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Plant Community Structure, Fire Disturbance, and Recovery in Mangrove Swamps of the Waini Peninsula, Guyana

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Soil fires during the 1997 to 1998 El Niño caused high mortality among mangroves of Waini Peninsula, a potential protected area. Impacts and early recovery were investigated, with baseline floristic and ecological analyses.

Plant species and communities were surveyed. 118 species were documented. Approximately 64.6 km^2 of swampland were burned, 26.6 km^2 classified as mangrove, the largest reported mangrove fire. Regional, continental, and global floral affinities are explored. Of 240 species in five Waini and two inland communities, 79% occurred in only one; coastal vegetation exhibited high beta diversity. The Waini held many species with Neotropical (33%) and Pantropical (27%) distributions but few Guiana Shield endemics (1.6%). The presence of the Asian mangrove palm, *Nypa fruticans*, in the study area is examined, including extent, possible sources, potential spread, and reported dispersal to Trinidad.

Six 0.1-hectare *Avicennia* swamp vegetation plots were sampled over four years. Unburned swamp basal area was 21.25 m^2/ha, increasing 2.5% to 3.5% annually. Burned swamp basal area was at least 20.43 m^2/ha before fires, with estimated biomass greater than unburned swamp. Sapling, seedling, and herbaceous cover in the unburned swamp was low, and variable in the burned swamp, with probable hydrology links. Spatial patterns of *Avicennia* trees were generally overdispersed. Waini mangrove basal area and height approached worldwide medians; stem density was much lower. Unburned swamps near Waini Point are apparently younger than to the southeast, with irregular seedling recruitment.

In burned swamp regeneration, establishment distances of seedlings from parents had a mean of 24.2 meters for *Laguncularia*, 4.8 meters for *Avicennia*, and 8.9 meters for *Rhizophora*. Mangrove plantings explored restoration potentials. *Rhizophora* plantings were successful in burned swamp, given sufficient elevation. After 10.5 months, *Rhizophora racemosa* in unburned swamp was about half the height of those in burned areas (56 cm vs 129 cm); wet condition plantings outsurvived and outgrew drought plantings. No *Laguncularia* or *Avicennia* plantings survived, suggesting narrow hydrological requirements.

Geomorphology influences mangrove dispersal, establishment, population structure, and disturbance on the Waini Peninsula. Its mangrove swamps are unique in the Neotropics and valuable biologically and culturally.

Results here suggesting that the Waini flora is essentially separate from the Guiana Shield flora and bears more affinity to the Caribbean region are not surprising, but lends support to the idea that biodiversity studies and conservation efforts should be pursued with an awareness of that distinction.

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Cover: Keith David measuring a large *Avicennia germinans* tree encountered near the Waini River, along transect A. Photo Tom Hollowell, Smithsonian Institution.

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Plant Community Structure, Fire Disturbance, and Recovery in Mangrove Swamps of the Waini Peninsula, Guyana

by

Thomas H. Hollowell[1]

INTRODUCTION

The Waini Peninsula is the site of the majority of Guyana's remaining mangrove swamps. In the ongoing development of Guyana's protected areas system (EPA Guyana 2002), there has been a focus on the "Shell Beach" portion of the Waini Peninsula as a candidate site, primarily because of its extensive mangrove swamps and marine turtle nesting beaches (Humm 2001). The area is important beyond its uniqueness within Guyana, as the high-sediment coastline of the Guianas differs significantly from Caribbean mangrove settings that are most often studied in the Neotropics. There was a basic need for description of the plant communities in the prospective protected area, to provide baseline floristic and ecological information upon which future scientific research and monitoring can build. In the broader perspective, it is important within mangrove ecology to expand documentation of the variety of biotic elements, structures, and disturbances that occur in mangrove ecosystems, to provide for suitable understanding, protection, and management (Ellison 2002; Finn et al. 1998; Jiménez et al. 1985). The disturbance of the study site just prior to field work offered opportunities to address basic questions about the nature of mangrove dispersal and recovery.

As a basis for study, plant specimens were collected and identified, and a vouchered species list was assembled for the Waini Peninsula. Some of those collections expanded documented species ranges. The plant collection results were compared to other available botanical data for the region, at various scales, to place the Waini flora in environmental and biogeographic context.

In addition, the plant communities of the Waini Peninsula were classified, described, and mapped. As part of that task, the unusual phenomenon of large-scale fires in the mangrove swamps was documented, including estimates of the extent of impacted plant communities. Documentation of the fires formed a contribution to knowledge of disturbance types that have been known to affect mangrove systems. The fires occurred during the extreme El Niño event of 1997 to 1998, and so may have been linked to global climate change processes (Laurance 1998; Snedaker 1995).

Among the plant species present, the Asian mangrove species, *Nypa fruticans* Wurmb., was of particular interest and so was documented and reviewed in detail. *Nypa* Wurmb. is an exotic species that may spread in important riverine mangrove swamps of the Waini Peninsula region, making it a concern both in Guyana and neighboring countries.

Ecological vegetation plots were established and resampled to provide new information on the structure of the Waini Peninsula's coastal mangrove forests and on the initial course of regeneration in the fire-affected mangrove forests. Those structural data allowed comparisons with information on other mangrove systems of the world and will aid additional population structure and succession trend studies.

Mangrove zonation patterns have been attributed to both physical and chemical factors

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[1] Master of Science, George Mason University, 1992

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(McKee 1993, 1995b) and to abilities of various mangrove species to disperse and establish (Clarke et al. 2001b; McGuinness 1997a; Rabinowitz 1978a). To investigate possible factors in the fire-disturbed environment, trial plantings of mangrove species were undertaken in both disturbed and undisturbed habitats. The plantings tested the abilities of species to establish in local conditions, independent of their dispersal ability. The results might have implications for potential restoration approaches and provide information on the roles of dispersal limitation versus environmental conditions in mangrove regeneration.

The fire-affected swamps also presented a unique setting to test establishment patterns of mangrove propagules in an environment where coastal tides and currents were absent. A method was devised for sampling the establishment patterns of mangrove propagules from the scattered surviving parent trees in the burned swamps. The establishment data provide insights into the possible path of vegetation recovery.

These studies were a first attempt to assemble critical information that may serve to integrate the swamps of the Waini Peninsula into the broader understanding of mangrove ecology in the Neotropics, and to inform the continued establishment of Guyana's Protected Areas System. It is hoped that future studies will be encouraged to move beyond the work presented here. Because the chapters were written to be published separately, some repetition was inevitable, however it is hoped that it has been kept to a minimum.

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CHAPTER 1.
THE WAINI PENINSULA ENVIRONMENT AND ITS FLORA

INTRODUCTION

Any protected natural area is well served by the assembly of comprehensive baseline information and by ongoing environmental description and monitoring. The broad goal of this chapter is to provide a detailed, initial documentation of the plant species and plant communities of the Waini Peninsula, to serve as a foundation for future studies and management. The Waini Peninsula is a proposed reserve in northern Guyana that has been known for its marine turtle nesting beaches and conservation activities. It is also the location of long stretches of coastal mangrove swamps, freshwater swamps, and extensive intertidal mudflats that are habitat for many types of wildlife. Included are a description of the study site, a summary of the botanical collections made to document the flora, and descriptions of basic vegetation zones. The quantity of new distributional information revealed by plant collections activities is of scientific interest, as that allows insight into the state of basic knowledge about an area, which guides future data gathering efforts for research and conservation activities. A more accurate delineation of Guyana's mangrove communities, which are of high conservation concern, is desirable considering the wide variations in existing estimates for the country (Saenger et al. 1983; Snedaker 1986; Spalding et al. 1997). As part of the plant community description, an estimate was also made of areas affected by the 1998 soil fires on the Waini Peninsula. Those fires were unusual for their impact to large areas of mangrove swamp, which is an ecosystem type normally considered to be unaffected by fire. Appendix 1 provides additional review of mangrove ecology in Guyana, including relationships to fire in the wet tropics. Appendix 2 fully lists the plant species that were documented for the Waini Peninsula.

STUDY SITE

Guyana is located in northeastern South America on the Atlantic Ocean, just north of the Equator (Figure 1.1). The Waini Peninsula is a relatively undisturbed, coastal region of northern Guyana (Figure 1.2). It is the site of most of Guyana's remaining intact coastal ecosystems, including mangrove swamps, freshwater swamps, flooded savannas, and their associated fauna. The peninsula's "wild coast" stretches for more than 75 kilometers along the Atlantic Ocean, from near the Venezuelan border (59º 50' W, 8º 25' N), southeast almost to the mouth of the Pomeroon River (59º 05' W, 8º N). For this paper, the study area includes approximately the northern third of the Waini Peninsula, from

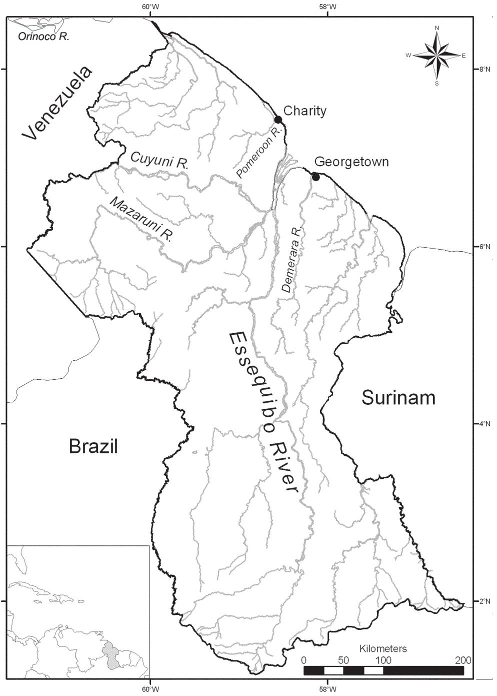


Figure 1.1. Location map of Guyana, with major rivers.

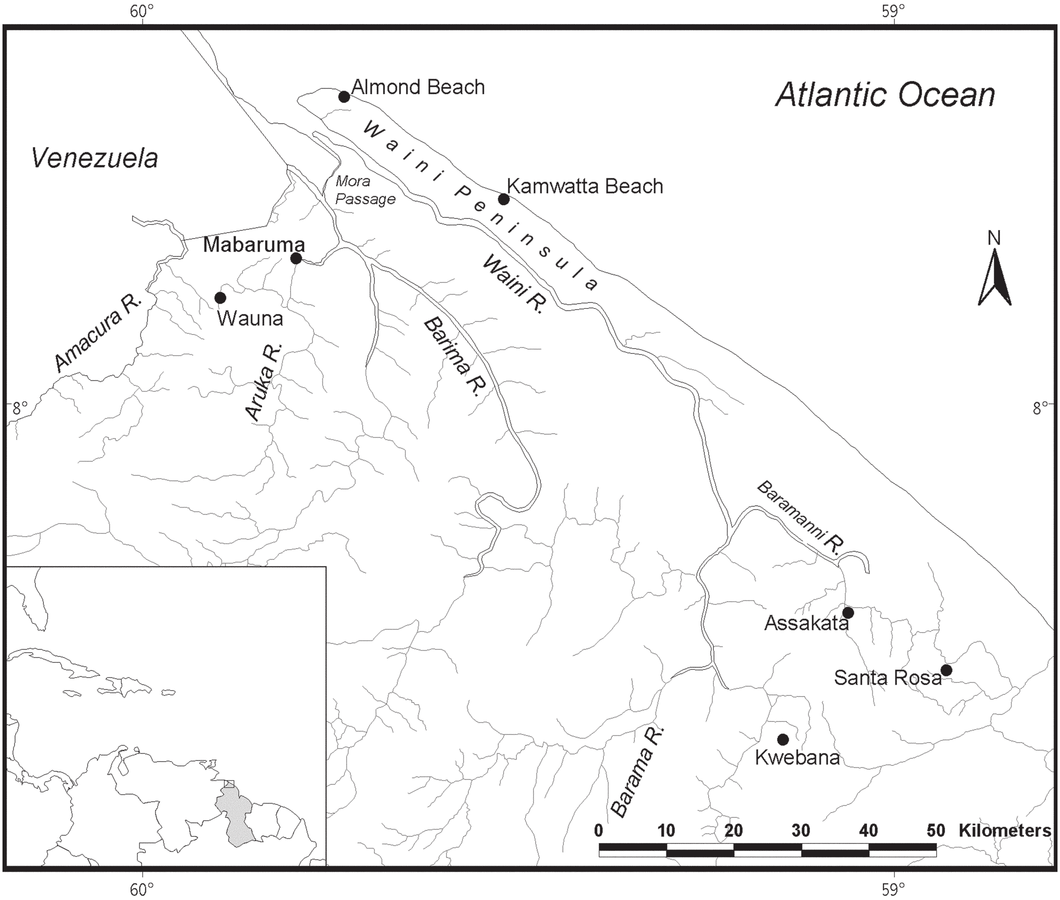


Figure 1.2. Site map of the Waini Peninsula, Guyana, with localities referred to in the text. The area framed comprises much of the Northwest District.

its northwestern point to 59º 30' W, covering a land area of about 190 km^2. That portion of the Waini Peninsula is also commonly referred to as "Shell Beach." The study area is part of a candidate site for Guyana's newly established National Protected Areas System (EPA Guyana 2004; Humm 2001), which at the time of this fieldwork consisted only of Kaieteur National Park (Kelloff 2003).

The coastal plain of Guyana is composed of fine sediments that primarily settled from waters of the current flowing from the Amazon River's mouth, which is over 1,000 kilometers to the southeast. Prior to colonization by European nations, most of the Guyana coast was probably lined by broad mangrove forests that graded into freshwater swamps and flooded savannas, and then into lowland tropical forests (Richardson 1987). In the more densely populated southeastern part of Guyana's coastal plain, around the capital Georgetown, those swamps and savannas were drained and converted to agriculture and settlements early in the country's colonial history. However, in the Northwest District of Guyana (also known as the Barima-Waini Division; Figure 2.1) there have been limitations on access to coastal lands: by land due to the absence of roads and presence of numerous swamps and rivers, and by sea because of the broad tidal mudflats extending up to several kilometers out from shore. As a result, long stretches of the coast have remained sparsely settled and largely unmodified.

Climate

Based on the life zone classification of Holdridge *et al* (1971), that combines influences of temperature, elevation, and rainfall, the Waini

Peninsula is capable of forming a Tropical Moist Forest. Because of its location near the equator, Guyana's climate is dominated by the equatorial trough and the seasonal movements of the intertropical convergence (ITC) (Snow 1976). The mean annual temperature for the coastal zone of Guyana is approximately 26.5ºC, with a 1°C to 1.5°C range between the mean temperatures of the warmest and coolest months, which coincide with the dry and wet seasons respectively. The trade winds consistently blow from the east-northeast or the east, with monthly mean speeds varying from 3 to 4 m/second. Precipitation patterns are characterized by two dry seasons and two wet seasons per year. The major wet season runs from April to August, with a minor wet season from November to February. Mean annual rainfall in the coastal area of the Northwest District has been reported from approximately 2,500 mm per year (Snow 1976) to 3,400 mm per year (K. Richardson, pers. comm.). The wettest month is sometimes reported as June, with an mean rainfall of 400 mm (Snow 1976), or January with a mean rainfall of 500 mm (K. Richardson, pers. comm.). During a typical year in the stronger dry season of February-April, only 5 to 10 days per month receive rainfall (Snow 1976).

Snow (1976) noted that a zone of minimum rainfall probably occurs along a narrow band of the coast of northern South America, with a peak in precipitation reached less than 50 kilometers inland, caused by effects of increased surface roughness of forests upon air leaving the ocean. This has been confirmed by many observations (Hollowell, unpublished) of rain developing several kilometers inland from the Waini Peninsula while extreme coastal areas remained dry. The typically low number of rain days in the dry season, combined with reduced rainfall immediately along the coast and a drought caused by a strong El Niño event, led to extremely dry conditions in the coastal forests of the Waini Peninsula in 1997-1998.

Geomorphology

The coastal plain sediments of the Guianas were deposited in recent times on the margins of the Guiana Shield, which is a natural geological unit characterized by ancient bedrock with sandstone and igneous highlands (Gibbs & Barron 1993; Huber 1995a). The Guiana Shield is geologically distinct from the more recently uplifted Andean highlands. It is bounded for the most part by the Atlantic Ocean to the east, the Orinoco River to the north and west, and the Negro and Amazon Rivers to the South. The Shield is widely considered to be a region of high biotic endemicity (Huber 1995c), possibly due to having served as a refugium for tropical forest species during prolonged periods of dry climate in the Pleistocene epoch (1.8 mya to 11,000 years bp), or due to the ancient, varied, and isolated landscapes of the region (Colinvaux 1987).

From the Orinoco Delta south to the Amazon River, the coast of South America is geologically referred to as a "passive margin," with deep sediments deposited over the tectonically stable Guiana Shield (Di Croce et al. 1999). That stability is reflected in estimates that relative sea level in the region has been relatively stationary since post-glacial rises ended perhaps 6,000 B.P., although sea levels possibly surpassed that of the present by as much as five meters from 6,000 to 3,000 B.P. (Pirazzoli 1991). By some accounts, the section of the Guyana coast including the Waini Peninsula has been subject to some uplift in recent geological times (Gibbs & Barron 1993), while others suggest that subsidence may have been a factor along the northwestern coast of Guyana (Brinkman & Pons 1968). Williams (1989) employed archaeological evidence to infer that subsidence in the Guyana's northwest ended around 3,400 years B.P. The presence of marine sediments on higher elevations in the central parts of the Waini Peninsula suggests that in geologically recent times, relative sea levels may have once been several meters higher than present or that moderate uplift has occurred. The area is close enough to a geologically active area beginning just south of Trinidad (Di Croce et al. 1999) that associated minor uplift or subsidence around the study site could be plausible.

The Shield's basement granites are estimated to be as far as 500 meters below the surface along Guyana's northwest coast (Di Croce et al. 1999). The coast of the Guianas is, in essence, the major portion of the coastal delta of the Amazon River. The Essequibo, Waini, and

Orinoco Rivers probably contribute a minor amount of sediment in comparison to the Amazon River. The coast is geomorphically similar to the coast of eastern Sumatra, based on an analysis of several coastal characteristics (Jelgersma et al. 1993). Both are deltaic environments with a wide coastal shelf, a prograding shore of very fine sediments, little subsidence or uplift, strong longshore transport, low wave energy, small tidal range, and no influence of tropical cyclones. A geomorphic classification commonly applied to this type of mangrove environment is River Dominated Alluvial Plain (Thom 1984; Woodroffe 1992).

The width of the lower coastal plain of Guyana varies about from about 75 kilometers at the Corentyne River on the Surinam border to 25 kilometers near the Venezuelan border (Vann 1969). The coastline is characterized by cycles of accretion and erosion of mudflat clay and silt sediments, which are known locally as "sling mud"(Richardson 1987; Wells & Coleman 1981). The Waini section of the coast has apparently been prograding, in a manner similar to the coastline of the Orinoco Delta to the northwest (Bureau of Economic Geology 2002). Along parts of the Guyana coast coastal currents have led to erosion loss of diked land, including land near Georgetown that was once populated or cultivated as recently as 1972; signs of these changes are visible in radar satellite imagery (Singhroy 1996). Sizable sediment deposits were colonized by mangroves, primarily *Avicennia*, between the Essequibo and Pomeroon Rivers in the 1990's (pers. obs).

Slow migration of the mudbanks along the coast leads to a smaller-scale cycle of shore erosion and redeposition that is unlike typical coastal dynamics that would produce relatively straight coastlines (Lakhan & Pepper 1997). As part of those cycles, coarser sand and shell fragments are released from the sediments and deposited to form beach ridges that may accumulate up to 200 meters in width (Prost 1989; Vann 1969). The beach ridges often isolate sections of mangrove forest from the sea. Along other stretches of the Waini coast waves wash directly into the mangrove forest. During the time of this field work (1997-2001), the widest beach ridge on the Waini Peninsula was Almond Beach, the location of a marine turtle monitoring camp (8° 23' 58'' N, 59° 45' 16" W) and base camp for these studies, where the ridge measured over 160 meters wide. That shell deposit was perhaps two meters deep and contained a lens of nearly fresh water (approximately 1 psu salinity, Hollowell, unpublished data). To illustrate the variability of the ridges, profiles were surveyed for one wide section and one narrow section of beach ridge, illustrated in Figures 1.3 and 1.4. The wider beach ridges roughly coincided with areas of mangrove swamp that dried adequately to

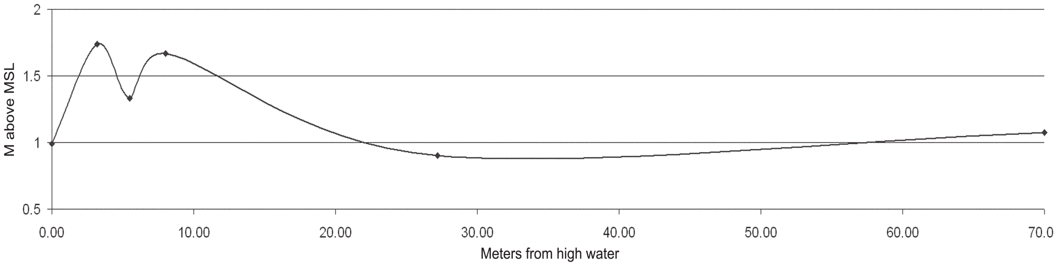


Figure 1.3. Beach profile between Almond Beach Camp and Waini Point, an area of narrow beach ridge near plots 1, 2 and 6. Beyond 25 m was *Avicennia* swamp, which borders the beach ridge with a low swale. It was not unusual for waves to spill sea water into the swamp during extreme tides. Profiles were started near the boundary between mudflats and shell substrate.

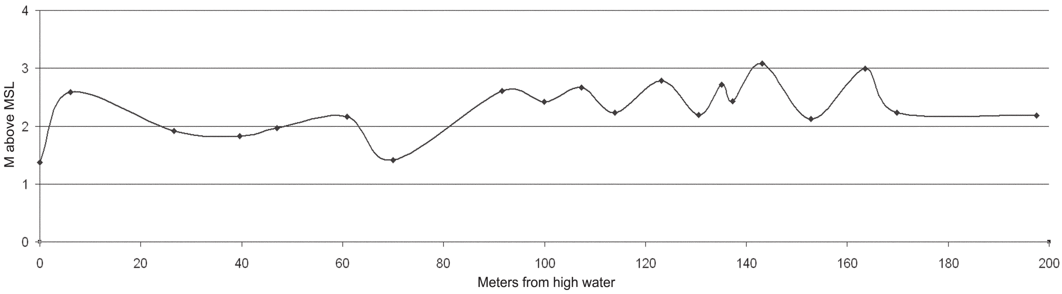


Figure 1.4. Beach profile at Almond Beach camp, near plots 2, 4 and 5, an area with a wide beach ridge that, at the time of survey in April 2001, had several small structures and gardens. The swale at 70 m was deeper in some places than shown, and formed a slightly brackish pond persisting through most dry seasons. Beyond 170 m was *Avicennia* swamp that burned in early 1998. Waves from extreme storms have flooded interior sections of the beach ridge, but rarely reached the mangrove swamp.

burn in the 1998 soil fires (Figure1.5).

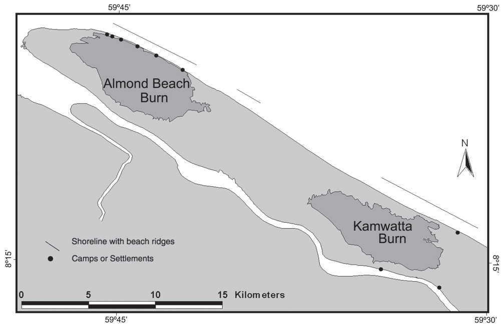


Figure 1.5. Location of beach ridges on the Waini Peninsula, shown in relation to burned areas and settlements or camps.

Inland beach ridges occur within the coastal mangrove swamps; these run approximately parallel to the present shoreline. Such ridges are evidence of long-term coastal accretion, as they represent former shorelines; they are often termed “cheniers” in the literature (Prost 1989, 1997; Wells & Coleman 1981), and the coast of the Guianas is one of the few true chenier coasts of the world. The region of South American cheniers stretches from the mouth of the Amazon River north through the Orinoco Delta (Bacon 1990). The other major chenier coast in the New World is the Louisiana chenier plain of the Mississippi River delta (Huh et al. 2001; Wells & Coleman 1981). On the Waini Peninsula, the largest cheniers rise about one meter above the surrounding swamp surface and support non-mangrove vegetation dominated by trees including *Terminalia catappa* L. and *Spondias mombin* L. Differences in hydrology, vegetation cover, or surface reflectance of shells often allow cheniers to be distinguishable in satellite imagery. The cheniers on the Waini Peninsula sometimes coincide with transitions in plant community composition. There are accounts from older residents of the Almond Beach area describing the largest chenier, now over 700 meters from the present shore, as having been the location of the shoreline within their memories; these accounts have not been confirmed, but could be subject to comparison with older maps and aerial photos. Vann (1969) also reports observations of shell ridges stranded up to 300 yards from shore that had been beach by the ocean 30 years earlier, corroborating the local accounts.

Like most coastal plant communities, those of the Waini Peninsula are influenced considerably by local geomorphic processes over time (Augustinus 1995; Thom 1967, 1975; Woodroffe 1992). Although direct building of land has been attributed to mangrove vegetation in early literature, that has been largely discounted (Woodroffe 1992). Still, mangroves probably play some role in securing land built up through geomorphic processes, both by slowing wave erosion and, as suggested by Wells and Coleman (1981), through new root biomass of *Avicennia* L. trees in newly colonized mudflats increasing substrate elevation enough to allow survival of a stand. Zones of recent coastal accretion are easily identified from the sea by bands of *Avicennia* saplings and small trees (Figure 1.6), while eroding shore segments are usually marked by fallen *Avicennia* trees (Figure 1.7).

Figure 1.6. *Avicennia* saplings recently established on new sediments in front of mature trees, on the Waini Peninsula coast just southeast of Kamwatta Beach.

Developing countries with populated low-lying land, such as Guyana, are particularly vulnerable to economic and environmental impacts from sea level increases (Gabche et al. 2000). A sea level rise in the 0.09 to 0.88 meter range has been predicted by the year 2100 (IPCC 2001), and the Government of Guyana estimates that the entire Waini Peninsula would be severely affected by a one meter rise in sea level (EPA Guyana 2000). Sea level rise could result in substantial changes in the extent of mangrove ecosystems world-wide (Pernetta 1993). To survive under such circumstances, mangrove communities must either migrate inland or survive on accreting substrates. In general, high sediment input mangrove systems such on the coast of the Guianas are more likely to withstand moderately rising sea levels (Field 1995), particularly in contrast to Caribbean mangrove systems that are often situated on slowly accreting peat substrates (Ellison 1993; Ellison & Stoddart 1991; Parkinson et al. 1994). Although the coastal plain of the Guianas could serve as a refuge for mangrove communities, in populated areas any landward migration of mangrove forests would be impossible.

Figure 1.7. Shore erosion along the Waini Peninsula coast between Almond Beach and Kamwatta Beach, showing fallen *Avicennia* trees. During higher tides waves wash over a very small beach ridge and into the forest.

Mangrove systems along the Guyana coast might be subject to accelerated isolation from tidal influence if sedimentation increases as a result of changes in upland land uses that cause erosion, as has been reported on parts of coastal Thailand (Panapitukkul et al. 1998).

Soils

The soils of the Waini Peninsula are the product of slow accretion of very fine sediments in very deep layers over recent geological time (Brinkman & Pons 1968; Gibbs & Barron 1993). Soils of the Waini Peninsula have been classified as Demerara Series, Coronie deposits, of the Comowine phase (Brinkman & Pons 1968), which are marine clays with high base saturation, deposited less than 1,000 years ago. The clay soils of the Waini Peninsula swamps are comparable to those of the Wia Wia reserve of coastal Surinam, which were described by Pons and Pons (1975) as typic Endoaqerts (at the time, termed Typic Haplaquepts). The Waini soils could alternately be classified as Vertisols since they marginally meet the requirement of forming cracks on a regular basis (Soil Survey Staff 1998), as observed during droughts of extreme dry seasons. These young, extremely fine clay soils are highly reduced by anaerobic conditions during long periods of inundation. Such reduced soils are indicated by a gleyed color (grey, low chroma color), most often measured on the Waini Peninsula at 7.5 YR 4/1 using the standard Munsell soil color system (Munsell Color 1992). The shallower portions of those soils included high chroma mottles, around Munsell color 7.5 YR 4/4, that usually result from seasonal fluctuation of water tables. There was little horizon development other than a surface layer of organic material that ranges from 5-15 cm in thickness. Most of the mangrove swamp soils of the Waini Peninsula had such organic horizons, again similar to those reported for Surinam's coastal mangrove swamps (Pons & Pons 1975). In the Waini Peninsula's more inland Mixed Freshwater swamps, the organic horizon was observed to be as much as 15-20 cm thick, but was minimal in areas where the upper soil layers had been burned in 1998. Such organic layers are quite shallow compared to "pegasse" peat that is several meters deep in coastal plain swamps located farther inland than the Waini Peninsula sites, most notably the *Mauritia flexuosa* L.f. palm savannas in the Santa Rosa vicinity of the Northwest District (van Andel 2000a).

The beach ridges and cheniers are composed of fine shell fragments with minimal coarse sand. These very young soils can be classified as typic Psammaquents or Psamments (Soil Survey Staff 1998), with fine shell materials probably derived from both riverine and oceanic sources (Brinkman & Pons 1968). The offshore mudflats could possibly be classified as Halic Typic Hydraquents, although they are likely unsuitable for colonization (Soil Survey Staff 1998), in which case they should be considered non-soil, being too frequently inundated and/or unstable to usually support plant growth.

Since the Waini Peninsula was deposited slowly by accretion of marine sediments, the interior area has probably been above sea level longer than land near the ocean, and land nearer to Waini Point may be more recent than the southeastern portion of the Peninsula. Older deposits have been subject to more leaching of salts by rains, greater accumulation of organic matter from vegetation, and possible changes in elevation. Generally, soil salinity is higher near the ocean, limiting the number of plant species that may become established. The soils of the interior Mixed Freshwater swamps are similar to those of the Coastal Mangrove swamps, being very fine, gray clays of marine origin. The porewater salinity of these soils was generally low enough, less than 10 psu (Hollowell, unpublished data), to allow non-mangrove plant communities.

The Venezuelan state of Delta Amacuro borders Guyana's Northwest District; it is largely situated on the coastal plain, with alluvial and marine soils similar to those of the Waini Peninsula and the coastal plain of Guyana. The southern third of Delta Amacuro is geologically part of the Guiana Shield, with soils derived mostly from granitic bedrock (Huber 1995a). This includes part of the low mountains of the Serranía Imataca along its border with the state of Bolívar. Those mountains are primarily composed of granitic bedrock with greenstones, similar to the mountains of Guyana's Northwest District but distinct from the sandstones and intrusive rocks of the Pakaraima mountains to the south.

The Waini Peninsula Fires of 1997-1998

The El Niño event of 1997-1998 was one of the more substantial that have been recorded (Trenberth 1999). Severe flooding occurred in northwestern South America, while there was a substantial decrease in rainfall intensity and frequency in northeastern South America. Guyana was one of the hardest hit countries, along with neighboring portions of Venezuela and Brazil. Below normal rains began in the Guyana region in June 1997. By March 1998, parts of Guyana had rainfall deficits of more than 1,000 mm and river flows approximately 20 percent of normal (WMO 1999). Minor fires resulting from that drought were reported for small, white-sand areas in Guyana (Hammond & Steege 1998). Widespread, uncontrolled forest fires were also reported during that time from the state of Roraima, in northern Brazil, just west of southern Guyana, affecting 12,000 km^2 to 33,000 km^2 of forest (Barbosa & Fearnside 1999; Barbosa et al. 2003; Cochrane & Schulze 1998). Also during that period, droughts led to fires of even greater extent in Indonesia, destroying over 50,000 km^2 of forest and causing widespread respiratory problems downwind (Kinnaird & O'Brien 1998; Legg & Laumonier 1999; Trenberth 1999).

Although unusual for mangrove ecosystems, the 1998 soil fires on the Waini Peninsula have been poorly documented. There were apparently no reports in the Guyanese media, and limited knowledge of the fires reached any governmental offices. One brief report of possible fires in the Waini Peninsula area occurred in the literature, based on satellite detection during March 1998 (Grégoire et al. 1998). That report was based on analysis of AVHRR 1-kilometer resolution satellite imagery, where a single point of possible fire was detected near the northwestern end of the Waini Peninsula. The same report indicated fires in mangroves and coastal vegetation in Surinam, and predicted serious consequences including increased coastal erosion and impacts on fisheries.

According to residents, the Waini peninsula fires were initiated by multiple, unintended escapes of agricultural fires at small settlements on coastal beach ridges. Spontaneous combustion of peat soils might be a slight possibility during droughts (Lindeman 1953; Viosca 1931), although the peat of the Almond Beach swamps was probably not thick enough to present that risk. Residents of Almond Beach have recounted carrying water in attempts to extinguish soil fires early in their course. The fires burned for several months, working through the swamp forest from late 1997 until the return of rains in April 1998. During that period, smoke often made navigation on the Waini River difficult.

Two extensive areas of the Waini Peninsula swamps were burned. The Almond Beach burn ran adjacent to the Atlantic beach ridge from the Peninsula's northernmost settlement at Almond Beach, the site of a marine turtle monitoring camp, to the last coastal settlement in the vicinity, about 7 kilometers to the southeast. For several years following the fires, crowns of dead standing *Avicennia* trees at the Almond Beach burn were visible from the ocean. The Kamwatta burn occurred about 20 kilometers to the southeast of Almond Beach. Those fires came within 250 meters of the ocean near Kamwatta Beach (Figure 1.2), where a temporary marine turtle monitoring camp was located. Possible outliers of the Kamwatta burn were visible along short stretches of the Waini River near homesteads.

Tree mortality was very high as a result of both of these burns. The mortality resulted from at least two factors: the high fire sensitivity of mangrove plants, and the manner in which the fires passed twice through many areas, with the first pass burning upper organic soil horizons (5-15 cm thick near Almond Beach), and second pass additionally fueled by leaves fallen from shocked and newly killed trees (local inhabitants, pers. comm). Cochrane (1998) refers to similar double fires in upland tropical forests following the accumulation of dead leaves on the forest floor.

MATERIALS AND METHODS

Plant Collection Field Work

For characterization of the flora of the Waini Peninsula, plant specimens were collected, identified and processed for deposit in herbaria to provide vouchers for a guide to the plants of the Waini Peninsula, vouchers for the composition of plant communities, and vouchers for ecological plots in the local mangrove swamp. At least one collection was made of each species encountered, including any plants that were potentially distinct from other species previously collected.

Plant collections were made on field trips from 1997 through 2001. Fertile plant material was selected in the field; at least three duplicate collections were made whenever possible to provide sheets for the herbaria at the University of Guyana's (GRB) Centre for the Study of Biological Diversity (CSBD) and at the Smithsonian Institution (US). Sterile collections were made in only a few cases when no fertile material was found. Associated plant description, habitat, and location data were recorded, with geographic coordinates recorded using a hand-held Geographic Positioning System (GPS) with an accuracy of 15 meters. Specimens were field pressed and air dried in the Almond Beach camp on the Waini Peninsula. Air drying of botanical collections in the field can be impractical in the wet interior of Guyana, where the common practice has been interim preservation in an ethanol solution. However, field drying is often possible in the relatively dry, windy environment of the Almond Beach camp. Because of that, the collections of Hollowell number series from 200 to 754 were not treated with any preservatives. All specimens were transported to the CSBD for any final drying, sorting, and processing for export permits.

Where possible, photographs were taken of species collected in the area. Copies of selected slides and image files are held by the Smithsonian Institution and by the CSBD. It is planned to use those photographs as part of an illustrated listing of plant species in a separate volume.

Plant Identification, Classification and Distribution

Plants were identified using available botanical keys, most notably treatments from the *Flora of the Guianas* (Görts-van Rijn 1985 - 2006) and the *Flora of the Venezuelan Guayana* (Steyermark et al. 1995 - 2005). As neither of these are complete, numerous other publications were also utilized (e.g., various regional floras and guides (Gentry 1993; Lanjouw 1964-; Lasser 1964-1992; Pulle 1932-; Ribeiro et al. 1999), botanical journal articles, and botanical monographs). The U.S. National Herbarium at the Smithsonian Institution (US) was a valuable reference for confirming determinations and resolving problems. In several cases, identifications were provided by specialists in particular plant families.

Following identification, name data were added to the Smithsonian's Biological Diversity of the Guianas Shield's (BDG) plant collection database, labels were produced for all duplicate specimens, and the specimens were distributed. The first duplicate sheet of all collections was returned to the University of Guyana's (BRG), and the second duplicate was mounted for the US National Herbarium. Any additional sheets were distributed to various herbaria in the United States, South America, and Europe. Collection and identification information were included with specimens returned to the CSBD.

Plant nomenclature was standardized and synonyms obtained from the Smithsonian's Biological Diversity of the Guiana Shield Program (BDG) database for the *Checklist of the plants of the Guiana Shield*, on which Boggan et al. (1997) and Hollowell et al. (2001) were based.

Plant Species List

Species were placed on the Waini Peninsula plant species list if they were collected or observed in the study area (west of 59° 30' W). Cultivated plants were not included in most instances, except if they were considered dominant in sizable areas of the vegetation or if they were naturalized or likely to become naturalized. Authors of plant names were listed following the Latin name and were standardized according to Brummitt and Powell (1992). Synonyms included with species lists were obtained from the *Checklist of the Plants of the Guiana Shield* database (Boggan et al. 1997; Hollowell et al. 2001), as well as from the *Flora of the Venezuelan Guayana* (Steyermark et al. 1995 - 2005) and nomenclatural databases (Missouri Botanical Garden 1995-present; Plant Names Project 1999-present). Synonyms are listed alphabetically by genus and specific epithet, along with the currently accepted name of that species.

Plant Communities

The vegetation on the Waini Peninsula was classified into four basic types, from the coast to the Waini River: 1) Beaches, 2) Coastal Mangrove swamps, 3) Mixed Freshwater swamps, and 4) Riverine Mangrove swamps. Most of the vegetation of the Waini Peninsula was dominated by typical beach, mangrove, and freshwater swamp species of the Neotropics. That dominance was presumably influenced by both the limiting factor of salinity and the high availability of fruits and seeds dispersed by the ocean. In that setting, the characteristics of available plant species were also important in determining community composition and zonation. A previous estimate of plant communities on the Waini Peninsula was given in the *Preliminary Vegetation Map of Guyana* (Huber et al. 1995), adapted in Figure 1.8. Here, those boundaries have been refined through interpretation of Landsat 7 Enhanced Thematic Mapper plus (ETM$^+$) imagery and fieldwork, including GPS georeferenced plant collections and notes made during transects across the Peninsula.

Burned Area Delineation

A post-burn Landsat ETM$^+$ scene with little

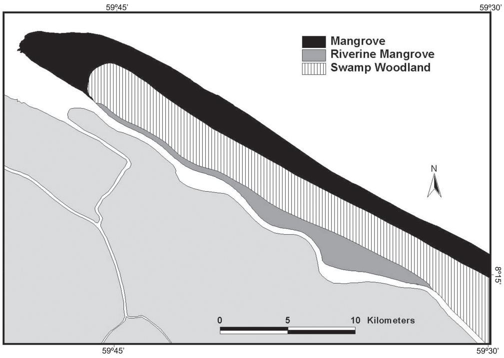


Figure 1.8. Classifications for the Waini Peninsula from the *Preliminary Vegetation Map of Guyana* (Huber et al. 1995) digitized onto a UTM base digitized from satellite imagery. Riverine Mangrove swamps were not differentiated from Coastal Mangrove swamps in the original map, but are shown here based on their location along the Waini River. The map's areas of Mangrove swamp are 74.8 km^2, Riverine Mangrove 25.2 km^2, and Swamp Woodland 95.0 km^2.

cloud cover over the area of interest on the Waini Peninsula was identified. That scene was acquired on 3 December 1999, about 20 months after the end of the Waini Peninsula soil fires, covering Path 232, Row 54. The U.S. Geological Survey EROS Data Center provided the scene in "GeoTIFF" format, which is readily displayed with standard Geographic Information System (GIS) software, Universal Transverse Mercator (UTM) projection for Zone 21 north, central meridian -57º, and processed with systematic geometric and radiometric corrections. Landsat ETM$^+$ images have a spatial resolution of approximately 28.5 meters in visible and infrared bands. The scene was cropped to the area of interest, 59º30' to 59º49’30''W and 8º12' to 8º25’N, approximately 35.8 kilometers x 25.2 kilometers covering about 902 km^2, including appoximately195 km^2 of the Waini Peninsula. For initial field work, a false color composite

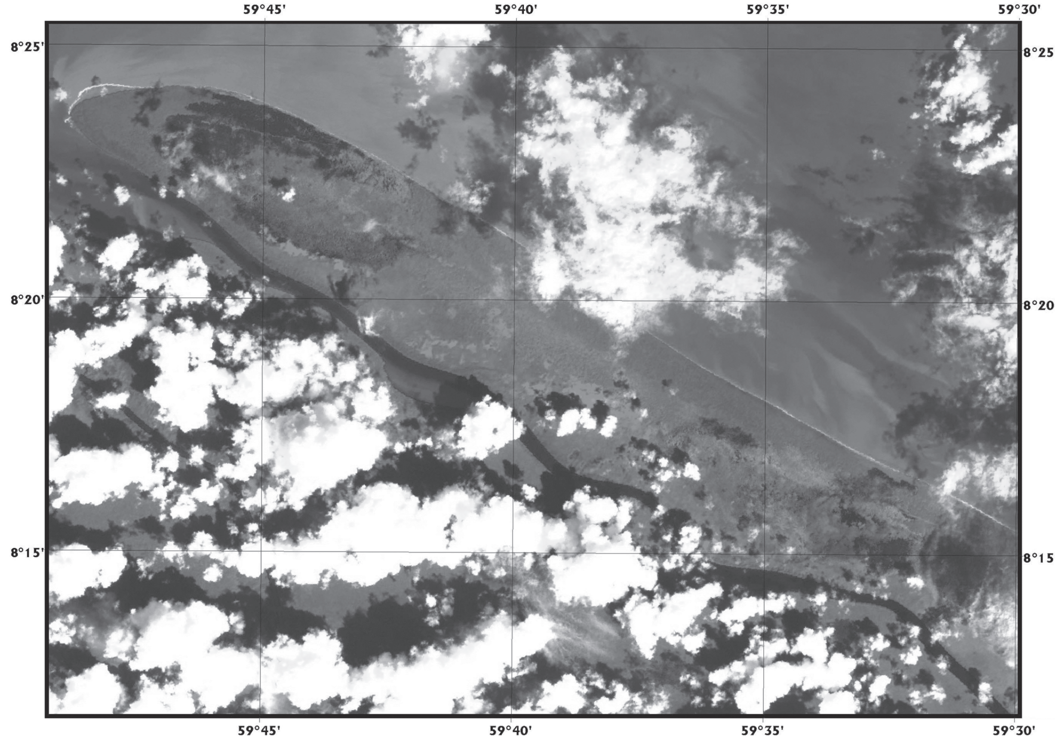


Figure 1.9. Landsat ETM+ display of a portion of the scene for path 232 row 54, 3 December 1999, cropped to show the upper Waini Peninsula. The clouds in the lower left portion of the view were typical for most areas of land of the full scene. The Almond Beach burn near Waini Point was much more distinct in false color composite (FCC) display than the Kamwatta burn at lower right, which was characterized by less open water and more recovering vegetation; the Kamwatta area of the scene was subject to confusion from nearby clouds and cloud shadows.

(FCC) scene was composed in ArcView 3.3 (ESRI 2002), using band 2 (green, 0.53 - 0.61 µm), band 3 (red, 0.63-0.69 µm), and band 4 (near-infrared, 0.78-0.90 µm) (Figure 1.9, in grayscale).

Japanese Earth Resources Satellite (JERS-1) Synthetic Aperture Radar images from October 1995 were obtained from the Global Rain Forest Mapping Project (2001). The image was registered in ArcView by creation of a 'world file' (ESRI 2002) with coordinates of the point of origin and the fraction of a degree represented by one pixel on each axis. Features visible in the JERS image (Figure 1.10) served as an additional guide for delineation of pre-burn plant community boundaries.

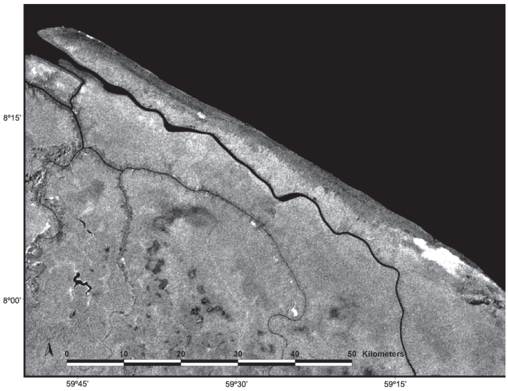


Figure 1.10. JERS-1 radar image of the entire Waini Peninsula, acquired in October 1995, resolution 3 arc-seconds, about 95 meters at the latitude of this image. On the coastal plain, dark areas primarily represent open water and smooth moist surfaces, while areas of high return represent distinct settlements or areas of flooded, intact forest, which is the likely interpretation along the coast near the right side of the image. Hills are visible along the center of the left edge, near the Northwest District's administrative seat, Mabaruma.

Ground-truth transects were made across the Waini Peninsula in and near the Almond Beach burn in April and October 2001. Two transects were made through central parts of the burn, and two others were made near each end of the burn (Figure 1.11). Transects were spaced approximately 2.5 to 3.5 km apart. Transect A crossed the Peninsula near its northwestern end, in unburned forest. Transect B was made from the vicinity of Almond Beach camp across burned swampland. Transect C started just east of the Almond Beach school, crossing burned swampland and intact forest near the Waini River. Transect D was intended to pass beyond the southeastern end the Almond Beach burn, however was adapted in the field to coincide with a boundary of the burn. Transect E was a shorter exploration made beyond the southeastern limit of the Almond Beach burn.

Along the transects at localities with distinctive vegetation types, vegetation transitions, burn boundaries, or plant collection localities, coordinates were recorded using a GPS receiver, plant species at those locations were noted. Voucher specimens were collected wherever a species was previously uncollected or field identification was uncertain. Transects B and C were each traversed twice, due to the time required to initially clear or mark routes.

A post-burn profile was composed to provide a visual representation of plant communities across the Almond Beach burn at transect C. The first tropical forest survey utilizing profiles was apparently performed in Guyana (at that time British Guiana) by Davis and Richards (1933), detailing a mixed lowland forest on Moraballi Creek near the Essequibo River; for that study all trees along a narrow transect were cut and measured as the profile was drawn. While Ellison (2002) argued that mangrove community profiles are subjective representations of structure and zonation unless they are linked to quantitative data, generalized

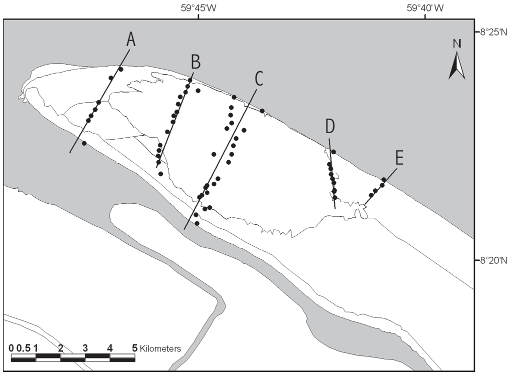


Figure 1.11. Positions of transects across the Almond Beach burn (B, C, D) and outside of the burn (A, E) on the Waini Peninsula. Points indicate locations of GPS readings where plant community information was gathered.

profiles have been of value for advancing concepts of variability among mangrove zonation patterns (Tomlinson 1986), and they can been useful for conveying system structure to policy makers and for providing background for later studies. Lindeman (1953) used profile diagrams for his descriptions of coastal vegetation in Surinam, along transects from 2 to 16 kilometers in length.

Pre-fire plant communities were manually drawn by on-screen digitization of polygons (Duke et al. 2003; Wilton & Saintilan 2000) in ArcView 3.3 GIS (ESRI 2002), following patterns visible in the 3 December 1999 Landsat ETM$^+$ FCC image, and in individual bands, combined with transect field data and observations. Patterns from the JERS-1 imagery assisted in community delineation, particularly in burned areas. Mangrove swamp areas were divided between pure *Avicennia* L. swamps, found near the coast, and Mixed Mangrove swamps with both *Avicennia* L. and *Rhizophora* L. trees. Non-mangrove freshwater swamp areas were divided between *Ficus* L.-*Euterpe* Mart. swamps and *Pterocarpus* dominated Mixed Freshwater swamps found closer to the Riverine Mangroves.

To estimate burned areas, Landsat ETM$^+$ bands 3 (red) and 4 (near infrared) were used in combination with data and observations from transects across the peninsula. Since different qualities of burned swamp could be discerned in the red and infrared bands, a separate delineation was performed for each band, using manual, on-screen digitization of polygons (Wilton & Saintilan 2000) with ArcView software (ESRI 2002). A linear contrast stretch was performed for each band, until boundaries between burns and intact forest, as observed in the field, became discernable. Polygons of the burn boundaries were digitized using the adjusted band images as a guide. A union of the band 3 and band 4 delineations was made to form polygons of total impacted areas in the Almond Beach and Kamwatta burns. Totals for burned areas were tabulated by vegetation type in ArcView 3.3, by intersection of polygons for plant communities with those for burned areas.

RESULTS

Plants of The Waini Peninsula

A total of 118 names of plant species documented for the Waini Peninsula are included in Appendix 2, with a synonymy. A more detailed analysis of the composition of the plants documented for the Waini Peninsula is presented in Chapter 2.

Plant Communities on the Waini Peninsula

Transect A crossed unburned, young *Avicennia* swamp forest with some areas of dense *Laguncularia* C.F.Caertn. shrub understory, into mixed mangrove forest with mature *Avicennia* and *Rhizophora* trees and often very dense *Acrostichum* L. fern understory, and finally into Riverine Mangrove forest dominated by *Rhizophora racemosa* G.Mey.. Transect B crossed through low elevation burned *Avicennia* forest, into burned Mixed Mangrove forest regenerating with broad expanses of *Typha* L. or shallow water and vines, and finally burned Mixed Freshwater forest, up to the Riverine Mangrove forest. Transect C ran through burned young *Avicennia* forest, across the largest chenier encountered in the area, into burned Mixed Mangrove forest, up a very shallow slope to the area of the highest elevations with a small *Roystonea* D.F.Cook. community, to a broad area of burned Mixed Swamp forest with some *Ficus* trees and many dead *Euterpe* palms, and often shallow water. Beyond that zone, elevation slowly decreases until near the river soil moisture apparently discouraged fires in 1998. There a belt of unburned Mixed Swamp forest was encountered, dominated by *Pterocarpus officinalis* Jacq. with occasional, extremely large *Avicennia* trees, and finally a band of Riverine Mangrove swamp up to 400 meters wide along the Waini river, dominated by *Rhizophora racemosa*. Transect C is detailed with a vegetation profile in Figure 1.12.

During the course of the transects it became evident that some areas not easily discernable in the Landsat FCC image had been burned.

Opposite - Figure 1.12. Plant community profile diagram across the Waini Peninsula at the Almond Beach burn.


NE
Beach
0 km
0.5 km
Chenier
1 km
"Palm Hill"
1.5 km
2 km
2.5 km
3 km
3.5 km
4 km
SW
4.5 km
5 km
5.3 km
Waini R.
Ficus
Roystonea
Rhizophora
Avicennia
Avicennia dead
Pterocarpus
Nypa
Laguncularia
Avicennia - fallen
Montrichardia
Typha
Acrostichum
Vines
Herbs

Transect D, on the southeastern end the Almond Beach burn, unexpectedly coincided with that boundary of the burn, which had been expected to be well outside of the burned area. It was determined at that time to follow the boundary and record characteristic points with GPS to provide additional information for delineation of burns. Transect E was a shorter investigation started beyond the southeastern limit of the Almond Beach burn. In that area of Mixed Mangrove swamp, progress on foot was slow, in part because of frequent *Rhizophora* prop-roots and occasional treefall disturbances with dense understory of *Acrostichum* ferns and vines. No transects were made into the Kamwatta burn. Because of confusion with nearby clouds on the Landsat FCC image, the extent of that burn was not fully apparent until a short excursion was made for about 1 kilometer into the area.

A map of approximate pre-burn plant communities of the Waini Peninsula is shown in Figure 1.13. Total areas are given by community type in the first column of Table 1.1.

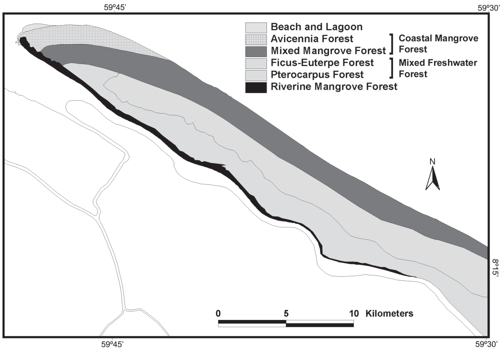


Figure 1.13. Plant communities of the Waini Peninsula prior to fires, estimated from the 3 December 1999 Landsat ETM$^+$ image and transects on the ground.

The area of *Avicennia* mangrove swamp near the tip of Waini Peninsula was approximately 11.7 km^2. Areas of three other plant community types were similar, with 56.9 km^2 of Mixed Mangrove swamp, 59.9 km^2 of *Ficus-Euterpe* swamp, 55.3 km^2 of Mixed Freshwater swamp, and 10.4 km^2 of Riverine Mangrove swamp. The small population of *Roystonea* palms was not discernable in satellite imagery, possibly due to minor cloud cover in the vicinity. The *Roystonea* population was estimated during field visits to cover less than 0.1 km^2.

- *Beaches*

Beach vegetation nearest to the ocean was composed of a few specialized vine, herb, and small shrub species (Figure 1.14), all of which are common along Neotropical coasts. Dominant beachfront vines were *Ipomoea pes-caprae* (L.) R. Br., *Canavalia rosea* (Sw.) DC., and *Passiflora foetida* L., all of which occurred out to the high water line. The common herb on the fore-beaches was *Sesuvium portulacastrum*

Figure 1.14. Typical Beach vegetation on the Waini Peninsula, with *Sesuvium portulacastrum* in the foreground and *Ipomoea pes-caprae* behind. Cultivated coconut (*Cocos nucifera*) trees are present in the background. The coarse texture of the shell substrate is apparent.

Table 1.1. Areas of Waini Peninsula plant communities in the Almond Beach and Kamwatta burns from manual delineations. Beach and lagoon areas were not affected by fires.

Forest type	**Waini Pre-burn**	**Almond Beach Burn**	**Kamwatta Burn**
Avicennia forest	11.7 km^2	5.2 km^2	*none*
Mixed Mangrove forest	56.9 km^2	15.7 km^2	5.5 km^2
Riverine Mangrove forest	10.4 km^2	*none*	*none*
Pterocarpus forest	55.3 km^2	2.9 km^2	5.4 km^2
Ficus-Euterpe forest	59.9 km^2	10.4 km^2	19.6 km^2
Total	**194.1 km^2**	**34.1 km^2**	**30.5 km^2**

(L.) L. Shrubs included *Conocarpus erectus* L. (a mangrove associate), *Talipariti tiliaceum* (L.) Fryxell (= *Hibiscus tiliaceus*L.), *Thespesia populnea* (L.) Sol. ex Corrêa, and *Caesalpinia bonduc* (L.) Roxb. These were occasionally interspersed with juveniles of mangrove species, particularly *Laguncularia racemosa* (L.) C.F. Gaertn. and *Avicennia germinans* (L.) Stearn. Apparently the shallow water over mud flats, the shell margins, or the high silt content of the coastal water are not conducive to the establishment of *Rhizophora* seedlings immediately along the coast (Pons & Pons 1975), although *Rhizophora* propagules were sometimes found stranded on the shell sand of the forebeach.

During field work, the beach ridges of the Waini coast ranged from a few meters to over 150 meters in width. Where these were sufficiently wide, somewhat higher diversity of shrubs and trees was found on the back beach towards the mangrove swamps, with species including *Spondias mombin* L., *Annona glabra* L. and *Morinda citrifolia* L. Just below the surface, the wider beach ridges contained lenses of nearly fresh water with salinity as low as 1 psu (Hollowell, unpublished). Because of available fresh water, the back beach was in places a site of agricultural activities. The dominant crop grown for trade was *Cocos nucifera* L. (Coconut), which grows well in the shell substrate over rich mud. *Manihot esculenta* Crantz (Cassava) is also commonly cultivated for community use, along with a variety of garden vegetables and ornamentals. Naturalized *Carica papaya* L. (Pawpaw, Papaya) was found frequently on beach ridges, usually 10 or more meters from the shore. *Terminalia catappa* L. (East Indian Almond) is a naturalized tree found on both beach ridges and higher cheniers farther inland. The small tree or shrub *Morinda citrifolia* L. (Noni), an Asian native widely known for medicinal values, is scattered in the back beach up to the margins of the mangrove swamp.

- *Coastal Mangrove Swamps*

Mangrove swamps are common along nearly all tropical shorelines where wave energy is low. They are dominated by woody plants with a tolerance to salt water (Tomlinson 1986). While mangrove species belong to several plant families, they have all developed structural and physiological adaptations to the salinity, waterlogged soils, and dispersal and establishment challenges of the coastal environment (Ball 1988). Adaptations include roots that function to exchange air and provide support in waterlogged soils, a capacity to exclude or secrete salt, and fruits that germinate at least partially while on the parent or during dispersal by water. The number of mangrove species is several times higher in the Western Pacific than the Atlantic region.

The Coastal Mangrove swamps were divided into two subsets, *Avicennia* forest and Mixed Mangrove forest (Figure 1.13). Swamp areas nearest to the ocean were most often dominated by *Avicennia germinans* (L.) Stearn (Black Mangrove, Courida) which reached 30 meters in height (Figure 1.15). Where the coastline has been accreting, *Avicennia germinans* is usually the first species to colonize a mudflat, and where monospecific stands of this species are found near the ocean, the trees often fell within a narrow range of intermediate diameters, suggesting that they might be the first generation on new land. A large area of this type occurred at the northwest end of the Waini Peninsula, including the swamp in the vicinity of Almond Beach. In the Mixed Mangrove swamp *Avicennia* was found with *Rhizophora*

Figure 1.15. A pure *Avicennia* Coastal Mangrove swamp near Waini Point, showing the dense carpet of pneumatophores. Trees in this area were measured as up to about 50 cm diameter and 32 meters in height. The pneumatophores allow gas exchange for the roots. Most of these trees lean to the west due to the soft soil and the prevailing trade winds.

mangle L. (Red Mangrove, Mangro) trees which may also reach heights of 30 meters or more. Farther to the southeast and inland from Almond Beach, the coastal forests are presumably older, and more diverse.

The third major mangrove species of the Neotropics, *Laguncularia racemosa* (L.) C.F. Gaertn. (White Mangrove, Kayara), does not often reach the stature of *Avicennia* or *Rhizophora* trees in the Guianas, but it was common as an understory shrub or treelet, as well as along the margins of coastal lagoons. *Laguncularia* has been observed in Guyana and other countries to be a very successful colonizer of swamps following disturbances (Baldwin et al. 2001; Delgado et al. 2001; Elster 2000; Roth 1992; Woodroffe 1983). The final dominant component of the mangrove swamp understory included two species of *Acrostichum* (Mangrove Fern, Monkey Bush). Those are similar, large terrestrial ferns; *Acrostichum aureum* L. was common throughout the mangrove swamps, while *Acrostichum danaeifolium* Langsd. & Fisch. is occasional in more inland locations. Either can become very dense in Mixed Mangrove swamp. The mangrove associate *Conocarpus erectus* L. was found on chenier ridges within the swamps and sometimes in the shrubby thickets along coastal lagoons and back beaches. As is typical for mangrove swamps around the world, the *Avicennia* swamps near the coast have a fairly open understory (Janzen 1985; Lugo 1986; Snedaker & Lahmann 1988), allowing easy walking, particularly during dry seasons.

Mangrove swamps along Guyana's Atlantic coast are well developed where they have been undisturbed by agriculture or urban development (Bacon 1990; Vann 1959, 1969; Wells & Coleman 1981). In places beach ridges separate swamps from tidal inundation, although waves at high tide often wash over narrower beach ridges and directly into the mangrove swamp. Those swamps behind beach ridges can also be referred to as occluded swamps, due to their separation from the sea. Such conditions have been documented in a few cases in the both the Neotropics (Lugo 1981; Stoddart et al. 1973; Vegas Vilarrúbia & Rull 2002; Woodroffe 1983) and the old world (Fosberg 1947; Steenis 1984; Woodroffe 1988). Within the classification of Lugo and Snedaker (1974) those swamps fall into the category of Basin Mangrove, and in some areas fit the classification of Hammock mangrove forest, a category added by Lugo (1980). Inlets into tidal streams are infrequent on the Waini Peninsula and can become blocked by sediment deposits, forming lagoons behind beach ridges.

The Coastal Mangrove swamps of the Guianas do not conform to the zonation pattern typically described for the low sediment swamps of the Caribbean, in which *Rhizophora* occupies the position closest to the sea, with *Avicennia* as a back mangrove species followed by *Laguncularia* and *Conocarpus* as species of the transition to freshwater swamp or upland. A pattern of zonation similar to that on the Waini Peninsula was also reported for the Wia Wia Bank in northeastern Surinam by Lindeman (1953), though he noted an absence of *Conocarpus*. That arrangement was also confirmed for French Guiana by Fromard (1998). There *Laguncularia* was reported to be at least as common as *Avicennia* in the pioneer coastal communities, though *Avicennia* still became the dominant species of mature coastal swamps.

- *Mixed Freshwater Swamps*

Towards the interior of the Waini Peninsula, the Coastal Mangrove swamp plant community graded into Mixed Freshwater swamp. The length of that transition varied but usually spanned one to two kilometers. In that zone, occasional *Avicennia germinans* (L.)Stearn trees and *Rhizophora* trees persist, usually as large individuals. The Mixed Freshwater swamp group was divided into two subsets, *Ficus* - *Euterpe* forest and *Pterocarpus* forest (Figure 1.13), which was mixed with several other tree and understory species. *Ficus* spp. trees were a significant component of the *Ficus-Euterpe* portion, particularly large *Ficus amazonica* (Miq.) Miq., of which several individuals survived the 1997-1998 soil fires in places where all other trees were killed. Individuals of *Ficus eximia* Schott, a similar member of the *Ficus citrifolia* group may also occur on the Waini Peninsula. In the center of the peninsula, parts of the swamp had been dominated by *Euterpe* cf. *oleracea* Mart. (Manicole palm) with scattered *Ficus*. In sections surveyed, all *Euterpe* trees had been killed by the recent fires, leaving numerous fallen trunks. After the fires those areas were very open and dominated by a mosaic of vines, *Typha*, sedges, and various herbs. During wet periods, scattered shallow pools with floating vegetation were common there.

The species richness of the Mixed Freshwater swamp increased in the *Pterocarpus* forest zone up to the transition to Riverine Mangrove swamps along the Waini River, in forests where *Pterocarpus officinalis* Jacq. (Corkwood) was common. Just before entering the Riverine Mangrove swamp, there was a belt dominated by *Pterocarpus* mixed with occasional, extremely large *Avicennia germinans* trees, some of which measured over two meters dbh (Figure 1.16); small *Avicennia* trees or seedlings were not common in that area. Some of these exceed the size of *Avicennia* trees at Maranhão, Brazil, reported by Lacerda et al. (2002) to grow in excess of one meter dbh. Fromard (1998) described a similar species zonation in French Guiana, moving inland up the rivers from Coastal Mangroves towards *Euterpe* and *Pterocarpus* forest with fewer, but very large, *Avicennia* and *Rhizophora* trees, which he attributed to increasing influence of riverine rather than tidal hydrology.

Figure 1.16. Mixed Freshwater forest near the transition to Riverine Mangrove forest. This *Avicennia germinans* tree was measured at over 2 meters dbh, though it was not measured above the buttresses. *Pterocarpus officinalis* trees were also found in this zone near the Waini River.

The trees *Machaerium lunatum* (L. f.) Ducke, *Inga ingoides* (Rich.) Willd., *Zygia latifolia* (L.) Fawc. & Rendle and *Clusia palmicida* Rich. ex Planch. & Triana were occasional in the Mixed Freshwater swamps, particularly in *Pterocarpus* zones. There the understory included *Cassipourea guianensis* Aubl., *Ilex guianensis* (Aubl.) Kuntze and *Malouetia tamaquarina* (Aubl.) A. DC., as well as several species of ferns including *Blechnum serrulatum* Rich., *Pteris pungens* Willd., and *Nephrolepis biserrata* (Sw.) Schott. Vines and lianas noted in those swamps included *Monstera adansonii* Schott, *Syngonium podophyllum* Schott, and *Hippocratea volubilis* L. as well as several vines that had become dominant in the burned swamp including *Cissus verticillata* (L.) Nicolson & C.E. Jarvis, and *Cydista aequinoctialis* (L.) Miers. While trees in the Coastal Mangrove swamps were host to few epiphytes, probably due to salinity from the ocean, several epiphytic species were found in the Mixed Freshwater swamps, including the bromeliads *Aechmea nudicaulis* (L.) Griseb. and *Guzmania lingulata* (L.) Mez, the cactus *Rhipsalis baccifera* (J.S. Muell.) Stearn, and the orchids *Epidendrum ciliare* L. and *Prosthechea aemula* (Lindl.) Higgins. Some epiphytic species were recorded in the Mixed Freshwater forest only as survivors on the branches of fallen trees killed by fires, including the cactus *Epiphyllum phyllanthus* (L.) Haw. and the orchid *Trichocentrum lanceanum* (Lindl.) M.W. Chase & N.H. Williams.

An unexpected feature of the Mixed Freshwater swamps was the isolated population of *Roystonea oleracea* (Jacq.) O.F. Cook, consisting of perhaps 120 scattered individuals of all sizes (Figure 1.17). That population survived the 1998 soil fires while most surrounding vegetation was killed except for a few large *Ficus* trees. Prior to the documentation of that population, no species of the genus *Roystonea* had been recorded in the Guianas outside of cultivation (Zona 1996). The remote

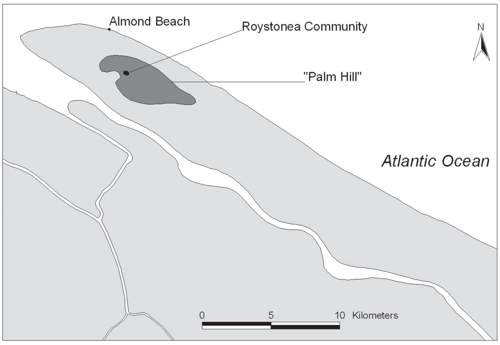


Figure 1.17. Location of the *Roystonea oleracea* community on the Waini Peninsula, within the approximate area of the elevated central zone of the peninsula that became known as “Palm Hill.” The initial excursion to the site was made on 8 April 2001 (Palm Sunday).

location of the population strongly suggested that it was not likely planted by people.

- *The Riverine Mangrove Swamps*

The swamps that line the tidal Waini River are inundated twice daily with brackish river water, since there are no barriers to tides similar to the beach ridges isolating many Coastal Mangrove swamps. That allows comparatively unimpeded dispersal of mangrove propagules in this zone, which may be partly responsible for the dominance of *Rhizophora racemosa* G. Mey., which fringes the Waini River and extends inland on the soft, muddy substrate to the tidal limit. That species is very similar to *R. mangle* in vegetative appearance, having similar conspicuous prop and aerial roots and indistinguishable leaves and bark. It differs distinctively from *R. mangle* in having 30 to 60 flowers per inflorescence, as compared to 2 to 3 for *Rhizophora mangle*; in having buds with obtuse apices as opposed to buds with acute apices in *Rhizophora mangle*; and in having propagules with much longer hypocotyls extending from the viviparous fruits, up to 50 cm. in length as opposed to hypocotyls up to 20 cm in length in *Rhizophora mangle* (Gray 1981). *Rhizophora racemosa* trees tend to have more aerial roots extending from higher branches to the water’s surface. Those two *Rhizophora* species have been considered by some to form the hybrid *Rhizophora* x *harrisonii* Leechm., which has been ascribed to similar brackish riverine habitats and is supposedly intermediate between the two species in reproductive morphology (Gray 1981; Tomlinson 1986). In practice, it was difficult to distinguish that putative hybrid from *R. racemosa*, and some specialists consider it to be synonymous with *R. racemosa* (Duke et al. 2001). In several descriptions of riverine mangroves in the Guianas, *R. racemosa* has been unmentioned, with only the name *R. mangle* used, although that is almost certainly inaccurate.

Figure 1.18. Riverine Mangrove forest dominated by *Rhizophora racemosa*. Some *Nypa fruticans* palms were in the understory (center background) and some fronds of the mangrove fern *Acrostichum* are visible in the foreground.

The Riverine Mangrove swamp understory was, in places, moderately dense with *Rhizophora* saplings and *Acrostichum aureum* ferns (Figure 1.18). The non-native mangrove palm *Nypa fruticans* Wurmb. was also common in the Riverine Mangrove swamp, sometimes in dense patches along river margins and often as an occasional component of the understory. Upriver, around 59° 30' W, *Nypa* was no longer present. At that point *Rhizophora* trees were also infrequent along the river margin, although they were observed as far up the Waini River as its confluence with the Barama River, and were seen occasionally on the Baramanni River. Along some segments of the Waini River the roots of *Rhizophora racemosa* were found covered with the red alga *Bostrichia* and occasionally with barnacles. Farther up the river, where the water became less brackish, freshwater swamp tree species including *Pterocarpus*, *Mora* Benth., *Machaerium* Pers., *Inga* Mill., *Euterpe* and *Pachira* Aubl. were increasingly common along the banks.

Burned Areas

The manual delineation using the Landsat red band (3) included 27.4 km^2 of burned vegetation at Almond Beach and 28.8 km^2 of burned vegetation at the Kamwatta (Figure 1.19). The major result of the fires detected in band 3 was apparently bare soil, which reflected red portions of the spectrum and appeared as light areas of the image. Using Landsat band 4 (near infrared), the manual delineation included 26.5 km^2 of burned vegetation at Almond Beach and 22.6 km^2 of burned vegetation at the Kamwatta site (Figure 1.20). That band was useful for detecting vegetation (high reflectance) and open water (low reflectance). The burned area totals were calculated by a union of the red and near infrared band results. The intersection of the total burns with the plant communities classifications provided areas of each community that were impacted. Totals burned areas for each plant community type and locality are given in Table 1.1. It was estimated that 34.5 km^2 of the forests in the Almond Beach area were burned, and 30.5 km^2 of the forests in the Kamwatta area were burned, for a total of 64.6 km^2 of burned forest for the entire area of interest on the Waini Peninsula (Figure 1.21). Areas of burns detected with each of the two Landsat bands are listed by locality in Table 1.2.

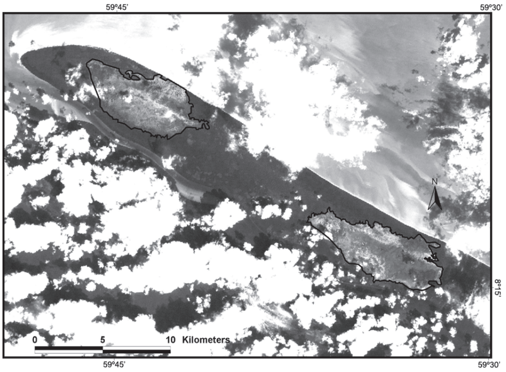


Figure 1.19. Manual delineation of burned areas using Landsat ETM$^+$ band 3, red.

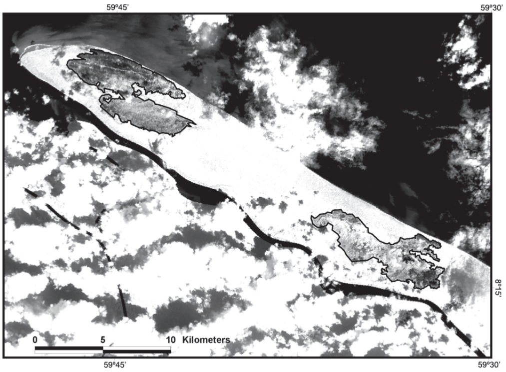


Figure 1.20. Manual delineation of burned areas using Landsat ETM$^+$ band 4, near infrared.

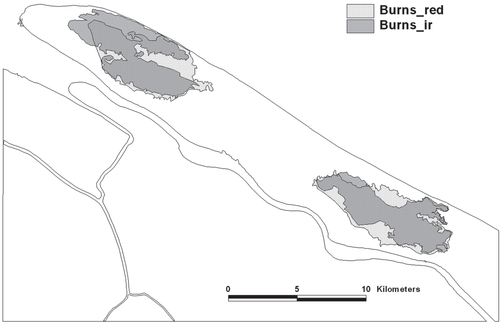


Figure 1.21. Combined areas of manual delineations of burns using the red and infrared bands from the December 3 1999 Landsat ETM$^+$ image. The total burned area was measured as 64.58 km^2.

Table 1.2. Manual burn delineation results by burn area and bands 3 (Red) and 4 (Near Infrared), for the Landsat ETM$^+$ image of 3 December 1999.

Band / area	km^2
IR Almond Beach	26.4
IR Kamwatta	21.9
RED Almond Beach	27.4
RED Kamwatta	28.7

The fires left large areas with few surviving mangrove trees to supply propagules for regeneration. After that large-scale disturbance, limitations on dispersal would likely retard recolonization by some species. Species that are wind or animal dispersed might be favored over those dependent on water dispersal. Additionally, variations of soil salinity levels would further influence the species that might become dominant. There has been substantial variation in initial recovery of burned areas.

In many locations, the initial regrowth after the fires in Coastal Mangrove swamp and Mixed Freshwater swamp was dominated by vines, most notably *Ipomoea tiliacea* (Willd.) Choisy, *Mikania micrantha* Kunth, *Cydista aequinoctialis* (L.) Miers and *Entada polystachya* (L.) DC. In places the tangle of vines became thick enough to walk upon nearly a meter above the ground (Figure 1.22). Other broad areas were dominated by dense, sometimes monospecific stands of herbaceous species such as *Acrostichum* ferns (Figure 1.23) or *Typha domingensis* Pers. (cattails) (Figure 1.24).

Figure 1.22. Heavy growth of vines three years after fires, in the former *Euterpe* swamp. The dominant species was *Ipomoea tiliacea*, which grew over tall stalks of *Montrichardia linifera*. In the distance nearer the Waini River was unburned Mixed Freshwater forest is visible, dominated by *Pterocarpus officinalis* interspersed with very large *Avicennia* trees.

Figure 1.23. Burned Coastal Mangrove forest near Kamwatta Beach, approximately three years after fires. This area had become dominated by dense *Acrostichum* ferns.

Figure 1.24. An expanse of *Typha* in burned *Avicennia* Coastal Mangrove forest, three years after the fires. It was estimated that this *Typha* stand covered up to 2.6 km2, starting approximately 1.4 km behind the Almond Beach camp, extending towards Waini Point.

Another distinctive vegetation type visible on Landsat ETM$^+$ imagery was a narrow band of dense herbaceous vegetation found in a few spots between burns on former *Ficus*-*Euterpe* swamp and Mixed Freshwater swamp near the river. *Acrostichum* ferns and the large, herbaceous aroid *Montrichardia* grew thickly there, mixed with several species of vine (Figure 1.25). Those areas were characterized by high

Figure 1.25. Vegetation in the belt of dense *Montrichardia* (broad leaves) and *Acrostichum* ferns near unburned Mixed Freshwater forest near the Waini River. Several months later this area was overrun with vines (pictured: Keith David).

reflectance in both infrared and red bands.

Burned areas in the pure *Avicennia* swamp of the northern portion of the Waini Peninsula were investigated in more detail with ecological plots (see Chapter 4). Those swamps suffered nearly full tree mortality and have undergone slow early regeneration. Initially, in wet seasons they were covered with deeper surface water than neighboring unburned areas, probably resulting from a combination of decreased transpiration and lowered elevation from combustion of the upper organic soil layer. When surface water was present they were dominated by floating vegetation, first *Lemna aequinoctialis* Welw., which was followed after the first year by *Limnobium laevigatum* (Humb. & Bonpl. ex Willd.) Heine (Figure 1.26). Such areas that were covered with floating plants were not distinguishable from forest in band 3 of the Landsat images, while sparse vegetation and bare soil were apparent. Areas of open, standing water were obvious in the near infrared band (4) due to very low return.

Fig. 1.26 Burned area in the pure *Avicennia* swamp of the northern portion of the Waini Peninsula. When surface water was present they were dominated by floating vegetation, first *Lemna aequinoctialis* Welw., followed by *Limnobium laevigatum* (Humb. & Bonpl. Ex willd.) Heine.

Later in those areas, shrubby *Laguncularia racemosa* (L.) C.F. Gaertn. trees became established; that species is often considered the most disturbance adapted of Neotropical mangrove species (Ball 1980; Elster 2000; Elster et al. 1999; Roth 1992; Woodroffe 1983), as it has the smallest, and so presumably most easily dispersed, propagules.

In areas that were not apparent as obviously burned in the FCC image but were actually recovering from fires, most were lightly to moderately covered with herbaceous vegetation including vines, *Typha*, and *Acrostichum*, which reflected adequate near-IR (band 4) to make them difficult to distinguish from undisturbed vegetation. Most of those areas were also slightly elevated and not covered with standing water or with highly saturated soils that contribute to low return in the near-IR.

The Kamwatta burn was the subject of limited field work, as it was not initially discerned in the Landsat FCC, perhaps due to limited areas of standing water, and confusion with adjacent areas of clouds and cloud shadows in the far southeastern part of the view. Nonetheless, manual delineation of the Kamwatta burn using separate bands 3 and 4 was practicable and consistent with preliminary field investigations in the area. In the future it would be useful to conduct additional field investigations in that area south of Kamwatta Beach to determine if fires had occurred there.

Plant Collections of Interest

Some plant collections made during field work were of particular interest because they represented new information on the ranges of species. In the first section, collections from the Waini Peninsula are covered, followed by collections made elsewhere in the Northwest District.

- *On the Waini Peninsula:*

Rhizoclonium africanum Kützing, Cladophoraceae, det. J. Norris, 2000: Hollowell, Arjoon and Chin 255, collected 4 November 1998. This algal species is newly recorded for the Guianas. It is known from mangrove swamps in Brazil, Central America, the Caribbean, and the west coast of Africa. Through introduction it is nearly pantropical in mangrove swamps (Guiry & Nic Dhonncha 2004). The collection was made just behind the beach ridge approximately 4 kilometers southeast of Waini Point. *Rhizoclonium* was collected on pneumatophores of *Avicennia* trees, and was very common in the wetter parts of the Coastal Mangrove swamps near the beach ridges.

Although green algae are photosynthetic protists rather than true plants, this is listed because the study of algae is typically grouped within the discipline of botany.

Amaranthus australis (A. Gray) J.D. Sauer, Amaranthaceae, det. T. Hollowell, 2001: Hollowell, A. James and Savory 352, collected 12 May 2000. This was apparently the second collection for Guyana; the other known collection was M.S. Grewal and H. Lall 305 (held at Utrecht Herbarium), from the Shell Beach area in 1977. The species is also known in the Guianas from two collections made in French Guiana and two collections made in Surinam (R.A. DeFilipps, pers. comm.). This collection was made to the southeast of Kamwatta Beach (see Figure 1.2), in open water of scrubby mangrove swamp that was possibly affected by a small fire around 1992 (Audley James, pers. comm).

Nypa fruticans Wurmb., Arecaceae, det. T. Hollowell, 1997: Hollowell et al. 213, collected 16 June 1997. This was the first known South American voucher for this Asian mangrove palm, collected along the banks of the Mora Passage between the mouth of the Waini River and the Barima River (Figure 1.2). *Nypa* is a monotypic genus and is unusual among both mangroves and palms because of its dichotomously branching, rhizomatous form (Tomlinson 1986; Tralau 1964); only the fronds and reproductive structures of *Nypa* extend above the riverbank mud. *Nypa* is common in Riverine Mangrove swamps along the tidal Waini River, Barima River, and Mora Passage. This species may be spreading in the Northwest District, displacing some native *Rhizophora racemosa* trees. *Nypa* fruits have been reported stranded on beaches in Trinidad (Bacon 2001). Plants have been recorded on the Caribbean coast of Panama (Duke 1991), and *Nypa* has become a widespread exotic species in the Niger Delta (Sunderland & Morakinyo 2002). It has long been utilized in Asia for many purposes, particularly thatching, but it has only rarely been observed in use in Guyana.

Roystonea oleracea (Jacq.) O.F. Cook, Arecaceae, det. T. Hollowell, 2002: Hollowell and Hinds 593, collected 21 October 2001. This was apparently the first record of native *Roystonea* for the Guianas. It was collected in fruit from the isolated population midway across the Waini Peninsula, with an elevation of 5-10 meters above sea level. It was composed of 50-60 mature trees up to 20 meters high, with a number of juvenile palms present (Figure 1.27). These palms may have been able to survive fires because palm cambium tissues are protected by their internal position (Cochrane 2003). The species was known from Venezuela including a few localities in Delta Amacuro and Bolívar states, and from Colombia. Some of those populations have been reported as native (Zona 1996). *Roystonea oleracea* also occurs in coastal swamps of Trinidad and Tobago (Bonadie 1998), and Barbados (Zona 1996), apparently in slightly elevated locations similar to that of the Waini Peninsula population. Species of *Roystonea* have been cultivated in cities and towns of the Guianas, but the Waini Peninsula population occurred far from any settlement and more than 20 kilometers from Mabaruma, the nearest town with cultivated *Roystonea*.

Fig. 1.27 The first native population of *Roystonea oleracea* (Jacq.) O.F. Cook found midway across the Waini Peninsula. This isolated population was composed of 50-60 mature trees up to 20 meter high, with a number of juvenile palms present.

Ipomoea violacea L., Convolvulaceae, det. T. Hollowell, 2002: Hollowell 217, collected 17 June 1997. This was possibly the second collection in Guyana of the white-flowered, coastal species. Collected along a narrow beach ridge west of Almond Beach. The other known specimen was collected by G.S. Jenman (collection number 5068, at US as *Ipomoea macrantha* Roem. & Schult.) in 1889 in "coastal lands" of Guyana. It is a widespread coastal vine in the Caribbean and has a nearly pantropical distribution.

Sesbania sericea (Willd.) DC., Fabaceae, det. T. Hollowell, 2000: Hollowell, A. James and Savory 351. Collected along a beach ridge swale to the southeast of Kamwatta Beach. The other known collection of this species from Guyana was made by A.S. Hitchcock (collection number 16626) in 1919, with the collection habitat listed as "among weeds" in the Georgetown Botanic Garden. The species is native to Asia, possibly to Sri Lanka (Howard 1976).

- In the Northwest District of Guyana:

Passiflora amicorum Wurdack, Passifloraceae, det. C. Feuillet, 2000: Hollowell and V. James 383, collected 16 May 2000. Collected on "Kissing Rock" hill north of Mabaruma. This was the first collection of the species for the Guianas; it was previously known only from Bolívar state of Venezuela. This red-flowered vine was growing upon low understory vegetation on a steep hillside, in partial shade.

Werauhia gigantea (Mart. ex Schult. f.) J.R. Grant. (=*Vriesea amazonica* (Baker) Mez.), Bromeliaceae, det. E.J. Gouda, 2002: Hollowell, A. James and V. James 386, collected 16 May 2000. This was apparently the second collection of the species in Guyana, the previous record being from Mabura Hill in central Guyana, collected by R. Ek (1997). This specimen was collected from the branches of a *Rhizophora racemosa* tree overhanging the Aruka River near "Kissing Rock" in the Mabaruma vicinity.

Habenaria sp. nov.? Orchidaceae, det. G. Carnevali, 2002. Hollowell and Hinds 607, collected 22 October 2001. This white-flowered, terrestrial orchid was not matched by other *Habenaria* species (fide Germán Carnevali, CICY) and is awaiting further examination. Collected on terra firme, approximately 100 meters from the Waini River well upriver from tidal influence, near an abandoned sawmill.

Miconia minutiflora (Bonpl.) DC. Melastomataceae, det. F. Almeda and D. Penneys, 2002. Hollowell and Hinds 724, collected 4 November 2001. This was the first collection of the species for Guyana. Specimens of this shrub were collected near the Wauna Oil Palm Estate, a small agricultural experimental station that is located about 12 kilometers to the west-southwest of Mabaruma.

DISCUSSION

These plant collections in Northwest Guyana were carried out as part of ecological research rather than as part of comprehensive plant collection expeditions. Dedicated collection efforts would almost certainly yield additional plant species records for the Waini Peninsula. The number of species records resulting from this fieldwork that were found to be of interest highlights the degree to which the flora of this lowland region has been under-sampled. Compared to remote interior areas in Guyana, the coastal plain of the Northwest District can be easily accessed, and additional field work might be relatively inexpensive for the information yielded. As the state of botanical research in Guyana advances, there will be more effort to understand species distributions at the level of a variety of ecosystems and for smaller political units. While existing specimen data can be modeled with GIS to investigate probable species distributions (Funk & Richardson 2002; Funk et al. 2005; Funk et al. 1999), the needs to verify models and produce more accurate and complete input data will always depend upon plant collecting expeditions. A substantial amount of fieldwork, plant identification, and museum work will be required to provide those specimens and data.

Changes in the global climate could have significant effects on Guyana's coastal ecosystems, changing the types of dominant plant communities. Increased severity of El Niño events could lead to higher fire frequencies on the northwest coast of Guyana, particularly if population pressure grows, increasing the chances of ignition. Guyana's occasional extreme droughts make it vulnerable to incremental forest degradation in which fires can play a key role (Cochrane 2002, 2003). The 1998 fires on the Waini Peninsula had severe impacts on coastal swamp habitats, and effects on forest composition are likely to persist. Fires among the Waini Peninsula mangroves were possibly less anomalous than they initially seem

(Lindeman 1953; Pons & Pons 1975), and may be a large-scale case of fire's role in maintaining mangrove/marsh boundaries, as documented for some other regions (Lugo 1997; Middleton 1999; Odum et al. 1982; Wade et al. 1980). The fires may represent an occasional phenomenon that has occurred in the coastal zone of the Guianas, where mangrove forests become isolated from the ocean, resulting in at least a temporary conversion to non-mangrove communities.

The Waini fires clearly provide a case for the inclusion of fire in the list of disturbances that can affect large areas of mangrove swamp (Finn et al. 1998; Jiménez et al. 1985). It is not known if the fires documented here were the first in those coastal swamps. Sampling for the presence of charcoal at promising sites in central portions of the Waini Peninsula might answer that question. Such potential sites could include areas of slightly higher elevation, and areas that are unusual in older imagery, particularly where breaks in forest are suspected.

The fires have also provided a natural experiment on the effects of disturbance on biodiversity and plant community structure (Field et al. 1998), and present continued opportunities for descriptive and comparative studies of mangroves in northeastern South America. Such studies of pre- and post-disturbance environments create baselines for future monitoring and analyses, and hopefully will encourage anticipation and prevention of fires. An effective mechanism for alerting environmental authorities and prompt field work are needed in rapidly changing, post-fire ecosystems, requiring commitment to conservation, monitoring, and response.

The assembly of background environmental information, including censuses of plant and animal species and mapping, are central to the description, understanding and management of protected areas and other sites of environmental importance. Such baseline biodiversity information is essential for monitoring changes over time, and makes comparative studies between sites possible. Catalogs of species are also a primary tool for utilization of protected areas for education, and it is hoped that the information presented here will be encourage additional scientific, conservation, and educational efforts.

CHAPTER 2

PLANTS OF THE WAINI PENINSULA IN REGIONAL AND GLOBAL CONTEXT

INTRODUCTION

The conservation value of a particular natural site may be derived not just from its species composition, but from the contrast of the species of the site with those of adjacent or related localities. This chapter investigates relationships between the Waini Peninsula flora and the species of nearby plant communities, the species of the Northwest District of Guyana, and the species of the adjacent Venezuelan state of Delta Amacuro. The phytogeographic affinities of the Waini Peninsula flora at the regional, continental, and global scales were explored through classification of species distribution ranges. Those comparisons also served as an example of the state of botanical knowledge on lowland forests in northeastern South America. Comparisons of Waini Peninsula plant communities were made with two coastal plain plant communities in the Northwest District near Santa Rosa, as documented by van Andel (2000a). Comparisons were also made of the Waini and Northwest District floras with the flora of the neighboring coastal Venezuelan state of Delta Amacuro, with the goal of understanding the level of diversity between the sites. This has implications both for the direction of additional basic research and ideally in the design of protected areas in the region. Finally, a regional and global phytogeographic analysis was made for the Waini flora. The questions addressed here include to what degree the flora of the Waini Peninsula is unique in relation to neighboring ecosystems, to all of Guyana, to the Guiana Shield region of northeastern South America, and to broader biogeographic areas. At the larger regional scales, the question is asked whether such coastal plain environments of the Guianas should be considered as part of the Guiana Shield flora or as units of a distinct Neotropical or Caribbean coastal flora. It is of interest whether additional botanical collection activities such as undertaken in this relatively low-diversity region of South America can add significantly to botanical knowledge.

Comparisons of species checklists covering areas of intermediate size have been used recently to analyze similarities and differences among sites that are candidates for protection or under consideration for additional detailed investigations (Clarke & Funk 2005; Clarke et al. 2001a; Kelloff 2002; Kelloff & Funk 2004). That approach relies only upon species presence and absence, allowing what may be an early opportunity for biodiversity analysis. Such qualitative data are frequently the only available information covering large parts of tropical South America. While ecological plot data sets can be very useful for detailed quantitative analyses, they have been available to date for small to moderately sized plots that are widely separated (Condit et al. 2002; Pitman et al. 1999; Pitman et al. 2001). As an alternative, qualitative species list-based data are comparatively easily compiled from existing publications such as regional florulas. Those sources can be augmented by data from the large, though often incompletely utilized reservoirs of information held in the world's herbaria (Funk 2003a, b). An important condition for validity of all scales of comparison is standardization of the biodiversity data utilized. This greatly facilitated by the availability of computerized nomenclatural databases, and for botanical research in particular, nomenclature including complete, linked synonymies. All of these data sources and data quality tools require substantial investment to create, maintain, and apply.

STUDY SITES AND BACKGROUND

The study site on the northern portion of Guyana's Waini Peninsula is described in detail in Chapter 1. Other localities mentioned in the text or from which data were utilized are indicated in Figure 2.1. Additional plant data were obtained or compiled for the sites listed below.

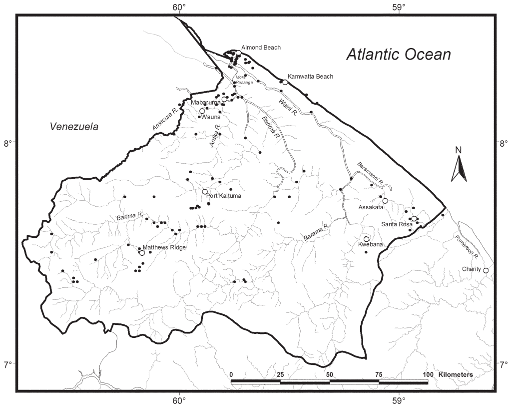


Figure 2.1. The Northwest District of Guyana, showing localities in the text. Georeferenced collection sites from this study and from herbarium specimens are indicated by the symbol •

Quackal and Manicole Plant Communities

The Quackal and Manicole plant communities are coastal plain vegetation types that were studied by van Andel (2000a), who considered them to grade into Coastal Mangrove swamps, making them of interest for comparison with the plant communities of the Waini Peninsula. Van Andel's research sites were located near Santa Rosa (7º41'N, 58º55'W) and Assakata (7º44'N, 59º04'W), in the southeastern portion of the Northwest District (Figure 2.1). She described the Quackal swamp woodland as dominated by *Tabebuia insignis* (Miq.) Sandwith, *Macrosamanea pubiramea* (Steud.) Barneby & J.W. Grimes, and *Symphonia globulifera* L. f. The manicole swamp was dominated by *Euterpe* palm species and was also rich in *Pentaclethra macroloba* (Willd.) Kuntze, *Symphonia globulifera* L. f., and *Virola surinamensis* (Rol. ex Rottb.) Warb. A comparison of the list of species collected from these two areas was also used to enhance the species list formed for the Northwest District.

The Northwest District

The Northwest District covers approximately 19,190 km^2, about 9.5 % of Guyana's total area. Of that area, approximately 1,000 km^2, or 5.5%, of the Northwest is contained within the Waini Peninsula, here considered to span from Waini Point to Baramanni Lake, including most of the district's Atlantic coastline. The 190 km^2 study area on the Waini Peninsula comprises about 1% of the area of the Northwest District. The only large town in the region is the administrative center Mabaruma, adjacent to Port Kumaka on the Aruka River (Figure 2.1). Most of the towns of the district are accessible via its many rivers.

Early major collection expeditions in the Northwest District were undertaken by the Schomburgk brothers and by J.S. de la Cruz. The German brothers Robert H. and Moritz Richard Schomburgk explored the Northwest in 1841, as part of work for the British Government in delineation of the boundaries of British Guiana (Schomburgk 1922; Schomburgk 1896). The basecamp for that expedition was at Port Kumaka. At the beginning of the expedition, the Schomburgk party camped on the beach ridge of Waini Point. They recorded no detailed description of the flora there, although Richard Schomburgk made an account of birdlife, as well as notes on the heat of the open sun, the plentiful mosquitos, and the types of small shells that make up the beach (Schomburgk 1922). Unfortunately, nearly all of the Schomburgk botanical specimens from that expedition were lost to mold and decay (van Dam 2002).

Juan S. de la Cruz was a plant collector for the New York Botanical Garden, working under contract to the prominent botanist H.A. Gleason (Ek 1990). Cruz collected in many regions of Guyana, particularly along the rivers of the Northwest District and the upper Mazaruni River basin. From an analysis of collecting dates on Cruz specimens, it appears that he made at least six collecting trips to the Northwest District. Two of these trips were extensive, in August to September 1921 and in May 1922. From the collection number ranges found, it is estimated that Cruz made over 1,400 plant collections in the Northwest from 1921 to 1927, approximately 80% of which are represented at the US National herbarium, according to database records of the BDG program.

More recently, Tinde van Andel (2000a; 2000b), of the University of Utrecht and

Tropenbos Foundation, made numerous plant collections in the Northwest from 1995-1997 as part of research on non-timber forest products in the region, including voucher collections for her ecological plots in the Santa Rosa vicinity, located just to the south of the Waini Peninsula. Those research sites start in freshwater forests apparently just inland of coastal plant communities that include some mangrove species. A summary of early botanical collectors who worked in the Northwest Region is given in Table 2.1. Georeferenced plant collection sites in the Northwest District are shown in Figure 2.1.

Delta Amacuro

The *Flora of the Venezuelan Guayana* (Steyermark et al. 1995 - 2005) includes listings of the plant species for the Venezuelan state of Delta Amacuro, located adjacent to the Northwest District of Guyana (Figure 2.2). This allowed a comparison to be made between the species known from the Northwest District and the species listed for Delta Amacuro. Waini Point is located within 6 kilometers of Delta Amacuro, which includes the large delta of the Orinoco River. North of the Waini Peninsula, the coastline of Delta Amacuro possesses vegetation predominantly of swamp forest and marshland along the Orinoco River's many distributaries.

The state of Delta Amacuro covers approximately 36,663 km^2, nearly twice the area of the Northwest District and approximately 8% of the 472,000 km^2 Venezuelan Guayana, which is the Venezuelan portion of the Guiana Shield region Gibbs & Barron, 1993) as covered in the floral treatment by Steyermark et al. (1995 - 2005). Huber (1995c), citing Pannier and Fraino

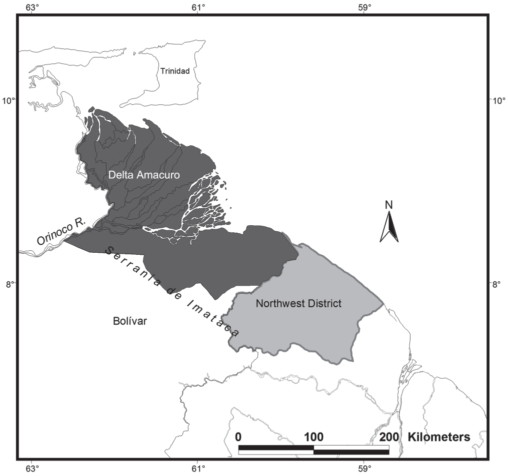


Figure 2.2. The location of the state of Delta Amacuro, Venezuela in relation to the Northwest District, Guyana.

Table 2.1. Major historical (pre-1980) collecting trips in Northwestern Guyana from US National Herbarium records.

Collector	Year	Localities
Schomburgk, M.R. and R H.	1841	Waini R., Mora Passage, Barima R., Aruka R.
Jenman, G.S.	1896	Barima R.
ImThurn, E.F.	1897	Aruka R., Barima R.
Bartlett, A.W.	1905	Aruka R., Barima R.
Beckett, J.E.	1906	Baramanni, Waini R.
Ward, R.	1907	Aruka R.
Hitchcock, A.S.	1920	Morawhanna, Issorora, Aruka R., Yarikita R., Amakura R.
Cruz, J.S. de la	1921-23,1927	Waini R., 'Marabo Shortcut', Barima R., Amakura R., Moruca R.
Altson, R.A.	1926	Mabaruma
Archer, W.A.	1934	Mabaruma, Aruka R., Barima R., Koriabo R., Wauna
Fanshawe, D.B.	1945	Waini R., Aruka R., Mabaruma
Cowan, R.S.	1955	Barima R.
Maguire, B.	1955	Matthew's Ridge
Mori, S.A.	1976	Matthew's Ridge
Maas, P.J.M.	1977	Aquero, Kwebana

de Pannier (1989), reported that 4,600 km^2 of the state, about 12.5% of the total area, was mangrove swamp, although that was possibly an overestimate resulting from inclusion of non-mangrove areas (Spalding et al. 1997). That compares to only 890 km^2 of mangrove swamp in the Northwest District of Guyana (Huber et al. 1995), which is about 4.6% of the district's total area. Although Delta Amacuro has a considerably larger area of lowlands, maximum elevations in Delta Amacuro and the Northwest District are similar. Elevations on Serranía de Imataca in Delta Amacuro exceed 500 meters at the border with Bolívar State, while in the Northwest District elevations approach 600 meters in the extreme western parts of the Barama River watershed at its border with Bolívar, and approach 500 meters in the headwaters of the Kaituma river and in the Kauramembu Mountains on its southern border with Guyana's Cuyuni-Mazaruni Division. The southern portion of Serranía Imataca extends into the Northwest and forms the upper watershed of the Barima River. Therefore, because of its proximity and comparable geomorphic setting, the flora of the Orinoco Delta might be expected to have a high degree of similarity to the flora of the Waini Peninsula.

The lower plant species diversity of the lowlands of Delta Amacuro, in comparison to the neighboring highlands of the Guiana Shield, has led to less interest in and under-sampling of its vegetation. For its area, far fewer collections have been made by early collecting expeditions in Delta Amacuro than in Amazonas or Bolívar. Out of more than 25,600 collections from the three states of the Venezuelan Guayana that have been databased from the US National Herbarium, only 4.8% were collected from Delta Amacuro. Although that region is not a likely source for many species new to science, its flora is possibly incompletely known, which can bias studies of regional diversity and conservation efforts.

Regional and Global Affinities of the Waini Peninsula Flora

The plant communities of the Waini Peninsula include many coastal species that have very broad distributions. In addition to this oceanic influence, the Peninsula makes up the outer edge of the coastal plain along the northeastern side of Guiana Shield. The Guiana Shield is a distinct geological and biological unit that is isolated in northeastern South America by broad surrounding lowlands and the Amazon, Negro and Orinoco River system (Gibbs & Barron 1993; Huber 1995a; Kelloff & Funk 2004). The degree to which proximity to the Shield's uplands is reflected in the Waini flora is a central question, as are the degrees to which other geographic affinities are apparent in the flora. In an effort to illuminate the floral affinities of one particular site, Kelloff and Funk (2004) performed a biogeographic analysis of the flora of Kaieteur National Park, Guyana, one of Guyana's few protected areas, located in central Guyana on sandstones of the Shield's Roraima formation. That analysis utilized a classification based on distribution ranges of each species to produce a summary of global affinities of the entire flora. In part, the inspiration for that method was the biogeographic investigations of British botanist Joseph Hooker (1817-1911), which have been summarized by Brundin (1966). Hooker's goal was to understand the history underlying the distributions of plant taxa of the Antarctic circumpolar regions. Also incorporated into the method here is the phytogeographic work of Leon Croizat (1964). However, where Croizat connected ranges of disparate taxa with linear "tracks," Kelloff and Funk grouped all species of a site of interest into a limited set of generalized, nested distribution classes for the biogeographic analysis.

METHODS

Comparison of the Waini Flora with Quackal and Manicole Plant Communities

Following the approach of Clarke et al. (2001a), a similarity matrix was assembled for the species present in a total of seven vegetation types. These included five vegetation types from the Waini peninsula: Beach, Coastal Mangrove forest, Mixed Freshwater forest, Riverine Mangrove forest, and Burned areas; and the two vegetation types drawn from van Andel's (2000a) ecological plots in the coastal plain of the Northwest District: Quackal swamp and Manicole swamp. Burned areas were included as a group to explore at what level they might bear similarity to any of the other plant communities. NTSYSpc (Rohlf 1997) statistical software was used for the clustering of those plant community data. Clustering was performed using simple matching coefficients, with the Sequential, Agglomerative, Hierarchical, and Nested clustering method (SAHN) and the Unweighted Pair-Group Method, Arithmetic average (UPGMA), based on algorithms from Sneath and Sokal (1973).

Possible sources of error in comparisons of plant communities included misidentification of plant specimens, which could change the amounts of overlap between communities. Misidentification was minimized by determination of specimens at major botanical institutions that host many specialists and have fairly complete, up to date collections for reference. Also of concern are incomplete or biased sampling, which may include under-sampling of trees and of plants sterile at the time of sampling, and differences in sampling effort and scale. Problems from assignment of species to particular vegetation types must be considered. Some of the species may be present in the beach community, since they are found in beach substrate, but are primarily on the margins of a neighboring community and might be best treated as outliers from that community. As with many of these vegetation groups, the beach community itself could be subdivided into finer units such as ocean front, central beach ridge, and back beach near mangrove swamps; similar concerns could be formed for a unit regarding boundaries. A final consideration is sampling bias, particularly the Quackal and Manicole samples which were obtained from one hectare plots, while the Waini samples were taken during sampling transects. However, these do represent a similar degree of sampling intensity for each vegetation type, and substantial possible disparity may be mitigated by the use of qualitative (presence/absence) rather than quantitative comparisons.

Northwest District

A checklist of plants of the Northwest District was assembled from five sources: 1) collections made on the Waini Peninsula during this study, 2) collections made in the Northwest District by the BDG program since 1986, 3) the dataset of Northwest District collections held at the US herbarium, 4) the 625 species listed by van Andel (2000b) based on her collections made in Guyana from 1995 to1997, and 5) some specimen information from online databases, e.g., the Missouri Botanical Garden's (1995-present) TROPICOS database, and the New York Botanical Garden's website (1996-present). The resulting names at the species level were matched with the database for the Checklist of the Plants of the Guiana Shield (Hollowell et al. 2001) to standardize nomenclature and correct errors. Those species known only from cultivation were not used in analyses but were included in the full checklist for the Northwest District (Appendix 3), and noted as cultivated. The status of species as cultivated was determined by literature checks in DeFilipps (1992), Boggan et al. (1997), van Andel (2000b), and Hollowell et al. (2001). Species that had apparently escaped cultivation and become naturalized were also noted. Taxa determined only to genus were included if they represented the only record for that genus. Contributions of recent collections to the lists were calculated as an indication of the status of knowledge of the region's flora.

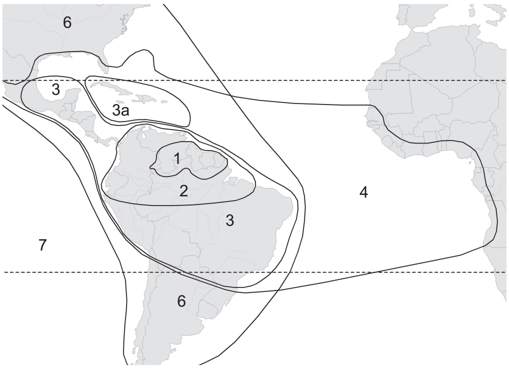


Figure 2.3. Nested floristic distribution zones used in analysis of plant species affinities for the Waini Peninsula. 1. Guiana Shield. 2. Northern South America. 3. Neotropical. 3a. Neotropical including Caribbean. 4. Neotropical and Western Africa. 5. South America (not indicated). 6. Western Hemisphere. 7. Pantropical, between 23.5° N and 23.5° S. 8. Cosmopolitan (not indicated). The Waini Peninsula flora had the greatest affinity (33%) with the Neotropical + Caribbean zone, followed by the Pantropical zone (27%).

Delta Amacuro

Comparisons with the flora of Delta Amacuro were made with species published in the *Flora of the Venezuelan Guayana* (Steyermark et al. 1995 - 2005), which included all pteridophytes (ferns) and spermatophyte families (seed bearing plants). Those were compared with species for the Northwest District of Guyana compiled to form the preliminary checklist given in Appendix 3, to estimate the amount of overlap between the floras of the two regions. Since the neighboring political divisions share similar geological and elevational properties, those species not included in the overlaps also suggest distributional records that might be found if collection efforts were continued. At the US National Herbarium, ongoing data collection of plant specimens collected in the Venezuelan Guayana, including Delta Amacuro, allowed an updated summary of historical collecting efforts in Delta Amacuro. Those are listed in Table 2.2. Although they were listed in an earlier compilation by Huber (1995b), R. Liesner and F. Delascio are not included because these researcher's names have been found on Delta Amacuro specimens only as secondary collectors with J. Steyermark in 1977.

Regional and Global Affinities

To analyze the Waini flora, all species were assigned to one of eight generalized, nested classes of biogeographic affinity: Guiana Shield, Northern South America, Neotropical (with a distinction between those included in or outside of the Antilles), Trans-Atlantic, Western Hemisphere, Pantropical, and Cosmopolitan. Those correspond to a subset of the classes

Table 2.2. Plant collectors in Delta Amacuro, Venezuela

Collector	Year	Localities
Rusby, H.H. and R.W. Squires	1896	Paloma, Manoa, Sacupana, Santa Catalina, Eleanor Creek
Bond, F.E., T.S. Gillin and S. Brown	1911	Caños of the Orinoco Delta
Curran, H.M. and M. Haman	1917	Caño Paijana, Isla de San Carlos, Caño Pedernales
Cardona, F.	1943	Puerto Caropita
Gines, H.	1952, 1954	Guayo, Isla Burojoida, Jotacuay, Teiua, Curiapo, Ibaruma, Los Piedras, Araguabisi, Puerto Baja, Koboima, Tobejuba, Wiuiquina
Wurdack, J.J. and J.V. Monachino	1955	Caño Jobure, Río Grande del Orinoco, Río Cuyubini, Río Acure, Río Ibaruma, Serrania Imataca, Río Guanamo
Steyermark, J.A.	1960, 1964, 1977	San Victor, Río Amacura, Río Cuyubini, Sierra Imataca, Cerro La Paloma, Río Acure, Río Grande, Caño Atoiba, Caño Jotajana, Caño Joba-Suburu (Caño Jota-Sabuca?).
Marcano-Berti, L. (with Zapata and Salcedo in 1977)	1964, 1965, 1977	East of Río Grande near border of Bolívar, Cano Araguao, Cano Arature, Caño Guiniquina
Breteler, F.J.	1966	Río Grande o Toro, near Bolívar border
Blanco, C.	1965, 1966	Río Grande, near Bolívar border
De Bruijn, J.	1967	Río Grande o Toro, near Bolívar border
Ruiz-Teran, L. and S. Lopez-Palacios	1973	La Ladera, Caño Mánamo, Pedernales
Davidse, G. and A.C. Gonzalez	1979	ESE of Los Castillos de Guayana, trail to the Rio San José
Aymard, G.	1987	Río Grande, Caño Orocoima
Fernández, A.	1987	Antonio Diaz
Montoya, S.	1993	Cerro Caño Acoima
Diaz, W.	1997	Mun. Tucupita Piacoa

employed by Kelloff and Funk (2004). The classifications are illustrated in the map in Figure 2.3.

The Guiana Shield distribution (1) includes species that are, fairly strictly, restricted to that geologic formation's igneous and sedimentary bedrock and areas influenced by that area's outwash. It includes southern Venezuela, most of the three Guianas, and parts of northern Brazil and scattered outliers in southeastern Colombia.

The Northern South America distribution (2) includes species found in the Guiana Shield as well as the Northern Andes, the continent's Pacific coast south to the arid Peruvian coast, and much of the Amazon Basin lowlands to about 7 degrees south. The Andes reach much higher elevations than the Guiana Shield highlands. Many of the habitats in this zone are wet to extremely wet.

The Neotropical distribution (3) includes all of the Americas between approximately 23.5 degrees north and 23.5 degrees south, with subclasses either including or excluding distribution in the Antilles (3a). Following climate patterns, this unit is mapped to the south of the Tropic of Capricorn on the Atlantic coast of South America, and to the north of that latitude on the Pacific coast, which is influenced by strong, cool ocean currents from the south.

The Trans-Atlantic distribution (4) accommodates species native to both the Neotropics and tropical Africa. Here this distribution is applied predominantly to mangrove species, thus the mapping in Figure 2.3 is adapted from the Atlantic-east Pacific distribution from mangroves by Tomlinson (1986)

The South American distribution (5) is essentially self-explanatory, and is indicated on Figure 2.3 only by the landmass of the continent.

The Western Hemisphere distribution (6) includes species adapted to a broad climate range. It includes species that extend into the subtropics and temperate zones of North and South America.

The Pantropical distribution (7) covers tropical areas nearly worldwide, from 23.5 degrees north to 23.5 degrees south.

Cosmopolitan (8) species are those known from both tropical, sub-tropical, and in some cases temperate areas, nearly worldwide. Here the Neotropical and Pantropical classifications both include species that might to some degree extend into the Subtropics.

RESULTS

Quackal and Manicole Communities

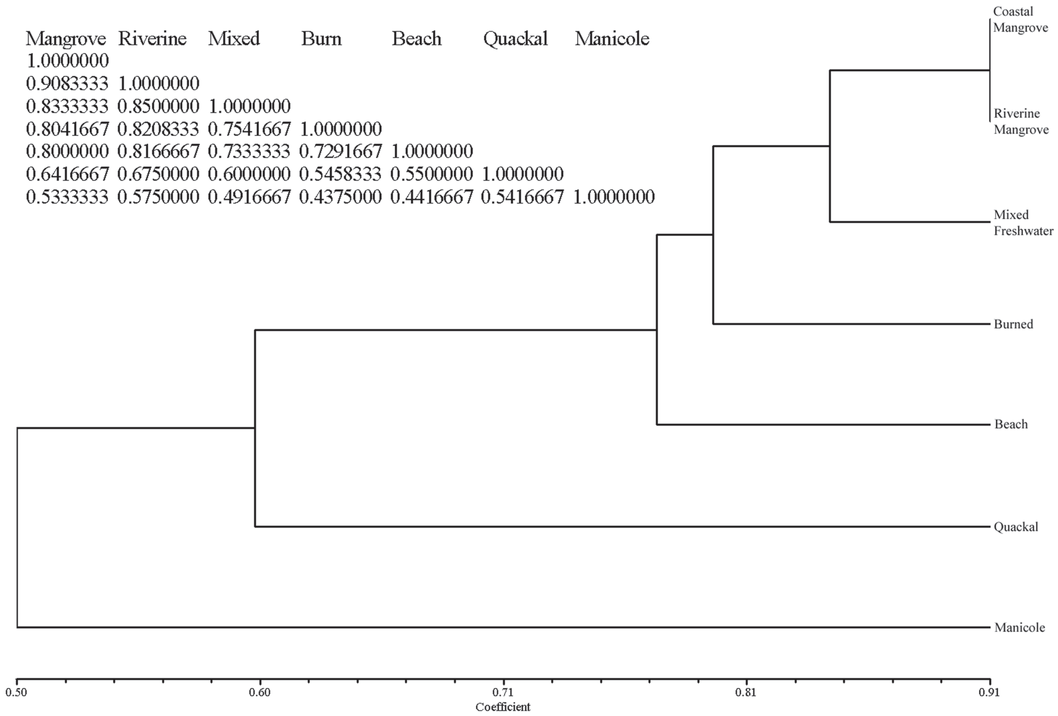
Forty-four species were shared between the 126 Waini species recorded and the list of all species recorded by van Andel for the entire District. That 35% overlap includes 5 species that are either cultivated or escaped from cultivation, *Cocos nucifera* L., *Luffa cylindrica* M.Roem., *Pedilanthus tithymaloides* (L.)Poit., *Gossypium barbadense* L., and *Jatropha gossypiifolia* L..

Only seven taxa were shared between the Waini Peninsula (126 species) and van Andel's Quackal and Manicole plots (138 species). That is approximately a 5.5 % overlap relative to the species of the Waini Peninsula. Of 240 total plant taxa for all sites, only 51 were shared in any way among the seven vegetation types.

Considered separately, collections resulting from this research on the Waini Peninsula and other sites in the Northwest added 99 species to the baseline list formed from historic collections, while van Andel (2000a) collections added 308 species to the baseline list. Thirteen of those species were added by both efforts.

The similarity matrix and tree matrix, displayed as a phenogram (similarity-based dendrogram), from the UPGMA clustering of the seven coastal plain communities are shown in Figure 2.4. A cophenetic matrix was formed from the UPGMA tree matrix and run against the original matrix to test the goodness of fit of the clustering results to the original data set, using a Mantel test for matrix correspondence (Rohlf 1997). That resulted in a high probability ($p = 0.995$) that a random Z-value would be less than the Z-value derived from the comparison of matrices, indicating a close fit in the UPGMA clustering. Alternate tests of single-link and complete-link clustering methods yielded phenograms very similar to those from UPGMA clustering, indicating that the clusters are quite distinct (Rohlf 1997).

Coastal Mangrove and Riverine Mangrove swamps clustered together. The two mangrove swamp types differed in part because different



Mangrove	Riverine	Mixed	Burn	Beach	Quackal	Manicole
1.0000000						
0.9083333	1.0000000					
0.8333333	0.8500000	1.0000000				
0.8041667	0.8208333	0.7541667	1.0000000			
0.8000000	0.8166667	0.7333333	0.7291667	1.0000000		
0.6416667	0.6750000	0.6000000	0.5458333	0.5500000	1.0000000	
0.5333333	0.5750000	0.4916667	0.4375000	0.4416667	0.5416667	1.0000000

Figure 2.4. Similarity matrix and cluster diagram for five major Waini Peninsula plant community types: Coastal Mangrove swamp, Riverine Mangrove swamp, Mixed Freshwater swamp, Burned areas, and Beach, as well as the Quackal and Manicole communities in southeastern Northwest Region (van Andel 2000a). Based on species presence and absence.

Rhizophora species were present, *R. mangle* in the Coastal swamp and *R. racemosa* in the Riverine swamp; the Riverine Mangrove community also contained a few epiphytic species while the coastal community contained none. Several species were included in Coastal but not Riverine Mangroves that were not strict halophytes; these were possibly excluded from the Riverine areas because they are not adapted to tidal fluctuations that are absent in the occluded Coastal swamps. Those mangrove vegetation types cluster together in part because of their low species richness (18 and 8 species respectively), although they shared only two species, *Acrostichum aureum* and *Avicennia germinans*. Those two species were also shared with the more diverse Mixed Freshwater swamp (34 species), with which the mangrove swamps clustered. The Mixed Freshwater swamp shared four species with Riverine Mangrove and one with Coastal Mangrove.

The Burned areas (39 species) clustered with the grouping of the above three communities, Coastal and Riverine Mangroves and Mixed Freshwater. Five of the ten species shared with those communities were remnants from mangrove swamps formerly in those burned areas, and the other five were colonists, including *Acrostichum* ferns from mangrove habitats and vines from Mixed Freshwater areas. Unaffected areas of these communities also surrounded the burned area and contributed seed for regeneration. The distinction of the burned areas from the previous three was due in part to the presence of a larger number of species, many of which are disturbance-adapted. Those include wind-dispersed species, members of the Amaranthaceae, vines, and floating and aquatic species that benefitted from the increases in open water. Among the wind dispersed species that were not found in the unburned swamps were *Typha domingensis* Pers., several ferns, *Mikania micrantha* Kunth, *Cydista aequinoctialis*, *Sarcostemma clausum*(Jacq.)Schult., *Entada polystachya* (L.)DC, and *Securidaca diversifolia* (L.)S.F.Blake. Animal dispersed species in the burned areas included *Coussapoa asperifolia* Trécul, *Aeschynomene sensitiva* Sw., *Heliconia psittacorum* L.f., *Hibiscus bifurcatus* Cav., and *Solanum stramoniifolium* Jacq. as well as several species of Amaranthaceae with tiny seeds that may be wind blown at times.

The Beach community (38 species) was primarily composed of species highly specialized for the coastal environment, many of which were not found in other vegetation zones. That community clustered with the four previous groups in part because of the presence of individuals of mangrove species and mangrove associates that were common in neighboring habitats, including *Laguncularia racemosa*, *Avicennia germinans* and *Conocarpus erectus*. Those occurred occasionally at the top of narrow beach ridges and often on beach borders of coastal lagoons. Some vines of the back beach were shared with the burned areas, including *Sarcostemma clausum*, *Cissus verticillata*, and *Ipomoea tiliacea* (Willd.)Choisy; *Vigna luteola* (Jacq.)Benth. was shared with Mixed Freshwater swamp.

None of the Beach taxa were present in either Quackal or Manicole communities. The similarity of those two communities with the other four Waini Peninsula communities was based on only seven shared species. The Quackal community as surveyed by van Andel was more diverse (70 species) than any one of the Waini Peninsula communities, probably reflecting low soil salinity because of its distance from the ocean (approximately 12 kilometers at the Quackal plot). Van Andel considered the Quackal vegetation type to grade into mangrove swamp; the four species that it shared with the Waini were *Euterpe oleracea*, *Clusia palmicida*, *Cassipourea guianensis* Aubl., and *Calyptranthes* sp., all shared with the Mixed Freshwater swamp community, which may have contributed to its clustering more closely than the Manicole community with the Waini communities.

The Manicole community was the richest of the seven (96 species) and also the most distant from coastal communities. The plot near Assakata village on the Baramanni River was approximately 17 kilometers from the Atlantic Ocean. This community had a significant overlap with the Quackal site, sharing 28 species. Of those, 18 are trees; the other shared species were divided among shrubs, herbs, and vines. The six species that those two sites shared with the Waini Peninsula communities were *Monstera adansonii, Euterpe oleracea*, *Clusia palmicida*, *Cassipourea guianensis*, *Pterocarpus officinalis,* and *Peperomia glabella* (Sw.)A.Dietr.. Although the Manicole community shared more species with the Waini Peninsula communities than the Quackal community shared with the Waini Peninsula, those species were drawn from the Manicole community's higher number of species, and the shared species were spread among several Waini communities. Four species were shared with the Mixed Freshwater community, the epiphyte *Peperomia* was shared with the Riverine Mangrove area, and the vine *Monstera* was shared with the Coastal Mangrove community. *Calyptranthes* sp. also occurred in Coastal Mangrove, Mixed Freshwater, and Quackal communities.

Of the 240 species from all seven sites, 189 (79%) were known from only one site; those were divided among 26 from Burned areas (66% of its species), 28 from the Beach community (76% of its species), 8 from Coastal Mangrove swamp (42% of its species), 17 from Mixed Freshwater swamp (50% of its species), 4 from Riverine Mangrove swamp (50% of its species), 41 from Quackal swamp (59% of its species), and 65 from Manicole swamp (68% of its species).

Northwest District

A preliminary list of 1449 vascular plant species from the Northwest District is given in Appendix 3. Those species were approximately 22% of the known vascular flora of Guyana, currently standing at 6,700 species (Boggan et al. 1997; Hollowell et al. 2001). Additionally, 105 cultivated species, one alga and six mosses were included on the list. Mosses and alga are poorly collected and analyzed in the Northwest District, as throughout the Guiana Shield, and are included with the hope of encouraging future research. A previous collections-based compilation for the Northwest District listed 484 species of vascular plants (BDG 2001). Collections made during these studies on the

Table 2.3. Rankings of the 20 most species rich families for the Northwest, all Guyana, and the Waini Peninsula. The nine families shared by all are listed in bold face type, and those families shared at two indicated in columns with an “x”.

GUYANA				NORTHWEST				WAINI			
	spp.	Prop.	Guy&Waini		spp.	Prop.	NW&Guy		spp.	Prop.	Waini&NW
Orchidaceae	603	8.15%		Rubiaceae	78	5.81%	x	**Fabaceae**	6	5.13%	
Rubiaceae	415	5.61%		**Fabaceae**	62	4.62%		**Araceae**	5	4.27%	
Poaceae	316	4.27%		**Orchidaceae**	57	4.24%		Convolvulaceae	5	4.27%	
Fabaceae	306	4.13%		Melastomataceae	51	3.80%	x	**Cyperaceae**	5	4.27%	
Melastomataceae	279	3.77%		**Poaceae**	51	3.80%		Amaranthaceae	4	3.42%	
Cyperaceae	274	3.70%		**Cyperaceae**	40	2.98%		Arecaceae	4	3.42%	x
Caesalpiniaceae	179	2.42%		**Mimosaceae**	37	2.76%		**Asteraceae**	4	3.42%	
Mimosaceae	172	2.32%		**Araceae**	33	2.46%		Malvaceae	4	3.42%	
Euphorbiaceae	167	2.26%		**Euphorbiaceae**	33	2.46%		**Orchidaceae**	4	3.42%	
Asteraceae	149	2.01%		**Asteraceae**	31	2.31%		**Poaceae**	4	3.42%	
Myrtaceae	144	1.95%	x	**Apocynaceae**	27	2.01%		**Apocynaceae**	3	2.56%	
Clusiaceae	127	1.72%		Caesalpiniaceae	26	1.94%	x	Bromeliaceae	3	2.56%	
Apocynaceae	117	1.58%		Arecaceae	25	1.86%		Combretaceae	3	2.56%	
Araceae	117	1.58%		Bignoniaceae	25	1.86%	x	**Mimosaceae**	3	2.56%	
Chrysobalanaceae	115	1.55%		Clusiaceae	25	1.86%	x	Moraceae	3	2.56%	
Piperaceae	111	1.50%		Chrysobalanaceae	24	1.79%	x	Pteridaceae	3	2.56%	
Bromeliaceae	110	1.49%	x	Malpighiaceae	24	1.79%		Rhizophoraceae	3	2.56%	
Bignoniaceae	109	1.47%		Piperaceae	24	1.79%	x	Cactaceae	2	1.71%	
Lauraceae	104	1.41%		Annonaceae	20	1.49%	x	**Euphorbiaceae**	2	1.71%	
Annonaceae	90	1.22%		Lauraceae	20	1.49%	x	Myrtaceae	2	1.71%	
	4004	**54.10%**			**713**	**53.09%**			**72**	**61.54%**	

Waini Peninsula and during incidental field trips farther inland in the Northwest were the only source for 90 species in the list. Of those, 53, approaching half of the Waini flora, were known only from Waini Peninsula collections, and those taxa are indicated in the list in Appendix 3.

To illustrate the relative composition of the regional flora at varying scales, Table 2.3 ranks the 20 most species-rich families for each of the three areas: the Northwest District, all Guyana, and the Waini Peninsula. The overall highest ranking family among all sites was Fabaceae (Papilionoid legumes), which ranked fourth in all Guyana, second in the Northwest, and first in the Waini flora. Nine families were shared in the top 20 families among all three areas: Fabaceae, Orchidaceae, Poaceae, Cyperaceae, Mimosaceae, Araceae, Euphorbiaceae, Asteraceae (Compositae) and Apocynaceae. Of the top 20 families, 18 were shared between the rankings of the Northwest District and all Guyana, while 11 of the top 20 families were shared between the Waini and all Guyana. The Arecaceae (Palmae), which ranked 14th in the Northwest were 23rd in the full Guyana rankings; the Malpighiaceae, which were ranked 19th in the Northwest were 21st in the Guyana rankings.

Table 2.4. Plant species collected on the Waini peninsula not listed for Delta Amacuro. One variety is also listed. Ten of these are primarily coastal, indicated by *.

Amaranthaceae	*Alternanthera sessilis*
Arecaceae	*Nypa fruticans* *
Aristolochiaceae	*Aristolochia trilobata*
Caricaceae	*Carica papaya*
Combretaceae	*Conocarpus erectus* *
Combretaceae	*Terminalia catappa* *
Convolvulaceae	*Ipomoea violacea* *
Cuscutaceae	*Cuscuta umbellata*
Fabaceae-Caesal.	*Caesalpinia bonduc* *
Fabaceae-Mimos.	*Entada polystachya*
Fabaceae-Papil.	*Sesbania sericea* *
Lygodiaceae	*Lygodium venustum*
Malvaceae	*Thespesia populnea* *
Myrtaceae	*Psidium guajava*
Orchidaceae	*Epidendrum ciliare*
Passifloraceae	*Passiflora foetida* var. *foetida*
Poaceae	*Paspalum distichum*
Poaceae	*Sporobolus virginicus* *
Pteridaceae	*Acrostichum danaeifolium* *
Rubiaceae	*Morinda citrifolia* *

Delta Amacuro

The *Flora of the Venezuelan Guayana* (Steyermark et al. 1995 - 2005) listed 1649 species of pteridophytes and spermatophytes for the state of Delta Amacuro. Among those species 193 (11.7%) were not listed for Guyana. Given the proximity and environmental similarities, a portion of those species might be expected to be found in the Guyana's Northwest District with additional collecting effort.

Also, several species were collected on the Waini Peninsula and in other parts of the Northwest District that were not listed for Delta Amacuro in the *Flora of the Venezuelan Guayana*. Table 2.4 lists 19 plant species and one variety that were collected in the Waini Peninsula vicinity that were not recorded for Delta Amacuro. In addition, the alga *Rhizoclonium africanum* apparently had not been documented for Delta Amacuro, although it is almost surely present in the coastal *Avicennia* swamps.

Appendix 4 lists plant species from the Northwest District that were not yet recorded from Delta Amacuro. Sources include records from this study's ancillary trips beyond the Waini Peninsula site to interior localities near Mabaruma and Kwebana (see Figure 2.1), as well as from collection-based literature (van Andel 2000b) and from specimens at the US National Herbarium. That list includes 517 species of vascular plants from the Northwest, without cultivated or naturalized species, more than 31% of the 1649 species currently known for that state.

Regional and Global Affinities

The strongest affinity of the Waini Peninsula flora was with the Neotropical distribution category including the Antilles (zones 3 + 3a in Figure 2.3), which accounted for approximately 33% of the Waini species. The next strongest affinity was with the Pantropical distribution category (zone 7), including approximately 27% of the species. The Neotropical - African, or transatlantic, distribution (zone 4) comprised about 10% of the species, including all mangrove and mangrove-associate taxa, being those in the genera *Avicennia*, *Laguncularia*, *Rhizophora*, and *Conocarpus*. Notably, only 1.6% of the

Table 2.5. Floral affinities of Waini Peninsula distribution categories, results, and comparison to the floral affinities in those categories for the Kaieteur Falls area (Kelloff and Funk 2004).

Zone	Distribution	WainiSpecies	WainiProportion	KaieteurProportion
3a	Neotropical (with Antilles)	42	32.8%	14.8%
7	Pantropical	35	27.3%	1.8%
4	Neotropical + Africa	13	10.2%	1.4%
3	Neotropical (excluding Antilles)	11	8.6%	11.6%
2	Northern South America	8	6.3%	26.1%
8	Cosmopolitan	8	6.3%	0.4%
5	South America	5	3.9%	0.2%
6	Western Hemisphere	4	3.1%	0.4%
1	Guiana Shield	2	1.6%	17.2%
	TOTAL	128	100%	73.9%

Waini species were found to have a distribution considered as restricted to the Guiana Shield region (zone 1). The totals for each distribution category are given in Table 2.5, by their rank in the Waini Peninsula flora, along with the corresponding proportion from Kelloff and Funk's (2004) analysis of Kaieteur National Park.

DISCUSSION

Quackal and Manicole Communities

The turnover of species, moving from the coastal communities inland into the Quackal and Manicole communities, showed a high level of beta diversity, the change in species composition across intermediate distances. That illustrated the contribution of the coastal plain flora to both species and landscape level diversity of Guyana. In the case of the Waini Peninsula, the species turnover is likely driven in part by changes in oceanic influence, particularly salinity, as well as by the results of ocean dispersal along the coast and perhaps increased precipitation inland from the ocean. Since a high proportion of species were found to be unique to each community, it might be expected that this trend continues in the inland direction. The implication of that for conservation is the liklihood that coastal plain diversity would be difficult to adequately represent within any small area. Rather, significantly broad transects of contiguous or intermittent sites along the gradient from ocean to highlands might be more effective as reserves.

The Manicole site shared more species, and a slightly higher proportion of its species, with the Waini flora than the Quackal site that actually clustered closer to the Waini communities. That illustrated how differences in species richness of the sites might play as significant a role in the outcome of the clustering method as the number of shared species.

The Mixed Freshwater swamp on the Waini Peninsula, some parts of which were dominated by *Euterpe* (Manicole) palms prior to the fires of 1998, may have held more species in common with van Andel's Manicole or Quackal sites before that disturbance. The Mixed Freshwater swamp was a distinct entity, containing elements characteristic of both types of mangrove communities, and it also possessed many unique species. Those were apparently plant species that could adequately tolerate the low to moderate salinity of the interior, although not higher salinities of the mangrove swamps. The Beach community was distinct from the other Waini communities because of the presence of coastal specialist species. The beach clustered with those communities in part because they shared species, and because of the lack of overlap with species of the more inland Manicole and Quackal communities. In the Burned areas, the increased species richness will probably be a short-term phenomenon. Several species that were present before the fires persisted or were quickly reestablished, while only a few of the most sensitive species were eliminated. The dominance of most of the disturbance-adapted species will likely be temporary, while others, such as *Typha*, may persist for long periods.

Northwest District

The family rankings illustrate moderate consistency at higher taxonomic levels between the countrywide flora and those of the Northwest District and the Waini Peninsula. Of families listed only in the Waini top ranking, most have a high component of wetland-adapted species, such as Malvaceae, Combretaceae, Moraceae, Rhizophoraceae, Arecaceae. Also represented for the Waini were disturbance adapted families such as Amaranthaceae, and Pteridaceae, and a family dominated by vines, the Convolvulaceae.

The number of species records contributed to the list for the Northwest District by recent collection efforts illustrates the incomplete state of investigations into the region's flora. Limited financial and professional resources require that collecting efforts be aimed at the localities most promising for shedding light on biodiversity and conservation questions. Associated with this, there is a great need to make additional historical collection data available for such analyses. Preparing additional museum specimen data is labor intensive but is cost effective in comparison to performing new fieldwork, and will provide increasingly useful data to answer biodiversity questions and guide future research. As biodiversity research efforts progress in Guyana, compilation of species distributions will likely become increasingly focused on the finer levels of detail, such as by political divisions within countries. The tendency to use political divisions should be tempered by the growing ability to analyze a growing body of georeferenced specimen data using climatic, geological, elevational, and distance data with geographic information systems, allowing questions to be more readily framed and answered in terms of environmental and ecological units.

Delta Amacuro

It is still not certain how much overlap should be expected for plant species of the Waini Peninsula and in Delta Amacuro. Collecting expeditions in almost any under-collected locality of the Guiana Shield region tend to yield new distributional records. Few botanical collections in Delta Amacuro have taken place along the coast near to Guyana; the closest known coastal collection locality is Punta Barima, more than 70 kilometers northwest along the Atlantic coast from the Waini Peninsula. Although both areas have similar coastal and estuarine environments, it was found that over 30% of the plants listed for the Northwest District are not known for Delta Amacuro. This difference can be compared to the same statistic for nearby areas. Twenty-one percent of Surinam's known vascular plant species are not recorded for French Guiana, and 18% are not recorded for Guyana. However, in comparison, for the diverse, mountainous Venezuelan segment of the Guiana Shield, 42% of the plant species listed for Bolívar state are currently not listed for Amazonas state (Steyermark et al. 1995 - 2005). Latitudinal and edaphic differences between the Northwest and Delta Amacuro, particularly the extensive deltaic environment found only in Delta Amacuro, in addition to the high overall level of endemicity in the Guiana Shield region, suggest that a sizable portion of the plant species listed in only one region will continue to be unnknown in the other. Still, only the assembly and analysis of additional collections can clarify the relationship between the two areas.

These comparisons highlight the incomplete state of botanical knowledge of these regions, and should serve as incentives and goals for plant specimen collecting efforts. They will also hopefully serve as encouragement for further analyses of the spatial patterns of the turnover of species in the tropics.

Regional and Global Affinities

The differences between affinities of the Waini Peninsula flora and those of the species of the interior Kaieteur location illustrated some interesting points. The coastal Waini communities included many species with broad ranges, with the four top categories being Neotropical and Pantropical distributions and the sixth ranked category being Cosmopolitan, which included a variety of herbs. The fifth-ranked category, Northern South America, and the last category, Guiana Shield, represented the two most species-rich groups for the Kaieteur area. The Neotropical distribution ranked fairly high at both sites, with the distribution including the Antilles being the highest ranked Waini group and the third ranked group of Kaieteur; the non-Antillean Neotropical species ranked fourth at both sites. The Neotropical affinities of the Waini Peninsula flora were strongly influenced by species with island distributions, which reflects its close association with the Atlantic Ocean.

The minimal presence within the Waini flora of species endemic to the Guiana Shield supports the idea that the Waini Peninsula should be treated as floristically distinct from the Shield, reflecting the effect of the Amazon-derived sediments that have buried the Shield's crystalline bedrock, often by hundreds of meters. The Atlantic Ocean is a dispersal vector that supplies propagules of species well adapted for the saline soils, and has an overwhelming influence on the flora. The Waini is actually fairly near to the geologic Shield, being less than 15 kilometers from the hills near the town of Mabaruma.

The lowlands of the Waini Peninsula, the Guyana coastal plain, and the Orinoco Delta section of Delta Amacuro should, in the strict sense, be excluded from definitions of the Guiana Shield in accounts of its flora and fauna as well as for conservation purposes. That does not reduce the importance of coastal habitats such as found on the Waini Peninsula. Rather, it should be a confirmation of that coastal area's distinctness on the regional level. Not only are those plant communities limited to a relatively narrow strip of coastal plain, bounded by ocean and the Guiana Shield, but their community structures and settings are different from the Antillean coastal plant communities because of their geomorphic position on the Amazon River's coastal delta, which is unique worldwide.

CONCLUSION

In the larger scope of Guyana's biodiversity, the Waini flora is not rich in rare endemic species from spectacular environments, such as are found on the isolated tepuis of the Guiana Shield. However, the coastal zone is a unique and limited unit of the landscapes of Guyana and northern South America. The peninsula is threatened in more ways than less accessible interior ecosystems, both from local sources from accidental fires, on the national level by unplanned settlement or unsustainable exploitation, and at the global level by climate changes that might increase the risk of fires and threaten this low-lying peninsula through sea-level rise.

Comparisons with other ecosystems in Guyana help to illustrate the high levels of beta diversity across the landscape in the low elevations of the coastal plain and highlight the need to gather more information from all ecosystem types in Guyana and neighboring Venezuela. The number of species records added for the Northwest by collections on the Waini alone highlights the incompleteness of knowledge of the flora of that region, and the number of species not recorded for Delta Amacuro shows a similar need for that Venezuelan state. As the level of botanical knowledge for a country grows, research moves towards compiling species distributions at regional levels, and analyses of species diversity and planning of collecting activities will become increasingly focused on gaps in regional knowledge.

In the future, additional collections from many herbaria should be entered into databases and standardized to improve the completeness of checklists and biodiversity analyses. With the tools of georeferenced data sets and GIS software, analyses may eventually be possible that utilize collection data in ways that link to and compliment both qualitative, spatially broad regional checklists and highly quantitative, spatially limited ecological plot studies. Through GIS analyses of adequate, high quality collections data, expeditions can be planned that effectively target under-sampled habitats in important areas (Funk et al. 2005).

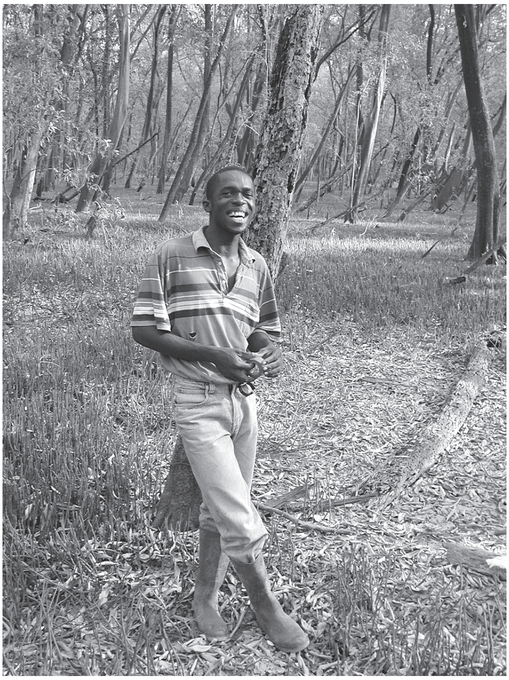
Results here suggesting that the Waini flora is essentially separate from the Guiana Shield flora and bears more affinity to the Caribbean region are not surprising, but lends support to the idea that biodiversity studies and conservation efforts should be pursued with an awareness of that distinction. The coastal plain should be excluded from the Guiana Shield when considered in any strict sense. In consideration of that, the coastal plain remains a unique ecosystem in Guyana that has suffered a high rate of disturbance and merits its share of study and protection.

This analysis of the plants of the Waini Peninsula should help to stimulate interest in the Waini Peninsula's inclusion in Guyana's fledgling Protected Areas System (EPA Guyana 2004; Kelloff 2003). Protected areas always benefit from the availability of plentiful information on the diversity of habitats and makeup of communities. Baseline information may be built upon and used for comparison with future surveys to increase understanding and benefit management in the face of rising population and climate change impacts. Documentation of local flora and fauna also increases the value of protected areas for educational purposes. On the Waini Peninsula, in large part because of sea turtle conservation activities, there has been a steady flow of local Amerindian students visiting Almond Beach. Students have been encouraged to take an interest in conservation issues and benefit from all additional information on the area.

While botanical diversity of the Waini Peninsula is modest in comparison to several other parts of Guyana, the area adds significantly to the diversity of landscapes found in the country. Similar coastal areas were long ago permanently converted to farm and urban land. The landscape also has substantial cultural significance, as the large majority of the population of Guyana has always lived in the country's coastal zone, and the Waini Peninsula is a prime example of that ecosystem type.

Doekie (Jackie) Arjoon and Chris Chin of the University of Guyana, in unburned *Avicennia* mangrove swamp near Waini Point, during Whittaker plot establishment in November 1998.

Keith David and Karen Redden on the prop roots of a *Rhizophora mangle* tree near the edge of the Kamwatta burn. A *Bromelia plumieri* plant (collection THH 413) is visible behind them.



Keith David of the University of Guyana, in the unburned *Avicennia* mangrove swamps near Waini Point, in April 2001. Keith also collected Lepidoptera specimens during this trip to the Waini Peninsula.

Karen Redden with the fruit of *Entada polystachya* (Fabaceae, collection THH 423) found along the central, vine covered portion of transect “C”, in early 2001.

CHAPTER 3.

THE MANGROVE PALM *NYPA FRUTICANS* WURMB.: A WIDESPREAD EXOTIC SPECIES IN NORTHWESTERN GUYANA

INTRODUCTION

Among the plant species present on the Waini Peninsula, *Nypa fruticans*, the Asian mangrove palm is of particular interest. One of the most pressing current issues in environmental conservation is detection, documentation, and management of invasive exotic species. That concern is exemplified by the widespread presence of *Nypa* in the Northwest District of Guyana. The growing appreciation of the ecological, social, and economic benefits of mangrove ecosystems has focused attention on potential threats, in terms of both the scientific and environmental policy. The goals of this chapter is to more fully document the presence of *Nypa* in South America, review information that might be relevant to understanding its arrival in the Northwest District of Guyana, and examine its possible sources and potential for spread within the region, as a basis for future research and appropriate management of the region's Riverine Mangroves.

NYPA HISTORY AND RANGE

Nypa fruticans Wurmb. is the only species in the monotypic genus *Nypa* Steck. It is native to the Indo-West Pacific region, thriving in high sediment estuaries from the Philippines to the Malay Peninsula, the Ganges Delta, Sri Lanka, and Northern Australia (Tomlinson 1986). *Nypa*'s trunk combines dichotomous branching and rhizomatous habit, and grows beneath mud, features unique among both mangroves and palms (Tomlinson 1973, 1986; Uhl & Dransfield 1987). It prefers habitats with moderate salinities and low wave energy. Those characteristics allow *Nypa* to form dense, monospecific patches in the intertidal zone along tropical estuaries.

Nypa is an ancient genus. Through analyses of fossil fruit and pollen evidence it has been documented as one of the earliest known mangrove genera, occurring in the Late Cretaceous period (about 70 mya) (Duke et al. 1997; Ellison et al. 1999; Gee 1989), and pollen representing *Nypa* is known from northern South America at that time (Graham 1995). *Nypa* was the dominant mangrove in the Neotropics, including the western Venezuelan coast, in the Middle Eocene period (45 mya) (Rull 1998, 2001) and was present in South America from the Maastrichtian stage of the late Cretaceous through the Eocene period (65-34 mya) (Gee 2001). It later disappeared from the Neotropics sometime after the Late Eocene (40 mya) (Gee 2001; Graham 1995; Tralau 1964), and has been restricted to Southeastern Asia since the Miocene epoch (20 mya) (Ellison et al. 1999). The ancient distributions of *Nypa* have been used as an illustration of the principle of continental drift (Raven & Axelrod 1975), and *Nypa* pollen is one of the earliest identifiable examples of a likely extant angiosperm species (Tomlinson 1986).

Throughout its modern natural range in Asia *Nypa* is heavily utilized. Descriptions of the species and discussions of its utility have been published for nearly a century (Conrado & Ayala 1906; Fong 1992; Halos 1981; Hamilton & Murphy 1988; Miah et al. 2003; Päivöke et al. 1984). It is particularly valued for its leaves which are used as thatching material (FAO 1994; Miah et al. 2003) and is also used for production of alcohol and vinegar derived from sap collected from the cut peduncle (Melana 1980; Miah et al. 2003; Päivöke et al. 1984). The hardened endosperm of *Nypa* has been used as a "vegetable ivory" similar to that of the Tagua Palm, *Phytelephas* Ruiz & Pav., of Central America and western South America, which in the past has been considered possibly *Nypa*'s closest relative within the Arecaceae. However that relationship has been refuted by recent molecular studies that place *Nypa* as a basal group sister to all other palms (Lewis & Doyle 2001) or basal if excluding the subfamily Calamoideae (Asmussen & Chase 2001), which includes the Moriche or Ité Palm *Mauritia*, a distinctive feature of the vegetation of the Venezuelan Llanos and the coastal plain swamps of Guyana.

NYPA FRUTICANS OUTSIDE OF ITS MODERN NATIVE RANGE

Nypa fruticans has become a widespread exotic species in some estuaries of Western Africa, where it was introduced in the early 20th century, particularly in the Niger Delta (Sunderland & Morakinyo 2002; Ukpong 1995). Duke (1991) first documented *Nypa* in the modern Neotropics from a small population at the mouth of Panama's Rio Majugual, in the vicinity of the Caribbean seaport Colón, near the northern, Caribbean end of the Panama Canal. More recently, viable *Nypa* fruits have been reported from beaches of Trinidad by Bacon (2001), who successfully germinated some of these stranded fruits in the laboratory. An initial account of *Nypa* populations along the rivers of the Northwest District of Guyana was given by Pritchard (1993), whose published segment on *Nypa* went largely unnoted within his general review of palms in Guyana. That knowledge of *Nypa*'s presence in Guyana has not been applied to subsequent discussions of *Nypa* in the Neotropics. In light of the increasing attention to the presence of *Nypa* outside of its native range and of its environmental implications, there is a need for further description and documentation of the populations established in Guyana.

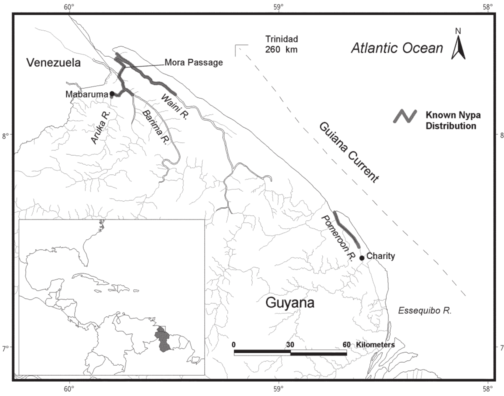


Figure 3.1. Map of northwestern Guyana, showing the known range of *Nypa*, from personal observations during river travel. The Guiana current flows in the direction of the Orinoco Delta and Trinidad.

Nypa's presence in Guyana also has bearing on recent speculation about the origin of *Nypa* propagules found stranded on beaches in Trinidad (Bacon 2001).

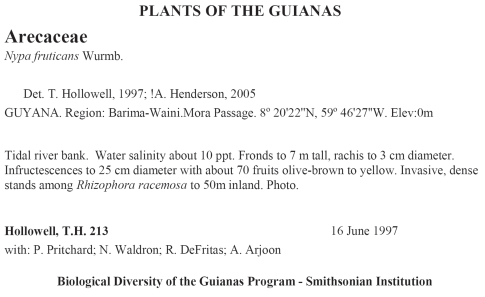
From 1997 to 2001, during investigations of coastal *Avicennia germinans* swamps in Northwestern Guyana, *Nypa* palms were observed along the banks of the Waini River as far as 42 kilometers upstream from the river's mouth. These colonies are thickest over most of the length of the Mora Passage, a connector between the Waini and the Barima Rivers. *Nypa* also grows along the Barima River from the Mora Passage to the Aruka River, and on the Aruka River as far upstream as the district administrative seat, Mabaruma. It is very likely that *Nypa* is present in Venezuela downstream along the Barima River as it flows towards the southern Orinoco Delta. Smaller colonies of *Nypa*, mentioned by Pritchard (1993), still exist on the Pomeroon River upstream nearly to the town of Charity. The currently observed range of *Nypa* in Guyana is shown in Figure 3.1.

Even the densest areas of *Nypa* along the Mora Passage (Figure 3.2) are mixed with the riverine red mangrove *Rhizophora racemosa* G.

Figure 3.2. *Nypa* growing along the banks of the Mora Passage, interspersed with the prop-rooted riverine red mangrove *Rhizophora racemosa*.

Mey., although *Nypa* sometimes dominates the river's fringe. *Nypa* is often scattered in the understory of the intertidal *Rhizophora racemosa* swamp. *Nypa* infructescences up to 25 cm in diameter, composed of approximately 70 fruits (Figure 3.3), are common in these populations. When mature, the spherical heads break up, and the viviparous fruits disperse with the currents. As part of recent fieldwork in the region a voucher collection of *Nypa fruticans* was made along the Mora Passage (Figure 3.4).

Figure 3.3. A *Nypa* infructescence collected as part of Hollowell et al. #213, from along the banks of the Mora Passage.



PLANTS OF THE GUIANAS

Arecaceae

Nypa fruticans Wurmb.

Det. T. Hollowell, 1997; !A. Henderson, 2005

GUYANA. Region: Barima-Waini.Mora Passage. 8º 20'22"N, 59º 46'27"W. Elev:0m

Tidal river bank. Water salinity about 10 ppt. Fronds to 7 m tall, rachis to 3 cm diameter. Infructescences to 25 cm diameter with about 70 fruits olive-brown to yellow. Invasive, dense stands among *Rhizophora racemosa* to 50m inland. Photo.

Hollowell, T.H. 213 16 June 1997

with: P. Pritchard; N. Waldron; R. DeFritas; A. Arjoon

Biological Diversity of the Guianas Program - Smithsonian Institution

Figure 3.4. Label information for the voucher collection of *Nypa fruticans* in the Northwest District of Guyana, as distributed with specimens.

Along the ocean beaches of the Waini Peninsula, germinated propagules are occasionally found stranded (Figure 3.5), similarly to those documented recently in Trinidad by Bacon (2001). Established *Nypa* plants have never been observed during many walks and boat trips along this part of Guyana's Atlantic coast. The entire coast of the Guianas is bordered by extensive mudflats, derived primarily from Amazon River sediments (Brinkman & Pons 1968; Gibbs & Barron 1993). This coastal habitat is apparently inhospitable to *Nypa*, possibly due to wave energy and the shifting nature of the mudflats. Neither has *Nypa* been seen in the *Avicennia* dominated mangrove swamps immediately behind the low coastal beach ridges along the Atlantic coast, and it is uncertain whether that habitat would be amenable to *Nypa*.

DISPERSAL OF *NYPA* TO TRINIDAD

Bacon (2001) suggested the possibility that *Nypa fruticans* propagules found stranded on beaches in Trinidad originated from known populations in West Africa and were dispersed by prevailing currents across the Atlantic ocean and north along the eastern coast of South America. In one day, along a 500 meter stretch of Manzanilla Beach in eastern Trinidad, Bacon and students collected a total of 53 *Nypa* propagules, including 12 viable propagules (Bacon 2001), which would be extraordinary if attributable to trans-Atlantic dispersal. Considering the trans-Atlantic distribution of several mangrove taxa, successful dispersal and establishment over these distances might occur rarely. However, the Atlantic Ocean is a formidable barrier (Duke et al. 2001), and

Figure 3.5. A viable *Nypa* propagule found stranded on the beach of the Waini Peninsula, approximately 5 km east of Waini Point. The beach is composed of small shell fragments; off the beach mudflats extend seaward for several kilometers.

dispersal even within mangrove biogeographic regions can be a limiting factor on distributions of some species (Duke et al. 1998). A high degree of separation of other trans-Atlantic mangrove species has also been supported by differences in the composition of foliar waxes between separated populations (Rafii et al. 1996). Trans-Atlantic dispersal is a consideration in the study of the limited number of plant genera and species with disjunctions; such dispersal events occur at long intervals, in the range required for speciation (Renner 2004).

The *Nypa* populations in Guyana provide plentiful propagule sources within effective dispersal range of Trinidad. The distance to be covered is approximately 260 kilometers directly along the prevailing Guiana Current from the mouth of the Waini River to Manzanilla Beach in Trinidad. Surface velocities of the Guiana Current range from 41 to 123 cm/second (Gyory et al. 2003), ideally allowing dispersal times from northwestern Guyana to Manzanilla Beach of 7.3 to 2.4 days respectively. In contrast, dispersal across the Atlantic Ocean is a daunting proposition. The South Equatorial Current flows approximately 6,000 kilometers from the Niger Delta across the Atlantic Ocean towards the mouth of the Amazon River. From satellite-tracked drift buoy data (WOCE Data Products Committee 2002), the current's maximum velocity appears to be around 60 cm/second and may commonly reach only 30 cm/second (Bonhoure et al. 2004). Under ideal conditions these velocities would translate to a dispersal time from Africa to South America of 4 to 8 months (Figure 3.6). That does not include an approximately 1,000 kilometers of additional dispersal in the more rapid Guiana current before reaching Trinidad over an estimated 15 - 45 days. Those dispersal times are around the upper limits suggested by floatation trials with other mangrove species; up to 5 months for *Avicennia marina* Vierh. (Clarke 1993) and over 107 days for *Rhizophora* (Rabinowitz 1978a). No published floatation data could be located for *Nypa* propagules.

POSSIBLE SOURCES OF PRESENT NEOTROPICAL *NYPA* POPULATIONS

Neither the *Nypa* populations in Guyana and Panama nor the propagules collected in Trinidad have an established source. *Nypa* has likely been present in northwest Guyana for several decades, and some elder inhabitants of far northwestern Guyana state that there is no time in memory that *Nypa* palms did not grow along the margins of the Mora Passage. As

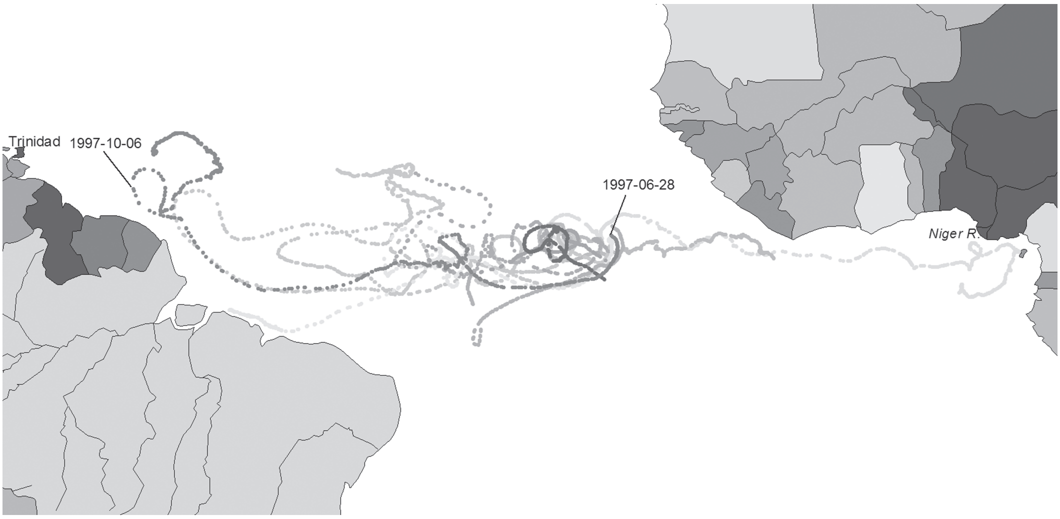


Figure 3.6. Mapped data points from 1997 WOCE drift buoy experiments (WOCE 2002) in the equatorial Atlantic Ocean. The indicated track is the fastest found for the South Equatorial Current, covering about half of the 6,000 km distance from the Niger Delta to the Guianas in approximately three months.

mentioned by Pritchard (1993), *Nypa* palms have been under cultivation for many decades in the Botanic Gardens in Guyana's capital, Georgetown. A 1955 guide to the Botanic Gardens (Anonymous 1955) describes *Nypa* in two ponds growing so vigorously that the ponds would be completely overrun if the palms were not regularly pruned. These were likely introduced in the late 19th century during the Botanic Garden's heyday under the direction of the British botanist George Jenman (McCracken 1997). Georgetown's extensive system of drainage canals certainly provides a feasible fruit dispersal route to the Atlantic Ocean and into the Guiana current, which flows towards Guyana's northwest coast (see Figure 3.1). *Nypa* fruits could then easily be carried by tidal fluxes into coastal rivers with moderate flows, such as the Pomeroon and Waini. Entry into river systems may be reinforced by estuarine circulation patterns that can drive mangrove propagules towards channel centers during flood tides and into slower currents close to river banks during ebb tides (Stieglitz & Ridd 2001). The distance from Georgetown to the mouth of the Waini River is about 260 kilometers, similar to the distance between the Waini and Trinidad. It is also possible that fruits from the live specimens in the Botanic Garden were intentionally introduced into the rivers of the Northwest District.

It is difficult to propose trans-Atlantic dispersal for the *Nypa* population that was reported from Panama. Among the logical explanations are intentional introduction, escape from cultivation (seeds are available on a few horticultural websites) or transport in ballast water from one of the many ships that travel through the Panama Canal. Duke (1991) did not speculate as to the source of introduction in Panama, but he rejected the idea that the population near Colón was a relict of the ancient *Nypa* distribution, on the basis that the plants would not have escaped detection for such a prolonged time; he did not discuss the possibility of trans-Atlantic dispersal.

Another scenario is the introduction of *Nypa* to northwestern Guyana by Dutch plantation owners, who were active in the region in the mid-18th century (Daly 1995), and maintained colonies on the Barima River (Schomburgk 1896). Erosion control could have been a concern of planters. Local people tell stories of the Mora Passage having once been so narrow that monkeys could travel on branches from one bank to another. Richard Schomburgk explored northwestern Guyana in 1841 with his brother Robert, while under contract to delineate the boundaries of British Guiana (van Dam 2002). He estimated the entrance to the Mora Passage to be only 116 feet (35 meters) wide, and he described the passage as a winding, natural waterway, with strong tidal currents (Schomburgk 1922). There are some anecdotal accounts (local inhabitants, pers. comm.) of the Mora Passage's origin as a canal planned by the Dutch and dug with slave labor. Vann (1969) estimated the width of the Mora Passage to be over 300 feet (92 meters) wide in 1956, and hypothesized that the waterway originated through crevassing and scouring by flood waters of the Barima River. He estimated that the Mora's depth had increased by nearly one half foot per year since measurements were made by the Schomburgk brothers. Measurements from 1999 Landsat satellite imagery (28.5 m resolution) show the Mora Passage as presently up to 200 meters wide along much of it course (Hollowell, unpublished). Regardless of the Mora Passage's origin, it appears that the Barima River has been increasingly captured by the Waini River via the Mora Passage. The strong tidal flows would encourage bank erosion, and eroded sediments may have contributed to a 6 kilometers long forested deposit which diverts the passage before it enters the mouth of the Waini River.

If *Nypa* has a long history in the area, it should have been recorded in botanical records. Both Robert and Richard Schomburgk were accomplished botanists; between them they described nearly 30 Guianan plant species that are still valid today (Boggan et al. 1997; Hollowell et al. 2001). In 1841 Robert Schomburgk (1896), reported numerous Trooli palms (*Manicaria saccifera* Gaertn.) and Manicole palms (*Euterpe* spp.) along the riverbanks between the mouth of the Aruka River and the Waini River, but he does not mention other palms along the banks, and it is unlikely that he would have confused either *Euterpe's* tall, thin form or *Manicaria*'s broad fronds with united pinnae with *Nypa*'s distinctive form. Robert's brother, Richard Schomburgk, reported *Euterpe* palms in his writings (1922), comparing their beauty to *Leopoldinia pulchra* Mart.:

> "Though the banks of the Mora had already claimed my entire interest, this was nevertheless very much more increased by those of the Barima. The loveliest of palms, *Euterpe oleracea* Mart., *Manicaria saccifera* Gaert., stretched their proud fronds up above the dark succulent mass of foliage and vied with the slender *Leopoldinia pulchra* Mart. both in beauty of growth and formation of leaf..."

Several other early plant collectors in Northwestern Guyana (Table 3.1) have also failed to record any presence of *Nypa*, although the chief mode of travel within this region was, and still is, by boat. In his detailed review of the riparian vegetation of Guyana, Fanshawe (1954), who traveled and collected plants in the Northwest, includes no mention of *Nypa*. Neither is *Nypa* listed in recent taxonomic treatments of palm species of the American tropics (Henderson 1995; Henderson et al. 1995), which require review of a high percentage of historical collections held in herbaria of the world. This should be considered with the knowledge that, compared to other plant groups, the large, and sometimes prickly, palms are typically under-collected.

ECOLOGICAL CONSIDERATIONS

It is useful to consider *Nypa*'s future in the estuarine mangrove swamps in terms of conditions for successful invasion listed by Lugo (1998) in his review of invasion of mangrove ecosystems. *Nypa* is an obligate halophyte, and so there is no reason to assume that the invasion is temporary. The conditions that *Nypa* has occupied in Guyana are typical of its native environment, along tidal river margins of moderate salinity. The invasion is not a response to microsite conditions, such as a period of freshwater inundation in a basin mangrove swamp. The major shift in the environment has been the increased disturbances of river banks and perhaps some increased sedimentation from disturbances in the watershed, which might be favorable to *Nypa* establishment. In northwestern Guyana, *Nypa* seems to have established frequently near homesteads or other areas of riverbank disturbance.

The small, though growing, human population in the region has not yet caused significant stresses in the riverine mangrove forests; harvesting of *Rhizophora* bark for tannins has been practiced on an small scale, although it is possibly increasing (Allan et al. 2002). The only event necessary for the *Nypa* invasion was probably the introduction of this well-adapted species to an environment from which it had been biogeographically isolated. So, while Lugo (1998) characterized mangrove

Table 3.1. Early plant collectors of the Northwest District of Guyana, from US National Herbarium holdings.

Collector	Year	Localities
Schomburgk, M.R. and R H.	1841	Waini R., Mora Passage, Barima R., Aruka R.
Jenman, G.S.	1896	Barima R.
ImThurn, E.F.	1897	Aruka R., Barima R.
Bartlett, A.W.	1905	Aruka R., Barima R.
Beckett, J.E.	1906	Baramanni, Waini R.
Ward, R.	1907	Aruka R.
Hitchcock, A.S.	1920	Morawhanna, Issorora, Aruka R., Yarikita R., Amakura R.
Cruz, J.S. de la	1922-23	Waini R., 'Marabo Shortcut', Barima R., Amakura R.
Altson, R.A.	1926	Mabaruma
Archer, W.A.	1934	Mabaruma, Aruka R., Barima R., Koriabo R., Wauna
Fanshawe, D.B.	1945	Waini R., Aruka R., Mabaruma
Cowan, R.S.	1955	Barima R.

ecosystems as difficult to invade and relatively easy to rehabilitate, this would not apply to invasion by the few species that are true mangroves, which total 70 species worldwide, according to Duke et al. (1998). In Hawaii and Tahiti, mangroves have been intentionally introduced to islands that were once mangrove-free, and have become nuisance species (Allen 1998). The mangrove fern *Acrostichum* is also sometimes considered a nuisance, due to interfere with regeneration in some disturbed mangrove swamps (Blanchard & Prado 1995; Ellison 2000a; Tomlinson 1986).

It is expected that the *Nypa* invasion in Guyana may be persistent, based in part of its current extensive distribution. The abilities of *Nypa* to spread vegetatively and to produce plentiful propagules enhance chances of its additional spread along the rivers of Guyana.

CONTROL OF *NYPA*

In its native range the control of *Nypa* is not a critical issue. In fact, in a few locations such as the Sundarbans of India, *Nypa* is reported to be under threat due to changes in hydrology and soil salinity (Badve & Sakurkar 2003; Sukhendu et al. 2002). In Nigeria, eradication of *Nypa* has been proposed by corporate and governmental agencies as a element of restoration of the Niger Delta (Sunderland & Morakinyo 2002), as attempts at *Nypa* control through increased utilization have not been effective. Efforts to control a few areas of the alien mangrove *Rhizophora* in Hawaii have been very expensive (Allen 1998). Surprisingly, there have been recommendations for *Nypa* plantings in the Volta estuary of Ghana, as part of efforts to remediate impacts of dam construction on the river (Rubin et al. 1998). Such unnecessary introductions should be viewed as ecologically risky in light of the nuisance that *Nypa* has become in Nigeria.

In Panama, the populations of *Nypa* that were documented by Duke (1991) in the Colón Free Zone of the Panama Canal have reportedly been destroyed by coastal construction activities (Neal Smith, Smithsonian Tropical Research Institute, pers. comm.), though possibly isolated individuals have survived in impoundments along the west shore of Bahia Limón to the west of Colón. Due to limited knowledge of its presence and extent, there is not yet any recognition of a need to control *Nypa* in Guyana; it is possible that increased utilization could serve as a minor control on its spread there. A few instances of *Nypa* harvest and thatching with *Nypa* fronds have been observed near the small settlement of Morawhanna at the western end of the Mora Passage, probably because the Trooli palm, *Manicaria saccifera* Gaertn. has become increasingly scarce, as its fronds are the preferred thatching material in the region.

NEEDS FOR ADDITIONAL STUDY

There is increasing concern about the increases in and effects of invasive plant species worldwide (Mack & Lonsdale 2001). The conservation community also needs information about this potentially aggressive exotic species, which could have significant effects on structure and function of important riverine mangrove communities. Due to their close connection with river waters, Guyana's riverine mangrove swamps, which are most susceptible to invasion by *Nypa*, may function more effectively as fish habitat and a source of nutrients and organic matter than the coastal mangroves isolated behind beach ridges (Ewel et al. 1998). Ecological research into the dynamics of competition between *Nypa* with *Rhizophora racemosa* and into the growth and reproduction of *Nypa* in Guyana would be useful in understanding the possible future of *Nypa* in the region and could inform considerations of control or restoration efforts, either through eradication or utilization.

The presence of *Nypa* in the Neotropics poses questions relevant to the study of biogeography. The feasibility of trans-Atlantic dispersal should be tested with floatation experiments on *Nypa* propagules, as demonstrated for mangrove species found in Panama by Rabinowitz (1978a), including assessment of viability at intervals (Duke et al. 1998). This might also include trials with varying salinities of water, which could affect buoyancy and viability, as the Guiana current can be diluted with substantial freshwater from the Amazon River. Molecular evidence may be useful in determining whether the sources of *Nypa* in Guyana, Trinidad, and Panama originated from African populations, introductions directly from Asia, or from the plants under cultivation in the Georgetown Botanical Garden. Possibly analyses of microsatellites would be a useful approach to molecular study of this issue (Godoy & Jordano 2001).

Records of the Dutch East Indies Company might hold information of possible introduction of *Nypa* to settlements in the Barima River area or other clues that may shed light on the history of the Mora Passage. An undertaking as ambitious as a 6 kilometers canal from the Barima River to the Waini River should also be documented in historical records.

Since they are restricted to brackish river fringes, these *Nypa* - *Rhizophora* swamps may be relatively easy to delineate and study. The extent of *Nypa* patches along rivers in Northwestern Guyana could be readily mapped by boat using a Global Positioning System (GPS), and resampling over a period of years would produce a picture of *Nypa* dynamics. Once a reasonable portion of the *Nypa* affected area is mapped, it may be possible to generalize that distribution to the entire region using large scale aerial photography (Manson et al. 2001; Wilton & Saintilan 2000) or high resolution, multispectral airborne imagery (Green et al. 1998); however, the more affordable Landsat imagery probably lacks adequate spatial resolution to detect fringing bands of *Nypa*.

The distributaries of the Orinoco River Delta should also be surveyed for populations of *Nypa*; it would not be surprising if it was found there. Those populations would represent additional sources for propagules that could be dispersed to Trinidad. If documented, the presence of *Nypa* in the Orinoco Delta should be of interest to Venezuelan botanists and conservation organizations. Certainly, any control strategies must be considered in light of many factors, with adequate attention to unintended effects.

CONCLUSIONS

Nypa as an invasive species appears to be an growing phenomenon in the tropical Atlantic Ocean region. If the source for *Nypa* in Guyana has been present for over a century in the Botanic Garden in Georgetown, but the species has only recently spread to the Mora Passage region, it can be concluded that initial colonization from intermediate distances might be uncommon, but once accomplished, local expansion may be rapid. It may only be a matter of time before *Nypa* becomes established as a nuisance in suitable sites of Trinidad and Venezuela’s Orinoco Delta. However, it should be noted that Duke (1991) warned of the inevitable spread of *Nypa* throughout the Central American Atlantic coastal region prior to its disappearance from Panama. Trinidad’s Nariva Swamp National Park may be of special concern, as it is located only a few kilometers to the south of Manzanilla Beach where so many viable *Nypa* propagules have been observed. Trinidad’s Caroni Swamp, near Port of Spain on the Gulf of Paria may also be vulnerable. The brackish waters of these areas should be monitored for *Nypa*. Documentation of the full extent of colonization and densities in northwestern South America and comparison with characteristics of *Nypa* in its native range could provide additional insight into the invasion and reasons for its success (Hierro et al. 2005). Understanding the regional history, dispersal, and ecology of this palm will be critical to mangrove conservation efforts.

Wiltshire Hinds in *Avicennia* forest with plentiful *Acrostichum* ferns and *Philodendron* vines, on transect "D" in November 2001.

Mangrove activities sometimes intersected with those of the Guyana Marine Turtle Conservation Society (GMTCS). On the way to reconnaissance of a burned area at Kamwatta Beach, Keith David, Karen Redden and Donald James of GMTCS help free a stranded Green Sea Turtle (*Chelonia mydas*). Over 100 eggs were also transported to a GMTCS nursery.

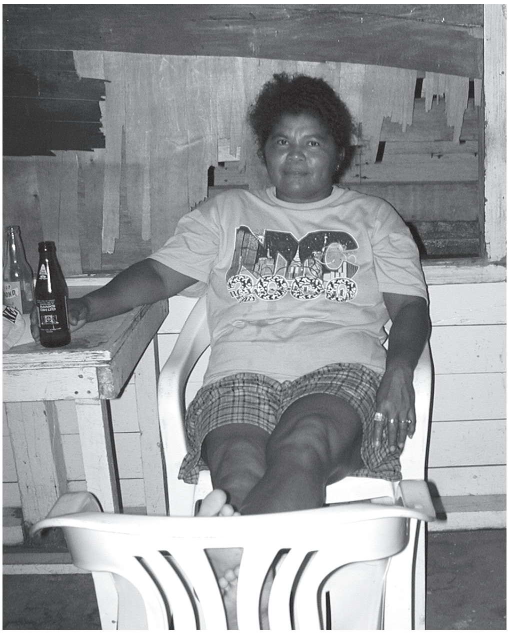
Professor Philip DaSilva of the University of Guyana, who provided support for research on the Waini Peninsula, at the front door of the Centre for the Study of Biological Diversity.

Wiltshire Hinds pressing the afternoon's plant specimens on the porch of the Kwebana guest house, November 2001. Kwebana is the site of an abandoned lumber mill on the Waini River upstream of tidal influence.

Amerindian students from Moruca inspect a Leatherback Sea Turtle (*Dermochelys coriacea*) recently hatched in the Almond Beach GMTCS nursery prior to releasing it that evening.

Romeo DeFritas, son of Violet and Audley James and a mainstay of the GMTCS, with hand chain-sawn *Rhizophora mangle* lumber harvested nearby for construction at the Almond Beach camp.

Audley James at Almond Beach camp, with his grandson Alex. A former turtle hunter, Audley became one of the key people in GMTCS.



Violet James, who with her husband Audley James and son Romeo DeFritas, managed many of the activities at the Almond Beach marine turtle monitoring camp.

CHAPTER 4.

STRUCTURE OF BURNED AND UNBURNED *AVICENNIA* FOREST, WAINI PENINSULA, GUYANA

INTRODUCTION

Fires burned across extensive parts of northeastern South America from 1997 to 1998 (Barbosa & Fearnside 1999; Cochrane & Schulze 1998), and at that time soil fires occurred in mangrove and freshwater swamps of the Waini Peninsula (Chapter 1, this manuscript). Those soil fires highlighted the need to improve understanding of the Waini Peninsula's mangrove ecosystems and their response to disturbances for the benefit of long-term management of the area.

Ecological plots have long been considered one of the best methods for collecting such detailed plant community information. Early mangrove studies were descriptive, often conveying species zonation of mangrove swamps and proposing explanations for the observations (Clarke & Hannon 1969; Davis 1940; Fosberg 1947; Lindeman 1953; Macnae 1963). Those studies frequently included vegetation profiles illustrating mangrove zonation patterns. Profiles are still occasionally produced, often incorporating information on physical characteristics such as soil type and salinity (Lindeman 1953; Odum et al. 1982; Thom 1967). One of the earliest quantitative ecological studies of mangroves was carried out by Golley et al. (1962) in Puerto Rico, in which biomass, carbon cycle measurements, and zoological trophic data were collected. By the 1970s, ecological plots were a fairly common method for census and description of mangrove swamps (Pool et al. 1977). Allometric formulas for estimating mangrove forest biomass using dbh values have been created for above-ground biomass in mangrove forests in Puerto Rico (Golley et al. 1962), French Guiana (Fromard et al. 1998) and Florida (Ross et al. 2001), and for above-ground plus root biomass in Pakistan (Snedaker et al. 1995). The mangroves of Guyana have been the subject of limited ecological study. Ramdass et al. (1997) collected plot data for an *Avicennia* forest near Alness Village on the country's southeastern coast. Mangrove litterfall dynamics were investigated by Chale (1996) near Onverwagt (see Figure 4.5) southeast of Georgetown, where high levels of small litter productivity were found, at 1771 $g/m^2/yr$, which is approximately double the typical rates reported for Caribbean mangroves and similar to values reported for tropical rainforests.

Mangrove research on the Waini Peninsula was carried out to address several questions about the nature of that plant community. If the coastal *Avicennia* forests have been recently established in stages on an accreting geomorphic formation, their structure should vary over space, with the more recently established stands possessing less biomass, and vary over time if stands are so recent as to have not approached a structural equilibrium of maturity. Mature stands that have not been disturbed should possess a relatively constant structure due to growth and mortality being balanced. The distribution in diameter classes of trees will indicate some aspects of population dynamics of stands. Data collected from the standing trees in the burned mangrove plots, within months after the fires, allowed reasonable comparisons with the living trees of the unburned plots. Also, spatial patterns of trees within those plots may reflect stand history. The early course and stability of plant community recovery immediately after disturbances may be assessed by observing initial changes in vegetation cover. It is also useful to compare the mangroves of the Guianas with those of the Neotropics and the world, in order to understand the ways in which they are either unique or similar.

The vegetation plot data in this study provide initial structural information on both intact and fire-affected mangrove ecosystems on the Waini Peninsula, and allow comparisons with values for other mangrove systems in several parts of the world. Early succession following the fires was investigated through analysis of the changes in herbaceous vegetation in the burned and unburned plots.

METHODS

Study Site

The study site was located near the northernmost point of Guyana, on the Waini Peninsula. Plots were established in two areas just inland of Almond Beach (8° 23' 58'' N, 59° 45' 16" W), a few kilometers to the east of Waini Point (Figure 4.1). In early 1998, parts of the mangrove forest of this area were killed by widespread soil fires, with the burn extending from the coastal beach ridge several kilometers into the interior of the peninsula. A detailed site description, listing of plant species of the Waini Peninsula, and description of the extent of the areas burned in the 1998 fires are given in Chapter 1.

A total of six plots were established, three in *Avicennia germinans* forest with high mortality from the fires and three in unburned *Avicennia* forest toward Waini Point from Almond Beach. The unburned plots were located in an area inland from a narrow beach ridge; burned plots were located inland from the Guyana Marine Turtle Conservation Society (GMTCS) camp, which is located on a broad beach ridge.

Data were also used from the one hectare Man and Biosphere style mangrove plot located near Alness Village (Ramdass et al. 1997), on southeastern Guyana's lower coastal plain, between the Corentyne and Berbice Rivers, (6º12'N, 57º18' W, see Figure 4.5). The Alness Village plot was located in a pure *Avicennia germinans* stand that had been utilized by cutting for poles by local residents. The use of the MAB

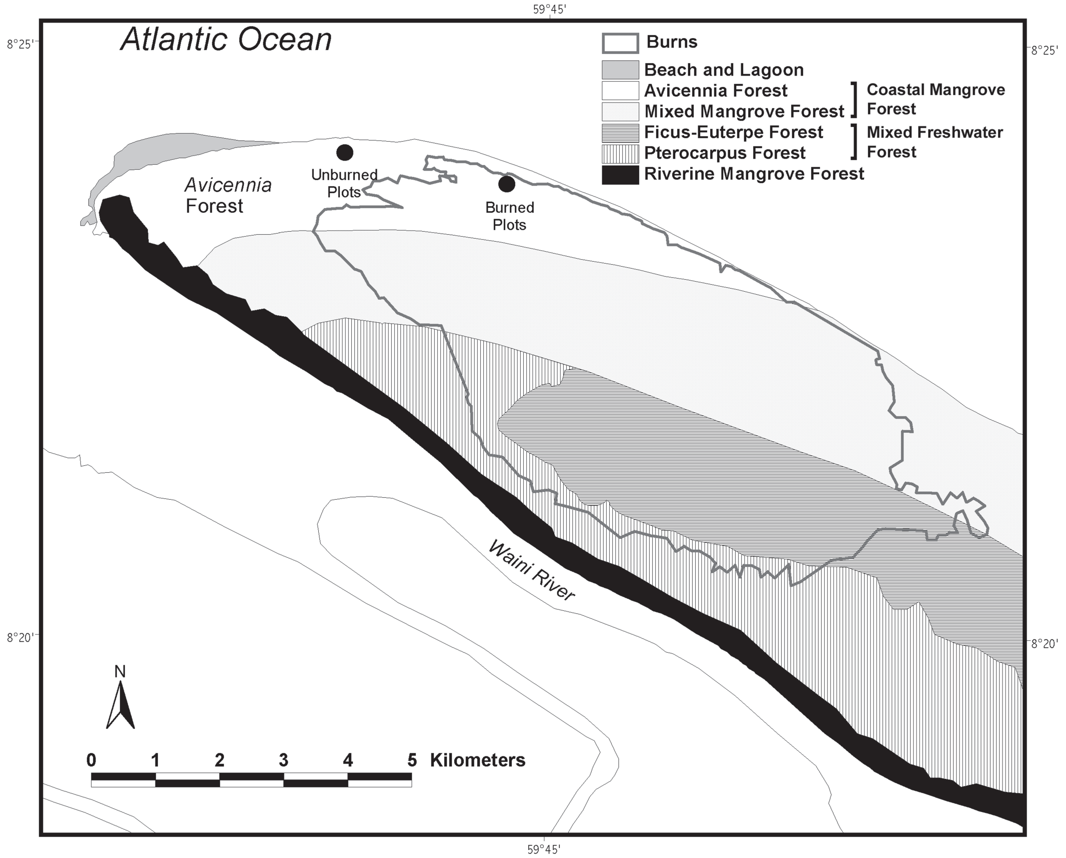


Figure 4.1. Location of modified Whittaker plots in burned and unburned *Avicennia* forest on the Waini Peninsula.

method made those data very comparable to data from the Almond Beach plots.

Plot Establishment

Three 0.1 ha modified Whittaker vegetation sampling plots (Campbell et al. 2002; SI/MAB 1998; Stohlgren et al. 1995; Whittaker 1960, 1973) were established for each treatment, being burned and unburned *Avicennia* swamp. Due to the low diversity of the plant community, having an essentially monospecific tree component and fewer than ten herbaceous species, that sampling area was determined to be adequate. The use of three randomly placed plots allowed for the reduction of placement biases and influences of small-scale irregularities in the forests. Features of the Dallmeier et al. (1992) one hectare plot protocol were adapted for use within the modified Whittaker plot layout, including tagging of all trees of 10 cm dbh or more and mapping of tree locations within the plot. The plots were established six to seven months after the end of fires and were re-sampled three times over a 35 month period in order to monitor changes in tree dbh and cover of seedlings and herbaceous vegetation. Trees in the burned area were measured for dbh and mapped only once, to capture information on pre-fire structure. The unburned forest plots were resampled twice to provide information about the growth rates and mortality of trees, and herbs and tree seedlings were resampled three times in both areas.

Each plot was laid out from a randomly placed corner stake. Corners were determined by measuring a randomly determined 50 to 250 meters along the boundary of the swamp either east or west parallel to the coast line, from a single starting point for each forest type. Then a randomly determined 100 to 300 meters inland was measured into the swamp perpendicular from the swamp edge. The GPS coordinates of those northeast plot corners (Table 4.1), along with the presence of durable tags, should allow relocation of the plots for several years. The northeast corner of each plot was marked with a steel rod. Each 0.1 ha plot was 20 m x 50 m in size, positioned with the long axis oriented east to west (Figure 4.2). The other three corners were established using a Tracon surveyor's compass and tape measure. All corners were marked with large, plastic surveyor's stakes. Plot boundaries were temporarily marked with string for convenience during the surveys. To utilize the tree mapping functions of SI/MAB Biomon software (Comiskey et al. 1999), each 50 m long plot was divided into two 20 m x 20 m quadrats and one 10 m x 20 m quadrat (Figure 4.3). To fully characterize the vegetation, separate measurements were made on herbaceous and woody plants.

For sampling of small woody plants, subplots of three sizes (A, B, C) were set within the 0.1 ha plots for collection of data on herbs and small woody plants. Those were not permanently marked. Ten "A" subplots of 0.5

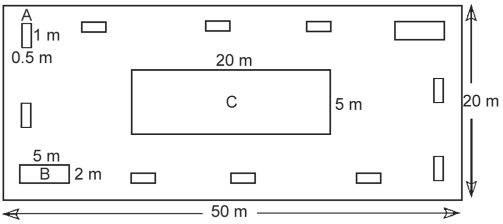


Figure 4.2. Layout of modified Whittaker plot and subplots. Adapted from Stohlgren et al. (1995) and Stohlgren and Chong (1997).

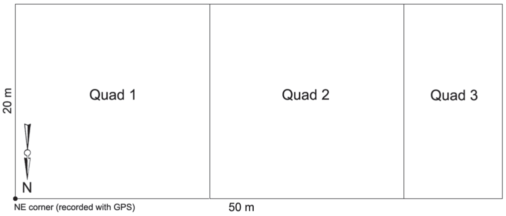


Figure 4.3. Division of the 0.1 ha plots into 20 m x 20 m quadrats compatible with the Biomon program's tree mapping.

Table 4.1. Coordinates of the northeast corners of the six 0.1 ha modified Whittaker plots, in decimal degrees, determined by GPS within 15 m.

Plot number	Latitude	Longitude
1 - Burned	8.40220	-59.77903
2 - Burned	8.40147	-59.78069
3 - Unburned	8.39744	-59.75664
4 - Unburned	8.39673	-59.75550
5 - Unburned	8.39617	-59.75522
6 - Burned	8.40156	-59.77733

m^2 in area, were sampled with a 1 m x 0.5 m frame dropped at 12 m intervals, four along each side and one at each end of each plot. Two "B" subplots placed in opposite corners were 10 m^2 in area, 2 m x 5 m in size. A central "C" subplot was 100 m^2, 20 m x 5 m in size.

All woody plants over 10 cm dbh were mapped by measuring distance from any two adjacent corners, and these measurements were converted to x-y coordinates, calculated by triangulation (Figure 4.4) using the Biomon program (Comiskey et al. 1999). All trees 10 cm dbh or greater were measured at breast height, the species recorded, and labeled with heavy aluminum tags stamped with the plot, subplot, and tree numbers, attached just above the dbh level.

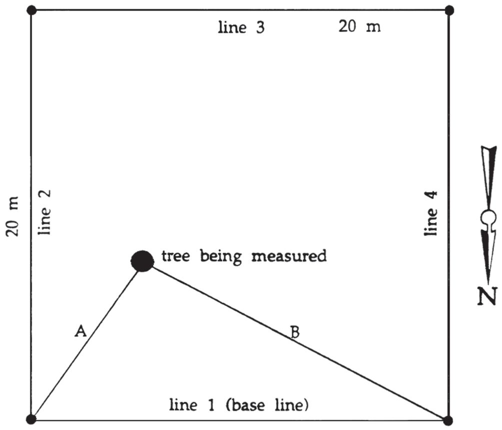


Figure 4.4. Mapping of tree locations in quadrats of SI-MAB plots using triangulation from any two corners. Adapted from Dallmeier et al. (1992).

Water level above or below the substrate was measured to provide basic data on hydrological changes that might have an influence on vegetation and to compare fluctuations in water table between the two sites. Two 10.2 cm (4 inch) diameter, 1.5 m long pvc well pipes were installed 0.75 m deep, one between the burned plots and one between the unburned plots. The bottoms of the well pipes were covered with several thicknesses of porous fiberglass screening, and the tops were provided with removable caps to prevent evaporation.

Measurements

For herbs and small woody plants, in each of the ten 'A' subplots the percent areal coverage of each herbaceous species was visually estimated and recorded. Plant species sampled as herbs included tree seedlings less than 1 cm dbh. In the two 'B' subplots all woody plants greater than or equal to1 cm but less than 5 cm dbh were measured and recorded. In the central "C" subplot all woody plants greater than or equal to 5 cm but less than 10 cm dbh were measured. Measurements were performed at the time of plot establishment in November 1998 and on three subsequent visits in May 2000, April 2001 and October 2001. The first two samplings occurred during fairly wet conditions, with standing water in both living and burned forests, while the April 2001 measurements were made during dry conditions, evidenced by cracking of soil surfaces in the burned swamp. The October 2001 measurements were made during moderately dry conditions, with no standing water in either plot area.

For woody plants, in each of the six 0.1-ha plots, dbh and height of all trees 10 cm dbh or greater were measured in November 1998. For the first census only tree heights were estimated using a simple clinometer at measured distances from the bases of trees. Height measurements were not made after the initial census. Trees were tagged and mapped within the quadrats, and the distances from corners were entered into the SI/MAB Biomon software. The status of each tree as living or dead was recorded; data from dead trees were not included in most analyses. The first census included *Avicennia* trees in the three burned plots that were killed by fire only a few months after their death. Subsequent large woody plant measurements were not made on the burned plots as the dead trees decayed. The three unburned plots were re-censussed for tree dbh at approximately 17 month intervals during May 2000 and October 2001. Basal areas were calculated from dbh using the formula $(0.5*\text{dbh})^2 * \pi$, and then expressed as m^2/hectare. All statistical tests, except where noted, were performed using the S-plus statistical software (Insightful Corporation 2001).

The water table was monitored with the use of a thin dip-stick marked in 1 cm increments. Water depth above or below the soil surface was measured monthly at both wells by marine turtle monitoring crew members, starting during the first plot samplings in November 1998 and continuing until the drought in March 2001.

Alness Village Plot

Data from the *Avicennia germinans* community at Alness Village in the Berbice River region (Figure 4.5) provided the only additional mangrove data from Guyana with which comparisons to Waini Peninsula mangrove physical structure and changes could be made, and effects of usage by local populations can be evaluated. As with the Almond Beach plots, the Dallmeier et al. (1992) plot method had been used to establish and census that 1 hectare plot in 1995 and 1996. Twenty-five quadrats of 400 m^2 each were set up in a 2-quadrat wide belt, with one row 10 quadrats long and the other 15 quadrats long (Figure 4.6). All trees of 10 cm or greater dbh were measured. Tree heights were recorded only in 1996, during the second census. These data were obtained from Ramdass et al. (1997); an electronic version of data from the Alness plot was not available, and so those data printed in the report were re-entered into the SI/MAB Biomon software.

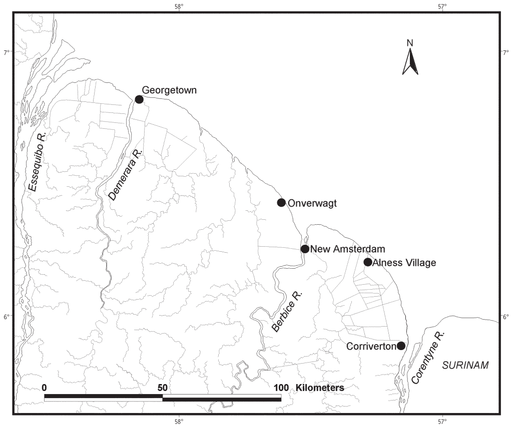


Figure 4.5. Location of Alness Village on the southeastern Guyana coast, site of an *Avicennia* forest 1 ha plot (Ramdass et al, 1997) and Onverwagt, site of an *Avicennia* litterfall study (Chale, 1996).

Dispersion Patterns of Trees

For an analysis of the arrangement of trees in these plots, the dispersion pattern of individuals was calculated. Data from the initial 1998 census only were used to measure dispersion for both the unburned and the burned plots. For each plot the XY coordinates of individuals were calculated using the SI/MAB Biomon program (Comiskey et al. 1999). The Chen and Getis (1998) Point Pattern Analysis (PPA) package was utilized through its on-line application (Aldstadt et al. 1998), using the nearest neighbor algorithm to determine whether the spatial pattern of individuals was random, clustered, or over-dispersed. The nearest neighbor analysis calculates distances between each point and the closest point and compares those distances to expected distance values from a random sample of points from a complete spatial randomness pattern (Chen & Getis 1998).

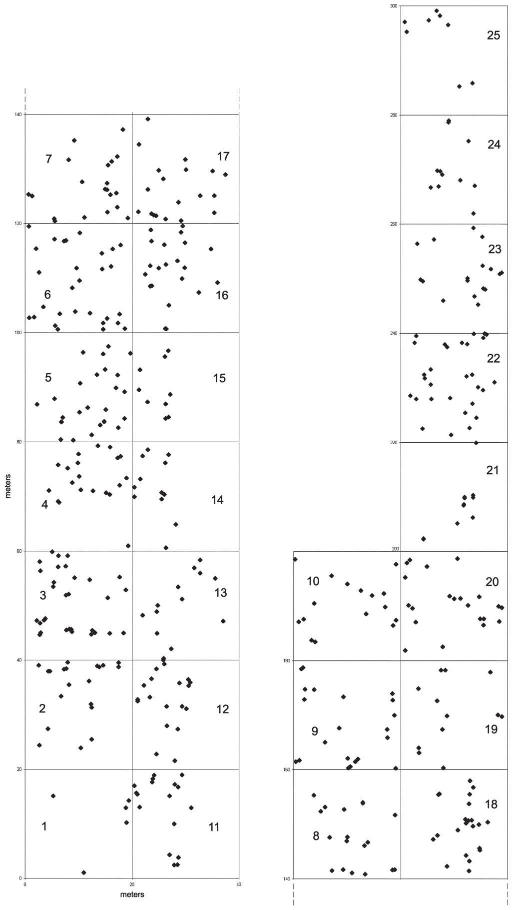


Figure 4.6. Layout of the Alness Village 1 hectare plot (Ramdass et al. 1997) with quadrat numbers and tree locations. Quadrats 1-20 were used for dispersion analysis. This diagram of the linear plot has been divided into two parts for display.

The output of the PPA program includes basic two dimensional statistics and a Z statistic (the standard normal variate) indicating the probability of significant clumping or over-dispersion.

The Alness Village 1 hectare plot was irregularly shaped, however a 0.8 ha portion formed a single rectangle two quadrats wide (Figure 4.6) providing data that was compatible with requirements for the PPA software. The XY coordinates for that rectangle were calculated from values for the component quadrats and run with the PPA software (Chen & Getis 1998).

Biomass

Using the allometric equations derived by Fromard et al. (1998), from *Avicennia* tree measurements in French Guiana, the above-ground biomass values for mangroves at Almond Beach and Alness Village were estimated for comparison with the values from French Guiana. The Fromard et al. (1998) formula for *Avicennia* trees above 4 cm dbh is: biomass = $0.14 * \text{dbh}^{2.4}$, with dbh in cm and the resulting biomass in kilograms; it includes dry weight of wood, leaves, fruit and flower, and above-ground roots. For comparison with swamps of Guyana, additional mangrove biomass values from the literature were assembled from reviews by Lugo and Snedaker (1974) and Fromard et al. (1998) and plotted.

Comparison with Other Plot Data

To further illustrate the relationship of the Waini Peninsula mangroves among mangrove ecosystems worldwide, basal area and stem density data for mangrove forests in several localities were compiled from sources in the literature (Bosire et al. 2003; Brocklehurst & Edmeades 2003; Cardona & Botero 1998; Chen & Twilley 1999; Cintrón et al. 1978; Fromard et al. 1998; Golley et al. 1962; Kjerfve 1998; Lacerda et al. 2002; Lugo & Cintrón 1975; Pool et al. 1977; Ramdass et al. 1997; Ross et al. 2001; Roth 1992; Sherman et al. 2000; Snedaker et al. 1992; Walters 2000). Any reported mean tree or canopy heights were recorded, as were the geomorphic type of the swamps. Where possible the site locations were assigned to 5-degree latitudinal classes.

RESULTS

Tree Mapping and Inventory

Maps of tree locations on the six plots are given in Figures 4.7 to 4.12. A total of 65 trees (64 dead, including trees likely killed by fires and recently fallen, and 1 living tree) were measured in the three combined 0.1-ha plots in the burned site (plots 1, 2, 6; Figures 4.7, 4.8, and 4.9), and 170 individual trees (dead and alive) over all three samplings in the unburned *Avicennia* swamp plots (plots 3, 4, 5; Figures 4.10, 4.11, and 4.12).

A. Dbh and Tree Height

In the unburned forest, differences from any one sampling to the next were not statistically significant (p= 0.558 for 1998 vs 2000 and p= 0.227 for 2000 vs 2001), while the difference approached the p=0.05 significance level between the first and last sampling (p= 0.076 for 1998 vs 2001), indicating that stand structure might be changing slowly over time, possibly to be interpreted as a fairly young forest maturing. Statistical tests paired by individual trees resulted in very low p-values, as would be expected since individual trees almost invariably change over time. The unpaired tests were more suitable for evaluation of overall stand structure.

The dbh of the trees remaining in the burned plots were measured after initial plot establishment in 1998, a few months after the end of fires. Trees in the burned plots which had apparently fallen recently were also measured, and it was assumed that any trees that were dead prior to the fires had been consumed. Dead trees in the unburned plots were omitted from these comparisons. For the unburned plots only the 1998 data were used for comparisons. Variances and skewness between these data were different enough to indicate use of non-parametric tests. Significant differences between dbh of burned and unburned plots were found with the non-parametric Wilcoxon rank-sum test, with a p-value of 0.004.

The maximum dbh recorded in the first sampling for trees at the burned site (65.5 cm) was higher than that of the unburned site (50 cm). The mean dbh value at the burned site of 31.3 cm was significantly higher than the value of 23.3 cm at the unburned site (p=0.0004,

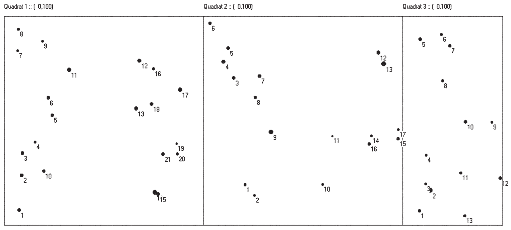


Figure 4.7. Plot 1, unburned *Avicennia* swamp at Almond Beach. The symbol size represents the relative size of each tree that was mapped.

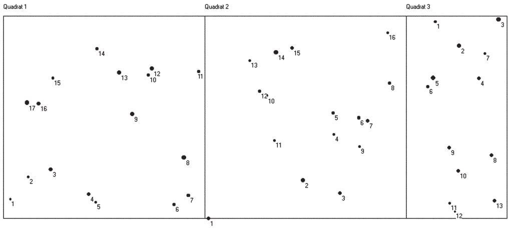


Figure 4.8. Plot 2, unburned *Avicennia* swamp at Almond Beach. The symbol size represents the relative size of each tree that was mapped.

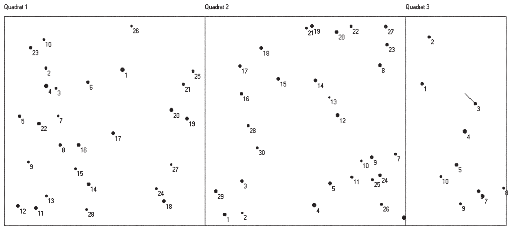


Figure 4.9. Plot 6, unburned *Avicennia* swamp at Almond Beach. The symbol size represents the relative size of each tree that was mapped. Lines extending from a symbol represent fallen trees and the direction of fall.

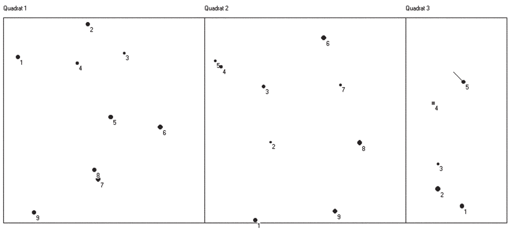


Figure 4.10. Plot 3, burned *Avicennia* swamp at Almond Beach. The symbol size represents the relative size of each tree that was mapped. Lines extending from a symbol represent fallen trees and the direction of fall; in the case of burned plots those were assumed to have been living trees prior to fires.

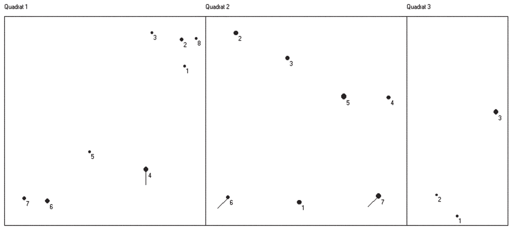


Figure 4.11. Plot 4, burned *Avicennia* swamp at Almond Beach. The symbol size represents the relative size of each tree that was mapped. Lines extending from a symbol represent fallen trees and the direction of fall; in the case of burned plots those were assumed to have been living trees prior to fires.

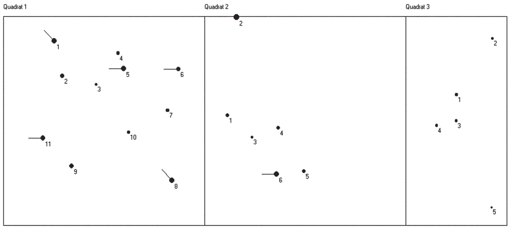


Figure 4.12. Plot 5, burned *Avicennia* swamp at Almond Beach. The symbol size represents the relative size of each tree that was mapped. Lines extending from a symbol represent fallen trees and the direction of fall; in the case of burned plots those were assumed to have been living trees prior to fires.

Welch's modified two-sample t-test). The median dbh values were 28.5 cm for the burned site and 23.1 cm for the unburned site. Diameter class frequencies for the burned plots are graphed in Figure 4.13, and for the unburned plots (2001 census) are shown in Figure 4.14. The 1997 Alness plot and the 1998 unburned plot at Almond Beach had markedly different structures. The Alness mean dbh values of 16.15 cm in 1995 and 16.49 cm in 1996 were not significantly different (t-test, p=0.59). The mean dbh was 23.3 cm at Almond Beach compared to 16.3 cm and at Alness; the median dbh at Almond Beach of 23.1 cm was significantly higher (p=0, Wilcoxon rank-sum test) than the median of 15 cm at Alness. For the Alness Village plots, a dbh distribution for the 1996 sampling is graphed in Figure 4.17.

Maximum tree heights were 36 meters in the burned forest and 34 meters in the unburned forest. Mean tree heights were 21.3 meters in the burned site and 18 meters in the unburned

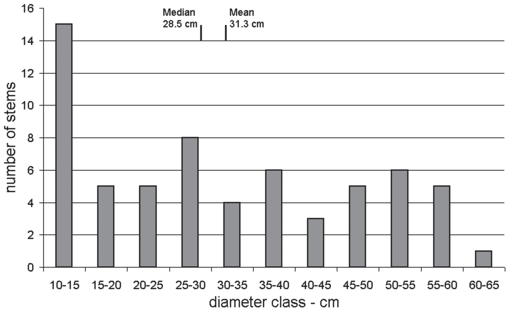


Figure 4.13. Dbh class distribution for the three burned plots combined (0.3 ha), at Almond Beach, from the 1998 sampling. Only living stems are assumed to have remained after the fire. Recently fallen trees killed in the fires were measured and included. The graph suggests periodic waves of successful recruitment. The higher frequency in the 25-30 cm size class is also seen in the unburned swamp.

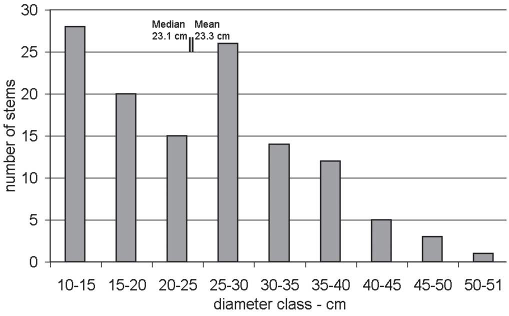


Figure 4.14. Dbh class distribution for the three unburned plots, combined (0.3 ha), at Almond Beach, 2001. Only living stems were included.

site; those were not significantly different (p= 0.268, Wilcoxon rank-sum test). A graph of tree height classes for unburned and burned plots is given in Figure 4.15. A plot of dbh vs height for all unbroken trees in all plots is provided in Figure 4.16; a logarithmic regression provided a best fit for those data, with a formula of y=12.066 Ln (x)-16.595, R^2=0.585, which could be employed to estimate tree height in other *Avicennia* forests. Tree height data were collected for Alness only in 1996, resulting in a mean height of 6.8 meters and a maximum height of 19 meters. Mean tree height at Alness was 6.8 meters compared to 20.7 meters at Almond Beach. The median tree height at Alness Village of 6 meters was significantly lower (p=0,

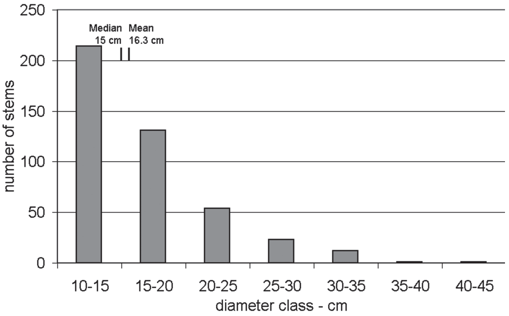


Figure 4.15. Dbh class distribution for 1996 sampling of the Alness Village plot (1 ha). (Ramdass et al. 1997). Only living stems are included. This plot is reported by the researchers as having been frequently disturbed.

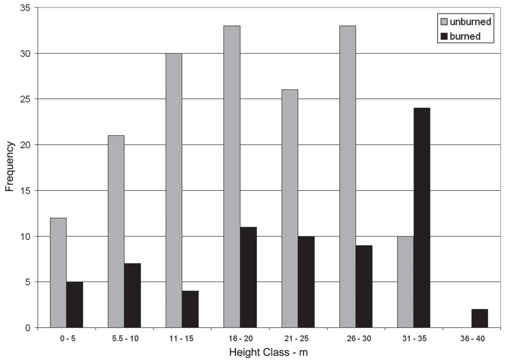


Figure 4.16. Height class distribution for trees in unburned and burned plots at Almond Beach, 1998 sampling. Mean tree heights were 21.3 m in the burned plots and 18 m in the unburned plots. Medians were not significantly different, (p= 0.268 using Wilcoxon ranksum test).

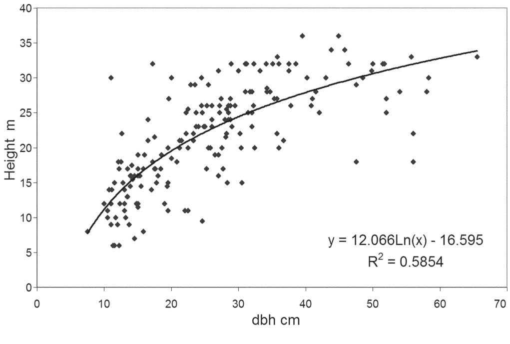


Figure 4.17. Tree diameter vs tree height for all unbroken trees in the Almond Beach plots, with a log-normal trend line.

Wilcoxon rank-sum test) than the 1998 Almond Beach unburned plot median of 21 meters. A graph of tree heights classes for the Alness Village plot is provided in Figure 4.18. Summary statistics for the plots over all years sampled are listed in Table 4.2.

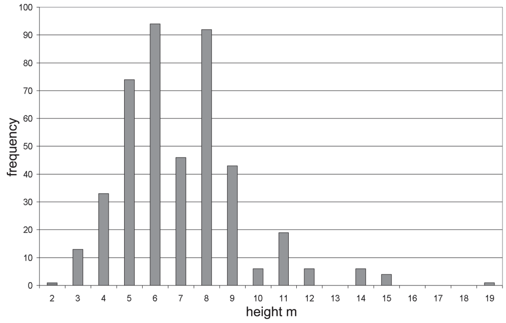


Figure 4.18. Alness Village plot tree height frequency distribution.

Table 4.2. Summary statistics for trees in unburned and burned plots at the Almond Beach sites and the Alness Village site

Site	dbh (cm)			Height (m)		
	Maximum	Mean	Median	Maximum	Mean	Median
Burned 1998	65.5	31.3	28.5	36	21.3	22
Unburned 1998	50.0	23.3	23.1	34	20.7	21
Unburned 2000	51.4	24.0	24.0	na	na	na
Unburned 2001	52.5	25.5	25.9	na	na	na
Alness 1995	47.5	16.1	14.95	na	na	na
Alness 1996	49.0	16.3	15.0	19	6.8	6

B. Basal Area

The basal area for trees that were located in the combined three burned plots, measured only in 1998, was 20.43 m^2/ha. The basal areas of living trees in the combined three unburned plots, were 21.25 m^2/ha in 1998, 22.36 m^2/ha in 2000 and 23.16 m^2/ha in 2001. Over the 34 month study period, basal area in the three unburned plots increased by 1.91 m^2/ha. Three pairs of t-tests were made to compare means between the three years for the grouped unburned plots. Between the three years variances of distributions were similar, therefore t-tests were acceptable; they were used for both paired and unpaired data. For the Alness Village plots sampled by Ramdass et al. (1997), basal areas were 10.07 m^2/ha in 1995 and 10.28 m^2/ha in 1996 (not significantly different, p=0.42).

C. Dispersion

For the unburned plots, nearest neighbor analysis of plot 1 resulted in an observed mean distance between trees of 2.22 m while the expected distance was 2.48 m, with a z-value of -1.16. This negative Z statistic value indicates that, while a clustered distribution was observed, it was not quite significantly different from a random distribution at the p=0.05 level. For plot 2 the mean distance between trees was 2.75 m with an expected distance of 2.66 m. The Z statistic obtained from the nearest-neighbor analysis suggested slightly over-dispersed (uniform) distribution, however the tendency was not significantly different from a random distribution, with Z=0.33. For plot 6 the mean distance between trees was 2.48, with an expected distance of 2.18. The Z statistic value of 1.686 indicated a tendency toward over-dispersion but slightly below statistical significance at the p=0.05 level.

For the three burned plots, all point pattern analyses resulted in positive Z statistic values indicative of over-dispersion, however with no significant tendencies (Z statistic values were < 1.96, p>0.05). Plot 3 data showed a mean distance between trees of 3.80 m, and an expected value of 3.28 m with a Z statistic value of 1.331. The mean distance between trees in plot 4 was 4.40 m, with an expected value of 3.83 m and a Z statistic value of 1.076. Plot 5 had an mean distance between trees of 3.80 m and an expected distance of 3.39 m with Z statistic value of 0.99.

The Alness Village plot nearest neighbor analysis found an mean distance between trees of 1.86 m, with an expected distance of 2.34 m, indicating a highly significant clustered distribution of trees for that plot (Z = -7.2114).

D. Density and Population Turnover in the *Avicennia* Forest

Stem densities between the two sites were very similar, with Alness density being 445 stems per ha compared to an Almond Beach unburned plot density of 440 stems per ha. Alness stem density decreased from 445 stems/ha to 436 stems/ha over the one year interval. In the three 0.1-ha unburned *Avicennia* plots, only four new trees entered the >10 cm population over the 34 month study period: two during the 1998-2000 interval and two during the 2000-2001 interval. Over the same intervals, a total of 29 trees died or disappeared from the living *Avicennia* plots, seven during the 1998-2000 interval and 22 during the 2000-2001 interval.

The number of living trees in the three unburned plots (0.3 ha total) was 132 in the 1998 census, 130 in 2000 and 115 in 2001, corresponding to per ha densities of 440, 433.3 and 383.3 stems respectively. The density of living trees therefore decreased in the first interval by 6.7 per ha and in the second interval by 50 per ha. In the burned plots, only 64 trees were located in the single census, a density of 213.3 trees per ha. The Alness Village plot had a density of 445 stems/ha in the first census and 436 stems/ha in the second census, a decrease of 9 stems/ha.

E. Biomass

Estimated biomass values for the Almond Beach plots and for the Ramdass et al. (1997) Alness Village plots are given with the corresponding basal areas in Table 4.3. The 1998 biomass value for the burned plots of 165,207 kg/ha was slightly higher than the unburned plot mean of 154,970 kg/ha, though the basal area totals for the burned plots was lower than for the unburned plots.

Table 4.3. Biomass and basal area values for plots at Almond Beach by site and year and for Alness Village by year. Biomass values were calculated from the allometric formula of Fromard et al. (1998).

Site	Biomass kg/ha	Basal area m^2/ha
Unburned 1998	145,637	21.25
Unburned 2000	155,641	22.36
Unburned 2001	163,632	23.16
Burned 1998	165,207	20.43
Alness 1995	58,605	10.07
Alness 1996	60,300	10.27

Worldwide biomass values gathered from the literature are summarized in descending order in Table 4.4 and graphed in Figure 4.19. The Guyana values from Almond Beach and Alness Village plots are emphasized (bold print) in both the graph and table. The maximum biomass value was 460,000 kg per ha, from a plot in Malaya, while the mean for all values, including dwarf and early successional stands, was 159,328 kg/ha, in the range of values from the Almond Beach plots.

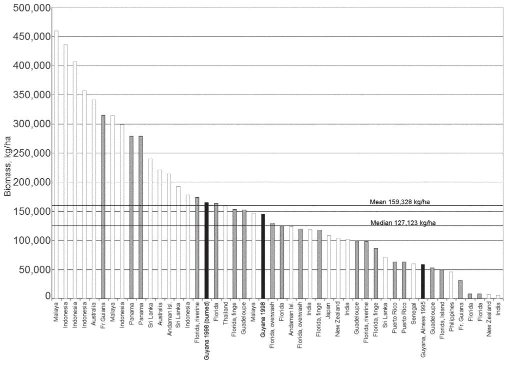


Figure 4.19. Mangrove biomass values (kg/ha) from compiled studies, sources included Lugo & Snedaker (1974) and Fromard (1998). Values from Guyana are shaded black, others from the Neotropics are in black, and values from the Asian-Pacific region are in white. Labels for values from this study are labeled in bold type. Units are in dry weight.

Small Woody Plants

The "B" subplots sampled very few individuals from 1 cm and less than 5 cm dbh (saplings). Only one living individual in the size range was recorded in all unburned plots over all census dates, an *Avicennia* sapling of 2.8 cm dbh in plot 6 in the October 2001 census. During that sampling there were 14 *Laguncularia* and four *Avicennia* saplings located in the "B" subplots of plot 4 in the burned swamp. The basal areas of these small saplings were 0.10

Table 4.4. Mangrove biomass values from 46 additional plot sites worldwide, compiled from the literature, in descending order. Values from Almond Beach and the Alness Village study are highlighted in bold face.

Biomass Values	Biomass kg/ha	Source
Malaya	460,000	Fromard, 1998
Indonesia	436,400	Fromard, 1998
Indonesia	406,600	Fromard, 1998
Indonesia	356,800	Fromard, 1998
Australia	341,000	Fromard, 1998
Fr. Guiana	315,000	Fromard, 1998
Malaya	314,000	Fromard, 1998
Indonesia	299,100	Fromard, 1998
Panama	279,212	Lugo & Snedaker, 1974
Panama	279,200	Fromard, 1998
Sri Lanka	240,000	Fromard, 1998
Australia	220,800	Fromard, 1998
Andaman Isl.	214,000	Fromard, 1998
Sri Lanka	193,000	Fromard, 1998
Indonesia	178,200	Fromard, 1998
Florida, riverine	173,900	Lugo & Snedaker, 1974
Guyana 1998 (burned)	**165,207**	**This study (Fromard equation)**
Florida	164,000	Fromard, 1998
Thailand	159,100	Fromard, 1998
Florida, fringe	152,868	Lugo & Snedaker, 1974
Guadeloupe	152,300	Fromard, 1998
Malaya	147,000	Fromard, 1998
Guyana 1998	**145,637**	**This study (Fromard equation)**
Florida, overwash	129,645	Lugo & Snedaker, 1974
Florida	124,600	Fromard, 1998
Andaman Isl.	124,000	Fromard, 1998
Florida, overwash	119,582	Lugo & Snedaker, 1974
India	118,700	Fromard, 1998
Florida, fringe	117,523	Lugo & Snedaker, 1974
Japan	108,100	Fromard, 1998
New Zealand	104,100	Fromard, 1998
India	101,900	Fromard, 1998
Guadeloupe	98,600	Fromard, 1998
Florida, riverine	98,218	Lugo & Snedaker, 1974
Florida, fringe	86,192	Lugo & Snedaker, 1974
Sri Lanka	71,000	Fromard, 1998
Puerto Rico	62,900	Fromard, 1998
Puerto Rico	62,850	Lugo & Snedaker, 1974
Senegal	60,000	Fromard, 1998
Guyana, Alness 1995	**58,605**	**Ramdass et al., 1998 (Fromard eq.)**
Guadeloupe	52,800	Fromard, 1998
Florida, Island	48,968	Lugo & Snedaker, 1974
Philippines	45,936	Lugo & Snedaker, 1974
Fr. Guiana	31,500	Fromard, 1998
Florida	8,200	Fromard, 1998
Florida	7,900	Fromard, 1998
New Zealand	6,800	Fromard, 1998
India	5,800	Fromard, 1998
Mean	159,328	
Median	127,123	
Max	460,000	
Min	5,800	

m^2/ha in the unburned swamp and 2.02 m^2/ha in the burned swamp. In the three 0.01 ha "C" subplots in the unburned swamp, only four saplings from 5 cm dbh up to 10 cm dbh were found in the three unburned "C" plots in the first census, six saplings in the second census, and seven in the third census, with total basal areas of 0.68, 0.87 and 1.1 m^2/ha respectively. A summary of changes in small woody plant basal areas is illustrated in Figure 4.20.

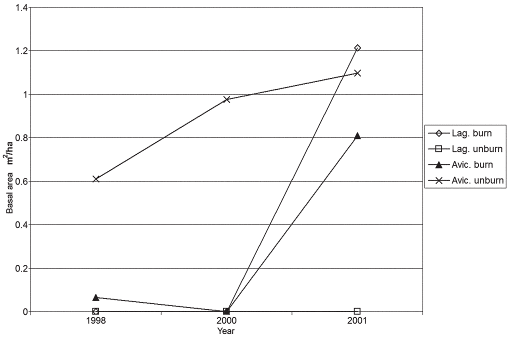


Figure 4.20. Changes in basal area for burned plots, for small woody plant species from 1 cm dbh to less than10 cm dbh, over three samplings.

Herbaceous Plants

Herbaceous vegetation composition varied dramatically over four samplings. The vegetation in both burned and unburned plot areas was influenced to a great degree by recent precipitation amounts and the levels of standing water in the swamp, which varied significantly.

In the unburned plots, the first sampling in November 1998 took place after a period of high rainfall, which was reflected in 33% areal coverage of the small floating aquatic plant *Lemna aequinoctialis* Welw. and some presence of *Rhizoclonium africanum* algae on pneumatophores of the *Avicennia* trees. Drier conditions prior to the second sampling in April 2000 apparently provided good conditions for germination of *Avicennia* propagules, when the highest coverage rate of those was recorded, at just over 2% . The third sampling in April 2001 followed an extended dry period, and almost no herbaceous vegetation was recorded other than a few *Avicennia* seedlings. For the final sampling of October 2001, conditions had been less dry, and there was a slight increase in the coverage of *Avicennia* seedlings.

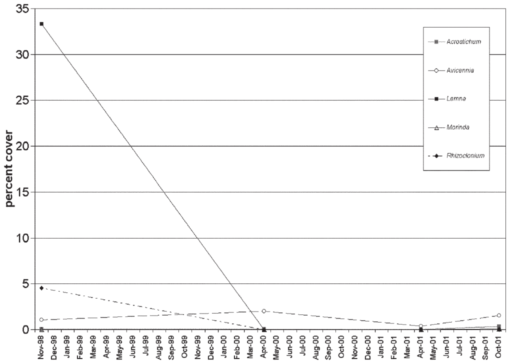


Figure 4.21. Changes in percent areal coverage of herbaceous species in unburned *Avicennia* plots, over four samplings, 1998-2001.

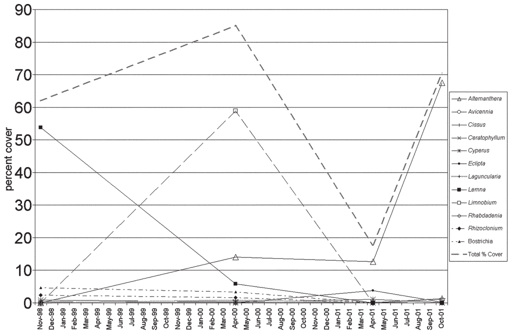


Figure 4.22. Changes in percent areal coverage of herbaceous species in burned *Avicennia* plots, over four samplings, 1998-2001.

While herbaceous vegetation was largely absent from the unburned *Avicennia* plots (Figure 4.21), it was present in the burned swamp throughout the samplings (Figure 4.22). The floating aquatic *Lemna aequinoctialis* was common for several months following the fires, with 53.8% cover during the 1998 sampling. During the May 2000 sampling, two years after the fires, the predominant floating aquatic vegetation was *Limnobium laevigatum* (Humb. & Bonpl. ex Willd.) Heine (58.8% cover), along with some spots of the sprawling terrestrial herb *Alternanthera sessilis* (L.) R.Br. ex DC (14% cover) and *Acrostichum* ferns on a few slightly elevated areas present in the vicinity but not sampled. The April 2001 sampling followed a strong dry season, and the dominant herbaceous vegetation in the burned areas was *Alternanthera* (12.6% cover). The final sampling in October 2001 also followed a dry season, and showed a sharp increase in dominance of *Alternanthera* (67.5% cover) in the burned area plots and an increase in seedlings of white mangrove *Laguncularia racemosa* (from 0.07% to 1.33% cover) which were concentrated in areas near the scattered surviving individuals of that species.

Chi square analyses were performed with herbaceous plants both burned and unburned plot data matrices by species over the four sampling periods (Table 4.5), testing for differences between expected and observed values of percent cover. Expected values were derived from the product of the percent coverage totals for the column and row of each combination of date and taxon, divided by the grand total for all combinations. Percent coverage for all "A" subplots in the three plots at each site were averaged. For both burned and unburned sites, differences in values for herbaceous cover were statistically significant between the species over the four samplings, with p < 0.001 in both burned and unburned habitats.

Table 4.5. Mean percent cover for herbaceous species over the four samplings in burned and unburned plots. These data presented in graphical form in Figure 4.21 for unburned plots and 4.23 for burned plots.

	Burned				Unburned			
	1998	2000	2001	2001b	1998	2000	2001	2001b
Acrostichum						0.03		0.33
Alternanthera		14.07	12.60	67.50				
Avicennia		0.03	0.13		0.37	2.03	0.37	1.63
Cissus		0.07						
Ceratophyllum	0.33							
Cyperus	0.83	0.37	1.13	0.07				
Eclipta			3.73	0.27				
Laguncularia		0.83	0.07	1.33				
Lemna	53.83	5.83			33.33			
Limnobium		58.83						
Morinda								0.07
Rhabdadenia			0.03	1.17				
Rhizoclonium	2.33	1.67			4.53			
Bostrichia	4.67	3.33						
Total % cover	**62.00**	**85.03**	**17.70**	**70.33**	**38.23**	**2.07**	**0.37**	**2.03**

Principal Components Analysis (PCA) allows summarization of multivariate data for visualization in two or three dimensional display, by determining optimal standardized linear combinations of many variables. PCA was performed using herbaceous data from all six plots over the four sampling dates from 1998 to 2001.

In the PCA Ordination, the three first axes (Figure 4.23) account for over 98% of the variance in this ordination (Figure 4.24). Three taxa have the major influence (loadings) on these components: *Alternanthera*, *Lemna*, and *Limnobium* (Figure 4.25). The principal components biplot graph displays the original taxon variables on the same axes with the transformed observations.

The *Lemna* vector represented the relative loadings of the two most important principal components for the 1998 sampling, trending towards the position of points for plots 3 (point #9), 4 (#13) and 5 (#17). The highest values for *Lemna* in plot 4 were nearly matched by those for plot 1 (#1). The *Limnobium* vector had as its extreme points the 2000 sampling in burned plots 3 (#10), 4 (#14) and 5 (#18). The *Alternanthera* vector showed extremes on the October 2001 sampling, in burned plots 3 (#12), 4 (#16) and 5 (#20). *Alternanthera* was also strongly represented in the March 2001 sampling in plot 4 (#15).

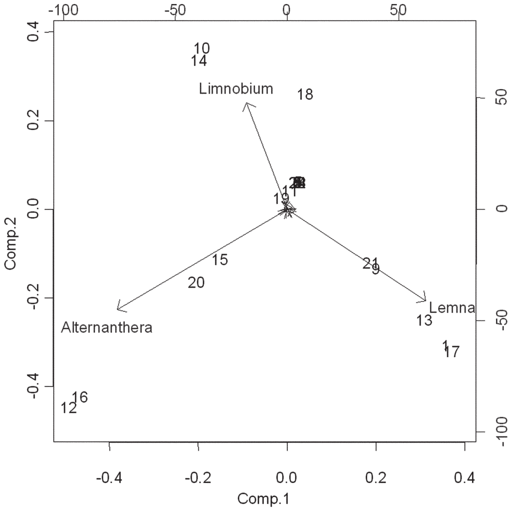


Figure 4.23. Principal Components Analysis (PCA) biplot for percent areal coverage of herbaceous vegetation in burned plots. The coverage for the floating aquatics *Lemna* and *Limnobium* and the annual herb *Alternanthera* account for most of the variance within the data.

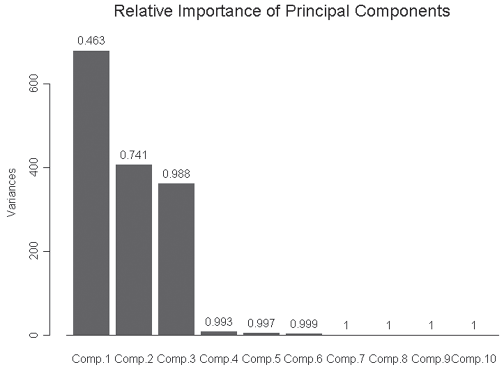


Figure 4.24. Relative importance of the Principal Components for herbaceous vegetation of burned plots. The cumulative importance for the first three components is 98.8%, indicating that they are overwhelmingly responsible for variances in these data.

All other species in the PCA ordination had minor cover and were outweighed by other taxa, and so clustered in the center of the graph. Except for the occurrence of moderate *Lemna* coverage in 1998, the unburned plots fell into that space because of very sparse herbaceous cover.

Well Levels

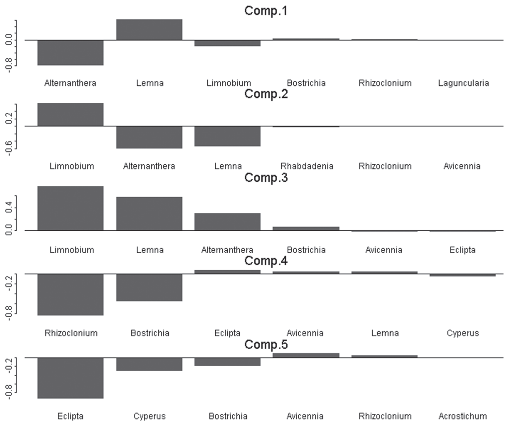


Figure 4.25. Loadings for the principal components for herb species in the burned plots.

Hydrology in the Waini Peninsula *Avicennia* swamps is dominated by rainfall, because tidal influence is limited by beach ridges along much of the coast. Outlets to the ocean are infrequent, and creeks draining the swamps often empty first into lagoons, some of which are above mean sea level, limiting tidal influence. Changes in the lagoon outlets can have significant influence on hydrology of the swamps near the coast. Well levels recorded in the burned and unburned *Avicennia* swamps are shown in Figure 4.26. Water levels in both burned and unburned plots followed very similar patterns of fluctuation, and remained above the

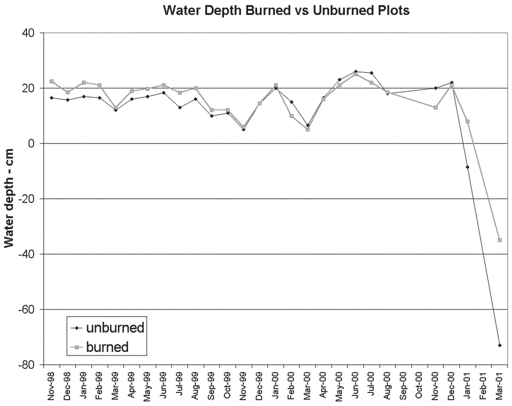


Figure 4.26. Well levels in burned and unburned areas over the period from the first to third samplings of herbaceous vegetation. A drought in early 2001 is conspicuous, though its severity was far less than the 1997-1998 drought that led to the fires on Waini Peninsula.

surface of the substrate until early 2001. Those peaked around 25 cm above the surface during wet seasons.

DISCUSSION

Guyana Plots

Avicennia swamps are typical of early succession on the coasts of the Guianas, as evidenced by monospecific bands of young trees on accreting parts of the coastline. This was evidenced by the *Avicennia* community documented here through the increases in size of individual trees between the "younger" area of the unburned plots and the burned plots in supposedly "older" areas farther from the Waini Point. There was also an increase in mean dbh and biomass within the unburned swamp over time, from sampling to sampling. The mean dbh value of the burned plots was significantly (p= 0.004) more than the mean for the unburned plots at Almond Beach, but it is also possible that some smaller living stems in the burned swamp were completely consumed by fire. Both the maximum diameters and maximum tree heights recorded in the burned swamp were also higher than in the unburned swamp, suggesting that the forest structures of the two areas were different before the fires, and that the burned area was a somewhat more mature mangrove stand. Probably neither stand had reached an equilibrium since their initial establishments. Basal areas of living trees in the unburned plots increased over both sampling intervals, 1.11 m^2/ha in the first interval and only 0.8 m^2/ha in the second, suggesting that it was a young, growing stand. An observed gradual increase in frequency of *Rhizophora* trees in the swamps along the Waini Peninsula coast to the southeast of Almond Beach also supported the idea that an equilibrium had not been reached.

The very low numbers of seedlings and trees less than 10 cm dbh also suggested that recruitment was poor, and occurred periodically rather than consistently from year to year. Dbh distributions of trees within the Almond Beach *Avicennia* swamps, with interspersed classes of high and low frequency, suggest periodic recruitment waves.

Although both median basal areas and tree heights were significantly higher at Almond Beach than at Alness Village, the occurrence of a few individuals with dbh similar to the maximum at Almond Beach (49 cm dbh vs 50 cm dbh) suggests that the Alness Village stand had been present for some time and might have matured to a structure similar to the Almond Beach stands, if undisturbed by tree cutting. Utilization impacts should be considered in the development of mangrove management plans. Prior to this Almond Beach plot study no data from Guyana were available to allow comparison with the Alness Village *Avicennia* forest.

Stem density also decreased slightly in the Alness Village plots over the one year interval, while basal area increased, although differences between the two years were not highly significant. Still, the increase suggested an *Avicennia* population that was growing and perhaps recovering from disturbance. Ramdass et al. (1997) conjectured that ongoing low-level disturbances occurred in that swamp, probably through periodic cutting, but he also believed that the visible tree tags in the Alness plots may have made local people may wary of utilizing those trees. Stem density data were available for 89 of the worldwide plots compiled from the literature, with values ranging from 267 stems/ha to 47,330 stems/ha. The combined Almond Beach unburned plots had a stem density of 413 stems/ha, compared to the compiled median of 3,120 stems/ha for all plots and the mean of 5,493.8 stems/ha. Stem densities from those plots are graphed with Almond Beach values in Figure 4.27.

Tree heights were compiled for 61 worldwide plots, with stand height values ranging from 2.9 meters to 23 meters; the median for those values was 10 meters and the mean 10.98 meters. That compares to mean heights of 18 meters in the unburned Almond Beach swamp and 21.3 meters in the burned swamp, with respective medians of 18 meters and 22.5 meters. The tallest trees at Almond beach were 34 meters in the unburned swamp and 36 meters in the burned swamp. In the Alness Village plot, out of 438 tree height measurements made in 1996, the mean tree height was 6.98 meters and the median 7 meters, with a maximum recorded tree height of 19 meters.

The Riverine Swamps on the Waini Peninsula were not sampled, however some large *Rhizophora* trees were observed along the rivers, and scattered, unusually large *Avicennia* trees were observed near the upland boundary of Riverine Swamps. The riverine systems are more frequently flushed than the coastal basin swamps, due to the latter's separation from tides by beach ridges. It is quite possible that higher basal area values occur in the Riverine Mangroves as a result of the lower salinity that was typical in those soils (generally >20 psu near the Atlantic beach ridges and <10 PSU from the central Waini Peninsula towards the Waini River, T. Hollowell, unpublished data). Additional research could allow insight into the relationship of soil salinity and hydrology with the forest composition or structure between the riverine and coastal swamps.

Dispersion

Over-dispersion of trees in mature forests might be attributable to heightened competition for light, nutrients and water among trees that are close to each other. Most of the Almond Beach plots were slightly over-dispersed, as might be expected for a maturing forest with individuals in competition (Wells & Getis 1999). Plot 1 exhibited a slightly clustered distribution. None of the results for the PPA tests were significant at the p= 0.05 level (z = ‴1.96), so although there were dispersion tendencies, the patterns were not significantly different from random.

In graphic representations of the plots (Figures 4.7 through 4.12) some linear patterns were discernable. Some of those patterns might have resulted from stranding during waves of seed dispersal, reflecting natural barriers such as slight variations in topography, fallen trees, or branches.

The Alness Village plot distribution of trees was significantly clustered, with a PPA p-value well below 0.05 (Z=-7.21). That may be a result

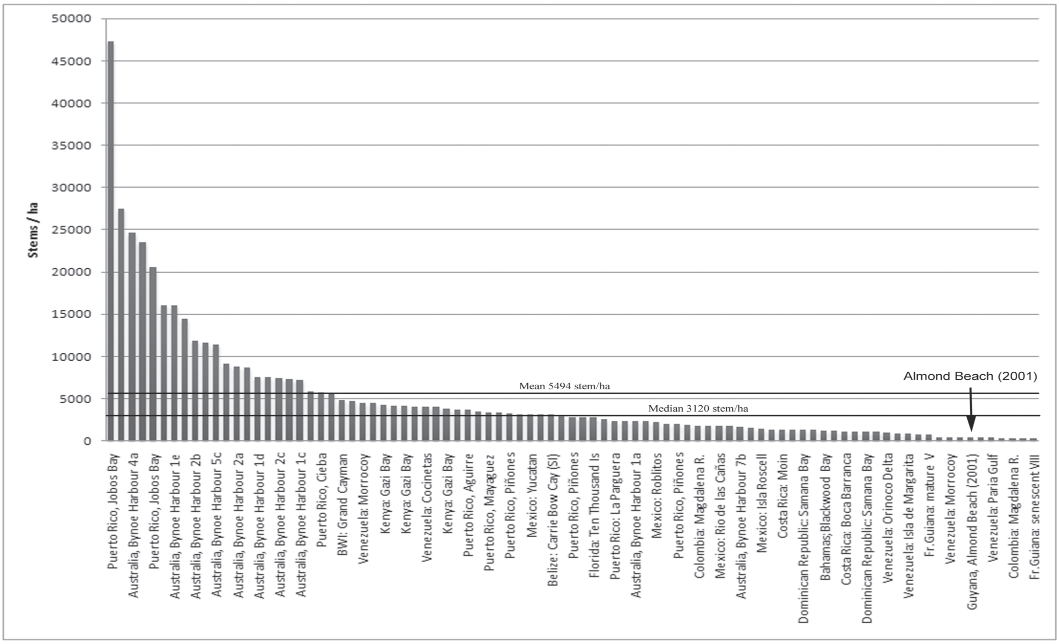


Figure 4.27. Stem densities per hectare, from 88 plot studies, including the Waini Peninsula. Many of the highest values were from Australian plots (Brocklehurst & Edmeades 2003). Guianas values are shaded black; the 4 highest of those were from French Guiana (Fromard et al. 1988), followed by Alness Village and the Almond Beach unburned plots (indicated by the arrow). The lowest value was for a senescent mangrove community in French Guiana.

of patchy disturbance patterns due to utilization. The clustering of individuals might also reflect localized *Avicennia* propagule sources or irregular stranding of propagules on logs, branches or slight variations in topography. Additionally, the clustering may be indicative of low levels of competition from thinning by utilization, which would keep basal area low (10.28 m^2/ha in 1996 vs 21.25 m^2/ha in 1998 for Almond Beach unburned plots) and prevent competition that might lead to overdispersion. In general, the dispersion results indicated that the Almond Beach *Avicennia* forests had been established long enough without disturbance for competition to begin to exhibit an overdispersed pattern (Wells & Getis 1999).

Biomass

While basal area values determined for the burned plots were lower than the unburned plots in the same year, estimated biomass values were slightly higher for the burned plots. It should also be noted that dbh measurements for trees in the burned forest were probably an underestimate of pre-burn structure, since the trees shed their bark shortly after fire mortality, and may have shrunken slightly during drying. It is possible that some live trees may have been entirely consumed during the fires, although it is more likely that only dead trees were consumed. Comparisons of biomass provide a variation on comparisons between stands. By transforming dbh data to account for the consequences of diameter changes, biomass values are more sensitive to differences in tree size, and they allow better differentiation between young stands with many small trees and mature stands with fewer but larger individuals. Allometric formulas such as those provided by Fromard et al. (1998) are a useful tool. The mean wood biomass value for the burned plots, 165,207 kg/ha, could contribute to an estimate of the amount of carbon that will be released to the atmosphere as the dead wood decomposes. Root biomass and soil would be responsible for additional carbon release from the fires. Snedaker et al. (1995) found that *Avicennia marina* trees in Pakistan had root biomass that was approximately 47-57% of total biomass, so assuming that Neotropical *Avicennia* is similar, carbon loss estimates for the fires might be doubled. During this field work, the depth of the organic layer lost to burning in the *Avicennia* swamp was estimated by an informal survey of length of pneumatophores above the soil surface in burned and unburned patches of swamp, under the assumption that pre-fire hydrology was similar between the sites. That yielded a difference between the means of 4.6 cm (N=40, p-value=0.001), which could be considered depth of organic soil lost in the fires. Organic soil samples were not collected for analyses of carbon content, but soil samples from similar sites could be obtained from the site for estimates in the future.

Comparisons with Worldwide Plot Basal Area Data

The compilation of plot values from studies in the literature yielded a total of 96 sites, of which 95 included basal area values and most included stem density values. The great majority of those data were drawn from studies that sampled all trees 2.5 cm dbh and greater. Almond Beach unburned plots had an almost negligible number of stems between 2.5 cm and 10 cm dbh, (only seven stems in the 5-10 cm range, representing additional basal area of only 1 cm/ha) making the Almond Beach data comparable to the compiled plot data.

Basal areas in the compiled plot data ranged from 1.17 m^2/ha to 96.4 m^2/ha. The mean basal area for the Almond Beach unburned plots was 23.2 m^2/ha, almost exactly the median value from the compiled sites of 23.25 m^2/ha and near the mean value of 25.6 m^2/ha.

Latitude classes could be determined for 94 of the compiled sites. There were no strong trends in mangrove basal area (m^2/ha) vs latitude, though possibly this could be demonstrated with a larger data set that was balanced in other factors. The non-parametric Kruskal-Wallis rank-sum test was used to compare the 6 latitude classes with 8 or more values, and resulted in a p-value = 0.167, indicating no statistically significant difference. Basal area values (m^2/ha) for the sites are grouped by latitude class in Figure 4.28.

Compiled basal area data were grouped by swamp geomorphic type according to the classification of Lugo and Snedaker (1974). Overwash type swamps were not included, as there was not an adequate number of values. There was no significant difference between fringing (coastal) and basin (interior) mangrove types (p-value = 0.84). Riverine swamp basal areas were significantly higher than either fringing or basin, with p= 0.005 for riverine vs fringing swamps and p= 0.019 for riverine vs basin swamps. Basal area values for the sites are grouped by geomorphic type in Figure 4.29.

Population Turnover in the *Avicennia* Forest

The higher rates of mortality observed during the interval between the second and third samplings might have been due to a moderate drought; precipitation in northern Guyana for January - June 2001 was less than 40% of the 1961-1990 average (Waple et al. 2002). Basal areas of living trees did increase over both of those intervals, 1.11 m^2/ha in the first interval and only 0.8 m^2/ha in the second. That indicates that the *Avicennia* forest sampled is still a young, growing stand that has not yet reached equilibrium since establishment. The loss of stems as the plots mature is a typical self-thinning pattern of a young forest. *Avicennia*, like other tropical tree species, does not form annual growth rings found in temperate trees, preventing direct analysis of population structure. However, patterns of fluctuating tree frequencies among dbh classes seen in both burned and unburned plots (Figures 4.15 and 4.16) suggest intermittent periods of recruitment, which is also consistent with variable numbers of seedlings in herbaceous layers of the plots, with the low number of sapling sized trees, and with the low success rates of plantings of *Avicennia* propagules (Chapter 5).

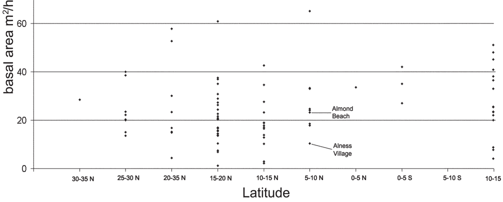


Figure 4.28. Compiled basal area values grouped into 5-degree latitudinal classes.

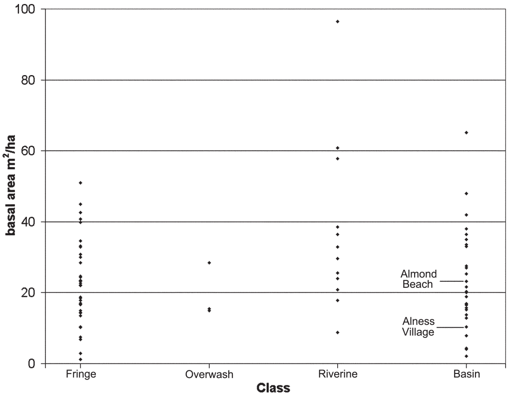


Figure 4.29. Compiled basal area values grouped by geomorphic type of the mangrove forests.

Herbs and Seedlings

Coverage of herbs in both burned and unburned plots was highly variable in both cover and species composition. In the unburned areas, there was significant cover of only *Lemna* during wet periods, with the alga *Rhizoclonium africanum* on *Avicennia* pneumatophores also apparent when swamps were flooded. There was almost no herbaceous cover in unburned swamps during dry periods, and what was observed mainly consisted of infrequent *Acrostichum* ferns.

The year of the sampling shows a strong relationship to species in the PCA ordination of the herbaceous data, most likely driven by variations in rainfall. While hydrology was apparently a major influence on herbaceous cover changes, other environmental factors such as nutrient levels could have an effect on competition between *Lemna* and *Limnobium*, as could timing of their dispersal to the burned site. *Lemna* was present in nearby unburned *Avicennia* forest, which may have given it an immediate advantage of proximity for early colonization, while *Limnobium* is possibly a more aggressive occupier of space in the open water of the burned swamp. *Alternanthera* is evidently comparatively drought resistant and almost maintained its 2000 level of coverage into the very dry sampling period in early 2001, after which it expanded further.

Avicennia seedlings seem to undergo cyclic establishments with high mortality and only very rare graduation to larger sizes. This is evidenced in the very sparse density of saplings and small trees that were found in the plots. In general, the young, unburned *Avicennia* forest conformed to common concepts of sparseness of mangrove understories (Janzen 1985; Lugo 1986), although exceptions were seen in dense understories that were observed in older, mixed mangrove stands in parts of the Waini Peninsula in areas of sparse canopy and treefall disturbance. In general, the number of understory and epiphytic species found in the mangrove swamps increased with distance from the ocean and its salinity. Certainly the set of plant species that can survive the salinity and anaerobic soils of mangrove swamps is limited, and that number may be further reduced when a forest is intact, in which case there would be high competition for light, nutrients and water. The unburned *Avicennia* forest would presumably have low rates of treefalls because it was a young stand, and so there would be fewer gaps with increased resources. The unburned forest plots were located near the ocean where soil salinities reached very high levels during droughts (in excess of 50 psu in October 2001, T. Hollowell, unpublished data), which may also have eliminated unadapted understory species. In the *Avicennia* forest near Waini Point there was additionally a very high density of pneumatophores, which play a role in limiting establishment or survival of understory species, although such an effect has apparently not yet been addressed in mangrove ecological studies. Snedaker and Lahmann (1988) had to impose a strict definition of mangrove communities, including frequent tidal inundation and lack of disturbance, in order to maintain the concept of a characteristically sparse mangrove understory. However, it may be best to accept that mangrove systems are so variable in geomorphology, hydrology, and disturbance regimes that understory densities can vary widely, with the stress of salinity favoring more extreme values at the low end.

Role of Water Levels

Water levels in the burned swamp had obvious effects on changes in herbaceous species presence and cover. In the burned swamp, standing water, bright sunlight, and increased nutrient levels led to high densities of floating aquatics, at first *Lemna aequinoctialis* (Figure 4.30) and later *Limnobium laevigatum* (Figure 4.31). For several months after the fires there were substantial areas of submerged filamentous green algae, probably flourishing in the elevated levels of nutrients released by the fires. The unburned *Avicennia* forest also had areas of substantial *Lemna* cover during the period of highest water. Surface water levels were farther above the substrate in the burned swamp after the fires due to both the lowering of the substrate by burning of organic layers and most likely reduced evapotranspiration from trees. When

Figure 4.30. Burned *Avicennia* forest near Almond Beach, at plot 5, in November 1998. The herbaceous vegetation is almost entirely dominated by the small floating aquatic *Lemna aequinoctialis*.

Figure 4.31. Burned *Avicennia* forest near Almond Beach, at plot 4, in May 2000. The herbaceous vegetation is dominated by the floating aquatic *Limnobium laevigatum*, with some scattered clumps of small *Acrostichum* ferns and *Cyperus*.

water levels in the burned swamp fell during droughts, the sprawling herb *Alternanthera sessilis*, which was found only on a few slightly elevated spots during earlier samplings, became the dominant herb (Figure 4.32). In later samplings of herbs in the burned plots, with the water table far below the surface, herbaceous vegetation was scarce, and the soil surface was covered with salt crystals. In the unburned forest, the drier periods also coincided with lower numbers of *Avicennia* seedlings sampled. In unburned plots following the drought, the increases in *Avicennia* tree dbh and basal area were also lower, with an mean increase of 0.3 cm dbh and 25.7 cm^2 basal area in the first (wetter) interval compared to 0.04 cm dbh and 18.5 cm^2 basal area in the second (drier) interval.

The water level in the burned plots was consistently slightly higher than in the unburned plots until early 2000, after which the level was slightly higher in the unburned plots. It is not certain whether that was attributable to changes in evapotranspiration as vegetation in the burned plots changed or if there were changes in the drainage via creeks and lagoons from the burned swamp. As the early 2001 drought intensified, water table levels in both areas dropped dramatically, with levels in the unburned swamp falling more, possibly because of continued evapotranspiration from trees of the mature forest, while in the burned swamp herbaceous vegetation cover fell sharply. When measurements were discontinued in March 2001, the water table in the unburned swamp was 73 cm below the surface, while in the burned area it was 35 cm below surface. After water levels in the burned swamp fell below the soil surface, evaporation would be greatly reduced, while in the unburned swamp the trees would continue to transport water into the atmosphere.

Figure 4.32. Burned *Avicennia* swamp near Almond Beach, between plots 4 and 6, in November 2001. The herbaceous vegetation is dominated by *Alternanthera sessilis*. There are also clusters of *Acrostichum* ferns and scattered young, shrubby *Laguncularia* trees (left foreground).

CONCLUSION

Many aspects of the mangrove forests of northern Waini Peninsula are linked to cycles of drought and rain, particularly because the swamps are often isolated from tidal influences. Dry periods may increase the chances of fire disturbances and serve to control presence of non-halophytic species. Wet periods may allow wider dispersal of propagules, and water levels may control which species can become established. Herbaceous vegetation was observed to vary greatly with wet and dry cycles. The data here have provided some evidence that these forests were recently established and that seedling recruitment has been intermittent. Coastal *Avicennia* swamps in the Waini Peninsula area have been apparently increasing in biomass over time. Many of the mangrove swamps of the northern part of the Waini Peninsula are near monocultures of *Avicennia*, however over time occasional dispersal of *Rhizophora* and *Laguncularia* may add to their species diversity, as part of the slow transition to a mixed coastal mangrove forest if they are undisturbed. It seems very likely that the forests of the Waini represent a chronosequence of plant community development, with the youngest, least developed areas found nearer to Waini Point. In comparison to mangrove swamps in other parts of the world, the Waini coastal mangroves are fairly average in basal area and biomass, but very low in stem density. The *Avicennia* dbh and height class distributions for both burned and unburned sites suggest that seedling recruitment has occurred in episodes, and that can help to explain the very low density of seedlings that were observed in the unburned swamp. It can be hypothesized that the low density reflects the climate-driven hydrological variations of the non-tidal swamps, with recruitment only occurring during rare periods of optimal conditions.

Following the soil fires, the species diversity of the disturbed coastal *Avicennia* swamps increased, primarily because of an increase in opportunistic species that disperse quickly into the available space. The herbaceous component of those post-disturbance swamps changed rapidly, apparently linked to fluctuations in the weather through its effects on hydrology and salinity. The composition of the tree community in the burned areas appears to be changing from a near monoculture of *Avicennia* to domination, for the immediate future, by *Laguncularia* trees, driven by scattered survivors of the species and effective dispersal of their relatively small fruits. In unburned swamps of Almond Beach *Laguncularia* is a common understory species at intermediate distances from the coast. *Laguncularia* is a comparatively weedy mangrove species and has been seldom observed to dominate mangrove forests in the Guianas, and it will be of great interest to know if that species will give way to other mangrove dominants.

The *Laguncularia* trees that initially colonized the burned site were generally very low and spreading, which could lead to a forest of low biomass. Some Amazonian forests have been found to return to pre-burning biomass and dbh values, although not of similar species composition, within 40 years (Ferreira & Prance 1999), and long-term monitoring of the forest structure in the Almond Beach burn would be useful for comparison to those observations, in order to see if mangrove systems behave similarly to upland tropical systems.

The mangrove forests of the Caribbean, which occur more often in areas of lower sedimentation, on calcareous substrates relatively low in nutrients, are generally more limited in extent than those of the Guianas (Sealey & Bustamante 1999). In several respects, the mangrove ecosystems of the Guianas are more geomorphically similar to those of high sediment coasts of South Asia rather than to those of the Caribbean (Jelgersma et al. 1993). For instance, in some river deltas of India *Avicennia* is considered the predominant pioneer (Blasco 1975), as the genus is in the Guianas. The *Avicennia* forests of the Guianas were shown here to be somewhat distinct from other Neotropical mangrove ecosystems, which might be a factor in decisions regarding their protection. The Amazon is the world's largest river, and its coastal delta is globally unique and includes the coast of the Guianas. This description of the most seaward portion of the Waini Peninsula swamps should serve to stimulate additional investigations and to raise awareness of the unique properties of the region's forests.

Lloyd Savory and some of his students from Moruca, including his daughter, after assisting with setup of some mangrove planting trials in burned Avicennia swamp near Almond Beach.

Annette Arjoon, a founder of the Guyana Marine Turtle Conservation Society, on Almond Beach in May 2000. The Almond Beach GMTCS camp was used as the base for these mangrove investigations.

Peter Pritchard, a marine turtle biologist and GMTCS collaborator, exhuming the skeleton of a Leatherback marine turtle that had been buried after washing ashore on Almond Beach several months earlier.

Students from Moruca returning to Almond Beach camp from Waini Point after a full night of beach patrol to monitor nesting marine turtles.

CHAPTER 5.
DISPERSAL AND ESTABLISHMENT OF MANGROVE PROPAGULES FOLLOWING FIRES

INTRODUCTION

In 1998 a mass mortality of trees in mangrove and freshwater swamps occurred after fires burned the soils of a large portion of the Waini Peninsula, Guyana. The affected mangrove swamps were primarily pure *Avicennia germinans* (black mangrove) stands. However, *Laguncularia racemosa* (white mangrove) trees were also present in the understory in scattered locations prior to the fires (see Chapter 4), and *Rhizophora mangle* (red mangrove) was present infrequently along the swamp margins by the beach ridge. Some scattered individuals of those species survived in the burned swamp. The path of early vegetation regeneration in these swamps will apparently be highly affected by the dispersal and establishment abilities of the surviving species in the environments after the fires.

This chapter provides an analysis of mangrove dispersal and establishment patterns, in order to establish whether mangrove dispersal, like terrestrial dispersal, is influenced by size of the seed or propagule. Such information has not been widely collected and analyzed for mangrove species in the Neotropics. A method was developed for collection of those data. Planting trials in the field with regional mangrove species were undertaken to provide additional information on establishment, independent of dispersal ability, in the environments of burned and unburned Waini Peninsula mangrove swamps. Information on the post-fire dispersal and establishment of mangrove species should allow insights into the early recovery process in the Waini Peninsula swamps.

Seed Dispersal

Early vegetation succession concepts such as described by Clements (1928) were largely deterministic, regarding disturbed plant communities as inexorably moving through a sequence of community stages towards a fixed climax determined primarily by climate, with vegetation modifying edaphic conditions through the stages. Such "facilitation" models gave little consideration to seed availability or plant life history traits and could not explain regeneration patterns observed after fire disturbances (Bond & van Wilgen 1996). Gleason (1927) began to incorporate the role of chance into concepts of vegetation change. Later Egler (1954) made a full distinction between the facilitation or "Relay Floristics" of Clementsian succession and an "Initial Floristic Composition" model in which the course of succession might depend on the species that survive or disperse to first colonize a disturbed site. Connell and Slatyer (1977) incorporated relay floristics and Egler's initial floristic composition concept into their set of three alternative models, which were applied to situations depending on organism adaptations, edaphic variables and the level and size of disturbances. Their elaboration of a variety of succession models reflected a growing recognition that plant communities are dynamic entities to which no single successional model can be applied (Pickett et al. 1989; White & Pickett 1985), and where seed availability is often a critical component.

Dispersal distribution curves, or seed shadows, for seeds from individual trees tend to follow leptokurtic pattern that peaks a short distance from the parent, with a long tail (Harper 1977; Willson & Traveset 2000). However, there is still limited data available for comparison and analysis of the dispersal curves for various modes (Willson & Traveset 2000). The tails of dispersal curves are difficult to model (Bullock & Clarke 2000), and the longest distance dispersal events may be the result of unusual high winds or turbulence, which can affect smaller fruits that are not normally thought of as wind dispersed (Jongejans & Telenius 2001). Extremely long-distance dispersal is rare, but it is probably important for colonization of suitable habitats after large-scale disturbances.

Dispersal in Mangrove Swamps

Coastal mangrove swamp attributes such as nutrient levels and salinity are strongly influenced by geomorphic setting (however see McKee 1993), so succession models based on organism modification of conditions may not be as applicable as the initial floristic composition, or inhibition model of Connell and Slatyer (1977). Therefore in the Waini Peninsula swamps, dispersal and establishment of species after a disturbance may have a strong influence on early recovery. Smaller disturbances such as tree falls are common in all mangrove swamps but would not have serious effect on species composition, as the short dispersal distances allow rapid regeneration (Baldwin et al. 2001; Clarke & Kerrigan 2000; Duke 2001; Sherman et al. 2000).

Water dispersal is the major mode of dispersal for mangrove propagules, which are typically transported by tidal currents. Water dispersal (hydrochory) is covered only briefly or not at all in dispersal ecology reviews (Chambers & MacMahon 1994; Harper 1977; Westoby et al. 1997). Water dispersal is understandably linked to currents for longer distance movement. Water dispersal has been observed to be directional in inland North American bottomland hardwood swamps, where dispersal distance was minimal at times of low water flow (Schneider & Sharitz 1988). As with a majority of species in wet tropical environments, mangrove establishment is restricted by the inability of seeds or propagules to lay dormant in a seed bank.

Some of the best known studies of mangrove dispersal properties were published by Rabinowitz (1978a; 1978b). She suggested that mangrove zonation may be controlled, in part, by variation in abilities of mangrove species to colonize segments of the intertidal zone, due to influences of size and shape of each species' propagules. The result would be propagule sorting on the seaward edge of swamps. The propagules of the three principal mangrove genera in the Neotropics and the Waini Peninsula area, *Rhizophora*, *Avicennia* and *Laguncularia*, are of distinctly different sizes. Rabinowitz's (1978a; 1978c) measurements of Neotropical mangrove propagule weights in Panama gave the mean weight of *Laguncularia* propagules as 0.41 grams, *Avicennia* as 1.1grams, *Rhizophora mangle* as 14.0 grams, and *Rhizophora racemosa* (cited as *R. harrisonii)* as 32.3 grams. These sizes are in general agreement with the those of propagules found in northern Guyana (Figure 5.1).

Most mangrove dispersal studies have been set in swamps with tidal currents. Mangrove dispersal is simplified in swamps that are rarely inundated by tides. Published reports of mangrove dispersal distances vary from only a

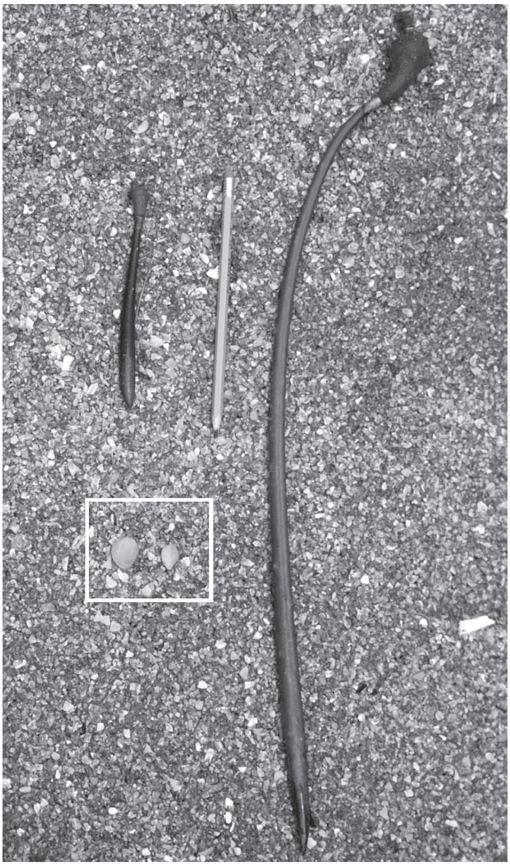


Figure 5.1. Propagules of *Rhizophora mangle*, *Rhizophora racemosa*, *Laguncularia racemosa*, and *Avicennia germinans* (from upper left, clockwise). The *Avicennia* and *Laguncularia* propagules are indicated in the box. For scale, the pencil is approximately 16 cm long.

few meters in a swamp in northwestern Australia with little tidal influence (McGuinness 1997a), to several or even tens of kilometers for *Avicennia marina* in tidal coastal environments (Clarke 1993). This author has found viable *Rhizophora mangle* propagules on beaches near Cape Hatteras, North Carolina, more than 850 kilometers along the Gulf Stream from the northernmost *Rhizophora* stands of Florida along the Indian River Lagoon.

As pointed out by McGuinness (1997a), there have been fairly few studies of the role of dispersal in mangrove community patterns. Rabinowitz's assertion that tidal sorting of propagules by size played a major role in mangrove zonation has been debated up to the present, with several more recent papers investigating physico-chemical correlates of zonation (Jiménez & Sauter 1991; López-Portillo & Ezcurra 1989; McKee 1993, 1995b; McKee & Faulkner 2000). The dominance of *Avicennia* on the seaward margins of the Guianas coast does not conform to the Rabinowitz tidal sorting model, possibly because of the unusual mudflat environment. Clarke et al. (2001b) suggest that tidal sorting may be less important in the zonation of Australian mangroves than establishment characteristics of species. On the mudflats of the Guianas, *Avicennia* may be best adapted to root quickly during extended periods of very low tides (Figure 5.2). Wells and Coleman (1981) proposed that rapid growth of newly established *Avicennia* stands on the mudflats of the Guianas might raise substrate elevation significantly with added root biomass, increasing the probability that new stands would persist.

Dispersal in Disturbed Mangrove Swamps

Only a few studies have addressed mangrove dispersal in disturbed sites. Blanchard and Prado (1995) found that establishment of *Rhizophora mangle* in cleared plots in Ecuador dropped off significantly 5 meters from plot edges, and Lema Vélez (2003) reported similar patterns in a disturbed site in Colombia. In studies of both oil spill and hurricane disturbances in Guadeloupe, *Rhizophora mangle* propagules were found to disperse very poorly in areas inland from coasts or rivers (Imbert et al. 2000). Elster et al. (1999) assumed that in a hydrologically disturbed mangrove swamp with little tidal influence, at Ciénaga Grande de Santa Marta, Colombia, large open areas remained bare because of dispersal limitations of mangrove propagules. If mangrove dispersal in non-tidal conditions is poor, the initial composition of a disturbed swamp might have lasting effects, since regeneration would be mostly dependent on very short range dispersal. In the burned swamps at Almond Beach, dispersal may have the most significant effect on which species dominate after the fires, and could influence how far mangrove trees will spread into areas where no parent trees survived.

In detailed studies of seed dispersal ecology, patterns of seed dispersal are separated from establishment success rates, generally through the use of seed traps. However, seedling establishment patterns have been used as a proxy for actual seed dispersal, where it is not critical to separate seed dispersal from establishment success (Nathan & Muller-Landau 2000). Establishment distance information can be a proxy for dispersal distance if the sites where seeds are deposited have fairly uniform establishment success rates. That is arguably the case for mangrove propagules in the non-tidal burned swamp at Almond Beach. Measurements

Figure 5.2. *Avicennia germinans* propagules and a germinated seedling on the mudflats at Almond Beach, Waini Peninsula. This image suggests that *Avicennia* may be able to take advantage of cracks in mudflats as a stable site for establishment. The germinating propagule is located approximately 2 meters out from the narrow beach ridge near the unburned *Avicennia* swamp plots.

of establishment distances are therefore a particularly useful and convenient method for predicting the spread of populations.

Sites where mangrove propagules tend to strand may also be favorable for establishment in the burned Almond Beach swamps. This was evidenced by clusters of seedlings at the edge of pools (Figure 5.3) or in shallow water along barriers such as logs, branches or masses of floating vegetation such as *Lemna* and *Limnobium* (Figure 5.4) that have been dense at times after the fires. In intact *Avicennia* swamps pneumatophores are often quite dense and apparently impede dispersal in the unburned swamp, and seeds are found among pneumatophores directly under parent trees (Figure 5.5). Since they are dispersed in early stages of germination, stranded mangrove propagules are relatively quick to advance to seedling status. In the open environment of the burned swamp at Almond Beach, established seedlings grew rapidly and reached reproductive status quickly, which would increase colonization rates.

Figure 5.3. *Laguncularia* seedlings concentrated in stranding lines, around the edge of a small pool, the result of very short distance dispersal. The branches of the parent tree are visible on the right. Photo taken October 2001.

To begin to answer some of the questions posed above, two experiments were set up. These were designed to test the dispersal properties of the three mangrove species and their ability to establish successfully in the swamp environments of the Waini Peninsula.

Figure 5.4. Clustering of *Avicennia* seedlings along minor barriers, here the branches of trees that were killed by the soil fires three years before this image was taken in April, 2001. The surviving parent tree was directly behind the photographer, about 2 meters from this cluster. This image also illustrates the condition of the soil surface during the minor drought at the time, cracked with salt accumulations on the surface. The other plants seen are the sedge *Cyperus odoratus*.

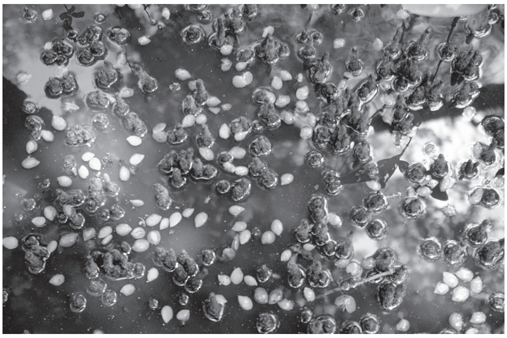


Figure 5.5. *Avicennia* propagules collected among pneumatophores under a parent tree in undisturbed non-tidal swamp behind a beach ridge, approximately 20 meters from the ocean.

METHODS

Study Site

The study site is located in the Almond Beach vicinity of Guyana's Waini Peninsula in, burned and unburned sections of *Avicennia* mangrove swamp. A detailed site description is given in Chapter 1. For this study, an area of approximately 0.75 km^2 was examined to locate suitable parent trees for the dispersal investigation, and planting trials were sited near the 0.1 ha vegetation monitoring plots in burned and unburned *Avicennia* swamp (see Figure 4.1).

Propagule Dispersal and Establishment

Most procedures for tracking dispersal of mangrove propagules have relied upon the marking of seeds on the parent tree and then attempting to find them in the environment following dispersal, or collection of data in a neighboring environment free from the subject species. In the case of the burned swamp at Almond Beach, parent *Laguncularia racemosa*, *Avicennia germinans*, and *Rhizophora mangle* trees were scattered to the degree that established seedlings encountered while moving from a parent in the downwind direction for 100 meters were likely derived from that parent. That, in addition to the absence of tidal currents from the swamps, provided a blank canvas of sorts, in which the supply and properties of propagules could be investigated.

In the burned *Avicennia* swamp, surviving reproductive trees were located near the Almond Beach camp. Establishment patterns were sampled for 16 *Avicennia* and 16 *Laguncularia* trees, while only five fertile *Rhizophora* parent trees were located. *Rhizophora* trees were rare in the area, occurring only along the swamp's boundary with the beach ridge, and those located were frequently without fruit. Some points considered as single *Laguncularia* parents were clusters of several shrubby individuals. A 5 meter wide transect was started at the edge of each parent tree's crown and followed for 100 meters in the direction of the prevailing winds, approximately toward the west-southwest (260 degrees). Transect width was tracked with a collapsible fiberglass dome tent pole, which covered the 5 meter wide swath when held perpendicular to the transect line and allowed to flex (Figure 5.6). The number of established seedlings (from plants with cotyledons exposed to plants 50 cm high) was recorded for each 0.1 meter of the transect. Significant barriers, generally logs and branches of fallen trees, were noted.

A simple initial model was formed to compare potential spread of *Laguncularia*, *Avicennia*, and *Rhizophora* in the burned *Avicennia* swamp at Almond Beach. Spatial buffering was performed in ArcView 3.3 (ESRI 2002), in which polygons of expected establishment distance are formed at a uniform distances from the parent trees according to species. Based on observations of the reproduction of these species in the burned swamp environment, it was assumed that *Laguncularia* reached reproductive age after about three years, *Avicennia* after about five years, and *Rhizophora* after about eight years. Buffers were generated for five generations of *Laguncularia*, three generations of *Avicennia*, and two generations of *Rhizophora*, or about 15 years (16 for *Rhizophora*).Mean establishment distances from the transects for each species were used as the distance that the range expanded from each individual over one generation.

Propagule Plantings

Plantings of propagules of four mangrove species were performed to assess the potentials of the common mangrove species in the area to establish and grow under a variety of hydrological conditions. Resulting information can then be considered in terms of different plant community succession models and potential ecosystem restoration strategies.

Mature propagules for the plantings were collected from surviving trees within or on the

Figure 5.6. Method for counting established *Laguncularia* using a "hip chain" measuring device and a pole spanning 5 meters when flexed. The area pictured was one of the most heavily vegetated with *Laguncularia* shrubs.

margins of the Almond Beach Swamp for *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*, and propagules of *Rhizophora racemosa* were collected from trees along the banks of the Mora Passage. *Avicennia* propagules were approximately 2-2.5 cm in length, *Laguncularia* propagules 1.5-2 cm in length, *Rhizophora mangle* propagules 15 cm in length, and *Rhizophora racemosa* propagules 35 cm in length (Figure 5.1).

Plantings were made in both burned and unburned swamp sites, during flooded and dry conditions, and at the normal swamp level and at a level elevated 15 cm above typical swamp surface level. Water levels at the time of the flooded plantings were well above the soil surface of the lower level plantings and a few cm above the soil surface of the elevated plantings. No surface water was present at an level at either site when dry condition plantings were made.

In the burned swamp site, plantings for the elevated treatment were made by anchoring aluminum flashing rings that were 20 cm-high and 1 m^2 area. The rings were anchored in place and filled to 15 cm with soil from nearby. In the unburned swamp site, a slightly elevated area existed in the planting area and was utilized for the elevated treatments. Water depths during the wet season plantings were similar between the treatments for the two sites. Sixteen propagules were planted for each treatment. The two *Rhizophora* species were planted by inserting propagules upright with points approximately 5 cm into the soil surface, while the *Laguncularia* and *Avicennia* propagules were secured in place with U-shaped thin wire clips. For the wet condition plantings, measurements were made after 10.5 and 17 months. Measurements were made for 1) the number of nodes on each seedling, 2) the height of each seedling, 3) the number of branches, and 4) the number of prop-roots developed in *Rhizophora* trees. The second, dry condition, planting was made of the same species in both burned and unburned areas, around the time of the first data collection for the wet season planting, in April 2001 during a moderate drought with no standing water in the swamps. The seedlings resulting from the dry condition plantings were measured after about 6 months, in October 2001.

RESULTS

Propagule Dispersal and Establishment

Sixteen *Laguncularia* and 16 *Avicennia* parent trees were located and sampled. Only five fertile *Rhizophora* parent trees were located in the vicinity, all growing along or near the swamp/beach ridge boundary. In the combined 100 meter transects, a total of 598 *Laguncularia* seedlings, 678 *Avicennia* seedlings, and 74 *Rhizophora* seedlings were sampled. Full counts for each species sampled are summarized in Table 5.1, and distribution curves based on those data are presented in Figure 5.7 for *Laguncularia*, Figure 5.8 for *Avicennia* and

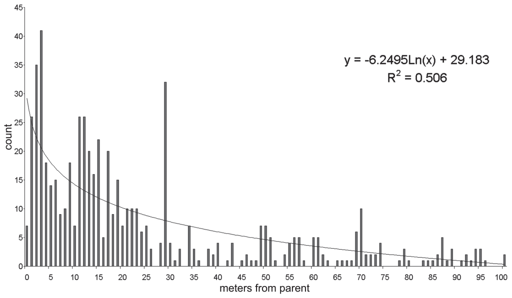


Figure 5.7. Dispersal curve for establishment of *Laguncularia* seedlings, for all 100 meter transects combined, with the logarithmic curve that best fitted those data.

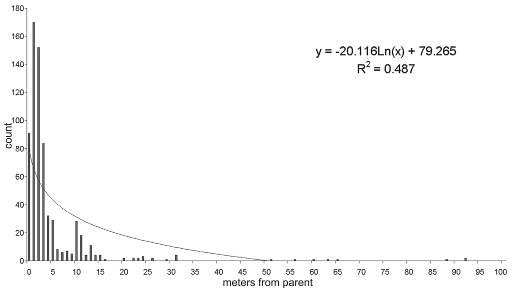


Figure 5.8. Establishment distance curve for *Avicennia* seedlings, combined 100 meter transects, with the logarithmic curve that best fitted those data.

Figure 5.9 for *Rhizophora*. The range of numbers of seedlings encountered from an individual parent varied from 2 to 155 in *Laguncularia*, 1 to 237 in *Avicennia*, and 3 to 39 in *Rhizophora*. The mean establishment distance was 24.2 meters for *Laguncularia*, 4.8 meters for *Avicennia*, and 8.9 meters for *Rhizophora*. Summary statistics for establishment distance measurements are given in Table 5.2.

The three resulting establishment distance data sets were tested for significant difference among themselves with pairs of Wilcoxon rank-sum tests (nonparametric, as distributions were not normal). In addition, a one-sample Kolmogorov-Smirnov test for each species was used to test if established seedlings distances were reasonably drawn from an exponential distribution with the mean for that species. In all Wilcoxon rank-sum tests of pairs of comparisons, p-values were less than 0.005. The maximum establishment distances recorded for each species were 100 meters for *Laguncularia*, 92.1 meters for *Avicennia*, and 49 meters for *Rhizophora*. All curves were significantly different from artificial uniform distributions of values ranging from 0 to the species maximum. In the case of *Laguncularia* ($p= 0.045$, one-sample Kolmogorov-Smirnov test) the distribution approached a less significant difference from 7 exponential distributions with the species' mean.

For graphing, the seedling establishment points were condensed into one meter interval groups. Those displayed degrees of bimodal or polymodal distributions, most distinctly in *Rhizophora* and *Avicennia*. Best-fit natural logarithmic lines were calculated for the dispersal data grouped into 1 meter increments, for the three species. The lognormal decay curves achieved a somewhat better fit to the data than linear or binomial curves. For *Laguncularia* the formula for the logarithmic curve was $y = -6.2495\mathrm{Ln}(x) + 29.183$, $R^2= 0.56$ (Figure 5.7), for *Avicennia* it was $y = -20.116\mathrm{Ln}(x) + 79.265$, $R^2 = 0.487$ (Figure 5.8) and for *Rhizophora* it was $y = -1.7536\mathrm{Ln}(x) + 7.1354$, $R^2 = 0.559$ (Figure 5.9). All three curves are displayed in a single graph in Figure 5.10.

For the buffering model, the mean distances obtained from the establishment transects were used: 24.2 meters for *Laguncularia*, 4.38 meters for *Avicennia*, and 8.94 meters for *Rhizophora*. The points modeled for *Rhizophora* and *Laguncularia* were those for all parent trees in the establishment transects, while 39 additional mature *Avicennia* trees were located in the area and marked with GPS, for a total of 55 used. One *Rhizophora* point was located to the west of the boundary that had been drawn for the Almond Beach burn, in an area the had apparently been impacted by scattered soil fires, without full mortality of the surrounding trees.

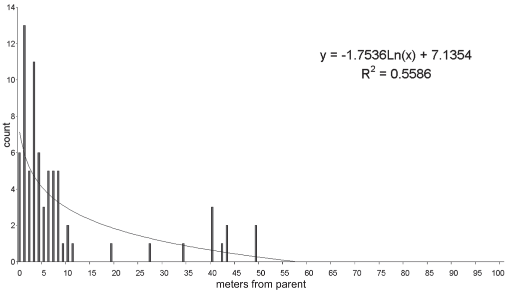


Figure 5.9. Dispersal curve for establishment of *Rhizophora* seedlings, for all 100 meter transects combined, with the logarithmic curve that best fitted those data.

The resulting buffer areas after the specified intervals were 57.4 ha for *Laguncularia*, 2.83 ha for *Avicennia*, and 1.0 ha for *Rhizophora*; out of the estimated 5.17 km^2 (517 ha) area of *Avicennia* swamp burned at the Almond Beach site. For *Laguncularia*, that equated to 11.1% of the burned area. The buffering result maps are shown in Figures 5.11, 5.12, and 5.13, respectively.

Propagule Plantings

In both burned and unburned treatments, plantings of the two *Rhizophora* species were the only species to survive to the first census, and all plantings of *Laguncularia* and *Avicennia* propagules failed. In the burned swamp, *Rhizophora racemosa* treatments grew robustly (Figure 5.14); however, substrate-level *R. mangle* experienced apparent full mortality. After the first 11 months in the burned treatment, the mean height of the 14 surviving elevated *R. mangle* seedlings was 71.5 cm, the mean height of the 16 elevated *R. racemosa* seedlings was 128.9 cm, and the mean height of the 16

Table 5.1. Number of seedlings found within one meter intervals away from parent trees, within a 5 meter wide band, totaled for all replicates within the three species sampled for establishment distance.

Avicennia		***Laguncularia***				***Rhizophora***	
m	count	m	count			m	count
0	91	0	7	47	1	0	6
1	170	1	26	48	1	1	13
2	152	2	35	49	7	2	5
3	84	3	41	50	7	3	11
4	32	4	18	51	5	4	6
5	29	5	14	52	1	5	3
6	8	6	15	54	2	6	5
7	6	7	9	55	4	7	5
8	7	8	10	56	5	8	5
9	5	9	18	57	5	9	1
10	28	10	7	58	1	10	2
11	18	11	26	60	5	11	1
12	4	12	26	61	5	19	1
13	11	13	20	62	2	27	1
14	4	14	16	63	1	34	1
15	4	15	22	65	1	40	3
16	1	16	5	66	1	42	1
20	2	17	20	67	1	43	2
22	2	18	9	68	1	49	2
23	2	19	15	69	6		
24	3	20	7	70	10		
26	2	21	10	71	2		
29	1	22	10	72	2		
31	4	23	10	73	2		
51	1	24	6	74	4		
56	1	25	7	78	1		
60	1	26	3	79	3		
63	1	28	4	80	1		
65	1	29	32	83	1		
88	1	30	4	84	1		
92	2	31	1	85	1		
		32	3	86	2		
		34	7	87	5		
		35	3	88	1		
		36	1	89	3		
		38	3	91	1		
		39	2	92	2		
		40	4	93	1		
		42	1	94	3		
		43	4	95	3		
		45	1	96	1		
		46	2	100	2		

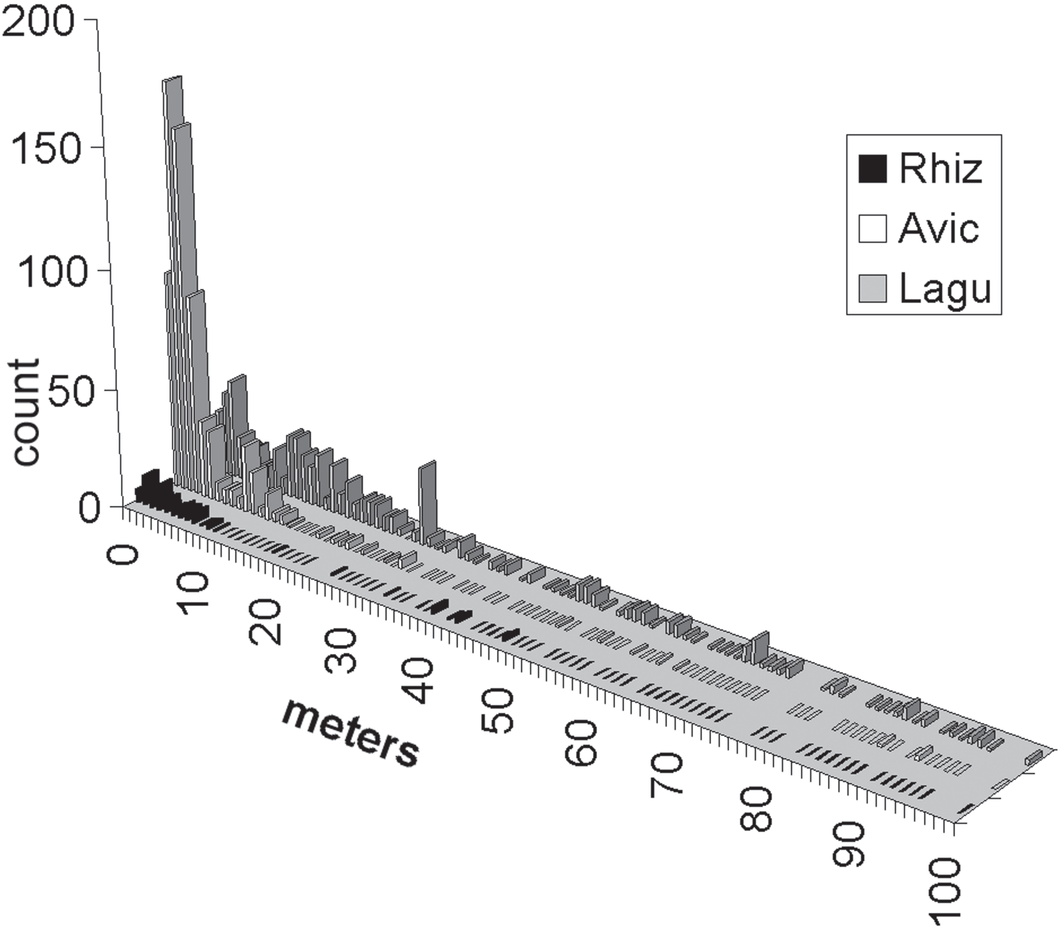


Figure 5.10. Comparison of seedling establishment distributions for *Rhizophora*, *Avicennia*, and *Laguncularia*, combined 100 meter transects.

Table 5.2. Summary values for establishment distance measurements.

	Avicennia	***Laguncularia***	***Rhizophora***
N	675	597	74
Mean	4.38	24.20	8.94
Mode	2.1	15.3	3.75
Minimum	0	0	0
Maximum	92.1	100	49
Std. Dev.	8.86	24.47	13.19
Variance	78.54	598.63	173.99

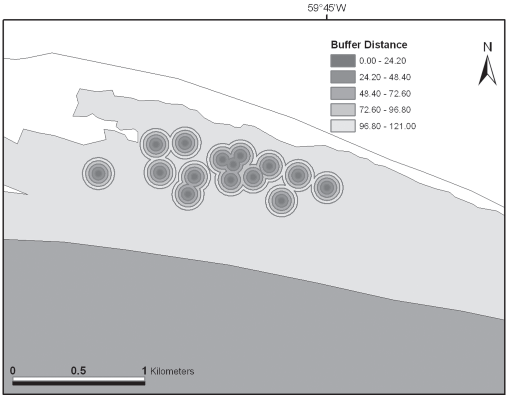


Figure 5.11. Graphic results of buffering of *Laguncularia* points in the Almond Beach swamp, based on five three-year generations. Total area covered was 57.4 ha.

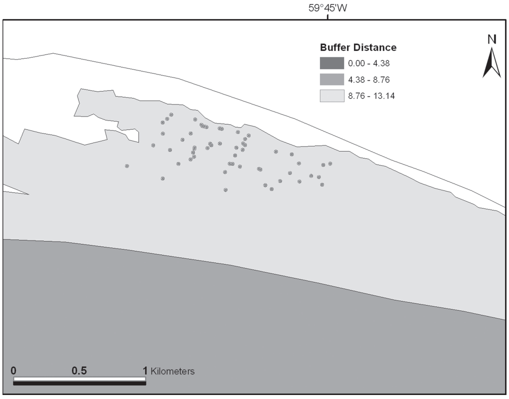


Figure 5.12. Graphic results of buffering of *Avicennia* points in the Almond Beach swamp, based on three five-year generations. Total area covered was 2.83 ha.

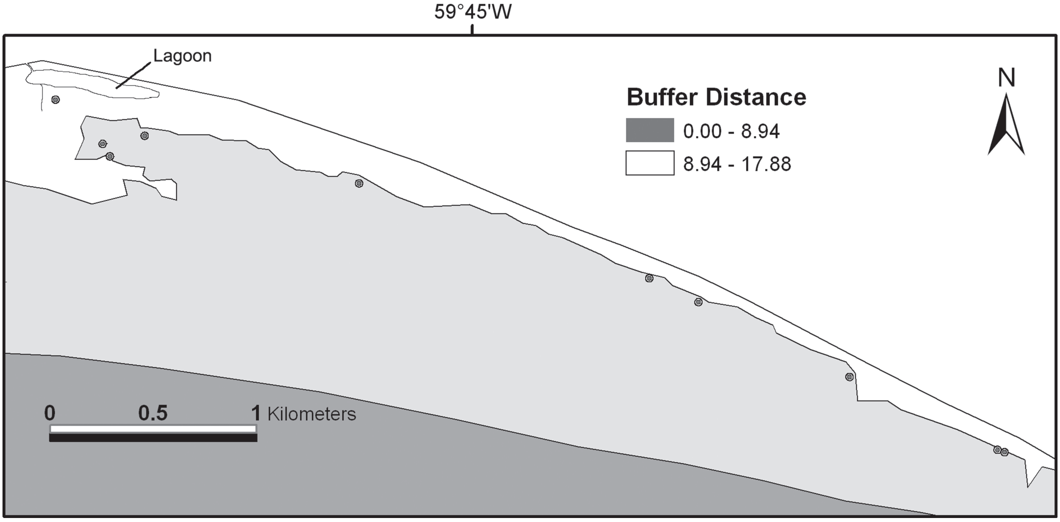


Figure 5.13. Graphic results of buffering of ten *Rhizophora* points in the Almond Beach swamp, based on two eight-year generations. The total area covered after that interval was 1 ha. The points included the five fertile trees used for establishment distance measurements and five others that were also located in the vicinity. The approximate location is indicated for the lagoon that sometimes connects the Almond Beach swamp to the sea.

substrate-level *R. racemosa* seedlings was 103.25 cm . At the second sampling 17 months after plantings there was no additional mortality; the mean height of the elevated *R. mangle* seedlings was 118.6 cm, the mean height of elevated *R. racemosa* seedlings was 197 cm, and the mean height of substrate-level *R. racemosa* was 159.4 cm. The mean values for height, node count, prop root count, and for the first measurement (10.5 months) are graphed in Figure 5.15, for the second measurement (17 months) in Figure 5.16 with the values and differences between the two dates listed in Table 5.3. It should be kept in mind that as planted, *Rhizophora racemosa* propagules were approximately 20 cm longer than *Rhizophora mangle* propagules. Height values for both *Rhizophora* species in the two habitats for both treatments are shown in Figure 5.17. A series of pairwise t-tests was used to compare the mean

Figure 5.14. *Rhizophora* plantings in April 2001, approximately 10½ months after establishment. Vegetation in the background is primarily *Acrostichum* ferns.

values for combinations of plantings since variances were fairly similar. A matrix of the resulting p-values is given in Table 5.4. For the height measure an analysis of variance (ANOVA) also showed high significance, approaching p=0, for all factors, habitat, elevation and species, with either the raw data or with seedling heights adjusted for the difference in length of propagules of the two species.

In the unburned swamp, survival and growth of both species of *Rhizophora* was much lower than in the burned swamp, where no *Laguncularia* or *Avicennia* again survived in any treatments. Dry season plantings also resulting in survival of only *Rhizophora* plants, and exhibited decreased survival and growth of those species, particularly in the unburned swamp. Values for the dry season plantings are summarized in Table 5.5 and graphed in Figure 5.18. During the dry season planting there was greater effect on *Rhizophora mangle* plantings, which displayed no survival in the elevated plantings and no survival in the unburned swamp. According to well data from the two

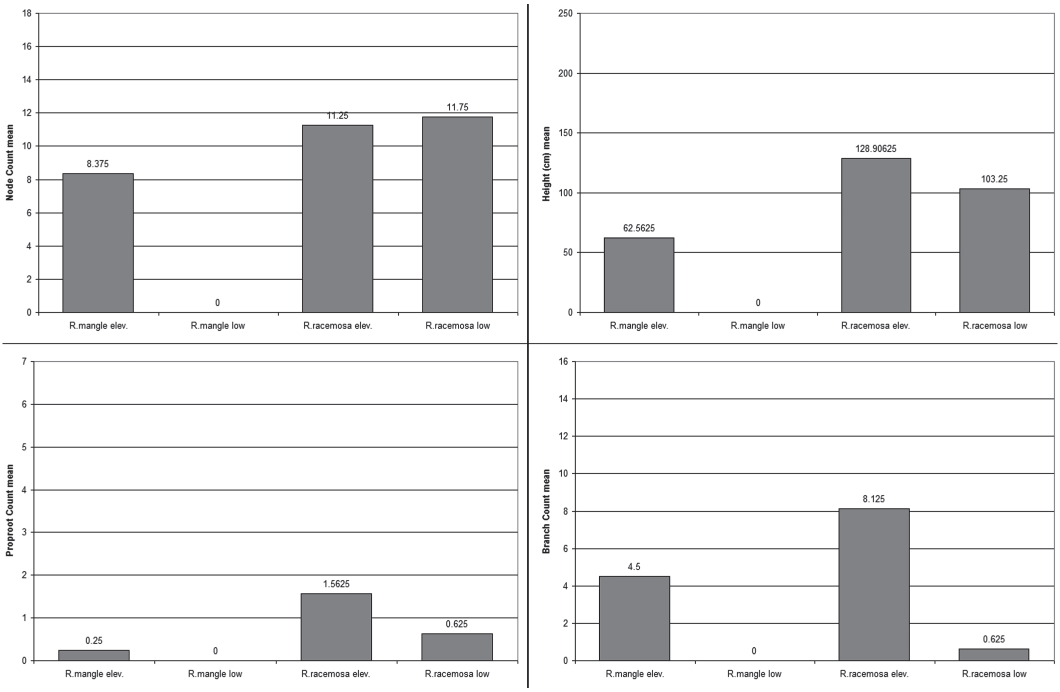


Figure 5.15. Graphs comparing *Rhizophora* planting results after 10.5 months, burned site. None of the shorter *Rhizophora mangle* propagules were noted as alive at low (substrate) elevation.

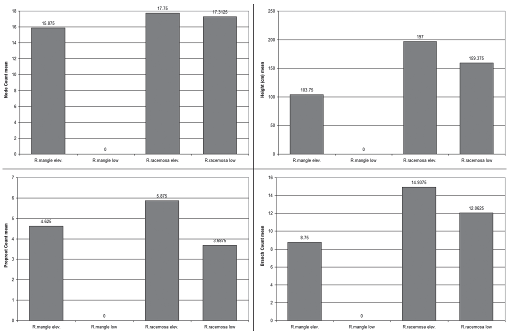


Figure 5.16. Graphs comparing *Rhizophora* planting results, burned site after 17 months.

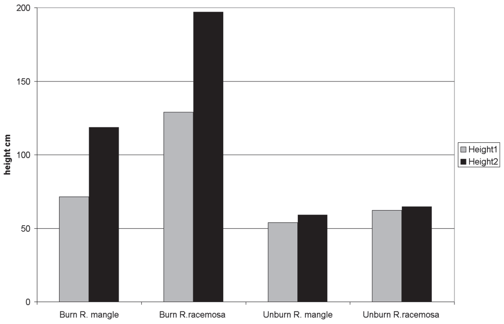


Figure 5.17. Mean seedling heights for both species of *Rhizophora* after 10.5 and 17 months, for surviving seedlings in elevated plantings, burned and unburned areas.

Table 5.3. Mean values for the variables measured for *Rhizophora* plantings made in wet conditions in May 2000, for the first sampling (11 mos.), the second sampling (17 mos.), and the difference between the means. These means are from values are for the surviving individuals only out of 16 planted in each treatment.

			Mean values, **first** sampling, survivors only				
			Nodes	Height (cm)	Prop roots	Branches	Survivors
Burned	elevated	*R. mangle*	9.6	71.5	0.3	5.2	14
		R. racemosa	11.25	128.9	1.6	8.1	16
	low	*R. mangle*	0	0	0	0	0
		R. racemosa	11.75	103.25	0.6	6.2	16
Unburned	elevated	*R. mangle*	6.1	53.9	0	0	10
		R. racemosa	6.3	62.2	0	0	14
	low	*R. mangle*	0	0	0	0	0
		R. racemosa	0	0	0	0	0
			Mean values, **second** sampling, survivors only				
			Nodes	Height (cm)	Prop roots	Branches	Survivors
Burned	elevated	*R. mangle*	18.1	118.6	5.3	10	14
		R. racemosa	17.75	197	5.9	14.9	16
	low	*R. mangle*	0	0	0	0	0
		R. racemosa	17.3	159.4	3.7	12.1	16
Unburned	elevated	*R. mangle*	8.6	59.1	0	0.6	10
		R. racemosa	6.8	64.8	0.1	0.1	9
	low	*R. mangle*	0	0	0	0	0
		R. racemosa	0	0	0	0	0
			Difference, first to second sampling, survivors only				
			Nodes	Height (cm)	Prop roots	Branches	Survivors
Burned	elevated	*R. mangle*	8.6	47.1	5.0	4.9	0
		R. racemosa	6.5	68.1	4.3	6.8	0
	low	*R. mangle*	0	0	0	0	0
		R. racemosa	5.6	56.1	3.1	5.9	0
Unburned	elevated	*R. mangle*	2.5	5.2	0	0.6	0
		R. racemosa	0.4	2.6	0.1	0.1	-5
	low	*R. mangle*	0	0	0	0	0
		R. racemosa	0	0	0	0	0

Table 5.4. Summary of P-values for pairwise t-tests between combinations of *Rhizophora mangle (R.m.)* and *Rhizophora racemosa (R.r.)* planting treatments in high vs low elevation plantings and burned vs unburned areas. Values significant at P=0.05 are shown in bold face.

	First planting, first census			
	Nodes	Height	Prop roots	Branches
R.m. vs *R.r.* low	n/a	n/a	n/a	n/a
R.m. vs *R.r.* high	**0.003**	**0**	**0.010**	**0.000**
R.r. hi vs low	0.219	**0**	0.065	**0.012**
R.m. burn vs unburn	**0.0005**	**0.006**	n/a	n/a
R.r. burn vs unburn	**0**	**0**	n/a	n/a
	First planting, second census			
	Nodes	Height	Prop roots	Branches
R.m. vs *R.r.* low	n/a	n/a	n/a	n/a
R.m. vs *R.r.* high	0.287	**0**	0.228	**0.0002**
R.r. hi vs low	0.542	**0.001**	**0.006**	**0.029**
R.m. burn vs unburn	**0**	**0**	n/a	n/a
R.r. burn vs unburn	**0**	**0**	n/a	n/a
	Second planting (dry season)			
	Nodes	Height	Prop roots	Branches
R.m. vs *R.r.* low	0.186	0.788	n/a	**0.032**
R.m. vs *R.r.* high	n/a	n/a	n/a	n/a
R.r. hi vs low	0.088	0.072	n/a	**0.025**
R.m. burn vs unburn	n/a	n/a	n/a	n/a
R.r. burn vs unburn	**0.033**	**0.036**	n/a	n/a

sites, the groundwater level in the unburned swamp was lower than the burned swamp, possibly caused by higher evapotranspiration from trees in the living forest. Other factors limiting survival and growth in the unburned site likely include shading and competition for nutrients and water. There were no observations suggesting that predation played a role in *Rhizophora* mortality in either site.

DISCUSSION

Propagule Dispersal and Establishment

Establishment patterns in the Almond Beach swamps were similar to those that might be expected in upland systems. Although in terms of Chambers and MacMahon's (1994) classification of dispersal movement phases, the water in the non-tidal Almond Beach swamp would qualify as Phase II dispersal, coming after the propagule first moves from parent to a surface, the establishment curves derived from the transects resemble a leptokurtic Phase I dispersal pattern, with a peak near the parent and a long tail. This is possibly attributable to the passive nature of the water that lacks substantial currents. The fits of the logarithmic curves calculated from the dispersal distance data were not particularly good for the three

Table 5.5. Mean values for variables measured for *Rhizophora* plantings made in drought conditions in April 2001.

	Nodes	Height (cm)	Prop roots	Branches	% Survival
R. mangle low	5.25	34.69	0	4.69	75
R.racemosa low	3.69	37.44	0	2.50	56
R.racemosa elev.	1.69	16.25	0	0.75	25
R.racemosa elev. unburn	0.81	8.63	0	0	25

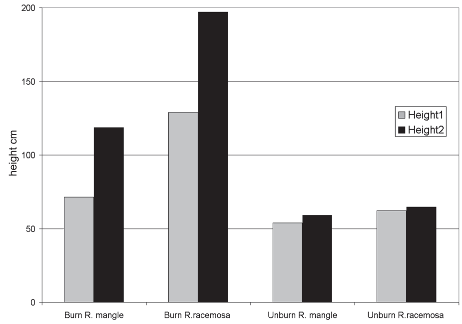


Figure 5.18. Dry season planting results. *R. racemosa* values are not corrected for its larger propagule length, approximately 20 cm. greater than *R. mangle*.

species, as all displayed typical irregular Phase I type distributions with a peak near the parents and with long tails. If there had been substantial Phase II dispersal it would be attributable to movement in water currents after falling from the parent, and it would have the effect of additional extension of tails of the curves. It is uncertain to what degree the patterns here reflect any seed movement from the time the fruits leave the parent tree and when they reach the water surface, such as during brief periods of high winds.

Propagule dispersal distance in the Almond Beach non-tidal environment was apparently related, in least in part, to the size of propagules. The smaller *Laguncularia* propagules were dispersed farther than *Avicennia* propagules. On the other hand, the mean distance for dispersal of the much larger *Rhizophora* propagules was higher than that of *Avicennia* (8.9 meters vs 4.4 meters). However, the maximum dispersal distance recorded for *Rhizophora* was lower than for *Avicennia* (92 meters vs 49 meters), although that may have been influenced by the greater number of *Avicennia* trees available for sampling and the much greater number of seedlings established from *Avicennia* parent trees.

The simplified environment of the burned mangrove swamp at Almond Beach provided a reduced number of variables in often present in natural dispersal experiments. In mangrove swamps the number of plant species present is limited, and water dispersal tends to deposit propagules where establishment rates are high (Middleton 2000). There is no seed bank or dormant phase for mangrove species, and animal dispersal is not an important factor. Fire-related mortality in the burned habitat limited the number of parent trees that might confuse dispersal or establishment patterns, which was reflected in these distinct establishment distance curves. The effects of predators have probably been initially reduced by fire disturbance. In the case of the Almond Beach swamp, beach ridge barriers block tidal and wave influences, making dispersal distance dependent primarily on water depth and minor currents generated by winds. The beach ridges also limit influx of propagules from outside sources. While the non-tidal setting is not typically utilized for dispersal studies in mangrove swamps, there are often sizable portions of mangrove systems that are isolated from regular tidal inundation. In some respects, the dispersal environments of Almond Beach mangrove swamps were more complex than that of the ocean/swamp edge studied by Rabinowitz 1978b.

While the results of the buffering trials provided an initial visual comparison of abilities to colonize the burned swamp, there is certainly a potential for more advanced propagule dispersal and establishment models to better predict species spread through consideration of the density of colonization events for each species, the probabilities that established seedlings might advance to reproductive age, and the potential for higher seed production of older individuals (Clark et al. 2001; He & Mladenoff 1999; Tews et al. 2004). Attention might also be given to correction for of the constant width of the transect from the trees, and the influenced of prevailing winds, which would call for a directional bias in the creation of buffers or chances of dispersal events.

It is interesting to note that some characteristics of "traditional" Neotropical mangrove zonation are apparent in the occluded, burned swamp once behind the beach ridges. *Rhizophora* is found nearest to the sea, and *Laguncularia* is more common several hundred meters inland, beyond the wettest area of the swamp. The swamp near the beach ridges is often a location of deepest water in the occluded swamps, and may allow some local movement of the larger *Rhizophora* propagules.

While ecological studies on fire-adapted plant communities tend to focus on life history traits rather than competition, in mangrove swamps it seems that hydrology will play a significant role in the path of recovery, along with closely linked factors such as soil salinity and soil redox potential, which affect nutrient availability. The importance of these factors is, however, contingent on availability of propagules, and the spread of tree species into burned areas of the Almond Beach swamp seems to be limited by the availability of propagules and patterns of dispersal and establishment success that are linked to small elevation differences and barriers that offer suitable establishment sites. Elster et al. (1999) found that in a hydrologically disturbed non-tidal mangrove swamp in Colombia, few propagules reached large areas that were remote from parent trees.

Difficulty of dispersal of the larger *Rhizophora* propagules into and within the Almond Beach swamps offer one explanation for their absence from the younger *Avicennia* swamps. Once introduced, the species apparently persists, as evidenced by increasing dominance of *Rhizophora* in coastal forests farther to the southeast on the peninsula, where the swamps behind beach ridges are arguably older and *Rhizophora* has had a longer time for colonization success. The vigorous growth of *Rhizophora* plantings at Almond Beach attest to its ability to thrive once dispersed to that location.

In a marked propagule experiment using the Asian mangrove *Ceriops tagal* (Perr.) C.B.Rob. (Rhizophoraceae), which has propagules similar in shape and size to those of *Rhizophora mangle*, McGuinness (1997a) found that 76% of marked propagules were found within 1 meter of the parent tree and 91% within 3 meters, and concluded that patterns of initial colonization may be reflected in zonation for long periods, and that long-term effects of competition within physico-chemical environments may be overestimated.

The burned environment at Almond Beach presented many barriers to dispersal of all mangrove species, and that effect was probably compounded by the lack of fluctuating water levels and currents from tides. Barriers of fallen dead trees have been cited as a probable factor in very slow colonization in hurricane disturbed *Rhizophora* swamps in Guadeloupe (Imbert et al. 2000). Patches of low herbaceous vegetation, usually *Alternanthera* or *Cyperus*, acted as barriers to dispersal against which many seedlings were stranded and became established. Similar phenomena were noted by Lema Vélez (2003) in Colombian mangroves, where *Batis maritima* L. plants blocked dispersal of propagules, and in North American *Taxodium* (bald cypress) swamps, where seeds were found concentrated non-randomly along logs, trees and other emergent obstacles (Schneider & Sharitz 1988). Clarke (1993) found that *Avicennia marina* propagules in Australia stranded at the line of highest water levels inside of swamps, where they shed their pericarps, became non-buoyant and established. All of those observations offer some support for application of the propagule sorting hypothesis proposed by Rabinowitz (1978b) to the physical environment of the non-tidal mangrove swamps at Almond Beach. Sorting in such swamp interiors is likely more complicated than along tidal coasts by barriers that block propagules differentially by size and by irregular patterns of water depth. At Almond Beach the smaller propagules of *Laguncularia* sometimes became established on top of mats of floating vegetation, extended their roots through water to the soil, and remained elevated on those roots after the water receded (Figure 5.19). That process provided a

Figure 5.19. Roots of a *Laguncularia* seedling that established on floating vegetation during high water. At lower right a string used to originally mark plots can be seen emerging from the roots. Remains of pneumatophores of *Avicennia* trees killed by the soil fires are also visible.

constantly moist, but never deeply inundated, surface that might be appropriate for such small fruits to germinate and establish successfully.

Ellison (2002) found across 44 worldwide sites from regions with a wide range of mangrove species richness, that within-site species richness maintained a linear relationship with regional species richness. It was concluded that mangrove forests may be unsaturated with available species and that a site's species composition may be more attributable to colonization abilities and propagule sorting, as proposed by Rabinowitz (1978a), rather than to differences in edaphic or competitive niches. At Almond Beach it was demonstrated that edaphic factors were not preventing establishment and growth of *Rhizophora* in regenerating burned mangrove swamp. During those studies a single creek drained the Almond Beach swamp into a lagoon that was only periodically open to the ocean. The northernmost *Rhizophora mangle* trees were located at that creek, which was possibly where propagules entered the occluded swamp, from which the species was able to disperse in deeper waters along the back of the beach ridge. The composition and patterns of Waini Peninsula coastal mangrove species seem to be influenced by dispersal, establishment ability and sorting in the early history of a swamp, which only later exhibits patterns influenced by edaphic factors and competition, along with the eventual migration of less easily dispersed species. Such development would depend on the absence of large-scale disturbances that would restore propagule availability and dispersal as dominant factors.

The establishment and composition of mangrove swamps in many parts of the world are apparently also influenced by propagule predation, particularly by herbivorous crabs (Dahdouh-Guebas et al. 1998; Lee 1998; McGuinness 1997b; Osborne & Smith 1990; Smith et al. 1989), though this may not necessarily be a major factor in mangrove swamp zonation (Sousa & Mitchell 1999). *Avicennia* propagules are most often cited as a preferred prey of herbivorous crabs (McGuinness 1997b; McKee 1995a; Smith 1987). In some populated areas propagule predation can also be dominated by domesticated animals (Lema Vélez et al. 2003). Zonation of mangrove swamps of Belize was found to be possibly influenced by predation of *Avicennia* propagules, though not of *Rhizophora* or *Laguncularia* (McKee 1995a). The herbivorous giant land crab *(Cardisoma guanhumi)* Latreille is common in the *Avicennia* swamps of the Guianas, including the unburned swamps near Almond Beach (Figure 5.20). However, *Cardisoma* crabs were absent from the burned swamp areas. When water levels were high in the burned swamps, *Callinectes* Stimpson crabs were observed. These crabs are carnivorous to omnivorous and are not mentioned in the literature as propagule predators. The potential role of *Cardisoma* crabs in population dynamics of *Avicennia* swamps, and therefore in eventual changes in species dominance in older Waini Peninsula swamps is an ecological interaction worthy of future study.

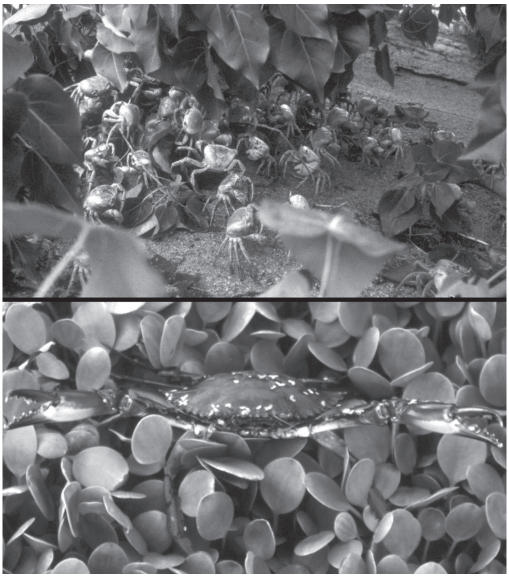


Figure 5.20. *Cardisoma guanhumi* and *Callinectes* crabs at Almond Beach. *Cardisoma* (above) is a common burrowing resident of the undisturbed *Avicennia* swamps and is possibly an *Avicennia* propagule predator. The large group of *Cardisoma* is assembled near the Atlantic Ocean during a full moon. In the burned *Avicennia* swamps *Callinectes* crabs (below) were often observed during periods of higher water; they are considered to be omnivorous to detritivorous. The *Callinectes* shown is on floating *Limnobium* plants.

Laguncularia has been noted by several authors for its function as a pioneer species in some mangrove swamps (Baldwin et al. 2001; Ball 1980; Delgado et al. 2001; Roth 1992; Tissot & Marius 1992; Woodroffe 1983), often becoming the dominant species early in regeneration of disturbed swamps. It produces a relatively large quantity of smaller propagules and has been described as shade intolerant and fast growing with high mortality rates (Roth 1992). Clarke (2000) felt that there were no gap specialists among Australia's mangroves, which lack a small-fruited genus such as *Laguncularia*.

While plant species richness in burned areas of the mangrove swamps of the Waini Peninsula was higher following the fires, many of those species were disturbance specialists; in some areas these will be temporary while in others they may dominate and prevent colonization by woody species. Smaller patches of post burn vegetation could be considered a diversification of the plant community with few negative effects (Hackney & de la Cruz 1981). However, at Almond Beach some large burned sections became quickly dominated by *Typha* and vines and will possibly recover very slowly and may be subject to additional fires during droughts. Dispersal and establishment of trees may be inhibited in these areas, which could remain a vestige of the fires for many years.

The Almond Beach fires may the beginning steps toward a landscape such as described by Pons and Pons (1975) for a section of coastal Surinam, where broad areas of herbaceous vegetation are found behind a coastal *Avicennia* belt. These landscapes are described as maintained by cyclical fire events. However, the authors offer no record of fires actually observed in areas dominated by mangrove vegetation. The recurring fires in Surinam may be analogous to those that maintain *Mauritia* palm and sedge marshes located farther inland on the Guyana coastal plain, most notably at Santa Rosa in Guyana's Northwest District.

Propagule Plantings

Although *Laguncularia* and *Avicennia* often display high germination rates in controlled experimental conditions (Steinke 1975), propagules of those species failed to establish or survive in field plantings. There were no explicit signs of predation at either site, however the potential propagule *Cardisoma* crabs were present in some locations near the unburned site. The failure of planting of smaller propagules is in agreement with results reported by Elster (2000) for a disturbed mangrove swamp in Colombia, where all propagules died within two months of planting in drying soils, with *Avicennia* and *Laguncularia* mortalities far higher than those of *Rhizophora* in most cases. Propagule mortality was described by Elster (2000) as being generally higher in open, disturbed sites and higher for smaller propagules, caused by environmental factors including dessication and unstable hydrology. Rabinowitz (1978c) also found far higher survivorship for *Rhizophora* seedlings compared to *Avicennia* or *Laguncularia* seedlings. It was demonstrated here that *Avicennia* and *Laguncularia* propagule establishment is sensitive to water level. While those species did not establish in planting trials, establishment along narrow strand lines was observed bearby, presumably where water levels were appropriate. Such sensitivity to hydrology has been noted for Cypress swamps in eastern North America (Middleton 2000). The morphology of *Rhizophora* propagules is significantly different from *Avicennia* and *Laguncularia* and affects the success of plantings. Some Asian mangrove plantations have been shown to be far more species poor than natural stands, with many species of natural stands absent; in the Philippines, *Rhizophora* is overwhelmingly preferred for ease of planting, high success rates, and usefulness/high economic value (Walters 2000). All of these findings illustrate why the large propagules of *Rhizophora* and other Rhizophoraceae are often the major type of mangrove planted in restoration efforts (Field 1998a; Field 1996), even though fairly high field survival rates have been reported for nursery reared seedlings of other mangrove species (Elster 2000; Rabinowitz 1978b). The planting results from Almond Beach are in general agreement with the concept that seeds with larger mass are well adapted for successful establishment and seedling survival (Westoby et al. 1997). In the case of planted *Rhizophora*, the advantages of the large, elongated propagule allow tolerance of deeper inundation and probably tolerance to lower moisture and nutrient availability during droughts. Advantages for establishment gained through larger size come at the expense of dispersal ability, which is especially apparent in the case of the non-tidal burned mangrove swamps at Almond Beach. At Almond Beach, the plantings of *Rhizophora* added well adapted species that were absent during early succession only because of dispersal limitation. Any large scale plantings could be viewed as a case of stepping ahead to a species composition that may be similar to one that would be attained naturally over time. *Rhizophora* is very easy to plant, and plantings of it are generally very successful. It is considered useful as timber and fuelwood, and some plantings near settlements could be considered and would not be out of place in view of potential long term plant community succession in the burned mangrove swamps. *Rhizophora mangle* propagules survived but grew comparatively poorly in dry season plantings, possibly because of their smaller size, and did poorly in deep water because of their shorter length. *Rhizophora racemosa* propagules had a higher chance of success through variations in hydrological conditions, probably because of their longer, more massive propagules. *Rhizophora racemosa* propagules are usually easier to collect due to their frequency along the margins of tidal rivers of the region. Because of the species' absence, establishment distance of *Rhizophora racemosa* was not tested in the Almond Beach swamps, but the longer propagules would likely disperse poorly in the shallow, non-tidal waters, and would potentially spread very slowly from any areas of plantings.

Just as Rabinowitz's (1978 a & b) tidal sorting hypotheses attributed mangrove zonation to differential establishment dependent on where each species was able to strand at high water, establishment in the burned swamp varied by water depth and the swamp's microtopography. The smaller *Laguncularia* and *Avicennia* propagules were observed to establish where they stranded, however they were not successful in this study's randomly placed planting sites where hydrological conditions were likely to be inappropriate. In the burned swamp, the success of naturally established *Laguncularia* in the very saline soils of drought conditions also suggests that zonation of that species is not necessarily driven by soil salinity in that area.

For restoration purposes, these results have indicated that species with smaller propagules would require a greater effort to establish successfully, and higher cost for growing and transporting seedlings. In light of the establishment distance results presented here, such effort would be unnecessary in the cases of *Laguncularia* and *Avicennia*, which develop seed over a period of as little as three years and can be expected to disperse and establish some seedlings over a distance up to 100 meters, even in a non-tidal interior swamp.

Nevertheless, in a majority of disturbance cases, natural regeneration is preferable for mangrove restoration (Field 1996; Lewis & Streever 2000), the exceptions generally being where large scale alterations to hydrology have taken place (Bacon 1975; Elster 2000; Elster et al. 1999; Elster & Polanía 2000; Lewis 1990, 1982). It is possible that plantings of mangrove seedlings might affect the success or course of natural colonization (Bosire et al. 2003). With that in mind, mangrove restoration and management efforts should not be undertaken without detailed investigation into potential ecological, social and economic costs and consequences (Alongi 2002; Ellison 2000a, b; Elster 2000; Field 1998a; Field 1996, 1998b; Hamilton & Snedaker 1984; Humm 2001; Lewis 1982, 2000; Lewis & Streever 2000; Macintosh & Ashton 2003).

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APPENDIX 1.
MANGROVE ECOSYSTEMS AND FIRE IN THE TROPICS AND GUYANA

This appendix is included to provide a literature review of information on mangrove ecosystems and fires in tropical forests to provide background on the 1997-1998 soil fires in the mangrove and freshwater swamps of the Waini Peninsula, Guyana.

MANGROVE ECOSYSTEMS

Mangroves are woody plants with adaptations to coastal conditions in the tropics. The word mangrove can also refer to communities of those plants. These plant communities are sometimes referred to as "mangal" to distinguish them from mangrove species or individual mangrove plants (Tomlinson 1986). The classification of a species as a mangrove species is physiological and functional, and these species have arisen from several relatively unrelated plant families. By the assessment of Duke et al. (1998) there are 71 true mangrove species in the world, including putative hybrids, divided among twenty families. The global distribution of these species is decidedly uneven, with 58 mangrove species occurring in the Indo-West Pacific region but only 8-13 species found in the America-East Pacific region; the causes for that disparity are among the primary questions in the study of mangrove biogeography.

True mangroves possess active or passive adaptations to exclude salt or secrete salt from leaves, "viviparous" propagules that are dispersed by water, generally in some stage of germination (which allows for rapid establishment of seedlings) aerenchymatous tissues (for delivering oxygen to and within roots in saturated, anoxic soils), and roots modified for anchoring the plant in saturated soils (as exemplified by the prop roots of the red mangrove *Rhizophora* and the shallow, lateral "cable" roots of the black mangrove *Avicennia*) (Tomlinson 1986). Some researchers define mangrove communities as occurring only in the intertidal zone, however communities of mangrove species beyond high tide are generally accepted as true mangroves, and that is consistent with long-accepted classifications of inland basin and "hammock" mangrove community types (Lugo & Cintrón 1975; Lugo & Snedaker 1974).

It has been estimated that about 25% of all tropical coasts are occupied by mangrove swamps (Tomlinson 1986). The communities are generally found along protected coasts with low wave energy, between 30ºN and 30?S latitude, with exact limits determined by minimum air temperatures, which in turn are influenced by ocean currents (Duke et al. 1998). Mangroves occur in geomorphological settings similar to those commonly occupied by herbaceous salt marshes in temperate regions. The communities can cover a wide range of structures and zonation patterns with relatively few species, as a result of both morphological and physiological elasticities of mangrove species that allow them to adapt to varied environments (Lugo & Snedaker 1974; Tomlinson 1986) and a lack of competition in marginal, saline habitats. Mangrove ecosystems are generally regarded as resilient from natural disturbances (Cintrón-Molero & Schaeffer-Novelli 1992), including shore erosion - accretion cycles and tropical cyclone damage (Baldwin et al. 2001; Conner et al. 1989; Imbert et al. 1996; Jiménez et al. 1985). Following severe disturbances, mangroves tend to display the rapid colonization characteristics of "pioneer" species, though in other aspects they possess characteristics of "climax" species such as large seeds and shade tolerance. Egler (1948) was an early researcher to conclude that mangrove communities generally followed a cyclic pattern, with rare establishment events and occasional catastrophic setbacks. Some researchers have suggested that mangrove community structures can be dependent upon periodic disturbance, and are adapted to persist in a cyclical succession pattern (Conner et al. 1989; Lugo 1980, 1997; Odum et al. 1982). Gaps created by small disturbances may play an important role in determining and maintaining mangrove forest structure (Duke 2001), particularly in lower rainfall environments (Ewel et al. 1998b).

Mangrove Values

Attitudes towards mangrove ecosystem values have changed from a regard for swamps as low value lands best avoided or drained and converted to upland uses, to an almost universal acceptance of mangrove's high ecological and economic values. These values certainly vary by species and community type (Ewel et al. 1998a). High productivity in some mangrove systems may be due in part to landscape positions that allow tidal subsidies, including contributions of marine and terrestrially derived sediments (Lugo & Snedaker 1974) and tidal flushing of soils. Biogeochemically, mangrove systems function similarly to other wetlands, serving as sinks and transformers of nutrients, building biomass in wood and soils, producing a steady supply of litter (Lugo & Snedaker 1974; Odum et al. 1982), and providing appropriate conditions for the trapping of sediments (Wolanski 1995). High productivity and complex physical structure often makes mangrove swamps important fish nursery areas (Marshall 1994), and mangrove loss has been associated with declines in coastal fisheries (Baran & Hambrey 1998; Christensen 1983; Nickerson 1999; Rittibhonbhun et al. 1993). While the diversity of plant species in mangrove swamps is rather low, some mangrove communities support a high density, biomass, and diversity of invertebrates as epibionts on the intertidal portion of roots (Ellison & Farnsworth 1992; Kathiresan & Bingham 2001; Rützler & Feller 1987; Rützler & Feller 1996). They can also host a high diversity of vertebrates utilizing the ground and canopy levels (Alongi 2002; Christensen 1983).

Mangroves can provide valuable protection of coastlines against erosion and storm surges. While early descriptions and works on mangrove ecology (Davis 1940; Fosberg 1947; Schomburgk 1922) reflected a common assumption that mangroves actually functioned as builders of coastal land, that has more recently been revealed as incorrect. Mangroves are, however, often credited with a major role in securing sediments which have accreted through forceful coastal geomorphic processes (Augustinus 1995; Thom 1975; Vann 1969; Woodroffe 1992) and in the protection of reefs by capturing terrestrial sediments (Bossi & Cintrón 1990; Kathiresan & Bingham 2001; Pernetta 1993).

Mangroves are utilized directly by local peoples for a wide variety of uses, most importantly fuelwood and charcoal, building materials, fibers, and tannin, as well as some foods and medicines (Alongi 2002; de la Cruz 1983; Dugan 1993; Kovacs 1999; Snedaker 1986; Tomlinson 1986). In parts of Asia mangroves are exploited commercially for lumber and wood chips for synthetic fiber production (Adeel & Pomeroy 2002; FAO 1994). In Guyana, mangroves are primarily exploited for fuelwood and poles for fishing seines and light construction, but some tanbark is still gathered (Allan et al. 2002). *Rhizophora* and occasionally *Avicennia* are also locally cut into planks for construction, and shoots of *Laguncularia* (White mangrove, Kayara) are woven into walls and fences (pers. obs.).

Mangrove Losses

Worldwide losses of mangroves have often been reported as approximately 50% of their original area. Such values have been disputed as unverified estimates that have simply been repeated in the conservation literature (Farnsworth & Ellison 1997). It has also been estimated that over one third of world mangroves were lost in the last 20 years of the 20th century, with the highest rates in the Americas (Valiela et al. 2001). The rate of loss of mangroves in many developing countries has been estimated to be around 1% per year (Ong 1995). More conservative studies based on known surveys, maps, and imagery have estimated that a total of perhaps one third of original mangrove area has been lost (Alongi 2002; Spalding et al. 1997). All of these studies are limited by the scarcity of accurate multi-date information utilizing consistent definitions of mangrove habitats (Blasco et al. 2001). Estimates of the extent of mangrove vegetation at regional scales have been considered highly variable by Alongi (2002), who noted that many are not based on reliable field surveys or ground-truthed imagery and that variations could also be attributed to inconsistencies in classifications of mangrove forests.

A common cause of mangrove degradation is alteration of either oceanic or terrestrial hydrology. Causes of hydrologic change have included dams (Colonnello & Medina 1998; Lacerda & Marins 2002; Medina et al. 2001; Rubin et al. 1998), diking, impoundment, channelization (Bacon 1975), poorly planned road construction (Jiménez et al. 1985; Lewis 1990; Lugo 2002), diversion of freshwater from swamps (Cardona & Botero 1998; Elster et al. 1999; Elster & Polanía 2000), and natural coastal morphology changes (Breen & Hill 1969). Planned conversion of mangroves is also a threat, particularly near urban areas, permanently destroying the resource. In Asia and parts of South and Central America, the establishment of aquaculture ponds, mostly for shrimp, has been a major problem (Alongi 2002; DeWalt et al. 1996; Epler 1992; Gujja & Finger-Stich 1996; Pons & Fislier 1991; Robadue 1995; Saenger et al. 1983; Twilley 1989; Weinstock 1994; Wolanski et al. 2000), as have salt production ponds (Stevenson 1997). Agricultural conversion of mangrove land has often failed in areas where acid-sulphate soils form through the oxidation of marine sediments (Hamilton & Snedaker 1984; Stevenson 1997). Urban and industrial conversion also have substantial permanent impacts, primarily from coastal zone related activities such as marina and port construction, landfills, and increasing waterside residential and estate construction (Alongi 2002; Bossi & Cintrón 1990; Ellison & Farnsworth 1996; Lugo 2002; Saenger et al. 1983; Valiela et al. 2001).

Sewage and chemical pollution can be substantial problems in many urban mangrove areas, and agricultural herbicide runoff has been implicated in some mangrove diebacks (Duke et al. 2003). Oil spills can have a particularly serious impact on mangrove ecosystems (Alongi 2002; Saenger et al. 1983). Essential air exchange, which takes place in the adventitious prop roots or pneumatophores in the intertidal range, is easily impeded by oil (Lewis 1990). Oil can be extremely persistent in the sediments of mangrove areas (Burns et al. 1994), resulting in widespread sublethal damages (Duke et al. 1997) with changes in community structure and productivity (Cintrón-Molero & Schaeffer-Novelli 1992; Garrity et al. 1994), although seedling establishment may be relatively unaffected in oil-polluted soils (Imbert et al. 2000).

FIRE IN THE TROPICS, WETLANDS, AND MANGROVE SWAMPS

Fires in most ecosystems are complex phenomena that vary appreciably depending on many factors, including vegetation type, topography, climate, fuel type, fuel arrangement, fire history. The influence of man is certainly increasing, including an increased risk of ignition and potential interruption of fires in dissected landscapes (Whelan 1995). The return frequency of fires varies among ecosystem types, from annually in some grasslands to over 1,000 years for some evergreen forests, and by some accounts, never for moist tropical forests (Whelan 1995). The concept of fire regimes suggests that some plant communities are adapted to fires, within certain limits. However the fire regime concept has drawbacks in light of the variable nature of fires, the great number of factors that must be considered to infer that regime, and the complications of alterations by human activities (Vogl 1975; Whelan 1995).

Succession concepts can be applied to fire recovery, but it must be recognized that each situation is unique according to combinations of species' life histories, the nature and patterns of disturbance, and the physical and chemical attributes of the disturbed environment (Noble & Slatyer 1981). Communities of fire-adapted species do not fit well into classical succession concepts, as these systems tend to remain in or rapidly return to their pre-fire species compositions after a fire because of the presence of persistent adults, roots, and seeds. In those cases, fire is an external factor causing only a temporary regression in an ongoing process

(Noble & Slatyer 1981). Gleason (1927) described a simple cyclical pattern of succession in fire-adapted plant communities. On the other hand, non fire-adapted communities may be good illustrations of successional concepts, since mortality is nearly full and reestablishment is mostly dependent on sources outside of the fire area. A typical species richness pattern for secondary succession often results, starting with an initial decrease in species followed by a sharp increase as many species invade, including disturbance specialists. Finally, a slow drop occurs, leveling off to those species best adapted for long term persistence in the developing environment (Whelan 1995). Along tropical coasts with saline soils, the expected endpoint of succession would be a return to dominance by mangrove species. That outcome would be influenced by the dispersal of mangrove propagules and any preceding occupation of disturbed sites by persistent, disturbance-adapted herbaceous species such as *Typha* (Miao et al. 2001; Newman et al. 1996; Smith & Newman 2001) or *Spartina*, and unfavorable changes that disturbances might have had on hydrology or nutrient availability, preventing mangrove dispersal or establishment, and thus setting the stage for a substantial shift in dominant species.

The most destructive wildfires are increasingly linked to human caused disturbances and ignitions. Fires in fire-adapted communities are more likely to be catastrophic when they occur outside of the usual fire season, or when the organisms in a community are not at all adapted to fire (Whelan 1995). Among forests types that may be considered non-fire adapted are tropical rain forests and swamp forests. Mangrove forests fall into both of those categories. Some fire adapted species may have life history traits that are incompatible with particular fire frequencies. For example, viable seeds may not have adequate time to be produced between frequent fires, or fire frequencies could fall to the point that species requiring fires for reproduction become locally extinct (Noble & Slatyer 1981).

One strategy allowing for tolerance to fire is through resistance of individual plants. Those species have evolved structures to protect critical living cells from the heat of fires, and thick, corky bark is a common adaptation. Mesophytic plant cells die at temperatures of only about 50-55ºC. The trees of tropical wet forests are typically thin-barked, making them vulnerable to fires (Uhl & Kauffman 1990). Persistent rootstocks of plants that re-sprout after fires are protected by the insulation of soils. Mangroves have neither of these adaptations; in addition to thin bark, sensitive root systems are often exposed to air or concentrated at shallow soil depths. Mortality from surface fires is higher if upper organic soil horizons burn rather than simply litter and dry herbaceous vegetation (Wade et al. 1980). In mangrove systems, saturation may slow soil decomposition and allow a buildup of organic matter. Mangroves generally have exposed or shallow roots possessing critical aerenchyma tissue and lenticels for gas exchange. With these conditions, almost any soil fire would be extremely damaging to mangroves; a large proportion of their sensitive roots would come into proximity or direct contact with the fuel. Not surprisingly, when soil fires burned in mangrove swamps of the Waini Peninsula there was nearly, full mortality of trees.

Laguncularia trees generally produce no aerial roots or sparse, small pneumatophores, which may have contributed to the survival of the Waini Peninsula soil fires by scattered small *Laguncularia* trees. These small trees may have also avoided mortality because of the scale of patchiness of the fires, while few large trees were unaffected. The patchiness of mortality together with the invasion rates of potential colonizers may play a major role in the path of recovery after a fire (Whelan 1995).

Post-fire physical conditions, such as surface temperatures, wind and nutrient levels, can be as influential upon the path of post-fire recovery as the characteristics of a fire itself, although these factors have been rarely studied (Whelan 1995). Fires are often used by people to release nutrients in preparation for cultivation in nutrient limited ecosystems; fire also volatilizes some nutrients, particularly nitrogen, which are lost to the atmosphere. Biogeochemical cycling of nutrients during and after fires is in need of more study, and certainly seemed to be a factor in the post-fire swamps of the Waini Peninsula, where released nutrients apparently stimulated growth of floating aquatic plants and algae and affected water openness for mangrove dispersal. Whelan (1995) lists pertinent questions that have been infrequently addressed in fire studies, including 1) What are seed dispersal distances in relation to the spatial patterns of fires? and 2) What are the responses of organisms to fires in historically fire-free environments? These questions are approached here in the context of the Waini Peninsula fires.

Fire in Tropical Ecosystems

Fire is an integral part of some ecosystems in the seasonal tropics, particularly dry seasonal forests and tropical savannas, where the plant species often have fire adaptations (Mueller-Dombois & Goldammer 1990). Because of that, investigations of fire dynamics in tropical South America have often focused on the burning of savanna ecosystems and agricultural uses (Eden 1964; Fearnside 1990; Hillis & Randall 1968). Primary tropical forests are generally unable to survive fires of even low intensity (Kauffman & Uhl 1990; Roberts 2000). Earlier writings on fire ecology tended to entirely pass over or minimally address effects of fire on humid tropical forests (Kozlowski & Ahlgren 1974), or focus only on damages from shifting cultivation and cattle ranching practices (Kauffman & Uhl 1990; Uhl & Buschbacher 1985). Attention has only recently been focused on the phenomenon of unintentional wildfires that can occur in wet tropical forests during periodic droughts (Cochrane 2001; Cochrane & Laurance 2002; Uhl 1998).

The El Niño Southern Oscillation (ENSO) periodically brings droughts to northwestern South America, while at the same time bringing extreme rains to the western coast around Ecuador and Peru (WMO 1999). “Mega-Niño” events have occurred periodically over the last two millennia, around 400, 700, 1000, and 1500 BP, and correlate with discontinuities in cultural artifacts; they are a possible cause of high linguistic heterogeneity in tropical South America (Meggers 1994). Evidence has also been found of charcoal deposits more than 2,000 years old in forests of French Guiana, suggesting that some fires could be non-human in origin (Charles-Dominique et al. 1998), and in the upper Rio Negro Basin on the Guiana Shield charcoal evidence has been found of fires occurring over 6000 years BP, nearly twice the estimated age of the oldest pottery shards from the region (Saldarriaga & West 1986).

Lindeman (1953) relays an account, by way of William Beebe, of extensive fires in the coastal area of Guyana during an extreme drought in 1837, listed by Quinn (1992) as a year of a greater than moderate El Niño phenomenon. That year fires destroyed the forest over a vast area in the freshwater *Mauritia* and *Mora* swamps of the Abary River region on the southeastern coastal plain of Guyana. More recently, attention was given to the occurrence of fires in relatively small, understory patches of disturbed evergreen forest on white sands in Guyana (Hammond & Steege 1998). These fires occurred during the fairly strong 1997-1998 El Niño event; they were rarely over 0.5 hectare in size.

While ignition through natural causes is possible, either accidental or intentional ignition by humans is considered to be the prime source of fires in Guyana and beyond (Hammond & Steege 1998; Kauffman & Uhl 1990; Lindeman 1953). Lindeman (1953) notes that cities and towns in the Guianas are built almost entirely of wood and lack lightning rods, yet do not experience structural fires from lightning strikes. In the Venezuelan portion of the Guiana Shield, as in Guyana, local people often ignite savanna fires that burn into adjacent forested areas. In these cultures fire is viewed positively as ‘cleansing,’ and as being especially useful for controlling populations of venomous snakes (Means 1995).

Fires become more likely in moist forests following most physical disturbances, which tend to result in higher daily temperature maxima and lower humidity, allowing litter on the forest floor to dry to the point where ignition is possible (Kauffman & Uhl 1990). Many kinds of disturbances, including fires, hurricanes and logging, can lead to an increase in the dominance of vines and other fine vegetation, which contribute to the fuel loading for future fires (Mueller-Dombois & Goldammer 1990).

There is a growing recognition that low intensity fires in the humid tropics can contribute to a positive feedback process that leads to impacts on ever wider land areas (Uhl 1998). Remote sensing studies in Brazil have indicated that once a forest has been selectively logged the risk of burning increases, and each time even a light fire occurs the probability of and severity of subsequent fires increase (Cochrane 2000). The probability of burning in an El Niño year also increases with selective logging (Cochrane 2000), and 90% of unintended forest fires in Amazonian Brazil are estimated to occur during El Niño years (Cochrane 2000). It has also been estimated that nearly 90% of fires in Amazonian Brazil have some relationship to a forest edge, with the length of the average fire return time bearing a positive relationship with distance from forest edge (Cochrane 2001). As forests become more fragmented their ratio of edge to area increases, and the increased tendency for fires to be initiated along forest edges suggests a cycle of increased frequency and impacts. Seemingly minor, accidental surface fires may cause significant impacts to tropical plant and animal communities and make forests far more vulnerable to larger fires (Laurance 2003). That apparently was the case when a severe dry season in 2003 led to fires over 20,000 km^2 or more in Roraima state of northern Brazil. Those lands were probably primed for additional fire by earlier fires during the El Niño event of 1998 (Barbosa & Fearnside 1999; Barbosa et al. 2003). Cochrane et al. (2002a) found that including the effects of unintended burns increased estimates of deforestation by 129 percent from 1993-1995 in Paragominas in Northeastern Brazil. These incremental, positive feedback augmented fire impacts may merit attention equal to that given to deforestation by agricultural clearing. Similar dynamics have possibly been at work in the Western Ghats of India over longer periods of time, where very short return intervals for fires and severe changes in species compositions of forests have been documented (Kodandapani et al. 2003). Tropical forest fires are often re-ignited by smouldering logs when litter conditions become dry (Cochrane et al. 2002b). During the early 2001 dry season on the Waini Peninsula, recently ignited fires were observed smoldering in fallen logs of trees killed during the 1998 fires; these sometimes spread a short distance in organic soils and dry herbaceous vegetation. Those re-burned areas generally had very sparse vegetation cover of scattered *Acrostichum* ferns and scrub *Laguncularia* and therefore dried quickly in the open sun.

Fire in Wetlands

While the idea of fire occurrence in wetlands may seem unusual, many wetlands pass through dry hydrologic conditions and may burn occasionally, though forested wetlands are rarely affected (Lugo 1995). Earlier studies of fire in wetlands have been predominantly confined to seasonally flooded herbaceous wetlands, tidal marshes and peatlands in North America (Kirby et al. 1988), often with a focus on prescribed burns for wildlife management (Cerulean & Engstrom 1995; Hackney & de la Cruz 1981). Many wetland types, including marshes, freshwater swamps, and mangrove swamps, are considered to be fire-independent systems, which generally require preparation for burning and deliberate ignition during dry periods (Vogl 1975). Nonetheless, fires in those types of ecosystems tend to be catastrophic, and recovery in burned wetlands is likely to include wide areas of weedy plants that can quite persistent. To avoid such results, controlled fires for management in marshes are typically set when the soil is damp, resulting in cover burns affecting only above ground biomass. Decomposition in wetlands often proceeds at a lower rate than production (Mitsch & Gosselink 1993), so that organic soils accumulate that, when ignited during drought or drawdown, usually fuel smoldering peat fires that produce copious smoke, which can pose serious visibility and health problems (Hungerford et al. 1995). Peat burns can result in open water and take many decades to recover; they are never considered a useful management tool (Nyman & Chabreck 1995). Some raised bogs and tidal marshes are subject to fires, and may possess some fire adapted species, in which case regeneration of vegetation can be rapid (Clarkson 1997; Timmins 1992).

Among forested wetlands, Cypress (*Taxodium distichum* Rich.) swamps are known to suffer infrequent fires with return frequencies of hundreds of years; these fires may play a limited role in stimulating seed production and therefore recruitment of seedlings (Cook & Ewel 1992; Ewel 1995; Glasser 1985). Although some varieties of Cypress may be more fire adapted than others, fires that burn significantly into organic soils will damage a high percentage of roots and kill most Cypress trees and all seedlings (Ewel 1995). Atlantic white cedar (*Chamaecyparis thyoides(*L.) Britton, Sterns & Poggenb.) wetlands in the Northeastern United States have been prehistorically disturbed by crown and soil fires, which apparently resulted in substantial declines in cedar populations, and which only after long periods were finally followed by regeneration (Motzkin et al. 1993). Fires in tropical wetlands are a very poorly studied phenomenon, being confined primarily to large-scale peat fires in Asia, particularly Indonesia, that have become associated with El Niño events (Fuller & Fulk 2001; Kinnaird & O'Brien 1998; Roberts 2000; Trenberth 1999). Fire is a factor in the maintenance and spread of *Mauritia* palms in the Llanos savannas of Venezuela and similar wet savannas of coastal Guyana (Middleton 1999; Myers 1990). The species composition of plant communities on and around the tepuis of the Guiana Shield in Southern Venezuela are also probably influenced by fires (Means 1995).

Fire in Mangrove Literature

In the terminology of Noble and Slatyer's (1980) vital attributes classification for successional pathways following disturbance, mangrove fires should be described as catastrophic events that do not normally occur over the life span of the affected species. The species of such systems have not been selected for and possess few mechanisms for rapid recovery.

There is limited information in the literature on the occurrence of fire in mangrove ecosystems. The few cases have been primarily concerned with small-scale mortality resulting from lightning strikes (Duke 2001; Sherman et al. 2000; Smith et al. 1994; Wade et al. 1980) with affected areas only in the range of 10 to 100 square meters. Colonization of these small lightning gaps may play a significant role in patterns of species distribution in some mangrove forests, particularly those forests that are not subject to large scale disturbances such as hurricanes (Duke 2001). Lugo (1980), in his work on mangrove succession and disturbance, mentioned only briefly the sensitivity to fire of raised "Hammock" mangrove swamps of the South Florida Everglades. Fires burning in adjacent marsh or upland vegetation have often been credited with maintenance of mangrove-marsh boundaries in Florida (Lugo 1997; Middleton 1999; Odum et al. 1982; Wade et al. 1980).

Vogl (1975) characterized mangrove swamps as fire independent systems in which fire leads to catastrophic results. His list of mangrove swamp properties that contribute to exclusion of fire included high water tables, rapid decomposition of organic fuel, few flammable oils, and sparse understories. He noted that fires in such systems are usually initiated by man during extreme droughts and result in high mortality, even from seemingly mild surface fires, and revegetation includes many weedy species. Without citing specific instances, Wade et al. (1980) also state that very low intensity, creeping soil fires easily kill mangroves. These observations are in agreement with the emerging understanding of the effects of surface fires on wet tropical forests in the Amazon basin (Cochrane 2003; Cochrane & Laurance 2002). Wade et al. (1980) also described cases of fires in dried dead mangrove debris left after hurricanes, as well as near the northern limits of mangrove vegetation in Florida frost killed mangroves are susceptible to fire. In very rare cases frost-killed leaves have ignited before dropping, causing intense mangrove crown fires.

In the Guianas, there has been minor documentation in the literature of fire in or near mangrove ecosystems. Lindeman (1953) mentions fire along parts of the Surinam shoreline, describing it as an infrequent agent that accelerates his model of succession in which *Avicennia* swamp forest gives way to *Eleocharis* R.Br. marsh. Pons and Pons (1975) also mention fires in *Avicennia* swamps isolated behind beach ridges at Little Orange Creek on the coast of Surinam, with the disturbance initiating various types of herbaceous vegetation. Their model describes a post-fire succession starting with shallow open water or *Eleocharis* meadows with *Avicennia* slowly colonizing. That returns to a "climax" of *Avicennia* swamp if undisturbed, or becomes arrested at a *Typha* marsh or *Cyperus-Montrichardia* marsh stage. Details are not given in the Pons and Pons paper about the extent of areas affected by fires, but maps are included indicating belts of *Eleocharis* up to 1 kilometer wide and patches of *Typha* on the inland margin of *Avicennia* swamps, some over 100 hectares in size. There, both of these herbaceous communities are described as persisting possibly as a result of recurring fires or other disturbances, however no specific fires were documented, and the frequency of fires is apparently low.

Observations at Almond Beach on the Waini Peninsula suggest that patterns of vegetation change on Guyana's coastline may follow pathways similar to those in Surinam (Lindeman 1953; Pons & Pons 1975), with shifts in the mangrove/marsh boundary occurring in a punctuated manner, initiated during extreme droughts by catastrophic fires that define a new boundary by burning forested areas that are no longer tidally inundated. The occluded mangrove swamps are then converted, at least for a time, to herbaceous, somewhat salt-tolerant vegetation.

Status of Mangroves in Guyana

Because the soils beyond Guyana's coastal plain are generally laterites or white sands with poor fertility, over 90% of the population lives on the coastal plain (Merrill 1993), with a sparse transportation system beyond the coast. That, in combination with a timber industry that has only recently reached large scales, has left mangroves as one of the most highly impacted forest types in Guyana (GFC & CIDA 1989).

The coast of the Guianas is credited with optimal growing conditions for the black mangrove *Avicennia germinans*, which is reported to reach heights of up to 100 feet in Surinam (Lindeman 1953; Vann 1959, 1969); similar heights have been observed in the coastal forests of the Waini Peninsula, and diameters in coastal swamps reach more than 50 cm, with exceptional diameters of over 2 meters for scattered mature trees found just inland of the Waini River (see Figure 1.16).

The zonation of species within mangrove communities in the Guianas is quite distinct from that typically described for the more often studied mangroves on calcareous substrates in the Caribbean (Lindeman & Mori 1989; West 1977). The black mangrove, *Avicennia germinans*, forms a moderate to wide band nearest the ocean. The red mangrove, *Rhizophora mangle*, the prop-rooted seaward species in most Caribbean communities, is mixed in to varying degrees behind the black mangroves (Granville 1992). Farther inland, forest composition grades into freshwater swamp (Bacon 1990). Red mangroves are also found along the banks of the tidal rivers in brackish water, usually as the riverine species *Rhizophora racemosa* G. Mey., a species with a narrower distribution in the Americas than *R. mangle*. The white mangrove *Laguncularia racemosa* is not a dominant tree in the mangroves of the Guianas, but is very common as an understory shrub or treelet.

The early colonization of Guyana by Dutch planters led to the diking of long stretches of coastline and tidal river banks for development of agricultural from coastal swamps and marshes. That affected almost all of the coastline southeast of the Pomeroon River, where the coastal plain is widest (Daly 1995). Daily operation and maintenance of the drainage and sea defense infrastructure places a great economic demand on the Guyanese economy and has at times been a significant focus of international assistance (Richardson 1987). Before reclamation, much of the coastal plain was covered by marshes and swamps, with areas closest to the sea periodically to frequently flooded by saline tides. The drainage of the coastal wetland soils probably resulted in subsidence from de-watering and oxidation of organic matter, leaving the land below mean sea level and making any restoration difficult.

No descriptions have been found of the extent of Guyana's mangroves prior to diking, but it is almost certain that a vast area was destroyed since the beginning of colonization (Richardson 1987). On the southeastern Guyana coast, many mangroves that remained outside of seawalls have disappeared from the effects of altered hydrology and erosion of sediments along the shore (Singhroy 1996). In some coastal areas sediment accretion outside of seawalls allows substantial colonization by *Avicennia*, such as has occurred on the coast between the Pomeroon and Essequibo Rivers (pers. obs.). These may be ephemeral and eventually be lost to erosion as mudbanks migrate along the coast.

Estimates of the current mangrove area in Guyana range from Spalding's (1997) 71,700 ha (whose methods were positively appraised by Alongi) to 80,000 ha (Snedaker 1986) with the highest area of 150,000 ha (Saenger et al. 1983) or slightly more (Huber et al. 1995). After agricultural conversion, the major threat to remaining mangroves in Guyana, both along the coast and in estuarine areas, was once fuelwood collection (GFC & CIDA 1989; Guyana Agency for Health 1992) which affected *Avicennia* as well as *Rhizophora*. These species are decreasingly utilized as sources for superior fuelwood, charcoal and tanbark, but are still harvested for construction and fishing poles (Allan et al. 2002). Mangroves near populated areas are highly degraded by intense use, evidenced by very low mean tree diameters in a 1 ha plot near Alness Village, where a mean dbh of 16 cm was recorded (Ramdass et al. 1997). Where mangrove swamps remain in Guyana they are credited with the stabilization of accreted sediments and erosion prevention (EPA Guyana 2000; GFC & CIDA 1989).

Fire Detection Resources

There are a growing number of resources that can alert resource managers and policy makers to wildfires, making timely reaction to events possible. NOAA's Operational Significant Event Imagery (http://www.osei.noaa.gov/Events/Fires/Guyana/), archives have included past events sensed by AVHRR channel 3 imagery. Only events for March 30, 1998 were available for Guyana, indicating no fire activity on the Waini Peninsula. The MODIS satellite has been operational since 2000, and provides 1 kilometer resolution fire and thermal anomaly data at a twice daily frequency that can be downloaded ready for use in GIS systems (http://modis-fire.umd.edu/). The National Geophysical Data Center's Satellite Fire Detection Viewer (http://map.ngdc.noaa.gov/website/firedetects/viewer.htm) provides recent possible fire data; the ABBA GOES-10 layer provides fire detections that include Guyana and can be downloaded for use in GIS systems. Ideally these data sources should be regularly monitored and analyzed to increase the likelihood that managers become aware of fires while they are in progress (Cochrane 2002). Another development advancing the detection of and communication about wildfires is the recent foundation of the Regional South America Wildland Fire Network (IFFN 2004), which is internationally funded by governmental and non-governmental organizations.

CONCLUSION

Like terrestrial forested ecosystems, mangrove ecosystems can vary widely in their structure and function. The mangroves of Guyana and not typical of the low sediment Caribbean systems most often studied and published on in the Neotropics, but fall well within the worldwide varieties of mangrove systems. As is true of many wetland types, they are dynamic systems, that change along with the hydrology and geomorphology of the landscape in which they are situated. In places like the coast of the Guianas, changes are accentuated by coastal sediment dynamics as well as by fluctuations of climate over time, possibly making the system increasingly vulnerable to disturbances such as fires. If understood, such disturbances can be anticipated and managed. On wild sections of the coast of the Guianas, that would primarily include suppression of fire ignition during extreme dry years, and connected efforts at education and planning of settlement and land use patterns. Such practices might have an impact on the frequency of fires, and the conservation of these ecologically and culturally valuable mangrove ecosystems.

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APPENDIX 2.
PLANT SPECIES LISTED FOR THE WAINI PENINSULA, WITH SYNONYMY

CHLOROPHYTES (Green Algae)

Cladophoraceae
Rhizoclonium africanum Kützing

PTERIDOPHYTES

Blechnaceae
Blechnum serrulatum Rich.

Lygodiaceae
Lygodium venustum Sw.

Oleandraceae
Nephrolepis biserrata (Sw.) Schott
Nephrolepis rivularis (Vahl) Mett. ex Krug

Parkeriaceae
Ceratopteris thalictroides (L.) Brongn.

Polypodiaceae
Campyloneurum phyllitidis (L.) C. Presl

Pteridaceae
Acrostichum aureum L.
Acrostichum danaeifolium Langsd. & Fisch.
Pteris pungens Willd.

DICOTILEDONEAE

Aizoaceae
Sesuvium portulacastrum (L.) L.

Amaranthaceae
Alternanthera sessilis (L.) R. Br. ex DC.
Amaranthus australis (A. Gray) J.D. Sauer
Amaranthus dubius Mart. ex Thell.
Blutaparon vermiculare (L.) Mears

Anacardiaceae
Spondias mombin L.

Annonaceae
Annona glabra L.

Apocynaceae
Allamanda cathartica L.
Malouetia tamaquarina (Aubl.) A. DC.
Rhabdadenia biflora (Jacq.) Müll. Arg.

Aristolochiaceae
Aristolochia trilobata L.

Asclepiadaceae
Sarcostemma clausum (Jacq.) Schult.

Asteraceae
Bidens alba (L.) DC.
Cyanthillium cinereum (L.) H. Rob.
Eclipta prostrata (L.) L.
Mikania micrantha Kunth
Pluchea odorata (L.) Cass.

Avicenniaceae
Avicennia germinans (L.) Stearn

Bignoniaceae
Cydista aequinoctialis (L.) Miers

Cactaceae
Epiphyllum phyllanthus (L.) Haw.
Rhipsalis baccifera (J.S. Muell.) Stearn

Caricaceae
Carica papaya L.

Cecropiaceae
Coussapoa asperifolia Trécul

Ceratophyllaceae
Ceratophyllum muricatum Cham.

Clusiaceae
Clusia palmicida Rich. ex Planch. & Triana

Combretaceae
Conocarpus erectus L.
Laguncularia racemosa (L.) C.F. Gaertn.
Terminalia catappa L.

Convolvulaceae
Ipomoea pes-caprae (L.) R. Br.
Ipomoea tiliacea (Willd.) Choisy

Ipomoea violacea L.
Merremia cissoides (Lam.) Hallier f.
Merremia umbellata (L.) Hallier f.

Cucurbitaceae
Melothria pendula L.

Cuscutaceae
Cuscuta umbellata Kunth

Euphorbiaceae
Euphorbia hirta L.
Manihot esculenta Crantz (cultivated)

Fabaceae-Caesal.
Caesalpinia bonduc (L.) Roxb.

Fabaceae-Mimos.
Entada polystachya (L.) DC.
Inga ingoides (Rich.) Willd.
Zygia latifolia (L.) Fawc. & Rendle

Fabaceae-Papil.
Aeschynomene sensitiva Sw.
Canavalia rosea (Sw.) DC.
Machaerium lunatum (L. f.) Ducke
Pterocarpus officinalis Jacq.
Sesbania sericea (Willd.) DC.
Vigna luteola (Jacq.) Benth.

Hippocrateaceae
Hippocratea volubilis L.

Lauraceae
Cassytha filiformis L.

Malpighiaceae
Stigmaphyllon bannisterioides (L.) C.E. Anderson

Malvaceae
Hibiscus bifurcatus Cav.
Talipariti tiliaceum (L.) Fryxell
Thespesia populnea (L.) Sol. ex Corrêa

Moraceae
Ficus amazonica (Miq.) Miq.
Ficus eximia Schott
Ficus maxima Mill.

Myrtaceae
Calyptranthes sp.
Psidium guajava L.

Nyctaginaceae
Boerhavia diffusa L.

Onagraceae
Ludwigia affinis (DC.) H. Hara
Ludwigia leptocarpa (Nutt.) H. Hara

Passifloraceae
Passiflora foetida L.

Piperaceae
Peperomia glabella (Sw.) A. Dietr.

Polygalaceae
Securidaca diversifolia (L.) S.F. Blake

Rhizophoraceae
Cassipourea guianensis Aubl.
Rhizophora mangle L.
Rhizophora racemosa G. Mey.

Rubiaceae
Morinda citrifolia L.

Sapindaceae
Paullinia pinnata L.

Scrophulariaceae
Capraria biflora L.

Solanaceae
Physalis angulata L.
Solanum stramoniifolium Jacq.

Vitaceae
Cissus verticillata (L.) Nicolson & C.E. Jarvis

MONOCOTILEDONEAE

Araceae
Anthurium gracile (Rudge) Schott
Monstera adansonii Schott
Montrichardia linifera (Arruda) Schott
Philodendron acutatum Schott
Syngonium podophyllum Schott

Arecaceae
Cocos nucifera L. (cultivated)
Desmoncus orthacanthos Mart.

Euterpe oleracea Mart.
Nypa fruticans Wurmb.
Roystonea oleracea (Jacq.) O.F. Cook

Bromeliaceae
Aechmea nudicaulis (L.) Griseb.
Bromelia plumieri (E. Morren) L.B. Sm.
Guzmania lingulata (L.) Mez

Costaceae
Costus arabicus L.

Cyperaceae
Cyperus ligularis L.
Cyperus odoratus L.
Cyperus polystachyos Rottb.
Eleocharis mutata (L.) Roem. & Schult.
Fimbristylis cymosa R. Br.

Dioscoreaceae
Dioscorea polygonoides Humb. & Bonpl. ex Willd.

Heliconiaceae
Heliconia psittacorum L.f.

Hydrocharitaceae
Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine

Lemnaceae
Lemna aequinoctialis Welw.

Liliaceae
Crinum erubescens L. f. ex Sol.

Orchidaceae
Dimerandra elegans ? (H. Focke) Siegerist
Epidendrum ciliare L.
Prosthechea aemula (Lindl.) W.E. Higgins
Trichocentrum lanceanum (Lindl.) M.W. Chase & N.H. Williams

Poaceae
Echinochloa polystachya (Kunth) Hitchc.
Leptochloa scabra Nees
Paspalum distichum L.
Sporobolus virginicus (L.) Kunth

Smilacaceae
Smilax cumanensis Humb. & Bonpl. ex Willd.

Typhaceae
Typha domingensis Pers.

Zingiberaceae
Renealmia alpinia (Rottb.) Maas

SYNONYMY

Achyranthes sessilis (L.) Desf. ex Steud. = *Alternanthera sessilis*
Acnida australis A. Gray = *Amaranthus australis*
Acnida cuspidata Bertero ex Spreng. = *Amaranthus australis*
Acrostichum guineense Gaudich. = *Acrostichum aureum*
Acrostichum lomarioides (Jenman) Jenman [nom. illeg.] = *Acrostichum danaeifolium*
Acrostichum thalictroides L. = *Ceratopteris thalictroides*
Agrostis littoralis Lam. = *Sporobolus virginicus*
Agrostis virginica L. = *Sporobolus virginicus*
Alpinia tubulata Ker Gawl. = *Renealmia alpinia*
Annona palustris L. = *Annona glabra*
Anthurium scolopendrinum (Ham.) Kunth = *Anthurium gracile*
Arum liniferum Arruda = *Montrichardia linifera*
Asclepias clausa Jacq. = *Sarcostemma clausum*
Aspidium biserratum Sw. = *Nephrolepis biserrata*
Aulizia ciliaris (L.) Salisb. = *Epidendrum ciliare*
Avicennia nitida Jacq. = *Avicennia germinans*
Avicennia tomentosa Jacq. = *Avicennia germinans*
Banisteria ovata Cav. = *Stigmaphyllon bannisterioides*
Bidens pilosa forma *radiata* Sch. Bip. = Bidens alba
Bignonia aequinoctialis L. = *Cydista aequinoctialis*
Bignonia picta Kunth = *Cydista aequinoctialis*
Bihai silvestris Gleason = *Heliconia psittacorum*
Blechnum indicum auct. non Burm. f. = *Blechnum serrulatum*
Boerhavia paniculata Rich. = *Boerhavia diffusa*
Boerhavia surinamensis Miq. = *Boerhavia diffusa*
Brachypterys borealis A. Juss. = *Stigmaphyllon bannisterioides*
Bromelia karatas L. = *Bromelia plumieri*

Bryonia guadalupensis Spreng. = *Melothria pendula*

Cacalia cinerea (L.) Kuntze = *Cyanthillium cinereum*

Cactus caripensis Kunth = *Rhipsalis baccifera*

Cactus phyllanthus L. = *Epiphyllum phyllanthus*

Calliandra latifolia (L.) Griseb. = *Zygia latifolia*

Calonyction tuba (Schltdl.) Colla = *Ipomoea violacea*

Cameraria tamaquarina Aubl. = *Malouetia tamaquarina*

Campyloneurum costatum (Kunze) C. Presl = *Campyloneurum phyllitidis*

Canavalia maritima Thouars = *Canavalia rosea*

Canavalia obtusifolia DC. = *Canavalia rosea*

Capraria hirsuta Kunth = *Capraria biflora*

Caraguata lingulata (L.) Lindl. = *Guzmania lingulata*

Caraguata splendens Planch. = *Guzmania lingulata*

Caraxeron vermicularis (L.) Raf. = *Blutaparon vermiculare*

Carica sativa Tussac = *Carica papaya*

Cassia paramariboensis Miq. = *Aeschynomene sensitiva*

Cassipourea belizensis Lundell = *Cassipourea guianensis*

Cassipourea elliptica (Sw.) Poir. = *Cassipourea guianensis*

Cassipourea macrodonta Standl. = *Cassipourea guianensis*

Cassipourea podantha Standl. = *Cassipourea guianensis*

Cassytha americana Nees = *Cassytha filiformis*

Cassytha baccifera Sol. ex J.S. Muell. = *Rhipsalis baccifera*

Ceratophyllum demersum L. var. *cristatum* (Spruce) K. Schum. = *Ceratophyllum muricatum*

Ceratophyllum lleranae Fassett = *Ceratophyllum muricatum*

Cereus caripensis (Kunth) DC. = *Rhipsalis baccifera*

Chamaesyce hirta (L.) Millsp. = *Euphorbia hirta*

Chrysodium aureum (L.) Mett. = *Acrostichum aureum*

Chrysodium lomarioides Jenman = *Acrostichum danaeifolium*

Cissus cordifolia L. = *Cissus verticillata*

Cissus sicyoides L. = *Cissus verticillata*

Conocarpus racemosa L. = *Laguncularia racemosa*

Convolvulus caracassanus Roem. & Schult. = *Merremia umbellata*

Convolvulus cissoides Lam. = *Merremia cissoides*

Convolvulus pes-caprae L. = *Ipomoea pes-caprae*

Convolvulus riparius Kunth = *Merremia cissoides*

Convolvulus tiliaceus Willd. = *Ipomoea tiliacea*

Convolvulus umbellatus L. = *Merremia umbellata*

Conyza cinerea L. = *Cyanthillium cinereum*

Conyza cortesii Kunth = *Pluchea odorata*

Conyza odorata L. = *Pluchea odorata*

Coreopsis alba L. = *Bidens alba*

Coronilla sericea Willd. = *Sesbania sericea*

Costus discolor Roscoe = *Costus arabicus*

Costus niveus G. Mey. = *Costus arabicus*

Costus ramosus Woodson = *Costus arabicus*

Crinum commelyni Jacq. = *Crinum erubescens*

Crinum guianense M. Roem. = *Crinum erubescens*

Crinum lancei Herbert ex Sweet = *Crinum erubescens*

Crinum lindleyanum Schult. f. ex Seub. = *Crinum erubescens*

Cynanchum clausum (Jacq.) Jacq. = *Sarcostemma clausum*

Cyperus eggersii Boeck. = *Cyperus odoratus*

Cyperus macrocephalus Liebm. = *Cyperus odoratus*

Desmoncus apureanus L.H. Bailey = *Desmoncus orthacanthos*

Desmoncus horridus Splitg. ex Mart. = *Desmoncus orthacanthos*

Desmoncus multijugus Steyerm. = *Desmoncus orthacanthos*

Desmoncus palustris Trail = *Desmoncus orthacanthos*

Desmoncus velezii L.H. Bailey & H.E. Moore = *Desmoncus orthacanthos*

Digitaria disticha (L.) Fiori & Paol. = *Paspalum distichum*

Digitaria paspalodes Michx. = *Paspalum distichum*

Dimerandra isthmii Schltr. = Dimerandra *elegans ?*

Dioscorea kegeliana Griseb. = *Dioscorea polygonoides*

Diplachne scabra (Nees) Nicora = *Leptochloa scabra*
Dolichos luteolus Jacq. = *Vigna luteola*
Dolichos maritimus Aubl. = *Canavalia rosea*
Dolichos roseus Sw. = *Canavalia rosea*
Drepanocarpus lunatus (L. f.) G. Mey. = *Machaerium lunatum*
Echinochloa polystachya var. *spectabilis* (Nees ex Trin.) Mart. Crov. = *Echinochloa polystachya*
Echinochloa spectabilis (Nees ex Trin.) Link = *Echinochloa polystachya*
Echites biflora Jacq. = *Rhabdadenia biflora*
Eclipta alba (L.) Hassk. = *Eclipta prostrata*
Elsota diversifolia (L.) S.F. Blake = *Securidaca diversifolia*
Encyclia aemula (Lindl.) Carnevali & I. Ramírez = *Prosthechea aemula*
Encyclia ciliaris (L.) Lemée = *Epidendrum ciliare*
Encyclia fragrans (Sw.) Lemée var. *aemula* (Lindl.) Dressler & G.E. Pollard = *Prosthechea aemula*
Entadopsis polystachya (L.) Britton = *Entada polystachya*
Epidendrum aemulum Lindl. = *Prosthechea aemula*
Epidendrum fragans auct. non Sw. 1788 = *Prosthechea aemula*
Epidendrum fragans Sw. var. *aemulum* (Lindl.) Barb. Rodr. = *Prosthechea aemula*
Epiphyllum hookeri Haw. = *Epiphyllum phyllanthus*
Epiphyllum phyllanthus (L.) Haw. var. *hookeri* (Haw.) Kimnach = *Epiphyllum phyllanthus*
Eupatorium denticulatum Vahl = *Mikania micrantha*
Euterpe badiocarpa Barb. Rodr. = *Euterpe oleracea*
Euterpe beardii Bailey = *Euterpe oleracea*
Euterpe edulis auct. = *Euterpe oleracea*
Feuilleea ingoides (Rich.) Kuntze = *Inga ingoides*
Ficus angustifolia (Miq.) Miq. = *Ficus amazonica*
Ficus expansa Pittier = *Ficus eximia*
Ficus foveata Pittier = *Ficus eximia*
Ficus foveolata Pittier = *Ficus eximia*
Ficus glandulosa Pittier = *Ficus eximia*
Ficus glaucescens (Liebm.) Miq. = *Ficus maxima*
Ficus guanarensis Pittier = *Ficus eximia*
Ficus parkeri Miq. = *Ficus maxima*
Ficus radula Humb. & Bonpl. ex Willd. = *Ficus maxima*
Ficus surinamensis Miq. = *Ficus amazonica*
Ficus turbinata Pittier = *Ficus eximia*
Fimbristylis cymosa R. Br. subsp. *spathacea* (Roth) T. Koyama = *Fimbristylis cymosa*
Fimbristylis glomerata (Retz.) Urb. = *Fimbristylis cymosa*
Fimbristylis obtusifolia (Vahl) Kunth = *Fimbristylis cymosa*
Fimbristylis spathacea Roth = *Fimbristylis cymosa*
Funastrum clausum (Jacq.) Schltr. = *Sarcostemma clausum*
Gomphrena sessilis L. = *Alternanthera sessilis*
Gomphrena vermicularis L. = *Blutaparon vermiculare*
Guilandina bonduc L. = *Caesalpinia bonduc*
Guzmania lingulata (L.) Mez var. *minor* (Mez) L.B. Sm. & Pittendr. = *Guzmania lingulata*
Guzmania minor Mez = *Guzmania lingulata*
Heliconia ballia Rich. = *Heliconia psittacorum*
Heliconia cannoidea Rich. = *Heliconia psittacorum*
Heliconia humilis (Aubl.) Jacq. = *Heliconia psittacorum*
Heliconia schomburgkiana Klotzsch = *Heliconia psittacorum*
Heliconia silvestris (Gleason) L.B. Sm. = *Heliconia psittacorum*
Hibiscus elatus Sw. = *Talipariti tiliaceum*
Hibiscus pernambucensis = *Talipariti tiliaceum*
Hibiscus populneus L. = *Thespesia populnea*
Hibiscus tiliaceus L. = *Talipariti tiliaceum*
Hippocratea laevigata Rich. = *Hippocratea volubilis*
Hydromystria laevigata (Humb. & Bonpl. ex Willd.) Díaz-Mir. & Philcox = *Limnobium laevigatum*
Hydromystria laevigata (Willd.) Hanzeker = *Limnobium laevigatum*
Ilex acuminata Willd. = *Ilex guianensis*
Ilex celastroides Klotzsch ex Garcke = *Ilex guianensis*
Ilex cumanensis Turcz. = *Ilex guianensis*
Ilex macoucoua Pers. = *Ilex guianensis*
Inga latifolia (L.) Willd. = *Zygia latifolia*
Ipomoea cissoides (Lam.) Griseb. fma. viscidula Meisn. = *Merremia cissoides*

Ipomoea macrantha Roem. & Schult. = *Ipomoea violacea*
Ipomoea mollicoma Miq. = *Merremia umbellata*
Ipomoea polyanthes Roem. & Schult. = *Merremia umbellata*
Ipomoea tuba (Schltdl.) G. Don = *Ipomoea violacea*
Iresine vermicularis (L.) Moq. = *Blutaparon vermiculare*
Isochilus elegans H. Focke = Dimerandra *elegans ?*
Jatropha manihot L. = *Manihot esculenta*
Jussiaea affinis DC. = *Ludwigia affinis*
Jussiaea aluligera Miq. = *Ludwigia leptocarpa*
Jussiaea hexamera Miq. = *Ludwigia affinis*
Jussiaea leptocarpa Nutt. = *Ludwigia leptocarpa*
Jussiaea leptocarpa Nutt. var. *aluligera* (Miq.) Jonker = *Ludwigia leptocarpa*
Jussiaea leptocarpa Nutt. var. *genuina* Munz = *Ludwigia leptocarpa*
Jussiaea leptocarpa Nutt. var. *meyeriana* (Kuntze) Munz = *Ludwigia leptocarpa*
Jussiaea surinamensis Miq. = *Ludwigia leptocarpa*
Jussiaea variabilis G. Mey. var. *affinis* (DC.) Kuntze = *Ludwigia affinis*
Jussiaea variabilis G. Mey. var. *meyeriana* Kuntze = *Ludwigia leptocarpa*
Karatas plumieri E. Morren = *Bromelia plumieri*
Lemna paucicostata Hegelm. = *Lemna aequinoctialis*
Leptochloa langloisii Vasey = *Leptochloa scabra*
Leptochloa liebmannii E. Fourn = *Leptochloa scabra*
Limnobium spongia (Bosc) Steud. subsp. *laevigatum* (Humb. & Bonpl. ex Willd.) Lowden = *Limnobium laevigatum*
Limnobium stoloniferum (G. Mey.) Griseb. = *Limnobium laevigatum*
Lophiaris fragrans Raf. = *Trichocentrum lanceanum*
Lophiaris lanceana (Lindl.) Braem = *Trichocentrum lanceanum*
Lygodium mexicanum C. Presl = *Lygodium venustum*
Lygodium polymorphum auct. non (Cav.) Kunth = *Lygodium venustum*
Macoucoua guianensis Aubl. = *Ilex guianensis*
Malouetia furfuracea Spruce ex Müll. Arg. = *Malouetia tamaquarina*
Malouetia guianensis (Aubl.) Miers = *Malouetia tamaquarina*
Malouetia obtusiloba A. DC. = *Malouetia tamaquarina*
Malouetia odorata DC. = *Malouetia tamaquarina*
Malpighia bannisterioides L. = *Stigmaphyllon bannisterioides*
Manihot diffusa Pohl = *Manihot esculenta*
Manihot dulcis Pax = *Manihot esculenta*
Manihot utilissima Pohl = *Manihot esculenta*
Mariscus ligularis (L.) Urb. = *Cyperus ligularis*
Melothria fluminensis Gardner = *Melothria pendula*
Melothria guadalupensis (Spreng.) Cogn. = *Melothria pendula*
Mikania denticulata (Vahl) Willd. = *Mikania micrantha*
Mikania orinocensis Kunth = *Mikania micrantha*
Milium distichum (L.) Muhl. = *Paspalum distichum*
Mimosa bipinnata Aubl. = *Entada polystachya*
Mimosa ingoides Rich. = *Inga ingoides*
Mimosa latifolia L. = *Zygia latifolia*
Mimosa polystachia L. = *Entada polystachya*
Moutouchi suberosa Aubl. = *Pterocarpus officinalis*
Musa humilis Aubl. = *Heliconia psittacorum*
Oncidium lanceanum Lindl. = *Trichocentrum lanceanum*
Oplismenus polystachyus Kunth = *Echinochloa polystachya*
Orelia grandiflora Aubl. = *Allamanda cathartica*
Panicum bonplandianum Steud. = *Echinochloa polystachya*
Panicum spectabile Nees ex Trin. = *Echinochloa polystachya*
Paullinia hostmannii Steud. = *Paullinia pinnata*
Pharmacosycea guyanensis Miq. = *Ficus maxima*
Phaseolus luteolus (Jacq.) Gagnep. = *Vigna luteola*
Philodendron cyclops A.D. Hawkes = *Philodendron acutatum*
Philoxerus vermicularis (L.) R. Br. = *Blutaparon vermiculare*
Phyllocactus phyllanthus (DC.) Link = *Epiphyllum phyllanthus*

Physalis capsicifolia Dunal = *Physalis angulata*
Physalis lanceifolia Nees = *Physalis angulata*
Piper glabellum Sw. = *Peperomia glabella*
Pithecellobium latifolium (L.) Benth. = *Zygia latifolia*
Pluchea cortesii (Kunth) DC. = *Pluchea odorata*
Polygala diversifolia L. = *Securidaca diversifolia*
Polypodium phyllitidis L. = *Campyloneurum phyllitidis*
Polypodium rivulare Vahl = *Nephrolepis rivularis*
Portulaca portulacastrum L. = *Sesuvium portulacastrum*
Pothos gracilis Rudge = *Anthurium gracile*
Pothos scolopendrinus Ham. = *Anthurium gracile*
Pteris biaurita var. *pungens* (Willd.) H. Christ = *Pteris pungens*
Pteris longicauda H. Christ = *Pteris pungens*
Pterocarpus draco L. = *Pterocarpus officinalis*
Pterocarpus lunatus L. f. = *Machaerium lunatum*
Pterocarpus suberosa (Aubl.) Pers. = *Pterocarpus officinalis*
Pycreus polystachyos (Rottb.) P. Beauv. = *Cyperus polystachyos*
Renealmia exaltata L. f. = *Renealmia alpinia*
Rhipsalis cassutha Gaertn. = *Rhipsalis baccifera*
Rhipsalis minutiflora K. Schum. = *Rhipsalis baccifera*
Rhizophora americana Nutt. = *Rhizophora mangle*
Rhizophora mangle var. *racemosa* (G. Mey.) Engl. = *Rhizophora racemosa*
Rhizophora mangle var. *samoensis* Hochr. = *Rhizophora mangle*
Rhizophora samoensis (Hochr.) Salvoza = *Rhizophora mangle*
Roystonea venezuelana L.H. Bailey = *Roystonea oleracea*
Salvinia laevigata Humb. & Bonpl. ex Willd. = *Limnobium laevigatum*
Sarcostemma cumanense Kunth = *Sarcostemma clausum*
Sarcostemma pubescens Kunth = *Sarcostemma clausum*
Scirpus glomeratus Retz. = *Fimbristylis cymosa*
Scirpus mutatus L. = *Eleocharis mutata*
Scirpus obtusifolius Vahl = *Fimbristylis cymosa*
Sesuvium acutifolium Miq. = *Sesuvium portulacastrum*
Smilax globifera G. Mey. = *Smilax cumanensis*
Smilax hostmanniana Kunth = *Smilax cumanensis*
Smilax pirarensis Kunth & M.R. Schomb. = *Smilax cumanensis*
Smilax surinamensis Miq. = *Smilax cumanensis*
Solanum demerarense Dunal = *Solanum stramoniifolium*
Solanum toxicarium Rich. = *Solanum stramoniifolium*
Solanum trichocarpum Miq. = *Solanum stramoniifolium*
Spondias lutea L. = *Spondias mombin*
Sporobolus littoralis (Lam.) Kunth = *Sporobolus virginicus*
Stigmaphyllon ovatum (Cav.) Nied. = *Stigmaphyllon bannisterioides*
Tillandsia lingulata L. = *Guzmania lingulata*
Torulinium ferax (Rich.) Urb. = *Cyperus odoratus*
Torulinium odoratum (L.) S.S. Hooper = *Cyperus odoratus*
Typha angustifolia var. *domingensis* (Pers.) Hemsl. = *Typha domingensis*
Typha tenuifolia Kunth = *Typha domingensis*
Typha truxillensis Kunth = *Typha domingensis*
Urostigma amazonicum Miq. = *Ficus amazonica*
Urostigma angustifolium Miq. = *Ficus amazonica*
Verbesina alba L. = *Eclipta prostrata*
Verbesina prostrata L. = *Eclipta prostrata*
Vernonia cinerea (L.) Less. = *Cyanthillium cinereum*
Vigna repens (L.) Kuntze = *Vigna luteola*
Vilfa virginica (L.) P. Beauv. = *Sporobolus virginicus*
Vitis sicyoides (L.) Baker = *Cissus verticillata*
Wedelia psammophila Poepp. = *Eclipta prostrata*
Willoughbya micrantha (Kunth) Rusby = *Mikania micrantha*
Willoughbya scandens Kuntze var. *orinocensis* (Kunth) Kuntze = *Mikania micrantha*

APPENDIX 3.
PRELIMINARY SPECIES LIST OF THE VASCULAR PLANTS OF THE NORTHWEST DISTRICT OF GUYANA

(* denotes taxon added by collections for this volume.)

LYCOPHYTES

Lycopodiaceae
Lycopodiella cernua (L.) Pic. Serm.

Selaginellaceae
Selaginella epirrhizos Spring
Selaginella parkeri (Hook. & Grev.) Spring
Selaginella porelloides (Lam.) Spring
Selaginella producta Baker

PTERIDOPHYTES

Adiantaceae
Adiantum latifolium Lam.
Adiantum phyllitidis J. Sm.
Pityrogramma calomelanos (L.) Link

Aspleniaceae
Asplenium cristatum Lam. *
Asplenium juglandifolium Lam.
Asplenium salicifolium L.
Asplenium serratum L.

Blechnaceae
Blechnum serrulatum Rich.

Cyatheaceae
Cnemidaria spectabilis (Kunze) R.M. Tryon
Cyathea cyatheoides (Desv.) K.U. Kramer
Cyathea microdonta (Desv.) Domin
Cyathea pungens (Willd.) Domin
Cyathea surinamensis (Miq.) Domin

Dennstaedtiaceae
Lindsaea lancea (L.) Bedd.
Lindsaea portoricensis Desv. *
Saccoloma elegans Kaulf.

Dryopteridaceae
Cyclodium meniscioides (Willd.) C. Presl
Didymochlaena truncatula (Sw.) J. Sm.
Polybotrya caudata Kunze

Gleicheniaceae
Dicranopteris pectinata (Willd.) Underw. [moss]

Grammitidaceae
Cochlidium serrulatum (Sw.) L.E. Bishop

Hymenophyllaceae
Trichomanes diversifrons (Bory) Mett. ex Sadeb.
Trichomanes martiusii C. Presl
Trichomanes polypodioides L.
Trichomanes radicans Sw.

Lomariopsidaceae
Elaphoglossum flaccidum (Fée) T. Moore
Elaphoglossum glabellum J. Sm.
Lomariopsis japurensis (Mart.) J. Sm.
Lomariopsis latiuscula (Maxon) Holttum

Lygodiaceae
Lygodium venustum Sw. *
Lygodium volubile Sw.

Metaxyaceae
Metaxya rostrata (Kunth) C. Presl

Oleandraceae
Nephrolepis biserrata (Sw.) Schott
Nephrolepis rivularis (Vahl) Mett. ex Krug

Parkeriaceae
Ceratopteris thalictroides (L.) Brongn. *

Polypodiaceae
Campyloneurum phyllitidis (L.) C. Presl
Campyloneurum repens (Aubl.) C. Presl
Dicranoglossum desvauxii (Klotzsch) Proctor

Microgramma fuscopunctata (Hook.) Vareschi
Microgramma lycopodioides (L.) Copel.
Microgramma persicariifolia (Schrad.) C. Presl
Microgramma reptans (Cav.) A.R. Sm.
Phlebodium aureum (L.) J. Sm. *
Phlebodium pseudoaureum (Cav.) Lellinger
Polypodium adnatum Kunze ex Klotzsch
Polypodium attenuatum Humb. & Bonpl. ex Willd.

Pteridaceae
Acrostichum aureum L. *
Acrostichum danaeifolium Langsd. & Fisch. *
Pteris altissima Poir.
Pteris pungens Willd. *

Schizaeaceae
Schizaea fluminensis Miers ex J.W. Sturm
Schizaea incurvata Schkuhr

Tectariaceae
Tectaria incisa Cav.
Tectaria trifoliata (L.) Cav.
Triplophyllum funestum (Kunze) Holttum

Thelypteridaceae
Thelypteris abrupta (Desv.) Proctor
Thelypteris interrupta (Willd.) K. Iwats.
Thelypteris leprieurii (Hook.) R.M. Tryon
Thelypteris opulenta (Kaulf.) Fosberg [naturalized]
Thelypteris serrata (Cav.) Alston

Vittariaceae
Anetium citrifolium (L.) Splitg.
Antrophyum cajenense (Desv.) Spreng.

Woodsiaceae
Diplazium celtidifolium Kunze

GYMNOSPERMS

Gnetaceae
Gnetum nodiflorum Brongn.

DICOTILEDONEAE

Acanthaceae
Aphelandra pulcherrima (Jacq.) Kunth
Asystasia gangetica (L.) T. Anderson [cultivated]
Blechum pyramidatum (Lam.) Urb. *
Justicia calycina (Nees) V.A.W. Graham
Justicia pectoralis Jacq.
Justicia secunda Vahl
Ruellia tuberosa L. [naturalized]
Thunbergia alata Bojer ex Sims [cultivated]
Thunbergia grandiflora (Roxb. ex Rottl.) Roxb. [cultivated]
Trichanthera gigantea (Bonpl.) Nees

Aizoaceae
Sesuvium portulacastrum (L.) L. *

Amaranthaceae
Alternanthera philoxeroides (Mart.) Griseb. *
Alternanthera sessilis (L.) R. Br. ex DC.
Alternanthera tenella Colla
Amaranthus australis (A. Gray) J.D. Sauer *
Amaranthus blitum L. *
Amaranthus dubius Mart. ex Thell.
Amaranthus viridis L.
Blutaparon vermiculare (L.) Mears *
Celosia argentea L. [cultivated]
Cyathula achyranthoides (Kunth) Moq.
Cyathula prostrata (L.) Blume
Gomphrena globosa L. [cultivated]
Iresine diffusa Humb. & Bonpl. ex Willd.

Anacardiaceae
Anacardium giganteum W. Hancock ex Engl.
Anacardium occidentale L.
Astronium lecointei Ducke
Mangifera indica L. [cultivated]
Spondias dulcis Parkinson [cultivated]
Spondias mombin L.
Tapirira guianensis Aubl.
Tapirira obtusa (Benth.) J.D. Mitch.
Thyrsodium guianense Sagot ex Marchand

Annonaceae
Anaxagorea dolichocarpa Sprague & Sandwith
Annona glabra L. *
Annona montana Macfad.
Annona muricata L. [cultivated]
Annona sericea Dunal
Annona symphyocarpa Sandwith
Bocageopsis multiflora (Mart.) R.E. Fr.
Duguetia calycina Benoist
Duguetia megalophylla R.E. Fr.
Duguetia pauciflora Rusby
Duguetia pycnastera Sandwith
Duguetia yeshidan Sandwith
Fusaea longifolia (Aubl.) Saff.

Guatteria flexilis R.E. Fr.
Guatteria schomburgkiana Mart.
Rollinia exsucca (DC. ex Dunal) A. DC.
Rollinia mucosa (Jacq.) Baill.
Unonopsis glaucopetala R.E. Fr.
Xylopia benthamii R.E. Fr.
Xylopia cayennensis Maas
Xylopia surinamensis R.E. Fr.

Apiaceae
Coriandrum sativum L. [cultivated]
Eryngium foetidum L.

Apocynaceae
Allamanda cathartica L.
Ambelania acida Aubl.
Aspidosperma cruentum Woodson
Aspidosperma excelsum Benth.
Aspidosperma marcgravianum Woodson
Catharanthus roseus (L.) G. Don [cultivated]
Condylocarpon intermedium Müll. Arg.
Forsteronia gracilis (Benth.) Müll. Arg.
Forsteronia guyanensis Müll. Arg.
Himatanthus articulatus (Vahl) Woodson
Himatanthus bracteatus (A. DC.) Woodson
Macoubea guianensis Aubl.
Malouetia flavescens (Willd. ex Roem. & Schult.) Müll. Arg.
Malouetia tamaquarina (Aubl.) A. DC. *
Mandevilla hirsuta (Rich.) K. Schum.
Mandevilla symphitocarpa (G. Mey.) Woodson
Mesechites trifida (Jacq.) Müll. Arg.
Odontadenia geminata (Hoffmanns. ex Roem. & Schult.) Müll. Arg.
Odontadenia macrantha (Roem. & Schult.) Markgr.
Odontadenia puncticulosa (Rich.) Pulle
Odontadenia sandwithiana Woodson
Plumeria inodora Jacq.
Prestonia tomentosa R. Br.
Rhabdadenia biflora (Jacq.) Müll. Arg.
Tabernaemontana disticha A. DC.
Tabernaemontana divaricata (L.) R. Br. ex Roem. & Schult.
Tabernaemontana heterophylla Vahl
Tabernaemontana lorifera (Miers) Leeuwenb.
Tabernaemontana undulata Vahl

Aquifoliaceae
Ilex guianensis (Aubl.) Kuntze
Ilex martiniana D. Don

Araliaceae
Oreopanax capitatus (Jacq.) Decne. & Planch.
Schefflera decaphylla (Seem.) Harms
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin

Aristolochiaceae
Aristolochia daemoninoxia Mast.
Aristolochia hians Willd.
Aristolochia rugosa Lam.
Aristolochia trilobata L. *

Asclepiadaceae
Asclepias curassavica L.
Blepharodon nitidus (Vell.) J.F. Macbr.
Matelea badilloi Morillo
Matelea stenopetala Sandwith
Sarcostemma clausum (Jacq.) Schult.
Stenomeria decalepis Turcz.
Tassadia propinqua Decne.

Asteraceae
Ageratum conyzoides L.
Bidens alba (L.) DC. *
Bidens cynapiifolia Kunth
Bidens pilosa L.
Chromolaena odorata (L.) R.M. King & H. Rob.
Clibadium surinamense L.
Clibadium sylvestre (Aubl.) Baill.
Conyza bonariensis (L.) Cronquist
Cosmos caudatus Kunth [cultivated]
Cosmos sulphureus Cav. [cultivated]
Cyanthillium cinereum (L.) H. Rob. [naturalized]
Cyrtocymura scorpioides (Lam.) H. Rob.
Eclipta prostrata (L.) L. *
Elephantopus mollis Kunth
Emilia sonchifolia (L.) DC. ex Wight
Erechtites hieracifolia (L.) Raf. ex DC.
Hebeclinium macrophyllum (L.) DC.
Mikania banisteriae DC.
Mikania congesta DC.
Mikania cordifolia (L. f.) Willd.
Mikania guaco Bonpl.
Mikania hookeriana DC.
Mikania micrantha Kunth
Mikania microptera DC.
Mikania parviflora (Aubl.) H. Karst.
Mikania psilostachya DC.
Mikania trinitaria DC.
Pluchea odorata (L.) Cass. *

Rolandra fruticosa (L.) Kuntze
Sonchus asper (L.) Hill *
Sphagneticola trilobata (L.) Pruski
Struchium sparganophorum (L.) Kuntze
Synedrella nodiflora (L.) Gaertn.
Tagetes erecta L. [cultivated]
Unxia camphorata L. f.
Wulffia baccata (L.) Kuntze
Zinnia elegans Jacq. [cultivated]

Avicenniaceae
Avicennia germinans (L.) Stearn

Balanophoraceae
Helosis cayennensis (Sw.) Spreng.

Basellaceae
Basella alba L. [cultivated]

Begoniaceae
Begonia humilis Dryand.

Bignoniaceae
Anemopaegma chrysoleucum (Kunth) Sandwith
Anemopaegma karstenii Bureau & K. Schum.
Anemopaegma oligoneuron (Sprague & Sandwith) A.H. Gentry
Arrabidaea candicans (Rich.) DC.
Callichlamys latifolia (Rich.) K. Schum.
Ceratophytum tetragonolobum (Jacq.) Sprague & Sandwith
Clytostoma binatum (Thunb.) Sandwith
Crescentia amazonica Ducke
Crescentia cujete L. [cultivated]
Cydista aequinoctialis (L.) Miers
Distictella elongata (Vahl) Urb.
Jacaranda copaia (Aubl.) D. Don
Jacaranda obtusifolia Bonpl.
Lundia densiflora DC.
Macfadyena uncata (T.F. Andrews) Sprague & Sandwith
Macfadyena unguis-cati (L.) A.H. Gentry
Mansoa kerere (Aubl.) A.H. Gentry
Martinella obovata (Kunth) Bureau & K. Schum.
Parabignonia steyermarkii Sandwith
Pleonotoma albiflora (Salzm. ex DC.) A.H. Gentry
Pleonotoma echitidea Sprague & Sandwith
Schlegelia spruceana K. Schum.
Schlegelia violacea (Aubl.) Griseb.
Tabebuia fluviatilis (Aubl.) DC.
Tabebuia insignis (Miq.) Sandwith
Tabebuia serratifolia (Vahl) G. Nicholson

Bixaceae
Bixa orellana L.

Bombacaceae
Catostemma commune Sandwith
Catostemma fragrans Benth.
Ceiba pentandra (L.) Gaertn.
Pachira aquatica Aubl.
Pachira insignis (Sw.) Sw. ex Savigny

Boraginaceae
Cordia curassavica (Jacq.) Roem. & Schult.
Cordia exaltata Lam.
Cordia fallax I.M. Johnst.
Cordia nodosa Lam.
Cordia schomburgkii DC.
Cordia sericicalyx DC.
Cordia tetrandra Aubl.
Heliotropium indicum L. [naturalized]
Tournefortia bicolor Sw.
Tournefortia cuspidata Kunth

Burseraceae
Protium decandrum (Aubl.) Marchand
Protium guianense (Aubl.) Marchand
Protium heptaphyllum (Aubl.) Marchand
Protium tenuifolium (Engl.) Engl.
Protium unifoliolatum Spruce ex Engl.
Tetragastris altissima (Aubl.) Swart
Trattinnickia boliviana (Swart) Daly
Trattinnickia burserifolia Mart.
Trattinnickia rhoifolia Willd.

Cabombaceae
Cabomba aquatica Aubl.

Cactaceae
Epiphyllum phyllanthus (L.) Haw.
Opuntia cochenillifera (L.) Mill. [cultivated]
Pereskia aculeata Mill. [naturalized]
Rhipsalis baccifera (J.S. Muell.) Stearn

Caesalpiniaceae
Bauhinia guianensis Aubl.
Bauhinia scala-simiae Sandwith
Bauhinia siqueiraei Ducke
Brownea coccinea Jacq.

Brownea grandiceps Jacq. *
Caesalpinia bonduc (L.) Roxb. *
Caesalpinia pulcherrima (L.) Sw. [cultivated]
Chamaecrista ramosa (Vogel) H.S. Irwin & Barneby
Crudia glaberrima (Steud.) J.F. Macbr.
Dicorynia guianensis Amshoff
Eperua falcata Aubl.
Eperua rubiginosa Miq.
Hymenaea courbaril L.
Macrolobium acaciifolium (Benth.) Benth.
Macrolobium angustifolium (Benth.) R.S. Cowan
Macrolobium bifolium (Aubl.) Pers.
Mora excelsa Benth.
Peltogyne venosa (Vahl) Benth.
Senna alata (L.) Roxb.
Senna bacillaris (L. f.) H.S. Irwin & Barneby
Senna multijuga (Rich.) H.S. Irwin & Barneby
Senna occidentalis (L.) Link
Senna quinquangulata (Rich.) H.S. Irwin & Barneby
Senna reticulata (Willd.) H.S. Irwin & Barneby
Senna sandwithiana H.S. Irwin & Barneby
Tachigali micropetala (Ducke) Zarucchi & Pipoly
Tachigali paniculata Aubl.

Campanulaceae
Centropogon cornutus (L.) Druce

Capparaceae
Cleome parviflora Kunth
Cleome serrata Jacq.
Cleome speciosa Raf.

Caricaceae
Carica papaya L. [naturalized]

Caryocaraceae
Caryocar microcarpum Ducke
Caryocar nuciferum L.

Casuarinaceae
Casuarina equisetifolia J.R. Forst. & G. Forst. [cultivated]

Cecropiaceae
Cecropia angulata I.W. Bailey
Cecropia obtusa Trécul
Cecropia peltata L.
Cecropia sciadophylla Mart.
Coussapoa asperifolia Trécul *
Coussapoa microcephala Trécul
Pourouma guianensis Aubl.

Celastraceae
Goupia glabra Aubl.
Maytenus guyanensis Klotzsch ex Reissek

Ceratophyllaceae
Ceratophyllum muricatum Cham. *

Chrysobalanaceae
Chrysobalanus icaco L.
Couepia parillo DC.
Hirtella paniculata Sw.
Hirtella racemosa Lam.
Hirtella silicea Griseb.
Hirtella triandra Sw.
Licania alba (Bernoulli) Cuatrec.
Licania apetala (E. Mey.) Fritsch
Licania boyanii Tutin
Licania densiflora Kleinhoonte
Licania divaricata Benth.
Licania guianensis (Aubl.) Griseb.
Licania heteromorpha Benth.
Licania incana Aubl.
Licania kunthiana Hook. f.
Licania laxiflora Fritsch
Licania majuscula Sagot
Licania membranacea Sagot ex Laness.
Licania micrantha Miq.
Licania octandra (Hoffmanns. ex Roem. & Schult.) Kuntze
Licania persaudii Fanshawe & Maguire
Licania rufescens Klotzsch ex Fritsch
Parinari campestris Aubl.
Parinari rodolphii Huber

Clusiaceae
Calophyllum brasiliense Cambess.
Caraipa richardiana Cambess.
Clusia cuneata Benth.
Clusia flavida (Benth.) Pipoly
Clusia gaudichaudii Choisy
Clusia grandiflora Splitg.
Clusia myriandra (Benth.) Planch. & Triana
Clusia nemorosa G. Mey.
Clusia palmicida Rich. ex Planch. & Triana
Clusia panapanari (Aubl.) Choisy
Mammea americana L. [cultivated]

Rheedia macrophylla (Mart.) Planch. & Triana
Rheedia virens Planch. & Triana
Symphonia globulifera L. f.
Tovomita brevistaminea Engl.
Tovomita calodictyos Sandwith
Tovomita choisyana Planch. & Triana
Tovomita obscura Sandwith
Tovomita schomburgkii Planch. & Triana
Vismia cayennensis (Jacq.) Pers.
Vismia gracilis Hieron.
Vismia guianensis (Aubl.) Choisy
Vismia japurensis Reichardt
Vismia laxiflora Reichardt
Vismia macrophylla Kunth
Vismia sessilifolia (Aubl.) Choisy

Combretaceae
Buchenavia grandis Ducke
Combretum cacoucia Exell ex Sandwith
Combretum fruticosum (Loefl.) Stuntz
Combretum laxum Jacq.
Conocarpus erectus L. *
Laguncularia racemosa (L.) C.F. Gaertn.
Terminalia amazonia (J.F. Gmel.) Exell
Terminalia catappa L. [naturalized]
Terminalia dichotoma G. Mey.

Connaraceae
Cnestidium guianense (G. Schellenb.) G. Schellenb.
Connarus coriaceus G. Schellenb.
Pseudoconnarus macrophyllus (Poepp.) Radlk.

Convolvulaceae
Aniseia martinicensis (Jacq.) Choisy
Dicranostyles sp.
Ipomoea asarifolia (Desr.) Roem. & Schult.
Ipomoea batatas (L.) Lam. [cultivated]
Ipomoea carnea Jacq.
Ipomoea indica (Burm.) Merr.
Ipomoea mauritiana Jacq.
Ipomoea pes-caprae (L.) R. Br. *
Ipomoea phillomega (Vell.) House
Ipomoea quamoclit L.
Ipomoea tiliacea (Willd.) Choisy
Ipomoea violacea L. *
Jacquemontia guyanensis (Aubl.) Meisn.
Jacquemontia tamnifolia (L.) Griseb.
Maripa scandens Aubl.
Merremia cissoides (Lam.) Hallier f. *
Merremia macrocalyx (Ruiz & Pav.) O'Donell
Merremia umbellata (L.) Hallier f. *

Crassulaceae
Kalanchoe integra (Medic.) O. Kuntze [cultivated]
Kalanchoe pinnata (Lam.) Pers. [cultivated]

Cucurbitaceae
Cayaponia jenmanii C. Jeffrey
Cayaponia simplicifolia ? (Naudin) Cogn.
Citrullus lanatus (Thunb.) Matsum. & Nakai [cultivated]
Cucumis melo L. [cultivated]
Cucumis sativus L. [cultivated]
Cucurbita moschata Duchesne [cultivated]
Gurania lobata (L.) Pruski
Gurania subumbellata (Miq.) Cogn.
Helmontia leptantha (Schltdl.) Cogn.
Lagenaria siceraria (Molina) Standl. [cultivated]
Luffa cylindrica (L.) M. Roem. [cultivated]
Melothria pendula L.
Momordica charantia L. [naturalized]
Posadaea sphaerocarpa Cogn.
Psiguria triphylla (Miq.) C. Jeffrey

Cuscutaceae
Cuscuta umbellata Kunth *

Cyrillaceae
Cyrilla racemiflora L.

Dichapetalaceae
Dichapetalum pedunculatum (DC.) Baill.
Tapura guianensis Aubl.

Dilleniaceae
Davilla kunthii A. St.-Hil.
Davilla nitida (Vahl) Kubitzki *
Doliocarpus dentatus (Aubl.) Standl.
Pinzona coriacea Mart. & Zucc.
Tetracera asperula Miq.
Tetracera tigarea DC.
Tetracera volubilis L.

Droseraceae
Drosera intermedia Hayne

Ebenaceae
Diospyros cayennensis A. DC.
Diospyros discolor Willd. [cultivated]
Diospyros guianensis (Aubl.) Gürke

Diospyros tetrandra Hiern

Elaeocarpaceae

Sloanea eichleri K. Schum.
Sloanea grandiflora Sm.
Sloanea guianensis (Aubl.) Benth.
Sloanea latifolia (Rich.) K. Schum.
Sloanea obtusifolia (Moric.) K. Schum.

Erythroxylaceae

Erythroxylum citrifolium A. St.-Hil.
Erythroxylum macrophyllum Cav.

Euphorbiaceae

Acalypha amentacea Roxb. [cultivated] *
Acalypha macrostachya Jacq.
Acalypha scandens Benth.
Alchornea discolor Poepp.
Alchornea triplinervia (Spreng.) Müll. Arg.
Alchorneopsis floribunda (Benth.) Müll. Arg.
Amanoa guianensis Aubl.
Chaetocarpus schomburgkianus (Kuntze) Pax & K. Hoffm.
Codiaeum variegatum (L.) A. Juss. [cultivated]
Conceveiba guianensis Aubl.
Croton cuneatus Klotzsch
Croton trinitatis Millsp.
Dalechampia brownsbergensis G.L. Webster & Armbr.
Drypetes fanshawei Sandwith
Euphorbia cotinifolia L.
Euphorbia hirta L. *
Euphorbia neriifolia L. [naturalized]
Euphorbia oerstediana (Klotzsch & Garcke) Boiss.
Euphorbia thymifolia L.
Hevea brasiliensis (Willd. ex A. Juss.) Müll. Arg. [cultivated]
Hieronyma alchorneoides Allemao
Jatropha curcas L. [cultivated]
Jatropha gossypiifolia L. [cultivated] *
Mabea piriri Aubl.
Manihot esculenta Crantz [cultivated]
Maprounea guianensis Aubl.
Microstachys corniculata (Vahl) Griseb.
Omphalea diandra L.
Pausandra martinii Baill.
Pedilanthus tithymaloides (L.) Poit. [cultivated]*
Pera glabrata (Schott) Poepp. ex Baill.
Phyllanthus brasiliensis (Aubl.) Poir.
Phyllanthus caribaeus Urb.
Phyllanthus stipulatus (Raf.) G.L. Webster
Phyllanthus urinaria L. [naturalized]
Plukenetia polyadenia Müll. Arg.
Ricinus communis L. [cultivated]
Sandwithia guyanensis Lanj.
Sapium jenmanii Hemsl.
Sapium paucinervium Hemsl.
Senefeldera sp.

Fabaceae

Aeschynomene sensitiva Sw. *
Alexa confusa Pittier
Alexa imperatricis (R.H. Schomb.) Baill.
Alexa surinamensis Yakovlev
Andira surinamensis (Bondt) Splitg. ex Amshoff
Cajanus cajan (L.) Millsp. [cultivated]
Calopogonium caeruleum (Benth.) C. Wright
Calopogonium mucunoides Desv.
Canavalia rosea (Sw.) DC. *
Centrosema brasilianum (L.) Benth.
Centrosema capitatum (Rich.) Amshoff
Centrosema molle Mart. ex Benth.
Centrosema plumieri (Turpin ex Pers.) Benth.
Clathrotropis brachypetala (Tul.) Kleinhoonte
Clitoria arborescens R. Br.
Crotalaria incana L.
Crotalaria nitens Kunth
Crotalaria stipularia Desv.
Dalbergia monetaria L. f.
Derris amazonica Killip
Derris pterocarpus (DC.) Killip
Desmodium adscendens (Sw.) DC.
Desmodium axillare (Sw.) DC.
Desmodium barbatum (L.) Benth.
Desmodium incanum DC.
Dioclea reflexa Hook. f.
Dioclea scabra (Rich.) R.H. Maxwell
Dioclea wilsonii Standl.
Diplotropis purpurea (Rich.) Amshoff
Dipteryx odorata (Aubl.) Willd.
Hymenolobium flavum Kleinhoonte
Indigofera suffruticosa Mill. [naturalized]
Lablab purpureus (L.) Sweet [cultivated]
Lonchocarpus chrysophyllus Kleinhoonte
Lonchocarpus heptaphyllus (Poir.) DC.
Lonchocarpus martynii A.C. Sm.
Lonchocarpus rufescens Benth.
Lonchocarpus sericeus (Poir.) Kunth ex DC.
Lonchocarpus spruceanus Benth.
Lonchocarpus utilis A.C. Sm.

Machaerium floribundum Benth.
Machaerium inundatum (Mart. ex Benth.) Ducke
Machaerium kegelii Meisn.
Machaerium leiophyllum (DC.) Benth.
Machaerium lunatum (L. f.) Ducke *
Machaerium quinatum (Aubl.) Sandwith
Mucuna urens (L.) Medik.
Muellera frutescens (Aubl.) Standl.
Ormosia coccinea (Aubl.) Jacks.
Ormosia coutinhoi Ducke
Ormosia nobilis Tul.
Phaseolus lunatus L. [cultivated]
Platymiscium pinnatum (Jacq.) Dugand
Pterocarpus officinalis Jacq.
Pterocarpus santalinoides L'Hér. ex DC.
Pueraria phaseoloides (Roxb.) Benth. [cultivated] *
Rhynchosia phaseoloides (Sw.) DC.
Sesbania sericea (Willd.) DC. *
Swartzia conferta Spruce ex Benth.
Swartzia guianensis (Aubl.) Urb.
Swartzia schomburgkii Benth.
Swartzia steyermarkii R.S. Cowan
Tephrosia sinapou (Buc'hoz) A. Chev.
Vatairea guianensis Aubl.
Vigna luteola (Jacq.) Benth.
Vigna sinensis (L.) Savi ex Hassk. [cultivated]
Vigna unguiculata (L.) Walp. [cultivated]
Zornia diphylla (L.) Pers.

Flacourtiaceae
Banara guianensis Aubl.
Casearia acuminata DC.
Casearia commersoniana Cambess.
Casearia guianensis (Aubl.) Urb.
Casearia javitensis Kunth
Casearia rusbyana Briq.
Flacourtia jangomas (Lour.) Raeusch. [cultivated]
Homalium guianense (Aubl.) Oken
Homalium racemosum Jacq.
Laetia procera (Poepp.) Eichler
Ryania speciosa Vahl
Xylosma benthamii (Tul.) Triana & Planch.

Gentianaceae
Chelonanthus alatus (Aubl.) Pulle
Chelonanthus purpurascens (Aubl.) Struwe, S. Nilsson & V.A.
Coutoubea ramosa Aubl.
Voyria aphylla (Jacq.) Pers.
Voyria aurantiaca Splitg.
Voyria pittieri (Standl.) L.O. Williams
Gesneriaceae
Besleria flavovirens Nees & Mart.
Chrysothemis pulchella (Donn ex Sims) Decne.
Chrysothemis villosa (Benth.) Leeuwenb.*
Codonanthe calcarata (Miq.) Hanst.
Codonanthe crassifolia (H. Focke) C.V. Morton
Drymonia serrulata (Jacq.) Mart. *
Nautilocalyx coccineus Feuillet & L.E. Skog
Nautilocalyx cordatus (Gleason) L.E. Skog
Nautilocalyx mimuloides (Benth.) C.V. Morton
Paradrymonia maculata (Hook. f.) Wiehler

Hippocrateaceae
Cheiloclinium cognatum (Miers) A.C. Sm.
Hippocratea volubilis L.
Peritassa pruinosa (Seem.) A.C. Sm.
Tontelea glabra A.C. Sm.

Humiriaceae
Humiria balsamifera Aubl.
Humiriastrum obovatum (Benth.) Cuatrec.
Sacoglottis cydonioides Cuatrec.

Hydrophyllaceae
Hydrolea spinosa L.

Icacinaceae
Discophora guianensis Miers
Emmotum fagifolium Ham.
Leretia cordata Vell.
Poraqueiba guianensis Aubl.

Lacistemataceae
Lacistema aggregatum (P.J. Bergius) Rusby

Lamiaceae
Coleus amboinicus Lour. [cultivated]
Coleus blumei Benth. [cultivated]
Coleus hybridus Hort. ex Cobeau [cultivated]
Hyptis lanceolata Poir.
Hyptis parkeri Benth.
Hyptis pectinata (L.) Poit.
Leonotis nepetifolia (L.) W.T. Aiton
Ocimum campechianum Mill.

Lauraceae
Aiouea guianensis Aubl.
Aniba guianensis Aubl.

Aniba hostmanniana (Nees) Mez
Aniba hypoglauca Sandwith
Aniba jenmanii Mez
Aniba kappleri Mez
Aniba terminalis Ducke
Cassytha filiformis L. *
Licaria debilis (Mez) Kosterm.
Licaria oppositifolia (Nees) Kosterm.
Nectandra amazonum Nees
Nectandra canescens Nees
Nectandra cuspidata Nees
Nectandra globosa (Aubl.) Mez
Ocotea cernua (Nees) Mez
Ocotea puberula (Rich.) Nees
Ocotea schomburgkiana (Nees) Mez
Ocotea splendens (Meisn.) Baill.
Ocotea tomentella Sandwith
Persea americana Mill. [cultivated]
Persea nivea Mez

Lecythidaceae
Couratari guianensis Aubl.
Couratari multiflora (Sm.) Eyma
Eschweilera alata A.C. Sm.
Eschweilera coriacea (DC.) S.A. Mori
Eschweilera decolorans Sandwith
Eschweilera micrantha (O. Berg) Miers
Eschweilera parviflora (Aubl.) Miers
Eschweilera sagotiana Miers
Eschweilera wachenheimii (Benoist) Sandwith
Gustavia augusta L.
Gustavia poeppigiana O. Berg
Lecythis chartacea O. Berg
Lecythis corrugata Poit.
Lecythis zabucajo Aubl.

Lentibulariaceae
Utricularia benjaminiana Oliv.
Utricularia foliosa L.
Utricularia myriocista A. St.-Hil. & Girard

Loganiaceae
Strychnos erichsonii M.R. Schomb. ex Progel
Strychnos mitscherlichii M.R. Schomb.
Strychnos toxifera R.H. Schomb. ex Benth.

Loranthaceae
Oryctanthus florulentus (Rich.) Tiegh.
Phthirusa pyrifolia (Kunth) Eichler
Phthirusa stelis (L.) Kuijt

Lythraceae
Cuphea melvilla Lindl.

Malpighiaceae
Banisteriopsis caapi (Griseb.) C.V. Morton
Banisteriopsis lucida (Rich.) Small
Banisteriopsis martiniana (A. Juss.) Cuatrec.
Burdachia sphaerocarpa A. Juss.
Byrsonima aerugo Sagot
Byrsonima crassifolia (L.) Kunth
Byrsonima spicata (Cav.) DC.
Byrsonima stipulacea A. Juss.
Diplopterys pauciflora (G. Mey.) Nied.
Heteropterys leona (Cav.) Exell
Heteropterys macrostachya A. Juss.
Hiraea fagifolia (DC.) A. Juss.
Hiraea faginea (Sw.) Nied.
Lophopterys euryptera Sandwith
Malpighia emarginata DC.
Mascagnia macrodisca (Triana & Planch.) Nied.
Mezia includens (Benth.) Cuatrec.
Spachea elegans (G. Mey.) A. Juss.
Stigmaphyllon bannisterioides (L.) C.E. Anderson
Stigmaphyllon convolvulifolium A. Juss.
Stigmaphyllon puberum (Rich.) A. Juss.
Stigmaphyllon sinuatum (DC.) A. Juss.
Tetrapterys discolor (G. Mey.) DC.
Tetrapterys fimbripetala A. Juss.

Malvaceae
Abelmoschus moschatus Medik.
Gossypium barbadense L. [cultivated]
Gossypium hirsutum L. [cultivated]
Hibiscus bifurcatus Cav.
Hibiscus furcellatus Desr.
Hibiscus rosa-sinensis L. [cultivated]
Hibiscus sabdariffa L. [cultivated]
Malachra alceifolia Jacq.
Pavonia fruticosa (Mill.) Fawc. & Rendle
Sida acuta Burm. f.
Sida glomerata Cav.
Sida linifolia Juss. ex Cav.
Sida rhombifolia L.
Sida setosa Mart. ex Colla
Talipariti tiliaceum (L.) Fryxell
Thespesia populnea (L.) Sol. ex Corr?a * [naturalized] *
Urena lobata L.

Marcgraviaceae
Marcgravia coriacea Vahl
Marcgravia magnibracteata Lanj. & Heerdt
Marcgravia pedunculosa Triana & Planch.
Marcgravia purpurea I.W. Bailey
Norantea guianensis Aubl.
Souroubea guianensis Aubl.

Melastomataceae
Aciotis annua (Mart. ex DC.) Triana
Aciotis indecora (Bonpl.) Triana
Aciotis ornata (Miq.) Gleason
Aciotis purpurascens (Aubl.) Triana
Bellucia grossularioides (L.) Triana
Clidemia capitellata (Bonpl.) D. Don
Clidemia conglomerata DC.
Clidemia dentata D. Don
Clidemia hirta (L.) D. Don
Clidemia japurensis DC.
Clidemia microthyrsa R.O. Williams
Clidemia pustulata DC.
Clidemia rubra (Aubl.) Mart.
Clidemia venosa (Gleason) Wurdack
Comolia villosa (Aubl.) Triana
Desmoscelis villosa (Aubl.) Naudin
Henriettea multiflora Naudin
Henriettea succosa (Aubl.) DC.
Henriettella caudata Gleason
Leandra divaricata (Naudin) Cogn.
Leandra rufescens (DC.) Cogn.
Loreya mespiloides Miq.
Miconia acinodendron (L.) Sweet
Miconia affinis DC.
Miconia bubalina (D. Don) Naudin
Miconia ceramicarpa (DC.) Cogn.
Miconia chrysophylla (Rich.) Urb.
Miconia ciliata (Rich.) DC.
Miconia egensis Cogn.
Miconia fragilis Naudin
Miconia gratissima Benth. ex Triana
Miconia hypoleuca (Benth.) Triana
Miconia ibaguensis (Bonpl.) Triana
Miconia lateriflora Cogn.
Miconia lepidota DC.
Miconia matthaei Naudin
Miconia minutiflora (Bonpl.) DC. *
Miconia mirabilis (Aubl.) L.O. Williams
Miconia myriantha Benth.
Miconia nervosa (Sm.) Triana
Miconia plukenetii Naudin
Miconia prasina (Sw.) DC.
Miconia pubipetala Miq.
Miconia racemosa (Aubl.) DC.
Miconia rubiginosa (Bonpl.) DC.
Miconia ruficalyx Gleason
Miconia serrulata (DC.) Naudin
Myriaspora egensis DC.
Nepsera aquatica (Aubl.) Naudin
Pterolepis glomerata (Rottb.) Miq.
Rhynchanthera dichotoma (Desr.) DC.
Tococa aristata Benth.

Meliaceae
Azadirachta indica A. Juss. [cultivated]
Carapa guianensis Aubl.
Cedrela odorata L.
Guarea guidonia (L.) Sleumer
Guarea pubescens (Rich.) A. Juss.
Trichilia rubra C. DC.
Trichilia schomburgkii C. DC.

Mendonciaceae
Mendoncia bivalvis (L. f.) Merr.
Mendoncia glabra (Poepp. & Endl.) Nees
Mendoncia hoffmannseggiana Nees

Menispermaceae
Cissampelos andromorpha DC.
Curarea candicans (Rich. ex DC.) Barneby & Krukoff
Orthomene schomburgkii (Miers) Barneby & Krukoff
Telitoxicum sp.

Menyanthaceae
Nymphoides indica (L.) Kuntze

Mimosaceae
Abarema jupunba (Willd.) Britton & Killip
Abarema laeta (Benth.) Barneby & J.W. Grimes
Abarema mataybifolia (Sandwith) Barneby & J.W. Grimes
Calliandra surinamensis Benth.
Entada polystachya (L.) DC. *
Hydrochorea corymbosa (Rich.) Barneby & J.W. Grimes
Hydrochorea gonggrijpii (Kleinhoonte) Barneby & J.W. Grimes
Inga acreana Harms
Inga acrocephala Steud.
Inga alba (Sw.) Willd.
Inga bourgonii (Aubl.) DC.

Inga edulis Mart.
Inga graciliflora Benth.
Inga gracilifolia Ducke
Inga huberi Ducke
Inga ingoides (Rich.) Willd. *
Inga java Pittier
Inga jenmanii Sandwith
Inga lateriflora Miq.
Inga leiocalycina Benth.
Inga marginata Willd.
Inga melinonis Sagot
Inga nobilis Willd.
Inga pezizifera Benth.
Inga pilosula (Rich.) J.F. Macbr.
Inga rubiginosa (Rich.) DC.
Inga sarmentosa Glaz. ex Harms
Inga sertulifera DC.
Inga splendens Willd.
Inga thibaudiana DC.
Inga umbellifera (Vahl) Steud. ex DC.
Macrosamanea pubiramea (Steud.) Barneby & J.W. Grimes
Mimosa polydactyla Humb. & Bonpl. ex Willd.
Mimosa myriadenia (Benth.) Benth. *
Pentaclethra macroloba (Willd.) Kuntze
Pithecellobium longiflorum Benth.
Zygia cataractae (Kunth) L. Rico
Zygia latifolia (L.) Fawc. & Rendle

Moraceae
Artocarpus altilis (Parkinson) Fosberg [cultivated]
Bagassa guianensis Aubl.
Brosimum guianense (Aubl.) Huber
Ficus amazonica (Miq.) Miq.
Ficus caballina Standl.
Ficus eximia Schott
Ficus gomelleira Kunth & Bouché
Ficus guianensis Desv. ex Ham.
Ficus malacocarpa Standl.
Ficus mathewsii (Miq.) Miq.
Ficus maxima Mill.
Ficus nymphaeifolia Mill.
Ficus paludica Standl.
Ficus paraensis (Miq.) Miq.
Ficus roraimensis C.C. Berg
Ficus trigona L. f.
Pseudolmedia laevis (Ruiz & Pav.) J.F. Macbr.

Moringaceae
Moringa oleifera Lam. [cultivated] *

Myristicaceae
Iryanthera juruensis Warb.
Iryanthera lancifolia Ducke *
Iryanthera macrophylla (Benth.) Warb.
Virola calophylla (Spruce) Warb.
Virola elongata (Benth.) Warb.
Virola sebifera Aubl.
Virola surinamensis (Rol. ex Rottb.) Warb.

Myrsinaceae
Ardisia guianensis (Aubl.) Mez
Cybianthus surinamensis (Spreng.) G. Agostini
Stylogyne orinocensis (Kunth) Mez

Myrtaceae
Calycolpus goetheanus (DC.) O. Berg
Calyptranthes sp.
Eugenia cucullata Amshoff
Eugenia florida DC.
Eugenia patrisii Vahl
Eugenia punicifolia (Kunth) DC.
Eugenia uniflora L. [cultivated]
Marlierea montana (Aubl.) Amshoff
Marlierea schomburgkiana O. Berg
Myrcia fallax (Rich.) DC.
Myrcia graciliflora Sagot
Myrcia guianensis (Aubl.) DC.
Myrcia servata McVaugh
Myrcia sylvatica (G. Mey.) DC.
Psidium cattleianum Sabine [cultivated]
Psidium guajava L. [naturalized]
Syzygium cumini (L.) Skeels [cultivated]
Syzygium jambos (L.) Alston [cultivated]
Syzygium malaccense (L.) Merr. & Perry [cultivated]

Nyctaginaceae
Boerhavia diffusa L. *
Guapira eggersiana (Heimerl) Lundell
Guapira salicifolia (Heimerl) Lundell
Neea constricta Spruce ex J.A. Schmidt
Neea floribunda Poepp. & Endl.

Nymphaeaceae
Nymphaea odorata Aiton
Nymphaea pulchella DC.
Nymphaea rudgeana G. Mey.

Ochnaceae
Ouratea candollei (Planch.) Tiegh.
Ouratea leblondii (Tiegh.) Lemée

Ouratea macrocarpa Sastre
Ouratea rorida Sastre
Sauvagesia elata Benth.
Sauvagesia erecta L.
Sauvagesia sprengelii A. St.-Hil.

Olacaceae
Heisteria maguirei Sleumer

Onagraceae
Ludwigia affinis (DC.) H. Hara
Ludwigia foliobracteolata (Munz) H. Hara
Ludwigia hyssopifolia (G. Don) Exell
Ludwigia latifolia (Benth.) H. Hara
Ludwigia leptocarpa (Nutt.) H. Hara *
Ludwigia nervosa (Poir.) H. Hara
Ludwigia octovalvis (Jacq.) P.H. Raven
Ludwigia torulosa (Arn.) H. Hara

Oxalidaceae
Averrhoa carambola L. [cultivated]
Oxalis barrelieri L.
Oxalis debilis Kunth

Passifloraceae
Passiflora amicorum Wurdack *
Passiflora auriculata Kunth
Passiflora cirrhiflora Juss.
Passiflora coccinea Aubl.
Passiflora foetida L.
Passiflora garckei Mast.
Passiflora glandulosa Cav.
Passiflora laurifolia L.
Passiflora nitida Kunth
Passiflora quadrangularis L. [cultivated]
Passiflora quadriglandulosa Rodschied

Phytolaccaceae
Microtea debilis Sw.
Petiveria alliacea L.
Phytolacca rivinoides Kunth & Bouché

Piperaceae
Peperomia duidana Trel. ex Gleason
Peperomia elongata Kunth
Peperomia glabella (Sw.) A. Dietr.
Peperomia macrostachya (Vahl) A. Dietr.
Peperomia magnoliifolia (Jacq.) A. Dietr.
Peperomia obtusifolia (L.) A. Dietr.
Peperomia pernambucensis Miq.
Peperomia rotundifolia (L.) Kunth
Peperomia serpens (Sw.) Loudon
Piper aduncum L.
Piper aequale Vahl
Piper anonifolium (Kunth) C. DC.
Piper arboreum Aubl.
Piper avellanum (Miq.) C. DC.
Piper coruscans Kunth
Piper dilatatum Rich.
Piper divaricatum G. Mey.
Piper glabrescens (Miq.) C. DC.
Piper hispidum Sw.
Piper hostmannianum (Miq.) C. DC.
Piper nigrispicum C. DC.
Piper peltatum L. *
Piper pseudoglabrescens Trel. & Yunck.
Piper pulleanum Yunck.

Polygalaceae
Bredemeyera densiflora A.W. Benn.
Moutabea guianensis Aubl.
Securidaca diversifolia (L.) S.F. Blake
Securidaca paniculata Rich.

Polygonaceae
Antigonon leptopus Hook. & Arn. [cultivated] *
Coccoloba ascendens Duss ex Lindau
Coccoloba densifrons Mart. ex Meisn.
Coccoloba marginata Benth.
Coccoloba parimensis Benth.
Polygonum punctatum Elliott
Triplaris weigeltiana (Rchb.) Kuntze

Portulacaceae
Portulaca oleracea L.
Portulaca pilosa L.
Portulaca sedifolia N.E. Br.

Quiinaceae
Quiina guianensis Aubl.
Quiina indigofera Sandwith

Rhamnaceae
Gouania lupuloides (L.) Urb. s.l.
Gouania polygama (Jacq.) Urb.

Rhizophoraceae
Cassipourea guianensis Aubl.
Cassipourea lasiocalyx Alston
Rhizophora x *harrisonii* Leechm. *?
Rhizophora mangle L.

Rhizophora racemosa G. Mey.

Rubiaceae

Amaioua corymbosa Kunth
Amaioua guianensis Aubl.
Bertiera guianensis Aubl.
Borreria assurgens (Ruiz & Pav.) Griseb.
Borreria capitata (Ruiz & Pav.) DC.
Borreria densiflora DC.
Borreria latifolia (Aubl.) K. Schum.
Borreria prostrata (Aubl.) Miq.
Borreria suaveolens G. Mey.
Borreria verticillata (L.) G. Mey.
Chimarrhis microcarpa Standl.
Cinchona sp. [cultivated]
Coccocypselum guianense (Aubl.) K. Schum.
Coccocypselum tontanea Kunth
Coffea arabica L. [cultivated]
Coffea liberica W. Bull ex Hiern [cultivated]
Cosmibuena grandiflora (Ruiz & Pav.) Rusby
Coussarea leptoloba (Spreng. ex Benth. & Hook. f.) Müll. Arg.
Coussarea violacea Aubl.
Diodia ocymifolia (Willd. ex Roem. & Schult.) Bremek.
Diodia sarmentosa Sw.
Duroia eriopila L. f.
Faramea guianensis (Aubl.) Bremek.
Faramea multiflora A. Rich. ex DC.
Genipa americana L.
Genipa spruceana Steyerm.
Geophila repens (L.) I.M. Johnst.
Geophila tenuis (Müll. Arg.) Standl.
Gonzalagunia bunchosioides Standl.
Gonzalagunia cornifolia (Kunth) Standl.
Gonzalagunia dicocca Cham. & Schltdl.
Gonzalagunia spicata (Lamb.) M. Gómez
Hamelia patens Jacq.
Hillia illustris (Vell.) K. Schum.
Ixora coccinea L. [cultivated]
Ixora schomburgkiana Benth.
Malanea hypoleuca Steyerm.
Malanea macrophylla Bartl. ex Griseb.
Morinda citrifolia L. [naturalized] *
Notopleura uliginosa (Sw.) Bremek.
Oldenlandia lancifolia (Schumach.) DC. [naturalized]
Palicourea crocea (Sw.) Roem. & Schult.
Palicourea croceoides Ham.
Palicourea guianensis Aubl.
Palicourea triphylla DC.
Posoqueria coriacea M. Martens & Galeotti
Posoqueria longiflora Aubl.
Posoqueria trinitatis DC.
Psychotria acuminata Benth.
Psychotria anceps Kunth
Psychotria apoda Steyerm.
Psychotria bahiensis DC.
Psychotria barbiflora DC.
Psychotria callithrix (Miq.) Steyerm.
Psychotria capitata Ruiz & Pav.
Psychotria cupularis (Müll. Arg.) Standl.
Psychotria deflexa DC.
Psychotria erecta (Aubl.) Standl. & Steyerm.
Psychotria gracilenta Müll. Arg.
Psychotria hoffmannseggiana (Willd. ex Roem. & Schult.) Müll.
Psychotria horizontalis Sw.
Psychotria iodotricha Müll. Arg.
Psychotria irwinii Steyerm.
Psychotria mapourioides DC.
Psychotria platypoda DC.
Psychotria poeppigiana Müll. Arg.
Psychotria racemosa Rich.
Psychotria tillettii Steyerm.
Psychotria ulviformis Steyerm.
Psychotria wessels-boeri Steyerm.
Randia armata (Sw.) DC.
Rudgea hostmanniana Benth.
Rudgea standleyana Steyerm.
Rudgea stipulacea (DC.) Steyerm.
Sabicea aspera Aubl.
Sabicea glabrescens Benth.
Sabicea oblongifolia (Miq.) Steyerm.
Sabicea velutina Benth.
Schradera polycephala DC.
Sipanea biflora (L. f.) Cham. & Schltdl.
Sipanea pratensis Aubl.
Uncaria guianensis (Aubl.) J.F. Gmel.
Uncaria tomentosa (Willd. ex Roem. & Schult.) DC.

Rutaceae

Citrus aurantifolia (Christm.) Swingle [cultivated]
Citrus aurantium L. [cultivated]
Citrus deliciosa Terr. [cultivated]
Citrus medica L. [cultivated]
Citrus paradisi Macfad. [cultivated]
Citrus reticulata Blanco [cultivated]
Citrus sinensis (L.) Osbeck [cultivated]
Ertela trifolia (L.) Kuntze

Murraya paniculata (L.) Jack [cultivated]
Zanthoxylum rhoifolium Lam.

Sabiaceae
Meliosma herbertii Rolfe [cultivated]

Sapindaceae
Allophylus racemosus Sw.
Cardiospermum halicacabum L.
Cupania hirsuta Radlk.
Cupania scrobiculata Rich.
Matayba camptoneura Radlk.
Matayba opaca Radlk.
Paullinia caloptera Radlk.
Paullinia capreolata (Aubl.) Radlk.
Paullinia hitchcockii Gleason
Paullinia pinnata L.
Paullinia rufescens Rich. ex Juss.
Paullinia xestophylla Radlk.
Pseudima frutescens (Aubl.) Radlk.
Serjania membranacea Splitg.
Serjania paucidentata DC.
Serjania pyramidata Radlk.
Talisia guianensis Aubl.
Talisia hemidasya Radlk.
Talisia hexaphylla Vahl

Sapotaceae
Chrysophyllum argenteum Jacq.
Chrysophyllum cainito L. [naturalized]
Chrysophyllum pomiferum (Eyma) T.D. Penn.
Chrysophyllum sanguinolentum (Pierre) Baehni
Manilkara bidentata (A. DC.) A. Chev.
Manilkara zapota (L.) P. Royen [cultivated]
Micropholis venulosa (Mart. & Eichler) Pierre
Pouteria ambelaniifolia (Sandwith) T.D. Penn.
Pouteria bilocularis (H. Winkl.) Baehni
Pouteria caimito (Ruiz & Pav.) Radlk.
Pouteria coriacea (Pierre) Pierre
Pouteria cuspidata (A. DC.) Baehni
Pouteria durlandii (Standl.) Baehni
Pouteria guianensis Aubl.
Pouteria hispida Eyma
Pouteria venosa (Mart.) Baehni
Pradosia schomburgkiana (A. DC.) Cronquist

Scrophulariaceae
Achetaria guianensis Pennell
Angelonia biflora Benth.
Asarina erubescens (D. Don) Pennell [cultivated]
Bacopa aquatica Aubl.
Capraria biflora L.
Lindernia crustacea (L.) F. Muell.
Lindernia diffusa (L.) Wettst.
Scoparia dulcis L.

Simaroubaceae
Picramnia guianensis (Aubl.) Jans.-Jac.
Picramnia latifolia Tul.
Quassia amara L. [naturalized]
Simarouba amara Aubl.

Siparunaceae
Siparuna decipiens (Tul.) A. DC.
Siparuna guianensis Aubl.

Solanaceae
Capsicum annuum L. [naturalized]
Cestrum latifolium Lam.
Markea camponoti Ducke
Markea longiflora Miers *
Nicotiana tabacum L. [cultivated]
Physalis angulata L.
Physalis pubescens L.
Solanum adhaerens Roem. & Schult.
Solanum asperum Rich.
Solanum leucocarpon Dunal
Solanum lycopersicum L. [cultivated]
Solanum pensile Sendtn.
Solanum rugosum Dunal
Solanum schlechtendalianum Walp.
Solanum stramoniifolium Jacq.
Solanum subinerme Jacq.

Sterculiaceae
Herrania kanukuensis R.E. Schult.
Herrania lemniscata (M.R. Schomb.) R.E. Schult.
Sterculia pruriens (Aubl.) K. Schum.
Sterculia rugosa R. Br.
Theobroma cacao L. [cultivated]
Waltheria indica L.

Theophrastaceae
Clavija lancifolia Desf.

Tiliaceae
Apeiba petoumo Aubl.
Corchorus aestuans L.
Triumfetta althaeoides Lam.

Turneraceae
Turnera scabra Millsp.
Turnera ulmifolia L.

Ulmaceae
Trema micrantha (L.) Blume

Urticaceae
Laportea aestuans (L.) Chew
Pilea pubescens Liebm.
Urera baccifera (L.) Gaudich. ex Wedd.

Verbenaceae
Aegiphila racemosa Vell.
Citharexylum macrophyllum Poir.
Clerodendrum fragrans (Vent.) Willd. [naturalized]
Lantana camara L.
Lippia alba (Mill.) N.E. Br.
Lippia micromera Schauer
Petrea volubilis L.
Priva lappulacea (L.) Pers.
Stachytarpheta cayennensis (Rich.) Vahl
Stachytarpheta jamaicensis (L.) Vahl
Vitex compressa Turcz.
Vitex stahelii Moldenke
Vitex triflora Vahl

Violaceae
Amphirrhox longifolia (St.-Hil.) Spreng.
Paypayrola grandiflora Tul.
Paypayrola longifolia Tul.
Rinorea flavescens (Aubl.) Kuntze
Rinorea pubiflora (Benth.) Sprague & Sandwith
Rinorea riana (DC.) Kuntze

Viscaceae
Phoradendron bathyoryctum Eichler
Phoradendron perrottetii (DC.) Eichler
Phoradendron piperoides (Kunth) Trel.
Phoradendron racemosum (Aubl.) Krug & Urb.

Vitaceae
Cissus erosa Rich.
Cissus verticillata (L.) Nicolson & C.E. Jarvis
Vochysiaceae
Vochysia guianensis Aubl.

MONOCOTILEDONEAE
Agavaceae
Agave americana L. [cultivated]
Furcraea foetida (L.) Haw.

Alismataceae
Sagittaria lancifolia L.
Araceae
Anthurium gracile (Rudge) Schott
Anthurium obtusum (Engl.) Grayum
Caladium bicolor (Aiton) Vent.
Caladium humboldtii Schott [cultivated]
Caladium schomburgkii Schott
Colocasia esculenta (L.) Schott [cultivated]
Dieffenbachia humilis Poepp.
Dieffenbachia paludicola N.E. Br. ex Gleason
Heteropsis flexuosa (Kunth) G.S. Bunting
Monstera adansonii Schott
Monstera obliqua Miq.
Montrichardia arborescens (L.) Schott
Montrichardia linifera (Arruda) Schott *
Philodendron acutatum Schott *
Philodendron brevispathum Schott
Philodendron deflexum Poepp. ex Schott
Philodendron fragrantissimum (Hook.) G. Don
Philodendron grandifolium (Jacq.) Schott
Philodendron hederaceum (Jacq.) Schott
Philodendron linnaei Kunth
Philodendron melinonii Brongn. ex Regel
Philodendron ornatum Schott
Philodendron pedatum (Hook.) Kunth
Philodendron rudgeanum Schott
Philodendron scandens K. Koch & Sello
Philodendron surinamense (Miq.) Engl.
Rhodospatha oblongata Poepp.
Spathiphyllum cannifolium (Dryand. ex Sims) Schott
Spathiphyllum cuspidatum Schott
Spathiphyllum maguirei G.S. Bunting
Stenospermation maguirei A.M.E. Jonker & Jonker *
Syngonium podophyllum Schott
Urospatha sagittifolia (Rudge) Schott
Xanthosoma belophyllum (Willd.) Schott [naturalized]
Xanthosoma brasiliense (Desf.) Engl. [cultivated]
Xanthosoma sagittifolium (L.) Schott [cultivated]
Xanthosoma undipes (K. Koch & C.D. Bouché) K. Koch

Arecaceae
Astrocaryum aculeatum G. Mey.

Astrocaryum gynacanthum Mart.
Astrocaryum vulgare Mart.
Attalea maripa (Aubl.) Mart.
Bactris acanthocarpa Mart.
Bactris brongniartii Mart.
Bactris campestris Poepp. ex Mart.
Bactris gasipaes Kunth [naturalized]
Bactris major Jacq.
Bactris maraja Mart.
Bactris oligoclada Burret
Bactris simplicifrons Mart.
Cocos nucifera L. [cultivated]
Desmoncus orthacanthos Mart.
Desmoncus polyacanthos Mart.
Elaeis guineensis Jacq. [cultivated]
Euterpe oleracea Mart.
Euterpe precatoria Mart.
Geonoma baculifera (Poit.) Kunth
Geonoma macrostachys Mart.
Geonoma maxima (Poit.) Kunth
Manicaria saccifera Gaertn.
Mauritia flexuosa L. f.
Nypa fruticans Wurmb. [naturalized] *
Oenocarpus bataua Mart.
Roystonea oleracea (Jacq.) O.F. Cook *
Socratea exorrhiza (Mart.) H. Wendl.

Bromeliaceae
Aechmea angustifolia Poepp. & Endl.
Aechmea bromeliifolia (Rudge) Baker
Aechmea lingulata (L.) Baker
Aechmea mertensii (G. Mey.) Schult. & Schult. f.
Aechmea nudicaulis (L.) Griseb.
Ananas comosus (L.) Merr. [naturalized]
Araeococcus micranthus Brongn.
Bromelia plumieri (E. Morren) L.B. Sm.
Disteganthus lateralis (L.B. Sm.) Gouda
Guzmania lingulata (L.) Mez
Guzmania monostachia (L.) Rusby ex Mez
Guzmania roezlii (E. Morren) Mez
Mezobromelia pleiosticha (Griseb.) Utley & H. Luther
Tillandsia bulbosa Hook.
Tillandsia monadelpha (E. Morren) Baker
Vriesea heliconioides (Kunth) Hook. ex Walp.
Vriesea procera (Mart. ex Schult. f.) Wittm. *
Werauhia gigantea (Mart. ex Schult. f.) J.R. Grant *

Burmanniaceae
Burmannia tenella Benth.

Cannaceae
Canna indica L. [cultivated]
Canna x *generalis* L.H. Bailey [cultivated]

Commelinaceae
Commelina diffusa Burm. f.
Commelina erecta L. *
Commelina rufipes Seub.
Dichorisandra hexandra (Aubl.) Standl.
Gibasis geniculata (Jacq.) Rohweder
Tripogandra serrulata (Vahl) Handlos

Costaceae
Costus amazonicus (Loes.) J.F. Macbr. [cultivated]
Costus arabicus L.
Costus congestiflorus Rich. ex Gagnep.
Costus erythrothyrsus Loes.
Costus guanaiensis Rusby
Costus scaber Ruiz & Pav.
Costus spiralis (Jacq.) Roscoe

Cyclanthaceae
Asplundia brachyphylla Harling
Asplundia glandulosa (Gleason) Harling
Asplundia gleasonii Harling
Asplundia guianensis Harling
Cyclanthus bipartitus Poit.
Evodianthus funifer (Poit.) Lindm.
Thoracocarpus bissectus (Vell.) Harling

Cyperaceae
Becquerelia cymosa Brongn.
Calyptrocarya bicolor (H. Pfeiff.) T. Koyama
Cyperus aggregatus (Willd.) Endl.
Cyperus articulatus L.
Cyperus comosus Poir.
Cyperus digitatus Roxb.
Cyperus haspan L.
Cyperus laxus Lam.
Cyperus ligularis L.
Cyperus luzulae (L.) Rottb. ex Retz.
Cyperus odoratus L.
Cyperus polystachyos Rottb. *
Cyperus simplex Kunth
Cyperus sphacelatus Rottb.

Cyperus surinamensis Rottb.
Diplasia karatifolia Rich.
Eleocharis interstincta (Vahl) Roem. & Schult.
Eleocharis mitrata (Griseb.) C.B. Clarke
Eleocharis mutata (L.) Roem. & Schult.
Eleocharis plicarhachis (Griseb.) Svenson
Eleocharis subfoliata C.B. Clarke
Fimbristylis cymosa R. Br. *
Fimbristylis dichotoma (L.) Vahl
Fimbristylis ferruginea (L.) Vahl
Fimbristylis miliacea (L.) Vahl
Fuirena umbellata Rottb.
Hypolytrum longifolium (Rich.) Nees
Kyllinga brevifolia Rottb.
Lagenocarpus guianensis Lindl. & Nees ex Nees
Rhynchospora cephalotes (L.) Vahl
Rhynchospora ciliata (Vahl) Kük.
Rhynchospora corymbosa (L.) Britton
Rhynchospora hassleri C.B. Clarke
Rhynchospora holoschoenoides (Rich.) Herter
Rhynchospora pubera (Vahl) Boeck.
Scleria latifolia Sw.
Scleria macrophylla J. Presl & C. Presl
Scleria melaleuca Rchb. ex Schltdl. & Cham.
Scleria microcarpa Nees ex Kunth
Scleria secans (L.) Urb.

Dioscoreaceae
Dioscorea alata L.
Dioscorea cayenensis Lam.
Dioscorea esculenta (Lour.) Prain [cultivated]
Dioscorea oblonga Gleason
Dioscorea pilosiuscula Bertero ex Spreng.
Dioscorea polygonoides Humb. & Bonpl. ex Willd.
Dioscorea riparia Kunth & R.H. Schomb.
Dioscorea samydea Griseb.
Dioscorea trichanthera Gleason
Dioscorea trifida L. f.

Eriocaulaceae
Paepalanthus bifidus (Schrad.) Kunth
Syngonanthus longipes Gleason
Syngonanthus umbellatus (Lam.) Ruhland
Tonina fluviatilis Aubl.

Haemodoraceae
Xiphidium caeruleum Aubl.

Heliconiaceae
Heliconia acuminata Rich.
Heliconia bihai (L.) L.
Heliconia chartacea Lane ex Barreiros
Heliconia hirsuta L. f.
Heliconia psittacorum L. f.
Heliconia richardiana Miq.
Heliconia spathocircinata Aristeg.
Musa x *paradisiaca* L. [cultivated]

Hydrocharitaceae
Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine *

Iridaceae
Eleutherine bulbosa (Mill.) Urb.

Lemnaceae
Lemna aequinoctialis Welw. *

Liliaceae
Aloe vera (L.) Burm. f. [cultivated]
Cordyline fructicosa (L.) A. Chev. [cultivated]
Crinum erubescens L. f. ex Sol.
Hippeastrum puniceum (Lam.) Kuntze
Hymenocallis littoralis (Jacq.) Salisb. [naturalized]
Hymenocallis tubiflora Salisb.

Marantaceae
Calathea cyclophora Baker
Calathea elliptica (Roscoe) K. Schum.
Calathea legrelleana (Linden) Regel
Calathea micans (Mathieu) Körn.
Calathea variegata Linden ex Körn.
Ischnosiphon arouma (Aubl.) Körn.
Ischnosiphon enigmaticus L. Andersson
Ischnosiphon foliosus Gleason
Ischnosiphon obliquus (Rudge) Körn.
Ischnosiphon puberulus Loes.
Maranta arundinacea L.
Monotagma spicatum (Aubl.) J.F. Macbr.

Orchidaceae
Brassia neglecta Rchb. f.
Brassia verrucosa Lindl.
Catasetum barbatum (Lindl.) Lindl.
Cyclopogon olivaceus (Rolfe) Schltr.
Dichaea picta Rchb. f.

Dichaea rendlei Gleason
Dimerandra elegans (H. Focke) Siegerist
Encyclia diurna (Jacq.) Schltr.
Encyclia granitica (Bateman ex Lindl.) Schltr.
Epidendrum anceps Jacq.
Epidendrum ciliare L. *
Epidendrum flexuosum G. Mey.
Epidendrum ibaguense Kunth
Epidendrum longicolle Lindl.
Epidendrum macrocarpum Rich.
Epidendrum nocturnum Jacq.
Epidendrum purpurascens H. Focke
Epidendrum rigidum Jacq.
Epidendrum strobiliferum Rchb. f.
Erycina pusilla (L.) N.H. Williams & M.W. Chase
Eulophia alta (L.) Fawc. & Rendle
Habenaria longicauda Hook.
Ionopsis utricularioides (Sw.) Lindl.
Jacquiniella sp.
Koellensteinia graminea (Lindl.) Rchb. f.
Lockhartia imbricata (Lam.) Hoehne
Maxillaria camaridii Rchb. f.
Maxillaria parviflora (Poepp. & Endl.) Garay
Maxillaria rufescens Lindl.
Maxillaria uncata Lindl.
Maxillaria villosa (Barb. Rodr.) Cogn.
Oncidium baueri Lindl.
Pleurothallis corniculata Lindl.
Pleurothallis exigua Cogn.
Pleurothallis glandulosa Ames
Pleurothallis lanceana Lodd.
Pleurothallis pruinosa Lindl.
Pleurothallis sclerophylla Lindl.
Pleurothallis yauaperyensis Barb. Rodr.
Polystachya concreta (Jacq.) Garay & H.R. Sweet
Prosthechea aemula (Lindl.) W.E. Higgins
Prosthechea vespa (Vell.) W.E. Higgins
Rodriguezia lanceolata Ruiz & Pav.
Scaphyglottis graminifolia (Ruiz & Pav.) Poepp. & Endl.
Scaphyglottis sickii Pabst
Selenipedium palmifolium (Lindl.) Rchb. f.
Sobralia sessilis Lindl.
Stanhopea grandiflora (Lodd.) Lindl.
Stelis argentata Lindl.
Trichocentrum lanceanum (Lindl.) M.W. Chase & N.H. Williams *
Trigonidium acuminatum Bateman ex Lindl.
Vanilla fimbriata Rolfe
Vanilla grandiflora Lindl.
Vanilla latisegmenta Ames & C. Schweinf.
Vanilla mexicana Mill.
Wullschlaegelia calcarata Benth.
Zygosepalum labiosum (Rich.) Garay

Poaceae
Acroceras zizanioides (Kunth) Dandy [naturalized]
Andropogon bicornis L.
Andropogon leucostachyus Kunth
Andropogon virgatus Desv. *
Axonopus compressus (Sw.) P. Beauv.
Bambusa vulgaris Schrad. ex J.C. Wendl. [cultivated]
Coix lacryma-jobi L. [naturalized]
Cymbopogon citratus (DC.) Stapf [naturalized]
Digitaria horizontalis Willd.
Echinochloa polystachya (Kunth) Hitchc. *
Eleusine indica (L.) Gaertn. [naturalized]
Eragrostis ciliaris (L.) R. Br. [naturalized]
Eragrostis tephrosanthos Schult.
Eragrostis unioloides (Retz.) Nees [naturalized]
Gynerium saccharoides ? Bonpl.
Gynerium sagittatum (Aubl.) P. Beauv.
Homolepis isocalycia (G. Mey.) Chase
Hymenachne amplexicaulis (Rudge) Nees
Hymenachne donacifolia (Raddi) Chase
Ichnanthus pallens (Sw.) Munro ex Benth.
Ichnanthus panicoides P. Beauv.
Ichnanthus ruprechtii Döll
Imperata contracta (Kunth) Hitchc.
Ischaemum timorense Kunth [naturalized]
Lasiacis ligulata Hitchc. & Chase
Leersia hexandra Sw.
Leptochloa scabra Nees
Leptochloa virgata (L.) P. Beauv.
Olyra latifolia L.
Olyra longifolia Kunth
Orthoclada laxa (Rich.) P. Beauv.
Oryza rufipogon Griff. [naturalized]
Panicum elephantipes Nees ex Trin.
Panicum laxum Sw.
Panicum millegrana Poir.
Panicum parvifolium Lam.
Panicum pilosum Sw.
Panicum polygonatum Schrad.

Panicum rudgei Roem. & Schult.
Panicum stoloniferum Poir.
Panicum trichoides Sw.
Paspalum conjugatum P.J. Bergius
Paspalum distichum L. *
Paspalum melanospermum Desv. ex Poir.
Paspalum millegrana Schrad.
Paspalum repens P.J. Bergius
Pharus latifolius L.
Piresia sympodica (Döll) Swallen
Saccharum officinarum L. [cultivated]
Sacciolepis striata (L.) Nash
Setaria parviflora (Poir.) Kerguélen
Setaria poiretiana (Schult.) Kunth
Sporobolus jacquemontii Kunth
Sporobolus virginicus (L.) Kunth *
Vetiveria zizanioides (L.) Nash [cultivated]
Zea mays L. [cultivated]

Pontederiaceae
Eichhornia azurea (Sw.) Kunth
Eichhornia diversifolia (Vahl) Urb.

Rapateaceae
Rapatea linearis Gleason
Rapatea paludosa Aubl.

Smilacaceae
Smilax cumanensis Humb. & Bonpl. ex Willd.
Smilax latipes Gleason
Smilax schomburgkiana Kunth

Taccaceae
Tacca parkeri Seem.

Triuridaceae
Sciaphila albescens Benth.

Typhaceae
Typha domingensis Pers. *

Xyridaceae
Xyris jupicai Rich.
Xyris laxifolia Mart.

Zingiberaceae
Aframomum melegueta K. Schum. [cultivated]
Curcuma zanthorrhiza Roxb. [cultivated]
Hedychium coronarium J. Koenig [naturalized]
Renealmia alpinia (Rottb.) Maas
Renealmia guianensis Maas
Renealmia orinocensis Rusby
Zingiber officinale Roscoe [cultivated]
Zingiber zerumbet (L.) Roscoe ex Sm. [cultivated]

APPENDIX 4.
SPECIES DISPARITIES BETWEEN THE NORTHWEST DISTRICT, GUYANA AND DELTA AMACURO, VENEZUELA

A: Taxa Found in the Northwest District not Recorded for Delta Amacuro

Including all Pteridophytes, and Spermatophytes (seed plants)

PTERIDOPHYTES

Lycopodiaceae
Lycopodiella cernua (L.) Pic. Serm.

Selaginellaceae
Selaginella parkeri (Hook. & Grev.) Spring
Selaginella porelloides (Lam.) Spring
Selaginella producta Baker

Aspleniaceae
Asplenium juglandifolium Lam.

Dennstaedtiaceae
Lindsaea lancea (L.) Bedd.
Lindsaea portoricensis Desv.
Saccoloma elegans Kaulf.

Grammitidaceae
Cochlidium serrulatum (Sw.) L.E. Bishop

Hymenophyllaceae
Trichomanes diversifrons (Bory) Mett. ex Sadeb.
Trichomanes martiusii C. Presl
Trichomanes polypodioides L.
Trichomanes radicans Sw.

Lomariopsidaceae
Elaphoglossum flaccidum (Fée) T. Moore
Elaphoglossum glabellum J. Sm.

Metaxyaceae
Metaxya rostrata (Kunth) C. Presl

Polypodiaceae
Dicranoglossum desvauxii (Klotzsch) Proctor
Microgramma fuscopunctata (Hook.) Vareschi
Phlebodium pseudoaureum (Cav.) Lellinger
Polypodium adnatum Kunze ex Klotzsch
Polypodium attenuatum Humb. & Bonpl. ex Willd.

Pteridaceae
Pteris altissima Poir.

Schizaeaceae
Schizaea fluminensis Miers ex J.W. Sturm
Schizaea incurvata Schkuhr

Tectariaceae
Triplophyllum funestum (Kunze) Holttum

Thelypteridaceae
Thelypteris interrupta (Willd.) K. Iwats.
Thelypteris leprieurii (Hook.) R.M. Tryon

Woodsiaceae
Diplazium celtidifolium Kunze

GYMNOSPERMS

Gnetaceae
Gnetum nodiflorum Brongn.

ANGIOSPERMS

Acanthaceae
Justicia pectoralis Jacq.

Agavaceae
Furcraea foetida (L.) Haw.

Alismataceae
Sagittaria lancifolia L.

Amaranthaceae
Alternanthera tenella Colla

Anacardiaceae
Anacardium giganteum W. Hancock ex Engl.
Anacardium occidentale L.
Astronium lecointei Ducke
Thyrsodium guianense Sagot ex Marchand

Annonaceae
Annona sericea Dunal
Annona symphyocarpa Sandwith
Bocageopsis multiflora (Mart.) R.E. Fr.
Duguetia calycina Benoist
Fusaea longifolia (Aubl.) Saff.
Guatteria schomburgkiana Mart.
Rollinia mucosa (Jacq.) Baill.
Xylopia benthamii R.E. Fr.
Xylopia cayennensis Maas
Xylopia surinamensis R.E. Fr.

Apocynaceae
Ambelania acida Aubl.
Himatanthus bracteatus (A. DC.) Woodson
Macoubea guianensis Aubl.
Odontadenia geminata (Hoffmanns. ex Roem. & Schult.) Müll. Arg.
Odontadenia puncticulosa (Rich.) Pulle
Odontadenia sandwithiana Woodson
Plumeria inodora Jacq.
Tabernaemontana disticha A. DC.
Tabernaemontana lorifera (Miers) Leeuwenb.

Araceae
Caladium bicolor (Aiton) Vent.
Caladium schomburgkii Schott
Dieffenbachia humilis Poepp.
Dieffenbachia paludicola N.E. Br. ex Gleason
Heteropsis flexuosa (Kunth) G.S. Bunting
Philodendron brevispathum Schott
Philodendron fragrantissimum (Hook.) G. Don
Philodendron hederaceum (Jacq.) Schott
Philodendron surinamense (Miq.) Engl.
Rhodospatha oblongata Poepp.
Spathiphyllum cuspidatum Schott
Spathiphyllum maguirei G.S. Bunting
Stenospermation maguirei A.M.E. Jonker & Jonker

Araliaceae
Schefflera decaphylla (Seem.) Harms

Arecaceae
Astrocaryum aculeatum G. Mey.
Astrocaryum vulgare Mart.
Bactris acanthocarpa Mart.
Bactris campestris Poepp. ex Mart.
Bactris oligoclada Burret
Bactris simplicifrons Mart.
Geonoma baculifera (Poit.) Kunth
Geonoma macrostachys Mart.

Aristolochiaceae
Aristolochia daemoninoxia Mast.
Aristolochia hians Willd.

Asclepiadaceae
Blepharodon nitidus (Vell.) J.F. Macbr.
Matelea badilloi Morillo
Matelea stenopetala Sandwith
Stenomeria decalepis Turcz.

Asteraceae
Clibadium surinamense L.
Clibadium sylvestre (Aubl.) Baill.
Conyza bonariensis (L.) Cronquist
Cyrtocymura scorpioides (Lam.) H. Rob.
Elephantopus mollis Kunth
Erechtites hieracifolia (L.) Raf. ex DC.
Mikania banisteriae DC.
Mikania cordifolia (L. f.) Willd.
Mikania hookeriana DC.
Mikania parviflora (Aubl.) H. Karst.
Mikania psilostachya DC.
Sonchus asper (L.) Hill
Sphagneticola trilobata (L.) Pruski
Unxia camphorata L. f.

Begoniaceae
Begonia humilis Dryand.

Bignoniaceae
Anemopaegma oligoneuron (Sprague & Sandwith) A.H. Gentry
Arrabidaea candicans (Rich.) DC.
Ceratophytum tetragonolobum (Jacq.) Sprague & Sandwith
Crescentia amazonica Ducke
Distictella elongata (Vahl) Urb.
Lundia densiflora DC.
Martinella obovata (Kunth) Bureau & K. Schum.
Pleonotoma echitidea Sprague & Sandwith
Schlegelia spruceana K. Schum.
Tabebuia serratifolia (Vahl) G. Nicholson

Bixaceae
Bixa orellana L.

Bombacaceae
Catostemma fragrans Benth.
Pachira insignis (Sw.) Sw. ex Savigny

Boraginaceae
Cordia schomburgkii DC.

Bromeliaceae
Aechmea angustifolia Poepp. & Endl.
Disteganthus lateralis (L.B. Sm.) Gouda
Vriesea heliconioides (Kunth) Hook. ex Walp.

Burmanniaceae
Burmannia tenella Benth.

Burseraceae
Protium unifoliolatum Spruce ex Engl.
Trattinnickia boliviana (Swart) Daly
Trattinnickia burserifolia Mart.

Caesalpiniaceae
Brownea grandiceps Jacq.
Chamaecrista ramosa (Vogel) H.S. Irwin & Barneby
Dicorynia guianensis Amshoff
Eperua falcata Aubl.
Eperua rubiginosa Miq.
Hymenaea courbaril L.
Macrolobium angustifolium (Benth.) R.S. Cowan
Peltogyne venosa (Vahl) Benth.
Senna alata (L.) Roxb.
Senna bacillaris (L. f.) H.S. Irwin & Barneby
Senna quinquangulata (Rich.) H.S. Irwin & Barneby
Senna reticulata (Willd.) H.S. Irwin & Barneby
Senna sandwithiana H.S. Irwin & Barneby
Tachigali micropetala (Ducke) Zarucchi & Pipoly

Capparaceae
Cleome serrata Jacq.
Cleome speciosa Raf.

Cecropiaceae
Cecropia obtusa Trécul
Coussapoa microcephala Trécul

Chrysobalanaceae
Couepia parillo DC.
Licania boyanii Tutin
Licania incana Aubl.
Licania kunthiana Hook. f.
Licania laxiflora Fritsch
Licania majuscula Sagot
Licania membranacea Sagot ex Laness.
Licania micrantha Miq.
Licania persaudii Fanshawe & Maguire

Clusiaceae
Clusia cuneata Benth.
Clusia gaudichaudii Choisy
Clusia myriandra (Benth.) Planch. & Triana
Rheedia virens Planch. & Triana
Tovomita calodictyos Sandwith
Tovomita choisyana Planch. & Triana
Tovomita obscura Sandwith
Tovomita schomburgkii Planch. & Triana
Vismia gracilis Hieron.
Vismia japurensis Reichardt
Vismia sessilifolia (Aubl.) Choisy

Combretaceae
Buchenavia grandis Ducke

Commelinaceae
Commelina erecta L.
Gibasis geniculata (Jacq.) Rohweder

Connaraceae
Connarus coriaceus G. Schellenb.
Pseudoconnarus macrophyllus (Poepp.) Radlk.

Convolvulaceae
Ipomoea asarifolia (Desr.) Roem. & Schult.
Ipomoea quamoclit L.

Costaceae
Costus erythrothyrsus Loes.
Costus guanaiensis Rusby
Costus spiralis (Jacq.) Roscoe

Cucurbitaceae
Cayaponia jenmanii C. Jeffrey
Helmontia leptantha (Schltdl.) Cogn.

Cyclanthaceae
Asplundia brachyphylla Harling

Asplundia glandulosa (Gleason) Harling
Asplundia gleasonii Harling
Asplundia guianensis Harling

Cyperaceae
Calyptrocarya bicolor (H. Pfeiff.) T. Koyama
Cyperus comosus Poir.
Cyperus simplex Kunth
Diplasia karatifolia Rich.
Eleocharis interstincta (Vahl) Roem. & Schult.
Eleocharis mitrata (Griseb.) C.B. Clarke
Eleocharis plicarhachis (Griseb.) Svenson
Eleocharis subfoliata C.B. Clarke
Fimbristylis ferruginea (L.) Vahl
Kyllinga brevifolia Rottb.
Rhynchospora cephalotes (L.) Vahl
Rhynchospora ciliata (Vahl) Kük.
Rhynchospora hassleri C.B. Clarke
Rhynchospora holoschoenoides (Rich.) Herter
Rhynchospora pubera (Vahl) Boeck.
Scleria macrophylla J. Presl & C. Presl

Cyrillaceae
Cyrilla racemiflora L.

Dichapetalaceae
Dichapetalum pedunculatum (DC.) Baill.

Dilleniaceae
Davilla nitida (Vahl) Kubitzki
Tetracera asperula Miq.

Dioscoreaceae
Dioscorea cayenensis Lam.
Dioscorea oblonga Gleason
Dioscorea pilosiuscula Bertero ex Spreng.
Dioscorea riparia Kunth & R.H. Schomb.
Dioscorea samydea Griseb.
Dioscorea trichanthera Gleason
Dioscorea trifida L. f.

Droseraceae
Drosera intermedia Hayne

Ebenaceae
Diospyros tetrandra Hiern

Elaeocarpaceae
Sloanea eichleri K. Schum.
Sloanea latifolia (Rich.) K. Schum.

Eriocaulaceae
Paepalanthus bifidus (Schrad.) Kunth
Syngonanthus longipes Gleason
Syngonanthus umbellatus (Lam.) Ruhland

Erythroxylaceae
Erythroxylum citrifolium A. St.-Hil.
Erythroxylum macrophyllum Cav.

Euphorbiaceae
Alchornea discolor Poepp.
Alchornea triplinervia (Spreng.) Müll. Arg.
Alchorneopsis floribunda (Benth.) Müll. Arg.
Croton cuneatus Klotzsch
Euphorbia cotinifolia L.
Euphorbia oerstediana (Klotzsch & Garcke) Boiss.
Euphorbia thymifolia L.
Microstachys corniculata (Vahl) Griseb.
Phyllanthus brasiliensis (Aubl.) Poir.

Fabaceae
Alexa confusa Pittier
Alexa surinamensis Yakovlev
Centrosema capitatum (Rich.) Amshoff
Crotalaria nitens Kunth
Crotalaria stipularia Desv.
Derris amazonica Killip
Derris pterocarpus (DC.) Killip
Desmodium axillare (Sw.) DC.
Dioclea scabra (Rich.) R.H. Maxwell
Dioclea wilsonii Standl.
Hymenolobium flavum Kleinhoonte
Lonchocarpus chrysophyllus Kleinhoonte
Lonchocarpus martynii A.C. Sm.
Lonchocarpus rufescens Benth.
Lonchocarpus spruceanus Benth.
Machaerium leiophyllum (DC.) Benth.
Machaerium quinatum (Aubl.) Sandwith
Ormosia coccinea (Aubl.) Jacks.
Ormosia coutinhoi Ducke
Ormosia nobilis Tul.
Platymiscium pinnatum (Jacq.) Dugand
Swartzia conferta Spruce ex Benth.
Swartzia guianensis (Aubl.) Urb.
Swartzia schomburgkii Benth.
Swartzia steyermarkii R.S. Cowan
Tephrosia sinapou (Buc'hoz) A. Chev.
Zornia diphylla (L.) Pers.

Flacourtiaceae
Banara guianensis Aubl.
Casearia acuminata DC.
Casearia javitensis Kunth
Ryania speciosa Vahl
Xylosma benthamii (Tul.) Triana & Planch.

Gentianaceae
Chelonanthus purpurascens (Aubl.) Struwe, S. Nilsson & V.A. Albert

Gesneriaceae
Besleria flavovirens Nees & Mart.
Chrysothemis villosa (Benth.) Leeuwenb.
Codonanthe calcarata (Miq.) Hanst.
Nautilocalyx coccineus Feuillet & L.E. Skog
Nautilocalyx cordatus (Gleason) L.E. Skog
Nautilocalyx mimuloides (Benth.) C.V. Morton
Paradrymonia maculata (Hook. f.) Wiehler

Heliconiaceae
Heliconia acuminata Rich.
Heliconia chartacea Lane ex Barreiros

Hippocrateaceae
Peritassa pruinosa (Seem.) A.C. Sm.
Tontelea glabra A.C. Sm.

Humiriaceae
Humiria balsamifera Aubl.
Humiriastrum obovatum (Benth.) Cuatrec.

Icacinaceae
Discophora guianensis Miers
Emmotum fagifolium Ham.
Poraqueiba guianensis Aubl.

Iridaceae
Eleutherine bulbosa (Mill.) Urb.

Lamiaceae
Hyptis parkeri Benth.

Lauraceae
Aiouea guianensis Aubl.
Aniba guianensis Aubl.
Aniba hostmanniana (Nees) Mez
Aniba hypoglauca Sandwith
Aniba jenmanii Mez
Aniba terminalis Ducke
Licaria oppositifolia (Nees) Kosterm.
Nectandra amazonum Nees
Ocotea puberula (Rich.) Nees
Ocotea splendens (Meisn.) Baill.
Persea nivea Mez

Lecythidaceae
Eschweilera alata A.C. Sm.
Eschweilera micrantha (O. Berg) Miers
Eschweilera sagotiana Miers
Eschweilera wachenheimii (Benoist) Sandwith

Lentibulariaceae
Utricularia benjaminiana Oliv.
Utricularia myriocista A. St.-Hil. & Girard

Liliaceae
Hippeastrum puniceum (Lam.) Kuntze

Loganiaceae
Strychnos erichsonii M.R. Schomb. ex Progel
Strychnos mitscherlichii M.R. Schomb.

Malpighiaceae
Banisteriopsis caapi (Griseb.) C.V. Morton
Burdachia sphaerocarpa A. Juss.
Diplopterys pauciflora (G. Mey.) Nied.
Heteropterys macrostachya A. Juss.
Hiraea fagifolia (DC.) A. Juss.
Mascagnia macrodisca (Triana & Planch.) Nied.
Mezia includens (Benth.) Cuatrec.
Stigmaphyllon convolvulifolium A. Juss.
Tetrapterys fimbripetala A. Juss.

Malvaceae
Sida glomerata Cav.
Urena lobata L.

Marantaceae
Calathea legrelleana (Linden) Regel
Calathea variegata Linden ex Körn.
Ischnosiphon enigmaticus L. Andersson
Ischnosiphon foliosus Gleason
Maranta arundinacea L.

Marcgraviaceae
Marcgravia magnibracteata Lanj. & Heerdt
Marcgravia purpurea I.W. Bailey

Melastomataceae
Aciotis annua (Mart. ex DC.) Triana
Aciotis indecora (Bonpl.) Triana

Bellucia grossularioides (L.) Triana
Clidemia capitellata (Bonpl.) D. Don
Clidemia dentata D. Don
Clidemia microthyrsa R.O. Williams
Clidemia rubra (Aubl.) Mart.
Clidemia venosa (Gleason) Wurdack
Comolia villosa (Aubl.) Triana
Desmoscelis villosa (Aubl.) Naudin
Henriettea succosa (Aubl.) DC.
Henriettella caudata Gleason
Loreya mespiloides Miq.
Miconia acinodendron (L.) Sweet
Miconia bubalina (D. Don) Naudin
Miconia ciliata (Rich.) DC.
Miconia egensis Cogn.
Miconia gratissima Benth. ex Triana
Miconia hypoleuca (Benth.) Triana
Miconia ibaguensis (Bonpl.) Triana
Miconia lepidota DC.
Miconia matthaei Naudin
Miconia minutiflora (Bonpl.) DC.
Miconia rubiginosa (Bonpl.) DC.
Myriaspora egensis DC.
Pterolepis glomerata (Rottb.) Miq.
Tococa aristata Benth.

Mendonciaceae
Mendoncia bivalvis (L. f.) Merr.
Mendoncia glabra (Poepp. & Endl.) Nees
Menispermaceae
Curarea candicans (Rich. ex DC.) Barneby & Krukoff

Menyanthaceae
Nymphoides indica (L.) Kuntze

Mimosaceae
Abarema jupunba (Willd.) Britton & Killip
Abarema laeta (Benth.) Barneby & J.W. Grimes
Abarema mataybifolia (Sandwith) Barneby & J.W. Grimes
Calliandra surinamensis Benth.
Hydrochorea corymbosa (Rich.) Barneby & J.W. Grimes
Hydrochorea gonggrijpii (Kleinhoonte) Barneby & J.W. Grimes
Inga acreana Harms
Inga acrocephala Steud.
Inga graciliflora Benth.
Inga java Pittier
Inga jenmanii Sandwith
Inga marginata Willd.
Inga pilosula (Rich.) J.F. Macbr.
Inga sarmentosa Glaz. ex Harms
Inga sertulifera DC.
Inga thibaudiana DC.
Macrosamanea pubiramea (Steud.) Barneby & J.W. Grimes

Moraceae
Bagassa guianensis Aubl.
Ficus mathewsii (Miq.) Miq.
Ficus roraimensis C.C. Berg

Myristicaceae
Iryanthera juruensis Warb.
Iryanthera macrophylla (Benth.) Warb.
Virola calophylla (Spruce) Warb.

Myrsinaceae
Stylogyne orinocensis (Kunth) Mez

Myrtaceae
Eugenia cucullata Amshoff
Eugenia punicifolia (Kunth) DC.
Myrcia graciliflora Sagot
Myrcia sylvatica (G. Mey.) DC.

Nyctaginaceae
Guapira salicifolia (Heimerl) Lundell
Neea constricta Spruce ex J.A. Schmidt
Neea floribunda Poepp. & Endl.

Nymphaeaceae
Nymphaea odorata Aiton

Ochnaceae
Ouratea candollei (Planch.) Tiegh.
Ouratea macrocarpa Sastre
Ouratea rorida Sastre
Sauvagesia sprengelii A. St.-Hil.

Onagraceae
Ludwigia nervosa (Poir.) H. Hara

Orchidaceae
Cyclopogon olivaceus (Rolfe) Schltr.
Dichaea rendlei Gleason
Encyclia diurna (Jacq.) Schltr.
Epidendrum anceps Jacq.
Epidendrum ibaguense Kunth
Epidendrum macrocarpum Rich.

Epidendrum purpurascens H. Focke
Maxillaria parviflora (Poepp. & Endl.) Garay
Maxillaria villosa (Barb. Rodr.) Cogn.
Pleurothallis exigua Cogn.
Pleurothallis lanceana Lodd.
Pleurothallis sclerophylla Lindl.
Pleurothallis yauaperyensis Barb. Rodr.
Selenipedium palmifolium (Lindl.) Rchb. f.
Vanilla fimbriata Rolfe
Vanilla grandiflora Lindl.
Vanilla latisegmenta Ames & C. Schweinf.
Wullschlaegelia calcarata Benth.

Oxalidaceae
Oxalis barrelieri L.
Oxalis debilis Kunth

Passifloraceae
Passiflora amicorum Wurdack
Passiflora cirrhiflora Juss.
Passiflora garckei Mast.
Passiflora glandulosa Cav.
Passiflora nitida Kunth

Piperaceae
Peperomia duidana Trel. ex Gleason
Peperomia pernambucensis Miq.
Peperomia rotundifolia (L.) Kunth
Piper aduncum L.
Piper avellanum (Miq.) C. DC.
Piper glabrescens (Miq.) C. DC.
Piper nigrispicum C. DC.
Piper pulleanum Yunck.

Poaceae
Andropogon leucostachyus Kunth
Eragrostis tephrosanthos Schult.
Gynerium saccharoides ? Bonpl.
Homolepis isocalycia (G. Mey.) Chase
Ichnanthus ruprechtii Döll
Imperata contracta (Kunth) Hitchc.
Panicum laxum Sw.
Panicum millegrana Poir.
Panicum polygonatum Schrad.
Panicum rudgei Roem. & Schult.
Panicum trichoides Sw.
Paspalum distichum L.
Paspalum repens P.J. Bergius
Piresia sympodica (Döll) Swallen
Sporobolus jacquemontii Kunth
Sporobolus virginicus (L.) Kunth

Polygalaceae
Bredemeyera densiflora A.W. Benn.
Moutabea guianensis Aubl.

Polygonaceae
Coccoloba densifrons Mart. ex Meisn.
Coccoloba parimensis Benth.

Rapateaceae
Rapatea linearis Gleason

Rhamnaceae
Gouania lupuloides (L.) Urb. s.l.

Rhizophoraceae
Cassipourea lasiocalyx Alston

Rubiaceae
Amaioua corymbosa Kunth
Borreria assurgens (Ruiz & Pav.) Griseb.
Borreria capitata (Ruiz & Pav.) DC.
Borreria densiflora DC.
Coccocypselum tontanea Kunth
Coussarea leptoloba (Spreng. ex Benth. & Hook. f.) Müll. Arg.
Coussarea violacea Aubl.
Faramea guianensis (Aubl.) Bremek.
Faramea multiflora A. Rich. ex DC.
Genipa spruceana Steyerm.
Geophila tenuis (Müll. Arg.) Standl.
Gonzalagunia bunchosioides Standl.
Gonzalagunia cornifolia (Kunth) Standl.
Gonzalagunia dicocca Cham. & Schltdl.
Gonzalagunia spicata (Lamb.) M. Gómez
Ixora schomburgkiana Benth.
Malanea hypoleuca Steyerm.
Palicourea guianensis Aubl.
Palicourea triphylla DC.
Posoqueria coriacea M. Martens & Galeotti
Posoqueria trinitatis DC.
Psychotria anceps Kunth
Psychotria bahiensis DC.
Psychotria barbiflora DC.
Psychotria callithrix (Miq.) Steyerm.
Psychotria capitata Ruiz & Pav.
Psychotria erecta (Aubl.) Standl. & Steyerm.
Psychotria horizontalis Sw.
Psychotria mapourioides DC.
Psychotria platypoda DC.
Psychotria tillettii Steyerm.
Psychotria ulviformis Steyerm.

Psychotria wessels-boeri Steyerm.
Rudgea standleyana Steyerm.
Rudgea stipulacea (DC.) Steyerm.
Sabicea aspera Aubl.
Sabicea velutina Benth.
Schradera polycephala DC.

Rutaceae
Ertela trifolia (L.) Kuntze
Zanthoxylum rhoifolium Lam.

Sapindaceae
Allophylus racemosus Sw.
Cupania scrobiculata Rich.
Matayba camptoneura Radlk.
Matayba opaca Radlk.
Paullinia caloptera Radlk.
Paullinia hitchcockii Gleason
Paullinia xestophylla Radlk.
Pseudima frutescens (Aubl.) Radlk.
Talisia guianensis Aubl.

Sapotaceae
Chrysophyllum pomiferum (Eyma) T.D. Penn.
Chrysophyllum sanguinolentum (Pierre) Baehni
Pouteria bilocularis (H. Winkl.) Baehni
Pouteria coriacea (Pierre) Pierre
Pouteria durlandii (Standl.) Baehni
Pouteria guianensis Aubl.
Pradosia schomburgkiana (A. DC.) Cronquist

Scrophulariaceae
Achetaria guianensis Pennell
Angelonia biflora Benth.
Lindernia diffusa (L.) Wettst.

Simaroubaceae
Picramnia guianensis (Aubl.) Jans.-Jac.

Smilacaceae
Smilax latipes Gleason

Solanaceae
Markea camponoti Ducke (possibly =*M. longiflora*)
Markea longiflora Miers
Solanum leucocarpon Dunal
Solanum rugosum Dunal
Solanum schlechtendalianum Walp.

Sterculiaceae
Herrania kanukuensis R.E. Schult.
Sterculia rugosa R. Br.

Taccaceae
Tacca parkeri Seem.

Theophrastaceae
Clavija lancifolia Desf.

Tiliaceae
Corchorus aestuans L.
Triumfetta althaeoides Lam.

Triuridaceae
Sciaphila albescens Benth.

Turneraceae
Turnera scabra Millsp.
Turnera ulmifolia L.

Urticaceae
Pilea pubescens Liebm.
Urera baccifera (L.) Gaudich. ex Wedd.

Verbenaceae
Aegiphila racemosa Vell.
Vitex compressa Turcz.
Vitex triflora Vahl

Violaceae
Paypayrola grandiflora Tul.
Rinorea flavescens (Aubl.) Kuntze

Viscaceae
Phoradendron bathyoryctum Eichler
Phoradendron perrottetii (DC.) Eichler

Vochysiaceae
Vochysia guianensis Aubl.

B: Taxa Found in Delta Amacuro but not Recorded for Guyana

Including all Pteridophytes, and Spermatophytes (seed plants)

LYCOPHYTES

Selaginellaceae
Selaginella cladorrhizans A. Braun

PTERIDOPHYTES

Adiantaceae
Cheilanthes bonariensis (Willd.) Proctor

Pteridaceae
Pteris tripartita Sw.

Thelypteridaceae
Thelypteris angustifolia (Willd.) Proctor

SPERMATOPHYTES

Acanthaceae
Barleria cristata L.
Barleria lupulina Lindl.
Justicia laevilinguis (Nees) Lindau
Justicia moritziana Wassh.
Sanchezia pennellii Leonard
Thunbergia erecta (Benth.) T. Anderson

Alismataceae
Echinodorus horizontalis Rataj
Sagittaria sprucei Micheli

Amaranthaceae
Celosia virgata Jacq.

Anacardiaceae
Astronium graveolens Jacq.

Aquifoliaceae
Ilex parvifructa Edwin

Araceae
Anthurium digitatum (Jacq.) G. Don
Philodendron delascioi G.S. Bunting
Philodendron fendleri K. Krause
Xanthosoma sagittifolium (L.) Schott

Aristolochiaceae
Aristolochia sprucei Mast.

Asclepiadaceae
Cynanchum strictum R.W. Holm

Asteraceae
Ambrosia peruviana Willd.
Ayapana trinitensis (Kuntze) R.M. King & H. Rob.
Oyedaea alba Pruski
Pseudogynoxys chenopodioides (Kunth) Cabrera
Spilanthes urens Jacq.
Tessaria integrifolia Ruiz & Pav.

Bignoniaceae
Arrabidaea chica (Bonpl.) B. Verl.
Memora patula Miers

Boraginaceae
Cordia dentata Poir.
Cordia panamensis Riley

Bromeliaceae
Hohenbergia stellata Schult. f.
Tillandsia balbisiana Schult. f.
Tillandsia elongata Kunth
Tillandsia gardneri Lindl.
Tillandsia polystachia (L.) L.

Caesalpiniaceae
Campsiandra implexicaulis Stergios
Chamaecrista pilosa (L.) Greene
Crudia aequalis Ducke
Senna spectabilis (DC.) H.S. Irwin & Barneby
Senna spinescens (Vogel) H.S. Irwin & Barneby

Capparaceae
Capparis osmantha Diels

Caprifoliaceae
Sambucus canadensis L.

Caryophyllaceae
Polycarpon apurense Kunth

Celastraceae
Elaeodendron xylocarpum (Vent.) DC.
Zinowiewia aymardii Steyerm.

Chrysobalanaceae
Licania latistipula Prance
Licania leucosepala Griseb.
Licania pyrifolia Griseb.

Clusiaceae
Clusia candelabrum Planch. & Triana
Clusia comans (Meisn.) Pipoly

Combretaceae
Combretum spinosum Bonpl.

Connaraceae
Connarus venezuelanus Baill.

Convolvulaceae
Ipomoea fimbriosepala Choisy
Maripa repens Rusby

Cucurbitaceae
Cayaponia metensis Cuatrec.
Fevillea cordifolia L.

Cyclanthaceae
Asplundia moritziana (Klotzsch) Harling

Cyperaceae
Bulbostylis svensoniana Steyerm.
Cyperus cornelii-ostenii Kük.
Cyperus felipponei Kük.
Cyperus gardneri Nees
Cyperus meyenianus Kunth

Elaeocarpaceae
Sloanea megacarpa Steyerm. & Marc.-Berti
Sloanea obtusifolia (Moric.) K. Schum.
Sloanea subpsilocarpa Steyerm.

Euphorbiaceae
Alchornea castaneifolia (Willd.) A. Juss.
Alchornea grandiflora Müll. Arg.
Croton bolivarensis Croizat
Dalechampia brownsbergensis G.L. Webster & Armbr.
Phyllanthus fluitans Benth. ex Müll. Arg.
Piranhea longepedunculata Jabl.
Plukenetia penninervia Müll. Arg.

Fabaceae
Cymbosema roseum Benth.
Dalbergia hygrophila (Mart. ex Benth.) Hoehne
Dalbergia subcymosa Ducke
Derris negrensis Benth.
Desmodium affine Schltdl.
Desmodium tortuosum (Sw.) DC.
Lonchocarpus fendleri Benth.
Lonchocarpus imatacensis Poppend.
Lonchocarpus sericeus (Poir.) Kunth ex DC.
Lonchocarpus tubicalyx Pittier ex Poppend.
Mucuna rostrata Benth.
Vatairea paraensis Ducke
Vigna longifolia (Benth.) Verdc.

Flacourtiaceae
Banara nitida Spruce ex Benth.
Banara orinocensis (Cuatrec.) Sleumer

Hippocrateaceae
Pristimera tenuiflora (Mart. ex Peyr.) A.C. Sm.

Lamiaceae
Hyptis brevipes Poit.

Lauraceae
Cinnamomum triplinerve (Ruiz & Pav.) Kosterm.
Nectandra pichurim (Kunth) Mez

Lemnaceae
Spirodela intermedia W. Koch

Loganiaceae
Strychnos mattogrossensis S. Moore

Loranthaceae
Psittacanthus acinarius (Mart.) Mart.

Lythraceae
Cuphea elliptica Koehne
Rotala ramosior (L.) Koehne

Malpighiaceae
Banisteriopsis lyrata B. Gates
Bunchosia armeniaca (Cav.) DC.
Clonodia complicata (Kunth) W.R. Anderson
Malpighia emarginata DC.
Mascagnia divaricata (Kunth) Nied.
Stigmaphyllon adenodon A. Juss.

Malvaceae
Abelmoschus moschatus Medik.
Cienfuegosia heterophylla (Vent.) Garcke
Urena sinuata L.
Wissadula hernandioides (L'Hér.) Garcke

Marantaceae
Calathea inocephala (Kuntze) H. Kenn. & Nicolson
Ctenanthe compressa (A. Dietr.) Eichler

Melastomataceae
Adelobotrys spruceana Cogn.
Clidemia acurensis Wurdack
Miconia borjensis Wurdack

Menispermaceae
Borismene japurensis (Mart.) Barneby

Mimosaceae
Enterolobium barinense L. Cardenas & H. Rodr.
Inga sapindoides Willd.
Macrosamanea spruceana (Benth.) Killip
Mimosa casta L.
Mimosa orinocoënsis Barneby

Moraceae
Clarisia racemosa Ruiz & Pav.
Ficus dendrocida Kunth

Myrtaceae
Calycorectes enormis McVaugh
Eugenia baileyi Britton
Syzygium malaccense (L.) Merr. & Perry

Nyctaginaceae
Guapira ferruginea (Klotsch ex Choisy) Lundell
Guapira marcano-bertii Steyerm.
Guapira rusbyana (Heimerl ex Standl.) Lundell
Neea davidsei Steyerm.

Olacaceae
Heisteria acuminata (Bonpl.) Engl.

Onagraceae
Ludwigia densiflora (Micheli) H. Hara

Orchidaceae
Campylocentrum lansbergii (Rchb. f.) Schltr.
Chelyorchis ampliata (Lindl.) Dressler & N.H. Williams
Dichaea panamensis Lindl.
Dichaea robusta Schltr.
Epidendrum congestoides Ames & C. Schweinf.
Lockhartia acuta (Lindl.) Rchb. f.
Macradenia rubescens Barb. Rodr.
Mormodes carnevaliana Salazar & G.A. Romero
Stelis santiagoensis Mansf.

Passifloraceae
Dilkea acuminata Mast.
Passiflora adenopoda DC.
Passiflora biflora Lam.
Passiflora cuneata Willd.
Passiflora cyanea Mast.
Passiflora suberosa L.
Passiflora subpeltata Ortega
Passiflora variolata Poepp. & Endl.

Piperaceae
Piper nigrum L.
Piper tenue Kunth

Poaceae
Brachiaria plantaginea (Link) Hitchc.
Guadua venezuelae Munro
Paspalum fasciculatum Willd. ex Flüggé

Polygalaceae
Moutabea sp. A
Securidaca bialata Benth.

Polygonaceae
Coccoloba declinata (Vell.) Mart.
Coccoloba fallax Lindau
Coccoloba spruceana Lindau
Polygonum ferrugineum Wedd.

Pontederiaceae
Heteranthera multiflora (Griseb.) C.N. Horn

Portulacaceae
Portulaca pusilla Kunth
Portulaca teretifolia Kunth

Rubiaceae
Chiococca pubescens Humb. & Bonpl. ex Roem. & Schult.
Diodia multiflora DC.
Psychotria occidentalis Steyerm.

Rutaceae
Angostura trifoliata (Willd.) T.S. Elias
Conchocarpus longifolius (A. St.-Hil.) Kallunki & Pirani
Neoraputia paraensis (Ducke) Emmerich
Zanthoxylum amapaense (Albuq.) P.G. Waterman
Zanthoxylum juniperinum Poepp.
Zanthoxylum martinicense (Lam.) DC.

Sapindaceae
Houssayanthus macrolophus (Radlk.) Hunz.

Sapotaceae
Diploon cuspidatum (Hoehne) Cronquist
Pouteria reticulata (Engl.) Eyma subsp. *reticulata*
Pradosia grisebachii (Pierre) T.D. Penn.

Scrophulariaceae
Bacopa innominata (M. Gómez) Alain
Mecardonia procumbens (Mill.) Small

Simaroubaceae
Simaba sp. A (sensu Steyermark et al.)

Solanaceae
Physalis cordata Mill.
Schwenckia micrantha Benth.
Solanum arboreum Dunal
Solanum lanceifolium Jacq.
Solanum seaforthianum Andrews

Sterculiaceae
Melochia manducata C. Wright
Melochia villosa (Mill.) Fawc. & Rendle
Sterculia abbreviata E.L. Taylor ex Mondragón
Sterculia apetala (Jacq.) H. Karst
Sterculia kayae P.E. Berry

Urticaceae
Boehmeria cylindrica (L.) Sw.
Phenax sonneratii (Poir.) Wedd.
Pilea fendleri Killip
Pilea involucrata (Sims) Urb.

Verbenaceae
Aegiphila perplexa Moldenke
Citharexylum poeppigii Walp.
Lantana glutinosa Poepp.

Viscaceae
Phoradendron berryi Rizzini

Vitaceae
Cissus alata Jacq.