VEGETATION

OF

THE RIO BRAVO CONSERVATION AND MANAGEMENT AREA, BELIZE

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SUMMARY

1. The Rio Bravo Conservation and Management Area covers 202,000 acres (82,000 hectares) in northwest Belize, Central America. This report presents a vegetation map of the 110,000 acre, western section of Rio Bravo and describes the different vegetation types in that section, with quantitative descriptions of some major forest types.

2. Rio Bravo is in the "subtropical moist" life zone. It receives about 1500 mm (60 in) of rain per year. January to May are usually dry months and the rest of the year is comparatively wet. Soils are derived from limestone. Topography includes level and gently rolling areas, hills, and escarpments with deep ravines.

3. Vegetation type is closely linked to topography and soils, especially as they affect soil moisture. The gently varying topography of much of Rio Bravo produces a long, shallow gradient of soil conditions and a correspondingly long continuum of subtly different forest types.

4. The Rio Bravo forest has regrown in the c. 1000 years since the decline of the ancient Maya. From the middle of the nineteenth century the area has been exploited for mahogany and later for chicle. There has also been some milpa agriculture and natural disturbances such as treefalls and hurricanes. But the vegetation remains largely intact.

5. Our vegetation map of this section of Rio Bravo is based on ground surveys, observations from a light plane, and patterns on a radar image of the area (Airborne Synthetic Aperture Radar). The map depicts **upland forest**, **transition forest**, **bajo swamp forest**, **cohune palm forest**, **riparian forest**, **marsh**, **mangrove**, **palmetto savanna**, **forest/milpa mosaic**, and **large milpa**. An additional vegetation type in the area, not shown on the map, is **lacustrine swamp forest**. **Upland forest**, **transition forest**, and **bajo swamp forest** cover about 46.2, 29.6, and 9.4 %, respectively, of this section of Rio Bravo.

6. **Upland forest** occurs on well-drained soils. Its canopy is 15-20 m high with some taller trees. In a one-hectare plot of dry **upland forest** we found 700 trees ≥ 10 cm dbh, of 56 species. In a hectare of mesic **upland forest** there were 450 trees of 48 species. *Pouteria reticulata*, *Drypetes brownii*, *Manilkara zapota*, *Pseudolmedia* sp., *Brosimum alicastrum*, *Sabal morrisiana*, *Hirtella americana*, and *Ampelocera hottlei* are dominant tree species in the **upland forest**. The subcanopy palm *Cryosophila stauracantha* is abundant. From place to place there is much variation in the species composition and structure of **upland forest**.

7. **Bajo swamp forest** is found on clay soils that are seasonally waterlogged and edaphically dry. It is a dense forest of small stems mostly three to five m tall. Many tree species are restricted to **bajo swamp forest**, while a few typical of dry **upland forest** are also found there. **Bajo swamp forest**, usually has a sedge groundlayer and sometimes dense "sawgrass".

8. **Transition forest** seems to occur in poorly-drained areas, intermediate between **upland forest** and **bajo swamp forest**. It largely resembles dry **upland forest** in structure, but is somewhat shorter, and has some features of **bajo swamp forest**. It shares tree species with both those forest

types. Some typical tree species of **transition forest** are *Calophyllum brasiliense*, *Gymnanthes lucida*, *Manilkara zapota*, *Matayba oppositifolia*, and *Metopium brownei*.

9. **Cohune palm forest** occurs on rich, well-drained soils. The canopy is 15-20 m high, with some taller trees. In a one-hectare plot of **cohune palm forest** we found 374 trees ≥ 10 cm dbh, of 46 species. *Attalea cohune*, the cohune palm, is a canopy dominant, but there are many other tree species, including most that are common in **upland forest**. **Cohune palm forest** soils are good for agriculture and the abundance of long-lived successional tree species in some stands are evidence of past clearing. These include such species as *Swietenia macrophylla*, *Cedrela mexicana*, *Spondias mombin*, and *Ficus* spp.

10. **Riparian forest** occurs along the temporarily flooded margins of the Rio Bravo. It tends to have a broken canopy, with much liana cover and occasional large emergent trees. In a one-hectare plot of cohune palm **riparian forest** we found 394 trees ≥ 10 cm dbh, of 59 species, the highest species tally among our plots. *Attalea cohune* was a dominant in this plot, as in some other areas of **riparian forest**, but it can also be uncommon in this forest type. Other species include some of those common in **upland forest** and such characteristic species as *Inga edulis*, *Bucida buceras*, *Pachira aquatica*, *Pterocarpus hayesii*, *Pithecellobium belizense*, and *Vachellia* spp.

11. There is a high degree of dominance in the species composition of Rio Bravo forests. In each of our one-hectare plots five to six species accounted for 50 % of the stems, while the remaining 50 % included 53 to 41 species. There were many uncommon and rare species; in each plot 15 to 19 species were represented by only one individual. Thirty-three species, of 118 total species, were represented by only one individual over all four one-hectare plots.

12. The distributions of most tree species are patchy, among and within forest types. Only 13 species, of 118 total species, were found in all four one-hectare plots (each plot in a different forest type); 65 were found in only one plot. There are many different patterns of distribution, from widespread and common to local and rare.

13. There is a high proportion of trees with known or possible commercial value in the forests of this section of Rio Bravo. Some are "old-growth" species, well represented as juveniles and seedlings in the forest, and these appear amenable to sustainable exploitation. Others, such as mahogany, do not seem to have adequate regeneration for sustainable harvest; their presence in the forest may be linked to major disturbances in the past such as hurricanes, and management for regeneration may require substantial intervention.

14. It is misleading to describe Rio Bravo's forests as "deciduous" or "semi-deciduous". Only a small proportion (6-7%) of the species or the individuals are leafless at any one time, except in restricted local patches. Although Rio Bravo forests have been subjected to significant human and natural disturbance, we think it is misleading to describe these forests as "secondary". The bulk of the trees in the canopy of the widespread forest types are old-growth species with substantial regeneration in the undisturbed understory, which indicates old-growth forest.

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I. THE RIO BRAVO CONSERVATION AND MANAGEMENT AREA

Introduction

The Rio Bravo Conservation and Management Area covers 82,000 hectares (202,000 acres) in northwest Belize, Central America (Figure 1). It is owned by the Programme for Belize and managed for conservation, research, and economic activities consistent with the protection of biological diversity. Until recently there had been no ecological information on Rio Bravo that could help the Programme devise management plans for the area. Basic to a management plan is information on vegetation types and their distribution over the landscape. This report begins with background information on the environment of Rio Bravo. We then present a vegetation map of the 110,000 acre (44,497 hectare), western section of Rio Bravo and descriptions of the vegetation types shown on the map, including quantitative information on structure and tree species composition in five plots in selected forest types at Rio Bravo.

We know of four vegetation maps of Belize. We have not seen the map published in 1934 (Anonymous 1934), but it was probably a simple treatment. Next was Lundell's (1945), which showed just four vegetation types in a small format for the whole country. Shelford (1963) added minor detail to Lundell's map. Wright et al. (1959) produced an excellent 1:250,000 vegetation map of Belize, distinguishing 34 major vegetation types and numerous variants. King et al. (1992) describe vegetation types associated with different "land systems" (based on soil and topography) mapped for northern Belize. For Rio Bravo our map improves on Wright et al. (1959) and King et al. (1992) by showing more detail and discriminating more finely among the local vegetation types.

So far as we know, we are presenting here the first quantitative descriptions of all tree species in forest plots in northern Belize. There is quantitative information for plots in southern Belize (Lundell 1940, Stevenson 1942, Smith 1945a, 1945b, Sutton 1991) and near Belmopan (Furley & Newey 1979). The results of those studies are from areas too distant to be relevant to Rio Bravo. The Belize Estates and Produce Company, former owner of Rio Bravo, inventoried Rio Bravo for a few commercially valuable tree species (see Discussion).

Climate

Rio Bravo lies between 17° and 18° N latitude, in the outer- or sub-tropics. Typical of this latitude, there is minor seasonal variation in temperature and much in precipitation, placing Rio Bravo in the *subtropical moist* life zone of the Holdridge Life Zone System (Holdridge et al. 1975, Hartshorn et al. 1984). This designation distinguishes the Rio Bravo area from the more uniformly wet and warm *tropical wet* and drier *subtropical dry* life zones. Temperature and rainfall data recorded at Chan Chich Lodge near Rio Bravo (Figure 2) suggest the seasonal climatic patterns prevailing in the area. But year-to-year variability is great, so we have derived the following general description for northwest Belize from Wright et al. (1959), Hartshorn et al. (1984), and King et al. (1992).

From November to January, daytime temperatures probably average about 24° C (75° F) and at night can dip below 10° C (50° F) when cold air arrives in a "norther". From April to September, daytime temperatures probably average about 26° C (80° F). The hottest period, with temperatures exceeding 32° C (90° F) is probably in April and May, toward the end of the dry season.

Total annual rainfall probably averages about 1500 mm (60 in). The wet season in this part of Belize usually extends from June to January and may exhibit two peaks. Rainfall can be high (200-250 mm per month) in June and July, when short, intense showers fall. By July soils usually become continuously moist. In some years rainfall decreases noticeably in August. It is again heavy in September and October before decreasing in December and January as the dry season approaches. February through April or May are dry (less than 100 mm per month). We emphasize that there is much year-to-year variation in amount of rainfall and in the length and intensity of dry and wet seasons. One dry season in the late 1980s extended five months without a trace of precipitation (T. Harding, pers. comm.). Supra-annually, there are cycles of wet and dry years.

Effective precipitation in the forest may be greater than what is measured at conventional weather stations. We have noticed considerable (up to 12 hrs) drip of condensing fog within the forest on many nights.

Easterly and northeasterly winds blow intermittently from February to September. From September to January northerly or northeasterly winds prevail.

Physical features

Rio Bravo is underlain by a geological formation known as the Yucatan Platform (Hartshorn et al. 1984). The Platform was under the ocean during the early Eocene (58-47 million years ago), when it accumulated marine sediments consolidating into limestone. Northern Belize emerged from the ocean in the Pliocene (13-2 million years ago). In this same period a trough opened along the eastern edge of the Platform, inducing slumping to the west along southwest-to-northeast fault lines. The slumping produced a series of terraces of successively increasing elevation proceeding west. Three of these terraces, fronted by steep escarpments (30-60 m high) cut by ravines, form the dominant topographic features of Rio Bravo (Figure 3). Elevations in this section of Rio Bravo rise from somewhat less than 20 m to 220 m above sea level. Rio Bravo is similar in topography, soils, and hydrology to adjacent areas of northern Belize, Mexico, and Guatemala, because all are located on the same Eocene rock formations.

One can visualize this section of Rio Bravo as composed of several physiographic regions that we name as follows (Figure 4). Starting at the east is "Booth's River Depression", a level expanse of the lowest ground in the area, bounded on three sides by higher terrain. Moving west, between Booth's River Escarpment and Rio Bravo Escarpment, are "Booth's River Upland" and the "Rio Bravo Embayment". Booth's River Upland is relatively level to rolling ground with patches of small hills. The Embayment is mostly low and level and includes the Rio Bravo floodplain running along the base of Rio Bravo Escarpment. The Rio Bravo Escarpment and the higher Lalucha Escarpment converge. Between them are the steep, hilly "Rio Bravo Terrace Upland" (Terrace Upland for short) in the northeast and the low, level "Rio Bravo Terrace Lowland" (Terrace Lowland) in the south. Extending west and north of the Lalucha Escarpment are the "Lalucha Uplands", a mix of steep hills, rolling ground, and level stretches. We will refer to these physiographic zones to describe the distribution of vegetation types and to draw a connection between topography and vegetation type.

King et al. (1992) present a "land systems" classification of Belize that is based on soils and topography. It is more useful than our system of physiographic regions for planning land uses, but it is less useful for visualizing and referring to relatively unified topographic regions within Rio Bravo. We were not aware of King et al.'s land systems until after we had designed our physiographic system. In future we will reconcile our system with theirs.

Much of the rainfall at Rio Bravo seeps through the porous limestone bedrock and flows away below ground. Surface streams are few and mostly ephemeral. But several springs with substantial perennial flow emerge along the base of the Rio Bravo Escarpment, form lagoons, and flow into the Rio Bravo. The Rio Bravo and Booth's River are the only perennial streams. They are narrow (usually no more than about 5 m across). The Rio Bravo occasionally floods to much broader widths, often as a result of rains well upstream in Guatemala, when it has rained little in Rio Bravo itself.

Rio Bravo contains scattered ponds (aguadas), a large marsh area, smaller marshes, and various types of swamps. Following conventional practice, we define marsh as a wetland with mostly herbaceous vegetation; swamp as a wetland with substantial woody vegetation. Further distinctions depend on the duration (perennial versus seasonal) and source (e.g. neighboring pond or stream) of flooding (Pope 1990).

We discuss some points about soils in later sections. See Wright et al. (1959), Hartshorn et al. (1984), and King et al. (1992) for more information on soils in Belize.

<u>Seasonality of the vegetation</u>

Flowering, fruiting, and leaf replacement are all highly seasonal at Rio Bravo. Each tree species has a different seasonal schedule, but many are similar enough that community patterns are evident. We have monitored flowering, fruiting and leaf replacement at Rio Bravo and will give detailed quantitative results in a later report, but some generalizations can be made now.

Flowering in terms of numbers of species and individual trees peaks in the mid to late dry season (March and April) and is least in the late wet season (December). Fruiting patterns are not so clear but fruit abundance appears to be relatively higher in the late dry season and early wet season (June). Leaf drop is highest in the dry season and new leaves appear mostly during the dry season and early wet season.

The great majority of trees at Rio Bravo are evergreen. The term "deciduous" (or even "semi-deciduous"), which has been applied to Rio Bravo's forests (e.g. Wright et al. 1959), gives an exaggerated impression of seasonal leaflessness in the forest. At any given time only a minority of Rio Bravo trees are leafless. From our observations of the leaf status of Rio Bravo trees and our inventories of tree species composition and abundance in forest plots, we estimate that no more than 6.9 % of the species become leafless or partly leafless for any period and that an equivalent of no more than 6.2 % of all tree individuals are leafless at a given time. Leaflessness is higher in **bajo swamp forest**. (See Appendix A for details of this analysis and more comments.)

The relationship among topography, soil, and vegetation

Every writer on the region's vegetation has emphasized the strong relationships among topography, soil, and vegetation. Topographic position (hilltop, upper slope, footslope, etc.) is correlated with soil type, soil moisture, and exposure, all of which affect vegetation directly (Furley & Newey 1979). Moreover, those same correlations probably induced the ancient Maya to farm certain topographic positions in certain ways. Since we assume that they used much of the landscape, anthropogenic historical factors correlated with topography would underlie and accentuate present topographic influences on vegetation.

Both Wright et al. (1959) and King et al. (1992) discuss soil-vegetation relationships that apply to the Rio Bravo area. We adapted a vegetation-topography-soil diagram from Wright et al. (1959) as a framework for understanding the distribution and the physical structure of the vegetation types at Rio Bravo (Figure 5). Because topography and resultant soil conditions so closely and consistently influence vegetation type, the gently varying topography of much of Rio Bravo produces a long, shallow gradient of soil conditions and a correspondingly long continuum of subtly different forest types. For example, the three vegetation types covering the largest area are arranged along the continuum of **upland forest** - **transition forest** - **bajo swamp forest** (cf. Lundell 1937, Schulze 1992).

History and disturbance

The number of ruined temples and houses (Guderjan 1991), and the traces of sophisticated agriculture and water management at Rio Bravo (Scarborough et al. 1992), indicate that a numerous population of the ancient Maya lived in the area. They undoubtedly cleared a large area of forest, and they farmed dry lands and wetlands. But a diversity of plant species would have survived if, as seems likely, the landscape was a complex mosaic of farmed plots, fallow of various ages, and patches of old growth in which timber and other products were harvested.

Forests have regrown over the landscape in the 1000 years since the decline of the Maya, and the distributions and abundances of different tree species today surely reflect, but in unknown ways, patterns set in motion by Maya land uses and during the early reestablishment of forest. Some researchers speculate that the Maya cultivated certain tree species (Barrera et al. 1977, Gómez-Pompa & Kaus 1990) whose descendants are consequently now common. But we are not aware of any convincing link between what is known about the ancient Maya and the present distribution and abundance of a tree species. For example, the present abundance of *Brosimum alicastrum* (ramon, breadnut) on ruins may simply reflect natural colonization and better survival on that substrate (Lambert & Arnason 1982), rather than ancient cultivation. Peters (1983), however, has shown that the genetic structure, if not the abundance, of the *Brosimum* population at Tikal is anomalous and may reflect local selection for a desirable strain by the Maya.

Since the decline of the ancient Maya there has been at least intermittent small-scale farming at Rio Bravo. Maya farmers were moved from the area when the Belize Estates and Produce Company began managing it in the 19th century. In the late 1970s and early 1980s many plots were cleared in the vicinity of the La Milpa ruins and along Booth's River Escarpment to grow marijuana. These plots are now growing back. More recent clearing is mainly limited to about 100 ha near the North Gate. (Cusick [1991] describes milpa agriculture at Rio Bravo.)

Since the early 1800s loggers have taken selected species (mainly *Swietenia macrophylla* [mahogany], *Cedrela mexicana* [spanish cedar], *Calophyllum brasiliense* [santa maria]), from Rio Bravo and have probably left no area unlogged. Selective logging has reduced the numbers of large trees of the target species, affected forest structure by removing some of the biggest canopy trees, creating roads, cutting fuelwood, and other incidental damage, and promoted regeneration of successional tree species. But probably no more than two or three trees have been removed per hectare of forest, so that while logging damage has been widespread it amounts to a small area in any block of forest, leaving a fairly complete forest cover and the bulk of the forest unaffected. We think that the term "secondary forest", sometimes applied to Rio Bravo, exaggerates the degree of past disturbance there (see Discussion).

Manilkara zapota (sapodilla) at Rio Bravo has been exploited for chicle sap, and the bark slashes on virtually all *M. zapota* greater than about 10 cm in diameter attest to the chicleros' thoroughness. A hurricane passed over the area in 1931 (Hartshorn et al. 1984), but any resultant direct damage is no longer evident.

II. METHODS

<u>Vegetation map</u>

Work on the ground, remote sensing, and overflights provided information for the map. We spent a year and a half doing research at a dozen fixed locations at Rio Bravo, and we explored many other areas on foot. To extrapolate from our ground work to the whole area we used the remote sensing technique known as Airborne Synthetic Aperture Radar (AIRSAR). The apparatus was flown in a NASA plane at about 9100 m, back and forth across Rio Bravo and adjoining areas, as part of the Tropical Rainforest Ecology Experiment (TREE) carried out by the Jet Propulsion Laboratory (JPL) in March 1990. AIRSAR detects physical features and water at the land surface. JPL rendered the AIRSAR data into an image whose colors and textures correspond well, with a few ambiguities, to topography and different vegetation types. By extrapolating from correspondences at known locations we were able to interpret the entire image for this section of Rio Bravo. In addition we have flown over Rio Bravo in a light plane many times, inspecting the vegetation and developing our interpretation of the radar image.

Using CAMRIS, a type of "Geographic Information System" and mapping program, we digitized the patterns from the AIRSAR image, as well as topography, major roads, and water-courses from the relevant sections of 1:50,000 topographic maps (Ministry of Overseas Development, UK), and drew the vegetation map.

Forest inventory plots

We established two one-hectare plots in **upland forest** (dry **upland forest** and mesic **upland forest** variants) and one each in **riparian forest** (cohune palm **riparian forest** variant) and **cohune palm forest** (forest types described below). The plots were belt transects 10 m wide and 1000 m long, marked every 20 m along a baseline. In each plot every free standing (i.e. not a liana or strangler) woody plant ≥ 10 cm dbh (diameter at breast height, 137.5 cm above ground) was mapped, measured for dbh (or the diameter above any buttresses), marked with a uniquely numbered aluminum tag, and identified. (For now, we base our analysis of species composition on our identifications of trees in the field, but we are processing voucher specimens for confirmation.) We also recorded the presence or absence of lianas or epiphytes in each tree. Lianas were "present" if any liana stem ≥ 1.0 cm diameter was touching the tree. Epiphytes were "present" if we could see with the naked eye any epiphytic vascular plant growing on the tree (mosses and lichens were not counted).

Bajo swamp forest has a high density of small stems, making a one-hectare sample impractical. In 400 m^2 of this forest type we marked, mapped, measured for dbh, and identified all self-supporting woody stems ≥ 2.5 cm dbh, and we recorded presence or absence of lianas and epiphytes. The 400 m^2 consisted of ten 2 x 20 m quadrats, one randomly positioned within, and parallel to, each 100 m segment of a 1000 m transect.

We describe the site of each plot in the respective Results sections.

Forest structure

We used Knight's (1963) methods to construct profile diagrams of dry **upland forest**, cohune palm **riparian forest**, and **bajo swamp forest**. Briefly, we used the point-centered quarter method to select trees (a sample ≥ 10 cm dbh and a sample between 2 and 10 cm dbh); measured the height of the uppermost canopy, lowest major branches, and canopy width of those trees; sketched their general form; and randomly chose among those measured a subset for use in a profile diagram. The diagram therefore does not show a particular, existing small area of forest but shows instead a statistically representative view of a small area of forest. Jennifer O'Hara drew the profile diagrams.

We also constructed "foliage height profiles" of dry **upland forest**, mesic **upland forest**, cohune palm **riparian forest**, **cohune palm forest**, **bajo swamp forest**, and **large milpa**. The profiles show the percent foliage cover in different height intervals above ground and are given in the companion report on birds of Rio Bravo (Mallory & Brokaw 1993).

III. VEGETATION MAP

The vegetation map (Figure 6) shows the distribution of 12 vegetation types in the 44,497 ha (110,000 acre) western section of Rio Bravo. Table 1 gives estimates of the absolute and percentage areas of these types in this section (plus the area of permanent clearings at the Rio

Bravo Research Station and at North Gate). In terms of area covered, **upland forest**, **transition forest**, and **bajo swamp forest** are the most important woody vegetation types.

TABLE 1 - Vegetation types shown on the map, with absolute and percent area covered. The area estimates are derived by CAMRIS (see text) from the digitized map data.

Vegetation	area (ha)	% of total
upland forest	20,537	46.1
transition forest	13,164	29.6
bajo swamp forest	4,167	9.4
marsh	2,792	6.3
riparian forest	2,669	6.0
undiff. Riparian	2,256	5.1
cohune palm riparian	274	0.6
royal palm riparian	139	0.3
mangrove	483	1.1
cohune palm forest	305	0.7
forest/small milpa	281	0.6
large milpa	82	0.2
palmetto savanna	44	0.1
permanent clearing	6	0.01
Total	44,530	100.0

The map has some flaws. According to JPL the AIRSAR image is somewhat distorted in places. That problem, and some inevitable errors in the digitizing process produced some inaccuracies in our map. For instance, in the southeast part of the map the area of **transition forest** is somewhat exaggerated. As mentioned, we could not interpret all parts of the AIRSAR image unambiguously and had to rely on informed speculation, and it was always difficult to decide where to draw boundaries in the frequent situations where vegetation types grade into each other. Finally, there is a limit to the scale of detail one can detect and depict. Rio Bravo is a mosaic of vegetation types and their variants; small pockets of contrasting vegetation exist within areas that are shown as homogeneous on the map.

Despite these flaws, the AIRSAR image was an excellent guide, and the tools and understanding we used on it have produced a reasonably accurate and detailed map. Further remote sensing work, and especially observations on the ground, will suggest corrections to the map, and we welcome all comments and criticisms.

IV. VEGETATION TYPES

We discuss the vegetation types in the order of declining area covered (Table 1), modified by logical relationships among them. Dry and mesic **upland forest**, **cohune palm forest**, and cohune palm **riparian forest**, where we did one-hectare plot studies, are treated in more detail, and we compare results from these sites in the Discussion section. We also include in the text a description of **lacustrine swamp forest**, a distinctive type which occurs in stands too small to show on the vegetation map.

The complete list of tree species found in the four one-hectare plots, common names, abundances per plot, and other information are given in Appendix B. Appendix C lists all the tree species we have recorded at Rio Bravo, including many not found in the plots, and Appendix D is a list of tagged trees on trails near the Rio Bravo Research Station, for use in learning to identify many species.

Upland Forest

1. Topographic distribution and soils

Upland forest covers the largest area of Rio Bravo. It on well-drained sites, usually where any degree of slope encourages drainage but in a few level areas also (Figure 6, cf. Figures 3 and 5). **Upland forest** occurs on the escarpment faces, where it can be especially tall, and extends in a large, mostly contiguous bloc over nearly all of the Rio Bravo Terrace Uplands and the extensive hilly parts of Lalucha Uplands. In the less hilly physiographic zones, such as parts of the Lalucha Uplands and Booth's River Uplands, its distribution is more fragmented (Figure 4).

Upland forest is found on a mosaic of calcareous soil types (Wright et al. 1954). Typically, these soils are shallow, gravelly, neutral or slightly acid, and of moderate fertility. On "normal" sites there is a clayey soil 30-38 cm deep; in rolling terrain there is a gravelly soil 7.5-15 cm. These soils vary greatly in their moisture holding capacity and thus support different kinds of **upland forest**. For our plot studies we distinguished mesic (moist but adequately drained) and dry **upland forests**. The mesic forest occurs on the relatively deep and moist, but well drained, soils of lower slopes, slope bottoms, and some level areas; the dry forest occurs on the shallow rocky soil of hill tops and slopes and covers more area than the mesic type. We could not distinguish the two on the radar image.

An example of dry **upland forest** can be seen on the Mahogany and Water Tank Trails near the Rio Bravo Research Station, while the first hundred or so meters of the Generator Trail, at the base of slope, pass through mesic **upland forest**.

2. Classification

In the broad context of neotropical vegetation types this forest is best referred to as "subtropical moist forest" (Holdridge 1971, Hartshorn et al. 1984.). The upland forest at Rio Bravo matches fairly well the "medium-high, semi-deciduous forest" in Pennington and Sarukhán (1968), but we question the aptness of "semi-deciduous" (see "Seasonality of the vegetation" and Appendix A). It has also been classified as "deciduous seasonal forest" in Wright et al. (1959), interpreting from Beard (1944), but of Beard's types the Rio Bravo forest corresponds better in structure to what he describes as "semi-evergreen seasonal forest" (but, as mentioned, we think semi-evergreen is misleading). In the context of Belize's vegetation, Wright describes this forest as "broadleaf forest rich in lime-loving species", indicating its occurrence on calcareous soil.

In structure and species composition the **upland forest** of Rio Bravo resembles forest in similar topographic situations extending through the northeastern Petén and southernmost Quintana Roo and Campeche (Lundell 1934). Rio Bravo **upland forest** is similar to much of the forest in Belize south of Rio Bravo and adjacent to the Guatemalan border, west of the Maya Mountains (Lundell 1940, Hartshorn et al. 1984, Brokaw 1992), and it shares many tree species with the forest in northeastern Belize but is probably better drained and taller. In comparison with the wetter, broadleaf forests of southern Belize, found east of the main divide of the Maya Mountains (and in the Upper Raspaculo watershed [Brokaw 1990]), Rio Bravo **upland forest** is shorter, has fewer epiphytes and probably fewer tree species, though there are still many plant species in common.

3. Structure

The taller trees in **upland forest** generally reach about 25 m, with a few to 30 m, while most upper canopy trees are 15-20 m (Figure 7). The dry **upland forest** tends to be shorter than the mesic **upland forest**, especially on exposed hilltops. The canopy of both types is usually uneven, consisting of tree crowns with gaps between them. Vertical structure is heterogeneous; layers of vegetation from top to bottom are not distinct. Buttressing is well expressed in some species, absent or moderate in many. Within **upland forest** there is much variation in canopy height and in tree size and density.

4. Tree species composition and size-class structure

The one-hectare study plot of dry **upland forest** was on hilly, exposed terrain on the Lalucha Escarpment above the Terrace Upland. Overall it appeared to be a comparatively dry location, but the transect did extend uphill along a slight gradient from more moist to more dry conditions. The mesic **upland forest** one-hectare plot was on level ground near the La Milpa Ruins, in the Lalucha Upland, and appeared to be an area of comparatively deep and moist soil.

We found 700 trees ≥ 10 cm dbh, of 56 species, in the dry **upland forest** plot, and 450 trees of 48 species in the mesic **upland forest** plot. The common species in each plot are given in Table 2. Note the high dominance of a few species. In each plot, a mere five species made up nearly 50 % of all the stems. *Pouteria reticulata* (zapotillo) and *Drypetes brownii* (male bullhoof) were among the top five in both plots. The important plant families (those represented at least twice in Table 2) among trees in the **upland forest** plots were Sapotaceae, Moraceae, Apocynaceae, Euphorbiaceae, Rubiaceae, Aceraceae (Palmae), Burseraceae, and Anacardiaceae. Sapotaceae is especially prominent, represented by four species (three *Pouteria* spp. and *Manilkara zapota* [sapodilla]) in each list in Table 2.

The bulk of the trees ≥ 10 cm dbh, especially in the dry **upland forest** plot, were between 10 and 25 cm dbh (Figures 8a and 8b). The largest diameter trees were an 84.7 cm *Pseudobombax* *ellipticum* (mapola) and a 94.0 cm *Brosimum alicastrum* (breadnut) in the dry and mesic plots, respectively.

5. Upland forest variants

We have seen several distinctive but minor variants of upland forest. North of the road from the Research Station to the La Milpa Ruins is a forest apparently on dry, flinty soil, with a thin canopy but some large trees, that includes oaks (*Quercus oleoides*) and many well-developed *Clusia* sp. (matapalo), a hemi-epiphytic tree. Then there are some relatively level areas with a loose substrate of pebbles and rocks to about 20 cm in maximum dimension, supporting a thin canopy of small trees and some locally unusual species (e.g. *Roupala montana*, Proteaceae). Lastly, we have seen unusually tall forest of large trees at some locations on escarpment faces (Figure 5). Wright et al. (1959) suggested this was due to more rapid breakup of soil parent material and better mixing of soil, with resultant higher availability of nutrients, on slopes than in level areas. It is also likely that plants on slope enjoy uniquely favorable water relations. Slope soils should be relatively moist, as they receive seepage from the perched water tables of the level area areas above them; at the same time slope soils are sufficiently well drained for good root growth.

TABLE 2 - The 15 most abundant tree species among all stems ≥ 10 cm dbh in two one-hectare **upland forest** plots at the Rio Bravo Conservation and Management Area, Belize. Also given are the percentage of all stems in the plots represented by each species, as well as the accumulated percentages of all stems as species are added in decreasing order of abundance.

a. DRY UPLAND FOREST - 700 stems, 56 species in one hectare.

species	number of stems	% of stems	cumulative % of stems
Pouteria reticulata	152	21.7	21.7
Manilkara zapota	59	8.4	30.1
Pseudolmedia sp.	58	8.3	38.4
Drypetes brownii	42	6.0	44.4
Hirtella americana	35	5.0	49.4
Drypetes laterifolia	35	5.0	54.4
Pouteria amygdalina	32	4.6	59.0
Aspidosperma cruentum	29	4.1	63.1
Metopium brownei	28	4.0	67.1
Pseudobombax ellipticum	28	4.0	71.1
Diospyros yatesiana	22	3.1	74.2
Pouteria spp.	15	2.1	76.3
Alseis yucatanensis	14	2.0	78.3
Bursera simaruba	14	2.0	80.3
Protium copal	11	1.6	81.9

b. MESIC UPLAND FOREST - 450 stems, 48 species in one hectare.

species	number of stems	% of stems	cumulative % of stems
Pouteria reticulata	69	15.3	15.3
Drypetes brownii	48	10.7	26.0
Sabal mauritiiformis	42	9.3	35.3
Ampelocera hottlei	35	7.8	43.1
Brosimum alicastrum	30	6.7	49.8
Trichilia minutiflora	30	6.7	56.5
Alseis yucatanensis	25	5.6	62.1
Pouteria spp.	21	4.7	66.8
Attalea cohune	18	4.0	70.8
Pouteria amygdalina	15	3.3	74.1
Aspidosperma cruentum	14	3.1	77.2
Protium copal	12	2.7	79.9
Spondias mombin	9	2.0	81.9
Manilkara zapota	8	1.8	83.7
Stemmadenia donnell-smithii	8	1.8	85.5

6. Other life forms

A higher percentage of trees had lianas and epiphytes in the mesic **upland forest** plot than in the dry **upland forest** plot (Table 3). A noteworthy liana at Rio Bravo is *Desmoncus* sp. (basket tie-tie) a climbing palm, or rattan. The epiphytes include orchids, aroids, bromeliads, ferns, pipers, and cacti and are fairly common but not profusely luxuriant as in wetter forests. Crustose lichens are common on tree trunks. The hemi-epiphytes *Clusia* spp. and *Ficus* spp., plants that germinate on a host tree and send roots to the ground, are occasional. *Rinorea* spp. (wild coffee), species in the Rubiaceae, and *Piper* spp., especially *Piper psilorachis*, are common shrubs or small trees. The understory palm, *Cryosophila stauracantha* (give and take), is abundant in upland forest and is one of the most characteristic plant species of Rio Bravo.

TABLE 3 - Percentage of trees with lianas and epiphytes in sample plots representing five forest types in the Rio Bravo Conservation and Management Area, Belize.

	% trees with	
Forest type	lianas	epiphytes
dry **upland forest**	38.8	9.6
mesic **upland forest**	54.7	11.4
bajo swamp forest	12.5	18.5
cohune palm forest	66.8	19.8
cohune palm **riparian forest**	72.6	17.3

Bajo swamp forest

Bajo swamp forest is a seasonally wet swamp forest, occurring in clay-filled, poorly drained, slight depressions that are scattered over Rio Bravo (Figure 5). The largest **bajo swamp forest** areas at Rio Bravo are in the northern part of the Rio Bravo Embayment, and in the Lalucha Upland, but they occur in all the physiographic regions in patches as small as a few hectares. **Bajo swamp forest** is a dense forest, with stems only 4 to 5 m tall and occasional emergent trees (Figure 9). Similar vegetation is found in the northwest Petén and in nearby Mexico ("tintal", Olmsted & Duran 1986).

Our **bajo swamp forest** corresponds roughly to Wright et al.'s (1959) "low marsh forest". We do not use "low marsh forest" because that name is a conjunction of mutually exclusive terms; a marsh (an herbaceous wetland) being so utterly different from a forest. In the Rio Bravo area **bajo swamp forests** are known as "scrubs". But that term should only be used locally; outside Rio Bravo it will be misunderstood, because elsewhere it is casually used for a range of vegetation types in low topographic situations, some very different from Rio Bravo "bajos". The **bajo swamp forest** study plot was in a 200 ha bajo swamp near the North Gate, in the Lalucha Upland.

Bajo swamp forest soils are saturated in the wet season (at times there is standing water), probably hindering root growth by inhibiting cell respiration. In the dry season the clay is "edaphically dry", meaning that it is moist but holds the water so tightly that it is unavailable to plants. Thus many of the trees have drought-adapted leaves: small, compound with small leaflets, or large but thick and leathery. Trunks are small: mean dbh in our 400 m^2 sample of all stems $\geq$ 2.5 cm dbh was 4.7 cm; of 313 stems measured only 10 were greater than 10 cm dbh. The largest was a 36.0 cm dbh *Haematoxylum campechianum* (logwood). Flaky bark is common. The percentage of stems with lianas is much less than in other forest types (Table 3). The percentage with vascular epiphytes is similar to the percentages in other forest types (Table 3), but epiphytes appear more prominent in **bajo swamp forest**, because here they are relatively large in relation to host stems and grow near eye level. Cacti, bromeliads, and orchids are well represented (Zimmerman & Olmsted 1992), as well as epiphytic mosses and lichens. Due to a thin, low canopy there is much light in the understory of bajo swamp, encouraging a ground cover of sedge, a good indicator of **bajo swamp forest** conditions. Tall sawgrass (*Scleria bracteata*, actually a sedge) grows in the lowest bajo swamps.

Bajo swamp forest contains many species not shared with other vegetation types, but several tree species typical of dry **upland forest** or **transition forest** grow, albeit stunted, in the taller bajo swamps, reflecting the value of adaptions to dryness in this habitat (Table 4). Likewise some species of xeric savannas are also found in **bajo swamp forest** (Table 4). We have not finished the quantitative analysis of species composition in our **Bajo swamp forest** plot, but *Croton* spp. were especially abundant, accounting for 21.7 % of all stems sampled. Composition and abundances can vary greatly among stands of **bajo swamp forest**. For example, the *Acoelorrhaphe wrightii* (cabbage palmetto), which is conspicuous from the air, seems to occur only in one **bajo swamp forest** in this section of Rio Bravo. A noteworthy species is *Haematoxylum campechianum* (logwood) whose wood was harvested for dye in the early history of Belize (see History of the Vegetation and Disturbance).

TABLE 4 - Tree species in **bajo swamp forest**

scientific name	common name
Small species (2-5 m tall), generally common	
Ardisia sp.	
Byrsonima bucidaefolia	crabboo
Chysobalanus icacos[1]	pigeon plum
Coccoloba reflexiflora[1]	wild grape
Croton spp.	
Erythroxylum guatemalense	redwood
Eugenia rhombea	
Gymnopodium cf. *ovatifolium*	bastard logwood
Krugiodendron ferreum[2]	axemaster
Sebastiana tuerckheimiana	white poisonwood
Myrica cerifera[1]	tea bark
Ouratea sp.	
Plumeria obtusa	zopilote
Rapanea guianensis	
Large species (5-10 m tall), generally uncommon	
Acoelorrhaphe wrightii[1] (palm)	cabbage palm, palmetto
Bucida buceras	bullet tree
Caesalpinia gaumeri[2]	bastard logwood
Calophyllum brasiliense[2]	santa maria
Cameraria latifolia[2]	savanna white poison wood
Clusia[2] sp.	matapalo
Haematoxylum campechianum	logwood
Manilkara zapota[2]	sapodilla, chicle
Metopium brownei[1, 2]	black poisonwood
Swietenia macrophylla	mahogany, caoba

[1]Also found in xeric savanna.
[2]Also found in dry **upland forest** or **transition forest**.

There is often a long gradient from extreme to moderate bajo swamp conditions, corresponding to the gradient from **bajo swamp forest** toward **transition forest** and making it hard to locate the edge of bajo swamps on the ground or the AIRSAR image. This gradient can be seen as one walks from the center of a bajo swamp (where one may find "gilgai", a lumpy surface typical of alternately wet and dry clay soil), out and up toward higher ground; although **bajo swamp forest** soil conditions and plants are still evident, the forest gets taller, with a more closed canopy and open understory, and has some species more characteristic of dry **upland forest**.

Transition forest

In any landscape there are transitions between vegetation types. At Rio Bravo **transition forest** deserves formal recognition because it covers so much area. It extends across the often long shallow gradient in topography between locations of **bajo swamp forest** and **upland forest**, occupying essentially level areas, where drainage and other soil characteristics are presumably intermediate between conditions in **bajo swamp forest** and **upland forest. Transition forest** is widespread in the flatlands of the Booth's River Uplands, the Rio Bravo Embayment, the Rio Bravo Terrace Lowlands, and the Lalucha Uplands (Figure 6).

As a transitional form this vegetation type is especially variable, and thus difficult to generalize about and hard to recognize. In structure and composition it usually more closely resembles dry **upland forest** or the taller forms of **bajo swamp forest** than it resembles short bajo swamp vegetation. It is generally somewhat shorter than **upland forest**. Characteristic species are *Calophyllum brasiliense* (santa maria), *Gymnanthes lucida* (false lignum vitae), *Manilkara zapota* (sapodilla), *Matayba oppositifolia* (boyjob), and *Metopium brownei* (black poison wood). Mahogany (*Swietenia macrophylla*) and timber species of secondary value (Lamb 1946) are present.

Cohune palm forest

Areas of deep, well-drained soil in uplands often support **cohune palm forest** (Figure 5), so named for the local abundance of the large (to 25 m) cohune palm (*Attalea cohune*). **Cohune palm forest** is found in patches in the southeastern part of the Booth's River Upland and in pockets at the base of slopes in the Terrace Upland and Terrace Lowland (Figure 6). The cohune palm is also abundant in some areas of **riparian forest** (see below). The radar image and our aerial surveys convince us that there is not nearly so much cohune dominated forest (upland or riparian) in this part of Rio Bravo as shown on Wright et al.'s (1959) vegetation map.

Cohune palm forest often occurs at the base of slopes, where patterns of soil deposition and drainage seem to produce suitable conditions. A change from level ground with much cohune to slope with no cohune is abrupt in places (cf. Tables 2a and 5). Furley (1975) described how fallen cohune fronds and the natural filling with organic matter of pits left by the deep, rotted bases of fallen cohunes produce a deep organic mulch. Thus cohune presence may be both consequence and cause of rich soil conditions. As a result cohune areas are favored for agriculture in Belize (where such stands are known as "cohune ridge", ridge in this context meaning forest stand and not denoting topography).

The **cohune palm forest** plot was located in a pocket of level ground between steep hills in the Terrace Upland, at the base of the Lalucha Escarpment, about 8 km south of the Research Station. In this plot we found 374 trees ≥ 10 cm dbh of 46 species, the lowest number of species among the four one-hectare plots (see Discussion). Table 5 shows common species. As in the **upland forest** plots, five species dominated this plot, making up 50 % of the stems (cohune nearly 20 %). Juvenile cohunes were common in the plot but were not inventoried. Most of the stems in the **cohune palm forest** plot were under 30 cm dbh (Figure 10). The largest specimen was an 87.9 cm dbh *Ampelocera hottlei* (female bullhoof). Lianas were common, and epiphytes were more frequent than in the other plots, reflecting the great abundance of epiphytes (ferns conspicuously) among the leaf bases of cohune palms.

TABLE 5 - The 15 most abundant tree species among all stems ≥ 10 cm dbh in a one-hectare plot of **cohune palm forest** at the Rio Bravo Conservation and Management Area, Belize. Also given are the percentage of all stems over the plot represented by each species, as well as the accumulated percentages of all stems as species are added in decreasing order of abundance. There were a total of 374 stems of 46 species in the plot.

species	number of stems	% of stems	cumulative % of stems
Attalea cohune	72	19.3	19.3
Drypetes brownii	47	12.8	32.1
Pouteria reticulata	25	6.7	38.8
Alseis yucatanensis	22	5.9	44.7
Trichilia minutiflora	20	5.4	50.1
Sabal morrisiana	19	5.1	55.2
Rinorea sp.	18	4.8	60.0
Stemmadenia donnell-smithii	18	4.8	64.8
Aspidosperma cruentum	17	4.6	69.4
Brosimum alicastrum	17	4.6	74.0
Pouteria spp.	10	2.7	76.7
Pseudolmedia sp.	8	2.1	78.8
Licaria peckii	6	1.6	80.4
Pouteria amygdalina	6	1.6	82.0
Trophis racemosa	5	1.3	83.3

At Xaxe Venic, a **cohune palm forest** area at the base of the Lalucha Escarpment west of Chan Chich (south of Programme for Belize lands), we found several species commonly that were not in the one-hectare plot described in this paper. The abundance of these species - *Spondias mombin* (hogpum), *Cedrela mexicana* (spanish cedar), *Cymbopetalum penduliflorum*, *Ficus glabrata* (amate), *Guazuma ulmifolia* (bay cedar) - suggests more recent disturbance at Xaxe Venic, possibly for agriculture, than in our one-hectare plot. *Guarea glabra* (cramantee) is also much more abundant at Xaxe Venic. Duck Ridge (on Programme land but outside the area considered here) is another **cohune palm forest** that seems to have been significantly disturbed 50-100 yr ago. It now supports much mahogany (*Swietenia macrophylla*), a species that regenerates in certain types of disturbed areas and would grow well in the conditions that also favor cohune.

Riparian forest

Riparian forest is a swamp forest that lines the perennial watercourses passing through forested parts of Rio Bravo. It is flooded seasonally and presumably has a deep, alluvial soil that is relatively moist throughout the year. Since it occurs on low-lying areas near watercourses its width is determined by local topography and varies greatly. In this part of Rio Bravo significant stands of **riparian forest** are restricted to areas adjacent to the Rio Bravo as it passes through the Rio Bravo Embayment and crosses the Booth's River Depression. Of course, the vegetation bordering even the smallest or most ephemeral streams is affected somewhat by flooding, but these areas are too small to concern us or to depict on a map.

Riparian forest is typically more heterogeneous in structure than **upland forest**. Many trees are leaning and it appears that stem anchorage is poor, probably because roots neither develop nor hold well in generally wet soil, and especially when the forest is flooded for a week or more. The result is a generally low main canopy and many gaps filled with tangly undergrowth and lianas, which also cover some of the lower tree crowns. But this forest is topped with scattered, large, emergent trees, of species that seem well adapted to these conditions and can remain upright (Figure 11), such as *Bucida buceras* (bullet tree) and *Pterocarpus hayesii*. Some areas of **riparian forest** mostly lack emergents, such as along the Rio Bravo in the northeast stretch of the Rio Bravo Embayment. Some patches, usually right on the river, are entirely low thickets, with a few short, liana-draped trees, and hardly merit the name forest.

There are two variants of **riparian forest** shown on the map, each characterized by a different abundant palm: cohune palm **riparian forest** and royal palm **riparian forest**. Our **riparian forest** one-hectare plot was in the cohune variant. Except for the abundance of *Attalea cohune* in that plot, the description of its composition will serve fairly well for **riparian forest** as a whole.

1. Cohune palm riparian forest

The cohune palm **riparian forest** plot ran for a kilometer parallel to the Rio Bravo, in the Rio Bravo Embayment and east of a point along the main road about 8 km south of the Research Station.

The one-hectare plot in cohune palm **riparian forest** contained 394 trees ≥ 10 cm dbh of 59 species, the highest number of species among the four plots. Table 6 lists common species. As in the other one-hectare plots, five species accounted for nearly half the individuals in the plot, *Attalea cohune* being the most abundant. Most trees were under 30 cm dbh (Figure 12); the largest was an 86.4 cm dbh *Pterocarpus hayesii*. The percentage of trees with lianas was higher than in any of the other study plots (Table 3), reflecting this forest's broken canopy.

Cohune palms, while common in this plot, were generally much shorter than in the upland **cohune palm forest** plot, which was on well drained ground, where trees are presumably more firmly rooted. Interestingly, these short cohunes flowered and fruited as abundantly as tall ones in the uplands, perhaps because they are just as exposed to light in this shorter forest as are the taller ones in tall forest.

A few other points should be made about **riparian forest** plants in addition to what is clear from the plot study. Some tree species, such as *Inga edulis* (bribri) and *Pachira aquatica* (provision tree) are virtually restricted to the very banks of the river. The spiny, *Bactris* spp. palms (porknoboy) are locally abundant and occur in clumps of thin stems sprouting from roots. Similarly, *Pithecellobium belizense* (turtlebone) seems to achieve its patchy abundance through clonal reproduction. In especially low areas spiny bamboos create a thick tangle. Free-standing figs (i.e. not stranglers) are comparatively abundant, at least in the cohune palm **riparian forest** variant. And finally, *Vachellia* spp. are especially important in this forest type.

TABLE 6 - The 16 most abundant tree species among all stems ≥ 10 cm dbh in a one-hectare plot of cohune palm **riparian forest** at the Rio Bravo Conservation and Management Area, Belize. Also given are the percentage of all stems over the plot represented by each species, as well as the accumulated percentages of all stems as species are added in decreasing order of abundance. There were a total of 394 stems of 59 species in the plot.

species	number of stems	% of stems	cumulative % of stems
Attalea cohune	71	18.0	18.0
Pouteria reticulata	37	9.4	27.4
Vachellia sp. 3	32	8.1	35.5
Pithecellobium belizense	31	7.9	43.4
Trophis racemosa	23	5.8	49.2
Drypetes brownii	18	4.6	53.8
Brosimum alicastrum	15	3.8	57.6
Guarea glabra	13	3.3	60.9
Lonchocarpus guatemalensis	9	2.3	63.1
Sabal mauritiiformis	9	2.3	65.4
Spondias mombin	9	2.3	67.7
Vachellia sp. 2	8	2.0	69.7
Casearia corymbosa	7	1.8	71.5
Chrysophyllum cainito	6	1.5	73.0
Protium copal	6	1.5	74.5
Pterocarpus hayesii	6	1.5	76.0

2. Royal palm riparian forest

Royal palm **riparian forest** is characterized by abundant, tall *Roystonea oleracea*, or royal palms. The only significant stand of this forest type we know of in Rio Bravo is at the northern end of Booth's River Depression, where the Rio Bravo crosses the Depression and joins Booth's River. Elsewhere on PFB lands we have seen a few *Roystonea oleracea* in swamps along the Rio Bravo and in small islands of woody vegetation in the northern part of Booth's River Depression.

This royal palm **riparian forest** is within a band of **riparian forest** that contrasts with the mostly herbaceous **marsh** (see below) covering nearby areas of the Booth's River Depression. Apparently the river has produced distinctive soil conditions within the Depression, probably by sediment deposition, as in a river delta, and of course by more frequent and prolonged flooding near the river, and this supports a distinctive vegetation type. Because we have only seen this swamp from the air, *Roystonea oleracea* is the only species we know to characterize it, but we suspect that there are other unusual plant species in this unusual habitat, in addition to species found in other **riparian forest** areas.

<u>Lacustrine swamp forest</u>

Lacustrine swamp forest occurs on the seasonally flooded margins of aguadas (small ponds) and lakes. The stands in this section of Rio Bravo are all small and do not show on the vegetation map, yet **lacustrine swamp forest** deserves recognition here because its tree species contrast clearly with those in surrounding **upland forest**, and there are larger areas of this forest type nearby (e.g. bordering Laguna Seca, just south of Programme for Belize land). Table 7 lists some species found in **lacustrine swamp forest**. Most of these can be seen at the large aguada southwest of and near the La Milpa ruins.

Table 7 - Some tree species found in **lacustrine swamp forest**.

scientific name	common name
Bactris spp.	porknoboy
Bucida buceras	bullet tree
Cassia grandis	bokoot, stinking toe
Calyptranthes chytraculia	
Enterolobium cyclocarpum	tubroos, guanacaste
Ficus spp. (free-standing)	fig, amate
Haematoxylum campechianum	logwood
Pachira aquatica	provision tree
Sapindus saponaria	soapseed tree
Tabebuia rosea	mayflower

Areas near the lagoons and streams formed by springs at the base of the Rio Bravo Escarpment have some lacustrine features, although we classified them as part of the **riparian forest** along the Rio Bravo. These are the only places we have seen *Licania platypus* (monkey apple) and *Alchornea latifolia* (fiddlewood) trees in this section of Rio Bravo.

<u>Marsh</u>

A large area of **marsh** covers much of Booth's River Depression. Smaller areas occur in the Rio Bravo Embayment scattered along the base of the Rio Bravo Escarpment, at a few sites in the Booth's River Uplands, and in the center of the largest **bajo swamp forest** in the Lalucha Upland. The largely herbaceous parts of some aguadas are **marsh**.

The Booth's River marsh occurs on wet, peaty clay. The part we visited at the base of Booth's River Escarpment was thigh-deep in water in April 1991, near the end of the dry season, but water may be generally deeper at this edge, if springs emerge there.

By definition, vegetation in **marsh** is mostly herbaceous, in Booth's River Marsh consisting of rushes (Juncaceae) and sedges (Cyperaceae). Some tree species in small hammocks (islands of woody vegetation) or on the fringes of large **marshes** include: *Roystonea oleracea* (royal palm), *Acoelorrhaphe wrightii* (cabbage palmetto), *Conocarpus erecta* (buttonwood), *Rhizophora mangle* (red mangrove), and *Annona glabra* (bobwood). The ancient Maya practiced "raised-field" agriculture (manipulating water and soil levels) in some **marshes**. This could still be affecting **marsh** hydrology and plant species composition.

<u>Mangrove</u>

In the southerly part of Booth's River Depression **marsh** grades into a large area of fairly continuous, shrubby *Rhizophora mangle*, the red mangrove, characterized by stilt roots. **Mangrove** is normally associated with seacoasts and saltwater. It seems unlikely that the Booth's River **mangrove** was established by seed dispersed from coastal areas, because *Rhizophora mangle* seeds are large and water dispersed. It is possible that these are relict stands from a period when the area may have been an embayment of the sea (Wright et al. 1959). The soil is wet, peaty clay. As for salinity, it is known that mangroves do not require saltwater, but King et al. (1992) suggest that this part of the Booth's River Depression may be somewhat saline. *Rhizophora mangle* is known from other inland locations in Belize. It some coastal areas it attains much greater height that at Rio Bravo.

<u>Palmetto savanna</u>

The northern extremity of Rio Bravo extends a short way into a wet **Palmetto savanna**. A savanna is a grassland with scattered trees. The transition from forest to savanna can be abrupt, reflecting a sharp change in soil. This savanna appears to be on wet, sandy soil, contrasting with better drained, flinty, clay soil of the abutting forest. (The presence of this savanna is clear on the radar image, but we have not actually seen it. Its vegetation and soil were described to us by J. D. Hensz).

Savanna areas in Belie tend to occur on sandy soils over an impervious "hardpan" of clay. In periods of heavy rain the upper layer becomes saturated, but in the dry season it is exceedingly arid. These savannas occasionally burn, but the bark and roots of the plants are well adapted to resist or recover from fire.

As the name implies, the characteristic tree of this **palmetto savanna** is the cabbage palm (*Acoelorrhaphe wrightii*), which is widespread in the wet savannas of Belize. Other trees in savannas we have seen elsewhere include *Byrsonima crassifolia* (crabboo), *Curatella americana* (yaha), *Pinus caribaea* (caribbean pine), *Quercus oleoides* (live oak), and the savanna species noted in Table 4.

Milpa, forest with milpas, and secondary forests

There are many abandoned milpas (farm plots) in Rio Bravo. The large ones, mostly near North Gate and along the northern stretches of the main road, are located on the vegetation map. Areas where there are many scattered, mostly smaller ones, around the La Milpa Ruins and along the northern part of Booth's River Escarpment, are indicated as **forest with milpa**. King et al.'s (1992) land classification map shows locations of many milpas at Rio Bravo.

Many of these milpas were cleared for marijuana cultivation and then abandoned 10 to 15 years ago; some near North Gate were used for subsistence and market farming recently (Cusick 1991). Abandoned milpas support secondary vegetation, composed largely of vines, shrubs, and trees described as light-demanding, shade intolerant, or secondary species (ecological, not economic, sense) or as pioneers (Table 8). Pioneers are also found in the areas periodically cut alongside the main road and in the larger logging and natural treefall gaps in the forest. Pioneers tend to have patchy distributions; one will notice nearly pure stands of different species along the main road. Trees in milpas also include many sprouts from stumps of the original forest.

TABLE 8 - Pioneer trees found in **milpa** and other second growth.

scientific name	common name
More common species	
Cecropia peltata	guarumo, trumpet
Guettarda combsii	glassy wood
Hampea trilobata	moho
Piper auritum	cowfoot
Thevetia ahouai	cojón de mico
Trichospermum grewiifolium	moho
Less common species	
Vachellia cookii	cockspur, bull's horn acacia
Calliandra belizense	
Bucida buceras[1]	bullet tree
Bursera simaruba	red gombolimbo
Cedrela mexicana	spanish cedar
Dendropanax arboreus	white gombolimbo
Ficus spp.	fig, amate
Metopium brownei	black poisonwood
Pseudobombax ellipticum	mapola
Sapium sp.	
Schizolobium parahyba	quamwood
Spondias mombin	hogplum
Swietenia macrophylla	mahogany, caoba
Vitex gaumeri	fiddlewood
Xylopia frutescens	polewood

[1]Especially in wet areas.

V. DISCUSSION

Our discussion derives largely from the results of the four, one-hectare plot studies. None of these plots fully represents a forest type, nor do they represent together the vegetation of this section of Rio Bravo. Yet we think these results do demonstrate some general features of Rio Bravo's forests.

Stem density

Among the plots the density of stems ≥ 10 cm dbh ranged from 374 to 700 per hectare (Table 9). The low density in the **cohune palm forest** probably results from the fact that so much growing space is taken up by the large juveniles of *Attalea cohune*, which, however substantial a plant they are, lack a definable stem and are not included in the tally of stems ≥ 10 cm dbh. The high density in the dry **upland forest** plot may be exceptional, but probably does indicate a generally high density of trees in that forest type, at least wherever there are exposed hill sites inhospitable to large trees, but allowing by compensation many small ones to fit in.

TABLE 9 - Totals from the four one-hectare plot studies.

Parameter	dry upland	mesic upland	cohune riparian	cohune palm		
stems	700	450	394	374	1918	(row summed over all four plots)
families	26	24	21	21	36	(total among all four plots)
species	56	48	59	46	118	(total among all four plots)
species unique to plot	19	10	27	9	65	(row summed over all four plots)
species with one individual	17	19	18	15	33	(one individual through all four plots)
species occurring in all four plots	13	13	13	13	13	
density (total stems/m²)	0.070	0.045	0.039	0.037		
commercial species						
species	17	15	15	15	28	(row summed over all four plots)
individuals	231	197	80	129	637	(total among all all four plots)

Tree species richness

The number of tree species ≥ 10 cm dbh in the plots ranged from 46 in the **cohune palm forest** to 59 in the cohune palm **riparian forest** (Table 9). The low number in the **cohune palm forest** plot is explained by the fact that it had the fewest stems, coupled with exceptionally high dominance of cohune and *Drypetes brownii* (male bullhoof), both factors militating against a high number of species. Yet the number of species in a plot is not simply correlated positively with the number of stems or negatively with the number of cohune palms. The dry **upland forest** had 304 more stems than the cohune-dominated cohune palm *riparian forest* plot, but the latter had three more species than the former. Thus other factors affect species richness. High tree species richness of riparian forests is probably a general characteristic in this section of Rio Bravo, and may be related to nutrient-rich alluvial soils, good soil moisture conditions, and high light levels (favoring a group of light-demanding trees) in the forest interior, resulting from unstable trees and proximity to the permanent edge maintained by the river. We should not overextend this generalization; other riparian forests may experience flooding so prolonged that few species tolerate it.

Forty-six to 59 tree species per hectare is probably typical of Rio Bravo. If we plot the accumulation of new species as a function of increments of area inventoried in the plots, we see that all four curves follow a similar trajectory and begin leveling off well before the one-hectare inventory is completed (Figure 13). These results suggest that it is unlikely that any hectare of Rio Bravo forest would contain much more than 59 or much fewer than 46 species. This is more species than would be found in a typical hectare of temperate zone forest but many fewer than would be found in moist forests closer to the equator (cf. Gentry 1988). The moist forests of southern Belize are richer than those at Rio Bravo.

The total of 56 species for the dry **upland forest** plot is probably a bit higher than the average would be for one hectare of that forest, even with 700 stems to tally, since the transect actually extends at its two ends into very dry and slightly mesic conditions, respectively, and therefore contains more species than would a transect representing medium conditions.

We found 118 tree species ≥ 10 cm dbh altogether in the four plots. We estimate that there are 250-300 tree species overall at Rio Bravo (Appendix C). Many of the additional species do occur in the forest types we studied, but are uncommon and by chance not occurring in the one-hectare sample plots, while some are restricted to habitats not sampled.

Tree species composition of Rio Bravo forests

When we plot the rate at which new species are encountered as a function of area inventoried we see that the curve is still rising at one hectare (Figure 13), indicating that we would continue to find new species as we add more area. Nonetheless, we judge that the plot data give a reliable indication of the common species and an approximation of the total number, if not exact composition, of species to be encountered in one hectare of a given forest type. No two hectares are ever the same. But the species that are especially common in our study plots will almost always be found in other areas with similar soil characteristics and disturbance history. It is the composition of the uncommon and rare species that will differ.

Of course we expect major differences between forest types. Of the 118 total species recorded among all four plots, only 13 (11%) occurred in all four plots, while 65 (55%) were found in only one plot, ranging from 27 found only in the cohune palm **riparian forest** plot to nine in the **cohune palm forest** plot (Table 9 and Appendix B).

To give some idea of the species that are most representative of the composition of forests in this section of Rio Bravo we list the 30 most abundant tree species over the four one- hectare plots combined (Table 10; see Appendix B for full composition of the plots). This list, however, is somewhat unrepresentative of Rio Bravo as a whole because it gives equal weight to the composition of each plot, while in fact cohune palm **riparian forest** and **cohune palm forest** are much less widespread than **upland forest**, and **transition forest** is not represented in the table at all. The particularly unrepresentative features of the table are the great abundance of *Attalea cohune*, the presence in the list of *Vachellia* sp. 3 and *Pithecellobium belizense* (turtlebone), which are limited in our plots to **riparian forest**, where they were abundant, and the lack of *Vitex gaumeri* (fiddlewood) and *Matayba oppositifolia* (boyjob), so typical of dry **upland forest** and **transition forest**, respectively. Otherwise Table 10 gives a good idea of the species one will most likely encounter in this section of Rio Bravo. In particular, the abundance of *Pouteria reticulata* (zapotillo), *Drypetes brownii* (male bullhoof) and other species at the top of the list definitely characterize this section of Rio Bravo. The understory palm *Cryosophila stauracantha* (give and take) is too small to have been counted in the plot studies, but it is probably the most abundant tree in this section of Rio Bravo.

TABLE 10 - The thirty most common tree species among all stems ≥ 10 cm dbh in four one-hectare plots (all plots combined) at the Rio Bravo Conservation and Management Area, Belize. There were 1918 stems of 118 different species in the four plots. Also given are the percentage of all stems over the four plots represented by each species, as well as the accumulated percentages of all stems as species are added in decreasing order of abundance.

species	number of stems	% of stems	cumulative % of stems
Pouteria reticulata	283	14.8	14.8
Attalea cohune	161	8.4	23.2
Drypetes brownii	155	8.1	31.3
Sabal mauritiiformis	78	4.1	35.4
Pseudolmedia sp.	73	3.8	39.2
Brosimum alicastrum	69	3.6	42.8
Manilkara zapota	67	3.5	46.3
Aspidosperma cruentum	64	3.3	49.6
Alseis yucatanensis	61	3.2	52.8
Pouteria amygdalina	55	2.9	55.7
Trichilia minutiflora	54	2.8	58.5
Pouteria spp.	48	2.5	61.0
Ampelocera hottlei	41	2.1	63.1
Hirtella americana	39	2.0	65.1
Drypetes laterifolia	37	1.9	67.0
Zygia sp.	33	1.7	68.7
Vachellia sp. 3	32	1.7	70.4
Protium copal	31	1.6	72.0
Metopium brownei	28	1.5	73.5
Pseudobombax ellipticum	28	1.5	75.0
Stemmadenia donnell-smithii	28	1.5	76.5
Trophis racemosa	28	1.5	78.0
Diospyros yatesiana	22	1.2	79.2
Guarea glabra	21	1.1	80.3
Rinorea sp.	18	0.9	81.2
Spondias mombin	18	0.9	82.1
Bursera simaruba	15	0.8	82.9
Simira salvadorensis	14	0.7	83.6
Vachellia cookii	13	0.7	84.3
Licaria peckii	12	0.6	84.9

Tree species abundances and distributions

There is a tremendous range in abundances among tree species at Rio Bravo; a few species are extremely abundant, many are moderately abundant, and most are uncommon. In each of the one-hectare plots no more than five or six species accounted for about 50 % of all stems (Tables 2, 5, 6), and over all four plots a mere eight extremely abundant species accounted for nearly 50 % of the total of 1918 stems. This means that the other 50 % of stems include from 40 to 53 species in the one-hectare plots and 110 species for the plots combined. Many of these species are quite uncommon. Within each plot 15 to 19 species were represented by only one individual, and of the 118 species overall 33 (28 %) were represented by only one individual tallied over all four plots. It is clever but accurate to say that "common species are rare, and rare species are common".

Dominance by a few and rarity of many species characterizes most tropical and temperate forests. To some extent this pattern is a sampling artifact: all species have patchy distributions, even in suitable habitat, and a given plot may simply happen to be in a place where a species is locally common or locally rare. Patterns of abundance also reflect habitat preferences, for example, rare species may be associated with rare microenvironments. Indeed, there are numerous explanations of species abundance patterns, but we only point out that every species has a different pattern, and we will illustrate the variety of different abundance and distribution patterns with the following examples from this section of Rio Bravo (cf. Appendix B):

-- *Drypetes brownii* (male bullhoof) and *Pouteria reticulata* (zapotillo) are both abundant and widely distributed.

-- *Aspidosperma cruentum* (mylady) is moderately common and widely distributed.

-- *Astronium graveolens* (glassy wood) and *Simira salvadorensis* (john crow redwood) are uncommon but widely distributed.

-- *Manilkara zapota* (sapodilla) is abundant, and *Metopium brownei* (black poisonwood) is common, in the more widespread forest types (**dry upland forest** and **transition forest**), but they rare or absent in some restricted forest types (**cohune palm forest**, cohune palm **riparian forest**).

-- *Zygia* sp. (turtlebone) is fairly abundant in a restricted forest type (**riparian forest**) but absent from others.

-- *Pseudobombax ellipticum* (mapola) is fairly abundant in a widespread forest type (dry **upland forest**) but absent from others.

-- *Trichilia minutiflora* (wild lime) and *Stemmadenia donnell-smithii* (cojotón) can be found in most forest types but are abundant only in two (**mesic upland forest** and **cohune palm forest**).

-- *Exostema mexicanum* (sabac-ché) is rare. One individual each was found in **dry** and **mesic upland forests**.

Disturbance and the maturity of Rio Bravo forests

We think that much of the Rio Bravo area was cleared of forest by the ancient Maya and that the forest has grown back and matured in the thousand or so years since their decline (see History of the Vegetation). But there have been significant disturbances in the forest since the time of the ancient Maya: natural mortality and fall of canopy trees, hurricane damage, milpa agriculture, and selective logging (cf. Brokaw 1986, Brokaw & Walker 1991, Uhl et al. 1982, Uhl & Viera 1989). How have these disturbances affected the structure and tree species composition of the forest at Rio Bravo?

Each of these disturbances involves damage to or removal of canopy trees. This increases light levels at the ground and alters soil conditions, promoting the germination and growth of tree species that cannot establish and grow in the shaded understory of undisturbed forest. Thus the frequency and extent of disturbance influence the relative proportions in the forest of "successional" tree species, those that require canopy opening for establishment, versus "old-growth" tree species, those that can establish in shaded understory. Both kinds of trees are well represented in the Rio Bravo forests.

If we look at the 30 most abundant species in the four one-hectare plots (Table 10), ten are old-growth species, judging from their fairly abundant presence (personal observation) as juveniles in the shaded understory (*Pouteria reticulata*, *Drypetes brownii*, *Attalea cohune*, *Sabal morrisiana*, *Pseudolmedia* sp., *Brosimum alicastrum*, *Manilkara zapota*, *Pouteria amygdalina*, *Trichilia minutiflora*, *Ampelocera hottlei*). Seven of the species (*Vachellia* sp. 3, *Metopium brownei*, *Pseudobombax ellipticum*, *Trophis racemosa*, *Spondias mombin*, *Bursera simaruba*, *Vachellia cookii*) are clearly successional species, because their juveniles are only found in disturbed areas (personal observation). The remaining 13 species are either intermediate in requirements or we do not know enough to classify them (but we do know that they are not highly disturbance-dependent).

The ten old-growth species in Table 10 are among the 12 most abundant species, and constitute the majority of the individuals, in the one-hectare plots. The successional species are among the less numerous in Table 10. These results support the view that the Rio Bravo forests are to a large extent old-growth, but in which there has been significant disturbance. And they agree with our knowledge of Rio Bravo's history, that it has been mostly forested since the ancient Maya, providing a suitable environment for shade tolerant, "old-growth" tree species; but that it has also been frequently disturbed in a patchwork fashion by humans and natural events, providing suitable microenvironments for disturbance-dependent, "successional" tree species. Thus Rio Bravo forests are not "primeval", or "virgin", or "undisturbed". But the majority of the individual, adult, canopy trees in the forest are "old-growth species, so it is incorrect to describe Rio Bravo forests overall, as some have, as "secondary". "Secondary" should be reserved for forests that have recently (say within 100 years) grown up from complete clearing or are much more highly disturbed than Rio Bravo forests.

It is obvious from the tree species composition at Rio Bravo, but not from direct evidence, that there have been major disturbances to the forest from time to time. Otherwise it is impossible to account for the abundance of several species, such as *Pseudobombax elliptica* (mapola) and

Swietenia macrophylla (mahogany). *Pseudobombax ellipticum* occurs fairly commonly as large adults in dry **upland forest** (Table 2), but its juveniles are found only in high light situations, such as along roads, and rarely, if ever, in natural treefall gaps or logging gaps within the forest. This pattern -- adult abundance but virtually no juveniles in the forest -- suggests that the forest suffered a major disturbance, perhaps a century ago, that opened much of the canopy, creating conditions not present now, and promoted regeneration of this species and others such as mahogany (see below). Hurricanes or fires are possible major disturbances.

Some management implications

1. Forestry

The forests of Rio Bravo contain a large volume of valuable or possibly valuable timber. The 118 species recorded in the one-hectare plots includes mahogany (*Swietenia macrophylla*) and spanish cedar (*Cedrela mexicana*) as well as 26 species of possible commercial value (Lamb 1946) (the species are noted in Appendix B). These species make up 637 (33 %) of the 1918 total stems in the plots (Table 10 and Appendix B). Most of these were in the upland forest plots (Table 10), but at Rio Bravo the forest types dominated by cohune palm seem to contain the highest densities of the especially valuable mahogany and spanish cedar (e.g. Duck Ridge).

Many of the commercial trees are old-growth species, are well represented as juveniles in the forest, and may be amenable to management with little or light intervention for sustained harvest. Others, such as mahogany and cedar are ecologically like *Pseudobombax ellipticum* (see above), do not appear to be reproducing adequately under present conditions, and may require heavy intervention, such as creation of small clearcuts, to maintain harvestable populations. The current studies at Hill Bank will elucidate the ecological and population characteristics of many of the commercial tree species and suggest ways to manage them sustainably.

Current stocking of mahogany and cedar in this section of Rio Bravo is unknown. The Belize Estates and Produce Company formerly owned Rio Bravo. They reported 0.4 mahogany and cedar 60-110 cm dbh per hectare, and 4.1 stems of these species $\geq$ 10 cm dbh per hectare, from a 1975 inventory of 2,028 km^2 of their land (Arnold et al. 1989, Table 3.11), which presumably included much of Rio Bravo. Many of these trees must have been harvested since 1975, because we doubt there are as many as 4.5 stems per hectare of these species, in any and all size classes, over much area of the forest today. (King et al. [1992, Table 26] erroneously reported the BEC data, intepreting stems/hectare given in Arnold et al. [1989] as stems/acre, and thereby inflating stocking by a factor of about 2.5 in their report.)

2. Biological diversity

The plot results show that uncommon or rare tree species make up a high percentage of the number of species found in a given area. Often these species may be common in another habitat, but many are rare everywhere. While unlikely, it is posible that clearing even a small forest area could eliminate all or a large part of the population of some tree species in Rio Bravo. There are some tree species for which we have noticed only one individual in the parts of Rio Bravo we have seen.

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FIGURE LEGENDS

Figure 1 - Location of the Rio Bravo Conservation and Mangement Area.

Figure 2 - Climate diagram, showing seasonal patterns of temperature and rainfall, based on averages over about five years at a location about 30 km from the study sites. (_ _ _) = rainfall; (+ + +) = temperature; fully shaded area = mean monthly rainfall > 100 mm; vertical lines area = relative humid period; stippled area = relative drought period.

Figure 3 - Elevation map of the 110,000 acre western section of the Rio Bravo Conservation and Mangement Area.

Figure 4 - Physiographic regions of the 110,000 acre western section of the Rio Bravo Conservation and Mangement Area. See text for explanation.

Figure 5 [not shown] - Relationships of topography, soil, and vegetation (from Wright et al. 1959). The diagram does not show some soil-vegetation types that are described in this report, and does show some types not described. Relevant vegetation types: 2, 2a, 2b = upland forest; 23 = bajo swamp forest; 34 = cohune palm forest. Relevant soil types: 13, 13a, 13b, 13c, 13h, 60 = upland, limestone-based soils; 56 = wetland clay. See Wright et al. (1959) for details.

Figure 6 - Vegetation map of the 110,000 acre western section of the Rio Bravo Conservation and Management Area.

Figure 7 - Profile of dry **upland forest**. Plot area is 40 x 10 m. Trees ≥ 2.5 cm dbh are shown. See text for explanation of method.

Figure 8a - Diameter class distribution of all trees ≥ 10 cm dbh in a one-hectare plot of dry **upland forest**.

Figure 8b - Diameter class distribution of all trees ≥ 10 cm dbh in a one-hectare plot of mesic **upland forest**.

Figure 9 - Profile of **bajo swamp forest**. Plot area is 30 x 1.0 m. Trees ≥ 2.5 cm dbh are shown. See text for explanation of method.

Figure 10 - Diameter class distribution of all trees ≥ 10 cm dbh in a one-hectare plot of **cohune palm forest**.

Figure 11 - Profile of cohune palm **riparian forest**. Plot area is 40 x 10 m. Trees ≥ 10 cm dbh are shown. See text for explanation of method.

Figure 12 - Diameter class distribution of all trees ≥ 10 cm dbh in a one-hectare plot of cohune palm **riparian forest**.

Figure 13 - The accumulation of species totals with increasing area sampled within one-hectare plots.

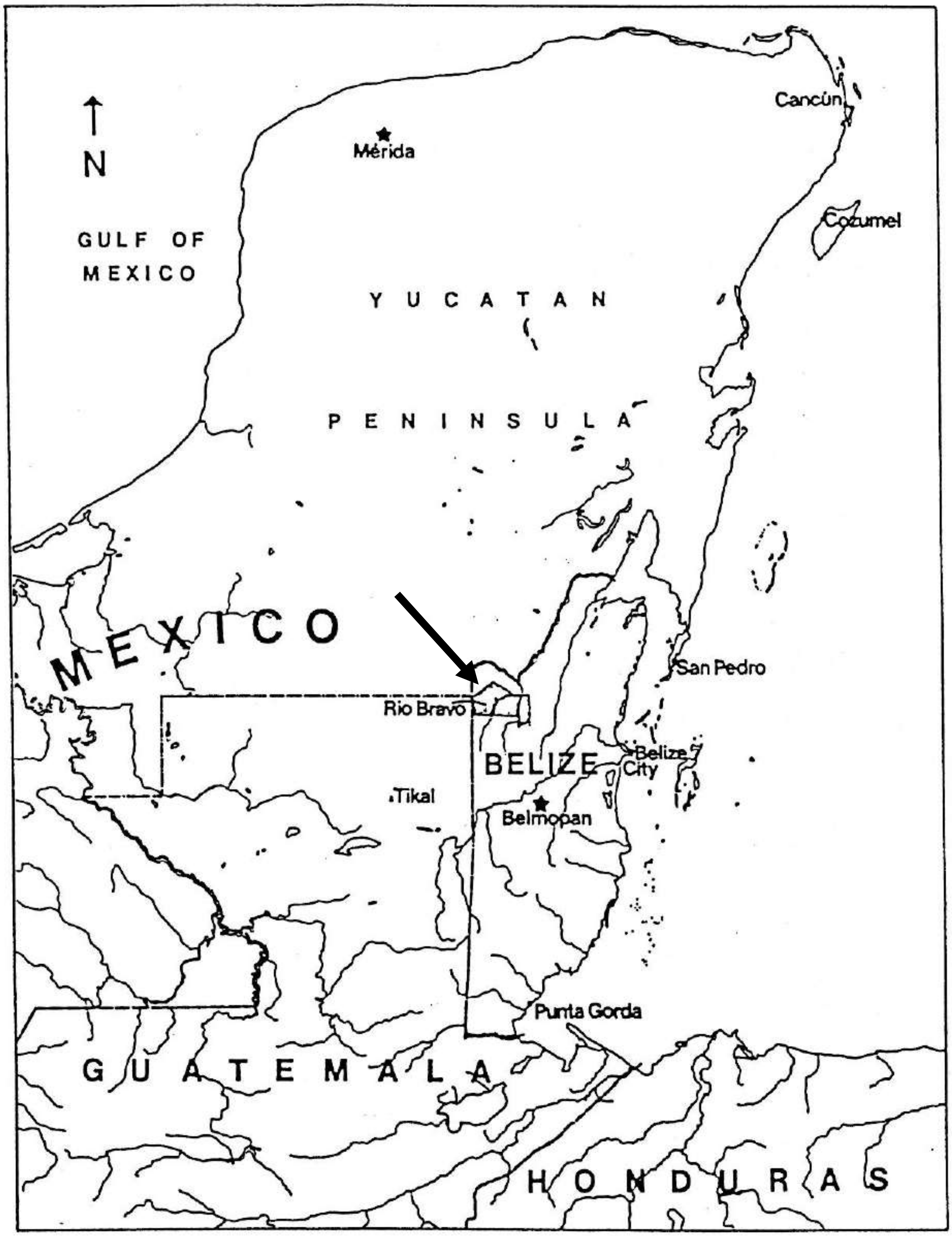


Figure 1 - Location of the Rio Bravo Conservation and Mangement Area.

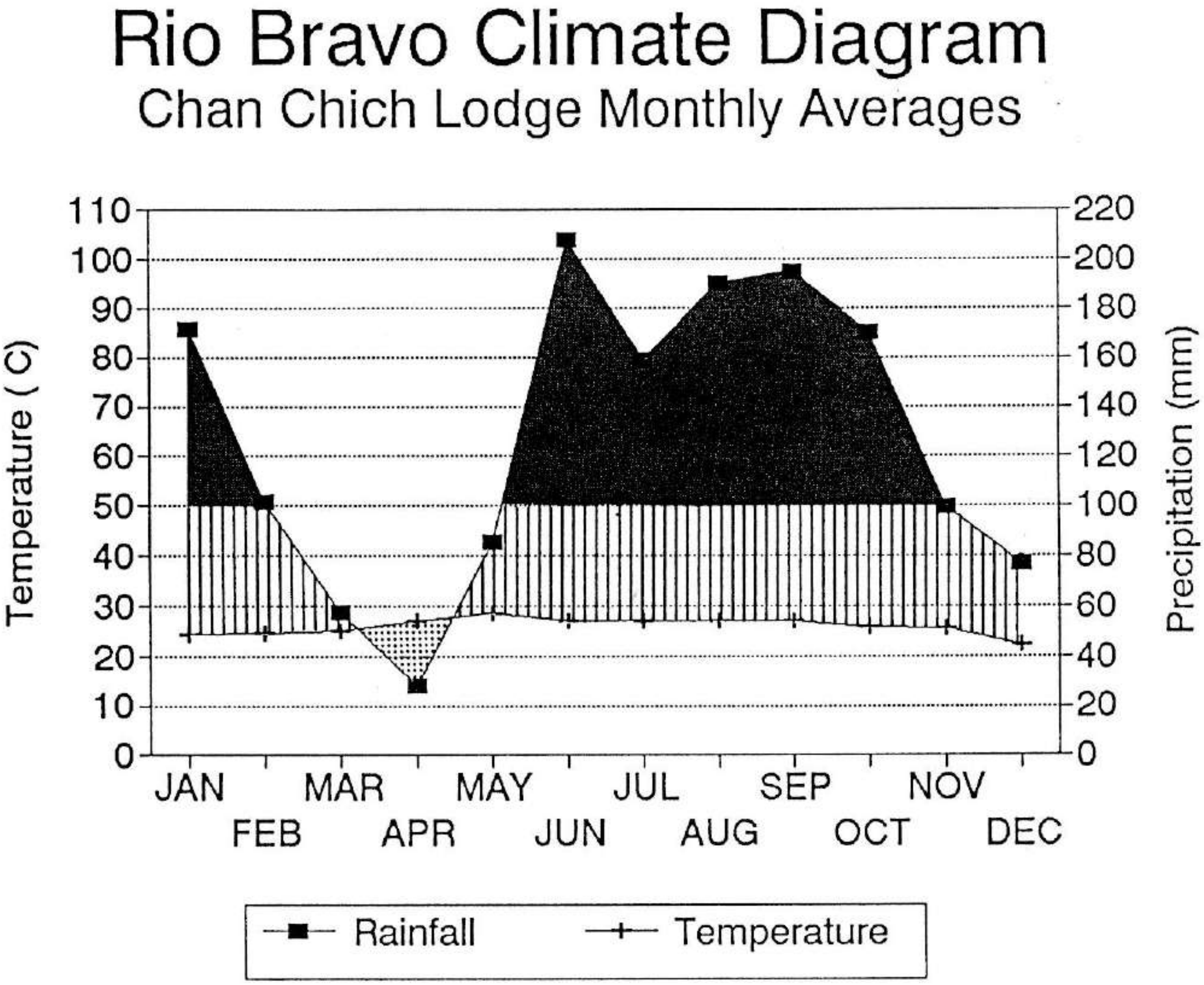


Figure 2 - Climate diagram, showing seasonal patterns of temperature and rainfall, based on averages over about five years at a location about 30 km from the study sites. Fully shaded area = mean monthly rainfall > 100 mm; vertical lines area = relative humid period; stippled area = relative drought period.

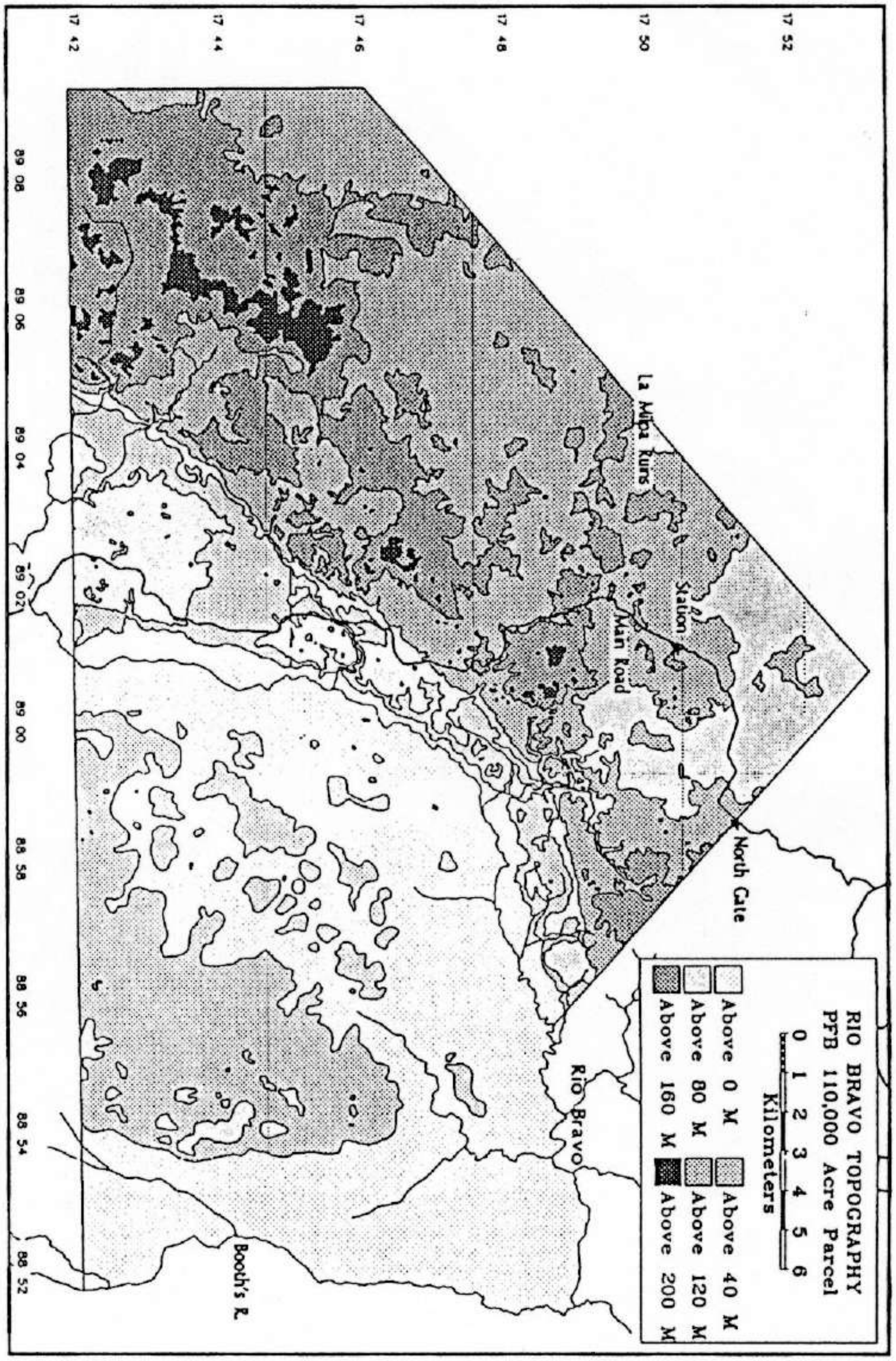


Figure 3 - Elevation map of the 110,000 acre western section of the Rio Bravo Conservation and Mangement Area.

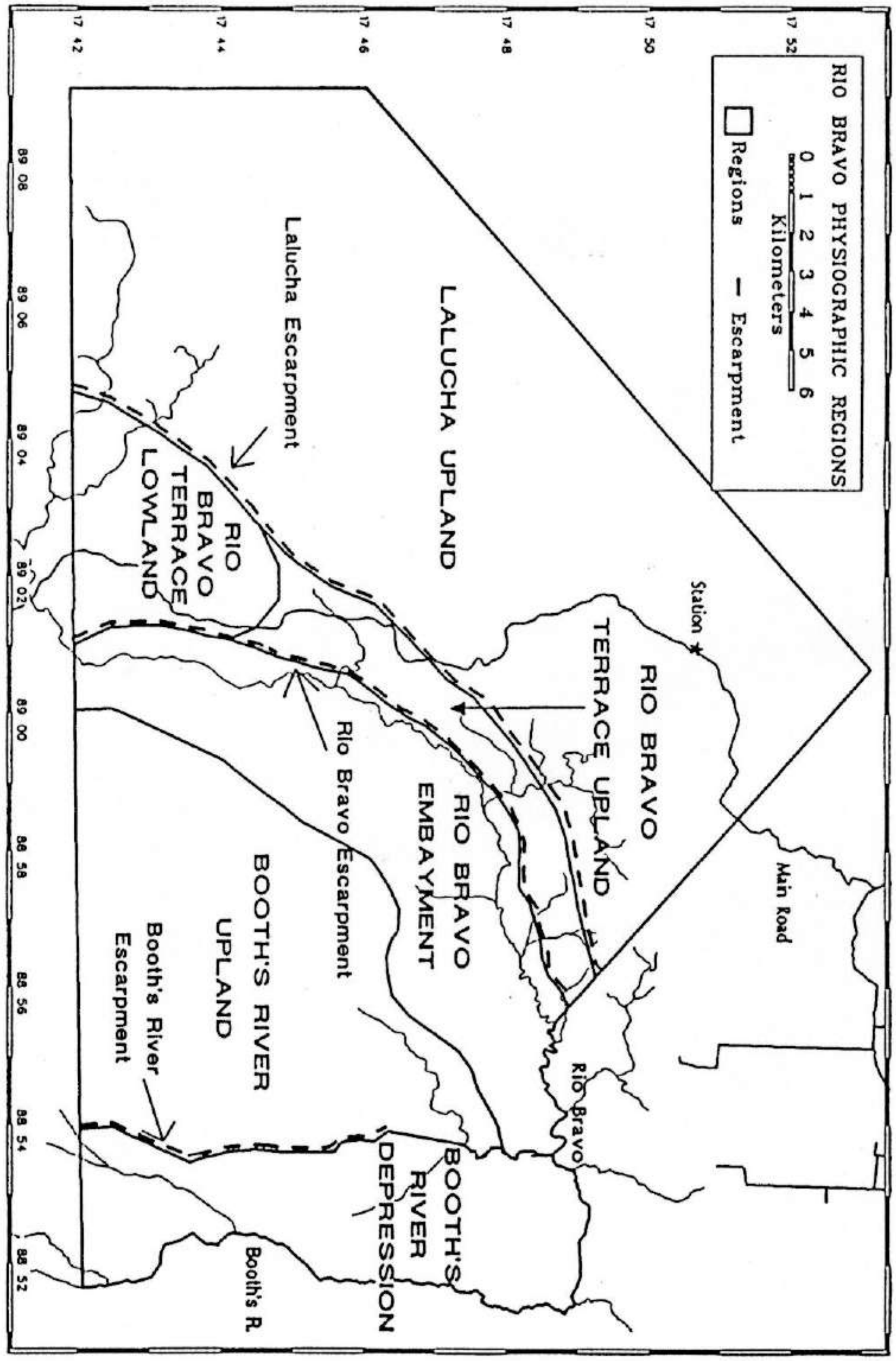
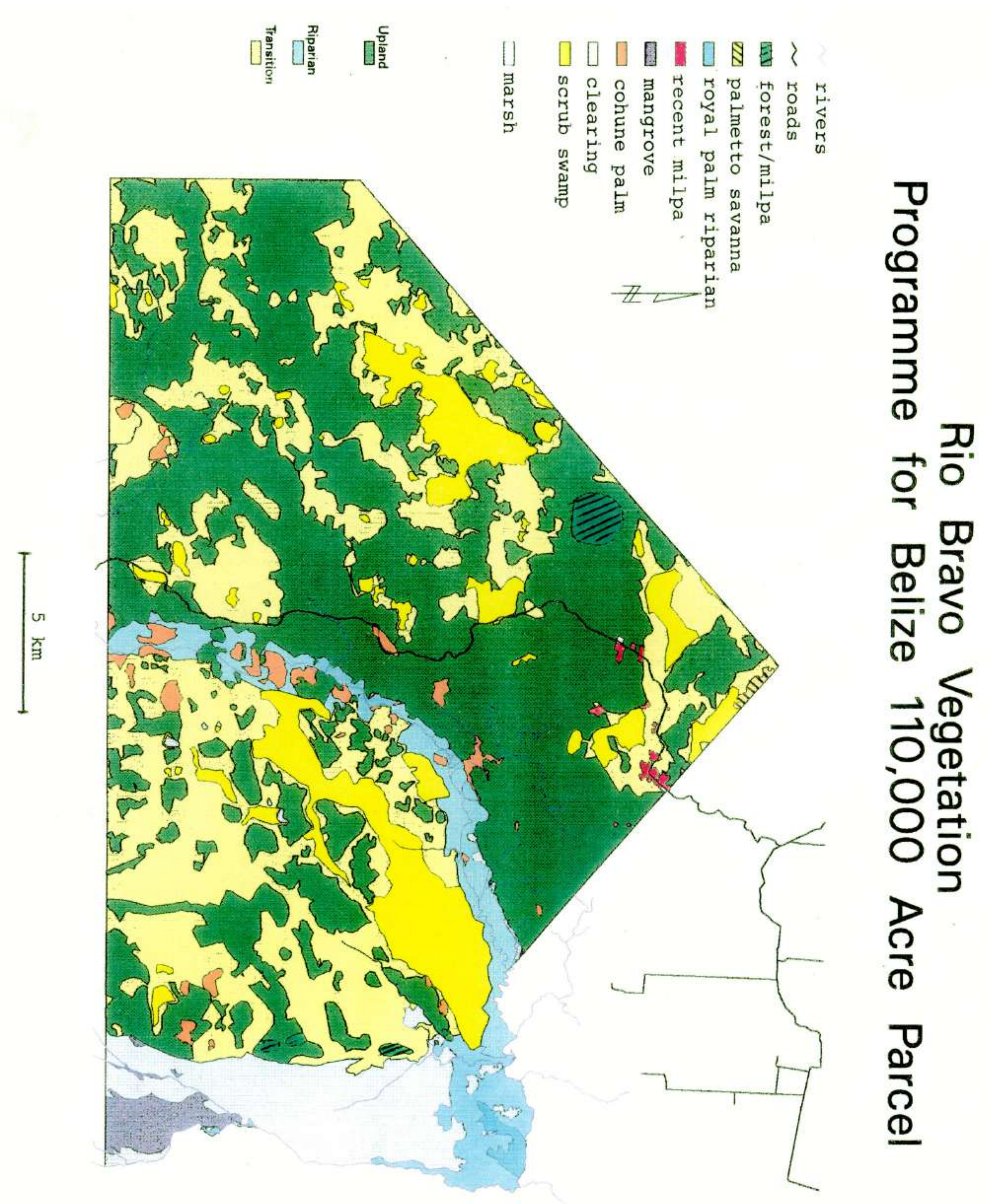


Figure 4 - Physiographic regions of the 110,000 acre western section of the Rio Bravo Conservation and Mangement Area. See text for explanation.

Figure 5 – Not shown

Figure 6


Rio Bravo Vegetation
Programme for Belize 110,000 Acre Parcel
rivers
roads
forest/milpa
palmetto savanna
royal palm riparian
recent milpa
mangrove
cohune palm
clearing
scrub swamp
marsh
Upland
Riparian
Transition
5 km

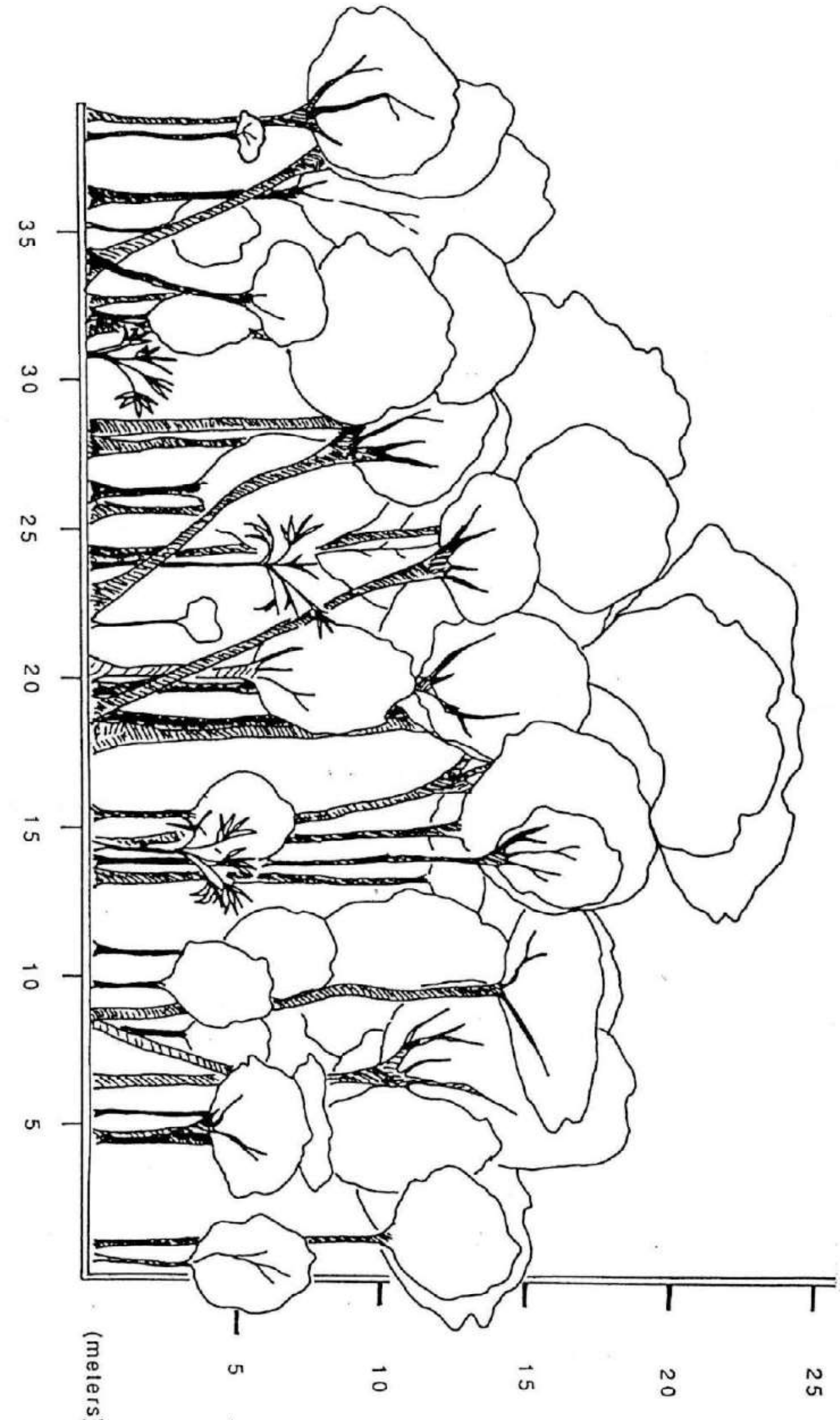


Figure 7 - Profile of dry **upland forest**. Plot area is 40 x 10 m. Trees ≥ 2.5 cm dbh are shown. See text for explanation of method. Drawing by Jenifer O'Hara. rawing by Jenifer O'Hara.

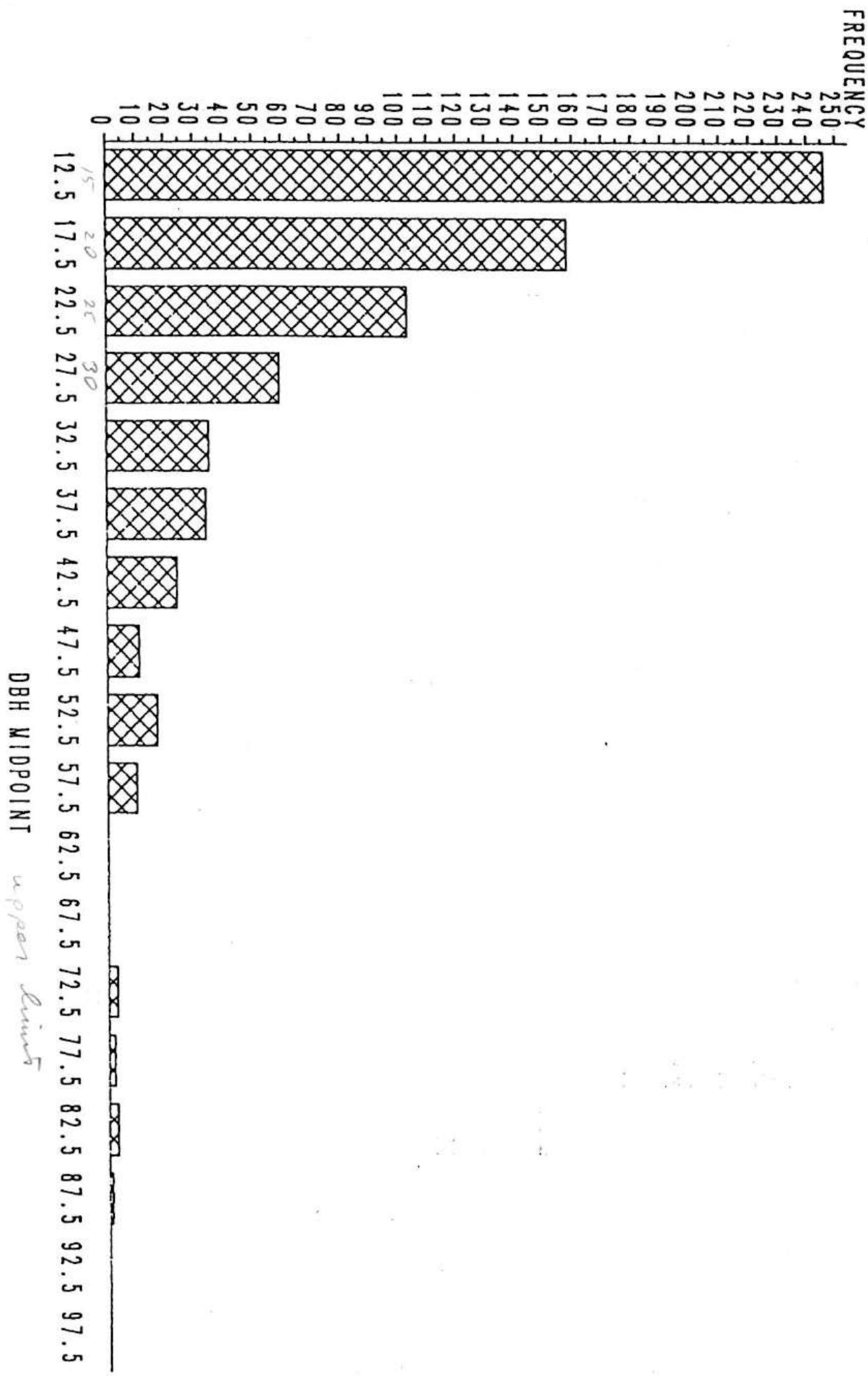


Figure 8a - Diameter class distribution of all trees ≥ 10 cm dbh in a one-hectare plot of dry **upland forest.**

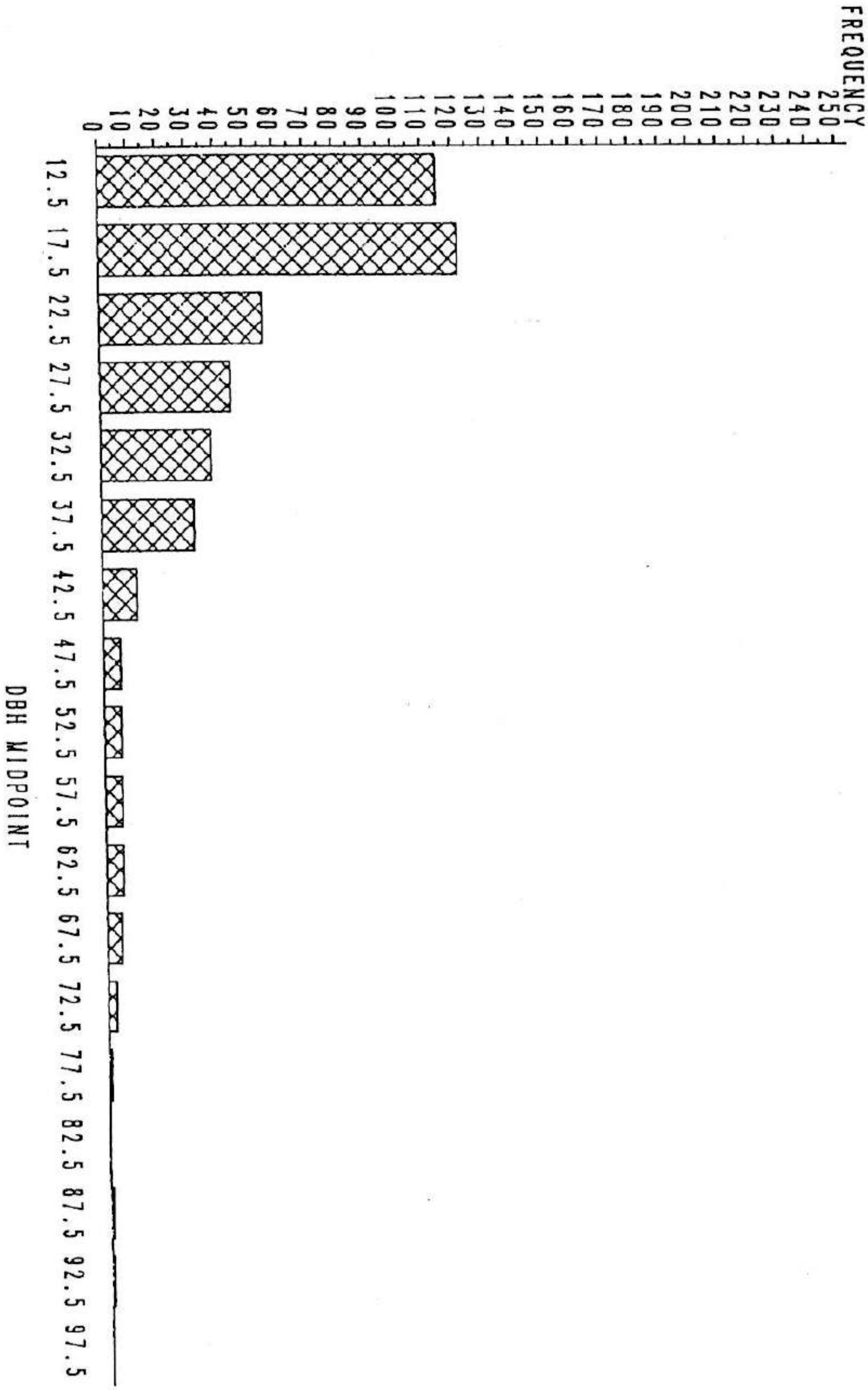


Figure 8b - Diameter class distribution of all trees ≥ 10 cm dbh in a one-hectare plot of mesic **upland forest.**

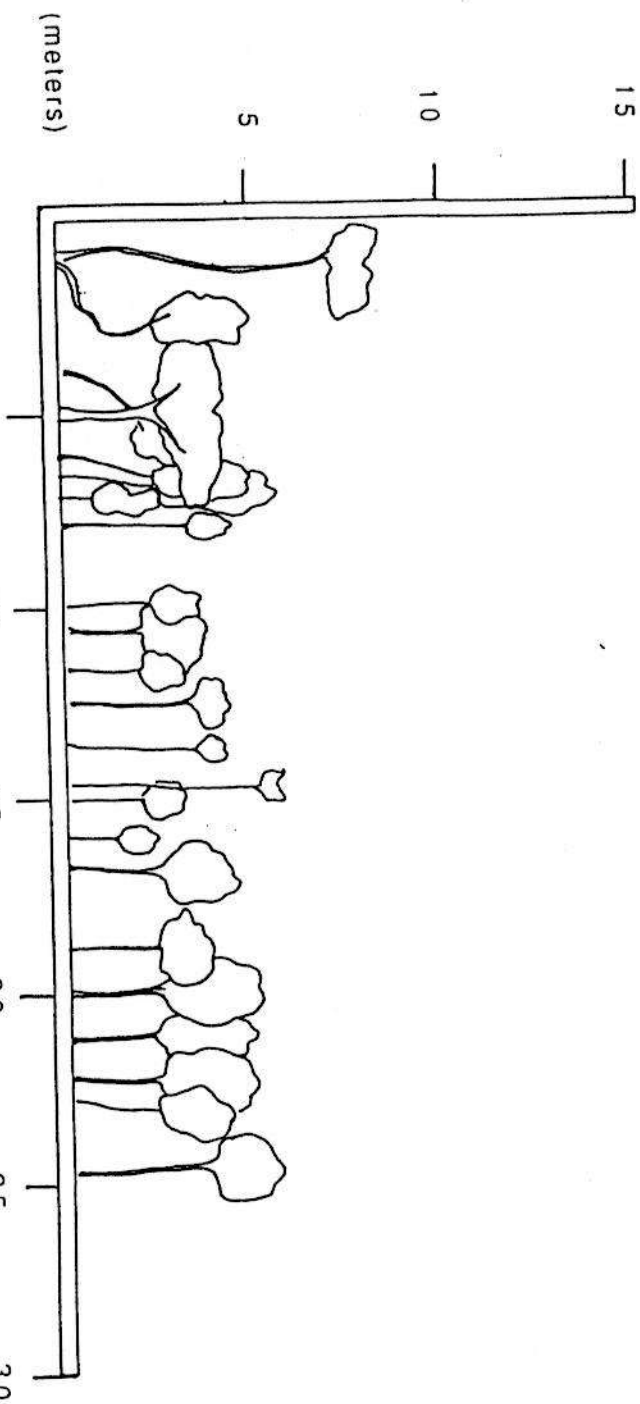


Figure 9 - Profile of **scrub swamp forest.** Plot area is 30 x 1.0 m. Trees ≥ 2.5 cm dbh are shown. See text for explanation of method. Drawing by Jennifer O'Hara.

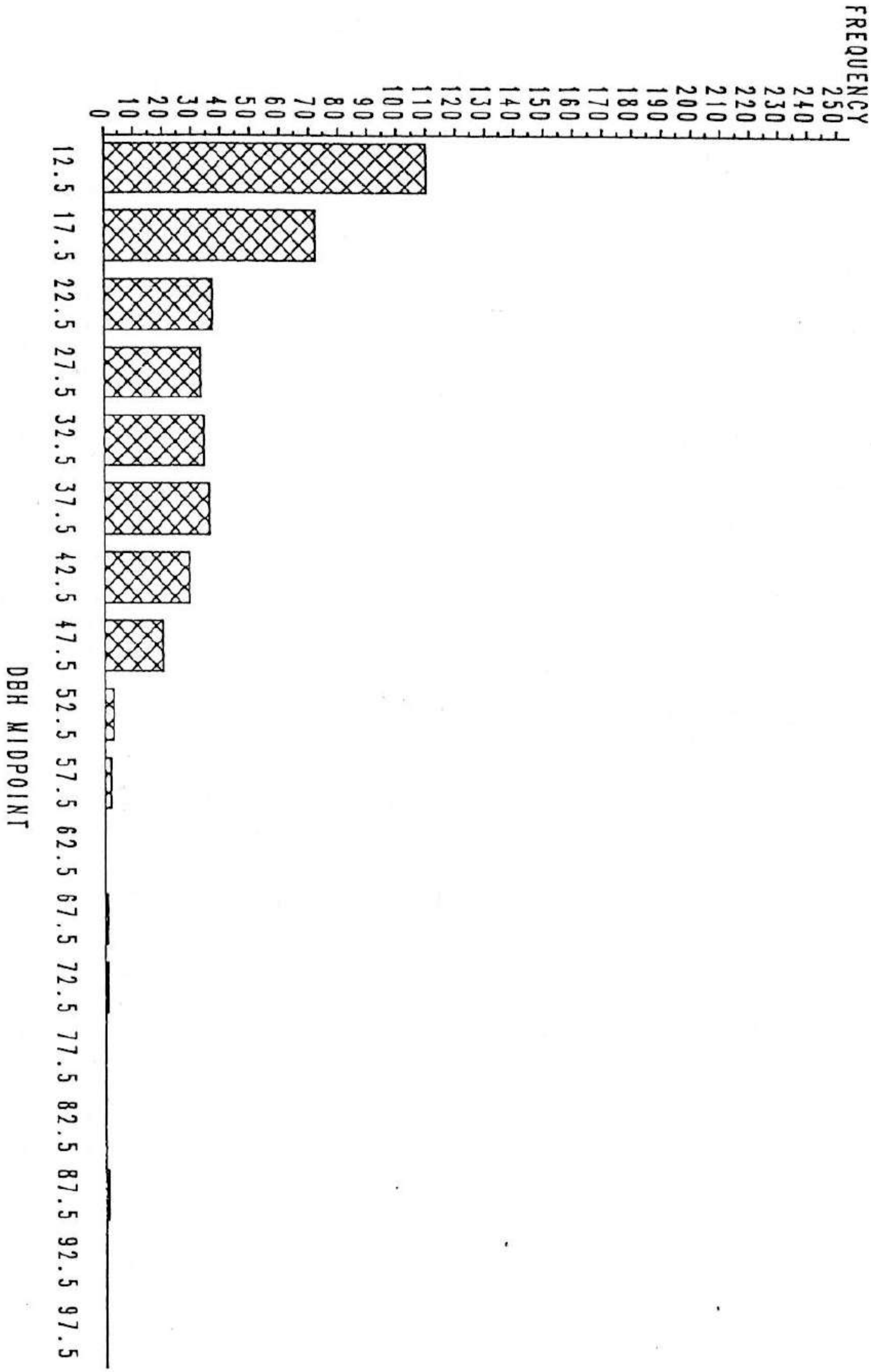


Figure 10 - Diameter class distribution of all trees ≥ 10 cm dbh in a one-hectare plot of **cohune palm forest.**

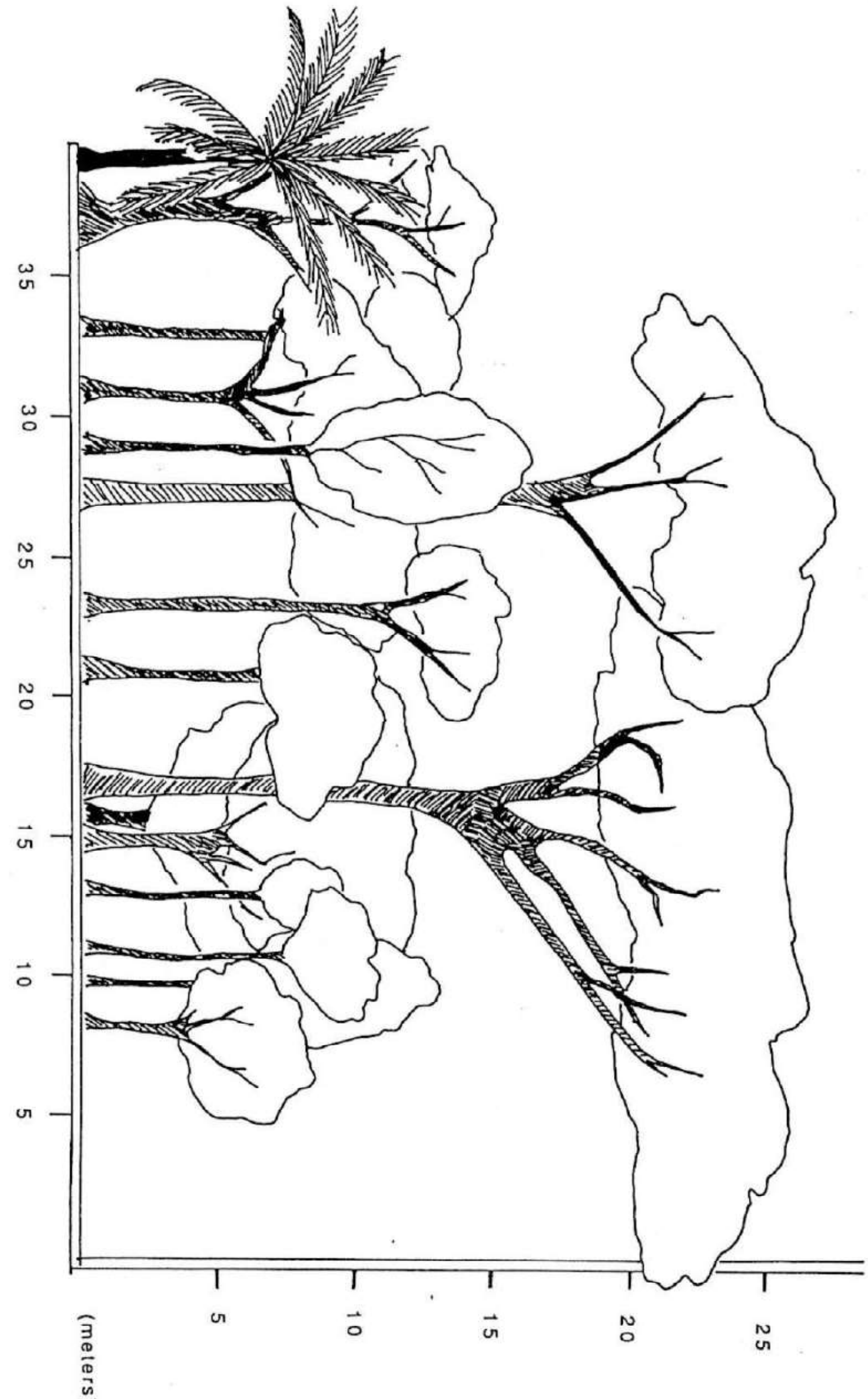


Figure 11 - Profile of cohune palm **riparian forest**. Plot area is 40 x 10 m. Trees ≥ 10 cm dbh are shown. Understory not shown. See text for explanation of method. Drawing by Jennifer O'Hara.

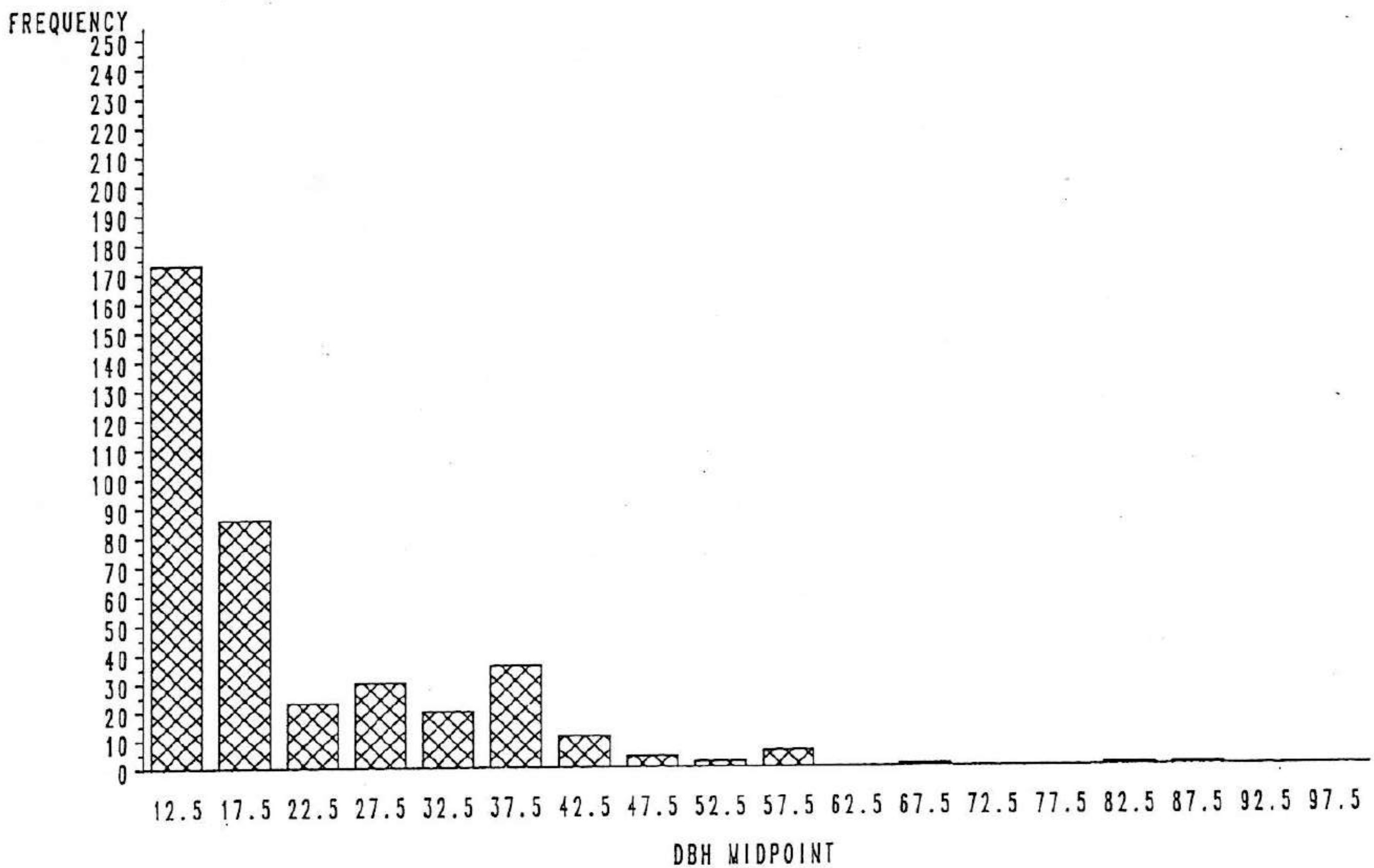


Figure 12 - Diameter class distribution of all trees ≥ 10 cm dbh in a one-hectare plot of cohune palm **riparian forest**.

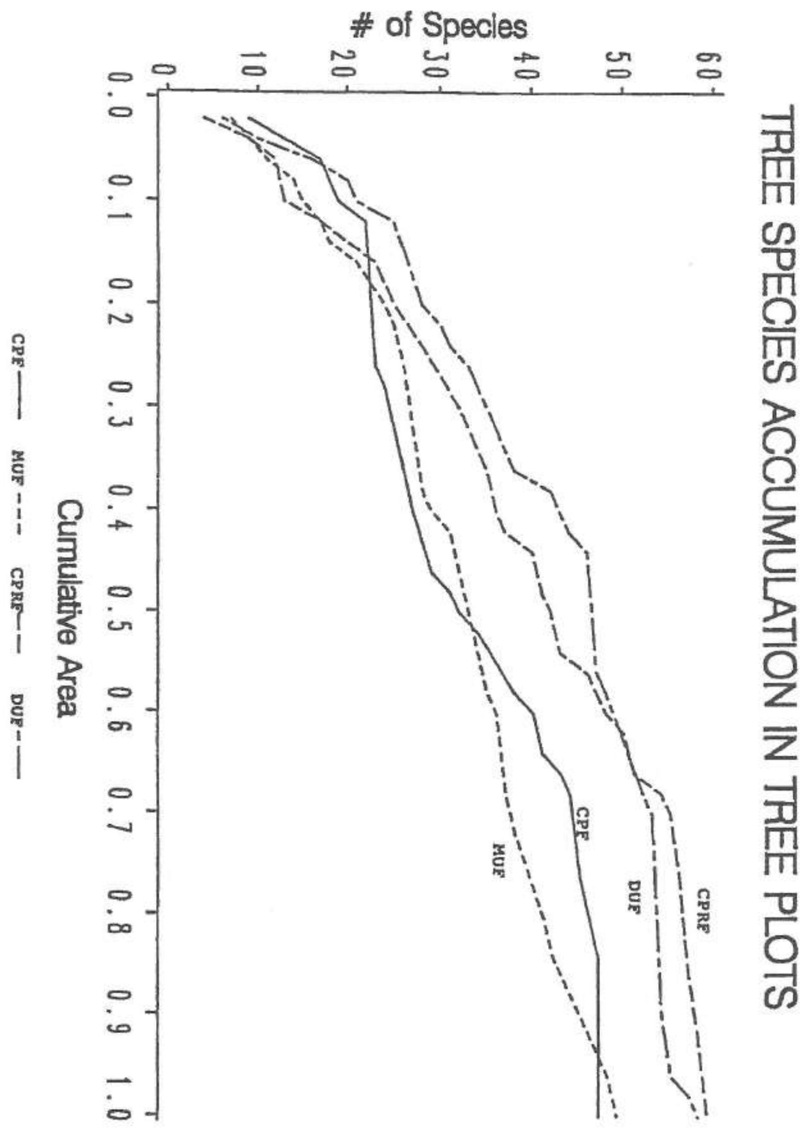


Figure 13 - The accumulation of species totals with increasing area sampled within one-hectare plots. CPF = cohune palm forest; MUF = mesic upland forest; CPRF = cohune palm riparian forest; DUF = dry upland forest.