of different ages will occur without major disruption of structure and biomass of the forest. This type of forest will probably continue accumulating biomass toward mature forest.

With the mature forest, living aboveground biomass reaches the largest values with differences in biomass values among stands depending on the productivity of the site, time of the last disturbance, and susceptibility of the site to wind damage. A temporary "steady stage" occurs when productivity is equal to losses. The duration of the "steady stage" will depend on natural or anthropogenic disturbances. If the loss of trees in the stand is over a short period, due to fire and windthrow, living biomass will reduce drastically to levels of successional stands 30 to 40 years old or younger. If the reduction of canopy trees is gradual, because of senescence, suppression, or competition, the stand will remain essentially unchanged.

SUMMARY

Changes in biomass from 10- to 80-year-old and mature forest stands were studied in the tierra firme forests of the Upper Rio Negro region of Colombia and Venezuela. To estimate aboveground biomass in each stand, regression equations were developed from trees harvested in the field according to dbh, height, and wood density. Regressions were then applied to the data collected in each stand to describe biomass amounts by stand. A similar approach was utilized to estimate aboveground dead and belowground root biomass. Aboveground biomass differences up to 48% were found in some of the stands. The high variability in biomass in some of the stands is probably the result of

natural disturbances such as windthrows that seem to occur frequently in this region.

Biomass of tree components accumulates at different rates. Leaf and twig biomass reach maximum values early in succession, remaining relatively constant and independent of total aboveground biomass. Branch biomass attains maximum values between 40 and 80 years, but high variability occurs among these stands. Branch biomass values in MTF are close to the largest figures reported for 60- to 80-year-old stands and have low variability. Stem biomass increases through time, gaining maximum values at MTF. Fifty percent of stem biomass is reached with 80-year-old stands.

Aboveground dead biomass still remains high 14 years after disturbance of the former forest. The lowest dead biomass is attained at 20 years. Dead biomass then increases, reaching the largest value at MTF. However, some of the stands between 60 and 80 years old also attain high values.

Belowground root biomass was greater in MTF than in successional stands. The proportion of root biomass in the upper 30 cm accounts for 78 to 94% of the total. Fine root biomass in successional stands was 49 to 95% of those at MTF. Large roots were found only in stands older than 40 years.

Aboveground biomass increases linearly throughout the first 40 years, but is highly variable depending on frequency of past disturbances, intensity of land use, and soil characteristics. No significant changes occur for the next 40 years, but small declines appear between 60 to 80 years when canopy dominants begin dying. The

largest aboveground biomass values are found at MTF, but there is high variability among and within stands. This variability is a result of the dissimilar characteristics among the sites and the stress caused by natural disturbances. Large dead biomass values and numerous tree falls indicate increased dynamics at mature stages. Under certain natural conditions, e.g., simultaneous death of several large trees, biomass of an MTF may decrease, approaching values close to those found in 30- to 40-year-old stands. Aboveground living biomass in the URN accumulates very slowly. Approximately 140 to 190 years are required for an abandoned farm to attain a biomass value comparable to that of an MTF. Recovery is five to seven times longer in the URN compared to tropical rain forests in other areas. Soils low in nutrients contribute to the slow recovery of the forests in the URN.

In the URN region, some patches of mature forests decline in living biomass, others accumulate biomass as part of the recovery process, and others remain stable. The mature forests are generally in equilibrium with periods of instability of unpredictable duration, according to environmental and biological conditions.

CHAPTER 6

CONCLUSIONS

This study provides evidence of periodic disturbances in the Amazon forests of the Upper Rio Negro region of Colombia and Venezuela. Charcoal was found in most of the tierra firme forest stands, and ceramic shards were found at two of the stands, indicating human habitation in the interior of the Amazon forests. Radiocarbon dates of charcoal varied from the present to 6260 years before present, but most of the dates correspond to a period within the last 3000 years. Thermoluminescence analysis showed ceramic shard ages to be 460 to 3750 years old. The presence of charcoal in the rain forests of the Upper Rio Negro suggests that this region has been subjected to fire during extreme dry periods and indicates periods of human disturbance for the last 3000 years.

The research discussed in this dissertation shows that the slash-and-burn regime of the tierra firme forests has had a continuing influence on the present composition and structure of the forest vegetation. Species diversity increases significantly during the first 80 years of forest succession; the most rapid increase is in the first 10 years. Both successional and mature forest stands were characterized by high density of stems in smaller size classes; the mature forests show an increased number of stems in the larger size classes. Analyses of the data collected for this study show that successional development to a mature tierra firme forest in the Upper Rio Negro region is slower than the recovery time for forests in other

tropical areas. From 140 to 200 years are required for an abandoned agricultural plot to approximate the basal area and biomass of a mature forest.

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APPENDIXES

APPENDIX A

Table A.1

Dominant species in the 9- to 14-year-old stands with their RIV up to 60%.

Stand	Species name	Relative*				Relative*
		Frequency	Density	Basal area	Importance value	Importance value
I	Vismia japurensis Reich	20.0	42.85	37.26	100.12	33.37
	Cecropia sp.	30.0	23.80	25.17	78.98	26.32
II	Vismia japurensis Reich	25.0	35.29	35.99	96.29	32.09
	Bellucia grossularioides (L.) Triana	16.6	23.52	21.61	61.80	20.60
	Cecropia sp.	16.6	11.76	17.49	45.92	15.30
III	Bellucia grossularioides (L.) Triana	15.78	24.13	22.21	62.14	20.71
	Ocotea opifera Mart	5.26	20.68	18.51	44.47	14.82
	One unidentified species (Bombacaceae)	15.78	13.79	10.64	40.22	13.40
	Sapindus saponaria L.	5.26	5.17	10.33	20.77	6.92
	Alcornea sp.	5.26	5.17	6.72	17.15	5.71
IV	Bellucia grossularioides (L.) Triana	23.07	37.03	38.76	98.88	32.96
	Vismia japurensis Reich	23.07	29.62	29.06	81.77	27.25

*Percent of all individuals $\geq$ 10 cm dbh.

Table A.2

Dominant species in the 20-year-old stands with their RIV up to 60%.

Stand	Species name	Relative*				Relative*
		Frequency	Density	Basal area	Importance value	Importance value
V	Vochysia sp.	9.52	22.22	31.70	63.44	21.14
	Sclerolobium sp.	4.76	18.51	16.24	39.52	13.17
	Goupia glabra Aublet	14.28	9.25	8.09	31.64	10.54
	Vismia lauriformis (Lam.) Choisy	9.52	7.40	5.76	22.69	7.56
	Bellucia grossularioides (L.) Triana	9.52	7.40	4.62	21.55	7.18
	Bellucia sp.	9.52	5.55	5.38	20.46	6.82
VI	Inga sp.	5.26	16.0	12.97	34.23	11.41
	Vismia japurensis Reich	10.52	12.0	11.49	34.02	11.34
	Astrocaryium sp.	10.52	8.0	10.79	29.31	9.77
	One unidentified species	5.26	8.0	8.25	21.51	7.17
	Guatteria schomburgkiana Martius	5.26	4.0	5.18	18.45	6.15
	Alcornea sp.	5.26	4.0	7.69	16.96	5.65
	One unidentified species	5.26	4.0	6.87	16.13	5.37
	Caryocar glabrum (Aubl.) Pers	5.26	4.0	5.94	15.20	5.06
VII	Astrocaryium sp.	14.28	31.57	35.53	81.39	27.13
	Vismia lauriformis (Lam.) Choisy	14.28	13.15	11.45	38.89	12.96
	Myrcia bracteata (Rich.) D.C.	9.52	15.78	10.84	36.15	12.05
	Vismia japurensis Reich	14.28	10.52	11.06	35.87	11.95
VIII	One unidentified species	8.82	14.28	16.16	39.27	13.09
	Ocotea opifera Mart	8.82	8.16	10.81	27.80	9.26
	Bellucia sp.	8.82	8.16	6.45	23.43	7.81
	Alcornea sp.	5.88	4.08	11.25	21.22	7.07
	Inga sp.	5.88	6.12	6.62	18.63	6.21
	Sclerolobium sp.	2.94	10.20	5.48	16.83	5.61
	Sapindus saponaria L.	2.94	2.04	9.17	14.16	4.72
	Conceveiba guianensis Aublet	5.88	4.08	4.00	13.96	4.65

*Percent of all individuals $\geq$ 10 cm dbh.

Table A.3

Dominant species in the 30- to 40-year-old stands with their RIV up to 60%.

Stand	Species name	Relative*				Relative*
		Frequency	Density	Basal area	Importance value	Importance value
IX	Goupia glabra Aublet	15	20.68	23.91	59.59	19.86
	Bellucia grossularioides (L.) Triana	15	17.24	14.56	46.80	15.60
	Guatteria schomburgkiana Martius	10	10.34	10.89	31.23	10.41
	Ocotea esmeralda Moldenke ex Gleas	10	6.89	5.96	22.86	7.62
	Miconia dispar Bentham	10	6.89	5.75	22.64	7.54
	Eperua purpurea Bentham	5	10.34	7.06	22.41	7.47
X	Eperua purpurea Bentham	12	32.65	26.62	71.27	23.75
	Humeria balsamifera (Aublet) St Hil	8	14.28	15.02	37.31	12.43
	Goupia glabra Aublet	8	12.24	14.28	34.52	11.50
	Astrocaryium sp.	8	6.12	4.74	18.87	6.29
	Micrandra spruccei (M-Arg) Shultes	8	4.08	1.90	13.98	4.66
	Dialium guianense (Aubl.) Sandw	4	2.04	6.39	12.43	4.14
XI	Bellucia grossularioides (L.) Triana	10.34	18.86	25.87	55.08	18.36
	Humeria balsamifera (Aublet) St Hil	10.34	16.98	23.24	50.57	16.85
	Goupia glabra Aublet	10.34	13.20	11.13	34.68	11.56
	Bellucia sp.	10.34	5.66	4.57	20.57	6.85
	Vismia japurensis Reich	10.34	5.66	4.54	20.55	6.85
	Clusia sp.	6.89	7.54	4.64	19.08	6.36
XII	Humeria balsamifera (Aublet) St Hil	14.28	50.79	53.66	118.74	39.58
	Eperua purpurea Bentham	4.76	17.46	16.44	38.67	12.89
	Vochysia obscura	9.52	4.76	5.15	19.44	6.48
	One unidentified species (Arecaeae)	9.52	4.76	1.62	15.91	5.30

*Percent of all individuals $\geq$ 10 cm dbh.

Table A.4

Dominant species in the 60-year-old stands with their RIV up to 60%.

Stand	Species name	Relative*			Importance value	Relative* Importance value
		Frequency	Density	Basal area		
XIII	Eperua purpurea Bentham	15.78	31.25	57.64	104.68	35.90
	Goupia glabra Aublet	15.78	21.87	17.06	54.73	18.25
	Protium sp.	10.52	9.37	5.51	25.42	8.47
XIV	Goupia glabra Aublet	7.14	18.60	16.19	41.93	13.97
	Vochysia obscura	3.57	6.97	15.49	26.04	8.68
	Jacaranda copaia (Aublet) D. Don	7.14	4.65	13.70	25.49	8.49
	Aspidosperma sp.	3.57	6.97	7.09	17.64	5.88
	Eperua purpurea Bentham	3.57	6.97	5.69	16.24	5.41
	Alcornea sp.	3.57	4.65	7.81	16.03	5.07
	Monopterix sp.	3.57	4.65	7.01	15.23	5.07
	One unidentified species	3.57	2.32	7.10	13.00	4.33
	Protium sp.	7.14	4.65	1.08	12.87	4.29
XV	Goupia glabra Aublet	10.34	15.90	19.26	46.21	15.40
	Alcornea sp.	10.34	13.63	20.12	44.10	14.70
	Vochysia obscura	3.44	2.27	15.07	20.79	6.93
	Conceveiba guianensis Aublet	6.89	6.81	6.92	20.63	6.87
	Ocotea sp.	6.89	4.54	3.47	14.91	4.97
	One unidentified species (Aracaceae)	3.44	6.81	1.86	12.13	4.04
	Licania silvae Prance	3.44	2.27	5.88	11.16	3.87
	Jacaranda copaia (Aublet) D. Don	3.44	4.54	2.98	10.97	3.65
	Rudgea klugii St.	3.44	4.54	2.78	10.78	3.59
	Sloanea sp.	3.44	4.54	2.48	10.47	3.49

*Percent of all individuals $\geq$ 10 cm dbh.

Table A.5

Dominant species in the 80-year-old stands with their RIV up to 60%.

Stand	Species name	Relative*				Relative*
		Frequency	Density	Basal area	Importance value	Importance value
XVI	Conceveiba guianensis Aublet	11.53	11.11	17.53	40.18	13.40
	One unidentified species (Arecaceae)	11.53	18.51	7.24	37.30	12.44
	Vochysia obscura	7.69	11.11	16.83	35.64	11.88
	Alcornea sp.	11.53	5.55	6.08	23.17	7.72
	Protium sp.	7.69	9.25	4.86	21.81	7.27
	Micrandra sprucei (M-Arg) Shultes	3.84	9.25	8.19	21.29	6.16
	Bellucia sp.	3.84	1.85	12.77	18.47	5.20
XVII	Vochysia obscura	8.57	13.51	23.05	45.14	15.04
	Aspidosperma sp.	8.57	10.81	20.76	40.14	13.38
	Paraqueiba sericea Tul	8.57	17.56	12.74	38.88	12.96
	Vochysia sp.	8.57	4.05	6.79	19.42	6.47
	One unidentified species	2.85	6.75	7.03	16.64	5.54
	Swartzia schomburgkii Bentham	5.71	4.05	2.36	12.13	4.04
	Xilopia spruceana Bentham	2.85	5.40	3.83	12.09	4.03
XVIII	Goupia glabra Aublet	7.69	12.06	22.74	42.50	14.18
	Sclerolobium sp.	5.12	10.34	13.09	28.57	9.53
	Bellucia sp.	5.12	6.89	10.49	22.51	7.51
	Protium sp.	5.12	6.89	5.75	17.77	5.93
	Alcornea sp.	5.12	3.44	8.52	17.09	5.70
	Astrocaryium sp.	5.12	6.89	5.03	17.05	5.69
	Bellucia glossularioides (L.) Triana	5.12	3.44	6.92	15.50	5.17
	Euterpe sp.	5.12	3.44	1.04	9.61	3.21
	Paraqueiba sericea Tul	2.56	1.72	4.92	9.21	3.07
	Ocotea opifera Mart	2.56	3.44	2.56	8.58	2.86
	Macrolobium limbatum Spruce cx Bentham	2.56	3.44	1.30	7.31	2.44
XIX	Eperua purpurea Bentham	10.34	28.00	29.70	68.04	22.68
	Vochysia sp.	6.89	12.00	12.94	31.84	10.61
	Humeria balsamifera (Aublet) St Hil	10.34	6.00	5.82	22.17	7.39
	Goupia glabra Aublet	6.89	6.00	8.10	21.00	7.00
	Inga sp.	3.44	6.00	9.98	19.43	6.47
	One unidentified species (Annonaceae)	6.89	4.00	4.19	15.09	5.03
	Protium sp.	3.44	6.00	3.77	13.22	4.40

*Percent of all individuals $\geq$ 10 cm dbh.

Table A.6

Dominant species in the MTF stands with their RIV up to 60%.

Stand	Species name	Relative* Frequency	Relative* Density	Relative* Basal area	Importance value	Relative* Importance value
XX	Unidentified species	7.5	13.72	10.44	31.70	10.58
	Cariocar glabrum (Aubl) Pers	5.0	3.92	18.11	27.03	9.02
	Micrandra sprucei (M-Arg) Shultes	2.5	3.92	18.29	24.71	8.24
	Mouriri uncithea Morley Wurdack	5.0	3.92	7.80	16.72	5.88
	One unidentified species	7.5	5.88	2.33	15.71	5.24
	Virola surinamensis	5.0	5.88	3.30	14.18	4.73
	Dialium guianense	2.5	3.92	6.39	12.81	4.27
	Xylopia spruceana Bentham	5.0	3.92	2.14	11.06	3.69
	Licania apetala (E Mey) Fritsch	5.0	3.92	2.10	11.02	3.68
	Iryanthera sp.	2.5	5.88	2.03	10.41	3.47
	Licania heteromorpha Bentham	5.0	3.92	1.37	10.30	3.44
	One unidentified species (Annonaceae)	2.5	3.92	2.33	9.60	3.20
XXI	Eperua purpurea Bentham	9.52	20.00	35.70	65.22	21.74
	Protium sp.	14.28	29.09	12.59	55.97	18.66
	Eschweilera sp.	14.28	10.90	4.75	29.95	9.98
	Monopterix sp.	4.76	10.90	8.68	24.35	8.12
	One unidentified species	9.52	3.63	9.77	22.93	7.64
XXII	Swartzia schomburgkii Bentham	5.40	5.88	34.04	45.32	15.12
	Jessemia batua (Mort) Burret	8.10	13.72	5.03	26.87	8.96
	One unidentified species	8.10	5.88	6.54	20.53	6.85
	Ocotea opifera Mart	5.40	3.92	7.46	16.79	5.60
	Conceveiba guianensis Aublet	5.40	3.92	5.55	14.88	4.96
	One unidentified species (Sapotaceae)	2.70	7.84	3.14	13.68	4.57
	Iryanthera sp.	5.40	5.88	1.58	12.87	4.29
	Dialium guianense	5.40	3.92	1.50	10.82	3.61
	Mouriri uncithea Morley Wurdack	2.70	1.96	6.14	10.81	3.61
XXIII	Swartzia schomburgkii Bentham	9.09	18.75	28.57	56.41	18.81
	One unidentified species (Leguminosae)	6.06	2.08	40.07	45.18	15.07
	Protium sp.	9.09	16.66	3.64	29.40	9.80
	Virola osteoploen	9.09	10.41	4.07	23.58	7.86
	Roucheria punctata aff Ducke	6.06	6.25	2.76	15.07	5.03
	Eschweilera collina Eyma	6.06	6.25	2.47	14.78	4.93

*Percent of all individuals $\geq$ 10 cm dbh.

Table A.7

Basal area changes through time. Numbers are means with one standard error, n = 4, except age class 60 with n = 3. Statistics were done using one way ANOVA and Duncan's multiple range test. Means designated with the same letter (in parentheses) were not significantly different at the $P \leq 0.05$ level.

dbh classes (cm)	Years since disturbance	Mean basal area (m^2/ha)	S.E.
1 ≤ to < 5	10	2.59 (AB)	0.26
	20	3.30 (A)	0.69
	35	2.75 (AB)	0.11
	60	1.98 (B)	0.22
	80	2.32 (AB)	0.20
	200	2.67 (AB)	0.23
5 ≤ to < 20	10	9.80 (A)	1.30
	20	11.39 (A)	0.88
	35	10.16 (A)	1.42
	60	6.13 (B)	0.12
	80	9.16 (A)	0.68
	200	9.31 (A)	0.39
20 ≤ to < 40	10	0.39 (D)	0.28
	20	2.24 (CD)	1.22
	35	5.40 (BC)	2.43
	60	10.79 (A)	1.19
	80	11.16 (A)	1.15
	200	8.88 (AB)	0.97
40 ≤ to < 60	10	0.00	
	20	0.00	
	35	0.28 (B)	0.28
	60	5.59 (A)	2.65
	80	1.33 (B)	0.79
	200	6.64 (A)	1.78
60 ≤ to 90	200	1.88	1.10
≥ 90	200	5.42	3.25
Totals	10	12.78 (C)	1.51
	20	16.92 (C)	0.89
	35	18.59 (BC)	2.41
	60	24.48 (B)	3.85
	80	23.98 (B)	0.88
	200	34.80 (A)	1.48

Table A.8

Broken crowns and standing dead trees by stand.

Stand	Years since disturbance	Broken crowns	Dead stems
I	9	0	NR*
II	11	0	NR
III	12	NR	NR
IV	14	21	NR
V	20	0	NR
VI	20	43	NR
VII	20	43	NR
VIII	20	87	NR
IX	30	0	60
X	35	0	76
XI	35	43	32
XII	40	16	36
XIII	60	43	36
XIV	60	0	0
XV	60	38	4
XVI	80	43	36
XVII	80	131	82
XVIII	80	21	56
XIX	80	150	72
XX	MTF	43	NR
XXI	MTF	43	44
XXII	MTF	12	40
XXIII	MTF	22	22

*NR = not recorded.

APPENDIX B

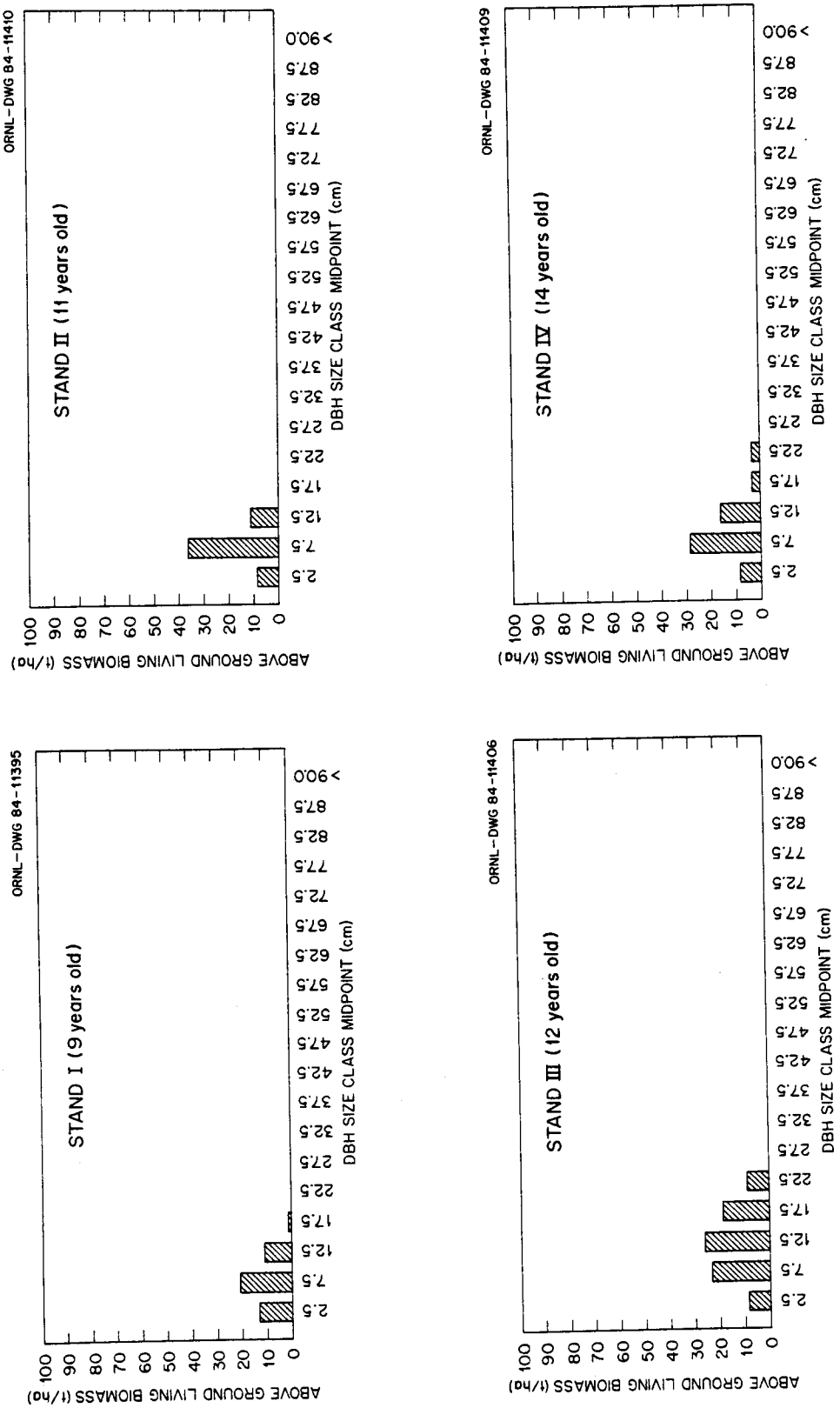

Figure B.1. Aboveground living biomass by dbh class for four, ~10-year-old, stands in the Upper Rio Negro region of Colombia and Venezuela.

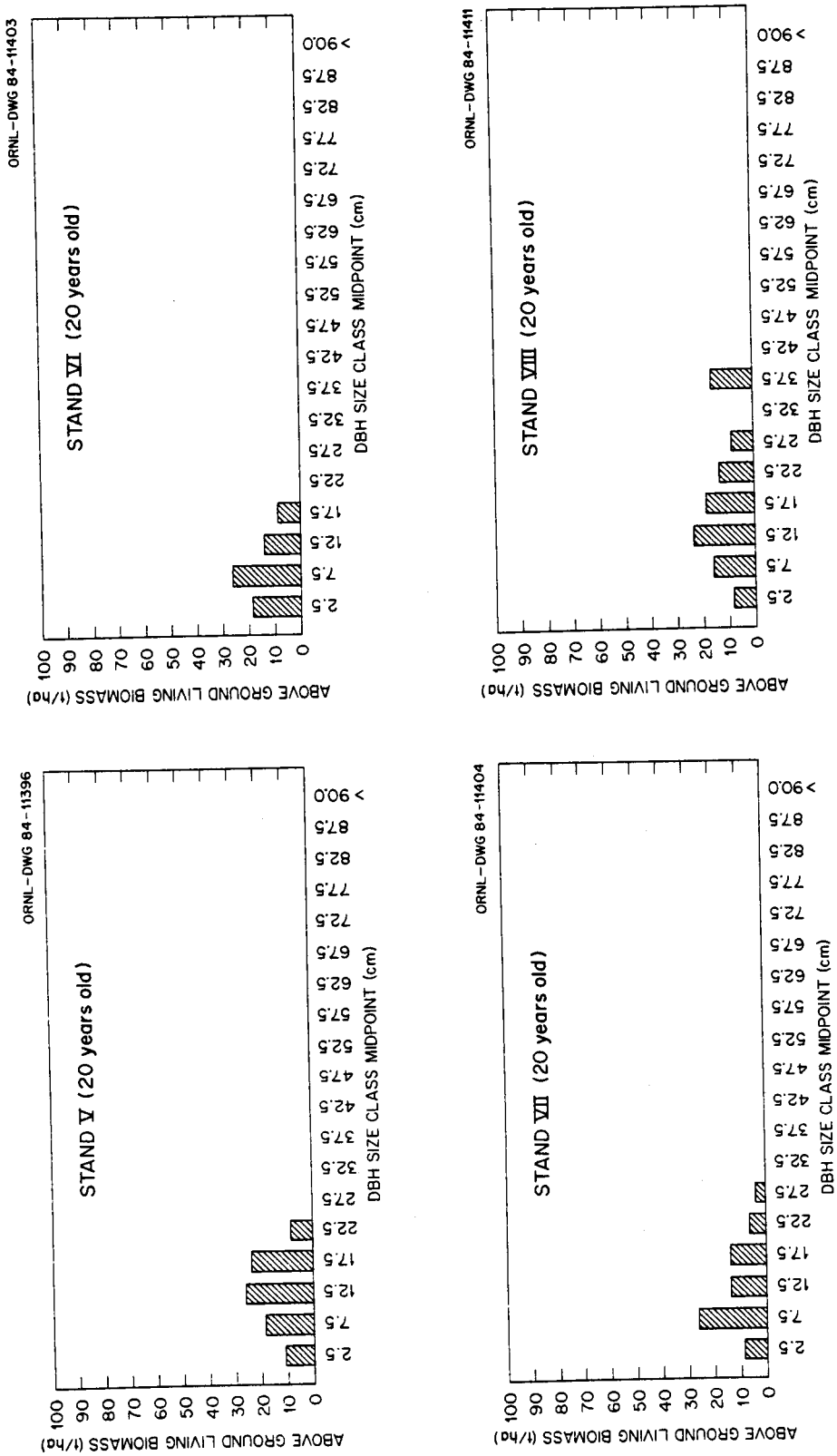

Figure B.2. Abovegound living biomass by dbh class for four, ~20-year-old, stands in the Upper Rio Negro region of Colombia and Venezuela.

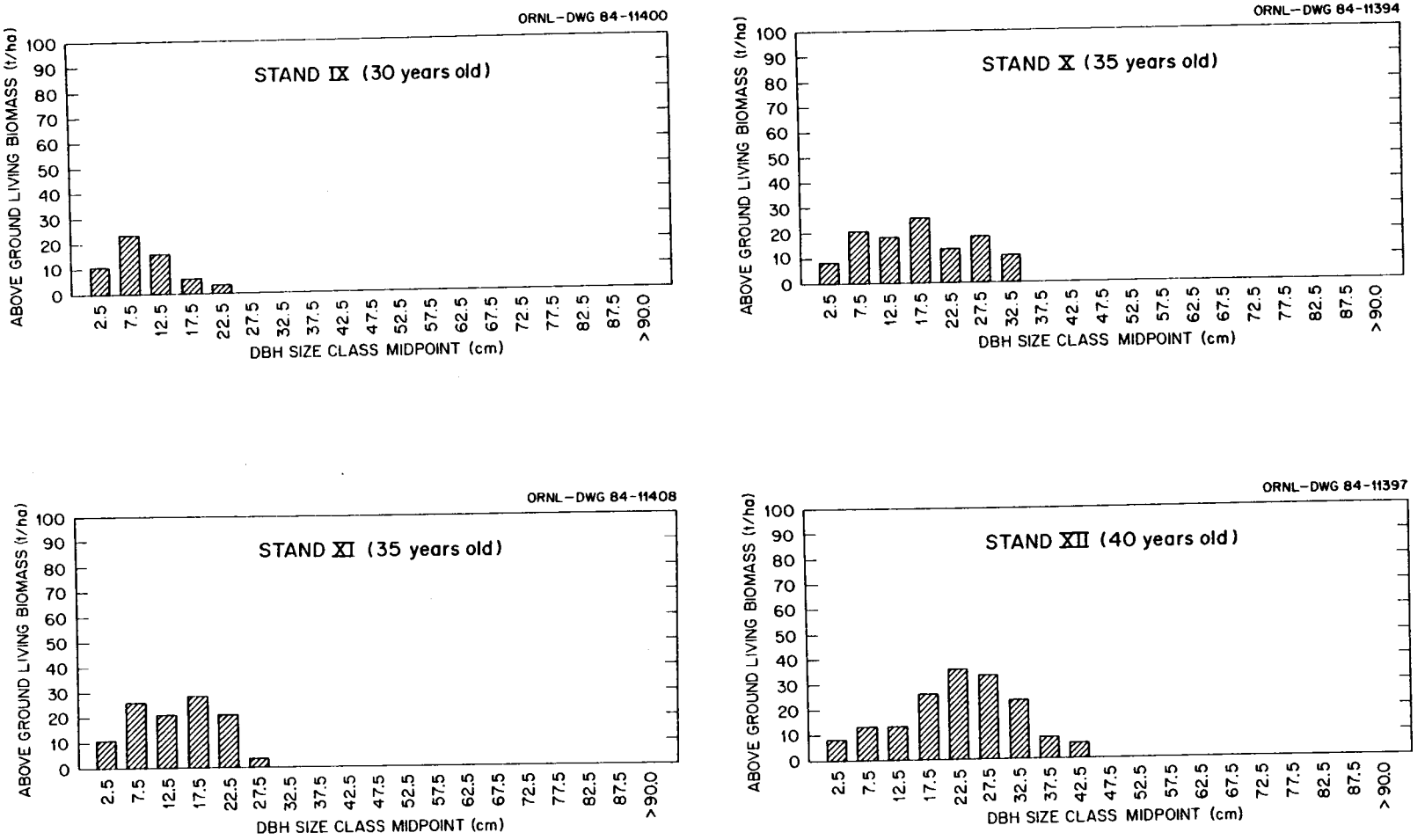

Figure B.3. Aboveground living biomass by dbh class for four, 30- to 40-year-old, stands in the Upper Rio Negro region of Colombia and Venezuela.

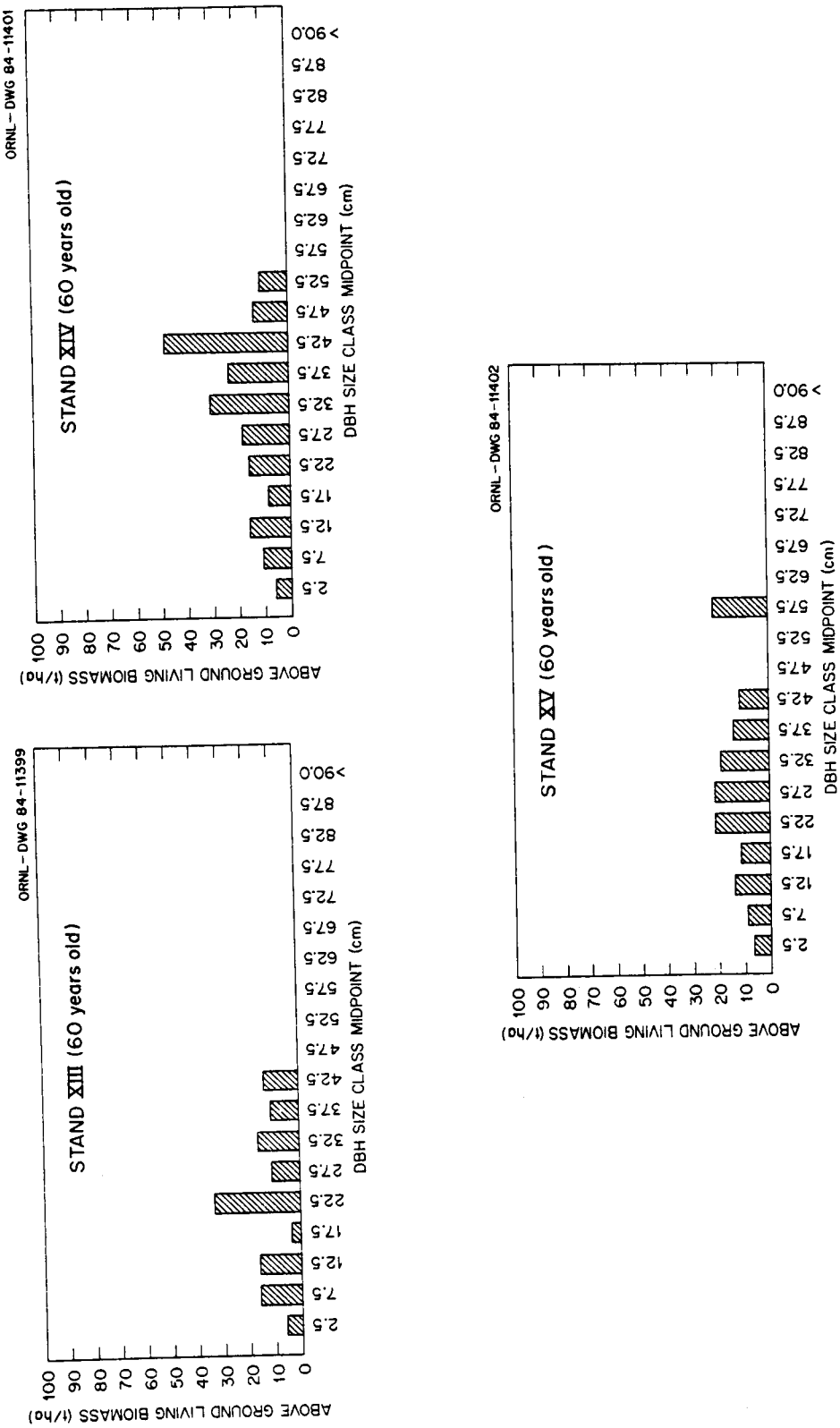

Figure B.4. Aboveground living biomass by dbh class for three, ~60-year-old, stands in the Upper Rio Negro region of Colombia and Venezuela.

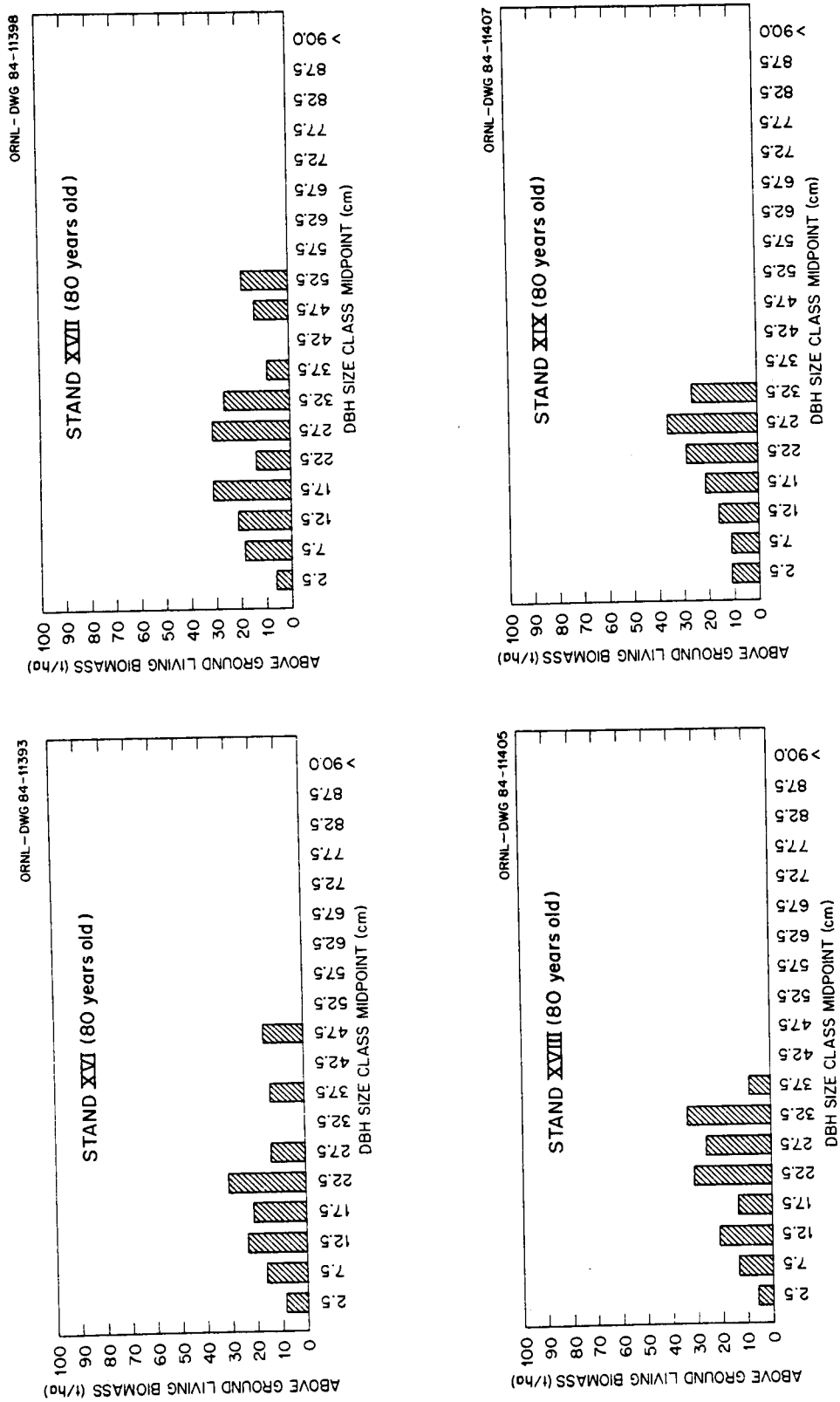

Figure B.5. Aboveground living biomass by dbh class for four, ~ 80-year-old, stands in the Upper Rio Negro region of Colombia and Venezuela.

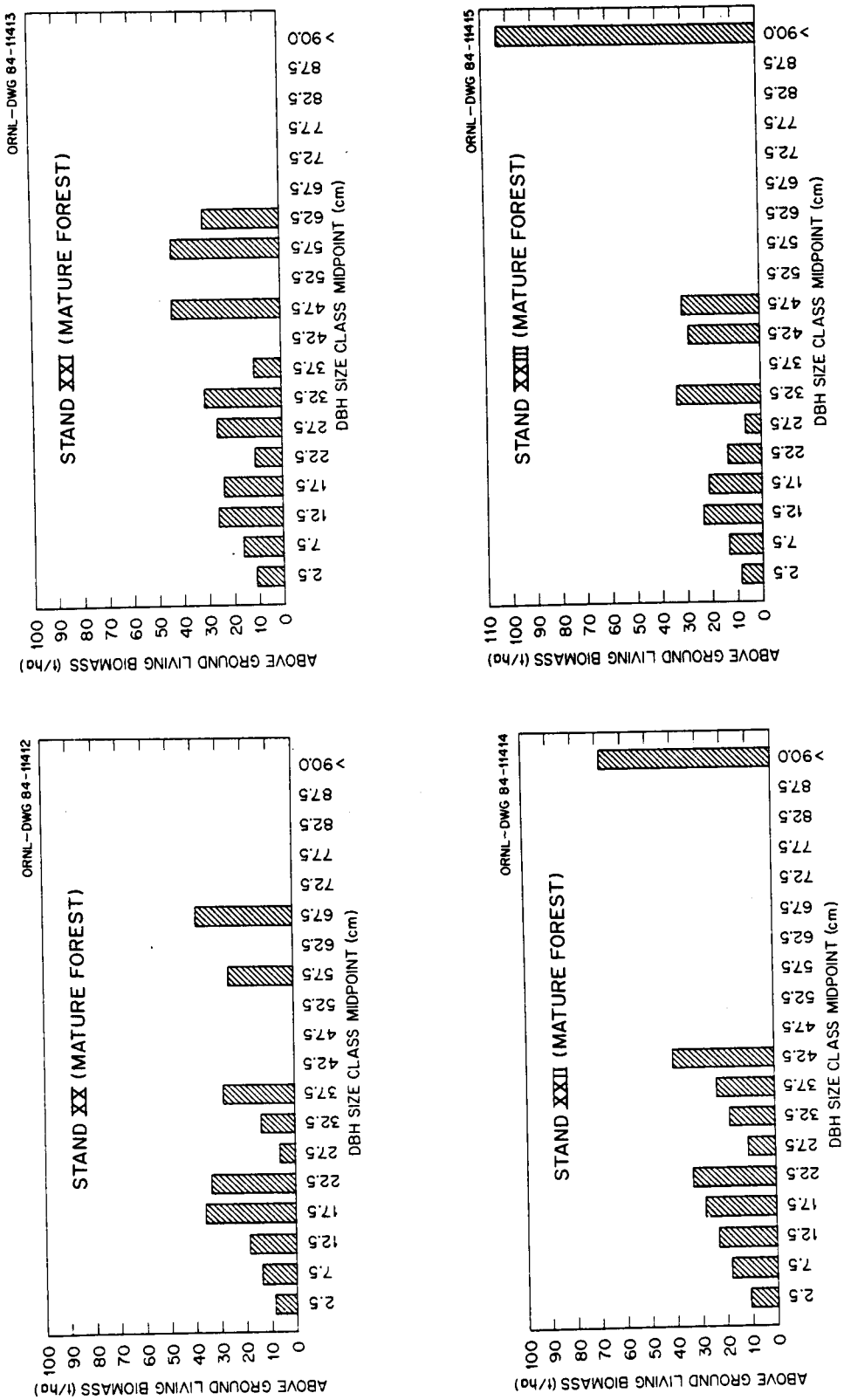

Figure B.6. Aboveground living biomass by dbh class for four, mature forest, stands in the Upper Rio Negro region of Colombia and Venezuela.

VITA

Juan Guillermo Saldarriaga was born in Cali, Colombia. He received a Bachelor of Science degree in Forestry Engineering from Universidad Nacional, sede Medellin, Colombia, in December 1975. He graduated from Universidad de los Andes, Merida, Venezuela, with a Master of Science degree in Forestry Management in 1979.