



HAL
open science

Ecology and patch dynamics of *Megaphrynium macrostachyum* (Benth.) Milne-Redh. (Marantaceae) in the south-west Central African Republic

Terry Brncic

► **To cite this version:**

Terry Brncic. Ecology and patch dynamics of *Megaphrynium macrostachyum* (Benth.) Milne-Redh. (Marantaceae) in the south-west Central African Republic. Environmental Sciences. University of Oxford [Oxford], 2003. English. NNT: . tel-04413152

HAL Id: tel-04413152

<https://hal.science/tel-04413152>

Submitted on 23 Jan 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

**Ecology and patch dynamics of *Megaphrynium macrostachyum*
(Benth.) Milne-Redh. (Marantaceae) in the south-west Central
African Republic**

Thesis submitted for the degree of Doctor of Philosophy
at Oxford University, Oxford, UK

Michaelmas term, 2002

Terry Brncic
Oxford Forestry Institute and Linacre College

**Ecology and patch dynamics of *Megaphrynium macrostachyum* (Benth.)
Milne-Redh. (Marantaceae) in the south-west Central African Republic**

Terry Brncic

Oxford Forestry Institute and Linacre College
Thesis submitted for the degree of Doctor of Philosophy
Michaelmas term, 2002

ABSTRACT

Herbs in the family Marantaceae are an important component of moist semi-evergreen central African forests and often occur in such abundance as to form a distinguishable forest sub-type with a very characteristic appearance. However, the mechanisms by which Marantaceae forests form and persist are unknown. This study was designed to elucidate the origins and mechanisms of maintenance of one type of Marantaceae forest made up of the giant herb *Megaphrynium macrostachyum* in the Central African Republic. *M. macrostachyum* often reaches high densities after logging, shifting cultivation, or fire, but there is no evidence that its abundance in the closed forest of the Ndakan study area is attributable to recent disturbance.

At the landscape-scale, *M. macrostachyum* distribution was closely associated with canopy openness and the abundance of subsoil charcoal. Charcoal was found at 47% of sites and, in addition, five sites were found to have pottery fragments dating back approximately 600 and 2200 years BP. These results strongly suggest that *M. macrostachyum* patches are a persistent form of secondary forest resulting from prehistoric anthropogenic disturbance.

M. macrostachyum patches were found to inhibit the establishment and growth of tree seedlings in gaps significantly, both by considerably reducing the amount of light reaching the forest floor and through underground root and rhizome competition. It is a highly light-dependent species that exhibits seed dormancy in understory light conditions for up to 7 months and germinates most successfully in large clearings. *M. macrostachyum* seeds are unlikely to germinate under their own herb canopy. Vegetative growth through rhizome expansion is therefore likely to be important for the maintenance of patches. Invasion of intact forest through the colonisation of small gaps is unlikely. This study on the ecology of *M. macrostachyum* suggests that it is currently suffering a gradual reduction in abundance as the forest matures in the Ndakan study area.

ACKNOWLEDGEMENTS

I would like to thank Nick Brown and David Harris for supervising my research. I am glad that David, who has long wondered about *Megaphrynium*, was eager to learn more.

My field assistants were invaluable to me, not just for helping to collect data, but also for their companionship and wonderful humour. I am grateful to Guy 'Papa Bonheur' Mbiti, Blaise Henri Bourguenzo, Gislain 'Loutou' Kossoe, Yassi, Yves, Hannah Irving, and Ceri Collingborn for their hard work at Ndakan.

A special thanks to the sentinel at Ndakan, Maurice Dodonue and his family, for their cheerful company and help in camp.

I am grateful to my friends and associates in the Central African Republic for their warm hospitality in allowing me to stay in their camps and houses. Allard Blom, Angelique Todd, Chloë Cippoletta, Nigel Orbell, Diane Doran, Patrick Mehlman, Alecia Lilly, Andrea Turkalo, and Lisa Steel. In Congo I thank Boo Maisels, Bryan Curran, and the Bomassa camp.

I would like to thank the Ministry of the Environment, Water, Forests, Hunting and Fishing; the Ministry of National Education and Scientific Research; and the Dzanga-Sangha Project in the Central African Republic for giving permission to carry out this study.

The Swanson International Scholarship and the Linacre House Trust have generously supported my studies at Oxford and a grant from the Trapnell Fund has greatly aided my field work.

Thanks to my friends with whom I had the privilege to work, for their advice, help and camaraderie: Caroline Bampfylde, Luis Fonts, Dan Bebber, Tom D. Evans, Tom Clements, Miguel Olvera-Vargas, Shonil Bhagwat, and Mary Menton.

I am very grateful to all of my friends and housemates in Oxford for making my time here so enjoyable. Special thanks to Chris Trigg for his support, lovely cooking, and wonderful friendship.

I will always be indebted to Eef Hogervorst, an amazing woman and superb friend, who constantly provided food, encouragement, sage advice, enthusiasm, and good company during my time in Oxford.

Above all, I would like to thank all of my family for their love and support. I owe everything to my mother and her love of learning. I am especially grateful to my mom and my Nona for their continuous encouragement.

1 Introduction

1.1 Marantaceae forests in Central Africa

The Central African rain forest block occupies approximately 1,800,000 km² in equatorial Africa, centred on the Congo Basin (IUCN 1992, Whitmore 1997). This forest mass can be classified into different vegetation zones defined by the structure and physiognomy of the component species (White 1983). Vegetation zones develop as a result of large-scale gradients in rainfall regimes, temperature, soil parent material, water availability, and altitude. Examples include dense evergreen rain forest, moist semi-deciduous forest, mangrove forest, swamp forest, or montane rain forest. The Congo basin is mainly lowland semi-evergreen rain forest with approximately one third of it existing as freshwater swamp forest (Whitmore 1997).

Within the context of broader vegetation zones in the Congo Basin there is much variation at a local level that is unexplained by the above environmental gradients. Within the moist semi-deciduous forest zone for example, 'Marantaceae forest' may be one such sub-type. Herbs in the family Marantaceae (arrowroot family) are an extremely important component of central African forests and often occur in such abundance as to form a distinguishable forest sub-type with a much-reduced tree canopy (Gibert 1984, Maisels 1999). Such Marantaceae forests are widespread in the moist semi-evergreen lowland forests of Central and West Africa, sometimes covering large areas up to 2500 km² (de Foresta 1990). Marantaceae forests are known to support some of the highest densities of western lowland gorillas (*Gorilla gorilla gorilla*), forest elephants (*Loxodonta africana cyclotis*), chimpanzees (*Pan troglodytes*) and some monkey species in Africa, making them a crucial habitat for African wildlife (Maisels 1999, Rogers and Williamson 1987, Tutin and Fernandez 1985). However, the mechanisms by which Marantaceae forests form and persist are unknown. Despite having low densities of trees and being recognised as extremely important habitats for forest mammals, no studies have been carried out to elucidate the mechanisms by which they are able to compete for space with trees. This study was designed to elucidate the mechanisms relevant to the formation and persistence of one type of Marantaceae forest made up of the giant herb *Megaphrynium*

macrostachyum (Benth.) Milne-Redh. in the Central African Republic in order to understand the role that this forest sub-type plays in the ecology of Central African forests.

Marantaceae forests are noted for the general sparseness of the tree canopy, lack of mid-storey trees and shrubs, and a dense understorey made up primarily of herbs in the families Marantaceae and Zingiberaceae (ginger family), though the species composition may vary from region to region. The first mention of this forest type comes from Le Testu in 1938 in southwestern Congo (Le Testu 1938, in Maley 1990). Letouzey (1968 in Fay 1997) described 'sparse forests with a low layer of Marantaceae' (*forêts clairsemées à strate inférieure de Marantacées*) in eastern Cameroon. This was shortened to 'sparse forests with Marantaceae' (*forêts clairsemées à Marantacées*) (de Foresta 1990), and translated to 'open canopy Marantaceae forest' by Fay (1997). In this thesis the term 'Marantaceae forest' will be used to describe all forest types which have a dense herbaceous layer made up primarily of any species of Marantaceae.

The Ndoki National Park in south-west Central African Republic (C.A.R.) is characterised by a high density of *Megaphrynium macrostachyum* and also supports one of the highest densities of gorillas in Central Africa (Fay 1997). *M. macrostachyum* occurs in *terra firme* forest with a relatively open canopy and low density of trees, especially in the middle size classes, resulting in the appearance of an open mid-storey. *M. macrostachyum* can form dense thickets up to 5 m high and over 30 m in diameter, which have very little tree regeneration beneath them. Other herbs that frequently appear in the understorey are *Ataenidia conferta*, *Sarcophrynium schweinfurthianum*, and *Haumania danckelmaniana* (all Marantaceae), but these do not form large patches in this area. *M. macrostachyum* patches have a distinct canopy layer made up of large, loosely overlapping leaves on long petioles emerging from underground rhizomes (see Figure 1.1). Beneath the herb layer, the understorey is open, with small animal trails running between clumped petioles. There are sometimes lianas or understorey shrubs, but few seedlings, including seedlings of *M. macrostachyum*. Outside of these dense patches, *M. macrostachyum* occurs as scattered, smaller individuals in the forest understorey. Although the forest is secondary in appearance, the study area is in a National Park which has never been

logged. Here there is no evidence of recent disturbance such as fire and the interior of the park has no roads or villages.

Figure 1.1 A dense *M. macrostachyum* patch in the Ndakan study area, Central African Republic.



1.1.1 The extent of Marantaceae forests

Marantaceae forests of the general form found in C.A.R. have been described throughout Central and West Africa. Since the early account by Le Testu (1938), descriptions of Marantaceae forests in many different regions have been published. These are summarised below by country.

Cameroon

In a floristic survey of Cameroon, Letouzey (1968, in Fay 1997) described Marantaceae forests as having a low density of trees and shrubs and a dense herbaceous layer made up primarily of *Haumania danckelmaniana*, *Ataenidia*

conferta (both Marantaceae), and *Whitfieldia elongata* (Acanthaceae). A large area of Marantaceae forest on the west side of Mount Cameroon was described by Maley and Brenac (1998) as a similar form of Marantaceae forest. The Marantaceae forests there are in a climate of 2350 mm of rainfall yr⁻¹, between an altitude of 500 and 2000 m a.s.l., higher and wetter than most sites with Marantaceae in central Africa.

Congo

De Foresta (1990) gave the name '*forêt clairsemées à Marantaceae*' to extensive forest types around the edges of isolated savannas in the Mayombe, southwestern Congo. He wrote of places in the Mayombe of up to 1 ha with dense Marantaceae (*Haumania liebrechtsiana*, *M. macrostachyum* and *Sarcophrynium* sp.) and Zingiberaceae (*Aframomum* sp.) with no trees at all. He observed that there were seedlings of forest trees below the herbs, but that they seemed to die before reaching the sapling stage.

The relationship between savanna-forest boundaries and Marantaceae was also noted by Gibert (1984), who classified the forest sub-type as 'clear forest' (*Les forêts claires*). De Saint Aubin (1948, in Gibert 1984) described the 'clear forest' as being made up of different proportions of Marantaceae and Zingiberaceae, depending on the type of disturbance or location. For example, abandoned plantations were often dominated by two species of Zingiberaceae, whereas near Odzala, *M. macrostachyum* was common. Next to savannas, where the canopy was even more open than in clear forest, *Haumania liebrechtsiana* dominated the understorey. He also observed abandoned agricultural fields and found them to be quickly invaded by different herbaceous assemblages, along with lianas and shrubs which formed an impenetrable evergreen sub-canopy rich in Marantaceae, Zingiberaceae and Commelinaceae. Gibert (1984) thought local differences in the makeup of Marantaceae forests might be due to soil variation. The large trees were generally of bad form and often covered with lianescent Marantaceae. He noted that in Marantaceae forests natural tree regeneration was rare, and in some places seemed impossible.

Within the 2844 km² Odzala National Park in northeastern Congo, half of the vegetation is considered 'clear forest' with widely spaced trees (about 20% canopy

cover) and a dense herb layer, and the rest is relatively closed canopy (80% canopy cover), but also with an understorey of abundant Marantaceae (Maisels 1999). North of the Park, one of the highest densities of Marantaceae is found, extending over 900 km² with only small areas of 'primary' rain forest and seasonally inundated forests near rivers (Vanleeuwe and Gautier-Hion 1998). Rollet (1963, in de Foresta 1990) estimated the extent of Marantaceae forest in this area as 2500 km². Species composition is primarily *Haumania liebrechtsiana*, *Megaphrynium* spp. and *Aframomum* spp. In the more closed canopy Marantaceae forest, *Sarcophrynium schweinfurthianum* is also common (Brugiere *et al.* 2000, Maisels 1999). Maisels noticed a distinct difference in the dominant herb species between the western part of the park as compared to the east and central. The west had an understorey of predominantly *Megaphrynium* sp., *Haumania liebrechtsiana*, and *Aframomum* spp., whereas the east and central had a thick growth of primarily *Haumania liebrechtsiana* up to 3 m tall. However, Maisels (1999) could see no obvious soil or geological variations to explain the change in Marantaceae species composition across the Odzala study site. Tree density and basal area of Marantaceae forests in Odzala are as little as one-third to one-half of that reported for Central African closed forests (Maisels 1999).

Gabon

In the Forêt des Abeilles, a particular vegetation formation was described in logged forest by Dhetchuvi (1996) as containing abundant herbs in the families Marantaceae, Zingiberaceae, and Costaceae. Herbs from these three families make up nearly 70% of the forest cover in loading bays and felling sites. The principal species comprising the secondary vegetation are *Aframomum* spp. and *Haumania liebrechtsiana*. However, within this secondary growth was abundant regeneration of primary forest tree species.

In the Lopé Reserve, Gabon, White (1995) describes Marantaceae forest as having about 85% canopy cover, very few middle-storey trees, and a characteristic open appearance. Species composition is mainly *Haumania liebrechtsiana*, *Megaphrynium macrostachyum*, and *Megaphrynium velutinum* along with *Ataenidia conferta* and *Aframomum* spp. In some sites herbaceous vegetation formed dense thickets which

carpeted the ground and rose to 5 m or more in tangled climbing towers. One of these sites had been logged in the past. Stem densities for *Megaphrynium* spp. were up to 4186 stems ha⁻¹ in the logged site and 1892 stems ha⁻¹ in another Marantaceae site which had not been logged. *H. liebrechtsiana* reached a density of 3606 stems ha⁻¹ in the logged site (White 1995). Higher densities were reported by Rogers (1987), who measured the overall mean density of Marantaceae and Zingiberaceae at Lopé (6800 stems ha⁻¹ and 860 stems ha⁻¹ respectively).

Zaire/DRC

A study of post-agricultural regeneration in Kisingani, Zaire (now DRC) suggested that an association of *M. macrostachyum* and *Aframomum laurentii* (Zingiberaceae) colonised abandoned fields, logging tracks, and the understorey of secondary forests (Lubini 1986). Bebwa (1990) reported that the biomass of the herbaceous layer in 2nd year fallow fields in Kisingani, Zaire was predominantly from *Aframomum laurentii*, *Palisota ambigua* (Commelinaceae), *Costus* sp. (Costaceae/Zingiberaceae) and *Thaumatococcus* (Marantaceae). Biomass of these species is approximately 7 times higher than that of woody species after 2 years. In the same region, Lejoly (1980, in Bebwa 1990) made similar observations.

West Africa

Similar forest types have been described in the Ivory Coast and Ghana (Jaffre 1985, Hawthorne 1993, Hall and Swaine 1981). Hawthorne (1993) described stands of Marantaceae and Zingiberaceae on logging skid trails and gaps, but they appeared less dominant than in other areas, with abundant regeneration of other forest species present.

Overall extent

It is difficult to determine precisely how much area is covered by Marantaceae forest. Attempts are being made to utilise high-resolution satellite imagery to try to classify and quantify the range of forest types in Central Africa (N. Laporte, pers. comm.). However, the variable composition of Marantaceae forest and the existence of

overstorey canopy in some areas make it difficult to assess using remote sensing. Fay (1995) suggests that the only places where Marantaceae forests do not occur are in areas of high rainfall which have evergreen forests dominated by one or a few tree species. These monodominant forests occur in patches throughout the Congo Basin, particularly in eastern DRC and the Atlantic coastal region of Central Africa. In the Ndakan study area, evergreen forest made up of *Gilbertiodendron dewevrei* exists which has a very sparse herbaceous layer, consisting predominantly of *Palisota* spp. In general, it appears that Marantaceae forest is more or less ubiquitous in semi-evergreen forest zones throughout Central Africa.

1.2 The importance of understorey herbs in Central African forests

The ubiquity of Marantaceae forests throughout the tropical forest region of Central Africa indicates that they probably occupy an important niche in forest ecology. In studies on the diet and ranging patterns of animals such as great apes, elephants and monkeys, herbs in the families of Marantaceae and Zingiberaceae consistently turn up as important, if not essential, food sources (Malenky and Stiles 1991, Rogers and Williamson 1987, Wrangham *et al.* 1993). Primatologists have given them the name Terrestrial Herbaceous Vegetation or THV. Comparative studies on the distribution of herbaceous vegetation in East and Central Africa have highlighted differences in herb species composition and abundance that has led to theories on the development of primate social behaviour, particularly the social differences between mountain gorillas, lowland gorillas, chimpanzees and bonobos (Doran and McNeilage 1998).

A significant proportion of western lowland gorilla diet consists of pith and leaves of large herbs (Nishihara 1995, Remis 1997b). The percentage of *M. macrostachyum* stems on gorilla feeding trails markedly increases in the dry season when tree fruits are not readily available (Fay 1997). *M. macrostachyum* is also frequently utilised as material for nest construction (Voysey 1995, Tutin *et al.* 1995, Rogers *et al.* 1998, Fay 1997, Blom 2001, Brugiere and Sakom 2001). In the Ndoki National Park in C.A.R., 38% of gorilla nests were built using *M. macrostachyum* and 59.5% of nesting sites for gorilla groups were located in *M. macrostachyum* patches, whereas only 4.8% were located in closed canopy forest (Fay 1997).

The significance of Marantaceae forests becomes apparent when animal abundances are compared between forest types. Sites with less herbaceous vegetation, especially those without Marantaceae forests, have much lower densities of gorillas (such as the Petit Loango Reserve in Gabon with 0.21 gorillas km⁻²) (Furuichi *et al.* 1997). The lack of gorillas in the Kibale Forest, Uganda, with similar rainfall to Lopé has been attributed to 100-times less THV biomass at the Kibale site, and an absence of Marantaceae forest (Wrangham *et al.* 1993). Herbaceous vegetation at the Ngotto forest, C.A.R. is sparse (42 out of 50 sample quadrats had no herbaceous stems) (Brugiere and Sakom 2001) compared to the Dzanga-Sangha Reserve just over a hundred kilometres to the south-west. The population density of gorillas in the Ngotto forest was estimated at 0.34-0.40 weaned gorillas km⁻², whereas gorilla density was estimated at 0.89-2.0 gorillas km⁻² for Dzanga-Sangha (Fay 1989, Carroll 1988). Odzala National Park in Congo has one of the largest expanses of Marantaceae forest in Africa and the highest recorded densities of western lowland gorillas (5.4 gorillas km⁻²) and chimpanzees (2.2 chimpanzees km⁻²).

Elephants preferentially feed in areas with dense herbaceous cover (Vanleeuwe and Gautier-Hion 1998). In Gabon, C.A.R., and Congo, elephant densities were found to be higher in Marantaceae forest than in closed-canopy forest (White *et al.* 1995, Fay 1991).

Humans also depend on herbs as important non-timber forest products. The broad leaves of several Marantaceae species are used extensively by people to cook food, construct roofs, and wrap food purchases in markets. The petioles are often used in the fabrication of mats and for ropes in securing loads (Dhetchuvi and Diafouka 1993, Dhetchuvi 1993, Leonard and Mullenders 1950). *M. macrostachyum* is one of the species most heavily exploited for the above uses.

1.3 The origin and maintenance of Marantaceae forests

Fay (1997) proposed several potential causes for the formation of Marantaceae forests in Central Africa. These were the ecology of the component herb species, human-caused forest disturbance, climate change, and the action of large herbivores. All of

these factors operate at different temporal and spatial scales. It is possible that various combinations of them contribute to Marantaceae forest formation in different areas.

The ecology of each herb species determines the range in which it occurs, and the mechanisms by which it might compete with tree species in tropical forests. Specific environmental factors such as soil moisture or fertility may control where herbs are able to occur within a region. For many understorey plants, the most limiting resource is light (Augspurger 1984). In forests, small-scale disturbance caused by tree-fall gaps is responsible for much of the light reaching the forest floor (Barton *et al.* 1989, Canham *et al.* 1990). Therefore, many forest herb species are dependent on tree-fall gaps to grow and reproduce (Collins *et al.* 1985, Smith *et al.* 1987). Dirzo (1992), for example, showed that total standing leaf area of understorey herbs was significantly affected by both gap age and size in a Mexican rain forest. When a tree-fall occurs, herbs may grow rapidly to occupy the gap. Marantaceae and Zingiberaceae are large (1.5 - 5 m tall) and can often form a dense, low canopy. They have a network of underground rhizomes which allow them to re-grow rapidly when disturbed by large mammals. These characteristics may make them aggressive competitors with tree seedlings in gaps. An extensive patch may develop from one or a few individuals which spread from underground rhizomes, expanding into successive or multiple tree-fall gaps. Alternatively it may take several generations of local seed dispersal to develop the characteristic dense herb cover. However, although many observations have been made of the limited tree regeneration within Marantaceae forests, the actual interaction between herbs and tree seedlings has never been studied. Nor has the relationship between environmental variables and herb distribution and abundance been tested.

Most Marantaceae forests occur over a much larger area than that of a tree-fall gap. This suggests that Marantaceae forest formation is the result of much larger forest disturbance, or that the herbs are able to inhibit tree regeneration long enough to expand over large areas. Large-scale disturbance and subsequent forest regeneration have been hypothesised to be principally responsible for some of the vegetation mosaics within tropical forests through normal successional pathways (Brokaw and Scheiner 1989, Pickett and White 1985, Denslow 1987). Disturbance such as that caused by a wind throw, fire, or agriculture often results in a change of the ecological

community to one dominated by pioneer species. Pioneer species are more capable of rapidly dispersing to new areas and may be more tolerant of harsh conditions associated with degraded sites such as soil compaction and extreme heat and light exposure (Woodward 1996). In tropical forests that have been disturbed by logging or agriculture, herbaceous weedy species are often among the first colonisers. After a period of time the secondary successional species are replaced by longer-lived, woody species, progressively more tolerant of shady conditions. Barring any further perturbations, the climax vegetation community eventually returns. These processes are a possible mechanism for the creation of a mosaic of vegetation types at different stages and species compositions throughout the forest that contribute to the overall biodiversity of tropical forests.

Although some areas of Marantaceae forest can be attributed to recent natural or human disturbance, large expanses of Marantaceae in currently undisturbed forests often do not appear to be related to any such evidence. Several authors have noted the frequent proximity of Marantaceae forests to savanna isolates and have hypothesised that the development of a dense herbaceous layer may be a stage of secondary succession in the re-colonisation of savannas by closed forest in Gabon and Congo (de Foresta 1990, Gibert 1984, White 1992). Evidence of long-term climate change in Central Africa is sparse compared to other regions of the world, but does suggest that at least in some regions, lowland forest was replaced by savanna during colder, drier periods in the Quaternary (Elenga and Vincens 1990, Elenga *et al.* 1994, Maley 1989, Schwartz *et al.* 1995, Vincens *et al.* 1998). As the climate returned to warmer and wetter conditions, the forest was able to once again invade the savannas, perhaps with Marantaceae species in the early successional community. White (1992) proposed that in Marantaceae forests, eventually a few trees manage to escape, gradually building up canopy cover, causing the herb densities to decrease and allowing mixed forest species to invade.

There are also some Marantaceae forests in sites with no evidence of recent disturbance or nearby savannas, and thus no obvious explanation for the occurrence of Marantaceae forest. However, there is increasing evidence that prehistoric human impacts were much more widespread than previously assumed in the Congo Basin (Elenga *et al.* 1992, de Maret 1985, Oslisly and Dechamps 1994). Although there is no

direct evidence thus far linking Marantaceae forests to prehistoric human disturbance, previous human settlements and slash-and-burn agriculture may have created large areas of disturbed forest that could then be colonised by herbs.

Dhetchuvi (1996) proposed that Marantaceae and Zingiberaceae herbs, which made up most of the regeneration in fallow fields and in logged sites, facilitated regeneration of the forest after disturbance. The facilitation model of succession states that early successional species modify the environment to make it more suitable for the invasion of later successional or climax species (Connell and Slatyer 1977). The appearance of established tree seedlings beneath a layer of Marantaceae and Zingiberaceae as observed in fallow fields in DRC and Ghana (Dhetchuvi 1996, Hawthorne 1993) suggests that these herbs may facilitate forest regeneration after human disturbance.

However, Marantaceae forests may have long-term effects on forest composition in two ways. As a stage in tropical forest succession, they may affect the species composition of later stages. Tree species which are better able to compete with herbaceous cover may become more abundant in the forest. This effect on succession has been noted for other forests. For example, in China, dense bamboo swards preempt space after canopy gap formation by increasing shoot production. The reduction of opportunities for establishment and growth of other woody species leads to a change in later species composition of the forest (Taylor and Zisheng 1988).

Conversely, de Foresta (1990) hypothesised that as progressive colonisation of Congolese savannas took place, vegetation followed a successional pattern from shrubs and lianas to pioneer trees. As pioneer trees were replaced by primary forest trees, an understorey layer of *H. liebrechtsiana* established and arrested further tree establishment. As primary forest trees then died, they were not replaced, thus following an alternative regeneration pathway that resulted in a permanently different forest type. Marantaceae forests might thus be a plagio-climax, which is defined as a 'stable vegetation community arising from a succession that has been deflected or arrested' (Allaby 1998). Brugière (2000) even put forward that Marantaceae forests may be colonising both savannas *and* closed-canopy forests given its apparent success in northern Congo.

This scenario requires that Marantaceae herbs inhibit the regeneration of tree species in disturbed areas. Inhibition occurs when early successional species prevent recruitment both of other early successional species and climax species. Further invasion is only possible if space is released by the death or disruption of the early successors (Connell and Slatyer 1977). Many examples of inhibition exist for temperate forests, with different mechanisms of competition used by early successional species. Bracken (*Pteridium aquilinum*) competition after timber harvests in south-west Australia has been shown to reduce the number of surviving Eucalyptus seedlings by 50% through competition for light (Tolhurst and Turvey 1992). In tropical succession, inhibition of gap regeneration has been demonstrated for lianas in moist semi-deciduous forest on Barro Colorado Island, Panama (Putz and Canham 1992, Schnitzer *et al.* 2000). This is probably due to the strangling or smothering of emerging saplings by climbing lianas. Several Marantaceae species, *Haumania* in particular, have a lianescent growth form which may be capable of physically interfering with seedling and sapling growth. Alternatively a dense carpet of slow-decomposing leaves, such as that shown for the climbing fern *Dicranopteris linearis* in Hawaii, may inhibit tree regeneration by reducing the light reaching the forest floor (Russell *et al.* 1998).

When pioneers are able to inhibit further regeneration, they may occupy a site for a considerable period of time. Because of this, large-scale disturbance events may leave their mark on the forest perhaps for a century or more. Marantaceae forest on Mount Cameroon was ascribed to previous forest deterioration due to climatic changes several thousand years ago (Maley and Brenac 1998). It persists even though the current climatic conditions are very different from other lowland areas where Marantaceae forest is described.

The action of large herbivores such as gorillas and elephants may contribute to the inhibition of tree regeneration in Marantaceae forests. Struhsaker *et al.* (1996), in Uganda, noted that the movement and feeding of elephants in herbaceous secondary forest after logging often damaged young trees, suppressing tree regeneration. Fay (1997) also suggests that disturbance of the herb canopy by large animals may play an important role in the dynamics of Marantaceae forests. Gorilla and elephant use of *M.*

macrostachyum patches often results in the flattening of leaves and the creation of gaps in the herbaceous canopy. Such disturbance may also damage tree seedlings that have managed to establish, allowing herbs to dominate again through rapid re-growth from rhizomes. This is the case in grassland ecosystems for example, where grazing is viewed as one of many possible causes for persistence of sub-climax vegetation (Bray 1989). Conversely, gorilla nest construction frequently results in the deposition of dung, containing many tree seeds, into herb patches (Voysey 1995). The actions of large herbivores may thus create opportunities for tree species to invade Marantaceae forests. However, Voysey's work suggests that seeds that are deposited into herbaceous gaps at gorilla nest sites may have difficulty establishing under a herbaceous canopy, and the thick, folded leaves of the nest itself present a barrier between the seeds and the soil.

1.4 Aim of thesis and overview of chapters

The development and persistence of Marantaceae forest would depend on several factors, including the right conditions for establishment, rapid growth and reproduction, resilience against large herbivore disturbance, the ability to maintain sufficient densities when overtopped by trees, and the inhibition of further tree regeneration. The purpose of this thesis is to investigate these assumptions by specifically focusing on one type of Marantaceae forest, *M. macrostachyum* patches in the Ndakan study area of the Dzanga-Ndoki National Park, C.A.R. The ecology and dynamics of *M. macrostachyum* patches will be examined in order to provide some insight into the complex interactions that result in the formation of Marantaceae forests. The specific aims of this thesis are to:

1. Examine which environmental factors may be controlling the distribution and abundance of *M. macrostachyum*.
2. Explore some of the possible reasons for *M. macrostachyum* patch formation in the Ndakan study area.
3. Determine if *M. macrostachyum* patches inhibit, facilitate, or have no effect on tree regeneration.
4. Examine some of the mechanisms by which *M. macrostachyum* may compete with other forest species.

5. Determine the growth and reproductive rates of common Marantaceae species in different light environments and relate this to their abundance in the Ndakan study area.

The chapters are structured as follows:

Chapter 2: The role of environmental variables in *M. macrostachyum* distribution

This chapter will test whether the abundance and distribution of *M. macrostachyum* and other herb species are dependent primarily on environmental variables in the Ndakan study area. Results are presented from a stratified random sampling design of 100 plots over a 10 km² area where herb abundances were counted and a suite of habitat variables were measured at each point.

Chapter 3: Climate change and prehistoric human disturbance in Central African rain forests

Chapter 3 examines the evidence for linking *M. macrostachyum* patches to prehistoric disturbance in the Ndakan study area and placing it into the context of long-term climate change.

Chapter 4: The effect of *M. macrostachyum* on tree regeneration

The performance of seeds and seedlings of other forest species in *M. macrostachyum* patches is compared with closed canopy forest and forest gaps without *M. macrostachyum* cover. The mechanisms by which *M. macrostachyum* may compete with tree seedlings are subsequently examined, including the relative importance of root and shoot competition. Measurements of Photosynthetically Active Radiation (PAR) below forest tree canopy and *M. macrostachyum* canopy are presented.

Chapter 5: The ecology of *M. macrostachyum*

The ecology of *M. macrostachyum* is described in this chapter, in particular the characteristics of the species (such as growth and reproductive rates) that may contribute to patch formation. Comparisons are made between behaviour in different forest light environments, as well as with other Marantaceae species which do not form patches in the Ndakan study area. Experiments are described which show the optimal light conditions for germination of three different Marantaceae species, including *M. macrostachyum*.

Chapter 6: Discussion and Conclusion

The final chapter summarises the conclusions of the thesis and highlights areas for further research.

1.5 The Ndakan Study site

Research was carried out at the Ndakan study site (2°21'N, 16°9'E) in the southern sector of the Dzanga-Ndoki National Park, which is part of a 4500 km² protected area in the Dzanga-Sangha Dense Forest Reserve in southwestern C.A.R. (Figure 1.2). The vegetation of the Dzanga-Ndoki National Park is characterised as a mosaic of mixed semi-deciduous, open-canopy forest with abundant *M. macrostachyum*, monodominant evergreen *Gilbertiodendron dewevrei* forest, and seasonally inundated forest. The density of *M. macrostachyum* was measured at 11096 leaves ha⁻¹ by Fay (1997), almost three times that of the most herb-abundant site at Lopé measured by White (1992). The climbing herb *Haumania danckelmaniana* numbered 6756 stems ha⁻¹, over twice the density of the congeneric *H. liebrechtsiana* at the Lopé site. The area has never been commercially logged.

Mean annual rainfall for this region is approximately 1300 - 1600 mm yr⁻¹ (CTFT 1967 cited in Fay 1997), with a measurement at Ndakan of approximately 1600 mm for the study period of July 1999 to July 2000 (see Figure 1.3). Rainfall tends to be bimodally distributed with wetter periods from August to November and March to May. December to February is quite dry, with rainfall less than 100 mm per month and water stress becomes apparent in the forest.

Figure 1.2 Map of the Ndakan study area in the southern sector of Dzanga-Ndoki National Park, Central African Republic.

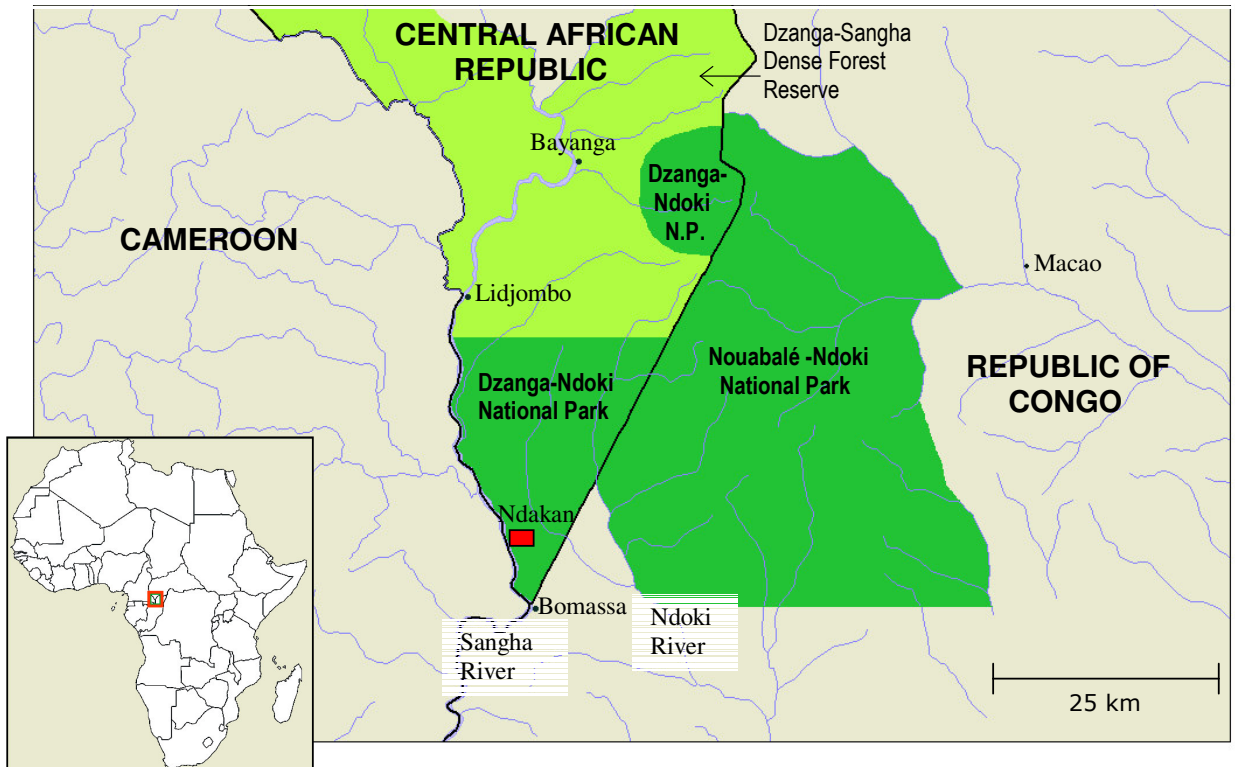
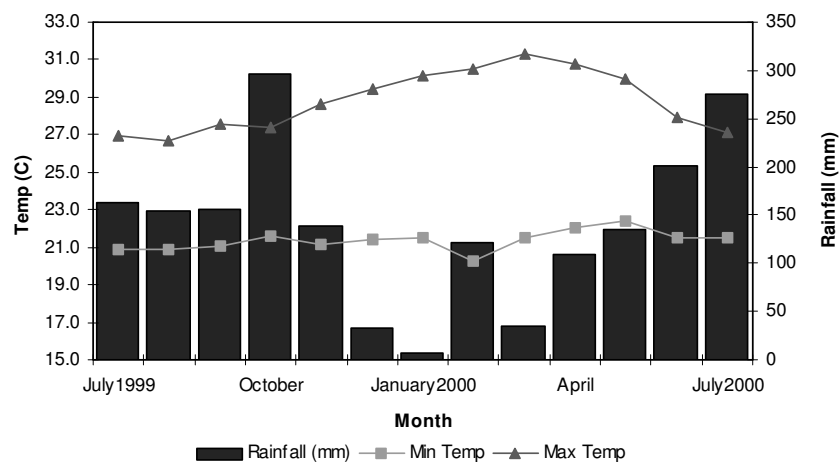


Figure 1.3 Mean monthly maximum and minimum temperatures and total monthly rainfall at Ndakan camp from July 1999 to July 2000.



Temperature is fairly constant throughout the year with a mean high temperature of 26° C and a mean low temperature of 21.5° C. The mean maximum temperature for the period from July 1999 to July 2000 at Ndakan was 28.7° C, and the mean minimum was 21.4° C. The altitude of the site is between 360 and 400 m a.s.l. with gentle topography.

Soils are generally ferrallitic alluvial or colluvial sands with some areas of hydromorphic soils in swamps. The majority of the area overlies Precambrian bedrock, with pre-Cretaceous sediments. In most places a thick layer of heavily leached red ferrasols overlies the bedrock. Alluvial deposits sometimes overlay and mix with ferrasols on the surface layer (Juo and Wilding 1996).

As described above, the Park has a high density of large mammals, including elephants, gorillas, and chimpanzees. Elephant density was recorded as 0.6 elephants km⁻², which is one of the highest in Central Africa (Fay 1991). Gorillas also had high abundances (1.6 individuals km⁻²), attributed to the open nature of the forest and the abundance of *M. macrostachyum* (Fay 1989).

The Park is uninhabited by people except for small fishing villages along the Sangha River. The Ndakan camp itself was a small village of about five houses which was abandoned in 1960 (Fay 1997).

2 The role of environmental variables in herb distribution

2.1 Background

2.1.1 Plant distributions and environmental variables

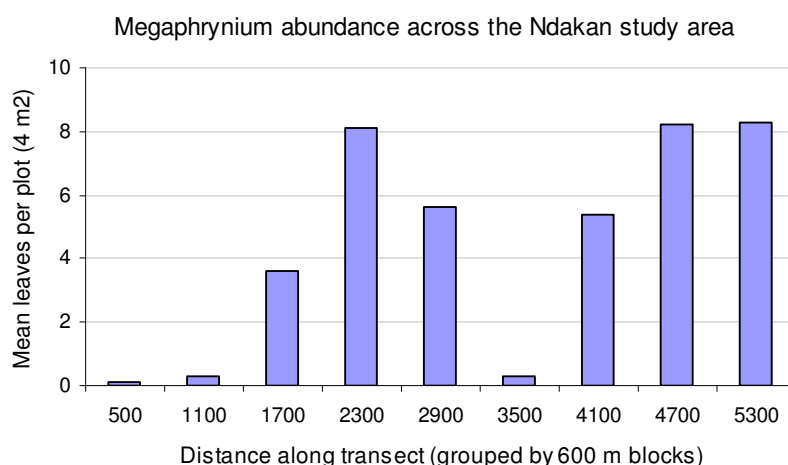
Climatic factors such as variations in rainfall, temperature, and seasonality are known to control the large-scale distribution and abundance of plant species (Gentry and Emmons 1987, Givnish 1999, Hall and Swaine 1981, Swaine 1996). On a landscape scale, plant distributions are often correlated with local environmental variables, primarily soil type and water availability, (Clark *et al.* 1999, Ashton 1976, Clinebell *et al.* 1995, Hutchinson *et al.* 1999, Newbery and Proctor 1984) and light (Augspurger 1984, Brokaw and Scheiner 1989, Denslow 1987, Raich and Gong 1990). Light is probably one of the most important factors affecting the distribution and abundance of many tropical understorey herbs. (Dirzo *et al.* 1992, Gentry and Emmons 1987, Smith *et al.* 1987). Often several environmental factors are inter-related. Soil characteristics and water availability are often highly correlated with topography (Beatty 1984, Newbery *et al.* 1996, Poulsen 1996). Less obvious relationships may exist, such as disturbance (from agriculture, logging, or fires) occurring more frequently on specific soil types (Robertson and Augspurger 1999, Hamilton *et al.* 1986, Poulsen 1996).

Still other species may have distributions better explained by biological factors such as complex relationships with other tree or herb species (Maguire and Forman 1983), or animal dispersers and herbivores (Ashton 1976, Horvitz and Schemske 1994, Janzen 1970, Ickes *et al.* 2001). Recent theoretical debates have also focused on the role of chance in species coexistence and distribution (Hubbell 2001, Bell 2000).

Several studies have shown that *M. macrostachyum* is associated with canopy openness (Fay 1997, Rogers and Williamson 1987). Fay (1997) measured the abundance and distribution of herbaceous vegetation in the Ndakan study area. He noted that *M. macrostachyum* was not evenly distributed throughout the study area, but appeared to increase in density at certain sections along a five km transect cut across the study area (Figure 2.1). It was noted that *M. macrostachyum* densities were

highest in sections of the trail with the lowest tree basal area and the greatest canopy openness, although when compared directly to adjacent plots, tree basal area and herb density were only slightly negatively correlated. Fay suggested that one reason for this unexpected outcome was that in plots with large basal areas and closed canopies, smaller ‘dwarf’ individuals were still relatively common. Although it was not tested, Fay also suggested that *M. macrostachyum* might prefer sandier soils which he thought predominated in the eastern half of the study area.

Figure 2.1 Graph redrawn from Fay (1995) summarising the distribution of *M. macrostachyum* along a 5.3 km transect through the Ndakan study area. The same transect is used as the baseline for the current study.



In Fay’s study, the number of *M. macrostachyum* leaves per 4 m² plot ranged from 0-180 with an average of 4.43. However, 82% of the plots had no *M. macrostachyum* leaves and 5% of the plots held 68% of the leaves. These figures suggest that *M. macrostachyum* is highly clumped in its distribution.

Objectives

The main objectives of this chapter are:

- To compare *M. macrostachyum* distribution directly to a suite of environmental variables in the Ndakan study area to determine which, if any, may control its presence and abundance at the landscape scale.

- To compare *M. macrostachyum* distribution to other species in the understorey herb community to determine whether *M. macrostachyum* responds differently to the same range of environmental factors.

2.2 Methods

2.2.1 Plot sampling and herb counts

Plot sampling was undertaken from June-Aug 2000 adjacent to the Ndakan camp in the Ndoki National Park, C.A.R. In order to experimentally examine herb responses to environmental factors, stratified random sampling of a 10 sq. km study area was employed (Kent and Coker 1994). The main trail running five km from the Sangha River to the seasonal Djeke River was used as a baseline from which to run 20 evenly spaced, perpendicular transects two km long. Using a random number generator, five random points were chosen on each transect for a total of 100 sample points. A Garmin 12 GPS or a topofil and compass were used to locate each of the points. Even with Selective Availability removed, the limited accuracy of the GPS could lead to bias in the placement of plots on a small scale because the clearest route was walked to reach a given point. Therefore, when an approximate point was reached, we proceeded another 15 m in a randomly chosen direction to arrive at each plot site.

Herb abundance

Within each 10 m² circular (1.78 m radius) plot, the identity and abundance of all herb species was assessed. Herbs were defined as non-woody plants which were rooted on the forest floor (Poulsen 1996). Clumping of plants sometimes made distinguishing individuals difficult without digging down to the rhizomes, so individuals were counted as separate plants if leaves were separated by more than 25 cm. Voucher specimens were deposited at the Daubeny Herbarium, Department of Plant Sciences, Oxford, UK (FHO) and Royal Botanic Gardens Edinburgh (E).

2.2.2 Habitat variables measured

At each of the sampling points a suite of variables was measured. Below is the justification for measuring each variable and a description of the methodology.

Soil properties

The predominant soil types in the study site are leached, discoloured, ferrallitic soils on alluvium or colluvium (Boulvert 1983 in Fay 1997). Because variation in soil types was known to exist across the study area, several soil variables were measured which could be used to indicate soil nutrient and water status. These were soil texture, pH, and soil colour. Directly adjacent to each herb plot, a soil pit was dug and a soil sample was collected from 30-45 cm depth. The samples were placed in labelled plastic bags, taken back to the camp, and analysed the same day.

Texture / Available Water Capacity

Soil texture is one of the most stable soil properties, and is useful as a basic indicator of soil physical and chemical properties, especially the available water capacity (AWC) of the soil (White 1979, Landon and Berryman 1991). AWC is the amount of water held by the soil which is available to plants for use. By definition it is the capacity of a soil to retain water between field capacity and permanent wilting point. Field capacity (FC) is the maximum water content that the soil will hold after gravitational drainage. Permanent wilting point (PWP) is the lower limit of water effectively available for plant use. Fine and medium textured soils such as clays, clay loams, silt loams generally retain more water than coarse, sandy loams or sands. However, they also release the water less easily to plants. Stones and gravel cause a reduction in water capacity. A soil containing 50% gravel will only have half the water storage capacity of a gravel free soil (Landon and Berryman 1991).

Soil texture was assessed by following a texture key and manually estimating sand, silt, and clay content of the sample. The soil textures were then converted to AWC values to obtain a continuous variable for the statistical analyses. AWC was estimated from a chart of tropical subsoils of different textures and stone contents (Pidgeon 1972). To compare the relative AWC estimates of each soil type, nine samples were brought back to the University of Oxford and tested using a pressure plate extractor with 15 bar and 1 bar ceramic plates (SoilMoisture Equipment Corp. Santa Barbara, CA). AWC is calculated as

$$FC - PWP \times BD$$

where FC is the % by weight of water held in the soil at 0.2 bar pressure, and PWP is the % by weight of water held in the soil at 15 bar pressure. BD is bulk density which is the dry mass of the soil divided by the original volume of the soil sample. Actual AWC was not calculated because bulk density was not measured in the field, but values generally range between 1.00 and 1.60 g cm⁻³ for clay, clay loam and silt loam and 1.20 to 1.80 g cm⁻³ for sands and sandy loams (Landon and Berryman 1991). The estimated AWC values obtained from the pressure plate extractor (not using bulk density) were then interpolated and assigned to the rest of the soil samples based on the hand texture classifications and estimated chart values.

pH

The availability of most nutrients is affected by soil acidity, measured as pH. Soil acidity has a marked control on plant growth through its effects on nutrient cycling, nitrogen mineralisation, soil fauna and the microbial population, on the concentrations of toxic aluminium in the soil solution, or on the availabilities of phosphorus and trace elements (Binkley and Vitousek 1989, Landon and Berryman 1991, Proctor *et al.* 1983). To measure pH, fresh soil samples were thoroughly mixed in a 1:1 volume ratio with distilled water. The mixture was stirred for four minutes with a glass rod. The slurry was allowed to sit for six minutes, stirred again for 30 seconds, then allowed to sit for another 4½ minutes. A calibrated digital pH metre (Piccolo, Hanna Instruments, Woonsocket, RI) was inserted into the mixture just below the surface and the reading recorded when stable (Landon and Berryman 1991).

Colour

Soil colours have long been used as a defining characteristic of soils and can serve as a proxy indicator of the nutrient properties of the soil. Soil colour depends on the parent material, the soil processes, amount of organic matter, and drainage. The hue of the soil can be roughly related to the amount of iron in the parent rock, and the oxidation rate of the iron in the soil. For example, high iron soils, commonly found in the tropics, tend to have a characteristic reddish-brown colour. Soil colour was measured by comparing fresh soil samples to the Revised Standard Soil Colour Charts (Oyama and Takehara 1967).

Light Characteristics

Canopy openness

At the centre of each circular plot, a canopy-scope was used as a relative measure to estimate the percent of canopy openness (Brown *et al.* 2000). This simple device is a piece of clear plastic marked with a grid of 25 evenly spaced black dots and is held 15 cm from the eye, related in principle to the moosehorn (Bonner 1967). Canopy openness is assessed by aiming the grid at the largest area of open sky and counting the number of dots that simultaneously overlay sky, unobscured by vegetation. The canopy-scope gives a good approximation of the amount of light reaching the forest floor at a single point in closed-canopy forest (Brown *et al.* 2000).

Tree Basal Area

From his sample of 100 m² plots, Fay (1997) estimated the tree basal area of the Ndakan study site to be low compared to other sites in Central Africa (23.2 m² ha⁻¹). Fay hypothesised that the low basal area over the whole site was part of the reason for high *M. macrostachyum* abundance at Ndakan. However, the herb plots he measured were not nested in the larger tree plots, and no correlation was found between tree basal area and *M. macrostachyum* abundance. In this study, the centre of each circular herb plot was used as the centre of a larger, 100 m² (.01 ha) circular plot (5.64 m radius) in which all trees >10 cm dbh were counted and measured with a dbh tape. Trees were counted if the centre of the tree was within the circle. Basal area was calculated in m² ha⁻¹.

Topography

The Ndakan study site is of relatively flat relief, with elevations varying between 360 and 400 m a.s.l. with no ridge-top and valley-bottom features. Small variations in the topography (called microtopography), such as pits and tip-up mounds are thought to have possible effects on species distributions (Svenning 1999). Although pits caused by the up-turned root plates of fallen trees were not common in this forest and were not encountered in the survey, small hills and termite mounds abound, and were categorised based on the size of the hill. Microtopography was classed into four

categories: 1=flat, 2=small hill (<3 m top to bottom), 3=medium hill (3-10 m top to bottom), 4=large hill (>10m top to bottom) or slope.

Other habitat variables

Charcoal

In an experimental soil pit, fragments of charcoal were found approximately 30-50 cm below the soil surface. It was thought that the charcoal might be from a past disturbance which might conceivably be linked to the current forest structure, and hence to the abundance of *M. macrostachyum*. Therefore, at each plot a soil pit was dug to a minimum depth of 60 cm and a minimum diameter of 50 cm and soil was searched carefully by hand for pieces of charcoal. If no charcoal was found, the pit was dug to a maximum depth of 1 m. Charcoal that was discovered was quantified and placed into plastic bags and later sun dried. A rating system was used to describe the abundance of charcoal in a given pit:

None (0);

Rare (1) – one or two flecks or small fragments (< 2 mm d), very difficult to find;

Occasional (2) – lots of flecks or a few small fragments;

Frequent (3) – four to ten small fragments or a few larger fragments (3-10 mm);

Common (4) – easy to find, moderate number of larger fragments;

Abundant (5) – very easy to find, many larger pieces (10-30 mm).

Macroscopic charcoal particles (>1 mm) remain near the source of the fire and therefore represent a local record of fire events (Clark and Patterson 1997). A higher abundance of larger fragments would indicate a localised, more recent, or more severe fire which consumed larger trees. Given the search method used, we were unlikely to find charcoal particles <1 mm in size which might have been carried from regional fires.

Fragments of pottery were also found in test pits. These were noted and collected when discovered in any of the sample plot pits. Pottery fragments were collected with surrounding soil and air-dried. They were transported to the UK and were thermoluminescence dated by the Luminescence Dating Laboratory in the Research

Laboratory for Archaeology and the History of Art at the University of Oxford (See chapter 3 for results).

Liana abundance

Lianas have been demonstrated to occupy canopy gap sites and significantly delay tree regeneration for many years (Schnitzer *et al.* 2000). They tend to be more abundant in younger forests (<40 years) than in older forests (>70 years) (Dewalt *et al.* 2000). Therefore, liana abundance may be an indicator of previous disturbance, as well as competing directly with ground herbs for light and nutrients in tree-fall gaps. Lianas rooted within the 1.78 m radius plots were counted.

Elephant or gorilla damage to trees and saplings

Several studies on the importance of herbaceous vegetation for diet and ranging behaviour of primates and elephants in Central Africa suggest that these large herbivores may actively maintain large Marantaceae patches by trampling tree seedlings or creating canopy gaps (Vanleeuwe and Gautier-Hion 1998, Voysey *et al.* 1999). Therefore, signs of gorilla or elephant damage to trees and saplings were noted at each point. Signs included broken or bent branches or stems and bark damage from rubbing or feeding.

2.2.3 Statistical Analyses

Modelling of species distributions in relation to this suite of environmental variables was done in two ways. First, Canonical Correspondence Analysis was used to detect major species-environmental gradients. Second, the presence or absence of each species was directly related to the environmental variables using binary logistic regression. Binary logistic regression was used because the high number of absences meant that the species data did not follow a normal distribution.

Canonical Correspondence Analysis

A direct comparison between species abundances and environmental variables was done using Canonical Correspondence Analysis in PC-ORD (McCune and Mefford 1999). CCA is an eigenvector ordination technique that also produces a multivariate

direct gradient analysis (Ter Braak 1986). CCA uses the weighted averages of species abundance data for each environmental variable, which gives an indication of where the species occurs along a particular environmental gradient. If an environmental variable gives a large dispersion between species, then that variable explains the species distribution well. By calculating the dispersion for each environmental variable, one can select the ‘best’ variable (Ter Braak 1987). Because a combination of variables may best explain the species distribution, CCA examines all linear combinations of environmental variables that maximise the dispersion of the species scores.

CCA is most likely to be useful when species responses are unimodal (hump-shaped) and there are many species, both conditions which make linear models invalid or impractical. However, when the response curves are simpler (e.g. linear), the results can still be expected to be adequate in a qualitative sense (Ter Braak 1987). CCA also relies on the assumption that the important underlying environmental variables have been measured (Ter Braak 1986). This is because the environmental matrix is being used to constrain the ordination results.

Treatment of data

Two corresponding matrices are required for CCA. In the main matrix, the rows are normally sites (plots) and the columns are species. In the second matrix, the rows are the same as in the main matrix, but the columns are environmental variables. To compare the explanatory power of different environmental variables, each environmental variable must first be standardised to mean 0 and variance 1. This removes arbitrariness in the units of measurement of the environmental variables and makes the canonical coefficients comparable to each other. PC-ORD centres and standardises the site scores automatically. Because the compound environmental gradients constructed by CCA are required to be linear combinations of environmental variables, non-linear transformation of several environmental variables was performed.

In CCA, species are weighted according to their totals. This gives high weight to species whose total abundance in the data matrix is low, thus exaggerating the

distinctiveness of samples containing several rare species (Faith *et al.* 1987, Minchin 1987). CCA may put these aberrant sites (with only rare species) at extreme ends of the ordination axes if the environmental variables are also somewhat aberrant. Therefore, rare species (those in fewer than 10% of plots) which behaved in this way were removed from the analysis.

CCA cannot cope with ordinal variables, which must either be treated as quantitative variables or nominal (dummy) variables. Ordinal variables were thus transformed into quantitative variables where necessary, and categorical variables which had a relative order were also treated as quantitative variables (such as colour).

Multicollinearity can occur when the environmental variables are strongly correlated with each other. When this happens, the canonical coefficients become less informative, but the intraset correlations are not affected (Ter Braak 1987). Multicollinearity between species is not a problem in CCA. A Spearman's rank correlation test was performed on all the environmental variables used in this analysis.

Interpretation of results

Eigenvalues

The first eigenvalue of CCA is equal to the maximised dispersion of species scores along the first CCA axis. The second and further axes are also maximised dispersions of species scores, but uncorrelated with the previous axes. The percentage variance of the weighted averages of the species explained by the two-dimensional diagram (goodness of fit) is calculated by taking $100 \times (\lambda_1 + \lambda_2) / (\text{sum of all eigenvalues})$, where λ_1 and λ_2 are the eigenvalues of the first two axes (Ter Braak 1986).

The dispersion along each axis and the relationship between environmental variables and species data was tested statistically by means of Monte Carlo permutation tests. The Monte Carlo permutation test assesses the null hypothesis that there is no relationship between the species and environmental matrices. It does this by randomly re-assigning the rows within the environmental matrix, destroying the relationship between the species and environmental matrices, but leaving the correlation structure

of the variables in the environmental matrix intact. This test was run with 2000 permutations.

Canonical coefficients and intraset correlations

The canonical coefficients define the ordination axes as linear combinations of the environmental variables. Intraset correlations are the correlation coefficients between the environmental variables and these ordination axes. The intraset correlations are indicators of which environmental variables were more important in structuring the ordination, but they are not necessarily an independent measure of the strength of relationship between communities and those environmental variables (Ter Braak 1986). The signs and relative magnitudes of the intraset correlations and the canonical coefficients describe the relative importance of each environmental variable for predicting the community composition. Both relate to the rate of change in community composition per unit change in the corresponding environmental variable. The difference between the two is that the canonical coefficient of a variable is calculated with other environmental variables held constant, whereas the intraset correlation value is calculated by allowing the other environmental variables to covary with it (Ter Braak 1986).

The coordinates for the environmental points are based on the interset correlations, which are the simple correlations between the environmental variables and the ordination axes, weighted by the eigenvalues of those axes (Ter Braak 1986)

The ordination diagram

The ordination diagram (biplot) of CCA displays sites, species, and environmental variables. Only the species points are displayed in this analysis. The environmental variables are represented by arrows where the longer the arrow, the greater its rate of change in the given direction. Longer arrows are more strongly correlated with the ordination axes than those with short arrows, and so more closely related to the pattern of community variation shown in the ordination diagram (Ter Braak 1987). Each arrow determines an axis in the diagram along which species are ranked according to their weighted averages in response to that variable. This can be determined by the projection of each species point on to the extension of an arrow. If the weighted

average projects beyond the end of an arrow, this implies a monotonic, rather than unimodal relationship with the environmental variable. This violates the assumption of unimodal species distributions, but CCA can still work well despite this (Ter Braak 1986).

However, species that are unrelated to the ordination axes tend to be placed in the centre of the ordination diagram along with species that have their true optima there. The true relationship can be determined by plotting sites by order of their scores on the first axis for each species and examining the abundance values along the axis. PC-ORD performs this function.

Binary Logistic Regression

Binary logistic regression regresses a dichotomous dependent variable on a set of independent variables (Hosmer and Lemeshow 1989). Logistic regression models were used to test the significance of relationships between individual species and the habitat variables used in the CCA. Akaike information criteria (AIC) (Akaike 1974) were used to compare alternative models. AIC penalises models with additional parameters, so the AIC selection criteria select the most parsimonious model. AIC is calculated as:

$$AIC_m = -2 \ln(L_m) + 2 p_m$$

where L_m is the sample log-likelihood for the m^{th} of M alternative models and p_m is the number of independent parameters estimated for the m^{th} model.

Binary logistic regression was done on presence-absence data of all herb species with at least 10 presences (7 species). A backwards stepwise model selection procedure was used, only removing habitat variables with p -values >0.05 . Multicollinearity between habitat variables was not greater than 0.5 in any case, so no variables were removed preliminarily. Interactions between variables were tested only if there was an ecological reason for doing so.

2.3 Results

2.3.1 Species

The ten most abundant herb species encountered in the sample plots are listed in Table 2.1 along with the percent of plots in which they were observed. The most frequent herb was *H. danckelmaniana* in 65% of the plots, followed by *M. macrostachyum* in 37% of the plots. The predominant species in the forest understorey at the Ndakan study site belong to the families of Marantaceae, Zingiberaceae, and Commelinaceae.

Table 2.1 The ten most abundant herb species found at the Ndakan study site.

Species	Family	% of plots
<i>Haumania danckelmaniana</i> (Braun & Schum.) M.-Redh.	Marantaceae	65
<i>Megaphrynium macrostachyum</i>	Marantaceae	37
<i>Ataenidia conferta</i> (Benth.) M.-Redh.	Marantaceae	24
<i>Sarcophrynium schweinfurthianum</i> (O. Kuntze) M.-Redh.	Marantaceae	22
<i>Aframomum thonneri</i> De Wild	Zingiberaceae	22
<i>Palisota brachythyrsa</i> Mildbr.	Comelinaceae	22
<i>Palisota ambigua</i> (P. Beauv.) C.B. Clarke	Comelinaceae	18
<i>Hypselodelphis scandens</i> Louis & Mullenders	Marantaceae	7
<i>Aframomum limbatum</i> (Oliv. & Hanb.) K. Schum.	Zingiberaceae	7
<i>Marantochloa congensis</i> (K. Schum.) J. Léonard & Mullenders	Marantaceae	4

2.3.2 Habitat characteristics of the Ndakan study site

Soil properties

Texture/Available Water Capacity

Figure 2.2 shows that the majority of soils in the study area were sandy silt loams and sandy loams. These two soil types also had the lowest mean AWC. Overall Mean AWC was 73.7 mm m⁻¹ (range 21-155). Gravel was present in 20 soil samples ranging from small amounts to 80% of the soil volume.

Figure 2.2 Frequency histogram of soil texture types in 100 plots in the study site. Soil types are coded as follows: CL=Clay Loam, fSCL=fine Sandy Clay Loam, fSL=fine Sandy Loam, fSZL=fine Sandy Silt Loam, LS=Loamy Sand, SC=Sandy Clay, SCL=Sandy Clay Loam, SL=Sandy Loam, SZL=Sandy Silt Loam, ZC=Silty Clay, ZCL=Silty Clay Loam, ZL=Silty Loam.

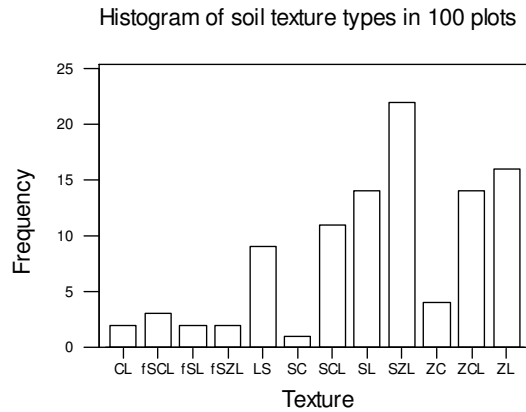
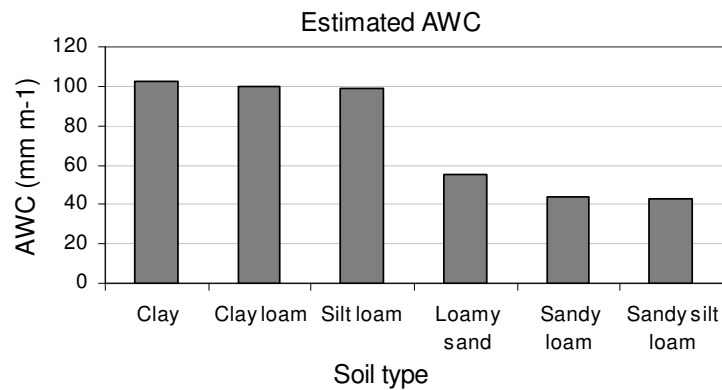


Figure 2.3 Graph of the AWC values measured with the pressure plate extractor for each group of soil textures found in the Ndakan study site.



Soils with a sandier texture had an AWC of around 50 mm m⁻¹, while silt loams, clays, and clay loams had approximately 100 mm m⁻¹ (Figure 2.3). Figure 2.4 shows the distribution of high and low AWC across the study site. From this map it appears that sandy soils predominate in the eastern half of the study area. All soils containing gravel were clustered in the north-west. Spearman’s rank correlation analysis (Table 2.2) showed AWC to be significantly correlated with soil colour and pH.

pH

Mean pH for the entire study site was 4.4 (range 3.8-5.5). Figure 2.5 shows the range of pH across the study site. This map shows that higher pH values were generally

found in the rocky, clay soils of the western half of the study site. Soils in the eastern half tended to be more acidic.

Soil colour

All soils fell into the range of reddish-brown (2.5 YR) to yellowish-brown (10 YR). Figure 2.6 shows the distribution of soil colour types across the study area. The relationship between soil AWC, pH, and colour can be seen from these figures, with the major soil gradients running east to west across the study area. The eastern soils are primarily weathered, acidic sandy soils, which change to higher pH, more iron-rich clay soils with frequent gravel in the western half of the plot.

Light variables

Canopy openness

78% of quadrats had continuous canopy cover with canopy-scope values of 5 or less. 8% of quadrats were in gaps with canopy-scope measurements between 6 and 11 (small gaps). 5% of plots were in medium gaps with canopy openness values of 12-18. Large gaps measuring 18-25 on the canopy-scope were at 11% of the quadrats. These figures are vastly higher than gap fractions measured in Neotropical forests (gap fraction is the proportion of the forest area under gaps. Range=1.4-7.5%) (Yavitt *et al.* 1995). However, the studies summarised in Yavitt all measured canopy gaps as vertical projections of holes (minimum 4 m²) in the canopy down to a maximum height 5 m above ground. This method does not take into account lateral light from adjacent canopy openings which the canopy-scope is able to measure. If canopy openness at Ndakan had been measured as vertical gaps, it may have been more comparable to the values reported for Neotropical forests. However, results from the canopy-scope do indicate that the canopy is fairly open at Ndakan.

Figure 2.4 Map of all sample plots in the Ndakan study area showing the distribution of soil types based on AWC values. Open circle, AWC < 87 mm m⁻¹ (sandy soils); Black square, AWC > 87 mm m⁻¹ (clay and loam soils). Diagonal arrows represent gravel presence in the soil sample.

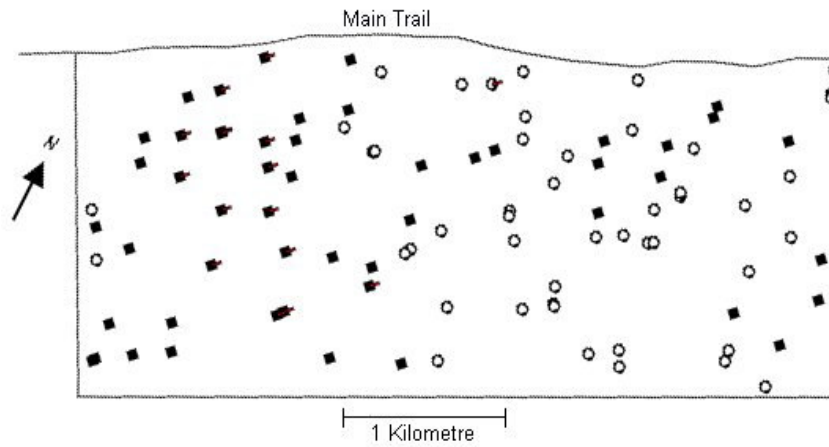


Figure 2.5 Map showing the distribution of pH categories. Open circles, pH 4.74-5.49; open squares, pH 4.38-4.74; black squares, pH 3.81-4.38.

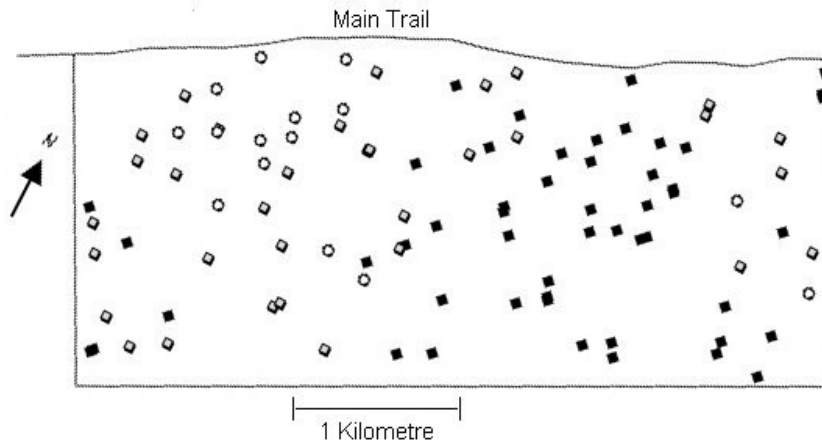
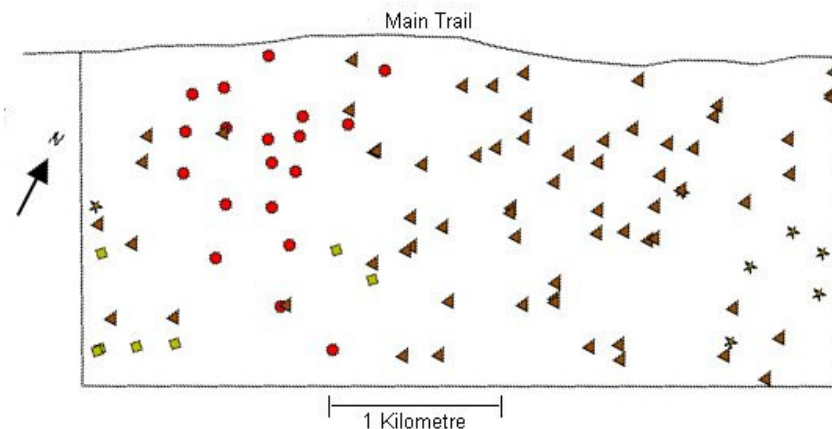


Figure 2.6 Map showing the distribution of soil colour over the study site. Red circles, 2.5 YR; brown triangles, 5 YR; stars 7.5 YR; yellow diamonds, 10 YR



Basal area

The average basal area of trees >10 cm dbh for the whole study area was 40.2 m² ha⁻¹. This is notably higher than the value of 23.4 m² ha⁻¹ reported by Fay (1995), but similar to values recorded in a forest in Gabon (White 1992). White (1992) reported tree basal area values in the Lopé Reserve between 29.6 and 40 m² ha⁻¹ for trees >10 cm dbh. The mean for African forests, presented in Fay (1997), was 34.1 m² ha⁻¹ for the same minimum diameter. The differences between this study and the Fay study may be due to the size and position of plots used to measure tree density. Fay used 200 m² circular plots along the main trail, whereas this study sampled 100 m² circular plots in a 2 km x 5 km area. Extrapolating to basal area per hectare values from smaller plots can inflate overall basal area measures, especially when a large-diameter tree falls within a plot. Tree basal area was not significantly correlated with canopy openness (Table 2.2).

Topography

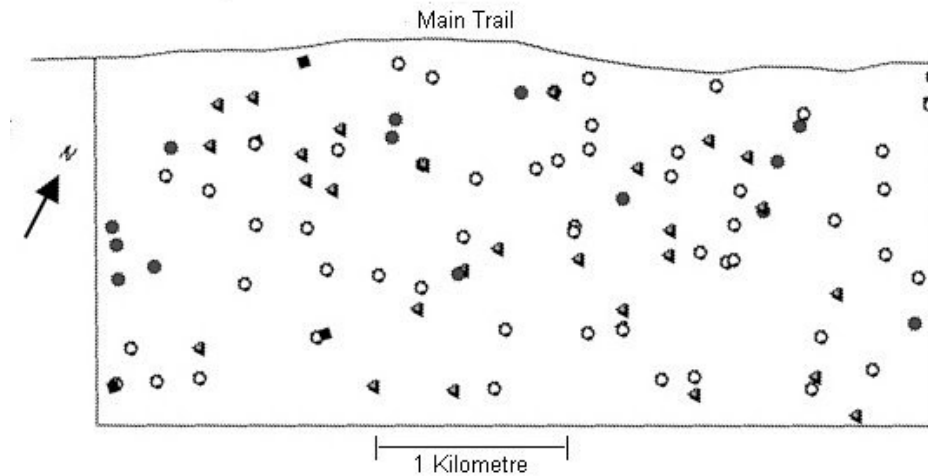
Topography did not vary much throughout the plot. The region is flat (rising 40 m over 5 km, and most plots (95%) were either flat or had small or medium-sized mounds. Because only 5% plots were located on large hills or true slopes, degree of slope and aspect were not included in the analyses. Large topographic differences, such as ridge top, slope and valley bottom did not exist in the study area. However, there was a significant correlation between microtopography and pH (GLM univariate analysis $F_{3,96}=4.06$, $p<0.01$). Tukey's pairwise post-hoc comparison showed that large hills or slopes had significantly higher pH than flat ground or medium-sized hills ($p<0.05$).

Other

Charcoal and pottery

Charcoal was found in 47 of the 100 soil pits, generally at a depth of 20-60 cm. Charcoal was mostly in the form of small fragments, but occasionally larger pieces were found. Frequent, common or abundant charcoal counts were found in 19 soil pits. Figure 2.7 is a map of the study area showing charcoal abundance of sample plots.

Figure 2.7 Map of the study area showing the locations of sub-soil charcoal. Charcoal abundance is shown as: Open circle=no charcoal; grey triangle=1-2; dark circle=3-4; black diamond=5.



Herbivore damage

Only two plots out of 100 had any signs of gorilla or elephant damage. The reasons for this are unclear as the Ndoki National Park has a high population of both species (Fay 1989, 1991). Such damage may be spatially concentrated in herb patches, so a figure of 2% for a random sample of all forest types is likely to be a reasonable estimate. Herbivore damage was not included in any of the analyses.

Liana abundance

Lianas were very abundant, with a mean of 2.7 lianas rooted in each plot (range 0-13).

2.3.3 Canonical Correspondence Analysis

Variables used in the analysis

The CCA main matrix was originally composed of abundance data for the 7 herb species that were present in more than 10% of the plots. These were *Haumania danckelmaniana*, *M. macrostachyum*, *Ataenidia conferta*, *Sarcophrynium schweinfurthianum*, *Aframomum thonneri*, *Palisota ambigua*, and *Palisota brachythyrssa*. However, *Palisota ambigua* was subsequently removed from the analysis after preliminary runs because it was not correlated with any of the

environmental variables measured, and yet had a strong effect on the second axis. Thus the final model included six species. Five plots had to be removed from the analysis because none of the species was present.

The second matrix was made up of microtopography, soil pH, soil AWC, soil colour, soil gravel content, canopy openness, charcoal abundance, liana abundance and tree basal area. Colour was included as a quantitative variable ranked on the amount of reddishness of the soil. Canopy openness and tree basal area were log transformed. Arcsine square root transformation was performed on percent gravel content. Aspect and slope were not used because most of study site was flat, and most slope angles were due to small hills (microtopography) rather than major slopes and valleys. Microtopography was converted into a quantitative variable based on the size of the hill or mound.

Results of CCA

Results from the Spearman's rank correlation test showed that none of the correlations between environmental variables were of sufficient strength to warrant removal from the analysis. Correlation between variables would have to be >0.8-0.9 to affect the analysis (Henderson 2003).

Table 2.2 Spearman's rank correlations among environmental variables in the second matrix

	pH	Soil colour	Gravel	AWC	Charcoal abundance	Canopy openness	Liana count	Tree basal area
microtopography	0.282**	-0.022	-0.057	0.163	-0.033	-0.186	-0.002	0.098
pH		-0.305**	0.484**	0.409**	0.065	0.029	0.066	-0.068
Soil colour			-0.499**	-0.125	0.026	0.168	-0.175	0.034
Gravel				0.360**	0.036	-0.241*	0.097	-0.133
AWC					-0.065	0.033	0.132	-0.193
Charcoal abund						-0.060	0.016	0.037
Canopy open.							0.060	-0.034
Liana count								-0.185

** Correlation is significant at the .01 level (2-tailed).

* Correlation is significant at the .05 level (2-tailed).

Table 2.3 shows the eigenvalues corresponding to the first three axes. These axes account for 23.8% of variance in community composition. Thus there is a substantial amount of residual variation in the community structure not explained by the measured environmental variables. Nonetheless, the results are still useful in pointing out the major trends in species distributions. The low eigenvalue for axis 3 suggests that it probably has little explanatory value for species distribution patterns, and indeed, it was not found to be significant in the Monte Carlo test ($p > 0.05$). Therefore, only the first two axes are discussed.

Table 2.3 Axis summary statistics for CCA showing three canonical axes. Total variance in species data = 2.5123

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.394	0.142	0.062
% of variance explained	15.7	5.6	2.5
Cumulative % explained	15.7	21.3	23.8
Pearson Correlation, Spp-Envt*	0.761	0.494	0.363
Kendall (Rank) Correlation Spp-Envt	0.450	0.223	0.291

* Correlation between sample scores for an axis derived from the species data and the sample scores that are linear combinations of the environmental variables. Set to 0.000 if axis is not canonical.

Results of the Monte Carlo randomisation test of the eigenvalues using 1999 runs are summarised in Tables 2.4 and 2.5. The probability of achieving eigenvalues greater than or equal to those of axes 1 and 2 was < 0.05 . This indicates that the amount of variation explained by the axes is significantly greater than by random chance. Similar results were obtained from the Monte Carlo test of species-environment correlations.

Table 2.4 Results of Monte Carlo permutations test on axis eigenvalues

Axis	Real data		Randomised data, 1999 runs		
	Eigenvalue	Mean	Minimum	Maximum	p
1	0.394	0.144	0.056	0.294	0.0005
2	0.142	0.080	0.029	0.191	0.0125
3	0.062	0.044	0.012	0.104	0.1000

p = proportion of randomised runs with eigenvalue greater than or equal to the observed eigenvalue

Table 2.5 Results of Monte Carlo permutations test on species-environment correlations

Axis	Real data		Randomised data, 1999 runs		
	Spp-Envr Corr.	Mean	Minimum	Maximum	p
1	0.761	0.483	0.299	0.677	0.0005
2	0.494	0.381	0.232	0.578	0.0185
3	0.363	0.304	0.150	0.486	0.1260

p = proportion of randomised runs with species-environment correlation greater than or equal to the observed species-environment correlation

The canonical coefficients and intraset correlations for each of the environmental variables indicate that pH and AWC were the most important variables for structuring the ordination along the first axis (2.6). Other soil variables such as soil colour and gravel content were also correlated with axis 1. The second axis was defined primarily by canopy openness, charcoal abundance, contrasted with liana abundance. CCA in this case separated out the herb community primarily on soil characteristics (axis 1) and disturbance variables (axis 2).

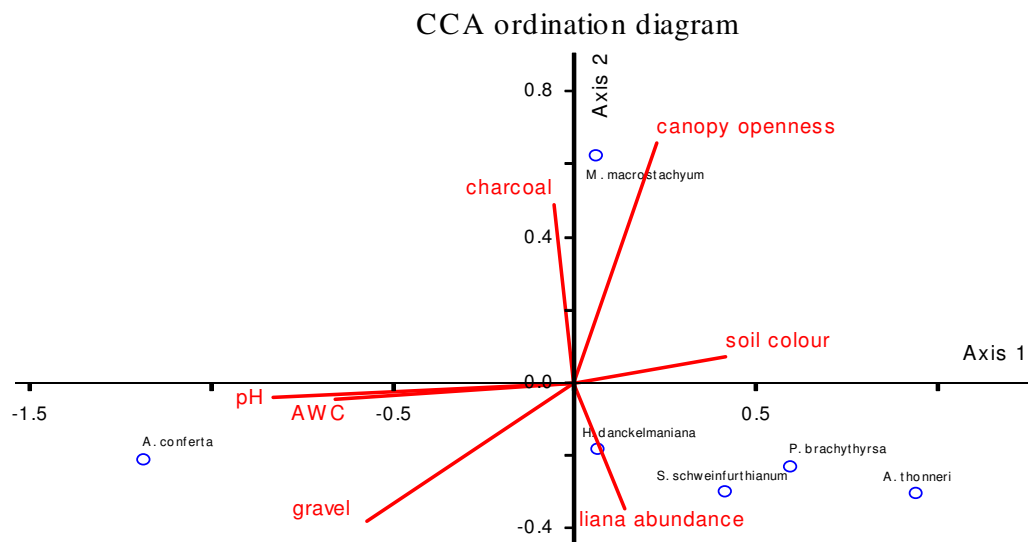
Table 2.6 Canonical coefficients and intraset correlations for 9 environmental variables

Variable	Canonical coefficients			Intraset correlations		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
microtopography	0.011	0.037	0.090	-0.085	0.039	0.023
pH	-0.523	0.070	-0.056	-0.828	-0.040	-0.151
soil colour	0.265	-0.182	0.477	0.418	0.075	0.519
AWC	-0.418	0.164	0.096	-0.659	-0.043	-0.035
charcoal abundance	-0.252	0.468	0.227	-0.056	0.491	0.072
canopy openness	0.051	0.661	-0.421	0.231	0.661	-0.465
liana abundance	0.193	-0.614	-0.453	0.140	-0.343	-0.629
tree basal area	-0.166	-0.103	0.380	-0.162	-0.174	0.604
soil gravel content	-0.180	-0.333	-0.104	-0.568	-0.380	-0.178

Despite the low amount of community variance explained (21.3% by the first two axes), meaningful patterns in species distribution were recognised. These were most strongly related to soil characters and disturbance characters. The ordination diagram

(Figure 2.8) shows that the first axis is a soil gradient on which higher pH sites have a redder soil with higher gravel content, and higher AWC (more clay). The correlations of the second axis show that places with more canopy openness have higher charcoal abundance. Liana count was negatively related to canopy openness, which can likely be attributed to the way that canopy openness was measured with the canopy-scope. Liana tangles often formed a dense canopy over a plot resulting in low canopy openness values even though the tree canopy may have been open. Also lianas were frequently abundant near the bases of large trees that served as their supports.

Figure 2.8 CCA ordination diagram of herb species and environmental variables. Species points are represented by circles. Environmental variables with canonical coefficients >0.200 are represented by red lines.



Soil characteristics that were correlated with axis 1 account for the greatest separation in the weighted averages of herb species. *A. conferta* mainly occurred on reddish-brown, clayey soils of high pH and high gravel content. Those on the right side of the diagram (*Aframomum thonneri*, *P. brachythyrsa*, and *S. schweinfurthianum*) were more closely grouped along the first axis. They were more abundant on yellowish-brown, sandy soils with lower pH and AWC. These herb species appear to exhibit a degree of niche differentiation along gradients in soil characteristics. However, they were not separated out at all by the second axis. *H. danckelmaniana* was located close

to the centre of the ordination diagram, which could be interpreted either as having its optima there or being uncorrelated with either of the axes. *M. macrostachyum* also occurred in the middle of axis 1, which indicated that it either preferred intermediate soil types or had no correlation with any soil characteristics. It was, on the other hand, more strongly associated with higher canopy openness and charcoal abundance (axis 2) than the other species. *M. macrostachyum* appeared highly correlated with disturbance variables and its abundance may therefore indicate areas with previous disturbance.

2.3.4 Binary logistic regression

M. macrostachyum

For *M. macrostachyum*, canopy openness and charcoal abundance were the best predictors of *M. macrostachyum* presence, and all competing models include these two variables. Competing models are shown in Table 2.7. The best model supported the results of the CCA analysis which also showed canopy openness and charcoal abundance as the two variables most related to *M. macrostachyum* abundance. *M. macrostachyum* also showed a slightly positive correlation with AWC, and a negative relationship with soil gravel content. The odds ratio (Exp (β)) of the model suggests that liana count was not significantly related to *M. macrostachyum* presence and closer examination of scatter plots of the data show the relationship to be spurious. Therefore, liana count was excluded from the final model, and model 4 was selected (Table 2.7).

The model predicted 76% of presences/absences correctly out of 100 sample plots. 85.7% of presences and 59.5% of absences were correctly classified by the model. Hosmer and Lemeshow goodness-of-fit test showed that the model predictions did not differ significantly from the observations ($\chi^2=8.342$, $df=8$, $p>0.05$). The null hypothesis that the coefficients of all terms in the model, except the constant, were zero was rejected ($\chi^2 = 32.70$, $df=4$, $p<0.001$) (Omnibus test of model coefficients).

Table 2.7 Competing models for logistic regression of *M. macrostachyum* presence/absence on environmental variables. Akaike information criteria (AIC) was used to choose the most parsimonious model. The best models are shaded.

Competing models:	-2 log likelihood	no. of parameters	AIC
1) Constant + canopy openness	116.856	2	120.856
2) Constant + canopy openness + charcoal abundance	109.613	3	115.613
Constant + canopy openness + charcoal abundance +			
3) AWC + gravel + liana count	96.530	6	108.530
4) AWC + gravel	99.091	5	109.091
5) AWC + gravel + liana count + tree ba	95.841	7	109.841
6) AWC + gravel + liana count + tree ba + pH	94.892	8	110.892
7) gravel + liana count	101.680	5	111.680
8) AWC + gravel + liana count + tree ba + pH + soil colour	94.699	9	112.699
9) All variables	94.663	10	114.663

Table 2.8 Environmental variables retained in the logistic regression model of *M. macrostachyum* presence/absence along with their coefficients, standard error, Wald statistic and significance, odds ratio ($\text{Exp}(\beta)$), and confidence intervals.

Variables in the equation	Coefficient			95% CI of $\text{Exp}(\beta)$				
	β	S.E.	Wald	df	Sig.	$\text{Exp}(\beta)$	lower	upper
Canopy openness	1.924	.598	10.362	1	.001	6.845	2.122	22.083
Charcoal abundance	.602	.196	9.469	1	.002	1.826	1.244	2.681
AWC	.019	.009	4.156	1	.041	1.019	1.001	1.039
Gravel content	-6.024	2.514	5.743	1	.017	.002	0.000	0.334
Constant	-1.397	1.053	1.759	1	.185	.247		

Haumania danckelmaniana

Binary logistic regression clarified the ambiguous results of the CCA for this species, which was located in the centre of the CCA ordination diagram. Several closely competing models for *H. danckelmaniana* were identified using Akaike information criteria (Table 2.9). All of the models included soil colour and gravel content as predictors of *H. danckelmaniana* presence. AIC included canopy openness, liana count, and tree basal area as factors needed to create the most parsimonious model.

However, the odds ratios suggested that only soil colour and gravel content were significant predictors of *H. danckelmaniana* presence (Table 2.10).

Table 2.9 Competing models for logistic regression of *H. danckelmaniana* presence/absence on environmental variables. Akaike information criteria (AIC) was used to choose the most parsimonious model. The best models are shaded.

Competing models:	-2 log likelihood	no. of parameters	AIC
1) Constant + soil colour + gravel	120.960	3	126.960
<u>Constant + soil colour + gravel +</u>			
2) canopy openness + liana count + tree ba	112.132	6	124.132
3) canopy openness + liana count	114.629	5	124.629
4) canopy openness + liana count + tree ba + charcoal	110.662	7	124.662
5) canopy openness + liana count + tree ba + charcoal + pH	109.016	8	125.016
6) canopy openness + tree ba	115.513	5	125.513
7) liana count + tree ba	115.911	5	125.911
8) all variables	106.384	10	126.384
9) canopy openness	119.017	4	127.017

Table 2.10 Environmental variables suggested for the most parsimonious logistic regression model of *H. danckelmaniana* presence/absence using AIC. Coefficients, standard error, Wald statistic and significance, odds ratio (Exp(β)), and 95% confidence intervals for the odds ratio are presented.

Variables in the equation	Coefficient β	S.E.	Wald	df	Sig.	Exp(β)	95% CI	
							lower	upper
Soil colour	-.295	.142	4.331	1	.037	.745	.564	.983
Gravel content	-3.378	1.537	4.832	1	.028	.034	.002	.693
Tree basal area	1.101	.593	3.449	1	.063	3.007	.941	9.609
Canopy openness	-1.443	.806	3.204	1	.073	.236	.049	1.147
Liana count	.811	.527	2.373	1	.123	2.251	.802	6.321
Constant	2.616	1.487	3.094	1	.079	13.687		

Model 1 was able to assign 70% of *H. danckelmaniana* presences and absences correctly. It correctly assigned 90.8% of the presences and 31.4% of the absences. Hosmer and Lemeshow goodness-of-fit test showed that the model predictions did not differ significantly from the observations ($\chi^2=2.566$, $df=3$, $p>0.1$). The model coefficients were significantly different from zero for model 1 ($\chi^2=8.530$, $df=2$, $p<0.05$, Omnibus test of model coefficients).

Both soil colour and gravel content were negatively related to *H. danckelmaniana* presence, indicating that *H. danckelmaniana* was most likely to occur in reddish-brown soils without gravel. These two soil variables are slightly correlated, with gravel occurring mostly in soils of reddish colour. This may reduce the apparent effect of soil colour on *H. danckelmaniana* presence. Canopy openness, tree basal area, and liana count may have some effect on *H. danckelmaniana* presence, but graphs of individual variables against species presence or absence indicated that the relationship with basal area and liana count was spurious. Canopy openness may have a slight negative association with *H. danckelmaniana* presence.

Ataenidia conferta

All competing models identified with AIC included pH as a significant predictor of *A. conferta* presence/absence (Table 2.11). Soil colour was also an important predictor which was shown to be significant in the model (Table 2.12). *A. conferta* was strongly associated with increased soil pH and reddish colour. These results concur well with the CCA analysis. Although AWC appeared in the most parsimonious AIC model, it was not a significant factor in the logistic regression. This may be due to the correlation of soil variables, and therefore AWC should be considered a potential predictor of *A. conferta* presence. Relationships with microtopography and tree basal area were examined by plotting the probability of *A. conferta* presence against both of the variables (graphs not shown). Results indicated that their effect on the model was spurious.

Table 2.11 Competing models for logistic regression of *A. conferta* presence/absence on environmental variables. Akaike information criteria (AIC) was used to choose the most parsimonious model. The best models are shaded.

Competing models:	-2 log likelihood	no. of parameters	AIC
Constant +			
1) pH + soil colour + AWC	85.121	4	93.121
2) pH + soil colour	87.221	3	93.221
3) pH + soil colour + AWC + microtopography + tree ba	81.913	6	93.913
4) pH + AWC	90.836	3	96.836
5) pH	93.701	2	97.701
6) all variables	81.461	10	101.461

Table 2.12 Environmental variables retained in the logistic regression model of *A. conferta* presence/absence along with their coefficients, standard error, Wald statistic and significance, odds ratio ($\text{Exp}(\beta)$), and confidence intervals.

Variables in the equation	Coefficient β	S.E.	Wald	df	Sig.	Exp(β)	95% CI	
							lower	upper
pH	3.035	.939	10.455	1	.001	20.806	3.305	130.976
Soil colour	-.376	.163	5.298	1	.021	.687	.499	.946
Constant	-13.050	4.420	8.717	1	.003	.000		

Model 2 was selected as the final model. It correctly assigned *A. conferta* presence/absence in 83% of sample plots. However, only 45.8% of presences were correctly assigned, although 94.7% of absences were predicted. The model coefficients were significantly different from zero ($\chi^2=22.995$, $df=2$, $p<0.001$). The final model was not significantly different from the observations (Hosmer and Lemeshow goodness-of-fit test $\chi^2=7.011$, $df=8$, $p>0.1$).

Aframomum thonneri

Results of the logistic regression for *Aframomum thonneri* indicate that pH is the primary predictor of its presence/absence (Table 2.13). Canopy openness was also found to be a significant factor in the model. Although AWC was included in the ‘best’ model, the odds ratio was not significant, thus it was excluded from the final model (Table 2.14). Again, this may be due in part to the correlation between pH and AWC, so AWC should be considered a potential predictor of *Aframomum thonneri* presence.

Table 2.13 Competing models for logistic regression of *Aframomum thonneri* presence/absence on environmental variables. Akaike information criteria (AIC) was used to choose the most parsimonious model. The best models are shaded.

Competing models:	-2 log (L)	no. of parameters	AIC
Constant +			
1) pH + canopy openness + AWC	77.023	4	85.028
2) pH + canopy openness	79.089	3	85.089
3) pH	87.238	2	91.238
4) all variables	72.676	10	92.676
5) canopy openness	99.846	2	103.846

Aframomum thonneri is strongly correlated with acidic soils. This is also shown by its appearance on the far right side of the CCA ordination diagram in Figure 2.8 (p. 39). In addition to soil acidity, increasing canopy openness was also a good predictor of *Aframomum thonneri* presence. However, the CCA ordination diagram did not show this relationship at all.

Table 2.14 Environmental variables retained in the logistic regression model of *Aframomum thonneri* presence/absence along with their coefficients, standard error, Wald statistic and significance, odds ratio (Exp(β)), and confidence intervals.

Variables in the equation	Coefficient β	S.E.	Wald	df	Sig.	Exp(β)	95% CI	
							lower	upper
pH	-6.695	1.973	11.513	1	.001	.001	.000	.059
canopy openness	1.724	.639	7.289	1	.007	5.608	1.604	19.608
Constant	26.900	8.321	10.452	1	.001	4.8E+11		

A test of the model coefficients shows them to be significantly different from zero ($\chi^2=26.293$, $df=2$, $p<0.001$). The model correctly predicted 83% of observations; 36.4% of presences and 96.2% of absences. The Hosmer and Lemeshow goodness-of-fit test indicated that the predictions for the presence/absence of *Aframomum thonneri* were not significantly different from observed values ($\chi^2=9.10$, $df=8$, $p>0.1$).

Sarcophrynium schweinfurthianum and *Palisota brachythyrsa*

For *S. schweinfurthianum* and *P. brachythyrsa*, the logistic regression ceased to provide satisfactory models. In both cases, the best model failed to predict any of the species presences, but rather, predicted that the species would be absent from all plots. For both species, this resulted in 88% of plots being correctly predicted as having absences. Thus the models were sufficient to provide ‘significant’ results, though they were somewhat unhelpful. Although pH is shown to be a significant predictor for both *S. schweinfurthianum* and *P. brachythyrsa*, it may be that the species optima were at an intermediate range of the pH values measured for this study. This creates a non-linear response curve that logistic regression cannot detect. Therefore, CCA is a more suitable analysis to predict the responses of these species.

2.4 Discussion

2.4.1 Critique of data analysis techniques

CCA and binary logistic regression proved to be complementary data analysis techniques for this complex set of ecological data. CCA was able to distinguish that the herb species in the Ndakan study area responded differently to a suite of environmental variables, and it portrayed that relationship in an easily interpretable diagram (Figure 2.8). Its strength was in predicting the distribution of species which could not be predicted well using binary logistic regression, such as *S. schweinfurthianum* and *P. brachythyrso*. CCA failed to identify the relationship between *Aframomum thonneri* and canopy openness, which was picked up in the logistic regression. This illustrates the two techniques are complimentary and the need to confirm results using different types of tests.

However, neither analysis dealt well with species that appeared infrequently in the sample plots. Species which appeared in less than approximately 10% of plots seemed to result in unreliable analyses. Species which occurred infrequently and were not correlated with any of the measured environmental variables tended to distort the CCA ordination by appearing at extreme ends of the axes. However, this also depended on the strength and shape of the relationships between the species and the predictor variables. Species which had stronger relationships to predictor variables, and had their optima near the end of an environmental gradient could still be adequately modelled by both methods (e.g. *Aframomum thonneri*). It is important to be aware of which species may cause this kind of distortion and remove them from the CCA analysis.

2.4.2 Distribution of herbs

Megaphrynium macrostachyum

Results show that the most significant habitat variables explaining *M. macrostachyum* presence were canopy openness and charcoal abundance. Soil factors did have an effect on *M. macrostachyum* distribution as well, with both AWC and gravel being

significant predictors in the logistic regression. The weak correlation with AWC was only slightly significant, but *M. macrostachyum* was strongly negatively correlated with soil gravel content. In the CCA, *M. macrostachyum* appeared towards the centre of axis 1 (Figure 2.8, p.39), indicating that although its abundance was strongly dependent on canopy openness and charcoal, it may have had its optimum at soils of intermediate AWC. However, the soils in this study were divided primarily between higher AWC, clay and clay loam soils and low AWC sandy soils. There were very few soil samples of ‘intermediate’ AWC value (60-90 mm m⁻¹, Figure 2.2). This suggests that perhaps the relationship with AWC was spurious, and that the negative relationship with gravel may have produced the distribution patterns observed by Fay (1997). Rather than being associated with primarily with sandier soils, *M. macrostachyum* may simply not be present in soils containing gravel, which were found only in samples in the western half of the study area.

The strong correlation of *M. macrostachyum* distribution with canopy openness and charcoal abundance indicates that it depends on some type of forest disturbance to establish. These results might perhaps be explained by small-scale tree-fall gaps or lightning fires that have opened up the canopy sufficiently for *M. macrostachyum* to temporarily establish. However, the depth at which the charcoal was found would suggest that the fires that produced the charcoal were generally not recent. When the discovery of pottery is also taken into account, a scenario emerges of a large-scale, past disturbance, such as slash and burn agriculture, which may have opened up large parts of the forest. The abundant *M. macrostachyum* in the forest today may have originated at that time and slowed the subsequent regeneration of trees. In such a case, the high canopy openness associated with *M. macrostachyum* may be a result of *M. macrostachyum* presence, rather than *M. macrostachyum* presence being a result of canopy openness.

Contrary to expectation, tree basal area was not associated with *M. macrostachyum* presence. Also there was no correlation between canopy openness and tree basal area. This is perhaps explained by an observation of Gibert (1984) in describing the formation of secondary forests from slash and burn agriculture. He observed that when people cut forest to establish fields that they often left very large trees which

were too large or difficult to cut or burn. Thus secondary forest often contains several trees of very large size. Also, the penetration of lateral light can produce understorey light environments under tall forest canopy that are equivalent to gap light environments (Clark *et al.* 1996). This scenario may explain the lack of expected correlation between *M. macrostachyum* abundance and tree basal area.

Other herb species

Of all the other abundant herb species in the Ndakan study area apart from *M. macrostachyum*, only *Aframomum thonneri* exhibited a correlation with canopy openness. This is consistent with observations of several *Aframomum* species occurring in dense patches at the edges of large swampy clearings within the forest, along logging roads, and as secondary vegetation in fallow agricultural land in other areas of central African forest (Bullock 1981, Dhetchuvi 1996). However, the distribution of *Aframomum thonneri* in this study was still primarily determined by soil pH. There are 16 species of *Aframomum* in the Dzanga-Sangha Dense Forest Reserve (Harris 2002). Several species often occur together in dense patches, such as *Aframomum thonneri* and *Aframomum limbatum*. Results from this study indicate that differential distributions along soil gradients may be one mechanism by which so many congeneric species of *Aframomum* co-exist in this forest.

The distributions and abundances of *H. dancklemaniana*, *A. conferta*, *S. schweinfurthianum*, and *P. brachythyrso* were correlated primarily with soil pH, colour, gravel content or AWC. None of these species form patches in the Ndakan study area. Only *S. schweinfurthianum* has been reported to be a major constituent of Marantaceae forests in other parts of central Africa, particularly in the Odzala Reserve, Congo (Maisels 1999, Maley 1990). These results suggest that it is limited at Ndakan either by soil conditions or some other factor not measured in this study. None of these four species was correlated with disturbance variables.

2.5 Conclusions and opportunities for further research

Data on the distribution of ground herbs in the Ndakan study site confirm that *M. macrostachyum* is associated primarily with disturbance variables, unlike most of the

other understorey herbs surveyed. The important question emerging from this work is whether or not the *M. macrostachyum* patches in the Ndakan study area are remnants from a previous large-scale disturbance which opened up the forest canopy. Its association with underground charcoal and lack of correlation with any of the measured soil variables suggests that this may be the case. If so, what is the scale of disturbance necessary for herb patch formation? The dynamics of herb patch formation and persistence are probably dependent on the extent of the disturbance, the dynamics of forest regeneration and the competitiveness of the herb species. These ideas will be addressed in later chapters.

The size of the study area and number of stratified random points should be sufficient to generalise these results throughout the larger forest block. However, most, if not all, of the Ndakan study site may have been affected by widespread disturbance in the recent or distant past. A wider-scale study looking at the same variables over a distance of tens to hundreds of kilometres may give a better picture of the factors influencing *M. macrostachyum* distribution and highlight other ecological gradients that may be significantly correlated. This information is likely to be useful in predicting the likelihood of *M. macrostachyum* patch formation in different areas and under different disturbance regimes.

Another interesting question emerging from this study is why *S. schweinfurthianum* and *A. conferta* are constituents of Marantaceae forests in other parts of central Africa and not in the Dzanga-Sangha Dense Forest Reserve. Indeed, why does the composition of Marantaceae forest differ throughout central African countries? These results suggest that environmental factors such as nutrient or water limitation may limit the ability of different herb species to respond to disturbance. Further studies should compare the ecology and species interactions within different types of Marantaceae forests in order to determine the causes of certain species associations.

3 Climate change and prehistoric human disturbance in Central African rain forests

3.1 Introduction

It is increasingly evident that African ecosystems were affected by rapid climate fluctuations and anthropogenic disturbance in the Holocene (Hamilton 1991, Elenga *et al.* 2000). For the dense forests of the lowland Congo Basin however, extremely little is known about the extent of climate-induced vegetation change or the impacts of prehistoric human settlement on modern forest structure. The purpose of this chapter is to examine the possibility that *M. macrostachyum* patches are a prolonged successional stage resulting from the effects of previous anthropogenic disturbance or climate change.

3.2 Background

3.2.1 Climate change in Late Quaternary Africa

Data available from research on African geomorphology, palynology, and ocean sediments shows that tropical forests were subject to strong climatic fluctuations throughout the Quaternary, which repeatedly altered the character and extent of the forest. The Quaternary was marked by approximately 20 'ice ages' where montane forests descended to lower elevations and savannas spread towards the equator (Hamilton 1991). These long periods were interspersed by shorter periods when forests were able to re-develop. In the upper Quaternary for example, the Maluekian period 70,000 - 40,000 years Before Present (BP), is believed to have been relatively dry with extensive deforestation. This was followed by the shorter Njilian period from 40,000 to 30,000 BP which was characterised by higher precipitation and reforestation. The Léopoldian period, 30,000 – 12,000 BP coincided with the Last Glacial Maximum of the northern latitudes (Eggert 1993, Maley 1993). Analyses of fossil pollen data from sites in East Africa, compared to modern pollen and climate data, show that during the last glaciation the climate changes were quite severe, with inferred temperature decreases of around 4-8° C accompanied by decreases in rainfall of approximately 30% (Bonnefille *et al.* 1990, Grove 1993, van Zinderen Bakker and

Coetzee 1988). As the Léopoldian reached its maximum ca. 18,000 BP, forests were drastically reduced, montane vegetation descended several hundred metres below its present level, and savannas covered much larger reaches of the Congo basin than today (Eggert 1993, Elenga *et al.* 1994, Hamilton 1991, Maley 1991, Vincens *et al.* 1999). As temperature and humidity increased towards 12,000 BP during the Kibangian phase, forests began recolonising savanna areas, reaching their maximum extent ca. 4000 BP (de Maret 1985, Maley 1993, Grove 1993).

Despite general agreement as to the effects and timing of these climatic fluctuations for Africa, precise data are available for only a handful of sites (van Zinderen Bakker and Coetzee 1988). At present, much of the palynological data available for Central Africa is from montane or savanna/woodland regions where slight fluctuations in climate are more likely to result in obvious vegetation changes. This may lead to an overestimate of these effects for the rest of the lowland Congo Basin where perhaps conditions were more stable. Several areas have been identified which appeared to have retained forest cover during the last major dry period and these have been labelled as forest 'refuges' (Maley 1991, Nichol 1999). However, knowledge of refugia sites at the present time is based on generalisations from a few well-studied areas and the true extent and severity of forest retreat is unknown for much of the Congo Basin.

There is strong evidence that Central Africa underwent further, rapid climate fluctuations and vegetation changes over the last three to four millennia (Maley 1992, Vincens *et al.* 1998, Vincens *et al.* 1999). The exact timing of these fluctuations appears to have varied from area to area and also depends on the methods used to detect it. Lake level changes that correspond to moisture levels show a regression between 4500-3000 BP indicating a drier period at this time in Ghana and in subtropical areas (Grove 1993). Using palynological techniques in swamps and lakes of the Atlantic equatorial region, an arid event was detected from ca. 3000 – 2000 BP (Vincens *et al.* 1998, Zogning *et al.* 1997, Elenga *et al.* 1994). For some areas of Central Africa this short, dry period caused the retraction of forest boundaries and the reopening of savannas that were thought to have been widespread during the Léopoldian period. Distinct features of the modern vegetation landscapes, in particular

secondary open grasslands and enclosed savannas of Congo and Gabon may be due to such recent changes (Schwartz *et al.* 1995, Vincens *et al.* 1994). The return of wetter conditions between 1900-700 BP may have allowed forests to re-develop throughout Central Africa, often in spite of human impacts, to reach their current extent and appearance (Vincens *et al.* 1999, Reynaud-Farrera *et al.* 1996, Maley 1992).

3.2.2 Human settlements

In addition to climate change, prehistoric human activities may have had an important influence on vegetation patterns. The immensity of the Congo Basin rain forest, 2500 km east-west and 1600 km north-south, was once perceived by scientists as a ‘transcontinental barrier’ to human settlement and migration (Eggert 1993). However, there is now evidence of human settlements in the Lopé region of Gabon dating back at least 60,000 BP (Oslisly and Peyrot 1992). Middle Stone Age lithic tools from Congo confirm that people had been present there at 20,000 – 18,000 BP (Lanfranchi *in de Maret* 1985). Both of these sites date within ‘glacial’ periods and were probably cooler and drier than now. It is very likely therefore that these areas were at least partially covered by savannas, although the exact landscapes used by people remain unknown.

As early as 3600 years ago, Neolithic groups are known to have reached central Gabon, which is now savanna-forest mosaic. There is also evidence that iron metallurgists arrived in the same region at around 2600 BP, spreading more rapidly and superseding the Neolithic groups (Oslisly and Fontugne 1993). The rapid expansion of Iron-age cultures as compared to Neolithic cultures may be due to climate-driven contraction of forests that facilitated migrations of people into the region. Alternatively, people living in or near remaining forests could have caused vegetation change in areas that otherwise might have been buffered from the more severe effects of climate fluctuations. In the Grass Fields of Cameroon, radiocarbon dates of charcoal indicate that human intervention within the forests dates back to 3000-2900 BP and has intensified since ca. 1000 BP, even after the return of wetter conditions (Kadomura 1984). Iron production demanded large amounts of fuel wood for the kilns, and provided more effective tools for forest clearance (Hall 1996, Oslisly and Dechamps 1994). Forest dwellers may have had lasting impacts on their

environment by their direct effects on the soil and vegetation or by the introduction of species such as the oil palm.

3.2.3 Significance of the oil palm

The oil palm, *Elaeis guineensis*, is a tree indigenous to Africa. Fossil oil palm pollen has been discovered in West Africa dating back to the Eocene, approximately 50 million years ago (Zaklinkaya and Prokofyev 1971 in Maley 1998), and fossilised remains of the endocarp found in Uganda have been dated to 6 million years BP (Ergo 1997). The earliest record of oil palm pollen in western Equatorial Africa is from SW Cameroon at around 8000 BP (Maley and Brenac 1998), much later than its appearance in East or West Africa. The oil palm occurs mainly throughout the lowland forest zones of western Central and West Africa, preferring sites that are warm, moist, close to water, and sufficiently open. It is a pioneer tree that is resistant to fire (Swaine and Hall 1983) and germinates more readily in burnt forest (Hawthorne 1995). It grows naturally in river valleys, savanna forest mosaic, swamp forest, and in secondary forests or forest edges (Letouzey 1978, Maley and Brenac 1998, Sowunmi 1999, Tuley 1995). In Cameroon, Letouzey (1978) described a naturally occurring belt of *Elaeis* trees more than 150 km long and 10 – 20 km wide, following the edge of the rain forest. However, it is almost always associated with human activity, where it thrives on cultivated land, allowing it to extend its range to more diverse environmental conditions (Hawthorne 1995).

The reason for its widespread success today is because of its economic importance as a crop both for domestic and commercial consumption. The most important use is the processing of the fruit for oil. Oil is pressed from both the soft pericarp and the hard kernel that is a staple for cooking, as well as being used for medicinal and cosmetic purposes. The tree itself is tapped to make an alcoholic drink (palm wine), and also is used for fuel and building materials. Today oil palm products are utilised throughout Central Africa, but in traditional settings it is not actively cultivated on a large scale. Rather, it propagates quite easily from discarded seeds (Eggert 1993).

The first evidence of human exploitation of oil palm seeds and fruits is from Bosumpra cave in Ghana approximately 5300 BP (Stahl 1993). Dependence on the

fruit may have led to its deliberate introduction to other sites in Central Africa, but this point is very much under debate. There is still no certainty about whether oil palm spread naturally to suitable environments or was planted by people (Eggert 1993). Existing palynological studies in West and Central Africa imply that the upsurges in oil palm pollen in the late Holocene as compared to earlier records were due to both natural and human factors. Sowunmi (1999) suggests that an increase in oil palm pollen indicates methods of land use favourable to its expansion, perhaps cultivation, though not necessarily cultivation of the oil palm itself. Combined with archaeological evidence of synchronous human occupation, pollen data show that it is likely that humans contributed to the expansion of oil palm in Central Africa (Elenga *et al.* 1992, Sowunmi 1999, Vincens *et al.* 1999).

It is of significant interest that in several places with prehistoric remains of oil palm, the modern forest supports no natural populations of the tree (Sowunmi 1999). In the Okomu Forest in Nigeria for example, an extensive layer of charcoal, pottery, and palm nuts dated to c. 1300 AD were found beneath mature mahogany forest (Jones 1955, White and Oates 1999). Systematic surveys in the dense forests of northern Republic of Congo and southwestern Central African Republic by Fay (1997) have turned up over 100 sites, including one near Ndakan, containing oil palm seeds that have been dated between 2340 and 990 years BP. These sites may have been ancient villages because oil palms do not occur naturally in the Nouabale-Ndoki National Park today. The distribution of dates show that oil palm frequencies increased until about 1700 BP and thereafter decreased until they disappeared ca. 1000 BP. This suggests that there was sufficient opening of the forest as to allow the proliferation of oil palm in the area for over a millennium.

3.2.4 Forest regeneration and Marantaceae

The structure and composition of a forest today may provide useful clues about the past if the specific processes of succession are understood. Where forest has been disturbed or destroyed, a typical successional pathway begins with the arrival of pioneer trees and shrubs that are then gradually replaced by climax forest species (Connell and Slatyer 1977). However, alternative pathways may develop that differ in species composition and behaviour from the normal successional route. Rather than

facilitate succession, early colonisers may delay forest regeneration for an extended period, or permanently change the climax vegetation community. The factors controlling the species composition of early succession are varied and perhaps stochastic. Site effects, climate change, and the type of disturbance all play an important role in determining the course of succession. Land uses such as shifting cultivation can have long lasting residual effects on soil nutrients, texture, and organic matter which can alter species composition (Kochummen and Ng 1977, Lawrence and Schlesinger 2001, Mesquita *et al.* 2001).

In the Brazilian Amazon, liana-rich forests which cover ca. 100,000 km² are thought to be late successional forests resulting from prehistoric anthropogenic settlements and shifting cultivation (Balee and Campbell 1990, Charles-Dominique *et al.* 1998). Heavy liana loads may weigh down woody stems, deforming them and reducing vigour. This in turn will increase the likelihood of future treefalls, bringing down multiple trees that are connected by lianas. Lianas easily survive this and are additionally favoured by the increased light and support structures (Uhl *et al.* 1988a). There are many examples of plant species which thrive on disturbed, degraded land, often forming monodominant persistent thickets, such as heath forest in Singapore (Sim *et al.* 1992), bracken in the U.K. (Marrs *et al.* 2000), gray dogwood in the U.S.A. (Dickinson *et al.* 1993), and *Dicranopteris linearis* in Hawaii (Russell *et al.* 1998).

As described in chapter 1, Marantaceae can be one of the main components of forest regeneration after treefalls, logging, and shifting cultivation in Central Africa. A model of long-term forest succession for Central African rain forests has been proposed by White (1992) for the Lopé Reserve in Gabon. At the Lopé Reserve, savanna isolates within the rain forest are thought to be remnants of more widespread savannas present during one of the last dry climatic phases. White hypothesised that as the climate became more humid, the forest began to spread out from its riverine refuges following several similar patterns of succession, gradually reducing the savannas to their present boundaries. He presented species compositions for seven major stages of this succession, two of which were different types of Marantaceae forest. The model is useful in that it allows Marantaceae forest types to be linked to past climatic change, but what cannot be determined from current vegetation studies is

the overall length of this process and the persistence of each stage. The abundance of Marantaceae forests in Central Africa may be prolonged successional stages where forest has been affected by climate change or anthropogenic disturbance.

The rather open forest at the Ndakan study site, containing many light demanding or secondary species such as *Myrianthus arboreus*, *Celtis adolfi-frederici*, dense liana tangles, and many *M. macrostachyum* patches, may still be in the process of recovering from some form of past forest loss. The amount of current rainfall at Ndakan (approx. 1500 mm y⁻¹) is similar to current rainfall at two sites in Congo that showed a change from forest to grassland or enclosed savanna between 2500–3000 BP (Vincens *et al.* 1999). The savannas only persist in those areas because of annual burning by humans. If this climate fluctuation affected the Ndakan area in a similar way then it is probable that forest vegetation disappeared from large areas and persisted only adjacent to rivers. Lack of continued human interference would have allowed the forest to regenerate as the climate became more humid since 2500 BP.

The discovery of ancient potsherds and charcoal in soil pits described in chapter 2 provide an indication that human settlements may have been one of the factors determining modern forest structure at Ndakan. The potsherds are direct evidence of human activity in the area. Luminescence dating can be done on quartz crystals in objects that have been fired, and does not require that they be in archaeological context. Therefore, potsherds were luminescence dated in order to; i) determine the antiquity of the potsherds, ii) determine whether the dates coincided with the dates of the oil palm deposits near Ndakan, iii) estimate the length of time that the forest may have been recovering and therefore the persistence of intermediate stages of succession i.e. *M. macrostachyum* patches, iv) try to place the artefacts in context with other archaeological records in the region.

3.3 Methods

3.3.1 Luminescence dating

Luminescence is the release of stored energy in mineral crystals, by heating or illumination, which was built up from natural radioactivity in the ground. Suitable

material for luminescence dating (sand or silt-sized grains of quartz and feldspar) is usually ubiquitous in pottery. When pottery is fired, stored energy in the crystal lattice of mineral grains is removed, resetting the grains effectively to zero. When the pottery is buried, the crystals begin to build up new energy from ionising radiation of the surrounding earth. Thus the amount of energy depends on the environmental dose rate (Gray (Gy)/time) and the elapsed time since burial (dosing period).

When artificially stimulated with light or heat the amount of light emitted by the quartz crystals (equivalent dose) is proportional to the total absorbed radiation dose. The equivalent dose (D_e) is measured in units of Gy. The equation for calculating the age of a sample is therefore:

$$\text{Duration of dosing period (age, years)} = D_e \text{ (Gy)} / \text{dose rate (Gy/1000 yrs)}$$

Potsherds from Ndakan were taken to the Luminescence Dating Laboratory in the Research Laboratory for Archaeology and the History of Art, University of Oxford. All analyses were performed by experts in the Dating Laboratory. Potsherd samples were broken in two and quartz grains drilled out from the broken surfaces for analysis by Optically Stimulated Luminescence (OSL) using the post-IR Blue technique (Banerjee *et al.* 2001).

Dose rate can be measured from samples of surrounding soil, but because of limited funding the environmental dose rate was not calculated. Rather it was roughly approximated by a luminescence dating expert to 1.5 – 3 Gy/ka, based on measured environmental dose rates from Britain (Barnett 2000). The equivalent dose was measured by OSL and averaged for three grains per sample.

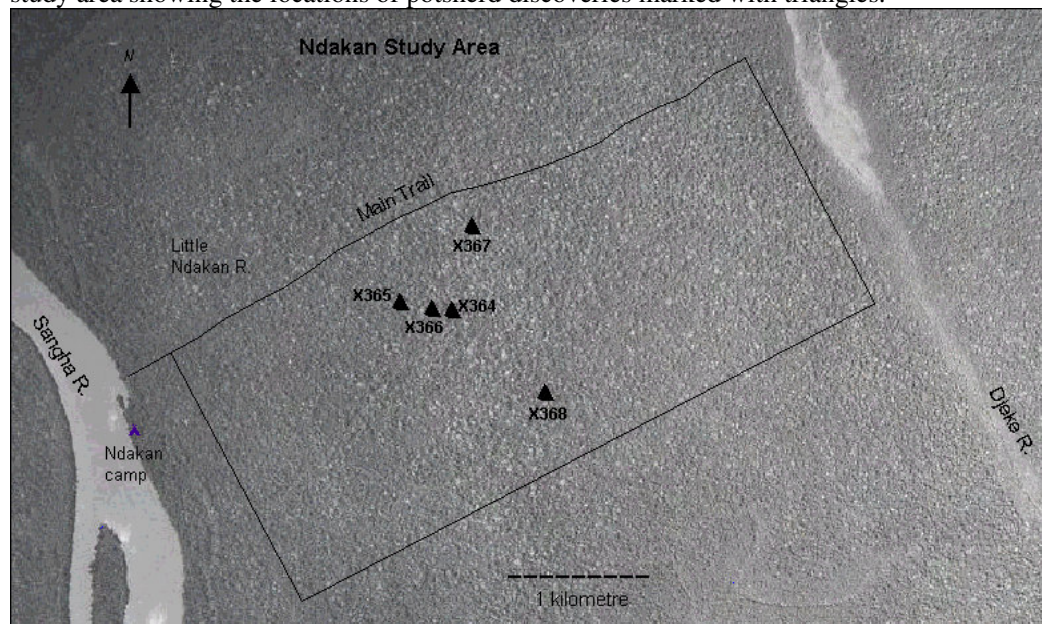
3.4 Results

3.4.1 Distribution and description of potsherds

Figure 3.1 is a map of the study area with locations of the potsherds. The potsherds came from three general locations within the study site. X364, X365, and X366 were

within a 250 m radius of each other. X367 was located roughly 700 m to the north. X368 was farther away, approximately 1 km to the southeast.

Figure 3.1 Map made using aerial photographs (ORSTOM, taken in 1962) of the Ndakan study area showing the locations of potsherd discoveries marked with triangles.



The potsherds were too fragmented to be able to determine pot morphology, and only one potsherd contained slightly visible designs. The fragments are generally a rough texture from weathering with black or reddish surfaces. Some are slightly curved. Figure 3.2 is a photograph of some of the potsherds found. Photographs of all samples are included in the Appendix. All potsherd sites also contained 'common' amounts of charcoal (classification explained in chapter 2) except for site X366, where charcoal was rare. Of the four potsherd sites discovered in the sample plots, only one had a *M. macrostachyum* patch present. Approximately 2 km inland from the camp, just 300 m south of the main trail, a worked, blade-like quartz flake was found in a test pit with a small amount of charcoal, but it has not been dated. By itself it is not sufficient to determine the stone working technology of the culture.

Figure 3.2 Potsherds from sample X368

3.4.2 Dates

As described above, the environmental dose rate was not measured from surrounding soil samples, but was estimated to be 1.5-3 Gy per thousand years. Therefore only a very approximate age can be given for the pottery. It can be said that the pottery is of some antiquity, of a magnitude of several thousand years (see Table 3.1). X364 and X365 had fairly consistent dates within the three sub-samples (low standard error). Using the given approximation for the environmental dose rate, X364, X365, and X366 date to roughly 2000 y old. X367 and X368 were somewhat younger, probably around 600 y old.

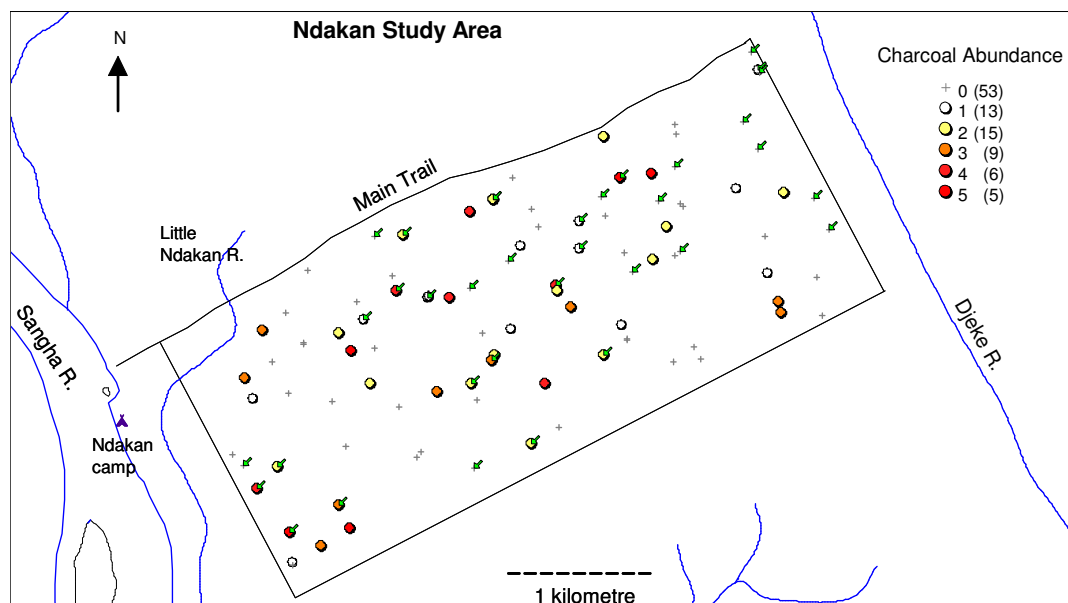
Table 3.1 Description of potsherds. Note that the approximate age range is calculated from an estimate of the environmental dose rate, without standard error (see text).

Potsherd no.	Ave. OSL reading Equivalent Dose (D_e) (Gy \pm SE)	Approx. age range (years BP) [not incl. SE]	Thickness (mm)	Designs present
X364	3.50 \pm 0.04	1100-2300	7.0-21.8	No
X365	4.24 \pm 0.19	1400-2800	8.8-10.0	No
X366	3.81 \pm 0.53	1200-2500	7.8-10.0	No
X367	1.39 \pm 0.99	460-920	10.1	No
X368	1.15 \pm 0.27	380-760	6.1-9.6	Yes

3.4.3 *Megaphrynium macrostachyum* patches and charcoal distributions

Charcoal was found in 47 out of 100 soil pits (Figure 3.3). Results from chapter 2 showed a significant association of *M. macrostachyum* presence with charcoal abundance. At each of the 100 plots surveyed in this study, *M. macrostachyum* patches were noted in addition to individual plants (Patches were defined as a cluster of >2 m tall *M. macrostachyum* plants over 5 m in diameter). A map of *M. macrostachyum* patch presence (as sampled in chapter 2) was overlaid with charcoal abundances in Figure 3.3. Although charcoal and *M. macrostachyum* patches do not overlap exactly, both are found together frequently.

Figure 3.3 Map of Ndakan study area with *M. macrostachyum* patch presence (from sample plots, chapter 2) marked by green arrows and charcoal abundance.



3.5 Discussion

3.5.1 Significance of pottery dates

Although precise measurements of the age of the pottery could not be made during this study, the antiquity of the potsherds offers important information for piecing together forest history at the Ndakan site. The most significant aspect of the potsherd discovery is that it contributes to evidence that Central African forests are not pristine

and that people were living near Ndakan at least 1400 years ago. The estimated range of dates of the potsherds coincides with the dates of oil palm nuts that were found by Fay (1997), strongly suggesting that in this region, humans were linked to the presence of oil palm. Palm nut deposits were found in southwestern C.A.R. and northern Congo dated between 2340 to 990 years BP. However, no oil palm nuts were found directly associated with pottery in the excavated pits. It is likely that this is due to the sampling strategy and the treatment of the palm fruits. Palm oil is generally processed in streams where water is used to float the oil (Fay 1997). Fay used the approach of walking along small streambeds searching for exposed palm nuts, so all of the palm nut deposits that he found were along watercourses. The sampling strategy of this study focused on an inland area away from most streams where village locations, if any, were entirely unknown. Palm nuts were found in two soil pits, but these were not associated with either charcoal or pottery. Had a known village site been excavated here it is almost certain that pottery and palm nuts would have been found together. At other similarly dated archaeological sites in Central Africa there is widespread evidence of the use of oil palm in connection with the presence of pottery (Eggert 1993).

3.5.2 Prehistoric peoples

The presence of potsherds at this site confirms prehistoric human presence in the area and provides useful data for comparison with other archaeological sites in central Africa. No iron artefacts were found in the Ndakan study area as evidence of iron smelting technology, but based on the closest archaeological sites of similar antiquity, the luminescence dates suggest that the makers of the older Ndakan pottery were likely to be either late Stone Age or early Iron Age peoples (de Maret 1985). By 2000 BP iron smelting was common west of the Sangha and Zaire rivers. The excavated sites of Pikundu-Mundu along the Sangha River and Likouala aux Herbes River in Congo contained pottery, stone tools, and iron slag, and dated between 2200 and 1980 BP (Eggert 1993). Further east however, the Batalimo (Maluba) complex on the Lobaye River in C.A.R. still remained Neolithic at 1600 BP (de Maret 1985, Vansina 1990). The younger potsherds from sample X368 and possibly X367 would almost certainly have belonged to Iron Age peoples.

The field of linguistics also provides clues to the migration patterns and cultural practices of early Congo Basin dwellers. Many independent groups of people throughout sub-Saharan Africa to southern Africa speak related languages (Vansina 1992). A sub-group of the Congo-Kordofanian language family is the Bantu language. The Bantu division shows remarkable similarity over its large range from West Africa through Central and into southern Africa (Phillipson 1993). The similarity of modern Bantu languages provides evidence that Bantu-speaking peoples expanded from Nigeria over the last several thousand years. At approximately 5000 BP they split into two branches, one migrating east along the rain forest-savanna boundary, and one south through the rain forest. The dates of their rapid expansion were established from linguistic studies which also suggest that pottery was in use by this time and farming was practised (Vansina 1990). Western Bantu speakers gradually occupied all of Central Africa and it is hypothesised that their successful dispersal may have been due to their farming technology (Oslisly and Fontugne 1993).

The occurrence of pottery is suggestive of increased sedentism and perhaps local food production (Stahl 1993, Eggert 1993). Presence of charring on the external surfaces of potsherds provides evidence of pots used for cooking as opposed to storage. The charred potsherds at Ndakan therefore suggest that local populations were sedentary and used pots to cook their food. Remains of staple foods, most likely yams, are rarely preserved, so it is difficult to ascertain diet or the degree to which cultivation was practised. Oil palms were probably utilised and encouraged, and therefore probably brought to the region by people (Sowunmi 1999). Intensive archaeological studies in the Ndakan area are expected to find far more extensive evidence of human settlements throughout the forest. Without further archaeological evidence of the cultural and technological status of these people, it is difficult to envisage their lifestyle and degree of impact on the environment.

3.5.3 Vegetation history and climate change

Today the forest in the southwestern C.A.R. is characterised as moist semi-evergreen forest, and is in a transition zone from evergreen forest in the south to dry deciduous forest and savanna 200 km to the north (Carroll 1992, White 1983). It is very likely that these forests, existing at an ecotone, were affected by the climate fluctuations

described for other parts of Africa in the last 4000 years. However, in order to determine this it is necessary to reconstruct vegetation history from detailed palynological and geochemical analyses. The nearest palynological study to the Ndakan site was done at Lake Télé in the Republic of Congo, approximately 100 km to the southeast in the same drainage system. The core from this lake dated to 6000 BP and the pollen analysis showed no evidence of surrounding grasslands in the last 6000 years (Laraque *et al.* 1998). Although the pollen analysis of the Lake Télé cores was limited, it does indicate that evergreen rain forest vegetation might not have varied as much as that of ecotonal semi-evergreen regions.

The area extending down between the Sangha and Djeke Rivers where most *M. macrostachyum* patches were found was also where all the pottery sites were located. This area away from the rivers may have been drier and more susceptible to forest loss during climatic fluctuations. In a period of drier climate 2000–3000 years ago, it is possible that savanna isolates were able to re-open. As these closed in, *M. macrostachyum* might have dominated the regeneration process at the forest edge, leaving the modern forest with extensive remnant patches. More local and detailed sediment studies are needed to ascertain the chronological and spatial relationship of human occupation, vegetation change, oil palm spread, and burning frequencies. For the Ndakan study area this also has important implications for the significance of *M. macrostachyum* patches as indicators of past disturbance. Data about long-term vegetation history are required to solidify the connection between prehistoric events and modern forest structure.

3.5.4 Association of potsherds, charcoal, and *M. macrostachyum*

The abundance of charcoal at Ndakan suggests that fire was a common feature of this forest in the past, though the exact causes of it are unknown. The frequency of charcoal in soil pits at 47% is much lower than the results for a similar study in the central Amazon Basin (Sanford *et al.* 1985). In an area with over twice the current rainfall as Ndakan (3530 mm y⁻¹), Sanford *et al.* found charcoal in 63 of the 96 pits they sampled, most frequently in *terra firme* forest. The charcoal from the Amazon study was found between 0 and 70 cm depth and dated between 250 and 6260 BP.

Fires may intentionally be set by humans for the purposes of hunting in a savanna landscape or clearance of forest for agriculture. However, they also occur naturally from lightning strikes within rain forests and more open forests can become vulnerable to extensive burning after short periods without rain (Tutin *et al.* 1996, Uhl *et al.* 1988b). Therefore the presence of charcoal itself does not necessarily indicate a drier climate regime or the presence of humans, though both of these would greatly increase the frequency of burning (Sanford *et al.* 1985). There is no record of recent large-scale fires in the Dzanga-Ndoki National Park. Small agricultural fields associated with fishing camps and small villages are located in a narrow area next to the Sangha River (Fay 1997). Charcoal found in the Ndakan study area may have originated either from localised lightning fires or prehistoric human disturbance.

Results from chapter 2 showed a significant association of *M. macrostachyum* presence with charcoal abundance. However, a quantitative comparison of charcoal abundance in other forest sites and different vegetation types, especially in areas with different overall *M. macrostachyum* densities, is essential for determining if previous fire is a factor in the development of *M. macrostachyum* patches.

Charcoal and *M. macrostachyum* patch locations seemed to occur predominantly in the central third of the study area. All five potsherd locations and the quartz flake that were found were also in the central area, which strongly suggests that there were several village sites, temporary camps, or agricultural fields in this area. Again, this could correspond to the re-opening of savanna between the rivers and the gradual regeneration of the forest in the last thousand years as the climate became more humid. According to White's hypothesis of savanna re-colonisation in Gabon, these patches may be the last visible evidence of pre-existing savannas at Ndakan. The *M. macrostachyum* and charcoal at the southern edge of the plot by the Sangha River may be due to human influences as well, perhaps villages that were occupied during the wet season when the low forest bordering the river was severely flooded.

3.5.5 Conclusions

Knowledge of forest history is important for the study and management of forests in the Congo Basin. In order to have a clear understanding of the contemporary

behaviour of an ecosystem, and the potential effects of altering that system, it is essential to take into consideration not just the immediate past but also ancient events that may continue to have long-term effects. Previous disturbance may mask normal environment-vegetation relationships. Existing forest and soil patterns may be the product of prehistoric anthropogenic activities rather than, or in combination with, contemporary environmental factors (Burslem *et al.* 2000, Foster *et al.* 1992, Fuller *et al.* 1998, Maley and Brenac 1998). Ecological studies that only examine modern environmental factors to explain patterns of tree distribution may come to false conclusions if forest history is not taken into account. An example of this comes from a study in Guinea which showed that ‘relic’ patches of forest thought to be remnants from extensive overexploitation had actually been planted into the arid landscape by inhabitants at village sites and encouraged by increasingly favourable climatic conditions from mid-nineteenth to the mid-twentieth centuries (Leach *et al.* 1994).

Conservation policies will also benefit from better understanding of the long-term dynamics of tropical forests. Awareness of the resilience of different forest types and the susceptibility to disturbance under changing climate conditions may aid managers in predicting responses to current and future threats (Noss 2001). This may be especially important when designating areas of conservation priority. Current environmental conditions favour the expansion of forests at the expense of these drier vegetation types. Without frequent burning by humans, savanna isolates would eventually disappear. This may be contrary to many existing forest management policies and will require decisions about what is the ‘natural’ ratio of savanna to forest. Savanna management policies may also have an impact on high conservation-value Marantaceae forests and thus the populations of animals such as gorillas and elephants.

It is clear that the forests around Ndakan have an extensive history of anthropogenic disturbance, as well as susceptibility to climatic fluctuations. It is probable that very few areas in the Congo Basin, even those that may have not been greatly affected by recent climate change, are pristine. The difficulty in describing forest history and its legacy for modern landscape lies in the dearth of known sites within tropical forests suitable for archaeological or palaeoecological study. Many more detailed studies of

sites like Ndakan are needed before the effects of climate change and anthropogenic disturbance on modern forest structure and composition can be disentangled. Finding archaeological sites in dense forest is a daunting task but may be aided by awareness of specific indicators that are relatively easy to locate. The appearance of oil palm nut deposits exposed in streambeds where there are no extant palm groves probably represents previous human activity. Abundant *M. macrostachyum* or Marantaceae patches certainly warrant further investigation as indicators of previous disturbance. Together, these two clues might be very useful in pinpointing areas of palaeoecological and archaeological interest. Ndakan is likely to be just one of many prehistoric human settlement sites existing underneath the rain forest of the Congo basin, yet to be discovered.

Finding, dating, and interpreting more sites is necessary to understand the interactions between people, oil palms, *M. macrostachyum* and climate change. Many questions remain to be addressed:

Did people migrate into a forested environment and clear forest to cultivate crops? Or did people inhabit savanna environments or live at the forest edge utilising both environments? Was oil palm brought to the region by humans, or did people settle near natural populations of palm groves? Can *M. macrostachyum* patches persist for hundreds of years, delaying forest regeneration?

3.5.6 Future work

The discovery of pottery in the Ndakan forest merely highlighted a very important topic in tropical forest ecology and provided starting blocks for further work in the area. Although the preliminary luminescence dates were adequate for the purposes of this thesis, it would be valuable to re-date the collected potsherds using the measured environmental dose rates. The more precise luminescence dates could then be more readily compared with the chronology of the palm nut dates from Fay (1997). Dating a sub-sample of the charcoal fragments and comparing charcoal date frequencies to the revised pottery dates would indicate if there was an increase in burning with arrival of humans. However, interpretation may be complicated because increased charcoal frequency may have resulted from natural causes, or may be associated with human activities that remain undiscovered.

A study area of 10-100 square kilometres may be a more appropriate scale at which to test for an association between charcoal and *M. macrostachyum*, especially if causes are related to climate change. Point counts within a small study area, similar to those done in the present study, should be repeated in different forest types, particularly with different *M. macrostachyum* densities. An overall pattern may arise between the size of the burns, time since burning and the density of *M. macrostachyum*. Standardised data should also be collected which would allow comparisons of charcoal densities between forests. Frequent burns over time may still affect soil nutrient quality hundreds of years later (Lawrence and Schlesinger 2001) and therefore may be an important environmental factor to take into consideration when assessing plant distributions.

A more intensive survey in the centre of the plot, based on the locations of potsherds, charcoal, and *M. macrostachyum* patches is likely to identify actual settlement sites. A purely archaeological study of settlement locations would reveal more information about the technological status and subsistence methods of the people who once lived there. Excavation at these sites would probably demonstrate the extensive use of oil palm by these cultures.

The advent of widespread, identifiable, anthropogenic disturbance in now remote sections of Central African rain forest provides an exceptional opportunity to combine ecological and palaeoecological methods in a detailed study of long-term tropical forest dynamics. With proper ecological knowledge, a study could be designed to examine late Holocene vegetation change in response to anthropogenic disturbance and climate change. Using *M. macrostachyum* patches and palm nut deposits to locate human artefacts could greatly increase our understanding of the extent, type and age of prehistoric anthropogenic disturbance in this region. Sediment cores subject to pollen, geochemical and microscopic charcoal analysis may provide a detailed enough record to disentangle the effects of climate change and anthropogenic disturbance on long-term vegetation dynamics and understand how climate change and disturbance interact to shape different forest communities over time.

4 The effect of *M. macrostachyum* on tree regeneration

4.1 Introduction

4.1.1 Models of succession

In summarising over 70 years of studies on succession, Connell and Slatyer (1977) propose that early successional species could have either a positive (facilitative), negative (inhibitory), or a neutral (tolerance) effect on later-invading species. Although most observations of Marantaceae forests suggest that these herbs act to inhibit tree regeneration (see Chapter 1), Dhetchuvi (1996) observed that within the secondary growth dominated by *Aframomum* spp. (Zingiberaceae) and *Haumania liebrechtsiana* (Marantaceae) during colonisation of fallow fields, there was abundant regeneration of primary forest tree species. In the Forêt des Abeilles, Gabon, where herbs from the families of Marantaceae, Zingiberaceae, and Costaceae make up nearly 70% of the forest cover in loading bays and felling sites, Dhetchuvi (1996) suggested that these herbs facilitate regeneration of the forest after logging. In addition, White's (1992) study concluded that Marantaceae forest is a successional stage between savanna and closed forest, suggesting that it may act to facilitate tree invasion of the savannas.

Despite its potential importance for forest dynamics in abandoned agricultural fields, logging sites and 'natural' forest, no studies have ever specifically tested the effect of Marantaceae forests on tree regeneration. The abundance of *M. macrostachyum* patches in the Ndakan study area make it a suitable place for examining the effect of one Marantaceae species on tree regeneration. Understanding how *M. macrostachyum* affects successional pathways may help predict some long-term effects of disturbance in Central African forests, and may help explain the distribution and abundance of such herb species.

Connell and Slatyer's three models offer testable hypotheses for assessing the effect of *M. macrostachyum* on later colonisers (specifically tree species). If *M. macrostachyum* facilitates the establishment of tree species in forest canopy gaps, tree

seeds would readily germinate and tree seedlings would perform better in a gap with *M. macrostachyum* than without, and better than closed canopy forest understorey. If *M. macrostachyum* inhibits the establishment of tree seedlings, germination and seedling performance would be highest in gaps without *M. macrostachyum*, and low in *M. macrostachyum* patches and closed canopy forest. The tolerance model predicts that *M. macrostachyum* has no effect on germination or performance of shade-tolerant species in a gap, and therefore these responses would be highest in gaps with and without *M. macrostachyum*, and lowest in closed canopy forest. Light-demanding species would still be inhibited under the tolerance model. Models and expected responses are summarised in Table 4.1.

Connell and Slatyer also propose that a further test of the three models comes from differences in the cause of death of early colonists. For the facilitation and tolerance models, *M. macrostachyum* would eventually be killed or shaded out by tree species. For the inhibition model to be appropriate, *M. macrostachyum* would have to be disturbed by external factors, such as large herbivores, for further invasion by other species to take place.

Table 4.1 Expected relative responses according to different successional models in germination, growth and survival of other plant species in gaps with intact *M. macrostachyum*, the same gap with a section of *M. macrostachyum* removed and closed canopy forest. + and – represent response relative to the other treatments. Treatments with the same symbols are expected to have similar responses.

Successional model	Plant response	<i>M. macrostachyum</i> gap	Gap with <i>M. macrostachyum</i> removed	Closed Canopy Forest
Inhibition	Total germination	-	+	-
	Germination time	+	-	+
	Survival	-	+	-
	Growth	-	+	-
Facilitation	Total germination	+	-	-
	Germination time	-	+	+
	Survival	+	-	-
	Growth	+	-	-
Tolerance	Total germination	+	+	-
	Germination time	-	-	+
	Survival	+	+	-
	Growth	+	+	-

4.1.2 Mechanisms of competition

The effect of early successional species on later invaders may include competition for resources, such as light, water, and soil nutrients. Light limitation in the forest understorey is often stated as the primary factor limiting seed germination and seedling establishment in tropical forest studies (Denslow *et al.* 1990, Hartshorn 1978, Hall and Swaine 1980, Raich and Gong 1990). Various studies indicate that the majority of tropical tree species require an opening in the canopy (i.e. increase in light level) at some point in their early life in order to reach maturity (Augspurger 1984, Denslow 1980), though individual species responses are variable (Clark and Clark 1993). Many studies in tropical rain forest dynamics have emphasised the extreme difference in light conditions between treefall gaps and nearby closed canopy forest understorey (Canham *et al.* 1990, Barton *et al.* 1989, Raich 1989, Whitmore *et al.* 1993). Light levels in tropical forest understorey have been measured at 1-2% full sunlight in tropical forests (Chazdon and Fetcher 1984, Clark *et al.* 1996, Raich 1989). The recognition of extreme light limitation under tropical forest canopies has produced a large body of research examining the importance of gaps in tropical forest dynamics (Brokaw and Scheiner 1989, Brokaw and Busing 2000, Dalling *et al.* 1998, Denslow 1980, Denslow 1987, Kennedy and Swaine 1992, Popma *et al.* 1988, Uhl *et al.* 1988, Whitmore 1978, Harshorn 1978).

Many studies have examined light quantity in canopy gaps (Barton *et al.* 1989, Chazdon and Fetcher 1984), but these measurements are often made in gaps with all understorey vegetation removed (Brown 1993). However, a fast growing herbaceous layer such as *M. macrostachyum*, may immediately overtop most advanced regeneration when a gap is created, significantly and quickly reducing available light levels. The question then arises as to the extent PAR (Photosynthetically Active Radiation) is reduced in a gap dominated by *M. macrostachyum*. For light competition to be a major factor in the maintenance of *M. macrostachyum* patches, PAR would have to be considerably reduced in gaps containing *M. macrostachyum*. Even an increase in light of 2% could be enough to cause a significant increase in height growth and survival of seedlings (Whitmore and Brown 1996).

Below-ground competition for water and soil nutrients has also been shown to be a mechanism by which early successional species may inhibit growth and survival of

later arrivals (Denslow *et al.* 1991, Lewis and Tanner 2000, Gerhardt 1996). Nutrient competition may be especially acute in tropical forest soils, where plants are often nutrient limited (Burslem *et al.* 1994, Veenendaal *et al.* 1996).

Another direct method of inhibiting later successional species is through the release of chemicals which are toxic to other plant species (allelopathy) (Rizvi *et al.* 1992). Allelopathy has been widely studied in agricultural and silvicultural systems, however, little is known about allelopathy in tropical forests. Responses may be species specific and therefore difficult to extrapolate to forest-wide processes in the diverse tropics (Gliessman 1976). The lack of germination beneath a given species is not sufficient evidence for allelopathy (Bazzaz and Pickett 1980), and other possible causes such as dispersal limitation, competition, and predation would need to be ruled out.

The exact mechanisms by which *M. macrostachyum* may compete with tree seedlings are unknown. Several factors relating to its physiognomy are likely to have detrimental effects on tree seedling establishment. The overlapping leaf layer may preempt light, re-creating shaded understory conditions for germinating seedlings. Furthermore, the dense network of roots and rhizomes may also compete for physical space, soil nutrients, and water, especially during the dry season when rainfall is low and the forest suffers water stress.

M. macrostachyum may also indirectly affect tree regeneration by attracting large herbivores which trample or uproot young seedlings. Smaller herbivores or granivores may also prefer secondary vegetation in gaps (Schupp *et al.* 1989). For example, disturbed forest in Bwindi National Park, Uganda had higher rodent populations than closed forest, resulting in higher seed predation rates than in closed canopy forest (Isabirye-Basuta and Kasenene 1987). Whitmore and Brown (1996) also noted that apical damage to Dipterocarp seedlings and saplings was more frequent in large gaps than in closed canopy forest and medium to small gaps.

The main objective of this chapter is to test whether the effect of *M. macrostachyum* patch presence on tree seedling establishment in gaps facilitates, inhibits, or has no

effect on later succession. The second objective of this chapter is to examine potential mechanisms by which *M. macrostachyum* may inhibit tree regeneration in gaps.

4.1.3 Hypotheses

Three experiments were performed to address the following specific hypotheses:

Hypothesis 1: M. macrostachyum affects seed germination of other plant species from the soil seed bank.

Hypothesis 2: M. macrostachyum in gaps differentially affects tree recruitment compared to gaps with other secondary vegetation and closed canopy forest.

Hypothesis 3: Competition from M. macrostachyum, either above- or below-ground, affects tree seedling establishment in M. macrostachyum patches.

Hypothesis 4: M. macrostachyum canopy alters light conditions in forest gaps.

4.2 Methods

4.2.1 Natural seed germination and seedling survival experiment (Hypothesis 1)

Experimental design

Germination from natural seed rain and the soil seed bank, and survival of the germinated seedlings, was monitored for 10 months in blocked experimental plots in ten different *M. macrostachyum* patches located in the Ndakan study area. Within each patch two 1 x 2 m plots were positioned on a north-south axis at a distance of 3 m from each other. The south plot was designated as the cut plot and all rooted *M. macrostachyum* leaves were cut to ground level. All overhanging leaves were also cut back to open a 1 x 2 m gap in the *M. macrostachyum* canopy. The north plot was designated the control *M. macrostachyum* plot and no leaves were cut in or around it. In addition to these two plots, a third plot was placed as close as possible to the patch in normal forest understorey not containing any *M. macrostachyum*. This was designated the forest plot and served as the overall control.

Plots were placed 3 m apart in order to minimise the effect of the cut plot on control *M. macrostachyum* light conditions, while maximising the similarity of seed rain into the plots. Distances between forest plots and *M. macrostachyum* plots ranged from 10 – 25 m. Similar patch conditions were chosen; i.e. all were located in tree canopy gaps and consisted predominantly of *M. macrostachyum* with few other lianes or trees interspersed. The size of canopy gap was estimated by measuring the long and short axes of the gap. Original *M. macrostachyum* leaf density was also measured in the plots.

The experiment was established in September 1999. In October 1999, bi-weekly censuses of new seedlings began and continued for ten months. This allowed measurements to be taken throughout wet and dry seasons. At each census, all new seedlings were given a unique number and marked with a metal tag. Dead or missing seedlings were noted. Unfortunately, we were not able to identify seedlings to species. After a few months it became apparent that *M. macrostachyum* leaves emerging from underground rhizomes, as well as leaning neighbour stems, would return the cut plots to their original level of cover. In April, the cut plots were re-cut and new *M. macrostachyum* leaves were cut as they emerged in order to maintain the experimental conditions.

Data analysis

Total germination in plots

The General Linear Model ANOVA was used (Minitab version 12) to assess differences between treatments. Because distances between replicate patches varied from 50 to 3000 m, potential seed rain was expected to be very different among patches. Therefore, data was blocked by patch in the analysis.

Seedling survival

The seedlings germinated continually from the seed bank or seed rain over the 40 weeks of the study. A proportion of seedlings were still alive at the end of the study, and are therefore counted as censored observations. The Kaplan-Meier survival function, or product-limit estimator, was used in SPSS (version 11) to estimate the

distribution of survival times from the sample because it handles censored data (Kaplan and Meier 1958). The Kaplan-Meier survival function estimates the survival function directly from the continual survival or failure times. The model is based on estimating conditional probabilities at each time point when an event occurs, and taking the product limit of those probabilities to estimate the survival rate at each point in time (Lee 1992).

For comparing survival between two or more treatments, the results from the Kaplan-Meier survival function were subject to a Log-rank test (SPSS). The Log-rank test is a non-parametric test that compares the equality of the different survival functions based on the rank ordering of survival times (PROPHET StatGuide 1996).

One assumption for the Kaplan-Meier and Log-rank test are that sample sizes are >30. In this case, each seedling was considered an independent sample, so sample size was large. Another assumption is that there are no systematic differences between censored and uncensored cases. Species of seedlings were not known in this case, so censored seedlings may have been of certain hardy species. Different patches may have had different suites of species growing in them. This was controlled for as much as possible analysing patches as blocks (strata in SPSS). Again, blocked treatments were laid out as closely as possible to increase the likelihood of similar seed sources within a patch.

4.2.2 Planted seed experiment (Hypotheses 2 & 3)

Experimental design

Both hypotheses were tested using introductions of seeds to evaluate species invasion success independent of variations in seed rain. Ten replicate plots (80 x 80 cm) were established in each of the following 5 conditions: **Closed Forest**, ***M. macrostachyum* patch**, and **Alternative Gap** (Gap with other low vegetation that is not made up of *M. macrostachyum*, e.g. lianas and shrubs); and within each *M. macrostachyum* patch, **Trenched** (all rhizomes of *M. macrostachyum* removed and a 1 m radius perimeter trench dug to 40 cm to prevent re-entry of adjacent rhizomes), **Bent** (rhizomes left intact, but all overhanging leaves of *M. macrostachyum* were tied back to allow sunlight to reach the ground), and again **Control *M. macrostachyum*** (Hypothesis 3).

A fourth treatment, trenched with overhanging leaves, representing the effects of shoot competition only, was not performed. Trenching within a *M. macrostachyum* patch would essentially open up a gap as well, thus not making the comparison valid. Root and shoot competition was assumed to be additive (Cahill 2002).

Plot locations

M. macrostachyum forest appears to fit two general types: those patches that are close to and interconnected with other patches, often covering large areas over 500 m in diameter, and those that are isolated, smaller, and more obviously associated with a single tree fall. Though the initial causes of patch formation and the age of each patch may differ, the physiognomy of the patches is very similar. One significant difference between these two types may be an increase in potential seed rain from surrounding trees in the smaller, isolated patches. Because this experiment was independent of variations in seed rain, both types of patches were used. The Closed Forest plot was located at the nearest point to the *M. macrostachyum* patch under forest canopy. Suitable Alternative Gaps without *M. macrostachyum* were rarely found near the *M. macrostachyum* patches or Closed Forest plots due to the fact that any gaps that were near *M. macrostachyum* patches usually had *M. macrostachyum* in them. Alternative Gaps were thus located by searching the study area for treefall gaps which had vegetation (shrubs, lianas) up to the height of 5 m, approximately similar to the height of *M. macrostachyum* canopy. These were found along the main trail, within 50-1000 m of the nearest *M. macrostachyum* patches.

Tree species

Tropical forests tend to have a high proportion of seeds dispersed by animals (Whitmore 1997). Gorillas and elephants frequent areas of secondary forest and gorillas may especially contribute to seed dispersal to *M. macrostachyum* patches with their frugivorous diet and habit of nightly nest building using stems of *M. macrostachyum* (Fay 1997, Voysey *et al.* 1999). Therefore, the tree species chosen for this experiment were those known to be important components of gorilla diet and therefore likely to end up in a *M. macrostachyum* patch. The species chosen were *Myrianthus arboreus*, a medium-sized tree (20 m) common in early successional

stages, open sites, and also in the Ndakan study area [Harris, 2002 #1035], *Tetrapleura tetraptera*, a tree (~25 m tall) often found near villages and in secondary forest (Heitz 1943), and *Greenwayodendron* syn *Polialthea suaveolens*, a shade-bearing species also common in the Ndakan study area (Fay 1997). All three species begin fruiting in May during what is normally the short wet season. Seeds were collected from ripe fruits found on the forest floor. The endocarp was removed and they were stored indoors until planting.

Between the 3rd to 7th of July 2000, 15 seeds of each of the three tree species were planted evenly spaced and in random order into each 80 x 80 cm plot. Starting three weeks after planting, a seedling census was done weekly for the next 2 months, then at 13 months and 17 months. Upon germination, the position of each emerging seedling was marked with a metal tag which permitted repeated censusing of the same individuals. Germination, survival, and damage to seedlings from predation or trampling was recorded during each census. Relative Growth Rates (RGR) were obtained from a maximum of 5 permanently marked seedlings per plot which had survived throughout the entire census. Height growth of seedlings was measured from the base to the terminal bud.

Data analysis

Seed germination percentages and percent of damaged seedlings were calculated for each treatment, arcsine transformed, and compared using ANOVA. For comparison between Trenched, Bent and Control *M. macrostachyum* plots, data were blocked by Patch. Density dependent effects between seedlings in the same plot were not considered to affect growth and survival because seedlings were spaced sufficiently, and were still relatively short at the end of the study.

Differences between treatments in mean germination time were calculated from the time of planting to the week when the seedling emerged. This was measured for the first four months of the study (July to October 2000). Seeds which germinated after October 2000 were not included in this analysis because, due to permit restrictions, the next census could not be completed until August 2001. Seeds which germinated and died in this interval would have been missed completely. Time to germination was

analysed only for those seeds which germinated and not all planted seeds because it was not possible to tell whether seeds that did not germinate were predated by animals, or may have germinated and died during the long intervals between the last three census times.

Relative Growth Rates were calculated as:

$$(\ln H_f - \ln H_0) / (T_1 - T_0)$$

where H_0 is the first measured height of the seedling at the start of the experiment (T_0), and H_f is the final height measured at the end of the experiment (T_1) (Hunt 1990). The measurement period was equivalent for all seedlings so $T_1 - T_0$ was given the value of 1 unit. General Linear Model univariate analysis (Minitab) was used to look at overall treatment differences. Because seedlings germinated at various times in relation to the measurement dates, seedling age was entered as a covariate into the model. Species and seedling damage were also entered as factors. Tukey's Post-hoc pairwise comparison was used to examine differences between pairs of treatments.

Survivorship was measured as for the first experiment, using Kaplan-Meier survival functions. A Log-rank pairwise comparison was done to examine differences between treatments.

4.2.3 PAR measurements in *M. macrostachyum* patches (Hypothesis 4)

Data collection

The quantity of PAR available to plants under different forest canopy conditions was measured using PAR quantum sensors (LI-190SA, LI-COR Inc. Lincoln, NE, USA) and PAR Special sensors (SKP 210, Skye Instruments, Llandrindod Wells, UK). When sensors from both models were placed adjacent to each other, measurements were within 5% of each other. Each sensor had a built-in bubble-level for making sure the sensors were vertical. Both models measure in micromoles per second per square meter ($\mu\text{mol s}^{-1}\text{m}^{-2}$). The PAR sensors were built-in or attached to LI-COR 1400 and Skye DataHog2 dataloggers which were set to record every 10 seconds throughout the

day. These readings were automatically averaged over 10-minute periods from 6:00 to 18:00hrs.

The Skye datalogger and PAR sensors were used to measure 100% full sunlight in a large clearing near the camp. The LI-COR datalogger with 4 external PAR quantum sensors was used to measure forest and *M. macrostachyum* understorey conditions. The 4 Li-Cor quantum PAR sensors were distributed as follows: 1 & 3) under *M. macrostachyum* canopy, 2) trenched plot or on a pole above the *M. macrostachyum* canopy (referred to as Gap), and 4) closed forest Understorey. These were directly compared to 100% full sunlight recorded at the camp with the DataHog2 for the same days. A total of 6 different *M. macrostachyum* patches were measured for 2-3 consecutive days each.

Data analysis

Graphs of PAR vs. Time were made which show light availability under the various canopy conditions. Results were averaged for the consecutive days at a site for the 12 hour period to get average PAR per treatment. The average for each treatment was then divided by the average of the Full Sun sensors to give percent full sunlight. *M. macrostachyum* PAR readings were also divided by the average Gap readings to estimate the percent of sunlight reaching the gap that then made it to the forest floor.

4.3 Results

4.3.1 Natural seed germination and seedling survival experiment

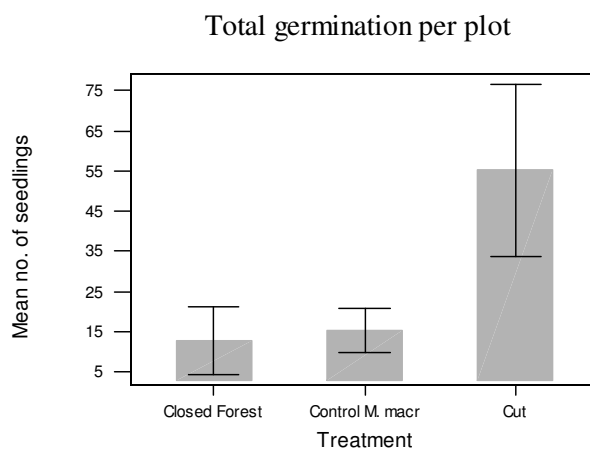
The ten gaps chosen for placing the experimental plots were between 160 and 960 m² in area with an average of 496 m². *M. macrostachyum* leaf densities within the plots averaged 25 m⁻² with a range of 15 – 46 leaves m⁻².

Total germination

Results show that when blocked by *M. macrostachyum* patch, there was a significant difference between treatments ($F_{2,18}=18.08$, $p<0.001$). Tukey's pairwise comparison showed that Cut plots were significantly different from Control *M. macrostachyum*

plots and Closed Forest plots ($p < 0.05$). Closed Forest and Control *M. macrostachyum* plots were not significantly different (See Fig. 4.1).

Figure 4.1 Comparison of total seed germination from soil seed bank and natural seed rain in *M. macrostachyum* patches (Control and Cut) and in closed forest understorey (Closed Forest). Bars are 95% confidence intervals.



Survivorship

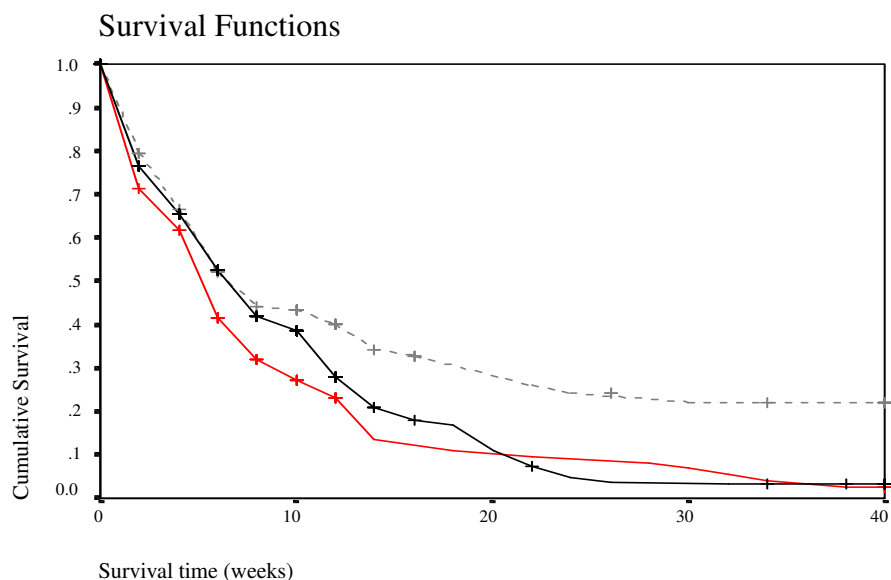
The sample sizes and percent of observations censored for the three treatments were: 1) Closed Forest $n=129$ (34.9% censored), 2) Control *M. macrostachyum* $n=155$ (18.1% censored), 3) Cut $n=562$ (24.7% censored). Overall $n=846$ (25.1% censored). The test statistics for overall comparison of Equality of Survival Distributions for Treatment (SPSS) were significant (Test statistic=12.23, d.f.=2, $p < 0.005$). Results of the post-hoc comparison are shown in Table 4.2. All three treatments are significantly different with seedlings in the Control Forest treatment surviving longer than Cut plots, which survived longer than Control *M. macrostachyum* plots ($p < 0.05$) (Figure 4.2).

Table 4.2 Log Rank Statistic and Significance for post-hoc comparisons of seedling survivorship. Results are adjusted for Patch.

	Cut	<i>M. macrostachyum</i>
<i>M. macrostachyum</i>	F=4.33	
	p<0.05	

Closed Forest	F=5.44 p<0.05	F=6.81 p<0.01
---------------	------------------	------------------

Figure 4.2 Graph of the survival functions for naturally germinated seedlings in *M. macrostachyum* patches - Control *M. macrostachyum* (Solid Red line) and Cut plot (Solid black line) - and in Closed Forest understory (Grey dashed line). Crosses represent censored observations.



4.3.2 Planted seed experiment

Percent of seeds germinating

Unfortunately, seeds of *Greenwayodendron suaveolens* used in this experiment failed to germinate until the census at 13 months and then did so in very small numbers. This species was therefore not included in any of the analyses. Of the two remaining species, *Myrianthus arboreus* had a relatively high germination rate, and showed significant differences in percent germination between treatments (*M. arboreus* $F_{4,45}=4.84$, $p<0.005$). Tukey's post-hoc pairwise comparison showed that there were significant differences between Alternative Gaps (with the lowest percent germination) and all other treatments ($p<0.05$) (Table 4.3). There was no significant difference between treatments within *M. macrostachyum* patches (i.e. Bent, Control *M. macrostachyum*, and Trenched), though there was a slight trend for Trenched plots to have higher percent germination. It is not obvious why Alternative Gaps would

have lower germination than all other treatments. One possible explanation may be higher seed predation rates at those sites.

Tetrapleura tetraptera had no significant differences between treatments (*T. tetraptera* $F_{4,45}=1.82$, $p>0.05$). Again, within *M. macrostachyum* patches there were no significant differences between treatments, though Trenched and Bent plots had slightly greater germination than *M. macrostachyum* plots (Results summarised in Table 4.3).

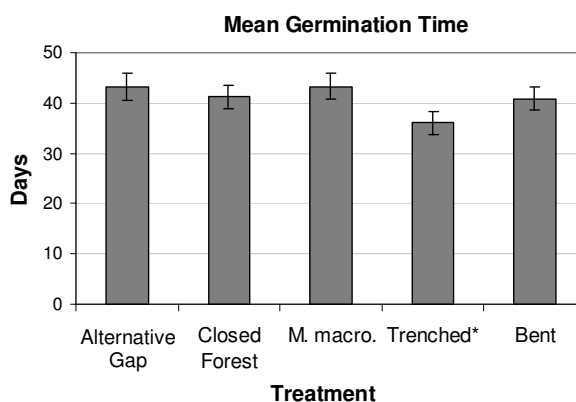
Table 4.3 Differences between treatments in mean percent of seeds germinated out of 150 planted per species per treatment. Different superscripts denote statistically different groups based on Tukey's post-hoc pairwise comparison, $p<0.05$.

Treatment	<i>Myrianthus arboreus</i> % germination	<i>Tetrapleura tetraptera</i> % germination
Alternative Gaps	71.3% ^a	50.6%
Closed Forest	86.0% ^b	62.7%
<i>M. macrostachyum</i>	92.6% ^b	56.0%
Bent	88.0% ^b	62.7%
Trenched	96.0% ^b	61.3%

Germination time

Both tree species showed similar patterns between treatments in mean germination time. There was a significant difference between treatments in the model ($F_{4,1031}=5.992$, $p<0.001$). Trenched plots had significantly shorter germination times than all other treatments ($p<0.05$, Tukeys HSD pairwise comparison) (See Figure 4.3).

Figure 4.3 Mean germination time of *M. arboreus* and *T. tetraptera*. Bars are 95% confidence intervals. Significant differences are denoted by asterisk.



Seedling injury or damage

The total number of seedlings suffering from slight damage was n=403, moderate damage n=23, and severe damage n=62. An overall comparison between treatments for each species showed that there was no significant difference in the percentage of seedlings suffering damage from predation or trampling between treatments (ANOVA for *M. arboreus* $F_{4,45}=0.78$, $p>0.1$, *T. tetraptera* $F_{4,45}=2.27$, $p>0.05$) (See Figures 4.4 and 4.5).

Figure 4.4 Comparison between treatments in percent of *M. arboreus* seedlings suffering damage during the census period. Bars are 95% confidence intervals.

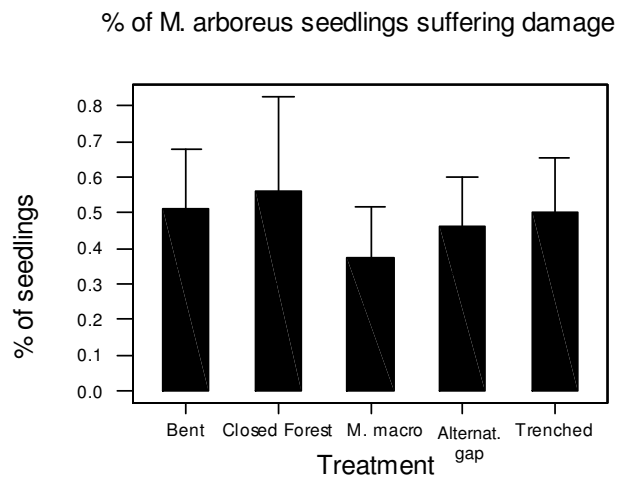
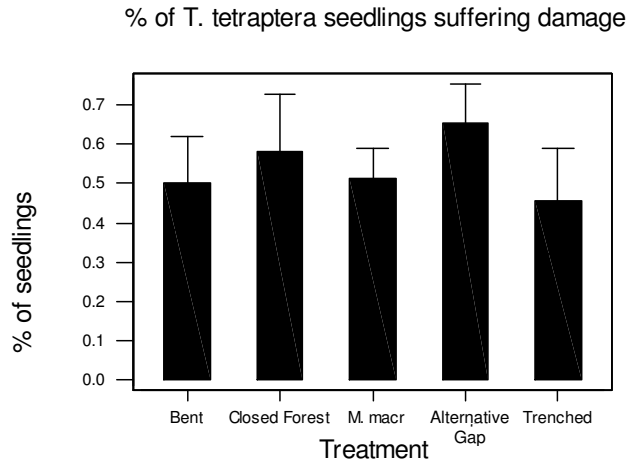


Figure 4.5 Comparison between treatments in percent of *T. tetraptera* seedlings suffering damage during the census period. Bars are 95% confidence intervals.



Slight damage where a few leaves were missing seemed to have no effect on the growth rate (ANOVA between slight damage and no damage not significant at $p > 0.1$). Less than 2% of damage was heavy damage where all leaves were missing.

Growth data

The effect of treatments on RGR was illustrated by plotting the residuals of the effect of Age at T_0 , Damage, and Species against Treatment for each species (Figures 4.6 and 4.7). The residuals are thus a measure of the error accounted for by Treatment.

Figure 4.6 Effect of Treatment on Relative Growth Rates for *M. arboreus*. Bars are 95% confidence intervals. Points with the same letters are not significantly different.

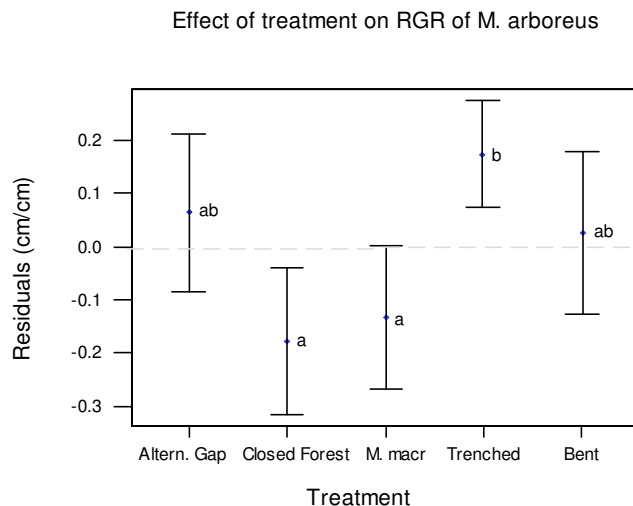
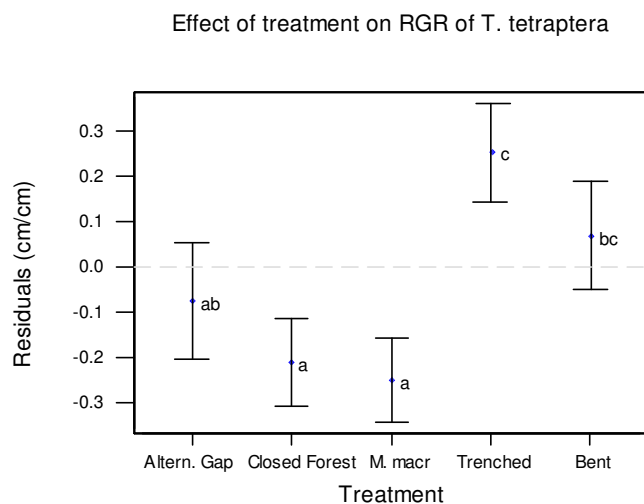


Figure 4.7 Effect of Treatment on Relative Growth Rates for *T. tetraptera*. Bars are 95% confidence intervals. Points with the same letters are not significantly different.



Because both species responded very similarly to the treatments, they were combined for GLM univariate analysis (Table 4.4). Results from the univariate analysis confirmed that there was a significant difference between treatments in Relative Growth Rate of seedlings. Tukey's pairwise comparison of the combined dataset revealed that seedlings in *M. macrostachyum* plots and Closed Forest had significantly lower Relative Growth Rates than Alternative Gap, Trenched and Bent plots ($p < 0.05$).

Table 4.4 GLM univariate analysis table for Relative Growth Rates of seedlings of *M. arboreus* and *T. tetraptera* planted into different treatment plots. Age at first measurement, seedling damage (Damage), and species were included as factors.

Source	d.f.	Seq SS	Adj SS	Adj MS	F	p
Age at T ₀	1	4.5599	0.2043	0.2043	1.58	0.210
Damage	2	12.2300	10.3988	5.1994	40.10	0.000
Species	1	3.4702	2.8909	2.8909	22.30	0.000
Treatment	4	7.2497	7.2497	1.8124	13.98	0.000
Error	285	36.9509	36.9509	0.1297		
Total	293	64.4607				

Seedling survival

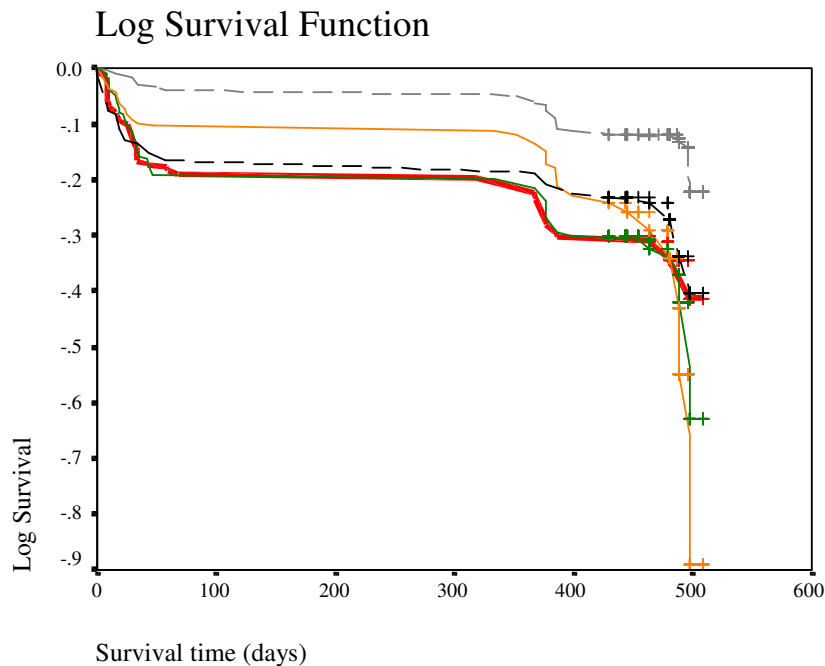
Table 4.5 shows the number of seedlings measured and the percentage of censored observations for each treatment at the end of the study.

Table 4.5 Sample sizes and percent of observations censored for the five treatments

	n	% censored observations
Alternative Gap	164	71.95%
Closed Forest	212	65.57%
<i>M. macrostachyum</i>	196	70.92%
Trenched	233	70.87%
Bent	215	59.07%
Total	1020	70.78%

The survivorship curves for planted tree seedlings in the five different treatments are shown in Figure 4.8. The test statistics for overall comparison of Equality of Survival Distributions for Treatment (SPSS) were significant (Test statistic=41.30, d.f.=4, $p < 0.001$). Results of the post-hoc comparison are shown in Table 4.6. There was no difference in survivorship between *M. macrostachyum*, Alternative Gap or Closed Forest treatments. Within *M. macrostachyum* patches, Trenched plots had significantly higher survivorship than Bent plots or *M. macrostachyum* plots. Bent plots were not significantly different from *M. macrostachyum* plots.

Figure 4.8 Graph of log survival vs. survival time for planted seedlings of *M. arboreus* and *T. tetraptera* in all five treatments. Lines represent treatments as follows: Trenched plots (grey dashed), Bent plots (orange), Alternative Gap (black dashed), Closed Forest understorey (green), and *M. macrostachyum* plots (thick red). Crosses represent censored observations. The long horizontal stretch in the middle represents a period when no seedling censuses were performed.

**Table 4.6** Log Rank Statistic and Significance for post-hoc comparison of Survival Analysis.

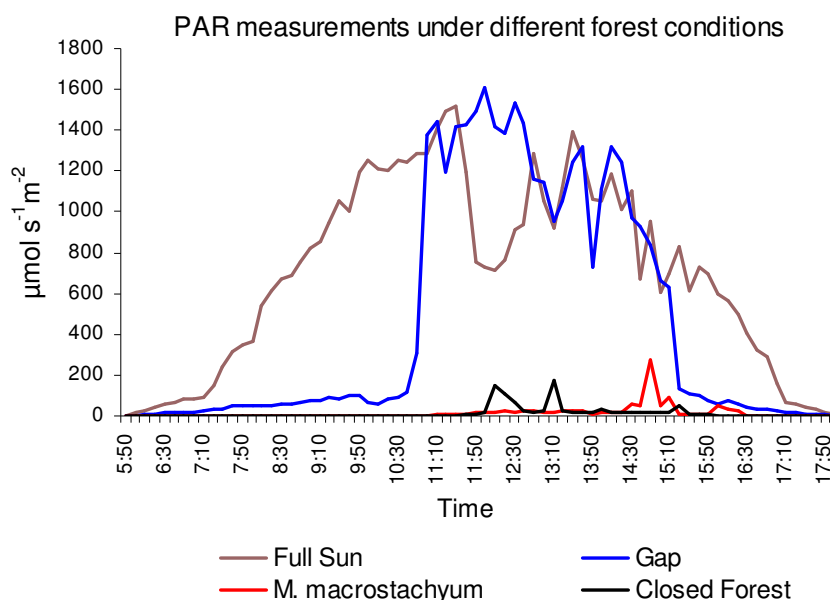
	Alternative Gap	<i>M. macrostachyum</i>
<i>M. macrostachyum</i>	F=0.28 p>0.1	
Closed Forest	F=1.71 p>0.1	F=0.63 p>0.1
	Trenched	<i>M. macrostachyum</i>
<i>M. macrostachyum</i>	F=17.92 p<0.001	
Bent	F=42.80 p<0.001	F=2.02 p>0.1

4.3.3 Light measurements

Figure 4.9 shows a comparison of typical PAR quantities throughout the day in 100% full sunlight, a forest canopy gap, beneath the *M. macrostachyum* layer within the same canopy gap, and in adjacent closed forest understorey. The lines representing the forest understorey and *M. macrostachyum* understorey are indistinguishable except

when short periods of weak sunflecks occasionally got through the canopy. The quantity of light of these sunflecks was much reduced from 100% full sunlight. Table 4.7 summarises the differences between the amount of PAR reaching the forest floor in canopy gaps, closed forest understorey, and beneath the *M. macrostachyum* layer within a canopy gap. In all six measurement periods, *M. macrostachyum* patches within forest canopy gaps permitted around 2% of full sun to reach the forest floor, creating light conditions similar to the closed forest understorey. The percentage of PAR entering the canopy gap that passed through the *M. macrostachyum* herb layer ranged from 2 – 11%.

Figure 4.9 Typical graph of ground-level PAR measurements measured concurrently from 6:00 to 18:00hrs in different forest conditions averaged over 3 consecutive days. Measurements for *M. macrostachyum* were taken in the same patch as the Gap measurements.



Comparison of percent full sunlight between Gap, Closed Forest, and *M. macrostachyum* were significantly different (ANOVA $F_{2,15}=15.32$, $p<0.001$). Tukey's pairwise comparison shows that gap light conditions under *M. macrostachyum* canopy are not significantly different from Closed Forest understorey ($p>0.05$). Canopy-scope values taken at the same location where PAR sensors were placed for gap measurements are presented in Table 4.7.

Table 4.7 Comparison of PAR levels in different forest types as percentage of Full Sun and *M. macrostachyum* as percentage of Gap sun. Measurements for consecutive days in the same site are pooled. Canopy-scope values are presented for each gap.

Chapter 4 - The effect of *M. macrostachyum* on tree regeneration

Dates measured	% of Full Sun PAR			<i>M. macrostachyum</i> as % of Gap PAR
	Gap	Closed Forest understorey	<i>M. macrostachyum</i>	
May 18-20	65%	2%	2%	3%
May 22-24	22%	3%	2%	11%
May 26-27	35%	1%	1%	2%
Aug 3-4	10%	1%	1%	9%
Aug 6-8	24%	0.40%	1%	4%
Aug 9-12	32%	1%	2%	5%

4.4 Discussion

4.4.1 Natural seed germination and seedling survival experiment

Hypothesis 1: M. macrostachyum affects seed germination of other plant species from the soil seed bank.

The results of this experiment indicate that *M. macrostachyum* inhibits the germination and survival of seeds from seed rain and the forest seed bank. The number of seeds germinating in Cut plots was significantly higher than both Control *M. macrostachyum* and Closed Forest plots, indicating that the *M. macrostachyum* canopy is able to suppress germination from the seed bank to a similar extent as a closed tree canopy. Cutting *M. macrostachyum* leaves to ground level released dormant seeds, indicating that low light levels below *M. macrostachyum* canopy may be the mechanism of seed suppression operating within the patches. This may also have been due to a reduction in allelopathic leaf leachate. But the proximity to other intact plants, and the fact that new *M. macrostachyum* leaves were continuously emerging within the plots from intact rhizomes, suggests that allelopathy is not an important mechanism for seedling inhibition.

Seedling survival, however, was highest in the Closed Forest understory, intermediate in the Cut plots and lowest in Control *M. macrostachyum* plots. Differences in survivorship between the treatments may have occurred if a different suite of species which had a different light response or growth characteristics germinated in the Closed Forest plots. For example, germination of mostly shade-tolerant seedlings may explain the higher survival rate in Closed Forest. However, Unfortunately, it was extremely difficult to identify the seedlings that germinated in the plots because many were very small and survived for only short periods of time. Thus species ecologies could not be taken into account. Survivorship in the Cut plot may have been higher if re-cutting of the *M. macrostachyum* leaves had taken place sooner. Shading of light demanding seedlings may have caused some to die. Re-cutting may have caused a drop in the survival function through sudden exposure of shade tolerant seedlings to too much direct sunlight. Seedlings in Cut plots also still faced root competition with *M. macrostachyum*, which may have contributed to low

survival rates. Differences in survivorship between Cut and Control *M. macrostachyum* plots indicate that light limitation is a significant factor affecting seedling survival in *M. macrostachyum* patches.

Alternatively, low survivorship in both *M. macrostachyum* Cut and Control plots may have been a possible consequence of allelopathy or increased herbivory rates within *M. macrostachyum* patches. However, survivorship curves in the planted seed experiment showed very different results for *M. arboreus* and *T. tetraptera*, with Bent and Trenched *M. macrostachyum* plots having higher survival than Closed Forest and Control *M. macrostachyum* plots (See Figure 4.9). If allelopathy is an important mechanism, these results show that its effect is indeed species specific. The possibility of increased gap seedling herbivory rates was addressed in the planted seed experiment.

4.4.2 Planted seed experiment

Hypothesis 2: M. macrostachyum in gaps differentially affects tree recruitment compared to gaps with other secondary vegetation and closed canopy forest.

M. arboreus and *T. tetraptera* are light demanding species. It was expected that they would germinate more readily in Alternative Gaps than in Closed Forest and *M. macrostachyum* patches. The opposite results perhaps can be explained by increased seed predation in gaps. The seeds of these two species are fairly large (8-15 mm long) and they were planted close to the surface, thus were visible to potential seed predators. Germination rates were quite high for all treatments, indicating that the two species may have a recalcitrant germination pattern (Garwood 1983, Roberts 1973). This may be an explanation for the similarities between treatments in germination rates. Mean germination time was also similar between the three treatments, again, implying recalcitrant seed strategies.

An increased seed predation rate in gaps was expected to be reflected in seedling damage as well. The data did not support this hypothesis as there were no differences in seedling damage between treatments. If herbivore damage to seedlings is density dependent, this may help explain increased seedling damage in the understorey

(Janzen 1970, Webb and Peart 1999). *M. arboreus* and *T. tetraptera* are two very common trees in the Ndakan study area. Seeds planted in the forest understorey were closer to conspecific adults, thus making them more susceptible to species-specific herbivores. Similar damage rates found between treatments may partially be due to the difficulty of determining whether dead or missing seedlings had been damaged first. This was only a partial picture of seedling damage, i.e. those seedlings that survived it.

Seedling growth rates clearly support the hypothesis that *M. macrostachyum* negatively affects tree performance in gaps compared to other successional vegetation. Survivorship curves however, were similar in Alternative Gaps, Closed Forest, and *M. macrostachyum* patches.

Overall seedling performance was very similar between *M. macrostachyum* and Closed Forest treatments. Alternative Gap responses were variable, but the null hypothesis can only be rejected with seedling growth data. Again there was not sufficient evidence from data on damage to seedlings to indicate whether *M. macrostachyum* patches were maintained indirectly by increased predation or herbivory on tree seedlings.

Hypothesis 3: Competition from M. macrostachyum, either above- or below-ground, affects tree seedling establishment in M. macrostachyum patches.

The null hypothesis could not be rejected using germination percentage data. Again, this may be because of recalcitrant seed strategies, as well as the obvious fact that seeds do not face root competition until they germinate. However, *M. macrostachyum* did increase the mean germination time of the seeds compared to Trenched plots. Lack of significant differences between *M. macrostachyum* plots and Bent plots may be explained by some shading at very low heights by the bent stems of *M. macrostachyum*.

There were significant differences between treatments when looking at growth and survival data. If a simple additive model of the relative effects of root and shoot competition is assumed, then shoot competition (the difference between *M. macrostachyum* RGR and Bent RGR) has almost twice the effect of root competition (the difference between Bent and Trenched RGR) on seedling growth. But Cahill

(2002) cautions that ‘root competition can increase the strength of shoot competition by compounding the negative effects of asymmetric competition for light’. The difference between *M. macrostachyum* and Bent plots does not necessarily represent the effect of above-ground competition for light, but only part of the interaction. What can be interpreted from these results is that above- and below-ground competition are both mechanisms by which *M. macrostachyum* may compete with later plant invaders at the seedling stage. The reduction in RGR is likely to be a minimum, given that during the period when seedling censuses could not be taken, experimental conditions could not always be maintained in the Trenched and Bent plots. Therefore the Relative Growth Rates for these two treatments reflect only partial treatment conditions. Furthermore, these *M. macrostachyum* gap conditions were somewhat optimal. Some *M. macrostachyum* patches have overhead canopy trees which would cause additional shading.

The high Relative Growth Rates in Bent and Trenched plots, which were in the centre of *M. macrostachyum* patches, suggests that allelopathy is not a mechanism of seedling suppression in *M. macrostachyum* patches.

Trenched plots had significantly higher seedling survivorship over the 17 months of the study than both Bent and *M. macrostachyum* plots. This supports the hypothesis that *M. macrostachyum* inhibits later regeneration through both root and shoot competition.

4.4.3 PAR measurements in *M. macrostachyum* patches

Hypothesis 4: M. macrostachyum canopy alters light conditions in forest gaps.

The null hypothesis is rejected by measurements which show that PAR levels in gaps occupied by *M. macrostachyum* patches are not significantly different from the understorey of closed canopy forest. However, much of the reduction in light below *M. macrostachyum* canopy may be due to a reduction in lateral light by the tree canopy surrounding the gap. 35 – 90% of potential incident PAR is already cut out by the surrounding forest before it reaches the *M. macrostachyum* canopy. Of light arriving in gaps, *M. macrostachyum* leaves reduce it by a further 89 – 98%. The

overall effect of *M. macrostachyum* is that it effectively negates the effect of canopy gaps on light levels reaching the forest floor.

4.5 Conclusions

Synthesis of observations throughout Central Africa suggest that *M. macrostachyum* is a mid-successional plant that occupies a niche between disturbed areas or savannas and mixed-species tropical forest. However, results from this study strongly suggest that *M. macrostachyum* closely fits the inhibition model in its effects on later tree regeneration in tropical forest gaps (See Table 4.8). This study suggests a mechanism by which *M. macrostachyum* can persist for extended periods in large patches - through direct competitive effects on seeds and seedlings of later arriving species. Indeed the question has been asked by many who have made observations in Marantaceae forests, ‘why are there trees at all?’

Table 4.8 Relative responses of seed germination and seedling performance of *M. arboreus* and *T. tetraptera*. Results from the natural seed germination and survival experiment are also shown, in parentheses. + and – symbols represent response relative to the other treatments. Treatments with the same symbol were not significantly different. All others are significant to $p < 0.05$. ‘Gap with *M. macrostachyum* removed’ column represents Trenched plots for planted seedling experiment and Cut plot for natural seed germination experiment.

Plant response		<i>M. macrostachyum</i> gap	Gap with <i>M.</i> <i>macrostachyum</i> removed	Closed Forest understorey
Results of this study	Total germination	+ (-)	+ (+)	+ (-)
	Germination time	+	-	+
	Survival	- (-)	+ (+)	- (++)
	Growth	-	+	-
Inhibition Model	Total germination	-	+	-
	Germination time	+	-	+
	Survival	-	+	-
	Growth	-	+	-

In addition to existing in large and small gaps, *M. macrostachyum* patches can be overtopped by a normal density of large diameter trees (see Chapter 2). Here the middle storey is greatly reduced and there is a general paucity of seedlings of other species. How is the forest canopy maintained? Brokaw (1983) suggests for herbaceous *Aechmea magdalenae* colonies on Barro Colorado Island, Panama, which similarly occur in patches, that canopy trees are still recruited, but from a much smaller pool of

saplings. The limited amount of tree regeneration that gets through the *M. macrostachyum* layer, perhaps in openings created by large herbivores, may be sufficient to maintain a canopy over the herbaceous layer.

Gorillas are thought to be important in the dispersal of tree seeds such as *T. tetraptera* and *M. arboreus*. They deposit many seeds at nest-sites in *M. macrostachyum* patches. Flattening of leaves through nest-building and feeding may provide a gap in the *M. macrostachyum* canopy where seedlings can establish. However, the hardy rhizomes of *M. macrostachyum* are able to survive uprooting by elephants and gorillas (personal observation), and the leaves grow back quickly. Ad-hoc experiments where patches were *M. macrostachyum* leaves were manually flattened show that they grow back to full canopy cover within a few months, which may take away any advantage given to seedlings. Light demanding species such as *T. tetraptera* and *M. arboreus* may then find survival difficult. Other personal observations in *M. macrostachyum* patches which have been razed and uprooted by elephants show similar results with vigorous re-sprouting from rhizomes and re-domination of the gap by *M. macrostachyum* (See figures 4.10 - 4.12).

These observations address the follow-on test of Connell and Slatyer's models: the cause of death of early colonists. The inhibition model would be supported if *M. macrostachyum* would have to be disturbed by external factors in order for other species to invade. *M. macrostachyum* seems to exhibit characteristics of a 'super-inhibitor', in that even when disturbed by elephants, it returns to dominate a gap.

Figure 4.10 Photo taken in July 1999 in a *M. macrostachyum* patch that had been razed by elephants. Short *M. macrostachyum* leaves are re-emerging from underground rhizomes.



Figure 4.11 Same perspective three months later in October 1999. Other species of plants are present.



Figure 4.12 Same perspective in July 2000, one year after original photo was taken. *M. macrostachyum* has completely re-dominated the gap and leaves are almost up to full height. Note the man standing in the middle of photo.



Possibilities for further research

In order to have a complete test of the models, the response of a shade tolerant species to *M. macrostachyum* cover should be studied. Due to the lack of germination by *Greenwayodendron suaveolens*, this could not be tested in this study.

If trees above *M. macrostachyum* patches are recruited from a reduced seedling pool, *M. macrostachyum* presence may influence the species composition of the forest. This could be tested by examining the abundance of seedling and sapling populations of selected tree species in closed-canopy forest vs. *M. macrostachyum* patches and gaps with other vegetation.

Short-term measurements of seedling performance in *M. macrostachyum* patches give an indication of possible interactions between herbs and trees. Longer-term observations of the same data would be far more valuable in showing what percent of seedlings can eventually make it through the *M. macrostachyum* canopy. It would also be of interest to know how long seedlings can survive below *M. macrostachyum* canopy.

Finally, controlled germination experiments using herbivore exclusion cages (always difficult with elephants), would be useful to clarify the role of herbivores in *M. macrostachyum* patch dynamics.

5 Herb responses to different light environments

5.1 Introduction

Plant species distributions have been shown to be determined by their physiological responses to the environment. Characteristics such as photosynthetic capacity, light compensation points, and nutrient-use efficiencies are reflected in the germination, growth, survival and reproduction rates for species in different habitats (Chazdon *et al.* 1996, Fredeen *et al.* 1996, Mulkey *et al.* 1991, Clark and Clark 1987, Kitajima *et al.* 1996). Ecological studies of plant species therefore, may offer explanations for observed distributions.

Germination requirements of a particular species play an important role in controlling their occurrence in different forest light environments. Raich (1990) found that optimal germination conditions determined for a species were similar to the distribution of adult individuals in mature and secondary forests. Several herb species which cannot survive as adults in shaded environments may persist in the forest understorey seed bank until light levels are increased through disturbance. However, Smith (1987) determined that most understorey herb species in a neotropical forest were poorly represented in the seed bank.

This may be because most forest understorey species persist in deep shade, taking advantage of the higher light conditions of occasional tree fall gaps to increase growth and reproduction (Mulkey *et al.* 1991, Levey 1990, Pinero and Sarukhan 1982, Smith *et al.* 1987, Collins and Pickett 1988). This suggests a scenario of suppression and release for most understorey herbs, not unlike that described for canopy tree seedlings (Whitmore and Brown 1996, Burton and Mueller-Dombois 1984, Van Der Meer *et al.* 1998, Augspurger 1984). Shade-tolerant herbs may have flexible photosynthetic responses, allowing them to adapt physiologically and morphologically to sudden changes in light levels such as that caused by a tree-fall gap.

Some studies of neotropical forest understorey herbs suggest that a high photosynthetic light saturation point is important to exploit a large treefall gap

(Rundel *et al.* 1998). This allows herbs to avoid photoinhibition and achieve faster growth rates and reproduction in higher light conditions while the conditions persist. However, high light saturation points have been shown to be correlated with high compensation points, meaning that plants able to take advantage of high light situations are poorly adapted to assimilating in low light conditions of the forest understorey (Bazzaz and Pickett 1980, Mulkey *et al.* 1993, Mulkey *et al.* 1991, Collins *et al.* 1985). Strongly gap-dependent species are likely to suffer mortality or decrease in size when the gap closes over.

Central African forest herbs might be expected to follow similar patterns. Published observations on the occurrence of herbaceous formations suggest that some species such as *M. macrostachyum* and *Aframomum laurentii* are capable of exploiting the very high light levels of abandoned agricultural fields (Lubini 1986, Bebwa 1990). These species also commonly colonise early successional or logged forest (Dhetchuvi *et al.* 1996), and many species appear in the understorey of closed forest. Species clearly differ in their light responses and some may show flexibility in their light requirements/tolerances which allow them to exploit a wide range of environments. This may explain why some herbs contribute to the make up of Marantaceae forests in some parts of central Africa, but also exist as isolated individuals in closed-canopy forest in others.

Reproductive success may also reflect optimal environments for some plant species. Many plant species can establish new individuals via both asexual and sexual reproduction. A benefit-cost model of reproductive strategy developed by Loehle (1987) predicts the ratio of allocation to sexual to vegetative reproduction based on a suite of factors. He describes several rules that act as testable alternatives for predicting the relative energy allocation to these two reproductive modes. One prediction is that increased resource levels (such as light or nutrients) will result in increased sexual reproduction. This may be because seed production is more nutrient costly (by weight) than vegetative production (Harper 1977, Muir 1995), or because the plant requires high light levels for germination and can sense the favourable conditions. Increased sexual allocation at low resource levels may be an attempt at dispersal to more favourable environments, either spatially or temporally. The exact

response of a species depends on its shade-tolerance, density-dependence, and the available resources. Patterns of reproductive allocation for *M. macrostachyum* may therefore be an indication of plant stress and colonisation strategy in different light environments.

M. macrostachyum distribution in the Ndakan study area was shown to be closely correlated with canopy openness (Chapter 2). In closed-canopy forest, Fay (1997) noted that *M. macrostachyum* seemed to occur in a ‘dwarf’ form, suggesting that it was suppressed by low light levels. It is unknown if these smaller individuals originated from seed germination in the understorey, or if they are remnants of larger individuals which grew in gaps that have since closed. The latter presents some interesting questions as to how long these suppressed herbs can survive in the understorey. Those species that can survive and grow in the understorey are more likely to be present when gap formation occurs, allowing more rapid gap colonisation and a competitive advantage against other species.

The response of *M. macrostachyum* to shaded conditions is an important aspect of its ecology which could elucidate whether the species is an obligate gap coloniser, or merely exploits temporary light conditions to increase growth and reproduction. Such information is crucial to understanding the patch dynamics of *M. macrostachyum* and the pathways by which patches form in the Ndakan study area. Furthermore, response to current Ndakan light environments will clarify the status of *M. macrostachyum* in the area, and confirm whether it is slowly disappearing after some large-scale former disturbance, or if it is continuing to colonise gaps in this forest.

5.1.1 Objectives

The aim of this chapter is to determine how the autecology of *M. macrostachyum* relates to its observed patterns of abundance and distribution. The questions addressed in this chapter focus on germination, growth, and reproduction in different light environments for *M. macrostachyum* and three other sympatric species in the same family. Specific questions asked are:

1. What are the differences in growth and reproduction between understorey and gap plants? Do ecological strategies (the relative importance vegetative vs. seed production) change in different light environments?
2. Do herbs in closed-forest understorey continue to grow (both in number of leaves and leaf height), or do they eventually die out?
3. What is the maximum rate of spread via rhizomes for *M. macrostachyum*?
4. Can *M. macrostachyum* germinate under closed forest canopy? What are the preferred germination environments for the different species?
5. To what extent are herb distributions related to their ecologies?

5.2 Methods

5.2.1 Description of species

Three other species of Marantaceae, common in the Ndakan study area and with similar morphologies, were chosen for an ecological comparison with *M. macrostachyum*. These species were *Sarcophrynium schweinfurthianum*, *Ataenidia conferta*, and *Megaphrynium trichogynum*. Detailed species descriptions are given in (Koechlen 1965). Here I describe characteristics that are especially relevant to this study.

All species have similar leaf morphologies, with a broad leaf blade emerging from an underground rhizome on a long petiole. The rhizomes extend horizontally below the ground, with successive leaves emerging from the rhizome. Slight differences exist in that *M. macrostachyum* generally sends out new leaves from one or both ends of the rhizome, extending the length of the stem in a linear manner (see Figure 5.1). The other species exhibit more leaf clumping, with new leaves often emerging out of the middle of a fan of older leaves, though they also emerge individually. *M. macrostachyum* bears inflorescences and fruit stalks about 2/3 of the way up the leaf

petiole. There are 2-3 seeds (about 1 cm long) per tri-lobed fruit. *M. macrostachyum* was the most common of the four species, found in 37% of plots surveyed (chapter 2).

Figure 5.1 Photo of whole-plant structure of *M. macrostachyum*. Label in photo is approximately 10 cm across.



A. conferta is exceptional in that it has an aerial stem, which branches and produces aerial rhizophores, giving it extra means of vegetative reproduction. In Ndakan, it reaches heights of approximately 3 m. It makes up part of the Marantaceae forests on Mt. Cameroon (Letouzey 1968), but does not form large, dense patches in the C.A.R. It was found in 24% of plots, and is often mixed with *S. schweinfurthianum*. Seeds are small (2-3 mm) and are borne inside leafy purple bracts emerging from the petiole.

M. trichogynum is the least common of the three species. It was only found as rare, scattered individuals in closed-canopy forest or in small gaps. It was observed to have a maximum leaf height of approximately 2 m in the Ndakan study area. Fruits are very similar to those of *M. macrostachyum*, though slightly smaller. It was not encountered in any of the survey plots.

S. schweinfurthianum was encountered in 22% of survey plots. It is known to be a component of Marantaceae forests in parts of Congo-Brazzaville (Brugière *et al.* 2000, de Foresta 1990, Maisels 1999), but does not occur in large dense patches in the C.A.R. Its maximum height is 3 m tall. The fruits are ovoid, and generally contain 2-3 seeds (<1 cm in length).

5.2.2 Growth and reproduction

In July and August 1999 (wet season), approximately 60 plants of each species were marked within 30 m of a 5 km trail bisecting the study area. Marked plants were 50 – 350 cm tall with a minimum of four leaves. Relative canopy openness above each plant was measured with a canopy-scope (see chapter 2), giving a relative quantification of canopy openness. Of the 60 plants, 30 were located in understory conditions and 30 were in forest canopy gaps. In reality, canopy openness varied continuously from values of 1 to >25. Understorey was therefore classified as <5 as measured with the canopy-scope, and gaps were defined as canopy openness >5. The gaps were later divided into three different categories; small gaps (canopy openness 6-11), medium gaps (12-18), and large gaps (>18), with approximately 10 plants of each species in each gap size. The purpose of this division was to examine the response of each species to gaps of different sizes and determine the responses of each species to different habitats.

All leaves of each plant were marked with flagging tape to allow repeated censusing of individual leaves. Original plant height was counted as the mature height of leaves that emerged at the beginning of the study. Plants were censused each month and the following data recorded:

- Number of new shoots
- Mature height of new shoots
- Number of dead leaves
- Number of flowers or buds
- Number of fruits
- For *A. conferta*, new aerial rhizophores were counted

- The change in total leaf number (plant size) was measured at the first and final censuses
- The change in total underground rhizome length was measured at the first and final censuses by measuring the distance between the two most distant leaves of the same plant.

Data analysis

Because Marantaceae stems (except for *A. conferta*) grow horizontally underground in the form of rhizomes, the Relative Growth Rate of plants was measured in two ways: the change in rhizome length, and the change in total number of leaves per plant over the duration of the study. Because growth was expected to increase with increasing plant size, Relative Growth Rates were calculated as

$$(\ln N_f - \ln N_0) / (T_1 - T_0)$$

Where N_f is the plant size (number of leaves or rhizome length) at the end of the study (T_1) and N_0 is the plant size or rhizome length at the beginning of the study (T_0). The measurement period was 1 yr for all plants.

Changes in plant height were analysed by comparing the original plant height to the mean mature height of all leaves that subsequently emerged for each plant. This value was the mean relative change in leaf height. Leaves were not counted if they did not reach maturity before the end of the study. It usually took 2-3 months for this to occur, so no leaf heights were included for leaves which emerged in the last two months of the study. Results were compared between gap sizes using GLM univariate analysis with month included in as a factor.

Larger plants have been shown to have greater reproductive output, so leaf production, leaf death, flowering and fruiting abundance were calculated as a proportion of the number of leaves per plant (Piñero and Sarukhàn 1982, Oyama 1990, De Steven *et al.* 1987). Differences between gap sizes for the above factors were analysed for each species using GLM univariate analysis (Minitab version 12).

5.2.3 Germination trials

Experimental design consisted of 1200 seeds of each species divided into: 3 light treatments x 4 replicate boxes per treatment x 100 seeds of each species per box. It was intended to include *M. trichogynum* in this study, but because it was relatively rare in the study site, sufficient seeds could not be found and it was not included. Seed boxes were constructed from local scrap timber. Each box (approximately 80 cm x 80 cm x 16 cm) was divided into four compartments, one for each species, and filled with a forest soil and sand mixture. Seeds were evenly spaced and planted just below the soil surface. All boxes were elevated at least 80 cm above the ground to avoid inundation during the wet season. The three light environments were shaded understorey, gap (approx. 30 m²), and clearing (approx. 1000 m²). Canopy openness at each site was measured using the canopy-scope. The clearing boxes were placed in three large former and current fields near the camp. Understorey and small gap boxes were placed within the forest near the three clearings.

Boxes were monitored for germinating seeds every two or three days for 7 months. However, the flooding that occurred almost immediately after planting in the late wet season was far more severe than expected and despite elevating them, 7 out of the original 12 seed boxes were submerged. Most of the submerged boxes were replanted in December 1999 after the flooding had subsided. These were monitored for 5 months. Sufficient numbers of seeds could not be found to completely repeat the experiment for *M. macrostachyum* at the later time of year. In total, after the replanting, there were 4 boxes in the closed forest understorey (one having only 81 seeds of *M. macrostachyum*), 4 in gaps (only 3 for *M. macrostachyum*), and 2 in large clearings.

Data analysis was done by comparing light treatments for each species using Kruskal-Wallis one-way analysis of variance.

5.3 Results

5.3.1 Growth and reproduction

The total number of plants sampled was reduced by the unforeseen affinity that elephants had for the flagging tape used to mark the leaves. During the dry season, passing elephants singled out marked plants and severely trampled them. Although most trampled leaves subsequently died, the plants generally survived. Thirty-two plants out of a total of 221 were trampled by elephants: 5 in the understorey, and 27 in gaps. *M. macrostachyum* was hardest hit, losing 15 of the 63 plants originally marked. Table 5.1 shows the number of plants of each species which were censused for the entire year in each light environment. *M. trichogynum* was almost exclusively found in the understorey. Only four were found in small gaps.

Table 5.1 Number of plants censused in closed-forest understorey and gaps of different sizes.

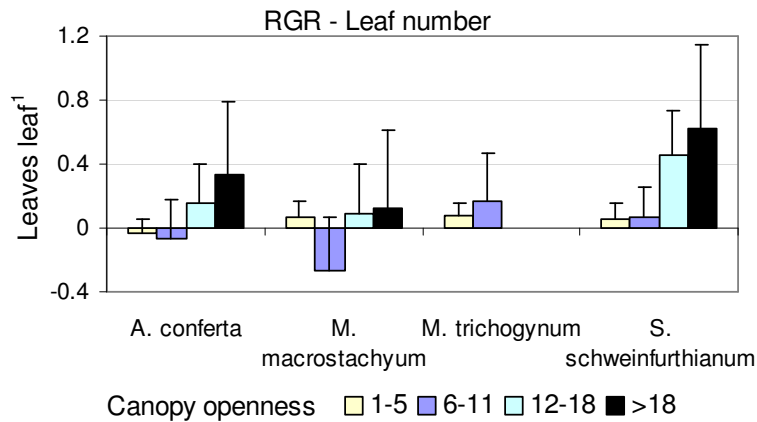
Canopy openness	<i>M. trichogynum</i>	<i>A. conferta</i>	<i>S. schweinfurthianum</i>	<i>M. macrostachyum</i>	Total
1-5	35	32	30	30	127
6-11	4	6	7	8	25
12-18	0	8	11	7	26
>18	0	4	4	3	11
Total	39	50	52	48	189

Relative Growth Rate -- number of leaves

Figure 5.2 summarises the mean RGR for each species, grouped by canopy openness categories. Change in *A. conferta* leaf number over time varied significantly in different gap sizes ($F_{3,48}=6.52$, $p<0.05$). *A. conferta* in shaded understorey and small gaps had fewer leaves at the end of the study than at the beginning. But in large gaps, they increased leaf number by over 30% in one year. For *M. macrostachyum*, the change in total number of leaves per plant over time was not significantly different between canopy openness categories ($F_{3,45}=0.00$, $p>>0.1$). The overall decrease in leaf number in small gaps (canopy openness 6-11) seems to be due to elevated leaf death rates in January, during the dry season. No *M. trichogynum* were found in larger gaps, so change in leaf number was only for canopy openness less than 11. Differences for *M. trichogynum* were not significant ($F_{3,37}=2.17$, $p>0.1$). *S. schweinfurthianum* showed a positive relationship between plant growth and canopy openness

($F_{3,50}=13.52$, $p<0.01$). Plants in medium and large gaps were significantly larger at the end of the study than plants in small gaps and shaded understorey (Tukey's pairwise comparison $p<0.05$).

Figure 5.2 Relative Growth Rate for total number of leaves per plant. Canopy openness is grouped into four categories. Bars are 95% confidence intervals.



Relative Growth Rate -- rhizome length

Differences in rhizome growth between gap sizes were significant for *M. macrostachyum*, with small gaps having significantly longer rhizome growth than plants in large gaps (Figure 5.3). The largest increase in rhizome length over the 1-yr study period was from 128 to 188 cm for *M. macrostachyum* located in a small gap. For the other three species there were no significant differences between light environment and rhizome growth rates.

New leaf production

Results are summarised in Figure 5.4 for each species in different light environments. All species showed higher leaf production rates in gaps than in closed-forest understorey. *A. conferta* had significantly different leaf production in the three light environments ($F_{3,46}=14.09$, $p<0.001$). Tukey's pairwise comparison showed higher leaf production in large gaps than in small and medium gaps and closed forest understorey ($p<0.05$). *S. schweinfurthianum* showed increasing leaf production rates with canopy openness, but only some differences were significant due to high

variation within light environments (Overall $F_{3,48}=18.64$, $p<0.001$). *M. macrostachyum* produced more leaves in gaps than in understorey, though only small and large gaps were significantly different (Overall $F_{3,48}=11.88$, $p<0.001$).

Figure 5.3 Relative Growth Rate of rhizome length in different light environments. Error bars are 95% confidence intervals.

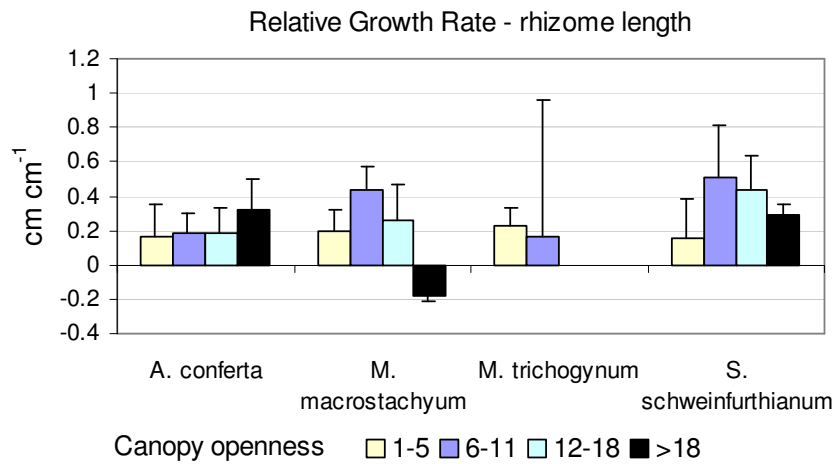
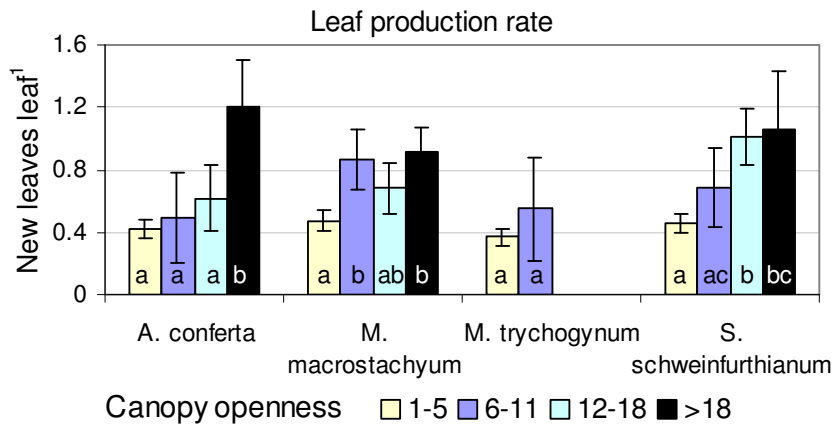


Figure 5.4 Leaf production rates given as total number of new leaves produced per leaf per year. Error bars represent 95% confidence intervals. Different letters represent significantly different leaf production rates within species.

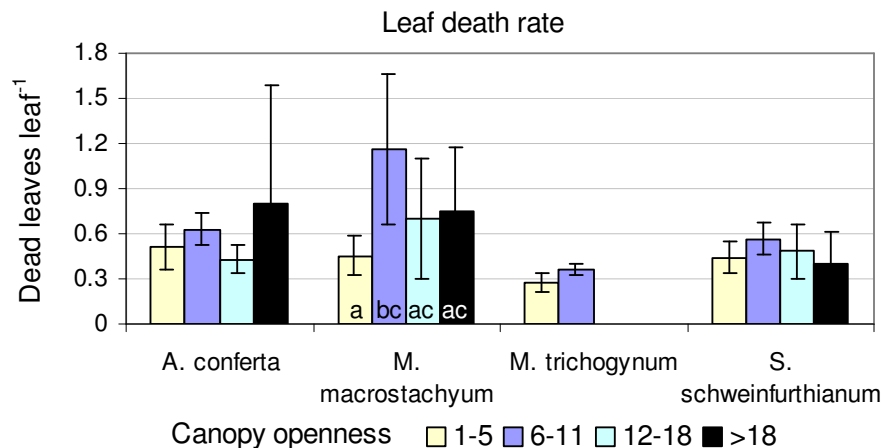


Leaf death rates

Leaf death rates fluctuated throughout the year, with a general tendency for all species to have higher leaf death rates (measured as number dead per total leaf number per plant) during the dry season. *M. macrostachyum* showed significant differences in

death rates between light environments ($F_{3,44}=5.12$, $p<0.005$). Tukey's pairwise comparison showed that the differences were between small gaps, with the highest death rate, and closed forest understorey ($p<0.05$). No other species showed significant differences in leaf death rates between light environments (Figure 5.5).

Figure 5.5 Leaf death rates given as total number of dead leaves per old leaf per year. Error bars represent 95% confidence intervals. Different letters represent significantly different leaf death rates within species.



Change in plant height

Figures 5.6 and 5.7 compare the heights of new leaves over the year to the heights of leaves produced at the beginning of the study. Almost all species showed a progressive decrease in leaf height in the understorey from August 1999 to May 2000 (the last time that leaves could be followed to maturity in this study). Apart from *A. conferta*, which produced shorter leaves primarily during the dry season (Jan and Feb), all species showed a trend of progressively decreasing leaf heights over the year. By the end of the study, new leaf heights had dropped an average of over 20% for each species.

Plants from all gap sizes were grouped together in Figure 5.7. New leaf heights were slightly greater than original leaf heights for the three species during the first half of the study, indicating that plants were getting taller or maintaining their original height. However, in March, after the dry season ended, successive leaf heights decreased. Only *S. schweinfurthianum* in gaps did not appear to decrease in height over time. It

produced taller leaves temporarily during the dry season. *M. macrostachyum* plants produced shorter leaves towards the end of the study period, on average, even in gaps. The decrease from March to May for all species in all environments may have to do with flowering and fruiting phenology. Plants may be investing extra resources into preparation for flowering and fruiting, which peaks in June and July for all four species (see Figures 5.14 and 5.15).

Figure 5.6 Mean relative change in height of successive new leaves from original height in closed-forest understory. Leaf heights measured for each month are a mean of those leaves which emerged in that month. Error bars represent 95% confidence intervals.

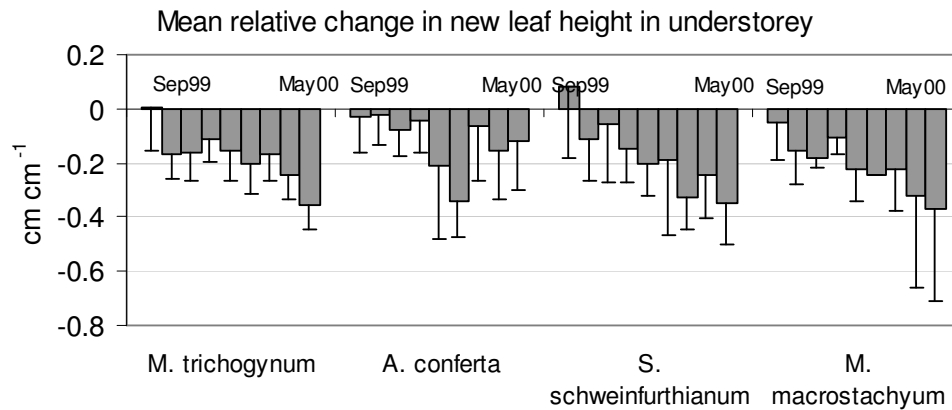
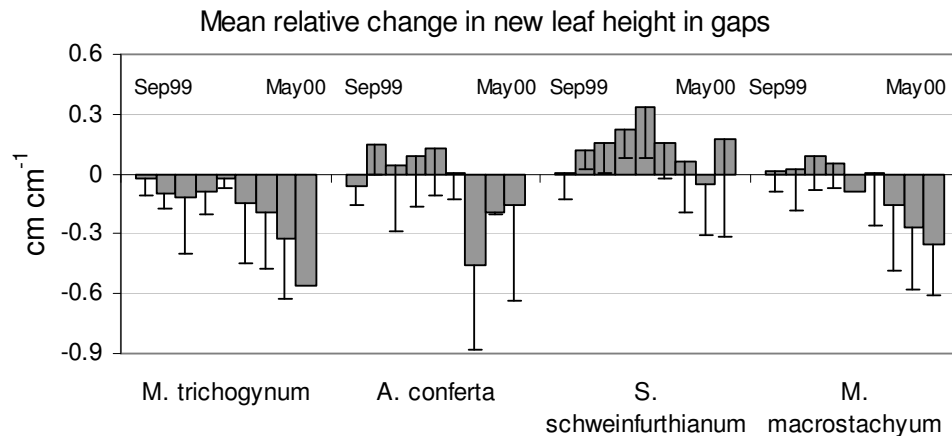
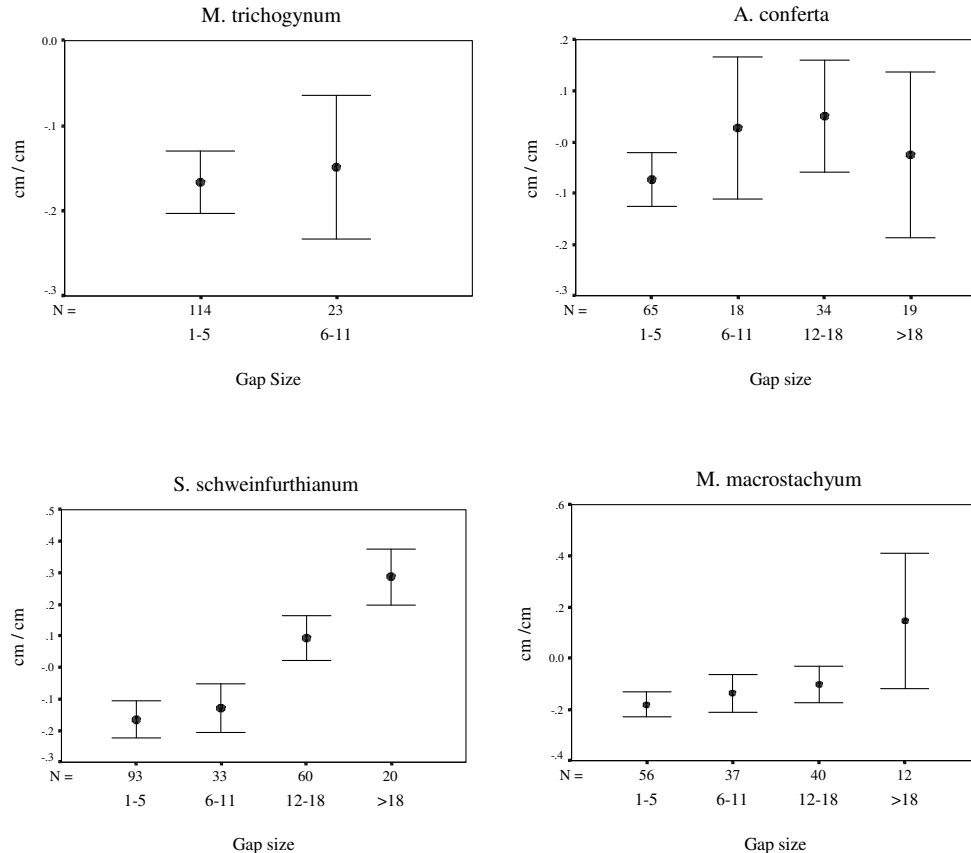


Figure 5.7 Mean relative change in height of successive new leaves from original height in all gaps. Leaf heights measured for each month are a mean of those leaves that emerged in that month. Error bars represent 95% confidence intervals.



The mean relative change in new leaf heights over the year for each species are compared for different gap sizes in Figure 5.8. In general, understorey conditions caused all species to produce shorter leaves over the year. *M. trichogynum* showed no differences in change in relative leaf height between understorey and small gaps ($F_{1,119}=0.0$, $p>0.5$) and decreased in both. *A. conferta* had similar performance at all light levels ($F_{3,103}=0.998$, $p>0.1$) and plants stayed approximately the same height over the year. New *S. schweinfurthianum* leaves showed significant differences in relative changes in leaf heights in different gap sizes ($F_{3,172}=20.93$, $p<0.001$). Tukey's pairwise comparison showed that plants in large gaps had a higher relative change in leaf height (and had positive growth over the year) than all other light environments ($p<0.05$). Plants in medium-sized gaps also had positive growth of new leaves and the relative change was significantly greater than small gaps and forest understorey where growth was negative ($p<0.05$).

Figure 5.8 Mean relative change in new leaf heights in different light environments as a percentage of leaf height at the beginning of the study. Error bars are 95% confidence intervals.

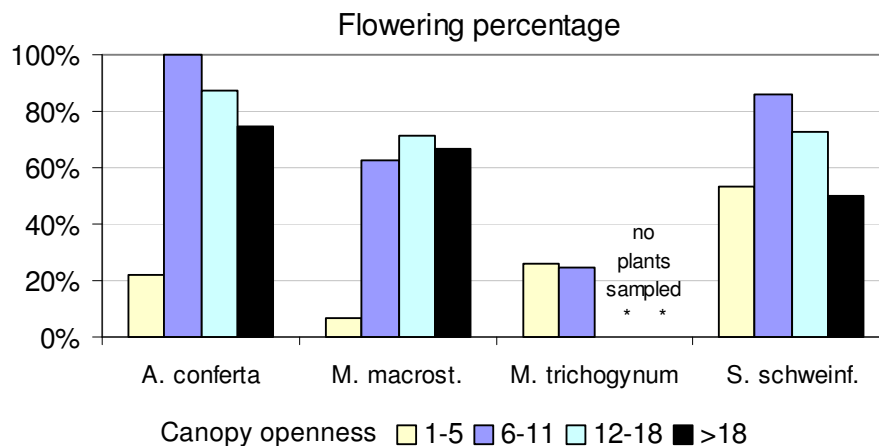


M. macrostachyum only exhibited positive leaf height growth in the largest gaps. There was a significant difference between light environments ($F_{3,111}=4.082$, $p<0.01$) with Tukey's pairwise comparison showing that large gaps had significantly higher relative growth than closed forest understorey, but no other differences were significant ($p<0.05$).

Probability of flowering and fruiting

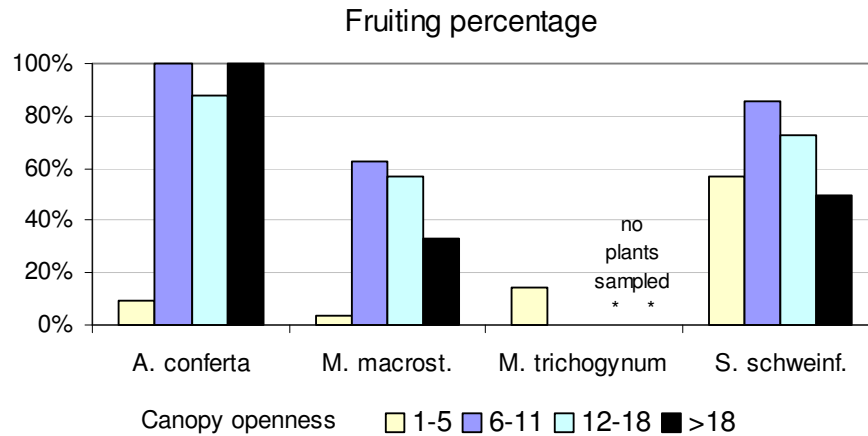
Figures 5.9 and 5.10 summarise the different flowering and fruiting patterns exhibited by each species in different light environments. *M. trichogynum* had similar flowering percentages between understorey and small gap sites. No data were available to compare with medium and large gaps. *A. conferta* had just over 20% of understorey plants flowering, and 100% of plants in small gaps. Flowering decreased to 75% in large gaps. *S. schweinfurthianum* had the highest percent of plants flowering in the understorey (53%). It was most likely to flower in small and medium-sized gaps. Only half of *S. schweinfurthianum* plants flowered in large gaps. *M. macrostachyum* showed the most dramatic differences between understorey and gaps in flowering percentages. Less than 10% of *M. macrostachyum* flowered in the understorey, whereas 60-70% of plants flowered in gaps of all three sizes.

Figure 5.9 Percent of plants flowering during the study in different light environments.



Fruiting patterns closely resembled those of flowering in different light environments. *A. conferta* was the most successful fruiter in gaps, with 93% of plants producing fruit (Figure 5.10). *M. macrostachyum* fruited less frequently in large gaps than it flowered, with just one-third of plants fruiting. However, the sample number of plants in large gaps was only 3, so it is possible that fruits were missed on one plant.

Figure 5.10 Percent of plants fruiting during the study in different light environments.



Flower and fruit abundance

Total number of flowers and fruit in relation to plant size (number of leaves) was compared between light environments for each species. Results were very similar for both flowering and fruiting (Figures 5.11 and 5.12). However, variance was extremely high for all light environments and all species. Therefore, statistical analyses showed no significant differences between light environments (Results not presented). Abundances did resemble patterns for probabilities of flowering and fruiting for each species. Of note is the low average fruiting and flowering abundances of *M. macrostachyum* in large gaps.

Figure 5.11 Relative flowering abundances of each species in different light environments. Error bars show 95% confidence intervals.

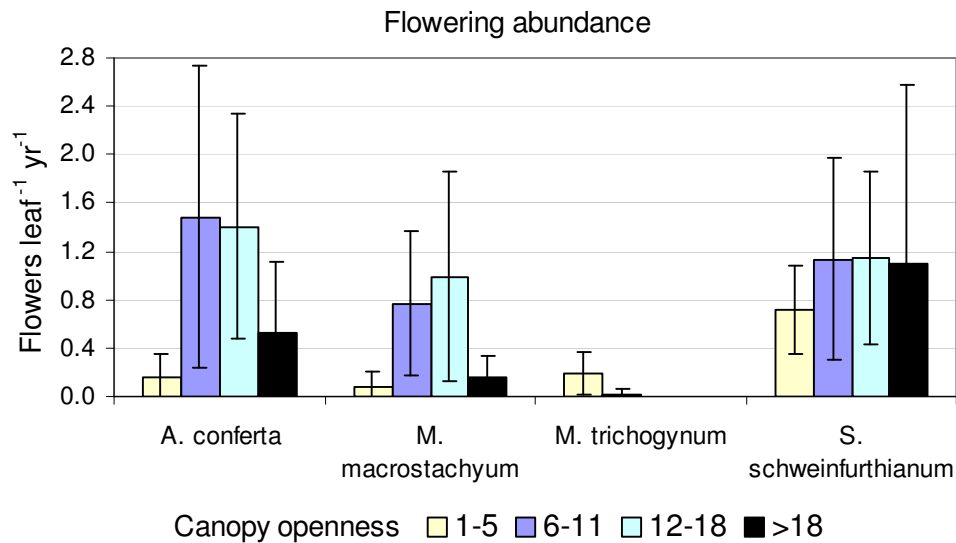
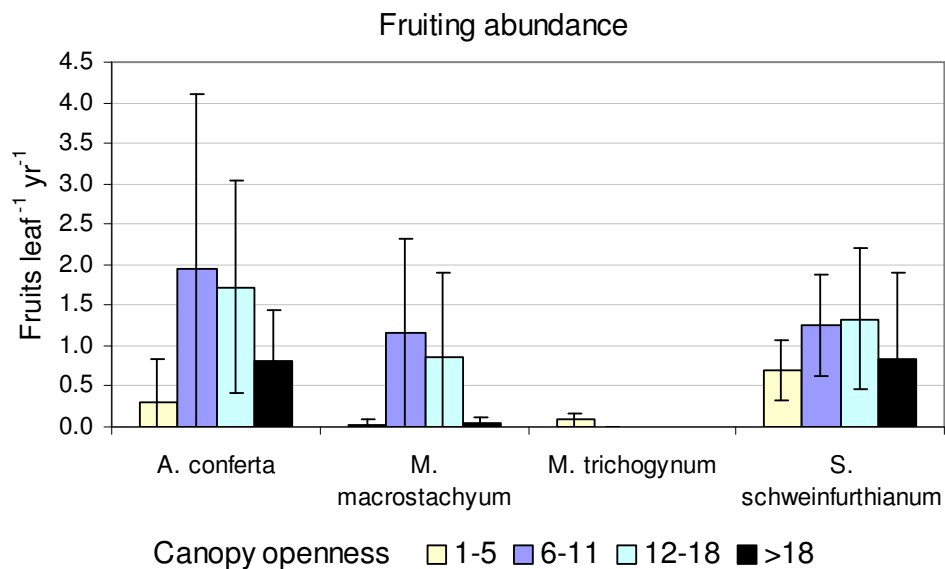


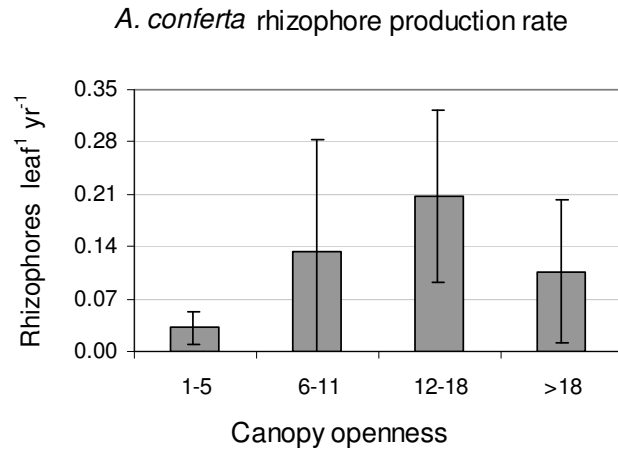
Figure 5.12 Relative fruiting abundances of each species in different light environments. Error bars show 95% confidence intervals.



Aerial rhizophore production

A. conferta rhizophore production rates were significantly different between light environments ($F_{3,46}=6.92$, $p<0.005$). Tukey's pairwise comparison showed that medium gaps had significantly higher rhizophore production rates than closed-forest understorey ($p<0.05$).

Figure 5.13 Rhizophore production rate for *A. conferta* in different light environments. Error bars are 95% confidence intervals.



Phenology

Figures 5.14 and 5.15 illustrate the flowering and fruiting phenologies of each species over the course of the one-year study period. Flowering and fruiting are at a maximum from May to July for all species and at a minimum during the dry season from December to February.

Figure 5.14 Flowering phenology of four Marantaceae species in the Ndakan study area.

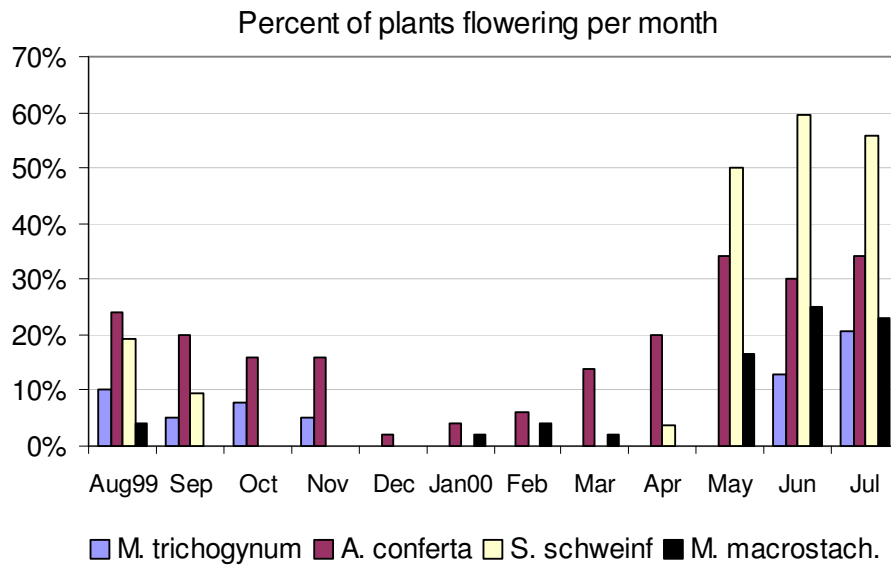
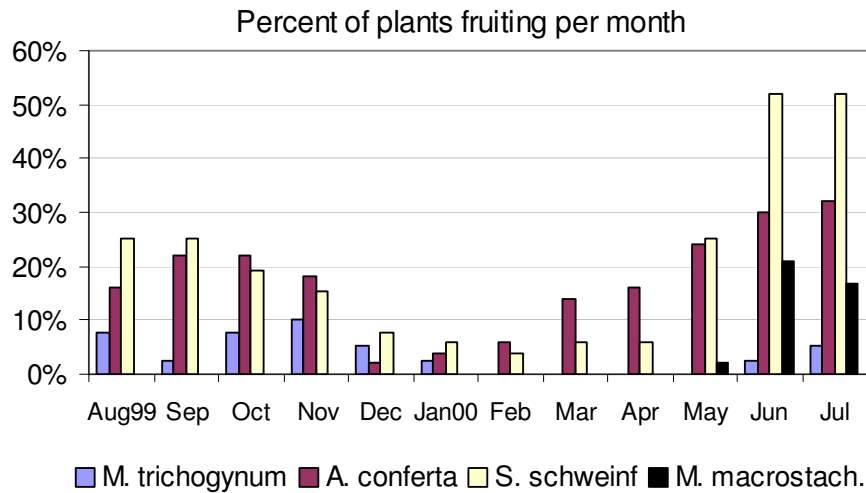


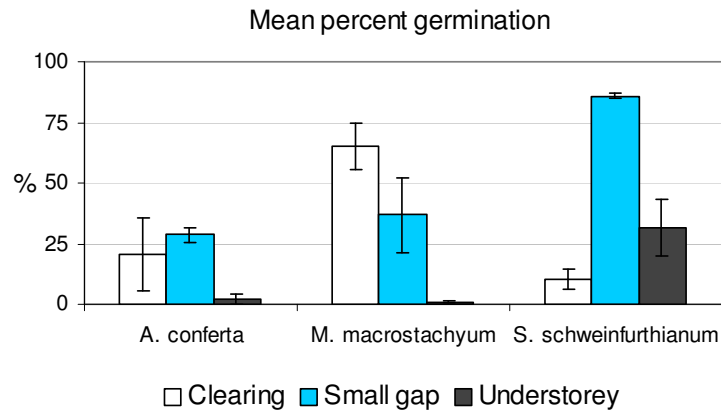
Figure 5.15 Fruiting phenology of four Marantaceae species in the Ndakan study area.

5.3.2 Germination

Canopy openness for closed-forest understorey boxes averaged 1-2 on the canopy-scope, and in gaps had values ranging between 11 and 15. Surprisingly, despite spending several weeks under water, many of the seeds in flooded boxes subsequently germinated, perhaps suggesting another mode of dispersal for Marantaceae herbs in seasonally flooded forest. These were only casual observations, as the experiment was re-done with different seeds and fresh soil.

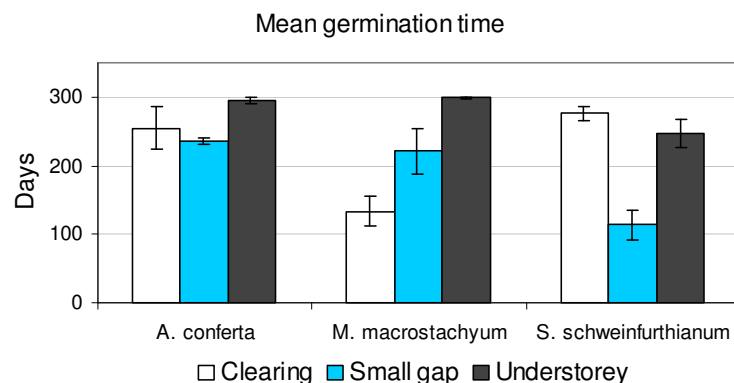
Kruskal-Wallis test for differences in mean percent germination of *A. conferta* at different light levels was significant ($H=6.22$, $df=2$, $p<0.05$). Results show that *M. macrostachyum* had the highest germination rate in large clearings and had almost no germination in closed forest understorey. *S. schweinfurthianum* preferred small gaps for germination and had lowest germination percentages in large clearings. It germinated more in closed forest understorey than the other two species. *A. conferta* had almost no germination in closed forest understorey, and approximately 25% germination in small gaps and large clearings (Figure 5.16).

Figure 5.16 Mean percent germination in different light environments. Error bars represent 95% confidence intervals.



Monitoring of the seed boxes stopped after approximately 7 months (unflooded boxes) and 5 months (replanted boxes). In order to calculate mean germination time, seeds that never germinated were given a germination time beyond the end of the study (arbitrary value of 300 days). Therefore the maximum germination time for boxes in which no seeds germinated was 300 days. Results of mean germination time in different light environments mirror germination percentages for each species (see Figure 5.17).

Figure 5.17 Mean germination time of seeds in different light environments. 300 days was given as the cut-off for seeds which did not germinate during the study period. Error bars are 95% confidence intervals.



To investigate whether these ungerminated seeds were dead or merely dormant, two of the closed forest understorey seed boxes which hadn't been flooded were moved to the edge of a large clearing in May 2000. Results are shown in Table 5.2. All species

responded to the change of environment with almost immediate germination, indicating that they can remain dormant in the forest understorey for at least 7 months.

Table 5.2 Change in total germination percentages in boxes that had been in closed forest understorey from October 1999 to May 2000 and then moved to the edge of a clearing.

	Seed Box	<i>M. macrostachyum</i>	<i>A. conferta</i>	<i>S. schweinfurthianum</i>
% Germinated	a	0	0	20
Oct - May	b	2	0	54
% germinated	a	72	45	46
May-Aug	b	54	28	81

5.4 Discussion

Cautions

The decision to divide the gap category into different sized gaps, although making behavioural patterns among species easier to distinguish, reduced the power of the analyses. Patterns might have been clearer if more individuals had been sampled in each gap size (or if fewer had been trampled by elephants). However, there may have been other causes for variation within gap categories that were not investigated. Differences in soil types across the study area might have contributed to the variance in performance of each species. Data from chapter 2 show that both *A. conferta* and *S. schweinfurthianum* distribution is significantly correlated with soil pH. Furthermore, gap conditions were taken solely on the canopy-scope measures, and ages or causes of formation were not known. Small gaps may have been formed by recent branch-falls, or from large, old gaps which had almost closed over. This could ultimately have an effect on the behaviour of each species. For example, Dirzo *et al.* (1992) demonstrated that for understorey herbs in Mexico, leaf production and percent of plants flowering were highest in intermediate-aged gaps. Individual plant ages might also have contributed to variation in responses to environmental conditions. Nothing is known about the lifespans of these species.

5.4.1 *Megaphrynium macrostachyum*

M. macrostachyum appears to be a very light demanding species. Leaf height changes per plant were negative in all but large gaps. The probability of flowering and fruiting was extremely low in the understorey. Germination took place primarily in large gaps and not at all in closed forest understorey. Therefore, *M. macrostachyum* ecology points to patch formation via seed germination in disturbed areas, with seeds remaining dormant in shade. These results suggest that *M. macrostachyum* has a high light compensation point, which allows it to grow quickly and dominate a clearing, but results in reduced growth in the understorey. Givnish (1988) proposed that for herb species, high light compensation points were correlated with greater investment in support structures. *M. macrostachyum* is by far the tallest of the non-lianescent Marantaceae species. Its tall, fast-growing leaves are likely to contribute to its competitive ability in large gaps and clearings.

M. macrostachyum has a high leaf turnover rate, as demonstrated by high leaf production and death rates, and relatively steady leaf number for the plants measured in this study. High leaf turnover is associated with high photosynthetic rates in a more gap-dependent species. This may result in a whole-plant negative carbon balance when light is limiting. Rapid growth and reproduction require high rates of carbon gain in short-lived leaves, which can amortize their cost quickly (Mulkey *et al.* 1991, Bongers and Popma 1990). Leaf turnover was slightly less for *A. conferta* and *S. schweinfurthianum* indicating that they may be more shade-tolerant. High leaf turnover may be a mechanism for *M. macrostachyum* to spread. The maximum observed rhizome spread for *M. macrostachyum* was 60 cm over a one-year period in a small gap. Successive leaves can grow simultaneously out from the ends of a rhizome as older leaves in the middle die off. As the rhizome rots and breaks apart, two now separated clones can continue growing in opposite directions. Depending on the lifespan of such clones, it is possible that large *M. macrostachyum* patches may be composed of clones from one or a few individuals. Given this, it is unclear why rhizome length decreased for *M. macrostachyum* in large gaps. Closer inspection of the raw data showed that 2 out of the 3 plants had large increases in leaf number, and all had a high leaf production rate. However, rhizomes may branch laterally, causing new leaves to emerge in the middle of the plant (Cain and Damman 1997). The

spatially concentrated leaf production in large gaps may contribute to patch formation by creating a dense leaf layer that blocks out light, and a dense rhizome layer that contributes to root competition. Evidence from other clonal herb species also shows that rhizomes produced in early successional habitats are shorter than those produced in late successional forest (Cain and Damman 1997).

The relative importance of vegetative vs. sexual reproduction plays a key role in *M. macrostachyum* ecology as well. High leaf production in gaps, coupled with a decrease in number of fruit produced, indicates that sexual reproduction becomes less important than vegetative reproduction in *M. macrostachyum* patches in disturbed areas. This makes sense for existing *M. macrostachyum* patches, where its own seeds may not germinate under the herb canopy, and vegetative growth may be the only successful means of propagation.

Aggregated *M. macrostachyum* in large gaps may also suffer reduced flowering and fruiting abundance due to density-dependent effects such as intraspecific competition for nutrients. Such a response has been shown for temperate daffodils, where vegetative reproduction was positively associated with plant density (measured as three-dimensional growing space), and underground bulb weight and flower production were negatively associated with density (Barkham 1980). However, several studies of tropical shrubs suggest that plants in natural higher densities produced fruit more successfully because of reduced flower predation (Piñero and Sarukhàn 1982), and increased fertilisation success (Silander 1978). The density of *M. macrostachyum* was not taken into consideration in this study. Not all individuals in large gaps were necessarily part of a patch and there might have been patches in some of the medium-sized gaps. This limits the ability to interpret these data in terms of density-dependence. Further study is needed to determine the exact causes of reduced fruit and flower abundance for *M. macrostachyum* in large gaps.

Invasion of intact forest through the successive occupation of small gaps for *M. macrostachyum* seems unlikely. Small and medium gaps may allow some *M. macrostachyum* to germinate, but leaf number and plant height decreased for small-gap plants in this study. Most likely, *M. macrostachyum* plants in small gaps are

remnants of a larger gap. Because inflorescences and infructescences are borne on the newest leaves, a high leaf production rate in small and medium gaps may contribute to the high probability of flowering and fruiting. Most of these seeds would end up in the seed bank unless dispersed by frugivores to other gaps.

5.4.2 *Ataenidia conferta*

A. conferta is an incredibly fecund species in gaps, with a very high probability of flowering and fruiting in gaps of all sizes. It fruits year-round, although less frequently in the dry season. However, the high probability of fruiting is offset by a very low germination rate of around 25% in gaps and clearings. Gap dependence for sexual reproduction is exhibited to some extent by a fruiting probability of 10% and almost no germination in closed-forest understorey. It does exhibit seed dormancy in the understorey, which may ultimately give it a higher germination rate.

The contribution of rhizophores to *A. conferta* populations may be substantial in small and medium gaps, although long-term data on the survival and growth of rhizophores would be essential to verify this.

The mean change in leaf height for the year was highly variable but essentially 0% for all gap environments, and only slightly negative in the understorey. It appears to take advantage of gaps of all sizes for sexual reproduction, growing in leaf number in medium and large gaps.

Through high rates of seed production and vegetative propagation, *A. conferta* seems capable of taking advantage of disturbances to increase in abundance, contributing to the make-up of Marantaceae forests. However, its maximum height of about 3 m, low leaf height increments, and dependence on soil pH may be the reasons it does not become a dominant species in Ndakan.

5.4.3 *Sarcophrynium schweinfurthianum*

S. schweinfurthianum showed a measure of flexibility in different light environments. For height growth and leaf production it performed better in gaps than in closed-forest

understorey, and performed best in large gaps. However, it fruited and flowered with similar frequency and abundance in understorey and gaps. Germination was best in medium-sized gaps and very poor in large clearings. *S. schweinfurthianum* is a major constituent of Marantaceae forests in the Odzala area of Congo, which may be due to less canopy cover (between 20 and 80%). However, it does not form patches with *M. macrostachyum* in Ndakan. Although it appears to perform well in all light environments, it may be constrained by soil nutrient status.

5.4.4 *Megaphrynium trichogynum*

M. trichogynum is rare throughout its range (D. Harris, pers. observation). Conclusions about how the ecology of *M. trichogynum* contributes to its distribution in the Ndakan study area are difficult to make due to its rarity. Where data were available, its performance in closed-canopy forest appeared to be similar to the other species in leaf production rate, change in new leaf height, change in leaf number, and leaf death rate. Where it appeared in small gaps it flowered less than other species and did not fruit.

5.5 Conclusion

In general, the other three species exhibited characteristics of light-flexible understorey species, which can persist in the understorey, but take advantage of gaps to grow and reproduce at elevated rates (Collins *et al.* 1985). *M. macrostachyum*, on the other hand, exhibits characteristics similar to ruderal species. Although it may persist for a time in the understorey, it is more likely to remain in the seed bank, where it may stay dormant for at least 7 months.

It has already been established in chapter 4 that once *M. macrostachyum* patches are formed within a gap, they can inhibit further tree regeneration. The other three Marantaceae herbs appear to lack the competitive ability of *M. macrostachyum* perhaps due to their shorter maximum height. This may result in their reduced abundance at Ndakan compared to *M. macrostachyum*. A further test of the inhibition model depends on the ability of the early successor to regenerate under its own canopy. *M. macrostachyum* seeds were not capable of germinating under the low light

levels of closed-canopy forest and needed at least a small light gap to germinate. Given that light levels under *M. macrostachyum* canopy are similarly low (chapter 4), it may not be able to germinate under its own canopy and may invest more in rhizome growth in large patches.

M. macrostachyum appears to be highly dependent on gaps for growth, reproduction, and germination. Bearing in mind the possibility of previous large-scale disturbance in the Ndakan study area, *M. macrostachyum* may be declining in relative abundance in this region as the forest gradually regenerates. Thus the density of *M. macrostachyum* in a forest may depend on the time since a previous large-scale disturbance.

Possibilities for future research

Plant phenology is known to fluctuate not only on a seasonal basis, but on a yearly basis as well (Chazdon 1992). Therefore a longer-term study of herb growth and reproduction, with more individuals in each gap size, may clarify some of the patterns seen in this study. The height decline in shaded understorey Marantaceae is especially of interest. Is this merely a seasonal consequence of the energy costs of flower and fruit production, or is it a symptom of an inability to assimilate at low light levels? What is the plant death rate for individuals in different light environments?

A large clue into the mechanisms of *M. macrostachyum* patch formation could come from studies of genetic relatedness within patches. The importance of clonal growth through the spread of underground rhizomes could be tested by using DNA fingerprinting techniques. Spatial distance between clones, combined with data from this study on rhizome growth rates could provide an estimate of the minimum life-span of a genetic individual.

Variation in growth data may be reduced by carrying out more controlled experiments using plants of known ages planted into different environments. It would also be interesting to directly test the assumption that *M. macrostachyum* cannot germinate under its own canopy with further planting trials.

The interaction with large herbivores and the consequences for patch maintenance or destruction is another potentially interesting area of research. Bullock (1981, 1978) showed that *Musa* (banana) plants and several species of *Aframomum* responded to damage by increasing the number of new shoots, thus eventually increasing overall stem density. Is this also the case for *M. macrostachyum*? Some preliminary indication of the consequences of elephant damage were gained from continued observations of the marked plants in this study which had been trampled. After six months new leaf height and total leaf number for most plants was still below original levels, indicating that damage significantly set back *M. macrostachyum* development and did not seem to result in increased shoot density. This supports the hypothesis that large herbivores may interrupt *M. macrostachyum* dominance and allow tree seedlings to reach the sapling stage. It could also indicate that *M. macrostachyum* is decreasing in abundance in Ndakan. However, in this case, trampling was severe (and apparently deliberate), and may not represent typical elephant or gorilla damage. Conflicting results were seen in 2 m² plots which had all leaves of *M. macrostachyum* cut to ground level (Natural seed germination experiment, chapter 4). After five months, plots had returned to their original densities and canopy cover by *M. macrostachyum*.

6 Conclusions

6.1 Thesis summary

Marantaceae forests are ubiquitous in lowland semi-evergreen forests in Central Africa and present an interesting puzzle regarding their origin and persistence. In Central Africa *Megaphrynium macrostachyum* often reaches high densities after logging, agriculture, or fire, but there is no evidence that its abundance in the closed forest of the Ndakan study area is attributable to recent disturbance. Most species of tropical forest herbs grow and reproduce more readily in sites that receive more light. However, *M. macrostachyum* is unusual because it occurs in this forest in large monodominant patches, where it appears to be capable of inhibiting or delaying tree regeneration. The main questions asked in this study were, what conditions are responsible for the formation of these patches, and what are the mechanisms by which these herbs compete with other forest species?

Experimental and descriptive studies of *M. macrostachyum* and other common herb species were carried out in the Central African Republic in order to understand the autecology and competitive interactions that control their local patterns of abundance and distribution.

The main findings of this thesis are summarised below:

- *M. macrostachyum* distribution was determined primarily by canopy openness and the abundance of sub-soil charcoal, unlike other common herb species in the Ndakan study area. These results strongly indicate that the abundance of *M. macrostachyum* and its existence in monodominant patches at Ndakan are related to some form of past disturbance involving fire. Other species, which included herbs in the families Marantaceae, Zingiberaceae, and Commelinaceae were associated with a variety of soil factors, primarily pH.
- Subsoil charcoal in the Ndakan study area was found in 47 out of 100 soil pits generally at depths between 10 and 60 cm. Charcoal was found most frequently at

a depth of 30-40 cm. In addition to charcoal, fragments of pottery were found in five soil pits between 20-60 cm of depth. These potsherds were luminescence dated to approximately 600 and 2200 years before present (BP). The pottery provides direct evidence that humans were living in the Ndakan area over the last two millennia. It also corroborates other evidence of potential human impact in the forest, notably the abundant fossilised seed deposits of the oil palm, of similar age, which were discovered throughout the region (Fay 1997). These data indicate that prehistoric human impact in this lowland forest region may be an important factor in modern forest structure, especially the development of Marantaceae forests. *M. macrostachyum* patches may be an indicator of such disturbance, persisting for hundreds if not thousands of years.

- Experiments in this study show that *M. macrostachyum* strongly inhibits the germination of seeds from the soil seed bank and from seed rain, and reduces the survival time of germinated seedlings. Within patches, cutting of *M. macrostachyum* leaves stimulated germination of seedlings of many different species whereas control plots remained more or less devoid of new seedlings. However, seedlings in plots where *M. macrostachyum* leaves were cut were quickly overshadowed as new shoots from underground rhizomes of *M. macrostachyum* vigorously re-emerged. Large herbivores may play a role in *M. macrostachyum* dynamics by occasionally creating areas of disturbance within these patches. It seems that this would have less of an impact on the growth and survival of *M. macrostachyum* than on young tree seedlings that have established below its canopy.
- Seeds from two common light-demanding tree species that were planted into tree-fall gaps, closed-forest understorey, and *M. macrostachyum* patches germinated equally and had similar survival rates in all three conditions. However, seedling height growth was significantly reduced in *M. macrostachyum* patches compared to tree-fall gaps that were occupied by other plant species. Growth rates for seeds planted into *M. macrostachyum* patches were not different from those of closed-forest understorey, supporting the hypothesis that *M. macrostachyum* acts to inhibit tree regeneration.

- The effect of the dense *M. macrostachyum* leaf layer on gap light conditions served to reduce Photosynthetically Active Radiation to the same levels as closed-forest understorey, approximately 1-2% full sunlight. It is suggested that this is the primary mechanism by which *M. macrostachyum* suppresses the establishment of other plant species. *M. macrostachyum* patches also inhibit tree seedling establishment through below-ground competition from roots and rhizomes.
- *M. macrostachyum* is a highly light-dependent species. The seeds exhibited dormancy in understorey light conditions for up to 7 months and germinated most successfully in large clearings. The length of new leaves became progressively shorter over the one-year study period in all but the largest gaps, even though leaf number increased for most plants. These factors suggest that invasion of intact forest through the colonisation of small gaps is unlikely. Smaller *M. macrostachyum* plants in closed-forest understorey are almost certainly remnants from individuals which established in gap conditions that have since closed over. In large patches where *M. macrostachyum* leaves reduce light conditions to that of closed-forest understorey, *M. macrostachyum* seeds are unlikely to germinate. Vegetative growth through rhizome expansion is therefore likely to be important for the maintenance of patches.

In conclusion, the *M. macrostachyum* patches in the Ndakan study area appear to have originated as much as several thousand years ago through extensive forest degradation either through climate change or the action of humans. It is likely that the succession of this forest may have been extensively delayed by the presence of *M. macrostachyum* patches. However, our knowledge of the ecology and patch dynamics of *M. macrostachyum* suggests that will suffer a gradual reduction in abundance as the forest matures.

6.2 Long-term tropical forest succession

How long does tropical forest succession take? This question is crucial as rainforests are under increasing threat from direct and indirect human impacts, including commercial logging, mining, and conversion to farmland. Data on long-term forest

succession is scarce, but those available are highly variable. Hartshorn (1980), working in neotropical forest in Costa Rica, proposed that tropical forests were very dynamic, with high tree turnover rates due to natural tree death. Hartshorn (1978) used gap size and frequency at La Selva to estimate a mature forest turnover rate of 118 ± 27 years. He therefore suggested successional rates of less than 500 years for tropical forests, even for old-field succession. However, this theory does not take into account the fact that gaps do not appear randomly and may repeat more frequently at certain sites (Young and Hubbell 1991), and tree death-rates are certainly species-specific.

Growth of pioneer trees is very rapid, and secondary succession can occur within a matter of years (Swaine and Hall 1983). However, continued succession from secondary forest to mature forest may take hundreds of years due to the very slow growth of mature forest species. For example, forests in the Darien, Panamá that had been cultivated for thousands of years by ancient agriculturalists were abandoned 350 years ago with the Spanish Conquest. Although the forest there now appears pristine, pollen data indicates that it is still in a process of recovery (Bush and Colinvaux 1994). A similar scenario of prehistoric shifting cultivation exists for the Xingu River Basin in Brazil, but large areas of the forest there are still secondary in appearance and are described as 'liana forests'. Forests in Nigeria classified as late secondary vegetation contain evidence of previous anthropogenic disturbance 700-750 years ago (White 1999). The effects of 19th century anthropogenic disturbance on the current forest composition in the Solomon Islands was thought to be greater than the impact of recent cyclones (Burslem *et al.* 2000). These studies give a minimum time-span for recovery, given that the forests mentioned still exhibit characters of secondary forests.

Permanent destruction of forests is likely only to occur on extremely infertile soils (Sim *et al.* 1992), where forests are in decline for climatic reasons (Laurance and Williamson 2001), or where destruction is so extensive as to eliminate propagule sources and dispersers. However, where regeneration is still possible, forest recovery after disturbance may be significantly delayed by the invasion of aggressive early secondary species which are able to inhibit further tree regeneration (Fike and Niering 1999, Niering *et al.* 1986, Russell *et al.* 1998, Schnitzer *et al.* 2000). Marantaceae forests in Central Africa probably act to inhibit tree regeneration after past large-scale

disturbance or climate change, seeming to result in a permanently different forest type. Further research is needed to determine if the various Marantaceae forests in Central Africa had similar disturbance-related origins, and to further test the temporal extent to which they inhibit tree regeneration.

6.3 Avenues for further research

In order to verify the development of Marantaceae forests following disturbance and ascertain the rates of forest regeneration, a longer-term record is necessary. One such record can be obtained through the palaeoecological record, using fossil pollen, plant macrofossils, charcoal and stable isotopes preserved in sedimentary sequences to reconstruct past vegetation dynamics (Elenga *et al.* 1994, Moscol-Olivera and Roche 1997, Dechamps *et al.* 1988, Bush *et al.* 2000). The Ndakan study area presents an ideal opportunity for examining a region where a finite period of human disturbance has been known to occur and the forest has subsequently regenerated. Palaeoecological methods could be used to study the environment before, during, and after the disturbance, monitoring successional changes and forest recovery for hundreds or even thousands of years. Such an approach, for example, has been successfully used to understand the patterns of succession following disturbance in the forests of Northeastern USA (Willis 1993, Foster and Zebryk 1993, Fuller *et al.* 1998).

Used in conjunction with satellite images and Geographic Information Systems, the palaeoecological record could be used to link contemporary forest types in the wider Ndoki River Region to their history. Such a study would provide detailed temporal and spatial data on the effects of prehistoric populations on the African rainforest and the long-term recovery of the forest after disturbance. This would be crucial for understanding the successional patterns that have contributed to current forest structure and composition. This also has important implications for current ecological research, as it would provide a baseline of forest history for those using short-term ecological experiments to study vegetation patterns and succession. Such GIS maps could also be used to pinpoint areas for further archaeological excavation within the dense rainforest, which has hitherto been an impractical task (Eggert 1993).

References

- Akaike, H. **1974**. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**:716-723.
- Allaby, M., editor. **1998**. A Dictionary of Plant Sciences, 2nd edition. Oxford University Press, Oxford.
- Anderson, M. C. **1964**. Studies of woodland light climate. *Journal of Ecology* **52**:27-41.
- Ashton, P. S. **1976**. Mixed Dipterocarp forest and its variation with habitat in the Malayan lowlands: a re-evaluation at Pasoh. *The Malaysian Forester* **39**:56-72.
- Augspurger, C. K. **1984a**. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* **72**:777-795.
- Augspurger, C. K. **1984b**. Seedling survival of tropical tree species: interactions of dispersal distance, light gaps and pathogens. *Ecology* **65**:1705-1712.
- Balee, W., and D. G. Campbell. **1990**. Evidence for the successional status of liana forest (Xingu River Basin, Amazonian Brazil). *Biotropica* **22**:36-47.
- Banerjee, D., A. S. Murray, L. Botter-Jensen, and A. Lang. **2001**. Equivalent dose estimation using a single aliquot of polymineral fine grains. *Radiation Measurements* **33**:73-94.
- Barkham, J. P. **1980**. Population dynamics of the wold daffodil (*Narcissus pseudonarcissus*). I. Clonal growth, seed reproduction, mortality and the effects of density. *Journal of Ecology* **68**:607-633.
- Barnett, S. **2000**. Luminescence dating of pottery from late prehistoric Britain. *Archaeometry* **42**:431-457.
- Barton, A. M., N. Fetcher, and S. Redhead. **1989**. The relationship between treefall gap size and light flux in a Neotropical rain forest in Costa Rica. *Journal of Tropical Ecology* **5**:437-439.
- Bazzaz, F. A., and S. T. A. Pickett. **1980**. Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics* **11**:287-310.
- Beatty, S. W. **1984**. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* **65**:1406-1419.
- Bebwa, B. **1990**. Biomasse et mineralomasses d'une jachère préforestière de deux ans dans les environs de Kisangani (Zaire). *Belgian Journal of Botany* **123**:92-102.
- Bell, G. **2000**. The distribution of abundance in neutral communities. *American Naturalist* **155**:606-617.
- Binkley, D., and P. Vitousek. **1989**. Soil nutrient availability. in R. W. Pearcy, J. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. *Plant Physiological Ecology*. Chapman & Hall, London.
- Blom, A., et al. **2001**. A survey of the apes in the Dzanga-Ndoki National Park, Central African Republic: a comparison between the census and survey methods of estimating the gorilla (*Gorilla gorilla gorilla*) and chimpanzee (*Pan troglodytes*) nest group density. *African Journal of Ecology* **39**:98 -105.
- Bongers, F., and J. Popma. **1990**. Leaf Dynamics of Seedlings of Rain Forest Species in Relation to Canopy Gaps. *Oecologia Berlin* **82**:122-127.
- Bonnefille, R., J. Roeland, and J. Guiot. **1990**. Temperature and rainfall estimates for the past 40,000 years in equatorial Africa. *Nature* **346**:347-349.
- Bonner, G. M. **1967**. Estimation of ground canopy density from ground measurements. *Journal of Forestry*:544-547.

- Bray, J. R. **1989**. The use of historical vegetation dynamics in interpreting prehistorical vegetation change. *Journal of the Royal Society of New Zealand* **19**:151-160.
- Brokaw, N., and R. T. Busing. **2000**. Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution* **15**:183-188.
- Brokaw, N. V. **1983**. Groundlayer dominance and apparent inhibition of the regeneration in tropical forests. *Tropical Ecology* **24**:194-200.
- Brokaw, N. V. L., and S. M. Scheiner. **1989**. Species composition in gaps and structure of a tropical forest. *Ecology* **70**:538-541.
- Brown, N., S. Jennings, P. Wheeler, and J. Nabe-Nielsen. **2000**. An improved method for the rapid assessment of forest understorey light environments. *Journal of Applied Ecology* **37**:1044-1053.
- Brown, N. D. **1993**. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. *Journal of Tropical Ecology* **9**:153-168.
- Brugière, D., S. Bougras, and A. Gautier-Hion. **2000**. Dynamique forestière et processus de colonisation-extinction: Relations faune-flore dans les forêts a marantacées d'Odzala. *Unpublished report-Projet Ecofac*.
- Brugière, D., and D. Sakom. **2001**. Population density and nesting, behaviour of lowland gorillas (*Gorilla gorilla gorilla*) in the Ngotto forest, Central African Republic. *Journal Of Zoology* **255**:251-259.
- Bullock, S. H. **1978**. Regeneration of *Musa* after feeding by Gorilla. *Biotropica* **10**:309.
- Bullock, S. H. **1981**. Dynamics of vegetative shoots of three species of *Aframomum* (Zingiberaceae) in Cameroon. *Adansonia* **20**:383-392.
- Burslem, D., I. M. Turner, and P. J. Grubb. **1994**. Mineral nutrient status of coastal hill Dipterocarp forest and Adinandra-Belukar in Singapore - Bioassays of nutrient limitation. *Journal of Tropical Ecology* **10**:579-599.
- Burslem, D. F. R. P., T. C. Whitmore, and G. C. Brown. **2000**. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *Journal of Ecology* **88**:1063-1078.
- Burton, P. J., and D. Mueller-Dombois. **1984**. Response of *Metrosideros polymorpha* seedlings to experimental canopy opening. *Ecology* **65**:779-791.
- Bush, M. B., and P. A. Colinvaux. **1994**. Tropical forest disturbance: paleoecological records from Darien, Panama. *Ecology* **75**:1761-1768.
- Bush, M. B., M. C. Miller, P. E. De Oliveira, and P. A. Colinvaux. **2000**. Two histories of environmental change and human disturbance in eastern lowland Amazonia. *Holocene* **10**:543-553.
- Cahill, J. F., Jr. **2002**. What evidence is necessary in studies which separate root and shoot competition along productivity gradients? *Journal of Ecology* **90**:201-205.
- Cain, M. L., and H. Damman. **1997**. Clonal growth and ramet performance in the woodland herb, *Asarum canadense*. *Journal of Ecology* **85**:883-897.
- Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. **1990**. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* **20**:620-631.
- Carroll, R. **1992**. Central African Republic. Pages 119-124 in J. A. Sayer, C.S. Harcourt, N.M. Collins, editor. *The Conservation Atlas of Tropical Forests of Africa*. MacMillan Publishers, Ltd., Cambridge.

- Carroll, R. W. **1988**. Relative density, range extension, and conservation potential of the lowland gorilla (*Gorilla gorilla gorilla*) in the Dzanga-Sangha region of southwestern Central African Republic. *Mammalia* **52**:309-323.
- Charles-Dominique, P., P. Blanc, D. Larpin, M.-P. Ledru, B. Riera, C. Sarthou, M. Servant, and C. Tardy. **1998**. Forest perturbations and biodiversity during the last ten thousand years in French Guiana. *Acta Oecologica* **19**:295-302.
- Chazdon, R. L. **1992**. Patterns of growth and reproduction of *Geonoma congesta*, a clustered understory palm. *Biotropica* **24**:43-51.
- Chazdon, R. L., and N. Fetcher. **1984**. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* **72**:553-564.
- Chazdon, R. L., R. W. Pearcy, D. W. Lee, N. Fetcher, S. S. Mulkey, and A. P. Smith. **1996**. Photosynthetic responses of tropical forest plants to contrasting light environments. Pages 5-55 in *Tropical forest plant ecophysiology*. Chapman & Hall, New York.
- Clark, D. A., and D. B. Clark. **1987**. Temporal and environmental patterns of reproduction in *Zamia skinneri*, a tropical rain forest cycad. *Journal of Ecology* **75**:135-150.
- Clark, D. B., and D. A. Clark. **1993**. Comparative analysis of microhabitat utilization by saplings of nine tree species in neotropical rain forest. *Biotropica* **25**:397-407.
- Clark, D. B., D. A. Clark, P. M. Rich, S. Weiss, and S. F. Oberbauer. **1996**. Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest. *Canadian Journal of Forest Research* **26**:747-757.
- Clark, D. B., M. W. Palmer, and D. A. Clark. **1999**. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* **80**:2662-2675.
- Clark, J. S., and W. A. I. Patterson. **1997**. Background and local charcoal in sediments: scales of fire evidence in the paleorecord. Pages 23-48 in J. S. Clark, H. Cachier, J. G. Goldammer, and B. Stocks, editors. *Sediment Records of Biomass Burning and Global Change*. Springer, Berlin.
- Clinebell, R. R. I., O. L. Phillips, A. H. Gentry, N. Stark, and H. Zuuring. **1995**. Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation* **4**:56-90.
- Collins, B. S., K. P. Dunne, S. T. A. Pickett, and P. S. White. **1985**. Responses of forest herbs to canopy gaps. Pages 217-234 in *The ecology of natural disturbance and patch dynamics*. Academic Press, Inc., London.
- Collins, B. S., and S. T. A. Pickett. **1988**. Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. *Journal of Ecology* **76**:437-450.
- Connell, J. H., and R. O. Slatyer. **1977**. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119-1144.
- Dalling, J. W., S. P. Hubbell, and K. Silvera. **1998**. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology* **86**:674-689.
- De Steven, D., D. M. Windsor, F. E. Putz, and B. de Leon. **1987**. Vegetative and reproductive phenologies of a palm assemblage in Panama. *Biotropica* **19**:342-356.
- Dechamps, R., R. Lanfranchi, A. Le-Cocq, and D. Schwartz. **1988**. Reconstruction of Quaternary environments through study of vegetable macroremains; Bateke

- area, PR Congo. *Palaeogeography, Palaeoclimatology, Palaeoecology* **66**:33-44.
- Denslow, J. S. **1980**. Gap partitioning among tropical rainforest trees. *Biotropica Supplement to Vol. 12*:46-55.
- Denslow, J. S. **1987**. Tropical rain forest gaps and tree species diversity. *Annual Review of Ecology and Systematics* **18**:431-451.
- Denslow, J. S., E. Newell, and A. M. Ellison. **1991**. The effect of understory palms and cyclanths on the growth and survival of *Inga* seedlings. *Biotropica* **23**:225-234.
- Denslow, J. S., J. T. Schultz, P. Vitousek, and B. R. Strain. **1990**. Growth responses of tropical shrubs to treefall gap environments. *Ecology* **71**:165-179.
- Dewalt, S. J., S. A. Schnitzer, and J. S. Denslow. **2000**. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology* **16**:1-19.
- Dhetchuvi, M. M. **1993**. Biology and Use of Some Species of Marantaceae in Zaire. *Belgian Journal of Botany* **126**:209-216.
- Dhetchuvi, M. M. **1996**. Aperçu sur les groupements secondaires à Marantaceae, Zingiberaceae et Costaceae de la Forêt des Abeilles (Gabon). Pages 145-149 in L. J. G. van der Maesen, X. M. van der Burgt, and J. M. van Medenbach de Rooy, editors. *The Biodiversity of African Plants*. Kluwer Academic Publishers, The Netherlands.
- Dhetchuvi, M. M., and A. Diafouka. **1993**. Les Marantaceae du Congo. *Fragm. Flor. Geobot.* **38**:401-450.
- Dickinson, M. B., F. E. Putz, and C. D. Canham. **1993**. Canopy gap closure in thickets of the clonal shrub, *Cornus racemosa*. *Bulletin of the Torrey Botanical Club* **120**:439-444.
- Dirzo, R., C. C. Horvitz, H. Quevedo, and M. A. Lopez. **1992**. The effects of gap size and age on the understorey herb community of a tropical Mexican rain forest. *Journal of Ecology* **80**:809-822.
- Doran, D. M., and A. McNeilage. **1998**. Gorilla ecology and behavior. *Evolutionary Anthropology*:120-131.
- Eggert, M. K. H. **1993**. Central Africa and the archaeology of the equatorial rainforest: reflections on some major topics. in T. Shaw, P. Sinclair, B. Andah, and A. Okpoko, editors. *The Archaeology of Africa: Food, Metals, Towns*. Routledge, London.
- Elenga, H., O. Peyron, R. Bonnefille, D. Jolly, R. Cheddadi, J. Guiot, V. Andrieu, S. Bottema, G. Buchet, B. J. L. De, A. C. Hamilton, J. Maley, R. Marchant, O. R. Perez, M. Reille, G. Riollet, L. Scott, H. Straka, D. Taylor, C. E. Van, A. Vincens, F. Laarif, and H. Jonson. **2000**. Pollen-based biome reconstruction for southern Europe and Africa 18,000 yr BP. *Journal of Biogeography* **27**:621-634.
- Elenga, H., D. Schwartz, and A. Vincens. **1992**. Changements climatiques et action anthropique sur le littoral congolais au cours de l'Holocène. *Bulletin de la Société Géologique de France* **163**:83-90.
- Elenga, H., D. Schwartz, and A. Vincens. **1994**. Pollen evidence of late Quaternary vegetation and inferred climate changes in Congo. *Palaeogeography, Palaeoclimatology, Palaeoecology* **109**:345-356.
- Elenga, H., and A. Vincens. **1990**. Paléoenvironnements quaternaires récents des plateaux Bateke (Congo); Etude palynologique des dépôts de la dépression du bois de Bilanko. Pages 271-282 in R. Lanfranchi and D. Schwartz, editors. *Paysages Quaternaires de l'Afrique Centrale Atlantique*. ORSTOM, Paris.

- Ergo, A. B. **1997**. Nouvelle evidence de l'origine africaine de l'*Elaeis guineensis* Jacq. par la decouverte de graines fossiles en Uganda. *Annales de Gembloux* **102**:191-201.
- Faith, D. P., P. R. Minchin, and L. Belbin. **1987**. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**:57-68.
- Fay, J. M. **1989**. Partial completion of a census of the western lowland gorilla (*Gorilla g. gorilla* (Savage and Wyman)) in southwestern Central African Republic. *Mammalia* **53**:202-214.
- Fay, J. M. **1991**. An elephant (*Loxodonta africana*) survey using dung counts in the forests of the Central African Republic. *Journal of Tropical Ecology* **7**:25-36.
- Fay, J. M. **1997**. *The ecology, social organization, populations, habitat and history of the western lowland gorilla (Gorilla gorilla gorilla Savage and Wyman 1847)*. Ph.D. Washington University.
- Fike, J., and W. A. Niering. **1999**. Four decades of old field vegetation development and the role of *Celastrus orbiculatus* in the northeastern United States. *Journal of Vegetation Science*. Aug. **10**:483-492.
- de Foresta, H. **1990**. Origine et evolution des savannes intramayombiennes (R.P. du Congo) II. Apports de la botanique forestiere. Pages 326-335 in R. Lanfranchi and D. Schwartz, editors. *Paysages Quaternaire de l'Afrique Centrale Atlantique*. ORSTOM, Paris.
- Foster, D. R., T. Zebryk, P. Schoonmaker, and A. Lezberg. **1992**. Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England. *Journal of Ecology* **80**:773-786.
- Foster, D. R., and T. M. Zebryk. **1993**. Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. *Ecology* **74**:982-998.
- Fredeen, A. L., C. B. Field, S. S. Mulkey, R. L. Chazdon, and A. P. Smith. **1996**. Ecophysiological constraints on the distribution of *Piper* species. Pages 597-618 in *Tropical forest plant ecophysiology*. Chapman & Hall, New York.
- Fuller, J. L., D. R. Foster, J. S. McLachlan, and N. Drake. **1998**. Impact of human activity on regional forest composition and dynamics in central New England. *Ecosystems* **1**:76-95.
- Furuichi, T., H. Inagaki, and S. Angoue-Ovono. **1997**. Population density of chimpanzees and gorillas in the Petit Loango Reserve, Gabon: Employing a new method to distinguish between nests of the two species. *International Journal of Primatology* **18**:1029-1046.
- Garwood, N. C. **1983**. Seed germination in a seasonal tropical forest in Panama; a community study. *Ecological Monographs* **53**:159-181.
- Gentry, A. H., and L. H. Emmons. **1987**. Geographical variation in fertility, phenology, and composition of the understory of neotropical forests. *Biotropica* **19**:216-227.
- Gerhardt, K. **1996**. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management* **82**:33-48.
- Gibert, G. **1984**. The Congolese forests: their geographical locations and types. *Bois et Forêts des Tropiques* **204**:3-19.
- Givnish, T. J. **1988**. Adaptation to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiology* **15**:63-92.
- Givnish, T. J. **1999**. On the causes of gradients in tropical tree diversity. *Journal of Ecology* **87**:193-210.

- Gliessman, S. R. **1976**. Allelopathy in a broad spectrum of environments as illustrated by bracken. *Botanical Journal of the Linnean Society* **73**:96-105.
- Grove, A. T. **1993**. Africa's climate in the Holocene. Pages 32-42 in T. Shaw, P. Sinclair, B. Andah, and A. Okpoko, editors. *The Archaeology of Africa: Food, Metals, Towns*. Routledge, London.
- Hall, J. B., and M. D. Swaine. **1980**. Seed stocks in Ghanaian forest soils. *Biotropica* **12**:256-263.
- Hall, J. B., and M. D. Swaine. **1981**. *Distribution and ecology of vascular plants in a tropical rain forest. Forest vegetation in Ghana*. Dr W. Junk Publishers, London.
- Hall, M. **1996**. *Archaeology Africa*. Natal Witness Printing & Publishing Co., Pietermaritzburg.
- Hamilton, A., D. Taylor, J. C. Vogel, and A. C. Hamilton. **1986**. Early forest clearance and environmental degradation in south-west Uganda. *Nature, UK* **320**:164-167.
- Hamilton, A. C. **1991**. History of climate and forests in tropical Africa during the last 8 Million years. *Climatic Change*:65-79.
- Harper, J. L. **1977**. *Population Biology of Plants*. Academic Press, New York.
- Harris, D. **2002**. The vascular plants of the Dzanga-Sangha Reserve, Central African Republic. *Scripta Botanica Belgica [Monographic series]*:1-286.
- Hartshorn, G. S. **1978**. Tree falls and tropical forest dynamics. Pages 617-638 in P. B. Tomlinson and M. H. Zimmermann, editors. *Tropical Trees as Living Systems*. Cambridge University Press, Cambridge.
- Hartshorn, G. S. **1980**. Neotropical forest dynamics. *Biotropica* **12**:23-30.
- Hawthorne, W.D. **1995**. *Ecological profiles of Ghanaian forest trees*. Nuffield Press, Abingdon.
- Hawthorne, W. D. **1993**. *Forest Regeneration After Logging*. Report no. 3, Overseas Development Administration.
- Heitz, H. **1943**. *La Forêt du Gabon*. Larose, Paris.
- Henderson, P. **2003**. Multivariate Statistics Software. PICSES Conservation Ltd.
- Horvitz, C. C., and D. W. Schemske. **1994**. Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. *Ecology* **75**:1949-1958.
- Hosmer, D. W., and S. Lemeshow. **1989**. *Applied Logistic Regression*. John Wiley & Sons, New York.
- Hubbell, S. P. **2001**. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, N.J.
- Hunt, R. **1990**. *Basic Growth Analysis*. Unwin Hyman, London.
- Hutchinson, T. F., R. E. J. Boerner, L. R. Iverson, S. Sutherland, and E. K. Sutherland. **1999**. Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (U.S.A.) *Quercus* forests. *Plant Ecology* **144**:177-189.
- Ickes, K., S. J. Dewalt, and S. Appanah. **2001**. Effects of native pigs (*Sus scrofa*) on woody understory vegetation in a Malaysian lowland rain forest. *Journal of Tropical Ecology* **17**:191-206.
- Isabirye-Basuta, G., and J. M. Kasenene. **1987**. Small rodent populations in selectively felled and mature tracts of Kibale Forest, Uganda. *Biotropica* **19**:260-266.
- IUCN. **1992**. *The Conservation Atlas of Tropical Forests. Africa*. MacMillan Publishers, Ltd., Cambridge.

- Jaffre, T. **1985**. Composition minerale et stock de bioelements dans la biomasse epigée des récrus forestiers en Cote d'Ivoire. *Acta Oecologia* **6**:233-246.
- Janzen, D. H. **1970**. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**:501-528.
- Jones, E. **1955**. Ecological studies of the rain forest of southern Nigeria IV. The plateau forest of the Okomu Forest Reserve, Part 1. The environment, the vegetation types of the forest, and the horizontal distribution of species. *Journal of Ecology* **43**:564-594.
- Juo, A. S. R., and L. P. Wilding. **1996**. Soils of the lowland forests of West and Central Africa. *Proceedings of the Royal Society of Edinburgh* **104B**:15-29.
- Kadomura, H. **1984**. *Natural and man-induced environmental changes in tropical Africa; case studies in Cameroon and Kenya; a preliminary report of the Tropical African Geomorphology and Late Quaternary Palaeoenvironments Research Project 1982/ 83*. Hokkaido University, Graduate School of Environmental Science, Division of Environmental Structure, Laboratory of Fundamental Research, Hokkaido, Japan.
- Kennedy, D. N., and M. D. Swaine. **1992**. Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rain forest. *Philosophical Transactions of the Royal Society of London, Series B* **335**:357-366.
- Kent, M., and P. Coker. **1994**. *Vegetation description and analysis : a practical approach*. John Wiley, Chichester.
- Kitajima, K., S. S. Mulkey, R. L. Chazdon, and A. P. Smith. **1996**. Ecophysiology of tropical tree seedlings. Pages 559-596 in *Tropical forest plant ecophysiology*. Chapman & Hall, New York.
- Kochummen, K., and F. Ng. **1977**. Natural plant succession after farming in Kepong. *Malaysian Forester* **40**:61-78.
- Koechlen, J. **1965**. *Flore du Cameroun*. Museum National d'histoire naturelle, Paris.
- Landon, J. R., and C. Berryman, editors. **1991**. *Booker tropical soil manual : a handbook for soil survey and agricultural land evaluation in the tropics and subtropics*. Longman Scientific & Technical, Harlow.
- Laraque, A., B. Pouyaud, R. Rocchia, E. Robin, I. Chaffaut, J. M. Moutsambote, B. Maziezoula, C. Censier, Y. Albouy, H. Elenga, H. Etcheber, M. Delaune, F. Sondag, and F. Gasse. **1998**. Origin and function of a closed depression in equatorial humid zones: the Lake Tele in North Congo. *Journal of Hydrology Amsterdam* **207**:236-253.
- Laurance, W. F., and G. B. Williamson. **2001**. Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conservation Biology*. **15**:1529-1535.
- Lawrence, D., and W. H. Schlesinger. **2001**. Changes in soil phosphorus during 200 years of shifting cultivation in Indonesia. *Ecology* **82**:2769-2780.
- Le Testu, G. **1938**. Note sur la vegetation dans le bassin de la Nyanga et de la Ngounie au Gabon. *Mem. Soc. Linn. Normandie, Nlle ser., Botanique* **1**:83-108.
- Leach, M., J. Fairhead, D. Millimouno, and M. Kamano. 1994. Social dynamics of environmental change in West Africa's forest-savanna mosaic. ESCOR of the Overseas Development Administration.
- Lee, E. T. **1992**. *Statistical methods for survival data analysis*, 2nd edition. John Wiley and Sons Inc., New York.
- Lejoly, J. **1980**. Le role des jachères dans la protection de l'environnement en zone tropicale humide. Pages 1-12 in *Communiqué à la 7e session de l'Ecole*

- Européenne d'Eté d'environnement*, Valladolid, U.L.B. Labo. de Bot. Syst et d'Ecol.
- Leonard, J., and W. Mullenders. **1950**. Clef Pratique des Marantacees Congolaises. *Bulletin de la Societe Royale de Botanique de Belgique* **83**:5-32.
- Letouzey, R. **1968**. Etude phytogeographique du Cameroun. in P. Lechevalier, editor. *Encyclopedie Biologique no.69*, Paris.
- Letouzey, R. **1978**. Notes phytogeographique sur les palmiers du Cameroun. *Adansonia* **18**:293-325.
- Levey, D. J. **1990**. Habitat-dependent fruiting behaviour of an understory tree, *Miconia centrodesma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology* **6**:409-420.
- Lewis, S. L., and E. V. J. Tanner. **2000**. Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. *Ecology* **81**:2525-2538.
- Loehle, C. **1987**. Partitioning of reproductive effort in clonal plants: a benefit-cost model. *Oikos* **49**:199-208.
- Lubini, A. **1986**. Vegetation adventice et postculturale de Kisangani et de la Tshopo (Haut-Zaire). *Bull. Jard. Bot. Nat. Belg.* **56**:315-348.
- Maguire, D. A., and R. T. T. Forman. **1983**. Herb cover effects on tree seedling patterns in a mature hemlock-hardwood forest. *Ecology* **64**:1367-1380.
- Maisels, F. 1999. Synthesis of information concerning the Park National d'Odzala, Congo. Projet ECOFAC - Composante Congo.
- Malenky, R. K., and E. W. Stiles. **1991**. Distribution of terrestrial herbaceous vegetation and its consumption by *Pan paniscus* in the Lomako Forest, Zaire. *American Journal of Primatology* **23**:153-169.
- Maley, J. **1989**. Late Quaternary climatic changes in the African rain forest; forest refugia and the major role of sea-surface temperature variations. Pages 585-616 in M. Leinen and M. Sarnthein, editors. *Paleoclimatology and paleometeorology; modern and past patterns of global atmospheric transport*. D. Reidel Publishing Company, Dordrecht-Boston, International.
- Maley, J. **1990**. L'histoire recent de la foret dense humide africaine: essai sur le dynamisme de quelques formations forestieres. Pages 367-382 in R. Lanfranchi and D. Schwartz, editors. *Paysages Quaternaires de l'Afrique Centrale Atlantique*. ORSTOM, Paris.
- Maley, J. **1991**. The African rain forest vegetation and palaeoenvironments during late Quaternary. *Climatic Change* **19**:79-98.
- Maley, J. **1992**. Mise en evidence d'une pejoration climatique entre ca. 2500 et 2000 ans B.P. en Afrique tropicale humide. *Bulletin de la Societe Geologique de France, Huitieme Serie* **163**:363-365.
- Maley, J. **1993**. The climatic and vegetational history of the equatorial regions of Africa during the upper Quaternary. in T. Shaw, P. Sinclair, B. Andah, and A. Okpoko, editors. *The Archaeology of Africa: food, metals, towns*. Routledge, London.
- Maley, J., and P. Brenac. **1998**. Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years B.P. *Review of Palaeobotany and Palynology* **99**:157-187.
- de Maret, P. **1985**. Recent archaeological research and dates from central Africa. *Journal of African History* **26**:129-148.

- Marrs, R. H., M. G. L. Duc, R. J. Mitchell, D. Goddard, S. Paterson, and R. J. Pakeman. **2000**. The ecology of bracken: Its role in succession and implications for control. *Annals of Botany* **85**:3-15.
- McCune, B., and M. J. Mefford. **1999**. *PC-ORD. Multivariate Analysis of Ecological Data*, 4th edition. MJM Software Design, Gleneden Beach, Oregon.
- Mesquita, R. C., K. Ickes, G. Ganade, and G. B. Williamson. **2001**. Alternative successional pathways in the Amazon Basin. *Journal of Ecology* **89**:528-537.
- Minchin, P. R. **1987**. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69**:89-107.
- Moscol-Olivera, M. C., and E. Roche. **1997**. Palynological analysis of a Holocene sedimentary sequence at Musisi-Karashoma (Kivu, Congo Democratic Republic). Climatic and human effects on the environment. *Geo Eco Trop* **21**:1-26.
- Muir, A. M. **1995**. The cost of reproduction to the clonal herb *Asarum canadense* (wild ginger). *Canadian Journal of Botany* **73**:1683-1686.
- Mulkey, S. S., A. P. Smith, and S. J. Wright. **1991**. Comparative life history and physiology of two understory Neotropical herbs. *Oecologia* **88**:263-273.
- Mulkey, S. S., S. J. Wright, and A. P. Smith. **1993**. Comparative physiology and demography of three Neotropical forest shrubs: Alternative shade-adaptive character syndromes. *Oecologia* **96**:526-536.
- Newbery, D. M., E. J. F. Campbell, J. Proctor, and M. J. Still. **1996**. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: Species composition and patterns in the understorey. *Vegetatio* **122**:193-220.
- Newbery, D. M., and J. Proctor. **1984**. Ecological studies in 4 contrasting lowland rain forests in Gunung Mulu National Park, Sarawak: 4. Associations between tree distribution and soil factors. *Journal of Ecology* **72**:475-494.
- Nichol, J. E. **1999**. Geomorphological evidence and Pleistocene refugia in Africa. *Geographical Journal* **165**:79-89.
- Niering, W. A., G. D. Dreyer, F. E. Egler, and J. P. J. Anderson. **1986**. Stability of a *Viburnum-Lentago* Shrub Community after 30 Years. *Bulletin of the Torrey Botanical Club* **113**:23-27.
- Nishihara, T. **1995**. Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National Park, Congo. *Primates* **36**:151-168.
- Noss, R. F. **2001**. Beyond Kyoto: Forest management in a time of rapid climate change. *Conservation Biology* **15**:578-590.
- Oslisly, R., and R. Dechamps. **1994**. Discovery of a 1500 BP burnt zone in the rainforest of Gabon. Anthropoc and palaeoclimatic implications. *Comptes Rendus, Academie des Sciences, Serie II: Sciences de la Terre et des Planetes* **318**:555-560.
- Oslisly, R., and M. Fontugne. **1993**. La Fin du stade néolithique et le début de l'age du fer dans la moyenne vallée de l'Ogooue au Gabon; problèmes chronologiques et changements culturels. *Comptes Rendus de l'Academie des Sciences, Série 2, Mécanique, Physique, Chimie, Sciences de l'Univers, Sciences de la Terre* **316**:997-1003.
- Oslisly, R., and B. Peyrot. **1992**. Un gisement du Paléolithique inférieur; la haute terrasse d'Elarmekora; moyenne vallée de l'Ogooue (Gabon); problèmes chronologiques et paléogéographiques. *Comptes Rendus de l'Academie des Sciences, Série 2, Mécanique, Physique, Chimie, Sciences de l'Univers, Sciences de la Terre* **314**:309-312.

- Oyama, K. **1990**. Variation in growth and reproduction in the Neotropical dioecious palm *Chamaedorea tepejilote*. *Journal of Ecology* **78**:648-663.
- Oyama, M., and H. Takehara. **1967**. *Revised Standard Soil Color Charts*, 2nd edition, Japan.
- Phillipson, D. W. **1993**. *African Archaeology*, 2nd edition. Cambridge University Press, Cambridge.
- Pickett, S. T. A., and P. S. White. **1985**. *The ecology of natural disturbance and patch dynamics*. Academic Press, Inc., London.
- Pidgeon, J. D. **1972**. The measurement and prediction of available water capacity of ferrallitic soils in Uganda. *Journal of Soil Science* **23**:431-441.
- Piñero, D., and J. Sarukhàn. **1982**. Reproductive behaviour and its individual variability in a tropical palm, *Astrocaryum mexicanum*. *Journal of Ecology* **70**:461-472.
- Popma, J., F. Bongers, M. Martinez-Ramos, and E. Veneklaas. **1988**. Pioneer species distribution in treefall gaps in Neotropical rain forest; a gap definition and its consequences. *Journal of Tropical Ecology* **4**:77-88.
- Poulsen, A. D. **1996**. Species richness and density of ground herbs within a plot of lowland rain forest in northwest Borneo. *Journal of Tropical Ecology* **21**:177-190.
- Proctor, J., J. M. Anderson, P. Chai, and H. W. Vallack. **1983**. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. *Journal of Ecology* **71**:237-260.
- Putz, F. E. **1980**. Lianas vs. trees [in Panama]. *Biotropica* **12**:224-225.
- Raich, J. W. **1989**. Seasonal and spatial variation in the light environment in a tropical Dipterocarp forest and gaps. *Biotropica* **21**:299-302.
- Raich, J. W., and W. K. Gong. **1990**. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *Journal of Tropical Ecology* **6**:203-217.
- Remis, M. J. **1997b**. Western lowland gorilla (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. *American Journal of Primatology* **43**:87-110.
- Reynaud-Farrera, I., J. Maley, and D. Wurrman. **1996**. Vegetation et climat dans les forets du Sud-Ouest Cameroun depuis 4770 ans BP: analyse pollinique des sediments du Lac Ossa. *Comptes Rendus de l'Academie de Sciences Serie IIa: Sciences de la Terre et des Planetes* **322**:749-758.
- Rizvi, S. J. H., H. Haque, V. K. Singh, and V. Rizvi. **1992**. A discipline called allelopathy. in S. J. H. Rizvi and V. Rizvi, editors. *Allelopathy: Basic and Applied Aspects*. Chapman & Hall, London.
- Roberts, E. H. **1973**. Predicting the storage life of seeds. *Seed Science and Technology* **1**:499-514.
- Robertson, K. M., and C. K. Augspurger. **1999**. Geomorphic processes and spatial patterns of primary forest succession on the Bogue Chitto River, USA. *Journal of Ecology* **87**:1052-1063.
- Rogers, E. M., and E. A. Williamson. **1987**. Density of herbaceous plants eaten by gorillas in Gabon: some preliminary data. *Biotropica* **19**:278-281.
- Rogers, M. E., B. C. Voysey, K. E. McDonald, R. J. Parnell, and C. E. G. Tutin. **1998**. Lowland gorillas and seed dispersal: The importance of nest sites. *American Journal of Primatology* **45**:45-68.
- Rollet, B. **1963**. *Introduction a l'inventaire forestier du nord Congo*. FAO, rapport no. 1782.

- Rundel, P. W., M. R. Sharifi, A. C. Gibson, and K. J. Esler. **1998**. Structural and physiological adaptation to light environments in neotropical *Heliconia* (Heliconiaceae). *Journal of Tropical Ecology* **14**:789-801.
- Russell, A. E., J. W. Raich, and P. M. Vitousek. **1998**. The ecology of the climbing fern *Dicranopteris linearis* on windward Mauna Loa, Hawaii. *Journal of Ecology* **86**:765-779.
- de Saint Aubin, G. 1948. Reconnaissance de la foret de la Sangha. Rapport Annuel des Services Forestiers pour 1948.
- Sanford, R. L., Jr., J. Saldarriaga, K. E. Clark, C. Uhl, and R. Herrera. **1985**. Amazon rain-forest fires. *Science* **227**:53-55.
- Schnitzer, S. A., J. W. Dalling, and W. P. Carson. **2000**. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology* **88**:655-666.
- Schupp, E. W., and E. J. Frost. **1989**. Differential predation of *Welfia georgii* seeds in treefall gaps and the forest understory. *Biotropica* **21**:200-203.
- Schwartz, D., R. Dechamps, H. Elenga, R. Lanfranchi, A. Mariotti, and A. Vincens. **1995**. *Les savanes du Congo; une vegetation specifique de l'Holocene superieur*. Report no. 31, Centre International Pour la Formation et les Echanges Geologiques.
- Silander, J. A. J. **1978**. Density-dependent control of reproductive success in *Cassia biflora*. *Biotropica* **10**:292-296.
- Sim, J., H. Tan, and I. Turner. **1992**. Adinandra belukar: an anthropogenic heath forest in Singapore. *Vegetatio* **102**:125-137.
- Smith, A. P., D. A. Clark, R. Dirzo, and N. Fetcher. **1987**. Responses of herbs of the understorey of a tropical forest to gaps caused by treefalls. *Revista de Biologia Tropical, Ecologia y ecofisiologia de plantas en los bosques mesoamericanos* **35**:111-118.
- Sowunmi, M. A. **1999**. The significance of the oil palm (*Elaeis guineensis* Jacq.) in the late Holocene environments of West and west central Africa: a further consideration. *Vegetation History and Archaeobotany* **8**:199-210.
- Stahl, A. B. **1993**. Intensification in the west African Late Stone Age: a view from central Ghana. in T. Shaw, P. Sinclair, B. Andah, and A. Okpoko, editors. *The Archaeology of Africa: Food, Metals, Towns*. Routledge, London.
- Struhsaker, T. T., J. S. Lwanga, and J. M. Kasenene. **1996**. Elephants, selective logging and forest regeneration in the Kibale Forest, Uganda. *Journal of Tropical Ecology* **12**:45-64.
- Svenning, J.-C. **1999**. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology* **87**:55-65.
- Swaine, M. D. **1996**. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *Journal of Ecology* **84**:419-428.
- Swaine, M. D., and J. B. Hall. **1983**. Early succession in tropical forests. *Journal of Ecology* **71**:601-627.
- Taylor, A. H., and Q. Zisheng. **1988**. Tree replacement patterns in subalpine *Abies* and *Betula* forests, Wolong Natural Reserve, China. *Vegetatio* **78**:141-115.
- Ter Braak, C. J. F. **1986**. Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**:1167-1179.
- Ter Braak, C. J. F. **1987**. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* **69**:69-77.

- Tolhurst, K. G., and N. D. Turvey. **1992**. Effects of bracken (*Pteridium esculentum* (Forst. f.) Cockayne) on eucalypt regeneration in west-central Victoria. *Forest Ecology and Management* **54**:45-67.
- Tuley, P. **1995**. *The Palms of Africa*. St. George Printing Works, Ltd., Redruth, Cornwall.
- Tutin, C. E. G., and M. Fernandez. **1985**. Foods consumed by sympatric populations of *Gorilla gorilla gorilla* and *Pan troglodites* in Gabon: Some preliminary data. *International Journal of Primatology* **6**:27-44.
- Tutin, C. E. G., R. J. Parnell, L. J. T. White, and M. Fernandez. **1995**. Nest building by lowland gorillas in the Lope Reserve, Gabon: Environmental influences and implications for censusing. *International Journal of Primatology* **16**:53-76.
- Tutin, C. E. G., L. J. T. White, and A. Mackanga Missandzou. **1996**. Lightning strike burns large forest tree in the Lope Reserve, Gabon. *Global Ecology and Biogeography Letters* **5**:36-41.
- Uhl, C., R. Buschbacher, and E. Serrao. **1988a**. Abandoned pastures in eastern Amazonia I. Patterns of plant succession. *Journal of Ecology* **76**:663-681.
- Uhl, C., K. Clark, N. Dezzo, and P. Maquirino. **1988b**. Vegetation dynamics in Amazonian treefall gaps. *Ecology* **69**:751-763.
- Uhl, C., J. B. Kauffman, and D. L. Cummings. **1988c**. Fire in the Venezuelan Amazon 2: Environmental conditions necessary for forest fires in the evergreen rainforest of Venezuela. *Oikos* **53**:176-184.
- Van Der Meer, P. J., F. J. Sterck, and F. Bongers. **1998**. Tree seedling performance in canopy gaps in a tropical rain forest at Nouragues, French Guiana. *Journal of Tropical Ecology* **14**:119-137.
- Vanleeuwe, H., and A. Gautier-Hion. **1998**. Forest elephant paths and movements at the Odzala National Park, Congo: the role of clearings and Marantaceae forest. *African Journal of Ecology* **36**:174-182.
- Vansina, J. **1990**. *Paths in the Rainforests*. James Currey Ltd, London.
- Vansina, J. **1992**. Habitat, Economy, and Society in the Central African Rain Forest. *Berg Occasional Papers in Anthropology* **1**:1-16.
- Veenendaal, E. M., M. D. Swaine, R. T. Lecha, M. F. Walsh, I. K. Abebrese, and K. Owusu Afriyie. **1996**. Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology* **10**:501-511.
- Vincens, A., G. Buchet, H. Elenga, M. Fournier, L. Martin, C. De Namur, D. Schwartz, M. Servant, and D. Wirrmann. **1994**. Changement majeur de la végétation du lac Sinnda (vallée du Niari, Sud-Congo) consécutif à l'assèchement climatique Holocène supérieur: apport de la palynologie. *Comptes Rendus, Academie des Sciences, Serie II: Sciences de la Terre et des Planetes* **318**:1521-1526.
- Vincens, A., D. Schwartz, J. Bertaux, H. Elenga, and C. De Namur. **1998**. Late Holocene climatic changes in western Equatorial Africa inferred from pollen from Lake Sinnda, southern Congo. *Quaternary Research* **50**:34-45.
- Vincens, A., D. Schwartz, H. Elenga, I. Reynaud Farrera, A. Alexandre, J. Bertaux, A. Mariotti, L. Martin, J. D. Meunier, F. Nguetsop, M. Servant, S. Servant Vildary, and D. Wirrmann. **1999**. Forest response to climate changes in Atlantic Equatorial Africa during the last 4000 years BP and inheritance on the modern landscapes. *Journal of Biogeography* **26**:879-885.
- Voysey, B. **1995**. *Seed Dispersal by gorillas in the Lopé Reserve, Gabon*. Ph.D. University of Edinburgh.

- Voysey, B. C., K. E. McDonald, M. E. Rogers, C. E. G. Tutin, and R. J. Parnell. **1999**. Gorillas and seed dispersal in the Lope Reserve, Gabon. II: Survival and growth of seedlings. *Journal of Tropical Ecology* **15**:39-60.
- Webb, C. O., and D. R. Peart. **1999**. Seedling density dependence promotes co-existence of Bornean rain forest trees. *Ecology* **80**:2006-2017.
- White, F. **1983**. The Guineo-Congolian regional centre of endemism. in *The Vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa*. UNESCO, Paris, France.
- White, L. J. T. **1992**. *Vegetation history and logging disturbance in the Lopé Reserve, Gabon*. Ph.D. Edinburgh, Edinburgh.
- White, L. J. T., and J. F. Oates. **1999**. New data on the history of the plateau forest of Okomu, southern Nigeria: an insight into how human disturbance has shaped the African rain forest. *Global Ecology and Biogeography* **8**:355-361.
- White, L. J. T., M. E. Rogers, C. E. G. Tutin, E. A. Williamson, and M. Fernandez. **1995**. Herbaceous vegetation in different forest types in the Lope Reserve, Gabon: implications for keystone food availability. *African Journal of Ecology* **33**:124-141.
- White, R. E. **1979**. *Introduction to the Principles and Practice of Soil Science*. Blackwell Scientific Publications, Oxford.
- Whitmore, T. C. **1978**. Gaps in the forest canopy. Pages 639-655 in P. B. Tomlinson and M. H. Zimmerman, editors. *Tropical trees as living systems*. Cambridge University Press, Cambridge.
- Whitmore, T. C. **1997**. *An Introduction to Tropical Rain Forests*, Second edition. Oxford University Press, Oxford.
- Whitmore, T. C., and N. D. Brown. **1996**. Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. *Philosophical Transactions of the Royal Society of London, Series B*:1195-1203.
- Whitmore, T. C., N. D. Brown, M. D. Swaine, D. Kennedy, C. I. Goodwin-Bailey, and W. K. Gong. **1993**. Use of hemispherical photographs in forest ecology: measurement of gap size and radiation totals in a Bornean tropical rain forest. *Journal of Tropical Ecology* **9**:131-151.
- Willis, K. J. **1993**. How old is ancient woodland. *TREE* **8**:427.
- Woodward, C. L. **1996**. Soil compaction and topsoil removal effects on soil properties and seedling growth in Amazonian Ecuador. *Forest Ecology and Management* **82**:197-209.
- Wragham, R. W., M. E. Rogers, and G. Isabirye-Basuta. **1993**. Ape food density in the ground layer in Kibale Forest, Uganda. *African Journal of Ecology* **31**:49-57.
- Yavitt, J. B., J. J. Battles, G. E. Battles, and D. H. Knight. **1995**. The canopy gap regime in a secondary Neotropical forest in Panama. *Journal of Tropical Ecology* **11**:392-402.
- Young, T. P., and S. P. Hubbell. **1991**. Crown asymmetry, treefalls, and repeat disturbance of broad-leaved forest gaps. *Ecology* **72**:1464-1471.
- van Zinderen Bakker, E. M., and J. A. Coetzee. **1988**. A review of Late Quaternary pollen studies in East, Central and Southern Africa. *Review of Palaeobotany and Palynology* **55**:155-174.
- Zogning, A., P. Giresse, J. Maley, and F. Gadel. **1997**. The late Holocene palaeoenvironment in the Lake Njupi area, West Cameroon; implications regarding the history of Lake Nyos. *Journal of African Earth Sciences* **24**:285-300.