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Assessment of the impact of a newly introduced free-ranging group of chimpanzees (*Pan troglodytes schweinfurthii*) on the vegetation of Ngamba Island, Lake Victoria, Uganda

by

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Meinen Eltern
in
Liebe und Dankbarkeit

&

Tim

the best of all companions

CONTENTS

SUMMARY

Assessment of the impact of a newly introduced free-ranging group of chimpanzees (*Pan troglodytes schweinfurthii*) on the vegetation of Ngamba Island, Lake Victoria Uganda

Claudia Ulrike Regina Schoene

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for the degree of
Magister Scientiae (Wildlife Management)

The purpose of the current research project was to undertake a thorough quantitative and qualitative survey of the vegetation on Ngamba Island. Based on the results of this survey suggestions are made for future management of the chimpanzees on the island.

It was assumed that the introduction of chimpanzees onto an island that was previously not inhabited by this species would have an (to be defined) impact on the environment in general, and the vegetation cover, in particular.

The woody vegetation was sampled and analysed using the varying quadrat plot method. This method gives the following results per (a) species, (b) stem growth form and (c) height class: 1. Canopy regime at different height levels; 2. Total projected canopy cover; and 3. Density.

The results of the vegetation analysis showed that at this stage the forest structure on Ngamba Island still represents a healthy secondary rain forest cover.

A major impact chimpanzees have on the woody vegetation cover of Ngamba Island is that they defoliate and destroy trees of all height classes.

The number of mature trees that a parent tree produces per fruiting period might often be as little as ≤ 1. Even though chimpanzees act as seed dispersers in their natural habitat the

impressive number of seeds dispersed by each individual chimpanzee is therefore put into perspective by the very low final recruitment rate. Resulting from the above it is postulated that the impact of the Ngamba Island chimpanzees as seed dispersers for selected woody vegetation species is of low importance if not negligible. It is by far outweighed by the destruction caused to the secondary rain forest cover of the Island by this newly introduced species.

Using different approaches and calculations to estimate the necessary home ranges for chimpanzees in a confined habitat the areas calculated range from 5 – 56 hectare per chimpanzee. Even though, there is an 11.2-fold difference between these estimates they indicate nevertheless, that Ngamba Island with an area of 42.40 ha of secondary rain forest cover and 16 adult and 17 juvenile chimpanzees is already highly overstocked.

In summary the impact the newly introduced species of chimpanzees on Ngamba Island will have over time on the secondary rain forest cover of their forest refuge is that of continuing destruction. Using a rate of destruction of about 0.05 ha per chimpanzee per year the secondary rain forest cover of Ngamba Island will be completely destroyed in 53 years with a stocking density of 16 adult chimpanzees. Increasing stocking density - also through maturing of the juvenile chimpanzees currently present on the Island into adulthood - will increase the rate of destruction of the woody vegetation cover of Ngamba Island proportionally.

CHAPTER 1

INTRODUCTION

The purpose of the current research project was to undertake a thorough quantitative and qualitative survey of the vegetation on Ngamba Island. Based on the results of this survey suggestions are made for future management of the chimpanzees on the island.

It was assumed that the introduction of chimpanzees onto an island that was previously not inhabited by this species would have an (to be defined) impact on the environment in general, and the vegetation cover, in particular.

The two previous vegetation surveys only provide a very broad overview of the vegetation of the island (Annex - Table 3 + 4). Furthermore, because the plant species identified in the surveys partly do not match and have subsequently been found also to be partly incorrect (Wanyamanganyi, pers. comm.[1]), they cannot be used as reliable baseline data for further vegetation-related studies.

It was considered essential to undertake a thorough survey especially of the woody and herbaceous vegetation of the island. Such a study should make it possible to evaluate and predict the impact of the chimpanzee population on the island vegetation over time. Wherever possible the data of the two former vegetation surveys (Kityo 1998, Zwick & Lloyd 1998b) will be taken into account and compared with the data collected during this study.

Taking into account the data collected during the present vegetation survey as well as the detailed data already available on the fauna and especially the bird population of the island, the ultimate purpose of the research project is to establish a Wildlife Management Plan for Ngamba Island.

Implementing this plan will then allow exact quantification of the impact of the chimpanzees on the environment of the island as a whole over time. Furthermore, following the survey, estimates of maximum chimpanzee stocking density considering the provision of a full food supply will be possible and can be taken into account for the future management of the island.

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[1] Wanyamaganyi, O. 2000. Department of Botany, Makerere University, Kampala, Uganda.

The following objectives have been set for this study:

1. To provide a detailed qualitative and quantitative description of the vegetation of Ngamba Island.

2. To model the impact of the newly introduced group of chimpanzees (*Pan troglodytes schweinfurthii*) on the island vegetation in the long-term, using different scenarios.

3. To provide a Wildlife Management Plan for Ngamba Island.

CHAPTER 2

NGAMBA ISLAND CHIMPANZEE SANCTUARY

WHY SANCTUARIES?

A sanctuary is defined in the Reader's Digest Oxford Complete Word finder as "a place where birds, wild animals, etc., are bred and protected" and as "a place of refuge..." (Tulloch 1993).

Over the last couple of decades chimpanzee sanctuaries have become more and more numerous all over Africa. Reasons for this steady growth being mainly (1) the rapid expansion of human populations locally, (2) an increase in the ongoing hunting of wild, forest-dwelling mammals, especially caused by the rapid expansion of the bush meat trade, and (3) the expansion of the commercial animal trade (Hladik 1974, Goodall 1994b, Ammann 1997-1998, Cox *et al.* 2000).

Many of the chimpanzees who are brought into the care of sanctuaries have been confiscated by government officials, or were once pets (Goodall 1994b, Cox *et al.* 2000, Rosen *et al.* 2001).

Many of the orphaned chimpanzees that arrive in Uganda have been smuggled out of the Democratic Republic of Congo (DRC) or are brought back from Ugandan soldiers returning home from fighting in the DRC. They are a 'by-product' of the bush meat hunting and consumption which includes primates in the DRC and are sold as pets, since they have no value as a meat source (Goodall 1994b, Ammann 1997-1998, Rosen *et al.* 2001).

Figure 2.1 illustrates the root causes for the need for sanctuaries.

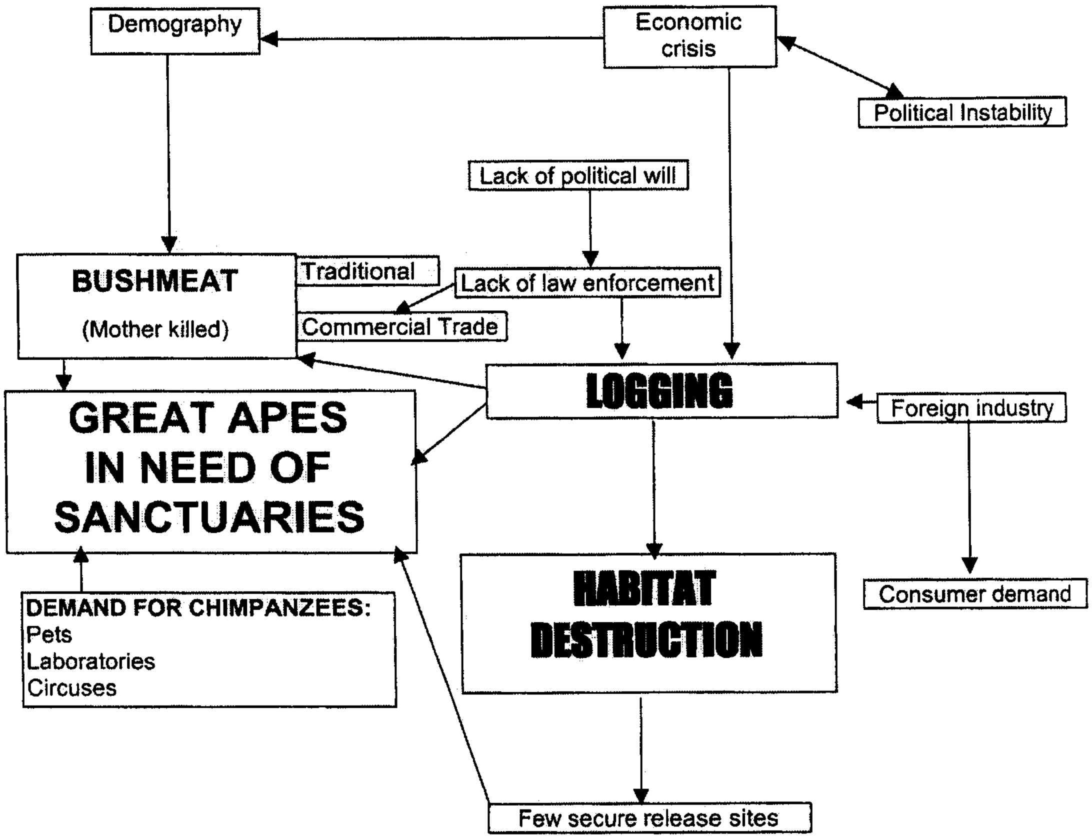

Figure 2.1: Root causes of the need for sanctuaries (redrawn after Cox *et al.* 2000 – with kind permission).

There are three main justifications for establishing and funding sanctuaries (Borner 1985, Goodall 1994b, Cox *et al.* 2000, Rosen *et al.* 2001):

1. *Education*: Local people can be introduced to their natural heritage and often for the first time in their lives have the chance to see chimpanzees and other primates close up and to observe their so 'human-like' behaviour.

2. *Tourism*: Attracting tourists and giving them the chance to observe chimpanzees close up will help sanctuaries to become self-supporting and to boost the economy of local people living around sanctuaries.

3. *Ethics*: Without sanctuaries, confiscated or illegally kept chimpanzees would either have to be euthanised or exposed to further mistreatment. This could surely be seen as contradictory in the effort to conserve the species and its habitat. A single chimpanzee, when given a name and reporting his or her individual history, can become an ambassador for the plight of his whole species if allowed to survive in a sanctuary.

Hannah & McGrew (1991) underline the importance of sanctuaries for the conservation of wild species. They state that "conservation of remaining wild populations and habitats should be the first priority, but rehabilitation projects should not be thought of as competing with the preservation of wild populations ... [T]here is always the possibility that, in the future, reproducing populations of apes maintained on islands could be released into suitable free-ranging sites."

Because of the constant influx of confiscated, mainly orphaned chimpanzees into sanctuaries all over Africa, even in non-range countries such as Kenya, South Africa and Zambia, a 'Pan-African Sanctuaries Alliance (PASA)' was founded in 2000 in Entebbe, Uganda (Cox *et al.* 2000). This alliance focuses on establishing practical recommendations on all aspects of sanctuary management and on enhancing and maintaining communication between the sanctuaries and between PASA and other great ape conservation projects ongoing in Africa (Cox *et al.* 2000, Rosen *et al.* 2001).

The Pan-African Sanctuary Alliance is intended to eventually be inclusive of all primates. It was founded under the facilitation of the Conservation Breeding Specialist Group (CBSG) in collaboration with the Primate Specialist Group of the International Union for Conservation of Nature and Natural Resources (IUCN) (Cox *et al.* 2000).

At the second PASA workshop in Limbe, Cameroon, 17 African primate sanctuaries from the following countries participated: Cameroon, DRC, Gabon, Guinea, Kenya, Nigeria, Republic of Congo, Sierra Leone, South Africa, Uganda and Zambia (Rosen *et al.* 2001).

The workshop proposed the following definitions:

"*PASA sanctuary*: A PASA sanctuary provides a safe and secure home for African apes and other primates in need. The welfare of the individual and the preservation of the species are of prime importance and are considered equally. The sanctuary operates in the context of an integrated approach to conservation, which can include rehabilitation and re-introduction."

"*Mission statement*: To support, assist and encourage member sanctuaries in their efforts to save Africa's great apes and other primates. PASA aims to accomplish this mission by campaigning locally and globally against the threats these species face in the wild, promoting the highest standards of captive animal husbandry, and by acting as a forum where sanctuaries can share information and discuss issues of mutual concern."

THE HISTORY OF NGAMBA ISLAND CHIMPANZEE SANCTUARY

Ngamba Island (S 00°06/E 32°39, 0.46 km^2, 1 160 m above sea level) in Lake Victoria, Uganda, was purchased by a Board of Trustees in 1998. This Board consists of the following members: Born Free Foundation; International Fund for Animal Welfare (IFAW); the Jane Goodall Institute (JGI); Taronga Zoo, Sydney, Australia, Uganda Wildlife Authority (UWA) and Uganda Wildlife Education Centre (UWEC - the new name and purpose of the former 'Entebbe Zoo'). The island is managed by JGI Uganda under joint directorship of Mrs Debbie Cox and Mrs Cherie (Monti) Montgomery.

Up to the date of purchase Ngamba Island was home to a small fishing community which inhabited a circumscribed area in the northern part of the island (Zwick & Lloyd 1998b, Möller pers. comm.[1]). After the purchase the community received compensation for their lost housing facilities and was translocated to a neighbouring island to join the existing fishing community there (Cox pers. comm.[2]).

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[1] Möller, W. 1999. Uganda Wildlife Education Centre, Entebbe, Uganda.

[2] Cox, D. 2000. Jane Goodall Institute Uganda, Entebbe, Uganda.

Since late 1998 the island has been used solely as a sanctuary for orphaned and confiscated chimpanzees. Only the northern area of the island, including the landing area, can be accessed freely. All the temporary buildings erected there by the fishing community have been demolished (Zwick & Lloyd 1998b, Möller pers. comm.[1]). The area now holds the night enclosure for the chimpanzees as well as some concrete-built houses with corrugated iron roofs for the caretakers of the chimpanzees, volunteers and researchers.

This area also includes a visitors' centre where information on the threats to the survival of chimpanzees in the wild and suggestions for possible solutions are displayed. A touring company transports tourists to and from the island, a maximum of two trips twice daily. The tourists receive an informal talk on the history of the island and its chimpanzees and afterwards have the opportunity to watch the morning (11:00 am) or afternoon (15:00 pm) feeding of the chimpanzees from the visitors' platform.

Origin of the Ngamba Island chimpanzees

The chimpanzees on the island were originally members of two separate groups. One of the groups had previously lived in 'The Isinga Island Chimpanzee Sanctuary' on Lake Edward, which is part of the Queen Elizabeth National Park. The second group had been kept at UWEC (Möller pers. comm.[1]). All chimpanzees of both groups originated from the Democratic Republic of Congo (DRC) and had been confiscated either from illegal traders, private owners or Ugandan soldiers returning from fighting in the war in the DRC and bringing with them a baby chimpanzee as a playmate for their children (Möller pers. comm.[1], Cox pers. comm.[2]).

Eventually, the group from Isinga Island was transferred to UWEC in 1998 and the two groups introduced to each other. Because of an increasing number of confiscated chimpanzees the capacity at UWEC quickly reached its limit. Thus, when the opportunity arose to purchase Ngamba Island to establish a chimpanzee sanctuary there, a Board of Trustees was formed to acquire the island (Chimpanzee Sanctuary and Wildlife Conservation Trust 1999, Cox pers. comm.[2]).

After the holding facility had been completed the first chimpanzees (juveniles and adult females) were brought to the island in October 1998. After a few days in the holding facility the chimpanzees were released into the fenced-off forest area. Each chimpanzee was followed by a volunteer who observed her behaviour in the new surroundings and collected samples of the vegetation chosen as food items by the chimpanzees (Chimpanzee Sanctuary and Wildlife

Conservation Trust 1999, Marshall pers. comm.[3]).

A fortnight later the adult male chimpanzees followed. The group reintegrated without any problems. Until December 1999 a total of 22 chimpanzees had been brought to the island. The 16 adult chimpanzees go out into the forest every day, while the juveniles are taken for infant walks at several mornings a week. The female chimpanzees receive anti-contraceptive implants every couple of years to prevent them from breeding (Möller pers. comm.[1], Cox pers. comm.[2]).

Future plans

The rate at which (infant) chimpanzees appear and are confiscated in Uganda has increased dramatically in recent years. While there had been a more or less 'steady influx' of about one chimpanzee every two years (0.5 chimp/year) until the year 1998 this rate has increased to 16 chimps in the two years of 1999 and 2000 (eight chimps/year) (Cox pers. comm.[4]).

Thus, until May 2001 the number of chimpanzees on the island has increased to a total of 33, consisting of 16 adults and 17 juveniles below the age of five years, while the remaining chimpanzees have been kept at UWEC (Cox pers. comm.[4]).

In the meantime, another area on neighbouring Nsadzi Island has been bought to be fenced off and transformed into a chimpanzee sanctuary by mid-2003 (Cox pers. comm.[4]). After completion of this second sanctuary, the number of chimpanzees remaining on Ngamba Island will be permanently reduced to 27, consisting of, in the long run, 12 adult and 15 juvenile chimpanzees under the age of five years. It is planned to transfer the four most dominant males to the new sanctuary, together with some females who promise no potential as surrogate mothers for orphaned juvenile chimpanzees. For every juvenile chimpanzee newly arriving onto Ngamba Island, one of the adult chimpanzees will be transferred to the new sanctuary on Nsadzi Island. At the same time the adult females who have proved themselves to be good surrogate mothers will remain on Ngamba Island (Cox pers. comm.[4]).

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[3] Marshall, S. 2000. Department of Psychology, St Andrews University, Scotland.

[4] Cox, D. 2001. Jane Goodall Institute Uganda, Entebbe, Uganda.

[5] Wanyamaganyi, O. 2000. Department of Botany, Makerere University, Kampala, Uganda.

PREVIOUS RESEARCH ON FLORA AND FAUNA OF NGAMBA ISLAND

Two Environmental Impact Assessments (EIAs)/Vegetation surveys had been undertaken on Ngamba Island before the release of the chimpanzees, one in August 1997 by Frontier-Uganda and the second by Kityo in the first half of 1998 (Kityo 1998, Zwick & Lloyd 1998b, Chimpanzee Sanctuary and Wildlife Conservation Trust 1999, Cox pers. comm.[2])

The Frontier report contains quite a detailed list of the fauna of Ngamba Island (Zwick & Lloyd 1998b). However, concerning the flora of the island the reports are incomplete and partially contradictory (Kityo 1998, Zwick & Lloyd 1998b, Chimpanzee Sanctuary and Wildlife Conservation Trust 1999, Cox pers. comm.[2], Wanyamaganyi pers. comm.[5]). The preliminary species list compiled from both vegetation surveys and the determined faunal species are listed in the Annex (Table 3 -5) (Kityo 1998, Zwick & Lloyd 1998b, Wilson & Schipper 2002).

Research has also been undertaken to determine the plant species used as food items by the chimpanzees. The first of two such surveys was conducted in October 1998 after the release of the adult females into the forest on Ngamba Island (Marshall 2000). The second one was conducted between December 1999 and May 2000. During this study the infant chimpanzees were accompanied on their morning forest walks and samples were collected of the vegetation they chose as food items (Marshall pers. comm.[3]). Lists of these plant species used as food items are provided in the Annex (Table 2) (Marshall 2000).

CHAPTER 3

STUDY AREA

LOCATION AND TOPOGRAPHY

The Lake Victoria region

Uganda (Figure 3.1 & 3.2) is a relatively small, landlocked country straddling the equator in East Africa. The country lies between N 04°07 and S 01°30 latitude and E 29°33 and E 35°20 longitude. It shares borders with Sudan in the north, Kenya in the east, Tanzania and Rwanda in the south and the Democratic Republic of the Congo in the west (Harcourt 1992) (Figure 3.1).

The largest part of Uganda is situated on the east-central African plateau at an altitude of between 900 to 1 500 m (Figure 3.2). Towards the north the plateau slopes downwards, forming gently rolling plains interrupted by occasional mountains and hills. In the south the topography consists of flat-topped hills and broad, frequently swampy valleys (Figure 3.2). The rift valley with its associated mountains and lakes runs through the west of the country (Figure 3.2). In this area the Ruwenzori rises to its highest peak at 5 119 m (Figure 3.2). In the east, three high volcanic mountains dominate: Mt Elgon (4 321 m), Mt Kadam (3 068 m), and Mt Moroto (3 083 m) (Harcourt 1992) (Figure 3.2).

The total area of Uganda is 235 880 km^2. One-sixth of this total area is made up of lakes, the biggest of which is Lake Victoria (Harcourt 1992) (Figure 3.1 & 3.2).

Lake Victoria

Lake Victoria lies in an equatorial basin between the escarpments of the eastern and western Rift Valleys of East Africa. It covers an area of 68 800 km^2 and extends 300 km from north to south and 280 km from east to west (Kendall 1969). The lake has a volume of 2 700 km^3. It is rather shallow, with a mean depth of 40 m and a maximum depth of 79 m (Lamb 1966, Kendall 1969) (Figure 3.1 & 3.2).

Figure 3.1: Africa indicating position of Uganda; Uganda – land area, lakes & neighbouring countries and location of study area in Lake Victoria, Uganda.

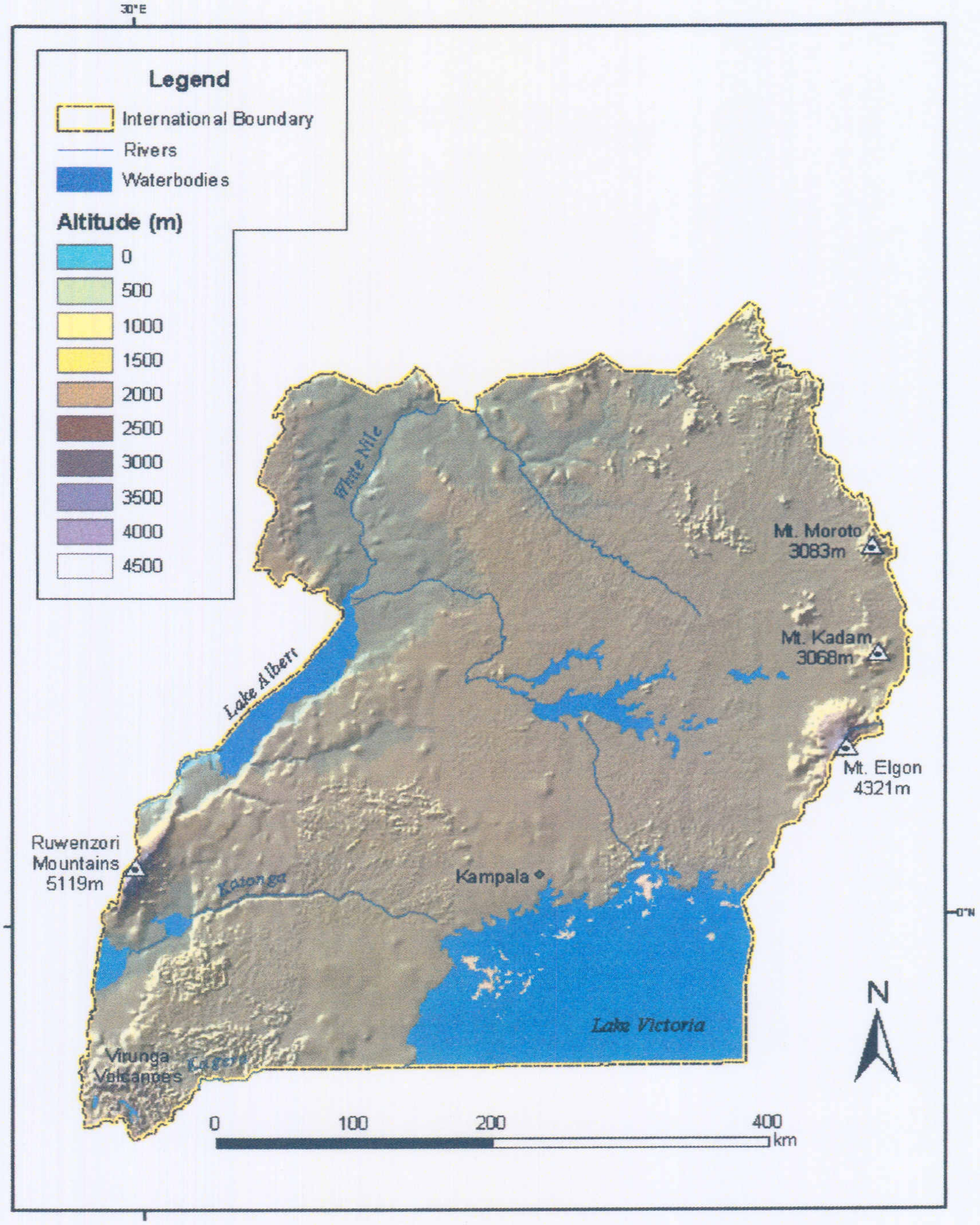

Figure 3.2: Uganda topography.

The Lake Victoria basin covers an area of 263 000 km^2 of which the lake occupies about one-fourth. The drainage of the lake is via the Nile River in the north, where it leaves the lake at Jinja (Kendall 1969). The shoreline of the lake, especially in the north and south, is very irregular and appears partially drowned. Straighter shorelines can be found in the southwest, southeast and northeast as a result of fault zones, resistant rocks or emergences (Kendall 1969). East and west of the lake its basin rises to over 1 000 m, forming highlands bordering the respective Rift Valleys, while locally in the north and south the watershed of the basin only rises to 25 m above lake level (Kendall 1969).

Volcanic emanations have covered part of the basin's periphery leading to regional uplift and Rift Valley formation (Kendall 1969). Thus, volcanics now constitute most of the lake's eastern watershed. In the northeast Mt Elgon volcano forms the corner of drainage, while in the west, with a less extensive igneous activity, only the Virunga vulcanos intrude on the basin (Kendall 1969) (Figure 3.2).

According to Kendall (1969) Lake Victoria's mean surface level prior to 1961 was 1 134 m above sea level. Even though the level has risen since then, all further references will be made to a presumed mean lake level of 1 134 m (Kendall 1969), a value which is also given by White (1983).

History

Lake Victoria originated in the middle or late Pleistocene (700 000 to 20 000 years B.P. - Tulloch 1993, Wahrig-Burfeind 1991) as a tectonically induced backwater through ponding of westwards flowing rivers (Kendall 1969). The lake was preceded by a west-to-east drainage system to which it now lies athwart, the earliest Lake Victoria was already very large and extended a considerable way to the west of its present position (Kendall 1969).

The backstopping of water was caused by uplifting of the land to the west of the present Lake Victoria basin. This uplifting began in the Miocene (> 700 000 years B.P. - Tulloch 1993, Wahrig-Burfeind 1991) and continued into the Pleistocene. Initially this uplifting was relatively slow and still allowed the westwards flowing rivers in the basin to maintain their direction of flow. The rate of uplifting increased and eventually caused river reversal and back-ponding in the middle to late Pleistocene. Through drowning of the two mature river systems of the *Kagera* in the west and the *Katonga* in the northwest Lake Victoria was originally formed (Kendall 1969). The remaining water is contributed by a number of smaller tributaries and through precipitation following evaporation from the Indian Ocean (Kendall 1969) (Figure 3.2).

Palaeogeology

Lake Victoria had three horizontally raised beaches during the last 12 000 years at 3, 12, and 18 m above the 1961 mean lake level. From 14 500 B.P. until about 12 000 B.P. the lake did not have an outlet. It also possessed a higher concentration in chemicals, especially carbon compounds, than today (Kendall 1969, Butzer *et al.* 1972).

During the period from 12 000 until 10 000 B.P. Lake Victoria had an outlet, coinciding with a rise in lake water level starting at around 12 000 B.P. (Kendall 1969, Butzer *et al.* 1972). Around 10 000 years ago the lake level dropped once again to about 12 m below the present level and the lake was closed once more (Kendall 1969, Butzer *et al.* 1972). After this period the lake level rose again and from about 9 500 B.P. Lake Victoria has had a constant drainage northward, forming the source of the White Nile (Kendall 1969, Butzer *et al.* 1972). From 9 500 until 6 500 B.P. the lake level was particularly high and it has been decreasing for the last 7 000 to 6 000 years reaching a particularly low level between 3 000 to 2 000 years ago (Kendall 1969, Butzer *et al.* 1972).

This fluctuation in mean lake level is typical for a number of East African lakes, such as Lake Turkana (Lake Rudolf), Lake Nakuru and Lake Naivasha (Lamb 1966, Butzer *et al.* 1972).

Lake level

The changes in lake levels were mainly induced by changes in climate, with a change in the precipitation/evaporation ratio being mainly responsible for subsequent changes in the mean lake level (Lamb 1966, Kendall 1969). Comparing modern rainfall conditions and water volume in the Victoria basin, Kendall (1969) concludes that from > 14 500 to 12 5000 years ago the climate must have been more arid than today to support a closed basin. Periods of higher rainfall are associated with higher lake levels (Kendall 1969).

Kendall (1969) calculates that at present Lake Victoria has a net water gain of 21 x 10^{12} litres per year. Tributaries deliver about 15 x 10^{12} to 16 x 10^{12} litres per year while the remaining volume is made up by rainfall (Kendall 1969). Kendall (1969) estimates that 90% of the lake's water income is lost again through evaporation (Kendall 1969). Lamb (1966) states an amount of 85%, with only the remaining 15% being lost by discharge through the Nile outlet.

Lamb (1966) argues that fluctuations in lake levels have been reported since measurements started. He concludes that such fluctuations should be expected to continue in the future with similar spacing as observed so far. Thus, high lake levels with peaks of up to half a metre above the ten year mean can be expected for two or three years in each decade (Lamb 1966).

Study sites

Ngamba Island is situated in the Ugandan part of Lake Victoria about 23 km southeast of Entebbe at S 00°06 and E 32°39 and an altitude of 1 160 m above sea level (Figure 3.1 & 6.1). It covers an area of 0.46 km^2 with a perimeter of 3 375.05 m (Meiklejohn pers. comm.[1]). Apart from a small area in the northern part of the island Ngamba Island is completely covered by moist evergreen secondary rain forest (Langdale-Brown *et al.* 1964) (Figure 6.1). The two control plots of the woody vegetation survey were situated in the north eastern part of neighbouring Nsadzi Island at S 00°05 and E 32°37 and a similar altitude as Ngamba Island (Figure 6.68).

CLIMATE

"The East African record ... presents a consistent picture of climatic change" (Kendall 1969).

Climate of tropical rain forests

The climate of the tropical rain forest is characterized by a high and very even temperature and heavy rainfall which is spread over the greater part of the year (Richards 1966). Throughout the rain forest belt these main features of the climate remain more or less similar. Even if considerable variations do occur, especially in the seasonal distribution of rainfall and temperature (Richards 1966).

Since the tropics are no natural climate boundaries, no simple latitudinal boundaries for the rain forest distribution can be given. Rather, in a climatologically sense, the tropical zone is

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[1] Meiklejohn, I.K. 2001. Department of Geography, University of Pretoria, Pretoria, R.S.A.

defined by the isotherm of 20 °C mean annual temperature, which ultimately depends on the uneven distribution of land and sea (Richards 1966).

In general terms it may be said, that the northern and southern climatic boundaries of the tropical rain forest formation type are mainly determined by precipitation, while its altitudinal boundaries are mainly determined by temperature (Richards 1939, 1966).

Rainfall

Uganda shows two different rainfall patterns. In the north of the country the rainfall is monomodal with one rainy season from April to October and a long and severe dry season for the rest of the year (Langdale-Brown *et al.* 1964, Hamilton 1974). The southern part of the country shows a bimodal rainfall pattern with a major rainy season from March to May and a minor rainy season from October to November (Langdale-Brown *et al.* 1964, Hamilton 1974). The two rainy seasons are separated by dry seasons up to three months in duration. However, the dry seasons are interrupted by occasional thunderstorms (Langdale-Brown *et al.* 1964).

Langdale-Brown *et al.* (1964) furthermore state a high variability in the quantity of precipitation throughout Uganda, with < 381 mm (15 inches) of rainfall in Karamoja, > 2 032 mm (80 inches) of rainfall in the Sese Islands and as much as 2 540 (100 inches) or more on the Ruwenzori Mountains.

The dividing line between the northern and southern rainfall profile can be roughly drawn from the northern end of Lake Albert in the west to Mbale in the east. It corresponds approximately with the northern limit of tropical rain forest as distinguishable from woodland at medium altitudes (Langdale-Brown *et al.* 1964, Hamilton 1974).

The mean annual rainfall for the years 1943 to 1959 was 1 549 mm (61 inches) for Entebbe and 1 245 mm (49 inches) for Jinja (Langdale-Brown *et al.* 1964). The mean annual rainfall at Entebbe ranged from 1 501 mm for the years 1901 to 1930, 1 605 mm (or 107% of the 01/30 mean) for the years 1956 to 1960, and 1 877 mm (or 125% of the 01/30 mean) for the years 1961 to 1964 (Lamb 1966).

Ngamba Island is located between Entebbe and Jinja and for the period between 1920 to 1980 the mean annual rainfall for Ngamba Island (at datum: S 00°06 / E 32°39) was 1 457 mm (Centre for Resource and Environmental Studies 1996, Erasmus, pers. com. [2]). Trends in rainfall patterns can be attributed to regularly occurring changes in large-scale atmospheric circulation which exert their effects over wide areas throughout the earth (Lamb 1966). However such drastic climatic changes as in 1960 are probably rare. Lamb (1966) compares this change in its magnitude and suddenness to the (in most cases opposite) climatic changes which took place around the 1890.

Figure 3.3 shows the monthly rainfall pattern during the study period. One peak appears in June and another one in October. The latter coincides with the peak of the second annual rainy season in the southern part of Uganda (Langdale-Brown *et al.* 1964). The total precipitation amounts to 528 mm during the six month study period.

Figure 3.4 shows the mean monthly rainfall pattern for the years 1920 to 1980 for the location S 00°06 / E 32°39, i.e. Ngamba Island. The bimodal rainfall pattern is clearly visible in Figure 3.4, with a major rainy season in March-April-May, and a minor one in October-November-December. This does not exactly coincide with Langdale-Brown *et al.'s* (1964) classification of the two annual rainy seasons in March-April and October-November.

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[2] Erasmus, B. 2002. Conservation Planning Unit, Dept. of Zoology and Entomology, University of Pretoria, R.S.A.

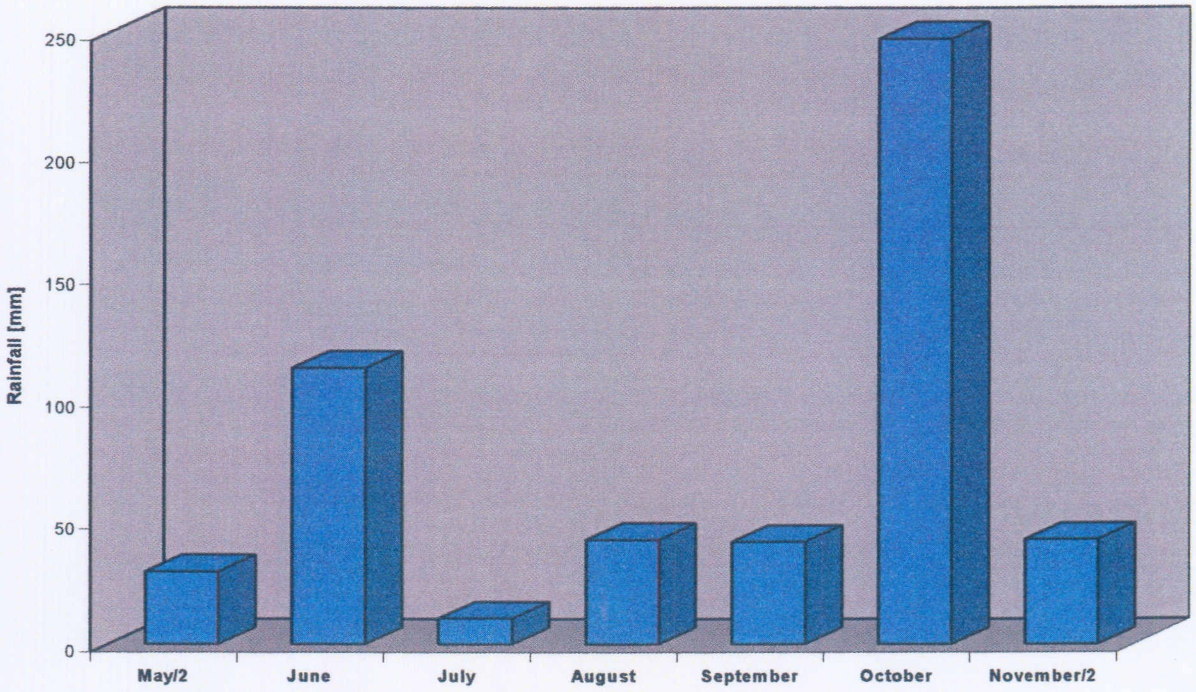

Figure 3.3: Monthly rainfall during study period – mid-May to mid-November 2000 for Ngamba Island.

Key: 🟦 Rainfall

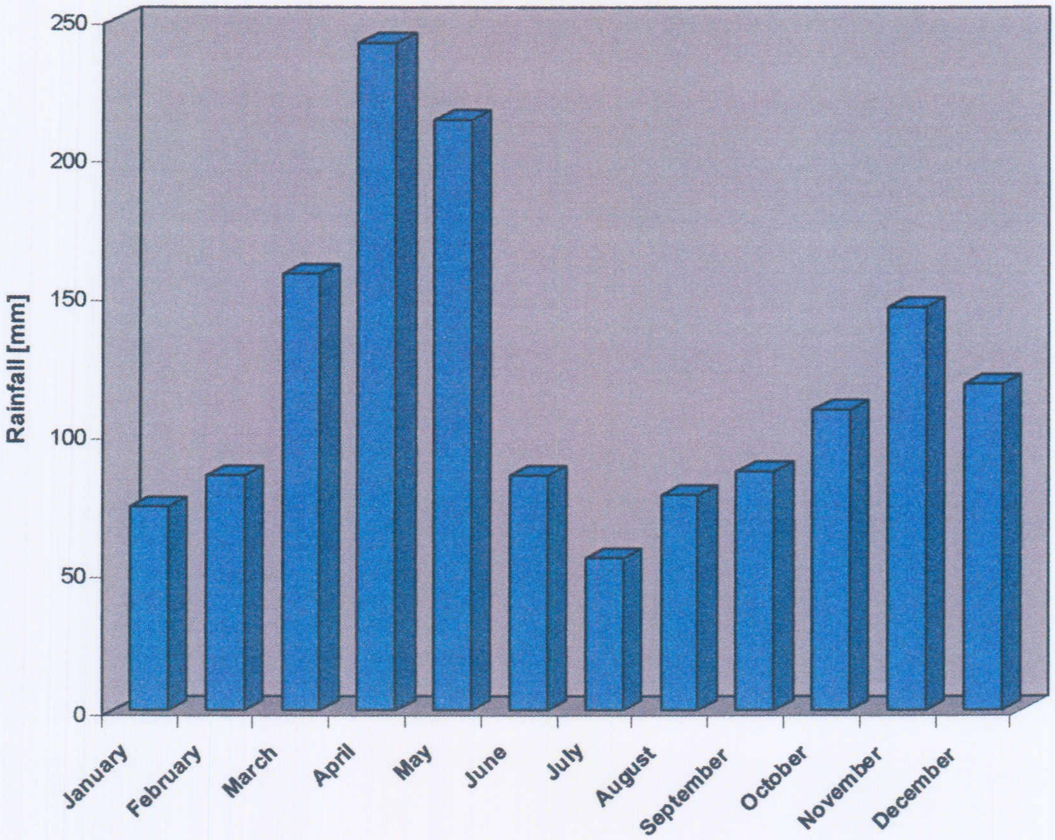

Figure 3.4: Monthly rainfall at S 00°06 / E 32°39 – mean from 1920 to 1980 (Centre for Resource and Environmental Studies 1996).

Key: 🟦 Rainfall

Temperature

Ngamba Island is located between Entebbe and Jinja and Langdale-Brown *et al.* (1964) list the following values for the year 1961:

Table 3.1: *Temperatures for Entebbe and Jinja meteorological stations for the year 1961*

Temperature [°C (°F)]	Meteorological station	
	Entebbe	Jinja
Mean annual maximum temperature [°C(°F)]	23.1 (73.5)	24.4 (76.0)
Mean annual minimum temperature [°C(°F)]	15.2 (59.3)	14.7 (58.4)
Mean annual temperature [°C(°F)]	19.1 (66.4)	19.6 (67.2)
Highest maximum temperature [°C(°F)]	26.7 (80.1)	30.1 (87.0)
Lowest minimum temperature [°C(°F)]	11.9 (53.5)	10.8 (51.5)

For the years from 1920 to 1980 the temperature values are as follows (Centre for Resource and Environmental Studies 1996, Erasmus pers. comm.[2])

Table 3.2: *Temperatures for Ngamba Island (S 00°06 / E 32°39) for the years 1920 to 1980*

Ngamba Island (Datum: S 000°06 / E 32°39)	
Mean yearly maximum temperature [°C]	26.1
Mean yearly minimum temperature [°C]	16.0
(mean yearly max. + mean yearly min.) / 2 [°C]	21.1
Mean maximum temperature [°C]	27.2
Mean minimum temperature [°C]	15.0

Figure 3.5 shows the mean monthly temperature and standard deviation (STD) on Ngamba Island during the study period from the middle of May until the middle of November 2000. During these months the mean temperature was always around 25ºC with a maximum standard deviation of ± 3ºC (Figure 3.5), indicating a "high and very even temperature" (Richards 1966) which is characteristic for tropical rain forest habitats.

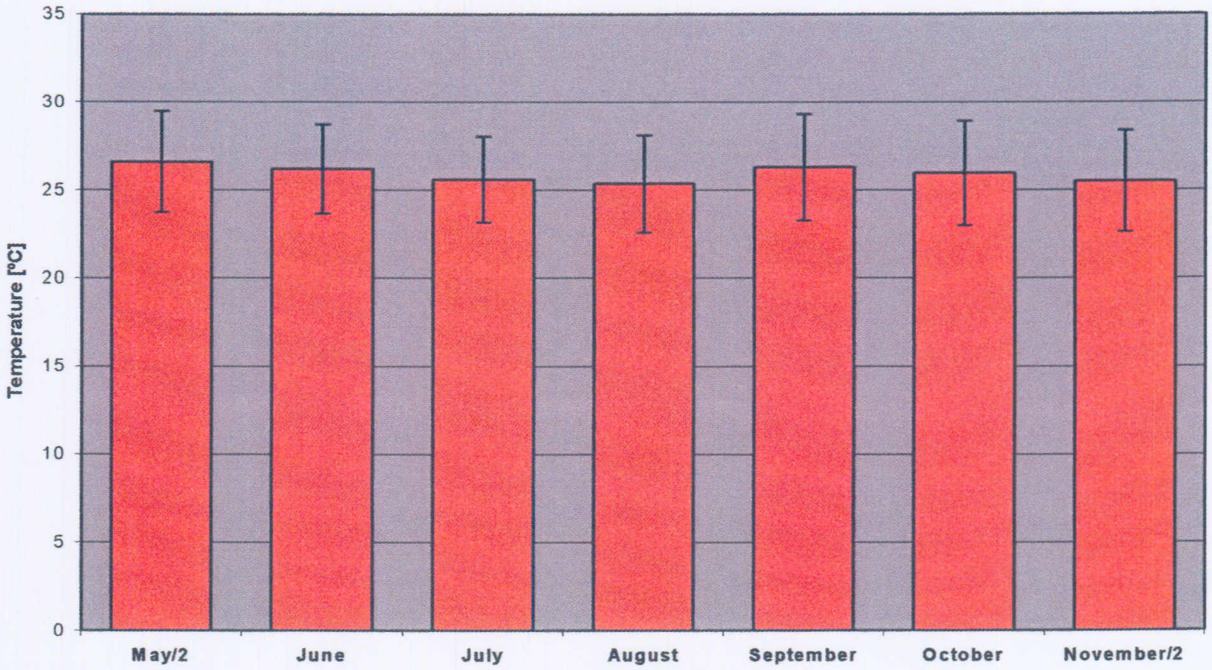

Figure 3.5: Mean monthly temperature during study period – mid-May to mid-November 2000 [Mean °C ± STD] for Ngamba Island.

Key: 🟥 Temperature

Figure 3.6 shows the mean monthly temperature at 08:00, 14:00 and 18:00 as well as the mean of the minimum and maximum temperatures during the six month study period. Again, the temperatures are relatively even throughout the months and the mean maximum (14:00) and minimum (08:00) temperatures do not differ with more than a maximum of 6.5°C.

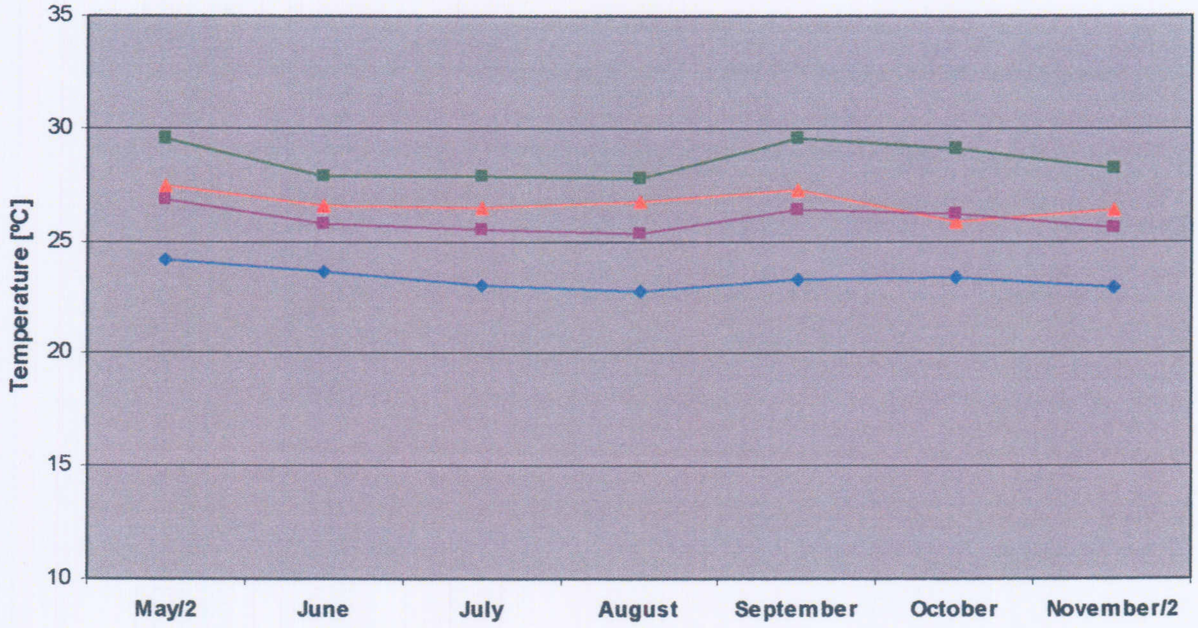

Figure 3.6: Monthly temperatures during study period: 08:00, 14:00, 18:00 & mean for Ngamba Island.

Key:

🟦 08:00
🟩 14:00
🟥 18:00
🟪 Mean

Figure 3.7 shows the mean temperature for the years 1920 to 1980 for the location S 00°06 and E 32°39, i.e. Ngamba Island. Like the rainfall data from 1920 to 1980 these data have been extracted for S 00°06 / E 32°39 from a CD containing digitized coordinates for the whole of Africa. The underlying Digital Elevation Model (DEM) has a standard error of between about 20 to 150 m, depending on the roughness of terrain. Overlaid on the DEM are monthly and annual mean values of rainfall and daily minimum and maximum temperatures for the years 1920 to 1980. These climate data have been subjected to comprehensive error detection and corrective procedures based on ANUDEM and ANUSPLIN. The standard error for the temperature values is about 0.5°C. The standard error of the rainfall values is between 5 - 15%.

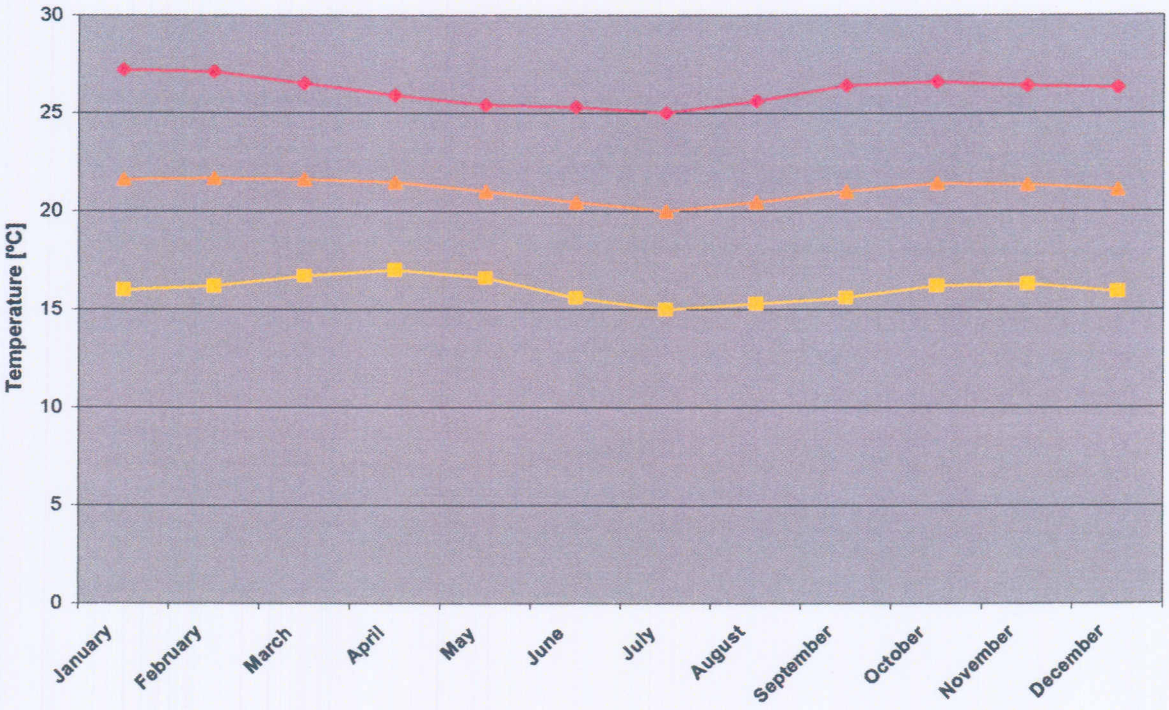

Figure 3.7: Monthly minimum, maximum & mean temperatures at S 00°06 / E 32°39 – mean of 1920 to 1980 (Centre for Resource and Environmental Studies 1996).

Key:

🟥 Maximum

🟨 Minimum

🟧 Mean

Even though, the mean temperature for these 61 years is about 5°C lower than for the mean during the study period, the general pattern, though slightly shifted in time, is still the same for both periods. The 5°C difference might at least partly be caused by the fact that the 08:00 temperature was taken as representative of the minimum temperature and not the real minimum (e.g. from a thermograph) which might be underlying the 1920 to 1980 data.

There is a slight decline in mean temperature from May until August, a slight increase of mean temperature from August to October leading into a second slight temperature decline towards November for the study period. The overall temperature pattern for 1920 to 1980 is slightly shifted in time with the lowest temperature occurring in July, followed by a slight increase in temperature until October/November and leading into a slight temperature decrease towards December. While the mean temperature during the study period never falls below 25°C, the lowest mean temperature for the years of 1920 to 1980 is 20°C in the month of July.

Relative humidity

For relative humidity Langdale-Brown *et al.* (1964) give the following values for 1961 (source: East African Meteorological Department):

Entebbe:	Mean of monthly means (06:00 am):	85%	lowest mean: 72%
	Mean of monthly means (12:00 noon):	67%	lowest mean: 55%
Jinja:	Mean of monthly means (06:00 am):	85%	lowest mean: 68%
	Mean of monthly means (12:00 noon):	61%	lowest mean: 41%.

Figure 3.8 shows the mean monthly relative humidity and standard deviation (STD) on Ngamba Island during the study period from the middle of May until the middle of November 2000. During these months the mean monthly relative humidity was always between 57 and 64 % with a relatively small maximum standard deviation of about ± 6 %.

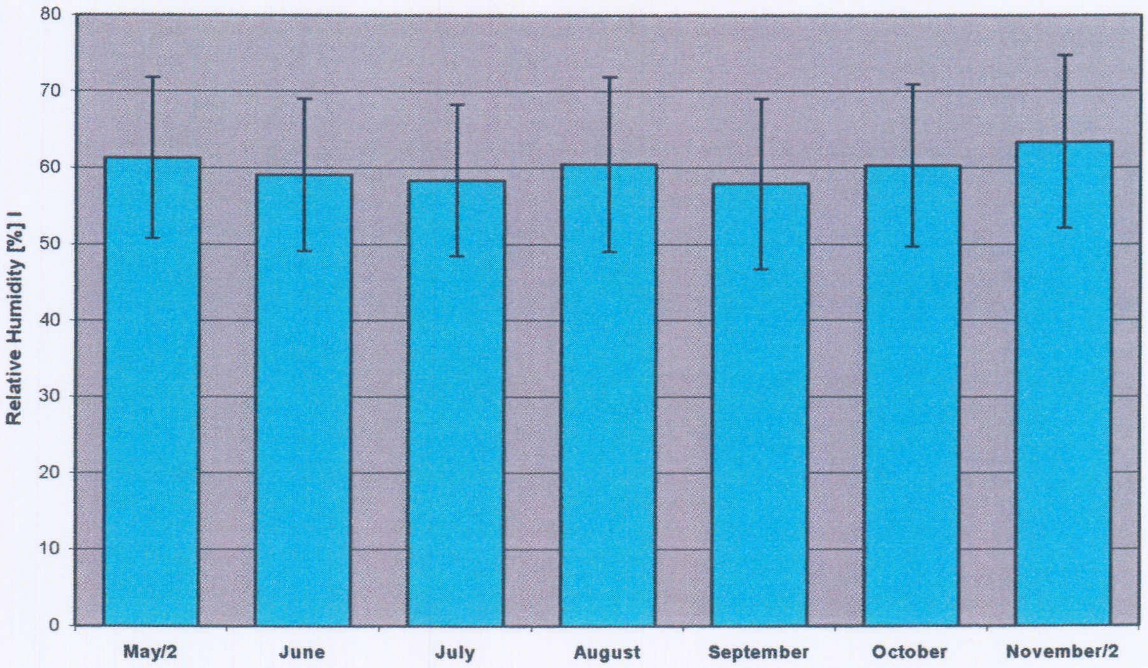

Figure 3.8: Mean monthly relative humidity during study period - mid-May to mid-November 2000 [Mean % ± STD] for Ngamba Island.

Key: 🟦 Relative humidity

Figure 3.9 shows the mean monthly relative humidity at 08:00, 14:00 and 18:00 as well as the mean of the minimum and maximum values during the six month study period. The range of values between the maximum (08:00) and minimum (14:00) mean values of relative humidity increases during the second half of the study period. The relative humidity at 08:00 and 14:00 behave rather similar and their values decrease and increase parallel to each other during the whole study period (Figure 3.9). While the relative humidity at 18:00 is very similar to that of 14:00 during the first half of the study period, its values behave inversely to the former from the middle of the study period (August 2000) onwards (Figure 3.9).

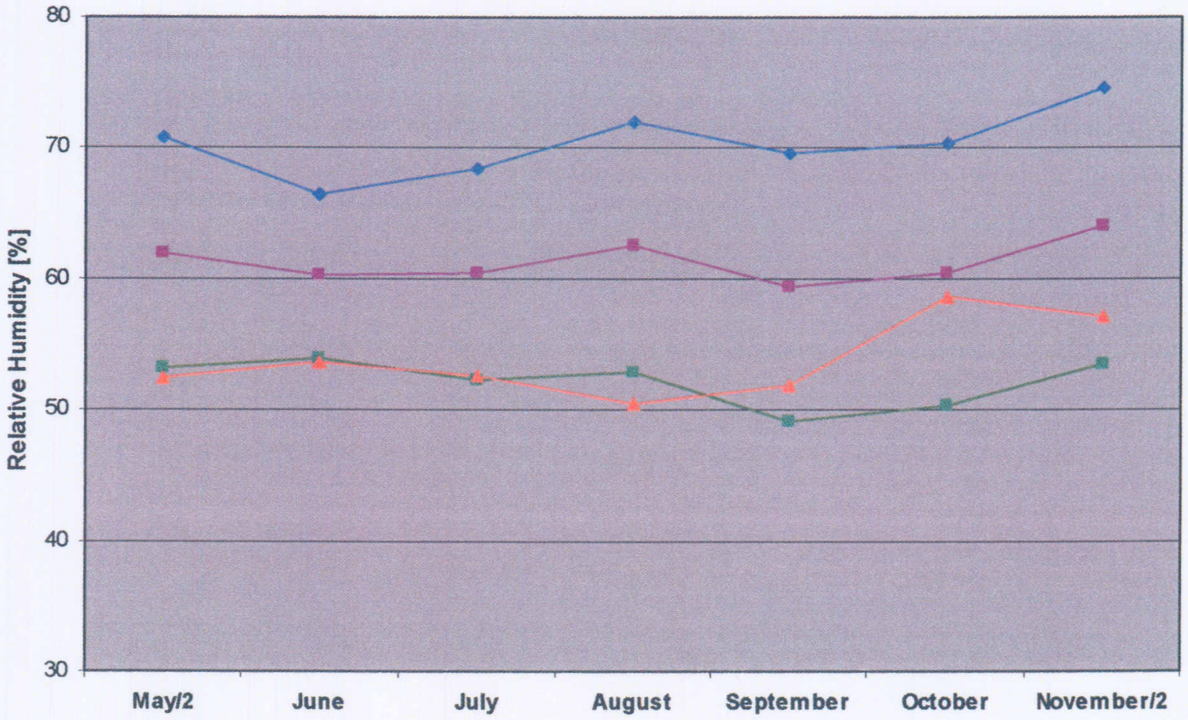

Figure 3.9: Monthly relative humidity (%) during study period 08:00, 14:00, 18:00 & mean for Ngamba Island.

Key:

🟦 08:00

🟩 14:00

🟥 18:00

🟪 Mean

The values for relative humidity at Entebbe from 1990 to 2000 are given in Figures 3.10 & 3.11 (Deutscher Wetterdienst 2001) and can be summarized as follows:

Entebbe Meteorological Station (N 01°00 / E 32°50):

Mean of monthly means (06:00 am):	87%	lowest mean: 84%
Mean of monthly means (12:00 noon):	72%	lowest mean: 65%

Figure 3.10 shows the mean monthly relative humidity at Entebbe meteorological station from 1990 to 2000. The mean relative humidity during the months of the study period (from mid-May until mid-November) ranges from 78 to 83 % and is hence on average about 20% higher during the years 1990 to 2000 compared with the values of the study period in the year 2000 on Ngamba Island (Figures 3.8 & 3.10). This might be due to a more arid climate on Ngamba Island compared to Entebbe meteorological station and / or to the fact, that minima and maxima where determined at slightly different times of day for the two locations. With a maximum of ± 16 % the standard deviation for the Entebbe data also shows a larger range than that for Ngamba Island (Figure 3.8 & 3.10).

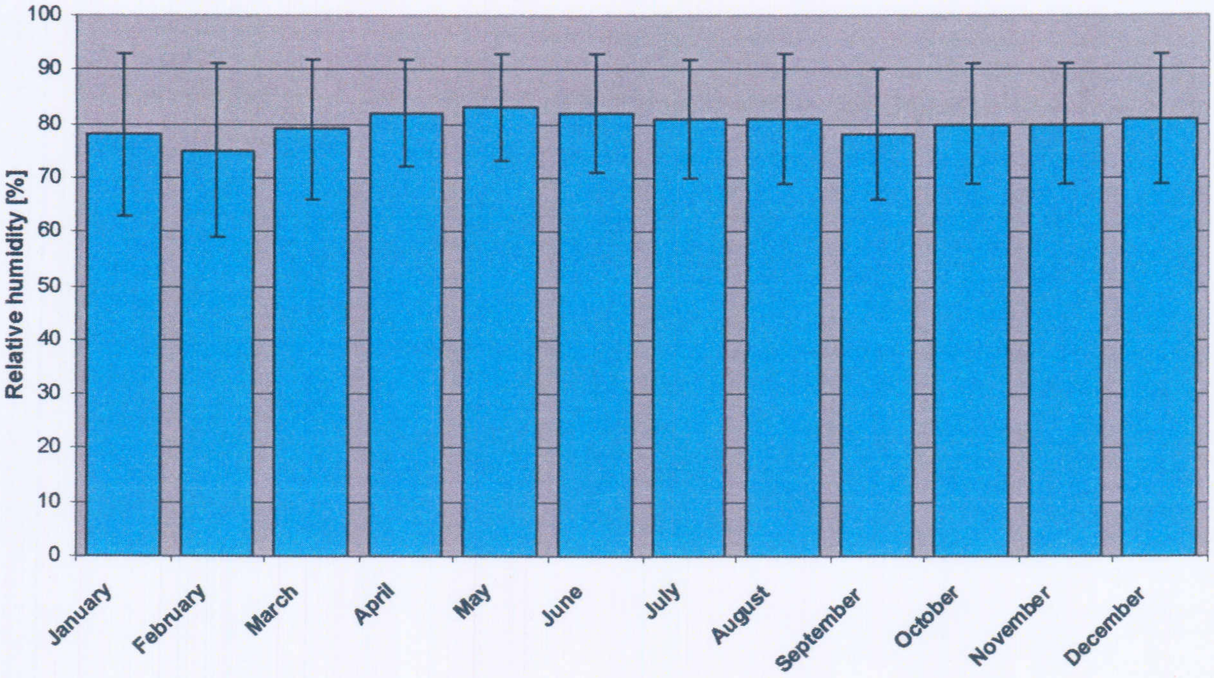

Figure 3.10: Mean monthly relative humidity [Mean % ± STD] at Entebbe Meteorological Station (N 01°00 / E 32°50) from 1990 - 2000 (n = 3 895) (Deutscher Wetterdienst 2001).

Key: 🟦 Relative humidity

Figure 3.11 shows the monthly minimum, maximum and mean relative humidity for Entebbe meteorological station for the years 1990 to 2000. Here again the values for maximum (06:00) and minimum (12:00) are on average about 20 % higher than those values measured at maximum (8:00) and minimum (14:00) during the study period on Ngamba Island (Figure 3.9 & 3.11). As stated above this is most likely due to the different time of day at which the measurements were taken at the two different locations.

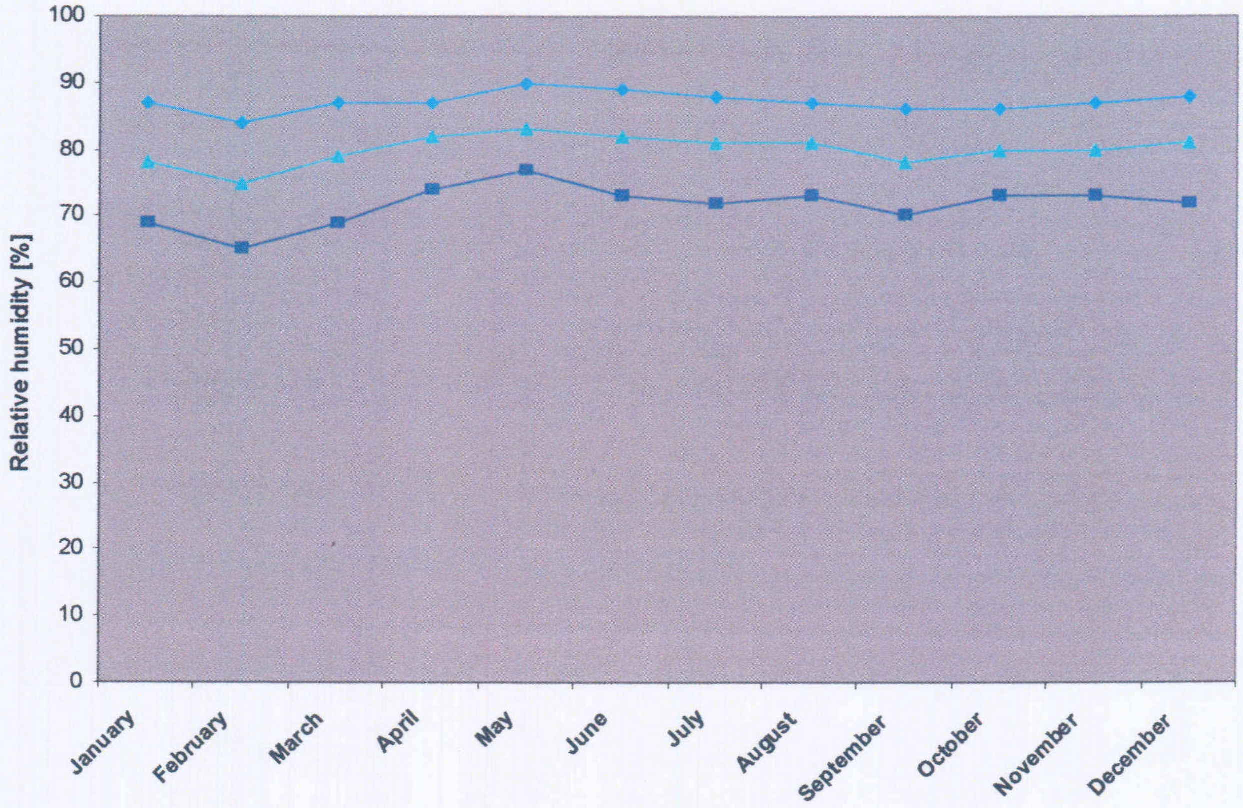

Figure 3.11: Monthly minimum, maximum & mean relative humidity [%] at Entebbe Meteorological Station (N 01°00 / E 32°50) from 1990 to 2000 (n = 3 895) (Deutscher Wetterdienst 2001).

Key:
🟦 06:00
🟦 12:00
🟦 Mean

Wind

The winds of Eastern Africa mainly come from an easterly direction supported by monsoons coming in from the northern hemisphere (Kendall 1969). However Newell (1960 in Kendall 1969) found conclusive evidence for a predominantly south to south easterly direction of the winds over Lake Victoria. This finding of a net southerly component is supported by the likewise directed, wind-generated currents of the lake through most of the year, and by the drift of thunderstorm tracks, the orientation of wave cut cliffs and long shore bars (Kendall 1969). Further evidence is given by precipitation patterns at different weather stations along the shores of Lake Victoria: upwind stations, such as Mwanza in the south (1 000 mm per year), receive considerably less precipitation than downwind stations, such as Entebbe in the north (1 500 mm per year) (Kendall 1969, Hamilton 1974).

Langdale-Brown *et al.* (1964) attribute the main seasonal rainfalls in Uganda to southeast monsoons coming from the Indian Ocean. For the dry season the authors state prevailing northeast winds occasionally interrupted by moist westerly winds which are responsible for additional "instability" rainfalls (Langdale-Brown *et al.* 1964). A summary of wind direction frequency from Entebbe Meteorological Station for the years from 1990 to 2000 shows a predominance of southerly winds, although northerly winds are nearly as frequent (Figure 3.12) (Deutscher Wetterdienst 2001).

In essence, all three observations agree on the fact that the major component of the winds over Lake Victoria is a strong southerly current.

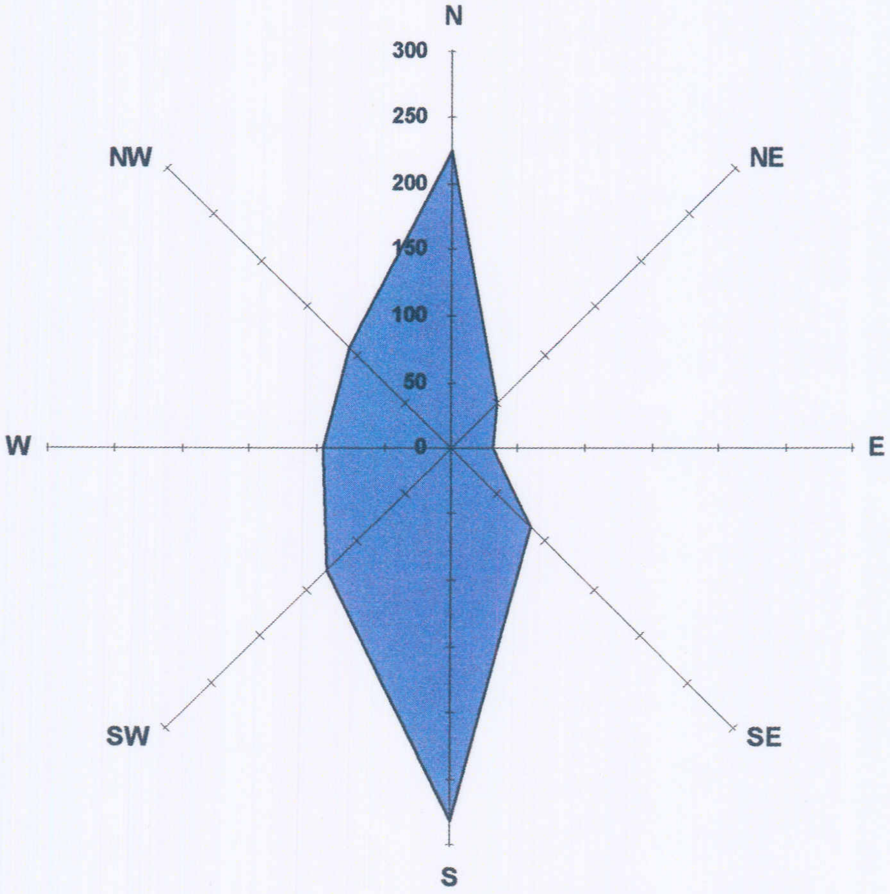

Figure 3.12: Wind rose showing the mean wind direction frequencies per 1000 recordings (n = 9 974) at Entebbe Meteorological Station for the years 1990 – 2000 (Deutscher Wetterdienst 2001).

Key: 🟦 Wind direction frequency

Wind velocity

Fons (1940) determined that the wind velocity is greatly decreased at the top of the crowns of the trees in a forest, and that it remains nearly constant in the canopy zone. This effect is mainly caused by the branches and foliage of the trees which (1) reduce wind velocity, and (2) render the distribution of wind velocity nearly uniform (Fons 1940). Several zones with different climatic conditions exist from the ground surface to the space above the crowns.

Figure 3.13 – 3.16 show the wind directions and wind velocities for Entebbe Meteorological Station for the years 1900 – 2000 (Deutscher Wetterdienst 2001). The majority of winds are feeble and comes from a southern and northern direction (Figure 3.13). Moderate to strong winds mainly come from a southern direction but are far less common (Figure 3.14). Strong to high winds occur rarely and are as frequent from the north as from the south (Figure 3.15); while heavy storms occur about twice a year and come mainly from the north (Figure 3.16).

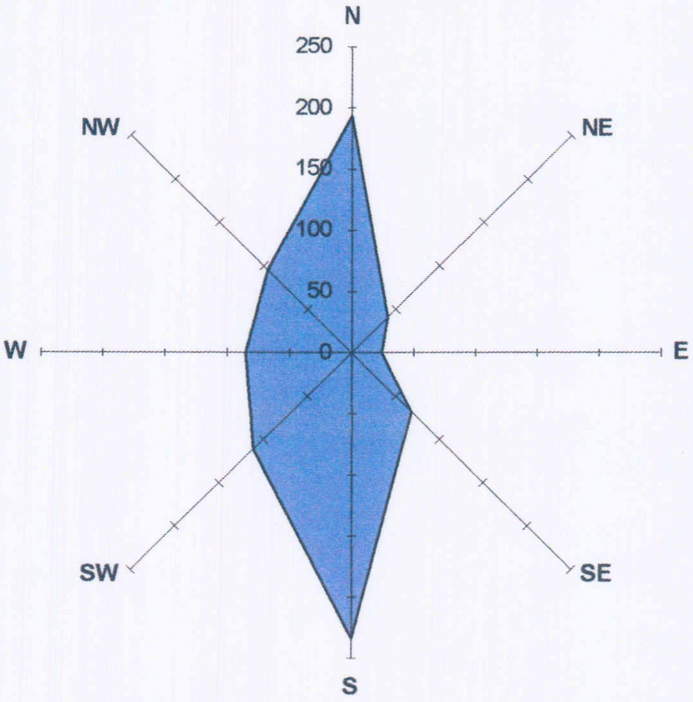

Figure 3.13: Wind rose showing the mean wind direction frequencies (n = 8 599) per year for feeble winds (0 – 10 knots = 0 – 19 km/h) at Entebbe Meteorological Station for the years 1990 – 2000 (Deutscher Wetterdienst 2001).

Key: 🟦 Wind direction frequency

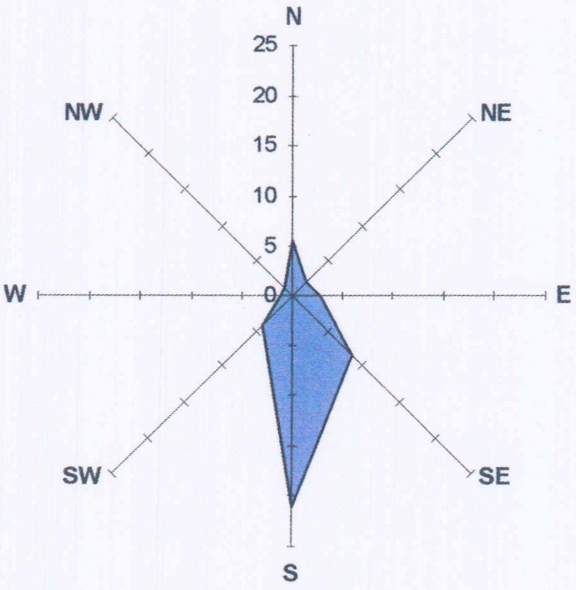

Figure 3.14: Wind rose showing the mean wind direction frequencies (n = 503) per year for moderate to strong winds (11 – 40 knots = 20 – 74 km/h) at Entebbe Meteorological Station for the years 1990 – 2000 (Deutscher Wetterdienst 2001).

Key: 🟦 Wind direction frequency

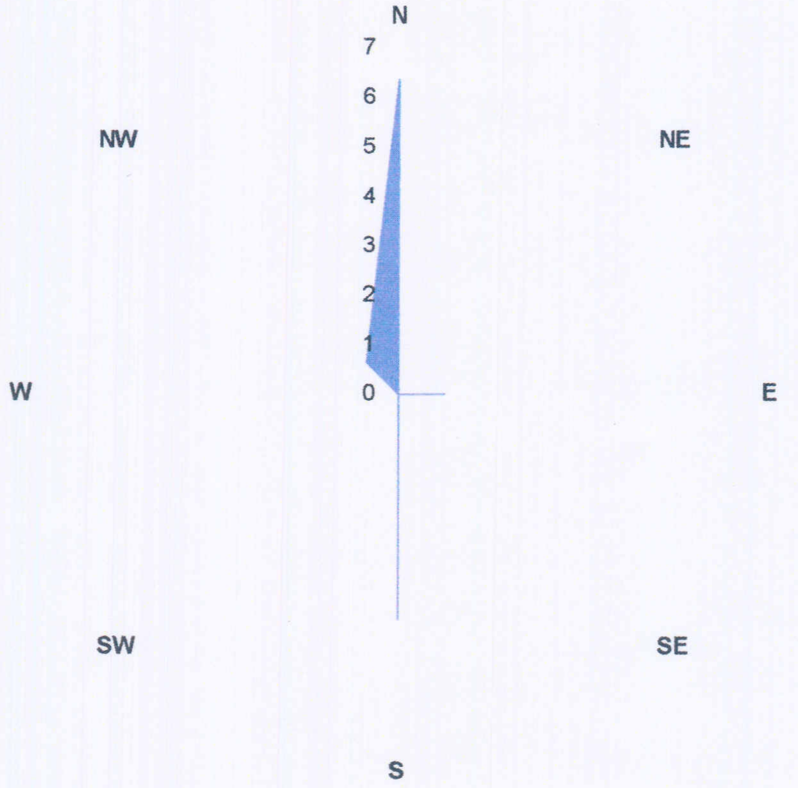

Figure 3.15: Wind rose showing the mean wind direction frequencies (n = 14) per ten-year period for strong to high winds (41 – 63 knots = 75 – 117 km/h) at Entebbe Meteorological Station for the years 1990 – 2000 (Deutscher Wetterdienst 2001).

Key: 🟦 Wind direction frequency

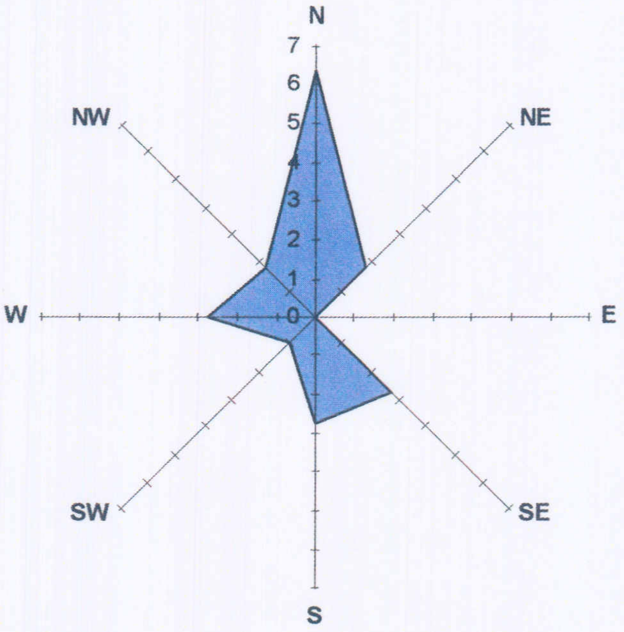

Figure 3.16: Wind rose showing the mean wind direction frequencies (n = 21) per ten-year period for heavy storms (> 64 knots = > 118 km/h) at Entebbe Meteorological Station for the years 1990 – 2000 (Deutscher Wetterdienst 2001).

Key: 🟦 Wind direction frequency

Geology & soil

The soils of tropical rain forests share certain characteristics (Eggeling 1947, Richards 1966):

colour: bright red or yellow
texture: generally loamy or clayey, but often sandy in the superficial layers
humus: low in humus content and mostly confined to the upper horizons
clay: relatively rich in aluminium and poor in silica
nutrients: generally deficient in plant nutrients
pH: usually deficient in bases and thus almost invariably acid.

Most forest soils of the damp tropics are lateritic, even if true laterite, i.e. the end product of laterization, "a mixture of aluminium and iron oxides with very little else", normally is never reached under rain forest conditions (Richards 1966). A lateritic soil according to Richards (1966) is a soil of which the silica/aluminium ratio is less than 2.0 in the clay fraction. *Laterite* in the sense of Richards (1966) should be comparable to the *ferralitic soils* or *ferralsoils* mentioned by Langdale-Brown *et al.* (1964). The red colour which is common in tropical soils, thus the term "tropical red earths", that are formed under conditions of unimpeded drainage is due to the abundance of iron oxides. The exact shade of the colour depends on the degree of hydration of the iron oxides (Richards 1966). Richards (1966) assumes that lateritic soils may be the most widespread soil type of the rain forest region, even if not all tropical soils are lateritic. This tropical red earth as a result of lateritic weathering is best seen on fragmental volcanic rocks (Richards 1966), such as those that are found on the islands in Lake Victoria.

The soils of the Lake Victoria basin are described by Kendall (1969) as being an abundance of silicate rocks and well-leached laterite soils (also: Thomas 1941). While Langdale-Brown *et al.* (1964) classify the soils of the Sese Islands as ferralitic soils (= ferralsols) on undifferentiated rock with a dominant red colour.

The soils of Ngamba Island show the typical acidity, (compare Results, Chapter 6) prevalent in a tropical rain forest habitat where soils are usually deficient in bases and thus almost invariably acid (Richards 1966) as well as generally deficient in plant nutrients (Richards 1966). They belong to the soil type named *ferrallitic soils* or ferralsols by Langdale–Brown *et al.* (1964) or *lateritic soils* by Richards (1966) with a dominant red colour and found on volcanic or undifferentiated rock in the tropics.

VEGETATION

Vegetation of tropical rain forests

“Evergreen, hygrophilous in character, at least 30 m high, but usually much taller, rich in thick-stemmed lianas and in woody as well as herbaceous epiphytes“ (Schimper 1903 in Richards 1966).

Primary tropical rain forest

This evergreen forest or primary tropical rain forest is, in ecological terms, according to Richards (1966), the climax vegetation of the equatorial climate. The author lists the following growth forms of primary tropical forest (Richards 1966):

A. Autotrophic plants (with chlorophyll)

1. Mechanically independent plants
   (a) Trees and ‘shrubs‘ } arranged in a number of strata
   (b) Herbs
2. Mechanically dependent plants
   (a) Climbers
   (b) Stranglers
   (c) Epiphytes (including semi-parasitic epiphytes)

B. Heterotrophic plants (without chlorophyll)

1. Saprophytes
2. Parasites

Secondary tropical rain forest

Richards (1966) defines a *typical secondary rain forest* as "the earlier seral stages found on areas which have been cultivated or exploited for timber, but not subsequently grazed or burnt."

Richards (1966) lists the following general characteristics of secondary rain forest:

1. It is lower and consists of trees of smaller average dimensions than those of primary forest.
2. Occasionally, trees of much larger dimensions than the average are found scattered through secondary forest, being 'leftovers' from the destruction of the original primary rain forest.
3. Young secondary forest is often remarkably regular and uniform in shape, but shows an abundance of small climbers and young saplings that gives it a dense and tangled appearance different to primary forest.
4. At a later stage in the succession an extremely irregular structure is characteristic.
5. Over time pioneer tree species become senescent and are often unable to regenerate under the new ecological conditions they have created. Thus, many trees in a large area may simultaneously become liable to wind throw or death from some other cause, leaving large gaps in the forest cover.
6. Slower-growing trees dominate the next phase of succession.
7. Lianas are typically abundant in secondary rain forest.
8. The different successional stages of secondary rain forest usually show a characteristic species composition, almost all secondary forest trees are light-demanding and intolerant of shade, but grow well in any opening or clearing of sufficient size.
9. Many secondary rain forest trees are unable to regenerate in their own shade and thus a community dominated by them necessarily lasts for only a single generation.
10. Secondary rain forest trees possess efficient means of seed dispersal as well as rapid growth.

Secondary succession in tropical Africa goes through three distinctive stages the first of which is marked by the invasion of herbaceous plants with rapid growth and a short life span. The second stage is followed by the invasion of perennial and 'suffrutescent' herbs in which herbaceous and woody climbing plants are abundant. Additionally, saplings are regenerating from seeds and resprouting from stumps that have survived in the soil. The third stage is also called the 'tree stage of the succession' and can again be divided into three different phases (Richards 1966, Ewel 1980).

During the first phase of the tree stage bushes and young trees become dominant and soon a tree canopy is formed. This phase is dominated by *Musanga cecropioides*, *Trema guineensis*, *Harungana madagascariensis* and *Pycnathus angolensis*. It reaches its optimum at 10 to 20 years of age and has a total duration of between 20 to 30 years (Richards 1966). The second phase is dominated by genera like *Bosqueia*, *Conopharyngia*, *Alstonia*, *Funtumia*, *Albizia*, *Pentaclethra*, *Sterculia*, *Ricinodendron*, *Fagara*, and *Ficus*. It reaches its optimum at 20 to 30 years after the beginning of the 'tree stage' and has a duration of about 50 years (Richards 1966). The third stage marks the gradual return to dominance of species characteristic of primary rain forest. This stage first becomes dominant 60 to 100 years after the beginning of the tree stage (Richards 1966).

Vegetation of Uganda

"Modern vegetational patterns have been greatly affected by human activity" (Kendall 1969).

Langdale-Brown *et al.* (1964) give a list of "Open Water, Crops and the Main Vegetation Types" for Uganda. They attribute the following percentage areas to the different land-use types:

Cropland	11.7%
High Altitude Grassland, Heath and Moorland	0.8%
Forest and Moist Thicket	4.6%
Well Drained Savanna (including Grass Savanna)	48.3%
Dry Thicket, Bushland and Steppe	7.5%
Communities on Sites with Impeded Drainage	7.9%
Permanent Swamp	3.9%
Open water	15.3%

The natural vegetation has been modified to a large extent by cutting, cultivation, burning, grazing and similar interferences by man according to Langdale-Brown *et al.* (1964). It is now often no longer possible to see the broad distribution of natural vegetation and what prevails is a mosaic of forest and derived savanna communities in the wetter areas to the northwest of Lake Victoria and in the Western Highlands (Langdale-Brown *et al.* 1964).

Figure 3.21 shows the Ecological Zones of Uganda as established by Langdale-Brown *et al.* (1964). Figure 3.22 indicates the Land Use of Uganda as delimited by Langdale-Brown *et al.* (1964) for the late 1950s and early 1960s. The establishment of the Ecological Zones was based on this latter map and additional climatic findings (Langdale-Brown *et al.* 1964).

Figure 3.23 has been drawn according to a map by Katende *et al.* (1995) and shows the main vegetation zones as identified in 1995.

Already in 1964 Langdale-Brown *et al.* (1964) reported a substantial impact of man on the vegetation of Uganda. They established that the mountainous vegetation had suffered least, still showing large areas of natural or semi-natural montane forest, high montane grassland and afro-alpine communities (Langdale-Brown *et al.* 1964). For the rest of the country the authors stated considerable changes in the vegetation due to annual or biennial grass fires, coupled with an overloading of traditional farming systems. This resulted in the prevalence of fire climax and seral communities constituting about 80% of the vegetation (Langdale-Brown *et al.* 1964).

Langdale-Brown *et al.* (1964) give four different areas of natural forest which are restricted by the prevailing rainfall patterns and altitude:

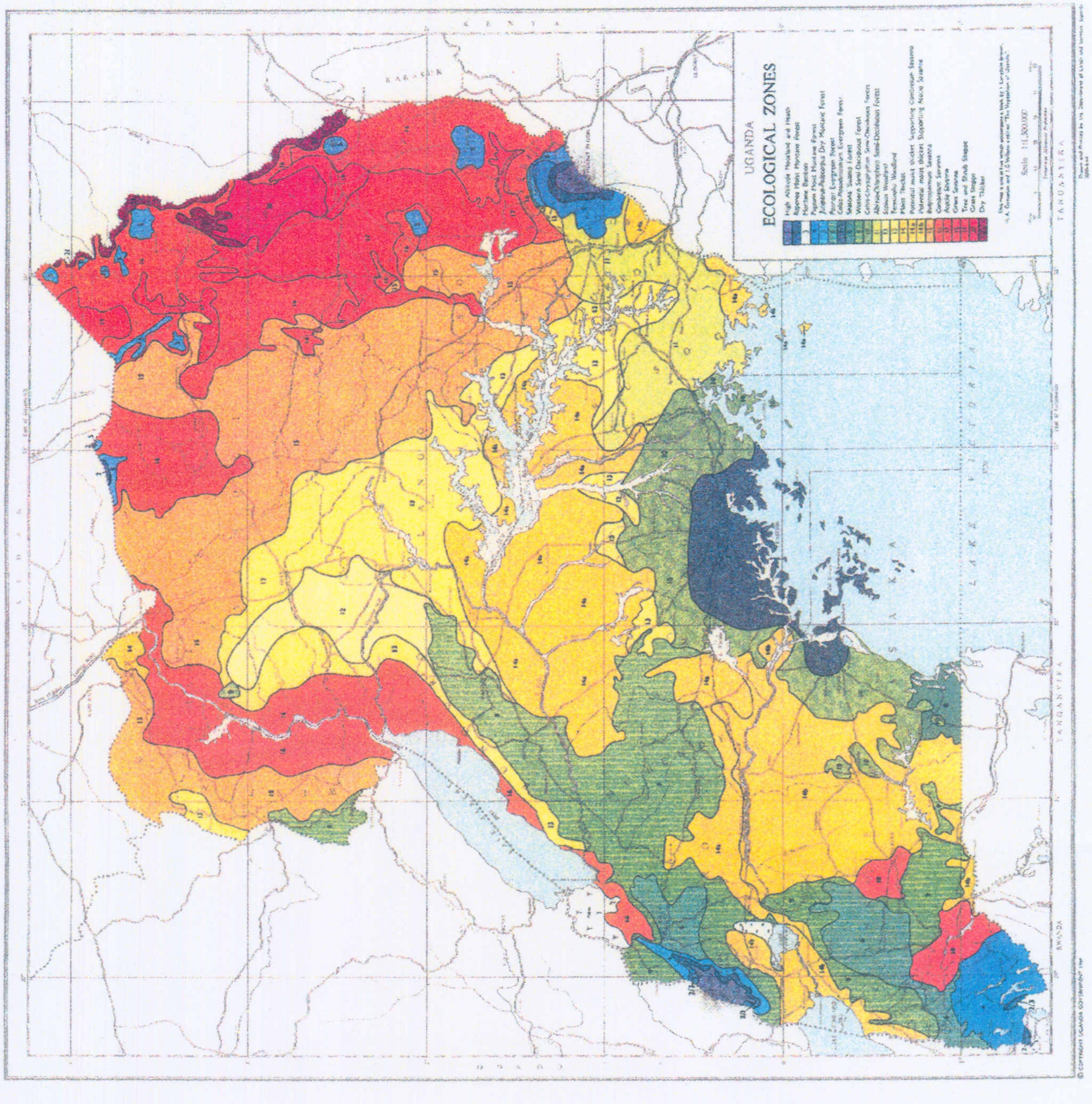

Figure 3.17: Ecological zones of Uganda (following Langdale-Brown *et al.* 1964).

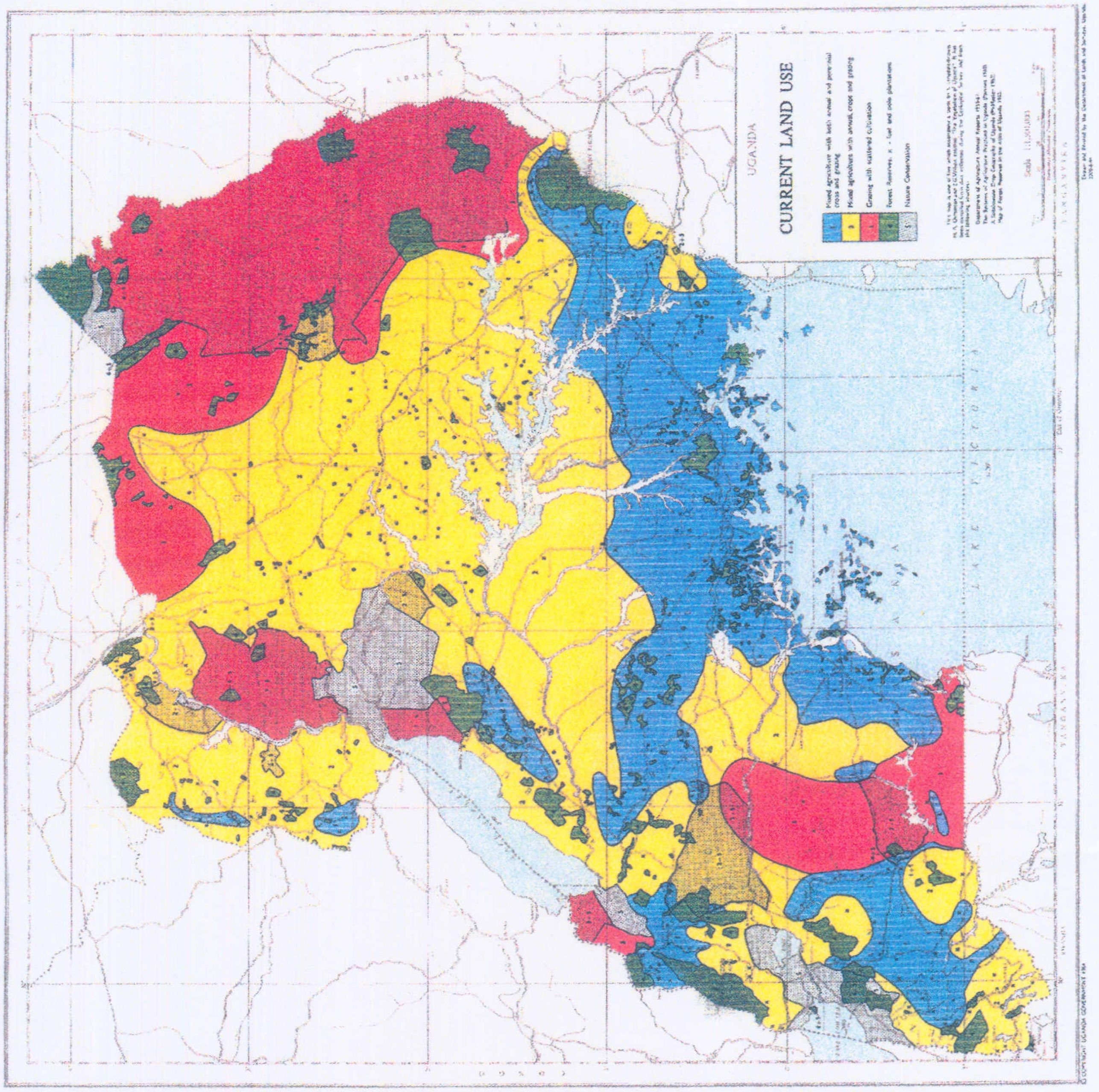

Figure 3.18: Land use of Uganda (following Langdale-Brown *et al.* 1964).

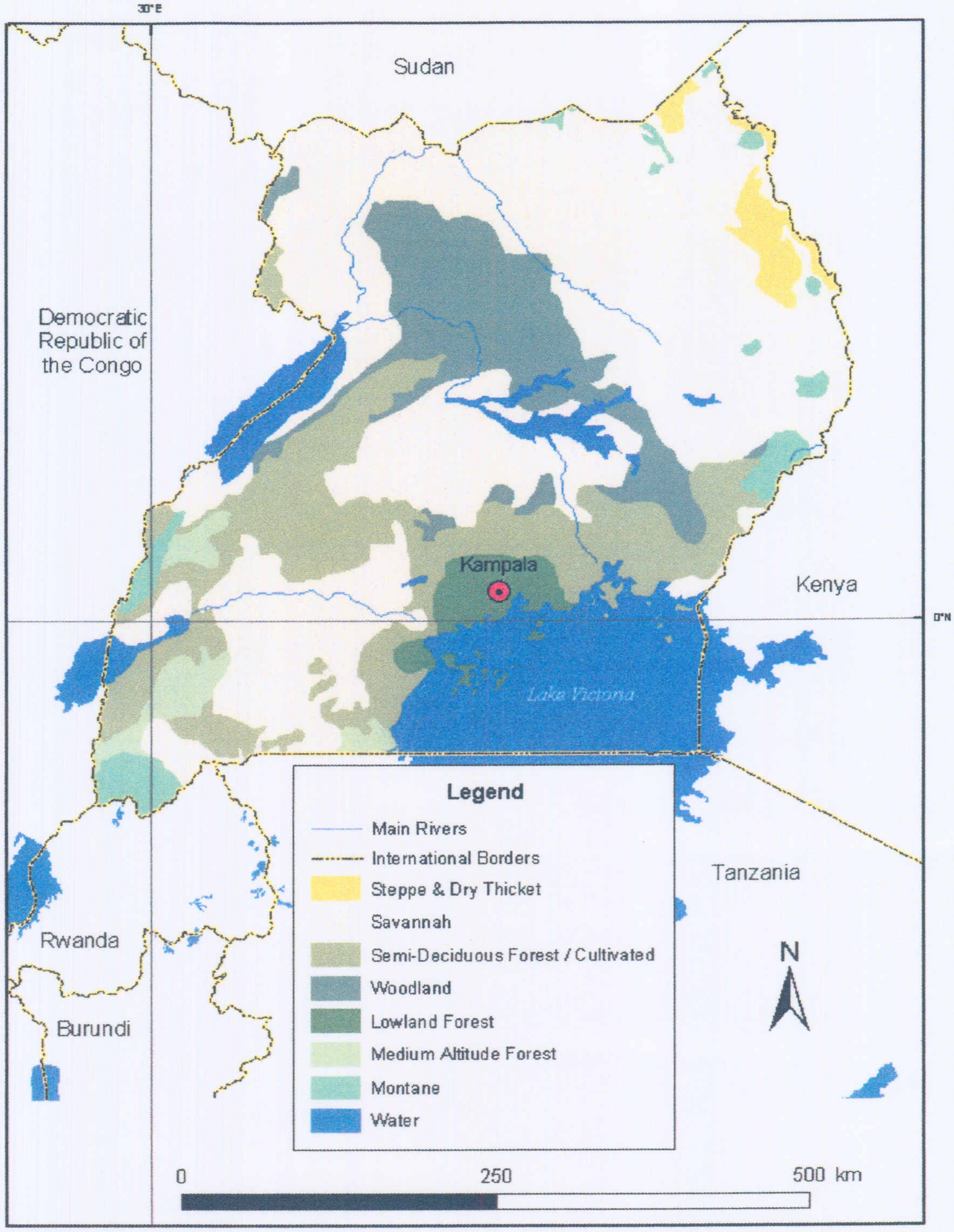

Figure 3.19: The main vegetation zones of Uganda (following Katende *et al.* 1995).

1. The high rainfall belt north-west of Lake Victoria
2. The high rainfall belt along the eastern side of the Western Rift Valley
3. A medium rainfall belt between the first two, where there are some young forests
4. The mountains over 1 524 m (5 000 feet) where orographic rainfall occurs.

Hamilton (1974) distinguishes only three different forest zones in Uganda, namely:

1. A region in the west including the shoulder of the Rift Valley and also extending in places into the Rift itself
2. The region around the northern shore of Lake Victoria
3. A number of isolated montane forests in the north and east.

Hamilton (1974) also classifies the Ugandan forests as floristically heterogeneous. Both articles determine temperature, moisture availability and human disturbances as the three most important factors that determine this varied floristic composition (Langdale-Brown *et al.* 1964, Hamilton 1974).

Until 3 000 years B.P. the vegetation in Uganda was mainly rainfall-dependent: when the climate changed from dry to wet around 12 000 B.P. lowland forest vegetation started to appear around the northern shore of Lake Victoria and replaced the prevailing grass-rich communities, around 10 000 B.P. a drier climate prevailed again and led to a reduction in forest cover, at about 9 500 B.P. the climate was humid again and the forest cover started spreading again and attained an evergreen character, while between 7 000 and 6 000 B.P. the forest became more semi-deciduous again, suggesting a shift to a drier or more seasonal climate.

After 3 000 B.P. the interpretation of climatic conditions based on pollen stratigraphy becomes less reliable since man started exercising his influence on the vegetation, mainly through deforestation (Langdale-Brown *et al.* 1964, Kendall 1969, Hamilton 1974, 1981). Present day vegetation of Uganda is still undergoing changes along rainfall gradients (Kendall 1969).

The Ugandan lowland forests are part of the Guineo-Congolian region (Hamilton 1974). The lowland forests show an increasing species poverty in plant and mammal species from west to east over the whole of Africa and also over Uganda itself. Hamilton (1974, 1976 & 1981) concludes that the lowland forest has spread fairly recently from refuge areas, namely the impenetrable Kayonza Forest, to the west of Ruwenzori and probably Sango Bay at the eastern shore of Lake Victoria, eastwards through Uganda. While forest mammals have spread into East Africa from three forest refuge areas in Upper Guinea, Cameroon-Gabon and Ruwenzori-Kivu (Kingdon 1971 in Hamilton 1974). In contrast, the avifauna is rather homogenous throughout the West and Central African lowland forests (Hamilton 1976).

Even though the spread of lowland forest was initiated through a climatic change about 12 000 years ago the direction of the spread can still be evaluated today. After a major climatic event there is usually a very long lag period until a forest ecosystem adjusts to a new equilibrium (Hamilton 1981).

For montane forest Hamilton (1976) states an opposite movement and a probable spread of species from east to west within West, Central and East Africa. He attributes these differences in spread of the two forest types mainly to differences in dispersal mechanisms and suitable climatic and edaphic conditions for the establishment of dispersed seeds (Hamilton 1976). For the recent past a more pronounced north-south movement of species of all vegetation types can be observed (Hamiltion 1976).

Langdale-Brown *et al.* (1964) make some general remarks about the forest structure in Uganda. The authors describe the Ugandan forests as rich in species and communities. The composition of these forests is mainly dependent on climatic conditions and drainage. Given a minimum depth of the soil, edaphic factors, such as nutrient content, seem to have little influence on the composition of forest stands (Langdale-Brown *et al.* 1964).

For many of the tropical tree communities it is not possible to determine the climax community, but stand tables suggest that the regeneration of trees is insufficient to maintain the present populations of mature trees (Langdale-Brown *et al.* 1964). The intermediate successional stages show the higher species richness and the least tendency for the dominance of only a few or one species, with the ground flora also differing widely between forest areas (Langdale-Brown *et al.* 1964).

The authors also observe that in the more mixed forests there is normally a smoothly decreasing number of trees in each size class from the smallest to the largest (Langdale-Brown *et al.* 1964). These forests also show an entirely arbitrary concentration of vegetation at certain levels (= strata), even if terms such as "emergents", "under storey" and "shrub layer" may still be used. This contrasts to forests with one dominant species where marked strata, occupied by mature individuals of one or a few species, can easily be distinguished (Langdale-Brown *et al.* 1964).

The authors observe a certain re-expansion of some of the Ugandan forests where there are no dense human, cattle or elephant populations. They ascribe this fact mainly to a depopulation of certain areas due to rinderpest, sleeping sickness or tribal strife (Langdale-Brown *et al.* 1964). This is especially true for the islands in the northwestern region of Lake Victoria. Following sleeping sickness epidemics between 1902 to 1906 many of the islands were depopulated and soon attained a forest cover again (Thomas 1941, Langdale-Brown *et al.* 1964). Many of these forests are distinct from the mainland forest vegetation often showing an abundance of *Uapaca guineensis*, a small to medium sized evergreen tree, which is for example ubiquitous on the Sese Islands while being hardly prevalent in the mainland forest vegetation (Langdale-Brown *et al.* 1964).

Since 1964 the population of Uganda has been expanding again and it seems more than likely that this newly formed cover of secondary rain forest has been deforested again in most of the areas on the mainland as well as on many of the Lake Victoria islands.

Vegetation on Ngamba Island

Figures 3.20 to 3.26 show photographs of the northern, eastern and southern shoreline of Ngamba Island taken from a boat, illustrating the landing area including housing facilities for chimpanzees and people, the area of herbaceous vegetation and the dense secondary rain forest cover of the remaining island.

Figure 3.20: View of the landing area, staff housing, chimpanzee enclosure and visitors platform in the northern corner of Ngamba Island.

Figure 3.21: View of the north eastern shoreline of Ngamba Island.

Figure 3.22: View of the eastern shoreline of Ngamba Island.

Figure 3.23: View of the easternmost point of Ngamba Island.

Figure 3.24: View of the south eastern corner of Ngamba Island.

Figure 3.25: View of the southern shoreline of Ngamba Island; note the much coarser water surface compared to the north eastern side.

Figure 3.26: View of the south western corner of Ngamba Island; note Nsadzi Island in the background left (arrow).

Figures 3.27 to 3.30 are taken from the visitors' platform and show the area of herbaceous vegetation where the chimpanzees assemble for the morning (11:00) and afternoon (15:00) feeding and where they can be observed by tourists. The assemblage of these pictures also shows an east to west panorama view of the transition of herbaceous vegetation in the north into secondary rain forest vegetation in the centre and south of the island.

Figure 3.27: View of the eastern corner of the grassland area on Ngamba Island from the visitors' platform; note Kimi Island in the middle and background left.

Figure 3.28: View of the transition between grassland and forested area on Ngamba Island showing part of the morning and afternoon outdoor feeding area and a chimpanzee path leading into the forest; note remnant group of forest trees and 'delayed' onset of forest.

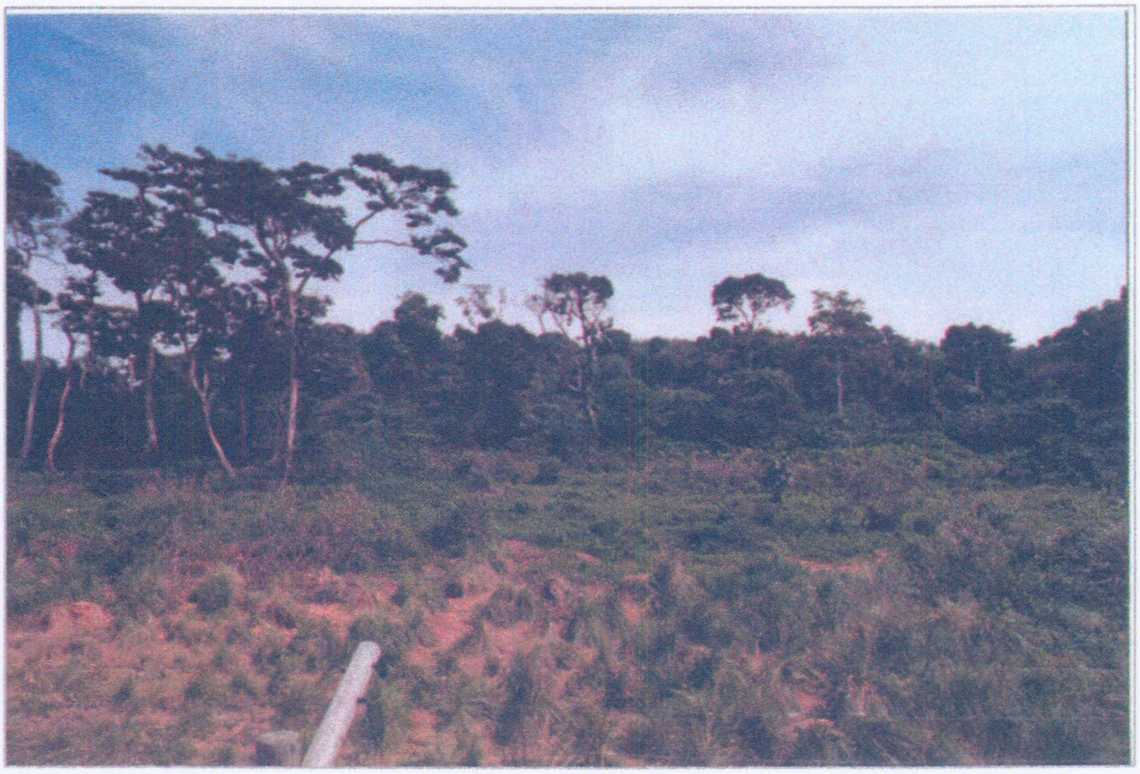

Figure 3.29: View of the central to western part of the grassland area on Ngamba Island and transition into the forested area; note single primary rainforest trees scattered throughout the secondary rain forest in the background.

Figure 3.30: View of the western corner of the grassland area on Ngamba Island.

Figures 3.31 to 3.35 show an aerial view of the secondary rain forest cover of Ngamba Island from the south westerly corner over the centre area to the easternmost outlayer of the island taken from a northerly direction. The “extremely irregular structure, typical of later successional stages of secondary rain forest vegetation” (Richards 1952), a number of upright dead trees especially in the western part of the island, “occasionally, trees of much larger dimensions than the average … usually … scattered through secondary forest, being ‘leftovers‘ from the destruction of the original primary rain forest“ (Richards 1952), and the open area in the eastern part of the island (Figure 3.34) can be distinguished.

Figure 3.31: Aerial view of the southwesterly corner of Ngamba Island taken from a northerly direction.

Figure 3.32: Aerial view of the southwest to central area of Ngamba Island taken from a northerly direction.

Figure 3.33: Aerial view of the central area of Ngamba Island taken from a northerly direction; note the calm lake surface on the northern side and the rough lake surface on the southern side of the island, indicating mainly southerly winds.

Figure 3.34: Aerial view of the eastern area of Ngamba Island showing the open area inside the forest towards the centre-left of the picture (arrow).

Figure 3.35: Aerial view of the easternmost point of Ngamba Island; note the open area in the forest in the centre-right of the picture.

Figures 3.36 to 3.40 show some impressions of the canopy cover of Ngamba Island's secondary rain forest cover taken from directly above. Smaller and larger gaps and a number of upright, dead and/or defoliated trees can be distinguished. Again, the irregularity of the vegetation and the variety of tree species contributing to the canopy cover are evident.

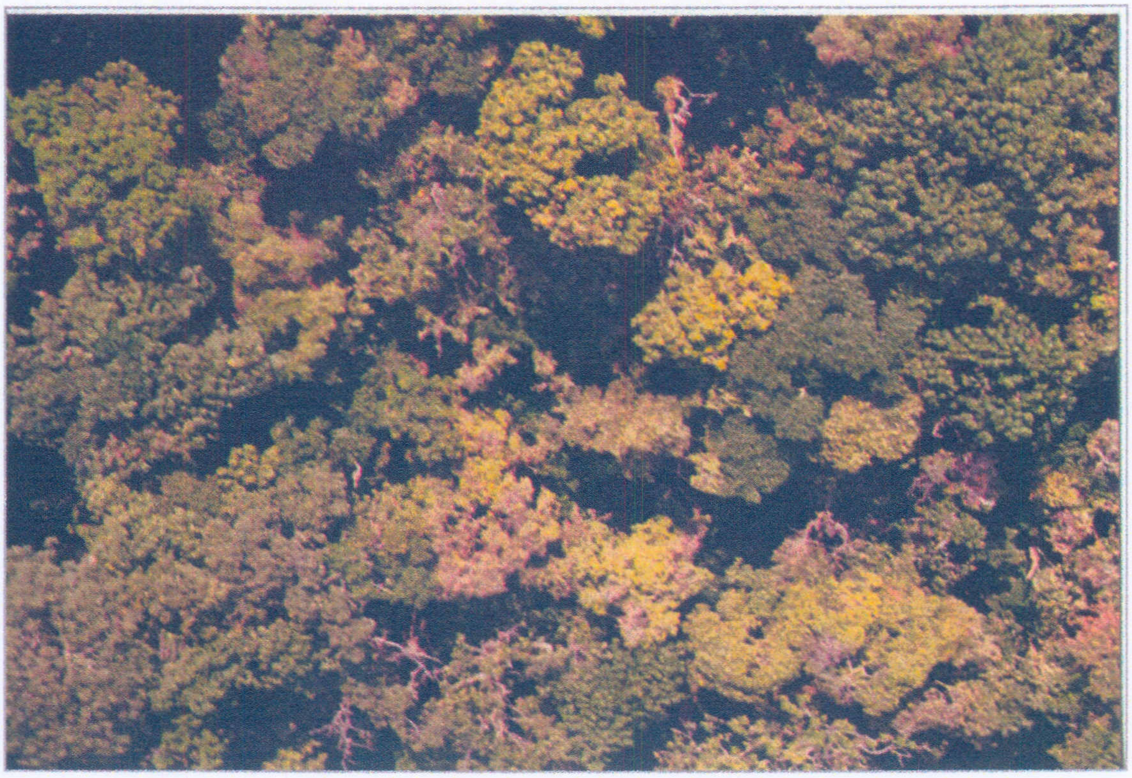

Figure 3.36: Aerial view of the closed but irregular canopy cover of the forested area on Ngamba Island.

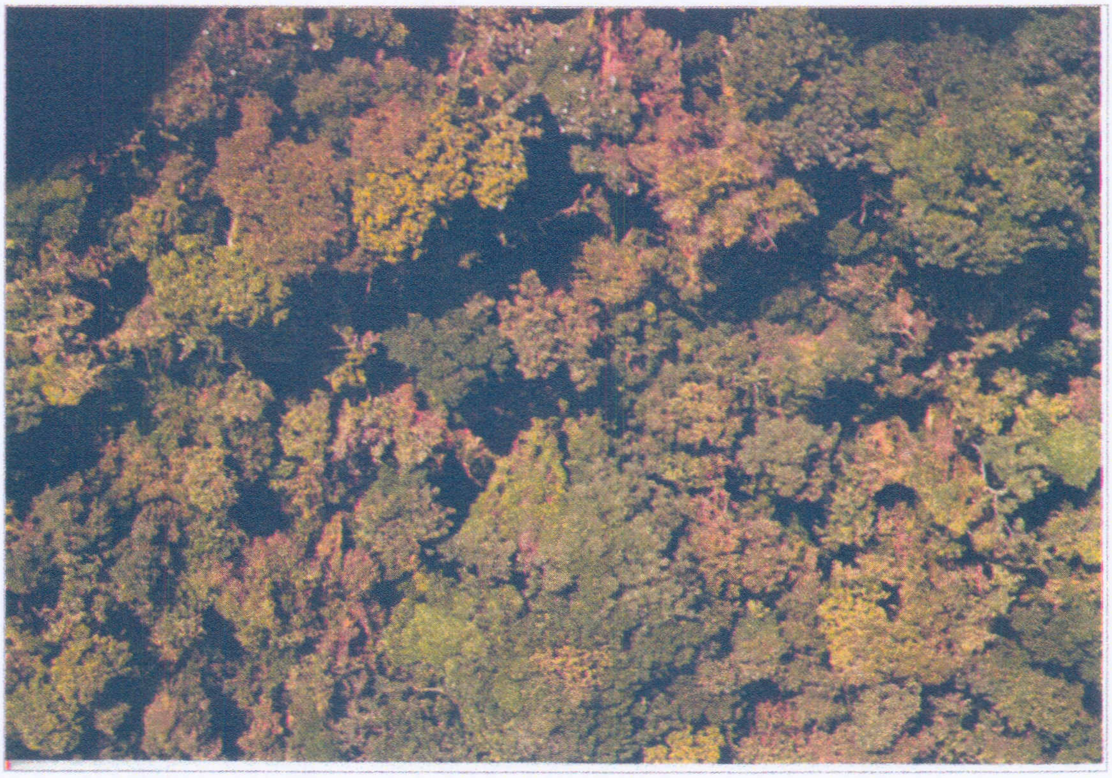

Figure 3.37: Aerial view of a more open area in the canopy cover of the forested area on Ngamba Island.

Figure 3.38: Aerial view of a more open area in the canopy cover of the forested area on Ngamba Island; note the defoliated tree in the foreground in the centre-right (arrow).

Figure 3.39: Aerial view of a partially refilled gap in the canopy cover of the forested area on Ngamba Island.

Figure 3.40: Aerial view of a further partially refilled gap in the canopy cover of the forested area on Ngamba Island; note the defoliated tree in the top centre-left of the picture.

FAUNA

The fauna of Ngamba Island consists mainly of over 200 different bird species (Annex – Table 5), a number of reptiles, e.g. the nile monitor lizard (*Varanus niloticus*), and as only natural occurring large mammal species, two hippopotami (*Hippopotamus amphibious*) (Annex – Table 5). Mainly small rodents and bats compose the small mammal fauna of the island (Annex – Table 5).

Nsadzi Island is also home for a number of bird and small rodent species. Furthermore, some livestock species are also present on this island, e.g. cattle and goats.

CHAPTER 4

LITERATURE REVIEW ON CHIMPANZEES - THEIR PAST, PRESENT AND BLEAK FUTURE

FREE-RANGING CHIMPANZEES

"It is my firm belief that unless we work together to change attitudes at all levels - from world leaders to the consumers of illegal bush meat - there will be no viable population of great apes in the wild within 50 years" (Dr Jane Goodall as cited in APE ALLIANCE 1998).

Phylogeny and distribution

Chimpanzees are part of the family Hominidae which encompasses all African apes and man and belongs to the order Primates (Ruvolo *et al.* 1991, Kingdon 1997). In contrast to monkeys which belong to the family Cercopithecoidea, all apes (and man) are tail-less. All chimpanzees belong to the genus *Pan* (Ruvolo *et al.* 1991, Kingdon 1997).

The genus *Pan* is divided into two species which are endemic to equatorial Africa. The one species is the "common" chimpanzee, *Pan troglodytes*, and the other species is the "pygmy" chimpanzee, *Pan paniscus*, or bonobo (McGrew 1989, Teleki 1989, 1994, Kortlandt 1997-1998). The genus *Pan* is confined to the African continent and the ranges of the two described species do not overlap (Gagneux *et al.* 2001).

Until recently *Pan troglodytes* was divided into three subspecies, namely (Latinen 1989, McGrew 1989, Teleki 1989, 1994, Erwin 1992, Gagneux *et al.* 2001):

Pan troglodytes troglodytes, Blumenbach, 1799
(Central African or bald chimpanzee)
Pan troglodytes schweinfurthii, Giglioli, 1872
(East African or long-haired chimpanzee).
Pan troglodytes verus, Schwarz, 1934
(West African, Upper Guinea, or masked chimpanzee)

Teleki (1989, 1994) describes the geographical range of the three *Pan troglodytes* subspecies as mutually exclusive *Pan troglodytes verus* is prominent in western Africa and its historical range extended from the Gambia River area to the west bank of the Niger River (Teleki 1989). *Pan troglodytes troglodytes* occupied the central African range from the east bank of the Niger River to the west bank of the Ubangi and Congo River (Teleki 1989). *Pan troglodytes schweinfurthii* occupied a range from the east bank of the Ubangi River and along the north bank of the Congo River to Lake Victoria and Lake Tanganyika (Teleki 1989). Bonobos only occur south of the Congo River (Gagneux 2001). Up until today, the range of both species has decreased substantially (McGrew 1989, Teleki 1989, 1994, Goodall 1994b). Teleki (1989) gives their range limits at 13° North and 7° South, with Senegal Oriental being the north western edge of the species' distribution and Shaba-Katanga in the DRC being the southernmost point of the chimpanzee's distribution (McGrew 1989).

Teleki (1989) lists 25 African countries in which chimpanzees were known to occur. He divides them according to the range of the three formerly known chimpanzee subspecies into (1) western African countries, namely, Benin, Gambia, Togo, Burkina Faso, Guinea-Bissau, Senegal, Ghana, Mali, Ivory Coast, Sierra Leone, Liberia and Guinea (*Pan troglodytes verus*), (2) central African countries, namely Nigeria, Angola (Cabinda), Central African Republic, Equatorial Guinea, Congo, Cameroon and Gabon (*Pan troglodytes troglodytes*) and (3) east African countries, namely Burundi, Rwanda, Sudan, Tanzania, Uganda and Zaïre (DRC) (*Pan troglodytes schweinfurthii*). Of these 25 countries two are known or believed to no longer have any viable chimpanzee population (Guinea-Bissau and Burundi) while in four countries (Benin, Gambia, Togo and Burkina Faso) chimpanzees have already been extinct for a while (Teleki 1989).

Gagneux *et al.* (2001) used mitochondrial DNA sequences and hyper variable nuclear micro satellite markers to investigate blood and faecal samples of chimpanzees in western, central and eastern Africa. Their results indicated that there is at least one newly-discovered, reproductively isolated chimpanzee population that is genetically distinct enough to form a new subspecies, *Pan troglodytes vellerosus*. Figure 4.1 shows the distribution of the four *Pan troglodytes* subspecies currently described: The range of *Pan troglodytes vellorosus* extends from the eastern bank of the Niger River to the western bank of the Sanga River, thus coinciding with the northwestern part of the range of *Pan troglodytes troglodytes* (Teleki 1989, Gagneux *et al.* 2001). These findings indicate that some geographical barriers, in this case the Sanga River, are of greater importance as a barrier for chimpanzee gene flow than was previously thought (Gonder *et al.* 1997, Gagneux *et al.* 2001).

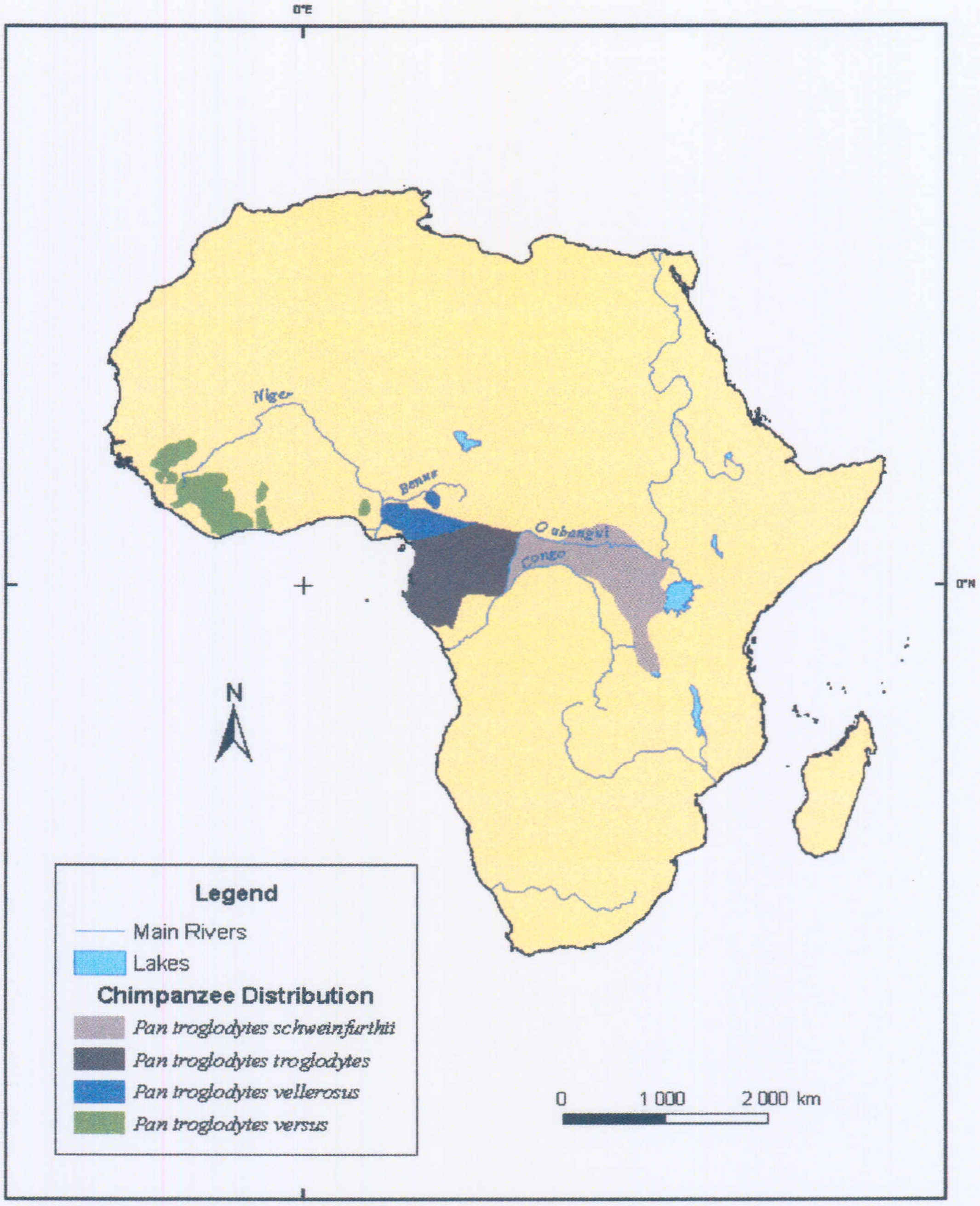

Figure 4.1: Distribution ranges of chimpanzee subspecies (Gagneux *et al.* 2001) – redrawn with kind permission from Pascal Gagneux.

At the same time, the results of the authors raised questions about the phylogenetic division of the eastern and western chimpanzee subspecies. Neither of the two subspecies forms monophyletic clusters with respect to each other. Some of the *Pan troglodytes troglodytes* sequences fall within the east African *Pan troglodytes schweinfurthii* sequences. This finding questions the Ubangi River as being a complete barrier between the ranges of the two subspecies, as was previously assumed (Teleki 1989, Gagneux *et al.* 2001). The authors state that extensive sampling of populations on either side of the river would be necessary to determine conclusively whether they are representatives of one or two subspecies (Gagneux *et al.* 2001). Gagneux *et al.* (2001) conclude that their findings indicate a more extensive gene flow between local chimpanzee populations than was previously thought and following patterns that are sometimes inconsistent with those documented through direct behavioural observations.

Mitochondrial DNA sequences allow conclusions about fairly recent events (tens to hundreds of thousands of years ago) in a species' evolution. On this time scale the authors determined an extensive within-subspecies gene flow for *Pan troglodytes schweinfurthii* and they consider this subspecies as having been panmictic at that point in time (Gagneux *et al.* 2001).

Current status and problems

"And what of the chimpanzees? ... But the question is purely academic. It could not be answered for countless thousands of years, and even *now* it is clear that the days of the great African forests are numbered. If the chimpanzees themselves survive in freedom, it will be in a few isolated patches of forest grudgingly conceded, where opportunities for genetic exchange between different social groups will be limited or impossible. And unless we act soon, our closest relatives may soon exist only in captivity, condemned, as a species, to human bondage" (Goodall 1998).

IUCN status and population size

The IUCN (2000a) lists chimpanzees, i.e. the genus *Pan*, as ***endangered***, giving the exact status as: EN A 2cd. This categorisation is explained as follows (IUCN 2000b):

En = Endangered
A = with population reduction in form of:
2 = at least 50%, projected or suspected to be met within the next 10 years or three generations, whichever is the longer, based on

c = a decline in area of occupancy, extent of occurrence and/or quality of habitat, and
d = actual or potential levels of exploitation.

Walter (pers. comm.[4]) gives the overall number of chimpanzees as 185 000 to 208 000, with about 2 500 of those animals officially registered as being held in captivity. The break down into subspecies / species is represented as follows (Walter pers.comm.):

Pan troglodytes schweinfurthii (East African Chimpanzee):	96 000
Pan troglodytes troglodytes (Central African Chimpanzee):	62 000
Pan troglodytes verus (West African Chimpanzee):	12 000 to 20 000
Pan troglodytes vellerosus (Nigeria Chimpanzee):	5 000
Pan paniscus (Bonobo):	10 000 to 25 000.

About 80 000 of those chimpanzees live in the Congo basin alone (Walter pers. comm.[3]) While *Pan troglodytes schweinfurthii* is the most abundant species in the wild, *Pan troglodytes verus* is the most abundant species in laboratories all over the world, but the second least abundant in the wild (Teleki 1989, Erwin 1992).

Chimpanzee study sites

A number of field studies have been undertaken on chimpanzee populations in Africa (Suzuki 1971, Baldwin & Teleki 1973, McGrew 1989, Teleki 1989, Goodall 1989, 1994a, Tutin & Fernandez 1991). Research into wild chimpanzees started as early as 1890 by R.L.Garner who built a cage in the west African jungle in which *he* could stay in safety while observing any chimpanzee passing by (Reynolds 1967, Goodall 1994b). Forty years later Henry Nissen continued studies in the wild in 1930 in Guinea (Goodall 1994b).

Only at the beginning of the sixties did field research into wild chimpanzee populations start in earnest in eastern Zaire, Gombe, and Mahale Mountains on the eastern shore of Lake Tanganyika in Tanzania (Goodall 1994b). Soon afterwards research on chimpanzees in Uganda was started (Reynolds & Reynolds 1965a, Reynolds 1967, Suzuki 1969, 1971, Baldwin & Teleki 1973, Goodall 1994b). Research on chimpanzees subsequently spread to west and central Africa (Baldwin & Teleki 1973, Goodall 1994b). McGrew (1989) divides the field research on wild chimpanzees in West Africa into long-term and short-term studies, mentioning the study of the

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[4] Walter, M.2001. Jane Goodall Institute, Munich, Germany.

Taï Forest chimpanzees, Ivory Coast, as the most important long-term study of the 1980s. Another long-term study site of great importance for chimpanzee (and gorilla) research is in the Lopé Reserve in Gabon (McGrew 1989, Tutin & Fernandez 1991, Goodall 1994b).

At some field study sites protected areas have been opened for tourism, partly as an additional income-generating activity for the surrounding local communities and the governments of the respective home range countries, and partly to create public awareness and to raise additional income for the project through funding coming from foreign visitors (Goodall 1989, Grieser Johns 1996).

Just as chimpanzees have had to become habituated to primatologists wanting to study them (Tutin & Fernandez 1991) they also had to become habituated to the regular influx of tourist groups into their home range (Grieser Johns 1996). Male and female chimpanzees react differently to this disturbance. Male chimpanzees mainly show aggression to the unusual human intruder, while female chimpanzees mainly react with protective behaviour towards infants and juvenile chimpanzees, most likely their own offspring, or with flight reactions (Tutin & Fernandez 1991, Grieser Johns 1996). Eventually, when habituation has been completed, the chimpanzees hardly take any notice any longer of the presence of the visiting tourist or scientist (Grieser Johns 1996, Goodall 1998).

This close encounter between non-human and human primates constitutes a significant health risk, mainly for the chimpanzee. Strict rules have to be complied with, e.g. regarding a minimum distance which has to be kept between the observer and the habituated chimpanzee(s), or regarding waste disposal of any kind by the tourists while in chimpanzee habitat (Grieser Johns 1996, Echroma *et al.* 1997).

Chimpanzees in Uganda

There have been and are several chimpanzee study sites in Uganda. The earliest site was established in the Budongo Forest in the early 1960s (Reynolds & Reynolds 1965a, Reynolds 1967, Albrecht 1976, Goodall 1994b). Albrecht (1976) lists a number of other forests in which chimpanzees occurred in the 1970s in Uganda: Bwindi, Kibale, Kasyoha, Kitomi, Kalinzu, Maramagambo and Ruwenzori, all of which are in the western region of the country close to the border of Zaïre and Rwanda. In 1976 a second study site was opened in the Kibale Forest of Uganda (Ghiglieri 1984, Goodall 1994b). The ecotourism component of the Kibale Forest Project was initiated in July 1991 as a further measure to conserve the chimpanzees and other primate species in the area and as a revenue-generating sustainable activity with the aim to benefit the local communities surrounding the park (Grieser Johns 1996). Today, the number of wild chimpanzees living in Uganda as estimated by a recent census in 1999/2000 is between 3 000 to 4 000 in 12 separated forest blocks of varying size (Cox pers. comm.[5]).

In summary, the chimpanzee is in imminent danger of extinction in all home range countries. The major threat the species faces is extinction of whole populations by the ever increasing bush meat trade, following the invasion by timber-logging companies, and habitat destruction and fragmentation through human encroachment. Research and/or eco-tourism projects which try to create awareness and sustainable income-generating activities are present in a number of these home range countries. However, the ongoing collection of behavioural data seems to mainly monitor the fast decline of the species, and until now has been unable to counteract this destructive trend in any significant way.

Threats

"All *Pan troglodytes* subspecies are vulnerable to extinction if the factors causing their decline continue to operate at the present pace" (Teleki 1989).

The wild chimpanzee populations still existing face several major threats to their survival (Suzuki 1971, Teleki 1989, 1994, Else 1991, Goodall 1989, 1994b, Bearder 1991, Oates 1995, Hart & Hall 1996, Ammann 1997-1998, Rose 1997-1998, Bermejo 1999):

Deforestation

According to Bearder (1991) even though the tropical forests of the world cover only about 7% of the land surface they contain nearly 50% of the total number of plant and animal species. The destruction of this habitat is pursued at a rate of about 20 to 40 hectare per minute globally (Bearder 1991). The destruction progresses rapidly and, if continued at this speed, there will be only isolated pockets of forest left in the middle of the 21 century (Bearder 1991, Hamilton 1992).

The main reason for this continuing destruction is a constantly progressing human encroachment due to a dramatic and unending increase in human population in the countries that constitute the equatorial forest belt (Teleki 1989, Goodall 1989, 1994b, 1998, Bearder 1991, Hamilton 1992, Oates 1995, Hart & Hall 1996, Bermejo 1999). This constant reduction of habitat

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[5] Cox, D. 2001. Jane Goodall Institute Uganda, Entebbe, Uganda.

leads to an increasing pressure on wild populations that very often respond with a decrease in population density through reduced reproduction (Medley 1993).

The habitat reduction does not occur in a circular way around intact forest habitats but rather in a haphazard way wherever need arises. It therefore also results in increasing fragmentation of the habitat, creating more and more edge-effect zones (Bearder 1991, Else 1991, Tutin & Fernandez 1991, Hamilton 1992, Medley 1993, Goodall 1994b, Oates 1995).

The increasing fragmentation and hence the increasing number of contact zones between forested and deforested areas also lead to an increase in primate-human contacts and interactions. This is disadvantageous to both species: through the close phylogenetic relation between human and non-human primates, and here especially to the chimpanzee (Ruvolo *et al.* 1991, Heltne 1994), both species also are susceptible to a number of each other's diseases and therefore constitute an infection risk to each other (Goodall 1994b, Rose 1997-1998, Gagneux *et al.* 2001).

As proven for HIV, Ebola and possibly other still unknown infectious agents, this increased interaction can be a lethal one for the human primate (Goodall 1994b, Rose 1997-1998, Gagneux *et al.* 2001, PROMED-MAIL 2001a+b, 2002a+b). On the other hand, the exposure, through human contact, to virus and other infectious disease agents to which the immune system of the forest-dwelling great ape is naive, can have disastrous consequences and reduce an entire population to such low numbers that it might be impossible to recover (Teleki 1989, Raub 1992, Goodall 1994b, 1998, Rose 1997-1998).

Another result of this increased interaction and close proximity is the easy accessibility to human food sources by non-human primates. They become pests and start raiding crop fields and human settlements where they sometimes even break into houses to steal food, while at the same time destroying a fair amount of the interior equipment as well (Johns & Skorupa 1987, Else 1991). Needless to say that this unfortunate trait of their non-human relatives does not endear these primates to the human population in their closest proximity. Instead, the latter use a number of strategies, from simple shouting to the use of traps and firearms, in an attempt to rid themselves of their intruders (Else 1991). This hostile attitude makes conservation efforts even more difficult to promote and achieve (Teleki 1989, Else 1991, Goodall 1994b, Rose 1997-1998).

However, well-intentioned and -perceived conservation projects can run the danger of undermining their own cause (Oates 1995). To prevent local communities from exploiting the resources inside the protected areas by trying to increase productivity and the standard of living in border zones around nature reserves and parks, these border zones might actually become 'too attractive' (Oates 1995). Oates (1995) gives an example from the Okomu Forest Reserve in Nigeria where the introduction of a 'development component' into the management of the park reversed the observed trend of population migration from the area. Through increased supply of crop seeds and infrastructure, immigrants from distant parts of the country were attracted to the area. At the same time no stringent measures were taken to enforce the compliance of the ever increasing community with the beforehand established conservation plan and objectives. Instead, the encroachment into the protected park area progressed steadily and led to even further habitat destruction (Oates 1995).

The Bush meat trade

The bush meat trade (Figures 4.2 – 4.5) is an ever increasing threat to chimpanzee and gorilla populations in many of the west and central African countries (Skorupa & Johns 1987, Teleki 1989, Goodall 1989, 1994b, Ammann 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998, Gagneux *et al.* 2001). Together with other forest-dwelling mammals, apes have been hunted for meat in equatorial Africa for millennia in a largely sustainable manner (Kortlandt 1984, Gagneux *et al.* 2001).

Figure 4.2: Bush meat in the forest (Photo: K. Ammann – with kind permission).

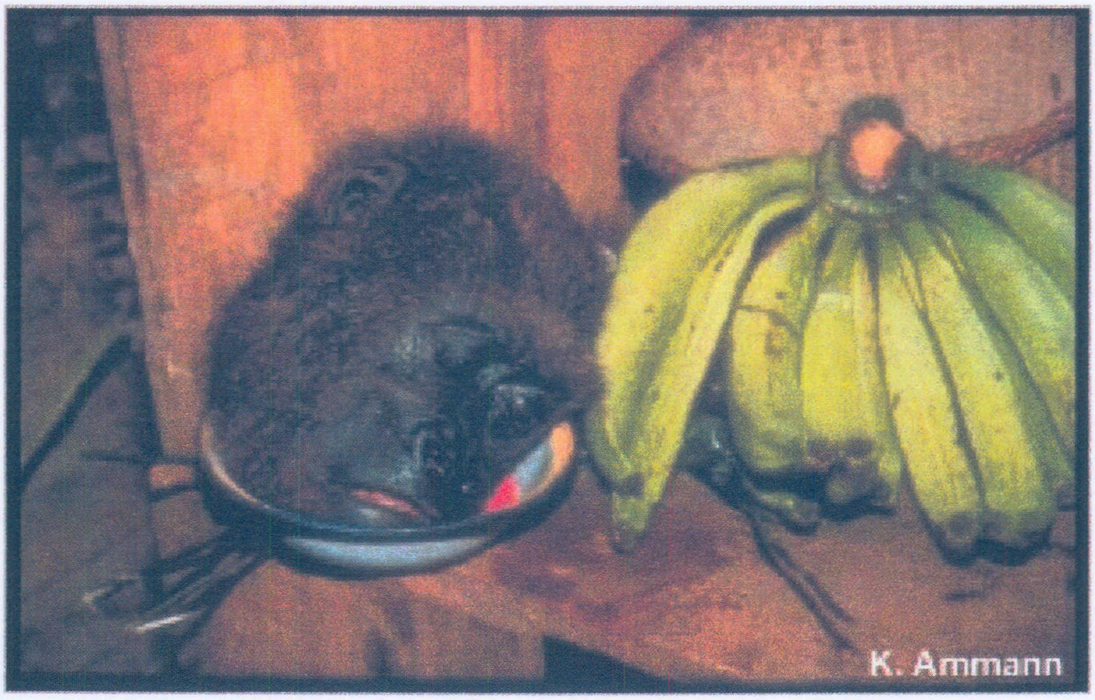

Figure 4.3: Bush meat at home (Photo: K. Ammann – with kind permission).

Figure 4.4: Smoked primate bush meat (Photo: K. Ammann – with kind permission).

Figure 4.5: Bush meat baby (Photo: K. Ammann – with kind permission).

A paramount new threat to the survival of the chimpanzee in the wild is the increasing commercialization of the bush meat trade that makes it unsustainable (Teleki, 1989, Goodall 1994b, 1998, Ammann 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998). This has been caused by the immense increase of commercial logging in a number of African countries inside the tropical forest realm. These logging companies, mainly based in European countries such as France, Germany, Italy, United Kingdom, and more recently also in Asia, open up the forests and bring with them a large number of employees that needs to be fed. The logging companies supply local hunters, very often pygmies, with automatic rifles to ensure hunting success (Teleki 1989, Ammann 1997-1998, Bowen-Jones 1997, Rose 1997-1998).

A newly constructed road system, established by the logging companies, provides easy access to previously inaccessible areas of tropical rain forest habitat. The hunters or, in most cases, their middlemen also use the vehicles of the logging companies to transport large quantities of bush meat to local markets and to the major markets in the urban centres of the west and central African countries (Ammann 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998).

Bush meat constitutes a major protein source in many African countries and the demand is constantly increasing especially in the large urban centres of west and central Africa (Amman 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998). It is this ever increasing urban demand that mainly fuels the bush meat trade. Bush meat attains much higher prices than livestock meat in most of the urban markets, whereas back in the villages this ratio is reversed. Thus, selling in distant urban markets is a very lucrative business which is even extended into neighbouring countries if the road infrastructure and the demand across the border are present (Ammann 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998).

The main targets for bush meat are primates and artiodactyls, especially duikers. Many of the hunted mammals are at risk from the bush meat trade and might well be brought to extinction if the hunting pressure continues or increases in the future (Teleki 1989, Goodall 1994b, 1998, Amman 1997-1998, Bowen-Jones 1997-1998, Rose 19997-1998).

Bowen-Jones (1997-1998) provides the following list of mammals believed to be at present threatened through the bush meat trade (also: APE ALLIANCE 1998):

Cephalophus duiker	Zebra duiker
Cephalophus jentinki	Jentink's duiker
Cephalophus leucogaster	White-bellied duiker
Cephalophus niger	Black duiker
Cephalophus ogilbyi	Ogilby's duiker
Cephalophus sylvicultor	Yellow-backed duiker
Cercopithecus diana	Diana monkey
Cercopithecus erythrogaster	White-throated monkey
Cercopithecus erythrotis	Red-eared monkey
Cercopithecus hamlyni	Owl faced monkey
Cercopithecus preussi	Preuss's monkey
Cercopithecus sclateri	Sclater's monkey
Cercopithecus solatus	Sun tailed monkey
Colobus satanas	Black colobus
Colobus vellerosus	Geoffrey's pied colobus
Gorilla gorilla	Gorilla
Hyemoschus aquaticus	Water chevrotain
Loxodonta africana	Forest elephant
Mandrillus leucophaeus	Drill
Mandrillus spinx	Mandrill
Pan paniscus	Bonobo
Pan troglodytes	Chimpanzee
Panthera pardus	Leopard
Procolobus badius, P. pennantii, P. preussi	Red colobus species
Profelis aurata	Golden cat
Smutsia (Manis) gigantea	Giant pangolin

A sad "by-product" of the bush meat trade is a large number of, especially chimpanzee, orphans. These young animals are too small to be of any value for their meat. Thus, they are often kept as pets in the villages of the hunters or sold as 'living toys' in the logging camps or the big cities, very often to expatriates (Teleki 1989, Goodall 1994b, 1998, Ammann 1997-1998, Bowen-Davies 1997-1998, Rose 1997-1998). Needless to say, not many of them survive this ordeal (Figure 4.5). The few who do eventually end up in cages or are chained in courtyards once they have become too big and strong and are causing too much damage in a 'civilized' home to still be suitable as a 'cute playmate' (Goodall 1994b, 1998, Ammann 1997-1998). Figures 4.2 – 4.5 are examples of the bush meat trade.

The logging of tropical rain forest and the bush meat trade are two unsustainable practices that will eventually lead to the destruction of a huge area with an exceptionally high biodiversity. Ammann (1997-1998) summarizes the prevailing attitude of the people involved in the trade as follows: "Increasing demand and decreasing supply will inevitably result in prices going up. With a limited resource, this will go on until the supply is exhausted, which, according to a Polish missionary, will elicit the response: » Why has God done that to us? «" (Ammann 1997-1998).

Chimpanzee trade

Despite a CITES (Convention on International Trade in Endangered Species of Fauna and Flora) agreement which has been signed by many of the African countries, a vast trade in wild chimpanzees is still ongoing, mainly providing young chimpanzees to laboratories in the United States and as pets or for the entertainment industry all over the world (Borner 1985, Carter 1988, Teleki 1989, Goodall 1998). Many of these chimpanzees are and have been taken from West African countries which explains the low number of *Pan troglodytes verus* in the wild and their exceptionally high abundance in many laboratories mainly in the United States and some of the European and Asian countries (Carter 1988, Teleki 1989).

It is estimated, that on average ten adult chimpanzees are killed when trying to obtain one young chimpanzee from a group of wild chimpanzees. Young chimpanzees are mainly taken while under the age of two years. During this time they still cling to their mother, who has to be shot to seize her infant. Adult male chimpanzees as well as the whole group often defend the dead mother and her infant and have to be shot as well to gain safe access to the youngster (Hladik 1974, Teleki 1989, Goodall 1998).

Teleki (1989) reports that due to the horrendous transport conditions and the appalling care the young chimpanzees receive on their very long journeys, only about one in five infants reach their new destinations alive. He calculates that sometimes as many as 29 chimpanzees are killed for one live infant chimpanzee arriving at his captive destination (Teleki 1989).

This trade in young chimpanzees has reduced the viable populations in the wild considerably and may push chimpanzees even further towards their extinction, since "time spans measured in decades, not in months or years, are needed for chimpanzee populations to recover once stability is lost" (Teleki *et al.* 1976 in Teleki 1989).

CHIMPANZEES IN CAPTIVITY

"In the milieu of captivity, the most important factor is man; apart from his immediate presence, the whole environment of the captive animal is as it were impregnated with man. Under such circumstances, the most important behavior pattern in freedom, flight from man, the enemy, becomes meaningless... The main problem set the animal in the reconstruction of its subjective world to suit captive conditions is to fit man into the new set of circumstances." (H. Hediger 1950)

"Island Chimpanzees"

Wilson & Elicker (1976) define the different environmental categories in which chimpanzees live, or are kept and in which they are studied:

Wild state:	Populations occurring within their natural range and foraging their habitat for all of their food (e.g. Mt. Assirik, Senegal).
Semi-wild state:	Populations occurring within their natural range which are also partially provisioned (e.g. Gombe National Park, Tanzania).
Free-ranging state:	Groups of primates released outside [or inside] their natural habitat into physically isolated areas where indigenous fauna and flora provide part of their food, and which are also provisioned (e.g. Ipassa, Gabon; Ngamba Island, Uganda).
Semi-free-ranging state:	Groups of primates [confined] to large outdoor man-made enclosures (e.g. Arnhem Zoo).
Caged state:	Individuals or small groups housed entirely indoors.

"Island chimpanzees", like the chimpanzees kept on Ngamba Island, can be considered as being *free-ranging,* even if they have the choice to retreat to their enclosure during night time.

There have been a number of projects where chimpanzees were released on islands either to *reintroduce* them into the wild or to keep them in an environment more suited to their needs for the purpose of establishing a breeding colony (Wilson & Elicker 1976, Pfeiffer & Koebner 1978, Maple 1979, Borner 1985, Carter 1988, Hannah & McGrew 1991).

According to Hannah & McGrew (1991) *rehabilitation* covers several release procedures, namely:

Release:	To set free captives, often with little or no follow-up of their fate.
Repatriation:	Animals are returned to the country of origin, usually from temperate climes to more hospitable tropical ones.
Translocation:	A shift from one wild site to another, with minimal time spent in between, in captivity. By definition, these are wild-born individuals, unlikely to acquire behavioural abnormalities in short-term human contact.
Reintroduction:	A term frequently used in the general context of 'restoration'.
Rehabilitation:	Used in the strict sense of training behavioural inadequate individuals in skills which allow them to survive with greater independence.

Figure 4.6 lists several island rehabilitation projects and shows the respective densities of chimpanzees in the areas where they have been released, expressed as the number of chimpanzees per km^2.

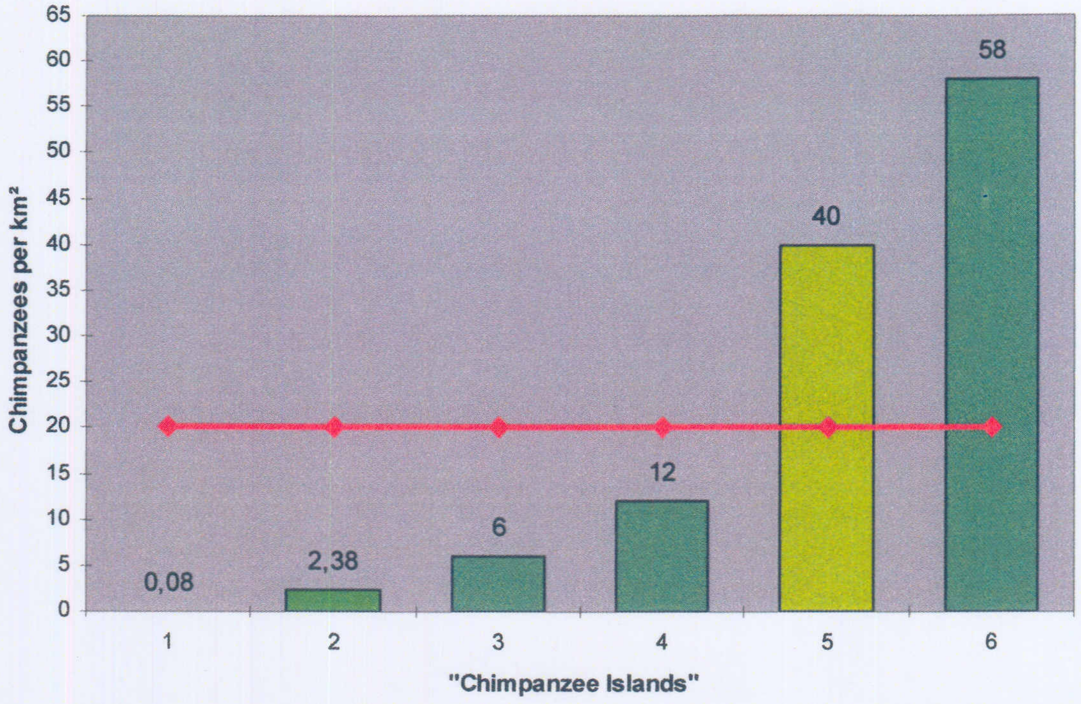

Figure 4.6: Chimpanzee densities in different Island habitats (all densities are given in: number of chimpanzees per square kilometre).

Key:

1. Rubondo Island, Lake Victoria, Tanzania: area: 240 km^2, number of chimpanzees: 20 (Borner 1985).
2. Average density of chimpanzees in the wild in a tropical rain forest habitat (Ghiglieri 1984).
3. Baboon Island, Gambia River, The Gambia: area: 490 ha, number of chimpanzees: 30 (Carter 1988).
4. Ipassa, near Makokou, Gabon: area: 65 ha, number of chimpanzees: 8 (Hladik 1973, 1974).
5. Ngamba Island, Lake Victoria, Uganda: area: 40 ha, number of chimpanzees: 16 (this study).
6. Island A + B, Little Bassa River, Liberia: area 85 ha, number of chimpanzees: 58 (Hannah & McGrew 1991)

Red line = Estimate by Jenkins (pers. comm.): 5 ha per chimpanzee for self sustainability.

The first project that released chimpanzees onto an island was the rehabilitation of chimpanzees onto Rubondo Island, Lake Victoria, Tanzania. This project was promoted by the Frankfurt Zoological Society and involved the release of 17 chimpanzees between 1966 and 1969. These animals had all been captured in the wild, then kept in several European zoos for different periods of time and eventually released into the forested Rubondo Island National Park. After two months, supplementary feeding was stopped. In 1985 it was estimated that ≥ 20 chimpanzees lived and successfully reproduced on the island (Borner 1985, Hannah & McGrew 1991). The density is about 0.08 chimpanzees per km^2 and is thus still below the mean density of 0.1 chimpanzee per km^2 given by Teleki (1989) for the density of wild populations in a savanna habitat. The *rehabilitation* of the Rubondo Island chimpanzees is an example for a *release* after *Repatriation* as defined by Hannah & McGrew (1991).

From 1968 to 1970 altogether eight chimpanzees were rehabilitated on the 'Ile aux Singes' Ipassa, in the Ivindo River, close to Makokou, Gabon. All individuals had spent a certain time of their life in a laboratory and were then released, with the original aim of reproducing and thus supplying new chimpanzees for research purposes on location (Hladik 1973, 1974, Hannah & McGrew 1991). The island has an area of 65 hectares and the density of the eight released chimpanzees thus equalled 12 chimpanzees per km^2. Thus 150 times that of the chimpanzees on Rubondo Island and about 40 times higher than the mean density of 0.3 chimpanzees per km^2 given by Teleki (1989) for chimpanzee densities in a tropical rain forest habitat, like the one found on Ipassa. However, these chimpanzees were provisioned with bananas to supplement the available food resources on the island (Hladik 1973, 1974). The chimpanzees eventually discovered that they could leave the island during low tide and wade back and forth to the mainland. Eventually, six of the eight were recaptured during one of their visits and brought back to the laboratory, while the remaining two escaped (Hannah & McGrew 1991).

Carter (1988) describes the *repatriation* of a number of chimpanzees from the United States to The Gambia during the late seventies. A number of locally confiscated chimpanzees were added to this group. Eventually, in late 1985, a second group was added and both groups together were released on Baboon Island in the Gambia River (Carter 1988, Hannah & McGrew 1991). The island covers an area of 490 ha and at present contains a group of over 30 chimpanzees who are provided with supplementary food. The chimpanzee density on Baboon Island is about 6 chimpanzees per km^2 (Carter 1988, Hannah & McGrew 1991).

Jenkins (pers. comm.[6]) estimates that for the self-sustainable survival of free-ranging chimpanzees in a tropical forest habitat at least 4 to 5 ha need to be allocated to every single chimpanzee to avoid a permanent destruction of the environment. This translates in a density of 20 chimpanzees per km^2, which is nearly 67 times higher than the mean number given by Teleki (1989) for wild populations.

On Ngamba Island, Lake Victoria, Uganda, the number of adult chimpanzees who are *free-ranging* in the forest during the day, is 16. To facilitate comparison between the island sites the number of juveniles is not considered since they only spend several hours a week inside the forest area. However, the damage caused by those youngsters is quite remarkable.

With a density of 40 chimpanzees per km^2, Ngamba Island has double the maximum density suggested for self-sustainable capacity of the area, as estimated by Jenkins. However, the Ngamba chimpanzees are provided with all the food they need and thus have the fruit and non-fruit food available in their forest habitat as 'extras'. The density of the Ngamba Island chimpanzees is about 133 times higher than the mean chimpanzee density as given by Teleki (1989) for a rain forest habitat.

There is a group of two islands (A + B) in Little Bassa River, Liberia, linked by mangrove swamps, which has an even higher density of chimpanzees (Hannah & McGrew 1991). These chimpanzees had been released from the local Vilab research laboratory (which is part of the Laboratory of Virology of the New York Blood Centre) and were supposed to be *reintroduced* into the wild after an adaptation to their natural habitat during their *release* period on Island A + B. With 68 chimpanzees per km^2 the density is 1.7 times higher than the density of adult chimpanzees on Ngamba Island (Hannah & McGrew 1991).

The most extreme example of chimpanzee density on an island rehabilitation site comes from Florida. Pfeiffer & Koebner (1978) released previously single-caged chimpanzees, after a short introduction phase, onto an 0.13 hectare island (Pfeiffer & Koebner 1978, Hannah & McGrew 1991). Altogether, eight chimpanzees originating from LEMSIP (The Laboratory for Experimental Medicine and Surgery in Primates, New York University School of Medicine) were brought to the island belonging to Lion Country Safari, West Palm Beach, Florida, U.S.A. (Pfeiffer & Koebner 1978). The chimpanzees were released on the island to study the social integration of previously single-caged chimpanzees and focusing especially on the alteration and persistence of pathological behaviour. The chimpanzee density on the island can be projected as being

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[6] Jenkins, P. 2001. Pandrillus, Calabar, Nigeria.

equal to 6 154 chimpanzees per km^2. Thus, the laconic remark of the authors that "the animals first destroyed the enclosure and most of the trees" does not come as a surprise (Pfeiffer & Koebner 1978). Furthermore, a picture showing part of the island also shows "the trees stripped of bark and most of their branches" (Pfeiffer & Koebner 1978).

The Yerkes Regional Primate Research Centre released laboratory chimpanzees on Bear Island, part of Ossabaw Island, Georgia, U.S.A., from June 1972 onwards (Wilson & Elicker 1976). Since reports vary regarding the size of the area available to the chimpanzees no comparisons can be made. Although some of the chimpanzees had died, the authors were still enthusiastic about the progress and outcome of their release operation in 1976 (Wilson & Elicker 1976). Maple (1979) reports that after five years and after a number of more animals had died, the chimpanzees were again removed from the island. The decision was partly made as a result of the constant danger of the animals drowning and the difficulty of maintaining the chimpanzees under absentee management conditions (Maple 1979).

Maple (1979) summarizes the major problem of island facilities for released chimpanzees as follows: "Another problem with islands is that unless they are quite large, the inhabitants will soon eat their way out of house and home. Therefore, it is often necessary to build artificial structures which provide shade and refuge should foliage be depleted".

Enclosure design

"To acknowledge that a captive primate is still a wild primate is the first and necessary step in providing for its needs" (Maple 1979).

Maple (1979) thus states that it is not enough to consider ape-keeping as being successful if *bearing and rearing of offspring*" has been fulfilled. This author considers the animal adequately housed and / or reared only if the captive animal is free of the bizarre behaviours of "stereotyped motor acts, autoerotic and autoagonistic behaviors" (Maple 1979).

An appropriate enclosure design is of utmost importance especially in zoos where the space of the captive chimpanzees is normally very restricted. It is compulsory that a stimulating environment is provided for all species in zoos (Latinen 1989), including "intellectual employment" for the inquisitive-minded chimpanzee (Kortlandt 1960/61). In short, outdoor and indoor facilities must be provided with appropriate "furniture" to ensure increased environmental diversity as well as physical and psychological stimulation (Kortlandt 1960/61, Reynolds &

Reynolds 1965a, Van Hooff 1973, Maple 1979, Latinen 1989, Coe 1992, Gold 1992).

The Arnhem Zoo is regarded as a prime example of provision of an adequate environment for its captive chimpanzees (Van Hooff 1973, Gold 1992). There is an outdoor and an indoor enclosure and the chimpanzees can choose freely where they want to pass their time; only in winter are they confined to the indoor enclosure alone (Van Hooff 1973, Gold 1992). That allows the chimpanzees to choose the temperature they feel most comfortable with and to find shelter and protection from the view of too curious visitors whenever they so desire (Kortlandt 1960/61, Wrangham 1992). A ditch separates the outdoor enclosure and chimpanzee forest from the public, thus providing a good view for the public undisturbed by an ugly fence construction (Van Hoof 1973).

An important consideration for enclosure design, indoors and outdoors, is to provide escape routes for young or subordinate individuals that enable them to escape attacks, and thus injury or accidental death, from superior adult chimpanzees (Kortlandt 1960/61, Van Hooff 1973).

Chimpanzees should never be kept alone and even in zoos, should be kept in groups, whenever possible (Kortlandt 1960/61, Reynolds & Reynolds 1965a, Maple 1979, Wrangham 1992).

Behavioural Enrichment

"Yet what is "freedom" but the relative number of choices available" (Coe 1992).

Chimpanzees in captivity often develop stereotypic or other atypical or undesirable behaviours such as regurgitation and reingestion, coprophagy, increased aggression, frequent throwing of sticks, stones or faeces, rocking, and self-mutilation (Reynolds & Reynolds 1965a, Van Hooff 1973, Maple 1979, de Waal 1994, Baker & Easley 1996). It is therefore generally agreed upon that as much natural behaviour as possible should be encouraged in all non-wild and non-semi-wild chimpanzees (Kortlandt 1960/61, Reynolds & Reynolds 1965a, Van Hooff 1973, Maple 1979, Redshaw & Mallinson 1991, Coe 1992, Gold 1992, de Waal 1994, Cox *et al.* 2000).

Behavioural enrichment can have many hues and colours, e.g. provision of natural and artificial climbing structures, including ropes and chains, tunnels, large rocks as outlooks, provision of old tyres and cut-off branches or straw as nesting material, provision of clothes and painting materials, hiding of food samples inside the enclosure, including the application of a colour code to indicate favourable or less-favourable food items, flexible feeding schedules and a frequent change of at least a certain number of provided toys to prevent boredom (Kortlandt 1960/61, Reynolds & Reynolds 1965a, Van Hooff 1973, Maple 1979, Gust 1989, Redshaw & Mallinson 1991, Coe 1992, Gold 1992, Wrangham 1992, de Waal 1994, Bloomsmith & Lambeth 1995, Fouts & Tukel Mills 1997, Cox *et al.* 2000).

How these considerations might be used to improve the well-being of free-ranging chimpanzees in a sanctuary environment while at the same time reducing the destruction of the natural habitat will be evaluated in detail in the discussion (Chapter 7).

CHIMPANZEE HABITAT

Kortlandt (1984) and Teleki (1989) provide maps giving the historical distribution of the two *Pan* species. When comparing these distribution ranges with White's (1983) classification of the vegetation of Africa it becomes obvious that chimpanzees are adapted to survival in a wide variety of habitats. "Chimpanzees utilize dry savannah-woodlands, mosaic grassland forests, and humid canopy rain forests, and live from sea level to at least 3 000 m elevation; however, the availability of permanent sources of surface water may be a key factor limiting the chimpanzees at the fringes of their geographical range" (Teleki 1989).

The centre of the chimpanzee's distribution range consists of White's (1983) "I. Guineo-Congolian regional centre of endemism". This is bordered to the south by the "X. Guinea-Congolian/Zambezian regional transition zone", to the north by the "XI. Guineo-Congolian/Sudanian regional transition zone" and to the east by the "XII. Lake Victoria regional mosaic". The marginal habitats of the chimpanzee distribution range reach into the "II. Zambezian regional centre of endemism" towards the south and into the "III. Sudanian centre of endemism" towards the north and north-west (White 1983, Kortlandt 1984, Teleki 1989).

According to Kortlandt (1984) the northern boundary of viable chimpanzee habitat is determined by the reduction in floristic richness, while the south-eastern boundary is determined by general climatic and ecological conditions.

The classification of vegetation types (originally) inhabited by chimpanzees varies more or less from author to author: Reynolds (1967) mentions habitat types such as 'tropical rain forest', 'montane forest' and 'tropical woodland', while Suzuki (1969) refers to the area where he studied chimpanzees in western Tanzania as 'savanna woodland' or 'miombo woodland'. Hladik (1974) describes the habitat of Mpassa as "la grande forêt dense sempervirente", i.e. dense, evergreen (rain) forest. Collins and McGrew (1988) compare three different habitats on the eastern shore of Lake Tanganyika: namely Bilenge, "mostly open woodland of *Brachystegia*, with relatively little riverine forest"; Kasoje, "predominantly forested with limited open vegetation"; both at Mahale Mountains and Gombe, "less open woodland, but extensive thicket woodland (or semi deciduous forest)". They ascribe these differences mainly to the differences in precipitation at the two locations. While these authors emphasise the difference in vegetation structure between the Mahale Mountains and the Gombe region, Nishida *et al.* (1983) consider these two habitats to be similar with a more extensive floral diversity at Mahale than at Gombe, due to higher rainfall at the former location.

McGrew *et al.* (1981) and Baldwin *et al.* (1982) differentiate five different vegetation types around Mt Assirik in the Park National du Niokolo-Koba, Senegal. This area is considered to be the "north western edge of the species distribution" (McGrew 1989). The authors list the following chimpanzee habitats with their associated vegetation, (1) gallery forest: tropical (or subtropical) semideciduous lowland forest, (2) woodland: drought-deciduous lowland woodland, (3) bamboo: flat-leaved savannah with isolated palms and deciduous trees, (4) grassland: narrow-leaved savanna with isolated palms and deciduous trees, and (5) plateau: narrow-leaved savannah with isolated deciduous shrubs (McGrew *et al.* 1981, Baldwin *et al.* 1982).

Bermejo (1999) distinguishes four major vegetation types as chimpanzee habitat in the Odzala National Park, northern Congo, namely (1) primary forest, on *terra firma* and inundated soils, (2) Marantaceae forest, i.e. evergreen forest with a dense under storey of Marantaceae species, (3) clearings, and (4) savannas. She subdivides the two forest types, i.e. Marantaceae forest and closed primary forest, according to their underlying soil conditions in (1) *terra firma* forest and (2) riparian forest, i.e. thicket, dense inundated and swamp forest (Bermejo 1999).

Eventually, White (1983) in his book "The vegetation of Africa" divides the whole of Africa into 21 different, so-called "phytochoria" or phytogeographic areas and defines the major vegetation types present. In the six phytochoria (I, II, III, X, XI, XII) which constitute viable chimpanzee habitat, the following vegetation types are represented (White 1983):

1. *Forest:* A continuous stand of trees at least 10 m tall, their crowns interlocking.
2. *Woodland*: An open stand of trees at least 8 m tall with a canopy cover of 40 per cent or more. The field layer is usually dominated by grasses.

3. *Bushland:* An open stand of bushes usually between 3 and 7 m tall with a canopy cover of 40 per cent or more.
4. *Thicket:* A closed stand of bushes and climbers usually between 3 and 7 m tall.
5. *Grassland:* Land covered with grasses and other herbs, either without woody plants or the latter not covering more than 10 per cent of the ground.
6. *Wooded grassland:* Land covered with grasses and other herbs, with woody plants covering between 10 and 40 per cent of the ground.
7. *Scrub forest:* Intermediate between forest and bushland or thicket.
8. *Transition woodland:* Intermediate between forest and woodland.
9. *Scrub woodland:* Stunted woodland less than 8 m tall or vegetation intermediate between woodland and bushland.

The tropical rain forest habitat

"Evergreen, hygrophilous in character, at least 30 m high, but usually much taller, rich in thick-stemmed lianes and in woody as well as herbaceous epiphytes" (Schimper 1903 in Richards 1966). In contrast to this description of the primary tropical rain forest vegetation Richards (1966) defines a *typical secondary rain forest* as "the earlier seral stages found on areas which have been cultivated or exploited for timber, but not subsequently grazed or burnt."

The general characteristics of tropical rain forests have already been described in Chapter 3. Today the prime tropical rain forest habitat of the chimpanzee is one faced by steady decline through (1) increasing human encroachment and (2) increasing commercial logging of timber (Brown 1981).

Logging and natural tree mortality

Figure 4.7 shows a train loaded with logged timber and the destruction caused by the infrastructure necessary for economic timber exploitation.

Figure 4.7: Train transporting timber logged in an African tropical rain forest.

General considerations

Myers (1980) believes that timber exploitation of tropical forest *per se* could be causing the effective conversion of somewhere between 17 700 and 29 000 km^2 of primary forest in the moist tropics each year.

Brown (1981) develops several suggestions for the protection of the remaining tropical forest areas. His underlying principle is to preserve as large an area as possible (Brown 1981). Brown (1981) considers the remaining patches of lowland and montane forest in Africa to follow *island biogeography theory* as far as the rate of species loss or turnover is concerned. Diamond (1981) differentiates between montane forest islands and lowland forest islands. He considers the former as *oceanic islands*, since they originally received their biota through long-distance dispersal and now show a species turnover around a constant equilibrium (Diamond 1981). The latter should be considered as *land-bridge islands*, formed by the continuous reduction of a formerly much larger area, which will experience a continued reduction of species numbers through decreased size until a new sustainable species density for the remaining area is reached (Diamond 1981).The most important feature of an oceanic island (montane or in the sea) is its proximity to a species source area to ensure constant influx of new species (Diamond 1981).

According to Brown (1981) there should be a number of measures and approaches to save the remaining forest habitat from further human encroachment and subsequent soil erosion:

1. Soil conservation
2. Intensification of agricultural practice to increase yield
3. Plantations which promote the cultivation of cash crops.

The latter point brings with it a number of risks: If a high-priced cash crop production is successful there will be the temptation to extend the cash crop area by reducing the protected forest habitat even further. These plantations often depend on a large amount of fire wood and thus the forest might have to give way to a further plantation of fast-growing tree species (Brown 1981). On the other hand, plantations, especially forest or tea plantations can be used as buffer zones between subsistence farming agriculture and its accompanying human encroachment and the conservation area. They can also act as fire breaks and livestock barriers (Brown 1981).

Brown's (1981) overall advice and conclusion is "to leave the [conservation] area strictly alone until the facts are better understood".

Bada (1989) fitted the 'Chapman-Richard Model' for the prediction of forest growth and yields to growth data of some secondary tree species in a mixed tropical forest.

His modified equation is as follows:

$$B^* = [n/k - C.e^{-(1-m)Kt}]^{1/(1-m)\ldots}$$

With B^* = the predicted basal area [of a specific tree species] at a given time
"t" = the initial time (i.e. from the time of girth measurement)
e = exponentiation constant (2.71828)
K, m, n = growth parameters best determined by the maximum likelihood method.

The growth variable "C" is derived as: $C = n/k = B^{(1-m)}$
With B = initial basal area.

This equation was adapted to four secondary tree species for which long term data were available. No significant differences were found between the predicted and the actual basal area. Although the author also found, that the degree of accuracy of stand basal area prediction with the model appeared to decrease with time, this decrease was not statistically significant (Bada 1989).

Riddoch *et al.* (1991) postulate that the successional status of a species is determined by the ability of this species' seedlings to exploit the light environment and nutrient supply which characterize a particular stage of canopy development (Riddoch *et al.* 1991). *Pioneer species* are those species with an enhanced capacity to utilize the high light environment associated with clearings or gaps in the canopy. Whereas *climax species* are those species which survive as saplings in deep shade (Riddoch *et al.* 1991). Although it was demonstrated that the respiration rates of shade-acclimated leaves of climax species were low compared to those of 'sun leaves' of pioneer species, the differences between the two species types were not such that a clear-cut prediction between their growth patterns and their exposure to light could be made (Riddoch *et al.* 1991). Light is therefore not the only variable of importance in determining seedling growth and successional status of a species. Other factors, such as humidity, temperature, and CO_2 also influence seedling growth of pioneer and climax species (Riddoch *et al.* 1991).

Pannell (1989) draws the attention towards a major problem caused by the increasing destruction of viable tropical forest habitat. Most of the rain forest tree species rely on animals for pollination and seed dispersal. As a result of the widespread destruction of the rain forest the presence of these animal seed dispersers can no longer be guaranteed (Martinéz-Ramos & Alvarez-Buylla 1986, Howe 1989, Pannell 1989, White 1994a, Hashimoto 1995).

The continued production of timber in the tropical rain forest belt depends on natural regeneration after logging. Representative and viable areas of tropical rain forest should therefore be retained within timber production areas to perpetuate viable populations of the plant and animal life typical of the local forest habitat (Pannell 1989). These areas should be totally and permanently protected from logging, burning, and other human disturbances and suitable breeding and roosting sites must be available. The protected animal populations furthermore should be large enough for a breeding population to persist after an attack by predators, pests or diseases (Pannall 1989).

Johns & Skorupa (1987) evaluated the response of primates to habitat disturbance by selective logging in a rain forest habitat. Selective logging here means the clearing of up to 10% of the trees from an area of forest while the residual stand is left to regenerate (Johns & Skorupa 1987). The authors found that some primate species can possibly survive alongside logging. In general body size and frugivory of a certain primate species explain 44% of the variation in species responses to moderate habitat disturbances (Johns & Skorupa 1987). Within any specific dietary strategy, large-bodied species are generally more sensitive to a forest disturbance than smaller-bodied species. When the authors controlled for the effects of dietetic diversity and body mass they found that diet type is very strongly correlated with survival ratios, being strongly positive for folivorous and strongly negative for frugivorous primate species (Johns & Skorupa 1987). The authors conclude that generally "*large-bodied frugivores* are the class of primates most vulnerable to habitat disturbance", which thus also and especially affects chimpanzees and their survival in disturbed habitats (Johns & Skorupa 1987).

Rain forest management in Uganda

Ugandan rain forests occur in three ecological zones (Table 4.1) (Harcourt 1992).

Table 4.1: *Estimates of forest extent in Uganda (following Harcourt 1992)*

Rain forests	Area [km^2]	% of land area
Lowland	6 318	3.2
Montane	2 212	1.1
Swamp	265	0.1
Total	*8 795*	*4.4*

Since 1929 the Ugandan government has been applying a forestry policy which is briefly outlined below (Harcourt 1992):

1929 – 1959 *Polycyclic felling system* – trees exceeding a minimum girth were harvested about every 30 years on a 60 to 90 year rotation.

No felling without prior systematic stock mapping by the Forestry Department was allowed. Only marked trees could be cut, while minimum girth limits were endorsed. Tree plantations were established for enrichment planting after timber harvest. Arboricide treatment was applied to remove undesirable trees. Since this system interfered relatively little with the natural state of the forest regeneration was mainly natural rather than by enrichment planting.

1960 – 1970 *Monocyclic felling system* – replacement of the polycyclic system.

No lower limit on the size of the trees cut. This system was a far more deleterious impact on forest wildlife and ecology of the forest than the polycyclic system.

1971 – 1986 Under Amin's regime – general break down of forest control.

Greater emphasis was put on short-term profit from timber extraction while Protective forestry was ignored. About 100 km^2 of forest were lost every year from 1981 to 1985.

1987 - Present Revised forest policy

Management of the forest to optimise economic and environmental benefits by ensuring that conversion of the forest resources to timber, charcoal and the like is carried out efficiently; that the forest estate is protected against encroachment, illegal tree cutting, fires, diseases and pests; and that sustainable methods are used for harvesting.

This policy might be difficult to put into practice. Ninety to 95 per cent of the wood consumed in the country is for fuel, most of it is even till today still coming from public land outside the forest reserves such as fuel wood plantations, small remnant patches of natural forest and woodland (Harcourt 1992). But Uganda has a high population growth rate of more than 3 per cent per year with the population having doubled since the 1960s (Harcourt 1992). The constant influx of immigrants from overcrowded districts will make it more and more difficult to sustainable protect the remaining Forest Reserves in Uganda (Harcourt 1992).

"No attention is given to the complex and fragile nature of the rain forest which has taken thousands of years to evolve to its present state and within our lifetime could be totally devastated by man“ (Struhsaker 1981).

Struhsaker (1981, 1987) is concerned about primate and forest conservation in Uganda. He found that the number of ape and monkey species in any medium to low altitude rain forest was dependent on the following major factors: (1) floral diversity, (2) proximity to upper Pleistocene forest refugia, and (3) the size of the forest (Struhsaker 1981, 1987).

Most non-human primates are forest-adapted. When evaluating primate species numbers in Uganda, Struhsaker (1981) found that the distance from Pleistocene forest refugia was inversely related to the number of anthropoid species present in the remaining forest habitats. This strongly supports the classification of those remaining forest habitats as *land-bridge islands* (Diamond 1981, Struhsaker 1981). Furthermore, Struhsaker (1981) established that the species diversity among these non-human primates is directly related to tree-species diversity and the diversity of anthropoid species depends on floristic diversity. It follows that protected forest habitats should be as large as possible to ensure high tree species richness to sustain a maximum species diversity of anthropoids (Struhsaker 1981).

Struhsaker (1981) gives the example of Kibale Forest Reserve which is subject to selective felling on a polycyclic basis, followed by ‘refining‘, i.e. the poisoning of undesirable trees. Often, these trees constitute an important part of the diet of primates inhabiting the forest, such as fig species for chimpanzees (Albrecht 1976). Struhsaker concludes that even selective logging has an adverse effect on most, if not all, primate species in the Kibale Forest Reserve. This author thus contradicts Harcourt (1992) who found, that a lightly logged forest will support primate populations in more or less the same way as an unlogged forest. Bowen-Jones (1997-1998) could find no example where selective logging has been practiced successfully alongside efforts to conserve floral and faunal species in the same habitat. The issue of selective logging and its effects therefore seems to be highly disputed and possibly to a large extent also dependent on forest type and tree-selection method regarding its impact on the forest habitat.

Struhsaker (1981) concludes his discussion with the following statement: “Conservation of primates essentially deals with the conservation of their habitat, the forest ecosystem… Clearly, the most important step to conserving rain forests and primates (including our own species) is to control this potentially disastrous growth rate of the human population“. Struhsaker (1987) underlines his view when stating that deforestation significantly exceeds afforestation.

The author furthermore stresses the fact that tropical rain forests additionally possess a high value by constituting "genetic storehouses". Struhsaker (1987) gives the examples of:

(1) *Foods* derived from tropical forests, such as coffee (*Coffea canephora*),

(2) *Medicines* derived from tropical forests, such as the use of traditional medicinal plants in eastern Africa and of plant-derived drugs and pharmaceuticals which were valued at US$ 16 billion in 1980 in the USA alone,

(3) *Natural pest control*, in the way that many natural predators of insect pests and valuable pesticides derived from forest plants might be used commercially and successfully in the biological control of agricultural pests, such as *Balanites wilsonia*, the fruit of which kills the snails carrying Bilharzia and water fleas transmitting guinea worms, and

(4) *Tree plantations and ornamentals* created by non-destructive harvesting of seeds to establish woodlots of indigenous tree species for domestic consumption, and of ornamental plants for export.

Skorupa & Kasenene (1984) use the rate of natural tree falls in Kibale Forest to develop a guideline for tropical forest management. The authors compared three forest blocks 12 years after logging had taken place at different intensities. The control area, K-30, had a size of about 300 ha of relatively undisturbed mature forest. In the past only about 3 to 4 stems per km^2 had been felled by pit-sawyers. Since 1970 the area had been protected from any interference and was thus used as 'undisturbed control forest' by Skorupa & Kasenene (1984) for their study. The second compartment, K-14, was about 390 ha in size and had been subjected to selective logging averaging about 14 m^3 per ha between May and December 1969. This plot was considered as being 'moderately disturbed' (Skorupa & Kasenene 1984). The third compartment, K-15, about 360 ha in size, had also been selectively logged between September 1968 and April 1969, averaging 21 m^3 per ha. This plot was considered to be heavily disturbed (Skorupa & Kasenene 1984).

The authors determined the mean annual rate of tree fall to be 1.4% for K-30, 1.3% for K-14, and 6.2% for K-15. Compared to data from mature forests in Malaysia, Skorupa & Kasenene (1984) consider a tree fall rate of 1.3% or 1.4 % as a natural tree fall rate. Whereas the tree fall rate of the heavily disturbed plot K-15 is significantly higher. Since the last logging occurred about 12 years ago in K-15, Skorupa & Kasenene (1984) consider most of the fallen trees in K-15 to have been healthy individuals that were simply uprooted by wind. They attribute the high tree fall rate to changes in forest structure that affect factors such as aerodynamic roughness, windbreak protection provided by neighbouring trees, and soil cohesion (Fons 1940, Skorupa & Kasenene 1984). The authors conclude that light to moderate logging rated as about 25% destruction, disrupted the regulatory process of natural tree fall only temporarily, if at all. Heavy disturbance or logging seriously disrupted the rate of natural tree fall, which is an integral component of any forest's dynamic balance, in Kibale Forest (Skorupa & Kasenene 1984). The authors consider a tree fall rate of up to 2.3% as normal and calculate an upper limit for forest destruction through logging in Kibale Forest as 35% (Skorupa & Kasenene 1984). They furthermore advise that mechanised selective timber harvesting in Kibale Forest may not be a sustainable means of timber exploitation, especially because of the high amount of incidental, i.e. non-marketable, destruction associated with logging (Skorupa & Kasenene 1984). According to these authors, pit-sawing greatly reduces this incidental destruction and might allow a non-disruptive level of destruction and timber exploitation for Kibale Forest (Skorupa & Kasenene 1984).

White (1994b) cites an example of commercial mechanised selective logging in the lowland rain forest of the Lopé Reserve, Gabon. The extraction rate was two trees per hectare, but incidental damage and cutting of trees that were not extracted, resulted in a mean loss of 2.8 trees ≥ 700 mm dbh (diameter at breast height) per hectare (White 1994b). Altogether, about 20% of trees > 700 mm dbh were lost during logging. Most of those were cut and extracted. The overall damage levels (to all trees) were between about 10 to 13%, while 28.3% of ground vegetation was altered and almost half of the canopy cover was disturbed (White 1994b). Compared to other African countries, White (1994b) still considers this level of damage caused by logging to be low in Gabon. Values for incidental damage in Nigerian rain forests are 44%, in Kibale Forest, Uganda, it is 25% in lightly logged and 50% in heavily logged forests, and the total damage per area in Bia South, Ghana, is estimated at 20% to 30% (White 1994b).

Intensive hunting normally occurs alongside most logging operations and indirectly affects forest dynamics. Hunting reduces primate numbers and since these primates also function as seed dispersers for a large number of trees in tropical rain forests, their decline might have an additional negative impact on forest regeneration after logging operations. Thus, even if sustainable timber logging theoretically seems possible it might be unsuccessful due to the secondary negative effects of the logging operations on the seed-dispersing fauna in tropical rain forests (White 1994b).

Logging had the following effects on forest structure and function (Chapman & Chapman 1997):

1. Growth rates in the most heavily logged areas were consistently lower than in the unlogged areas.

2. The lightly logged areas had similar growth rates to unlogged areas in the small size classes. Trees in the 300 to 500 mm dbh size cohort though showed elevated growth rates relative to the unlogged areas.

3. Mortality was highest in the heavily logged areas. Many deaths were occurring when healthy trees were knocked over by neighbouring tree falls (incidental damage).

4. There was no difference in the density or species richness of seedlings in the logged and unlogged areas.

5. Sapling density was lower in the heavily logged areas, thus suggesting a high level of seedling mortality in logged areas.

Chapman & Chapman (1997) suggest that the opening of the canopy cover which is created during logging, the lack of aggressive colonizing tree species, the activity of elephants that is concentrated in logged areas, and an aggressive herb community (also: Wrangham *et al.* 1993b), all combine to delay vegetation recovery after logging in Kibale Forest.

Lwanga *et al.* (2000) investigated the tree dynamics in Ngogo, Kibale Forest, Uganda, from 1975 to 1998. In that period species richness decreased by 3%, species diversity (H‘) declined slightly from 2.97 to 2.86, the number of trees recorded in the sample plots (height $\geq$ 10 m) decreased by 8%, and the basal area decreased from 49.48 m^2/ha to 48.68 m^2/ha (Lwanga *et al.* 2000). Only for a small number of tree species did stem abundance and basal area increase (Lwanga *et al.* 2000). Since the overall decrease in density at Ngogo was not accompanied by a significant decrease in basal area the authors conclude that the majority of trees that had died were small trees and that this loss of basal area was compensated for by the growth of larger trees (Lwanga 2000). Furthermore, the distribution of size classes for evaluated trees also showed that the smallest size class exhibited the largest decline in density (Lwanga *et al.* 2000).

A comparative study at Kanyawara, Kibale Forest, Uganda, showed that the same tree species which declined or did not change in number in Ngogo increased in number in Kanyawara (Lwanga *et al.* 2000). The authors suggest that more favourable light conditions on the forest floor in Kanyawara might favour seedling survival and sapling recruitment at that site (Lwanga *et al.* 2000).

Different tree species start fruit production at different ages. When considering a logging operation for timber extraction in a forest inhabited by (frugivorous) primate species, this fact should be taken into account. If a sufficient number of trees and tree species, which start fruit production at an early age, are kept and given the chance to recolonize in sufficient numbers, selective logging in a primate rain forest habitat should be possible without causing ever-lasting damage and/or decline of the primate species (Lwanga *et al.* 2002).

CHIMPANZEE SOCIAL STRUCTURE AND BEHAVIOUR

"The classic problems of survival in the wild are finding food, escaping predators and parasites, and avoiding bad weather. For chimpanzees, the set of solutions adopted by even a single population is surprisingly diverse..." (Wrangham 1994).

Community structure

Chimpanzees live in *fission-fusion* societies which are defined as follows: "social groups in which all members are rarely, if ever, together as a spatially discrete unit, and in which stable subgroups of specific adults do not recur daily, as one-male harems do." (Ghiglieri 1984).

This rare form of social system between mammals consists of a number of subgroups forming a community, which constantly varies in size and composition of their members over time (Kortlandt 1962, Reynolds 1967, Baldwin *et al.* 1982, Ghiglieri 1984, Cox *et al.* 2000). A *community* is defined here as "a group of chimpanzees acquainted with and tolerating one another" (Baldwin *et al.* 1982). Gagneux *et al.* (2001) give the typical community size as between 20 to 100 individuals.

Different authors have observed and described different numbers and kinds of groups. Kortlandt (1962) distinguished two different group forms in Zaïre, namely (1) *sexual groups* mainly formed by adult males and childless females, but often including a few mothers and infants, and (2) *nursery groups* consisting mainly of juveniles up to the age of puberty, the mothers of these juveniles and sometimes one or two of the adult males. Reynolds & Reynolds (1965a) distinguished four different group forms in Uganda's Budongo forest chimpanzees, i.e. (1) *bi-sexual adult parties*, (2) *all-male parties*, (3) *mother parties*, sometimes with childless females, and (4) *mixed parties*, i.e. a combination of all-male and mother parties. Suzuki (1969) coins the term *nomadic group* and defines it as a group "whose stability, in terms of time, is unknown but which has a certain behavioural coherence in its nomadic life in natural surroundings". The author then distinguishes five different types of nomadic groups in the savanna woodland of the Kasakati Basin at the eastern shore of Lake Tanganyika, western Tanzania, namely (1) *mixed nomadic groups*, (2) *adult nomadic groups*, (3) *mother nomadic groups*, (4) *male nomadic groups*, and (5) *lone individuals* (Suzuki 1969). Suzuki (1969) concludes that in general this area shows two forms of nomadic groups of chimpanzees, i.e. (1) lone individuals and (2) mixed nomadic groups containing individuals of both sexes and of various ages centring around one or more adult males.

On the other hand Goodall (1986) distinguishes eight different types of groups for the chimpanzees at Gombe, Tanzania, namely (1) *all male parties* of adult and/or adolescent males, (2) *a family unit* consisting of a mother and dependent offspring, at occasions including older offspring, (3) *nursery-units*, groups of family units that may include unrelated, childless females, (4) *mixed parties* of adult and/or adolescent males and females, (5) *sexual parties*, a mixed party with one or more females in oestrus, (6) *consortship* - exclusive relationships between an adult male and an adult female, (7) *gathering* - a large group containing at least one half of the community and one half of the adult males, and (8) *lone individuals* - single chimpanzees (Cox *et al.* 2000).

According to Ghiglieri (1984) chimpanzees aggregate in unstable travel and feeding parties and show a tendency to travel in "parties with non-random age-sex distribution" (Ghiglieri 1984). This author categorized chimpanzee travelling groups according to prevalent age-sex class representation and found that (1) *infants* always range together with their mothers, (2) *juveniles* often travel with their mothers and siblings, but they were also seen travelling solitary, with their siblings only or with parties containing no mothers and possibly also no siblings, (3) *sub adult males* mainly range with adult males though being reproductively inferior to them, (4) *adult males* range primarily with each other, (5) *adult females* travel mainly in units that consist of mothers and their dependent offspring, or in parties with other adult females, and (6) *adults of both sexes* sometimes travel with individuals of all life stages (Ghiglieri 1984).

Group sizes and composition change depending on habitat and season, and therefore reports differ from different research locations (Ghiglieri 1984). To be able to compare between-site group or party size Nishida (1994) suggests to firstly establish within-site party size reflecting daily, seasonal and annual change. As the most objective definition for *party size* he proposes "the largest party that includes at least one adult male (preferably the alpha male) in a day" (Nishida 1994). Chapman *et al.* (1994) list mean party sizes for chimpanzees and bonobos at different study sites summarized from different literature sources (Table 4.2).

Table 4.2: *Mean party sizes of chimpanzees at various locations in Africa (following Chapman et al. 1994)*

Study	Location	Mean party size
Ghiglieri 1984	Kibale (Ngogo), Uganda	2.6
Reynolds & Reynolds 1965b	Budongo, Uganda	3.9
Baldwin *et al.* 1982	Mt. Assirik, Senegal	4.0
Goodall 1968, 1986	Gombe, Tanzania	4.0
Chapman *et al.* 1994	Kibale (Kanyawara), Uganda	5.1
Sugiyama 1989	Bossou, Guinea	6.0
Nishida 1994	Mahale, Tanzania	6.2
Sabater Pi 1979	Okorobiko Mts., Equatorial Guinea	9.9
Teleki 1989	Taï, Ivory Coast	10.1

The ratio between adult females and males is > 1 in most chimpanzee communities (Ghiglieri 1984, Cox *et al.* 2000). Ghiglieri (1984) attributes this fact mainly to three different factors, namely (1) that females reach maturity a year or two earlier than males, (2) that females often temporarily emigrate to a neighbouring community, and might be included in both community counts, and (3) that it is mainly males who engage in displays and intercommunity combats and who might therefore be more frequently subject to accidental death or killing.

Ghiglieri (1984) gives the following age-class definitions for chimpanzees:

Infant:	0 - < 5 years
Juvenile:	5 - < 10 years
Sub adult:	10 - < 15 years
Adult:	≥ 15 years

Sugiyama (1969) in Ghiglieri (1984) additionally recognises babies (< 0.5 years) and classifies infants from 0.5 to 2 years only. Reynolds (1967) gives the age of sexual maturity for female chimpanzees between 7 and 10.75 years, and for male chimpanzees from 7 to 8 years. According to Goodall (1986) a chimpanzee is only considered to be an adult after s/he has reached sexual and social maturity.

Adult females frequently leave their home community and migrate to neighbouring communities to mate with the adult males there, so called "female exogamy", thereby ensuring a continuous mixing of gene pools (Ghiglieri 1984, Cox *et al.* 2000). Female chimpanzees give birth to an infant about every three to five years (Reynolds 1967, Goodall 1998) with pregnancy lasting an average of eight months (Kingdon 1997). According to Wrangham *et al.* (1994b) and Sugiyama (1989) mean interbirth interval ranges from 4.4 to 6.0 years, whereas Teleki (1989) estimates the average birth interval at 5.6 years and the beginning of a female chimpanzee's reproductive period at 12 years of age. Infants are normally nursed up to four or five years of age, while constantly being carried around by their mothers until at least three to four years of age. Yet, full independence only occurs around eight years of age (Goodall 1986, Teleki 1989). Infants who are orphaned before five years of age normally have a very small chance of survival even under normal wilderness conditions (Goodall 1986, Teleki 1989). Considering an expected reproductive span of about 25 years on average, the total number of offspring per female chimpanzee is not more than five per lifetime (Teleki 1989).

The existence of a male social network and a separate female social network has been established. The latter is considered to be much looser than the former, in most chimpanzee communities. The closer social interaction of male networks manifests itself for example in the fact that males groom each other much longer and more frequently than females interact in this way (Ghiglieri 1984, Nishida 1994, Cox *et al.* 2000). Furthermore, the range covered by the two networks is often not identical. The female network is considered to cover a smaller area of the community's home range but extends into the home range of a neighbouring community. The male network frequently covers the whole community home range, e.g. on patrol rounds (Ghiglieri 1984, Wrangham *et al.* 1994b, Cox *et al.* 2000).

When two different communities encounter this can result in extreme aggression, during which some members of the communities might even be killed and/or one of the communities might be dissolved as a result of this encounter (Goodall 1986, 1998, Cox *et al.* 2000).

Cognitive abilities

In a number of feeding experiments with six young, captive chimpanzees Menzel (1971, 1972) made some interesting discoveries concerning chimpanzees' spatial memory and their conversation about the environment.

The author discovered that in food hiding experiments chimpanzees will follow the one animal in the group who was present when the food items were hidden. This animal (a number of different individuals throughout the whole experiment) was able to remember the hiding place in the majority of cases (Menzel 1971). The leader of the group is also able to communicate to her/his ignorant companions whether the hidden item is a very desirable or less desirable food item or even a supposedly dangerous animal (e.g. a rubber snake) as well as information about the quantity of items hidden at one place (Menzel 1971).

Even if several food items were hidden at several locations the tested individual in most experiments remembered the majority of localities. When retrieving the items s/he followed the 'least distance principle' even in 'delayed response' tests (Menzel 1972). If several items were hidden non-randomly the chimpanzees would first recover the items in the area where most food samples were located and only then concentrate on the area with lower sample density (Menzel 1972). They would also first recover the preferred food items before recovering the less preferred items, while still following the least distance principle within each of the two categories, so-called 'cognitive mapping' (Menzel 1972).

This demonstrates immense cognitive and communicative abilities, but Menzel (1971, 1972) was not able to discover how the acquired and partly also processed information was passed on from the test animal to the ignorant control individuals in the group.

Locomotion

Chimpanzees are basically terrestrial but also arboreal, and they are able to travel four-, three- and two-legged (Kortlandt 1962, Reynolds & Reynolds 1965a, Reynolds 1967).

Doran & Hunt (1994) compared the locomotor behaviour of two chimpanzee subspecies (*Pan troglodytes schweinfurthii* from Mahale and Gombe, Tanzania, and *Pan troglodytes troglodytes* from Taï Forest, Ivory Coast) with each other and with the locomotor ability of the bonobo (*Pan paniscus* from Lomako, DRC). They distinguished five different categories of postural activity: (1) quadrupedalism, (2) quadrumanous climbing and scrambling, (3) suspensory behaviour, (4) bipedalism, and (5) leaping and diving. The authors concluded that there is far less variation in locomotor behaviour between sites and between subspecies than there is between the two species. Furthermore, they discovered that bonobos are more suspensory than chimpanzees and engage in more arboreal travel than chimpanzees who use terrestrial travel to move from one feeding place to the next (Doran & Hunt 1994).

Culture

Imanishi (1952) as cited in Wrangham *et al.* (1994b) defines *culture* as "socially transmitted adjustable behaviour".

The existence of culture in chimpanzee populations manifests itself for example in the existence of different tool using techniques by different chimpanzee communities in different countries and locations (Wrangham *et al.* 1994b, Cox *et al.* 2000). For example, while chimpanzees in Tongo, DRC, use moss sponges to soak up water from tree holes, the chimpanzees in Gombe, Tanzania, use leaf sponges, but the chimpanzees in Kibale Forest, Uganda, prefer the use of stem sponges for the same purpose (Goodall 1986, Wrangham *et al.* 1994b). On the other hand even though, ecological conditions and food availability may be quite similar for different chimpanzee communities at different locations, their food use may still vary considerably (Wrangham *et al.* 1994b, Cox *et al.* 2000).

The possession of *culture* is a special asset of chimpanzees and the great apes in general, which makes it even more difficult to draw a clear line between human and non-human primate societies.

Predators

Besides leopard and lion the main predator of chimpanzees is man (Kortlandt 1962, Reynolds 1967, Ghiglieri 1984, Nishida 1994). Ghiglieri (1984) also assumes spotted hyena to be a potential predator as well as crowned hawk-eagles who might also be a danger for infant chimpanzees. Captive chimpanzees when faced with stuffed leopards use sticks or throw stones to fend the potential predator off (Kortlandt 1962, Reynolds 1967).

Man, apart from hunting chimpanzees for bush meat, also constitutes a deadly threat through his use of snares and other devices to catch forest-dwelling small ruminants, like duikers. Especially young, inexperienced chimpanzees get caught in these snares and often only escape at the price of the loss of a hand or foot if not their life through gangrenous infection (Ghiglieri 1984, Ammann 1997-1998).

A rare and unexpected predator for the chimpanzee is the chimpanzee-self: Goodall (1998) reports on several infanticides followed by cannibalism by one of the adult females and her daughter among the Gombe chimpanzees.

Destructive behaviour

During their displays and also when leisurely sitting on tree branches while eating fruits and leaves or when building nests chimpanzees cause a lot of serious damage to the vegetation which constitutes part of their natural diet and shelter (Reynolds 1967, Baldwin *et al.* 1982, Ghiglieri 1984, Wrangham *et al.* 1994b, Grieser Johns 1996, Goodall 1998, Voysey *et al.* 1999a).

Reynolds (1967) lists several such activities in the Budongo Forest, Uganda: drumming on tree buttresses, drumming (rapid locomotion), throwing and shaking things (Reynolds 1967).

Baldwin *et al.* (1982) consider chimpanzee nests to be "reliable and durable traces of the distribution of chimpanzees", which indicates the permanent state of destruction of branches and leaves used for the construction of night and to a lesser extent also day nests. As an indicator for the life span of chimpanzee nests Ghiglieri (1984) used the "gradual recuperation of the tree".

When evaluating responses of chimpanzees to habituation and tourism in the Kibale Forest of Uganda Grieser Johns (1996) used the presence of *feeding noises* as one possible strategy to indicate and locate the presence of chimpanzees. She defines *feeding noises* as "... the tearing of branches, stripping of leaves off branches, munching noises" (Grieser Johns 1996).

Goodall (1998) gives a number of examples of Gombe chimpanzees accidentally or wilfully destroying vegetation during their everyday activities, such as displaying, infants playing, feeding and nesting. All these activities are potentially destructive to the trees and other vegetation used by the chimpanzees.

Voysey *et al.* (1999a) comment on the price trees have to pay if relying on great apes as seed dispersers. They believe that the tree's architecture, the structural quality of its wood and the position of fruits play an important role in the degree of damage a tree suffers for the benefit of seed dispersal by great apes (Voysey *et al.* 1999a) The authors also observe that trees specialised on great apes as seed dispersers seem to suffer less damage than generalists (Voysey *et al.* 1999a). Wrangham *et al.* (1994a) describe the destructive method of fruit collection by chimpanzees as follows: "ripe fruits were collected from small limbs that had been broken off by chimpanzees during their feeding". Van Hooff (1973) gives two examples of tree destruction by captive chimpanzees: (1) he observed apes at Holloman Air Force Base in New Mexico to tear off leaves, branches and bark from trees provided in the enclosure, and (2) found apes at Arnhem Zoo to peel off the bark from trees in their enclosure since they favoured the taste of the former's soft inside. Van Hooff (1973) expects those trees to eventually face complete defoliation and to "become one huge climbing frame in which the animals will be fully visible to the public" (Van Hooff 1973). Wilson & Elicker (1976) describe the waving of branches as one major component of displays performed by chimpanzees they released on Bear Island, Georgia, U.S.A. A similar destructive influence might be expected by chimpanzees when foraging for fruit in trees. Kortlandt (1960/61) ascribes the presence of a number of dead tree stumps inside a chimpanzee enclosure at the Institut Pasteur at Kindia in former French Guinea to the fact that all sprouts were generally eaten by these great apes. The author concludes that the destructive behaviour of chimpanzees through displays and sprout eating will lead over time to the complete destruction of woody vegetation in confined enclosures, such as zoos (Kortlandt 1960/61).

Jenkins (pers. comm.[4]) describes his experience when holding a group of originally 12 later 14 chimpanzees in an enclosure of 2.0 to 2.5 ha at Boki Ogi, Nigeria. The fenced-off area was completely covered with secondary rain forest. The chimpanzees ranged from 2.5 to 9 years and had a female:male ratio of approximately 1:1 (Jenkins pers. comm.). Chimpanzees were fed supplementary and water was freely available (Jenkins pers. comm.). The chimpanzees took about three to four years to completely destroy the secondary rain forest vegetation cover inside their enclosure (Jenkins pers. comm.). The destruction of trees was caused in the lower layers by playing infants, in the middle layers by fruit eating chimpanzees and in the high tree layers by the nest-building activities of adult chimpanzees (Jenkins pers. comm.).

Oppenheimer & Lang (1969) found that Gustavia trees had significantly more branches at a site *with* cebus monkeys than in a similar control site *without* monkeys. They suggest that the removal of terminal buds by the monkeys during feeding might release the lateral buds from apical dominance and thus induce increased branching (Oppenheimer & Lang 1969). An effect that might also be caused by chimpanzees feeding on buds in different fruiting trees.

Figures 4.8 to 4.17 show the destruction caused by chimpanzees (1) at Ngamba Island Chimpanzee Sanctuary (Figures 4.8 – 4.12) and (2) at Sweetwaters Chimpanzee Sanctuary in Nanyuki, Kenya (Figures 4.13 – 4.17).

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[4] Jenkins, P. 2001. Pandrillus, Calabar, Nigeria.

Figure 4.8: Young tree on Ngamba Island that has been defoliated and its branches broken off by infant chimpanzees during their forest walks.

Figure 4.9: One branch of a young tree has been broken off (arrow) by adult male chimpanzees displaying while foraging through the secondary rain forest on Ngamba Island.

Figure 4.10: Destruction caused to the undergrowth by adult chimpanzees while foraging, playing and feeding in the secondary rain forest on Ngamba Island.

Figure 4.11: Branches and stems of woody vegetation are bent and broken by the chimpanzees during their daily visits to the secondary rain forest on Ngamba Island.

Figure 4.12: An adult chimpanzee at his 'destructive work' in a tree on Ngamba Island.

Figure 4.13: Trees defoliated by chimpanzees at Sweetwaters Chimpanzee Sanctuary, Nanyuki, Kenya – with kind permission from A. Olivecrona, Sanctuary Manager.

Figure 4.14: Destruction of woody vegetation caused by chimpanzees at Sweetwater Chimpanzee Sanctuary, Nanyuki, Kenya – with kind permission from A. Olivecrona, Sanctuary Manager.

Figure 4.15: Destruction of woody vegetation (close up) at Sweetwaters Chimpanzee Sanctuary, Nanyuki, Kenya – with kind permission from A. Olivecrona, Sanctuary Manager.

Figure 4.16: Adult chimpanzee hunching next to a destroyed young tree at Sweetwaters Chimpanzee Sanctuary, Nanyuki, Kenya – with kind permission from A. Olivecrona, Sanctuary Manager.

Figure 4.17: Adult chimpanzee in 'display mood' with his hair slightly bristled – the tree in the background shows destruction caused by chimpanzees at Sweetwaters Chimpanzee Sanctuary, Nanyuki, Kenya – with kind permission from A. Olivecrona, Sanctuary Manager.

Chimpanzee ranging patterns

Animals living in groups share an area of land within which they forage, sleep, raise their young, and go about their other daily activities. The area so occupied is called 'home range' (Goodall 1986) and its size depends on a number of factors. The more important of those being: (1) the size and food requirements of the animal, (2) the number of individuals in the group, (3) the density of surrounding populations, and (4) the type of habitat (Goodall 1986).

According to Kortlandt (1984) the need for a very varied diet is the underlying factor determining the size of the home range of the chimpanzee. This need furthermore determines the carnivorous habits and the social organisation of this great ape species (Kortlandt 1984). Baldwin *et al.* (1982) give as general definition for chimpanzees' home range "the total area used for at least one year by members of a community of chimpanzees".

Metabolic principles

McNab (1963) examined the relationship between the size of the home range and mammalian body size. According to the author the size of the home range in wild mammals is determined by the rate of metabolism which in turn is dependent on body mass.

Following Kleiber's (1961) equation in McNab (1963) the basal rate of metabolism is calculated as follows:

$$M = k\,W^{0.75} = 70\,W^{0.75}$$

where: M = basal metabolic rate [kcal/day]
W = body mass [kg]
k = constant equal to 70.

Since there is also a linear relationship between the $\log_{10}$ of home range plotted against the $\log_{10}$ of body mass, in that the cost of locomotion per unit body mass is lower for larger animals which are thus expected to have larger home ranges (Schmidt-Nielsen 1972), the size of home range can eventually be expressed as being determined by the basal rate of metabolism:

$$R = 0.12\,M$$

where: R = size of home range [acres].

This equation represents just an approximation of the real relationship since it uses basal metabolic rate instead of total daily energy expenditure which would furthermore be temperature dependent (McNab 1963).

McNab (1963) found that the size of a species' range was dependent on the type of food this species consumes. He thus divided mammals into two broad categories, *food hunters* and *food croppers*. While the former have to 'hunt' for their food and include those species that are either granivorous, frugivorous, insectivorous, or carnivorous, the latter usually do not need to 'hunt', therefore have a smaller home range, and include those species that are either grazers or browsers (McNab 1963).

McNab (1963) adjusted his equation to correct for this difference in home range size for the two separate types of mammals, resulting in:

$R_h = 0.20\ M$ (for hunters)

$R_c = 0.05\ M$ (for croppers).

Thus, *food hunters*, like the chimpanzee, have about four times the home range size of *food croppers* with the same body mass.

This equation still does not consider the direct and indirect influences of weather and climate on the animal. Furthermore, it does not account for the fact that species with large home ranges usually cannot maintain locally dense populations because of the limited amount of energy available within a given area (McNab 1963).

Milton & May (1976) have developed McNab's equation further. These authors divide primates into (1) folivores, i.e. species who depend on mature or immature foliage as their staple diet, (2) frugivores, i.e.species who are primarily fruit eaters and take only a small amount of foliage and little or no protein, (3) generalist primary consumers, i.e. species who eat roughly equal proportions of both foliage and fruit and little or no animal protein, and (4) omnivores, i.e. species who seem to actively seek out and probably depend on animal protein (Milton & May 1976). The authors attribute frugivorous and omnivorous primates to McNab's *hunters* in their feeding habits and folivorous primates to McNab's *croppers* (Milton & May 1976). Milton & May (1976) conclude that folivorous primates occupy a smaller home range area for their body mass than do frugivorous and omnivorous primates. The authors furthermore state that primates in general occupy a smaller home range area per individual than solitary terrestrial mammals do, while primates living in social groups have a much larger total home range than individual solitary mammals (Milton & May 1976). Milton & May (1976) give three main factors which determine home range size, i.e. (1) *body size* of the animal, (2) *–vory* of an animal, e.g. frugivores tend to have larger home range sizes than folivores, and (3) *height of the tree canopy*, since the size of this third dimension adds to the density of resources per area and to the actual distance travelled in space per unit area and has an especially marked effect on the size of the home range of folivorous primates. Taking these considerations into account the authors arrive at the following equation to calculate the size of home range of individual *primate hunters*, which includes the chimpanzee (Milton & May 1976):

$$\text{Log } HR_i = 0.83 \text{ Log } BW - 2.17$$

With HR_i = size of home range [ha] of the individual
BW = body mass [g].

Milton & May (1976) are aware of certain shortcomings of this equation but consider it valid to at least give some idea of the relative amount of space required to provide adequate resources for individuals of a species.

Ghiglieri (1984) uses the same equation to calculate the home range for a single chimpanzee at Ngogo, Kibale Forest, western Uganda. He estimates the mean mass of an individual as 28.7 kg and arrives at a home range portion per Ngogo chimpanzee of 34 ha or 0.34 km^2. This would lead to a community home range for the 55 chimpanzees in his study group of 18.6 km^2, while from his census and nest count data the author estimated a home range of between 23.1 to 37.9 km^2 for the Ngogo community (Ghiglieri 1984). Ghiglieri (1984) criticises the equation developed by Milton & May (1976) in that it inherently underestimates the home range of chimpanzees. The reasons for that being that firstly the habitat type is not taken into account and secondly the diet has been generalized to that of a hypothetical model omnivore rather than that of a frugivore who has more specific and demanding foraging requirements (Ghiglieri 1984).

Home range and habitat type

Kortlandt (1984) criticises all above equations since they do not take into account the immense need for diversity of the chimpanzee's diet. According to him the minimum food diversity required for nutritional reasons mainly determines the necessary home range area for an individual and a community of chimpanzees in a given habitat (Kortlandt 1984). Based on this statement is the conclusion that in a habitat with a low or normal botanic diversity but a high carrying capacity, the number of chimpanzees in a community would amount to:

Population = range with minimum diversity x carrying capacity

With the size of the community being determined by the minimally required locomotor performance and the carrying capacity of the habitat (Kortlandt 1984).

In a habitat with a high botanical diversity but a quite low carrying capacity the number of chimpanzees in a community would amount to:

Population = maximum range x carrying capacity

With the size of the community being determined by the maximum (efficient) locomotor performance and the carrying capacity of the habitat (Kortlandt 1984).

The term *carrying capacity* has largely been replaced by the term *ecological capacity of the area*. Kortlandt (1984) uses the term *carrying capacity* to describe the long-term equilibrium of a population of animals under specific habitat conditions (Bothma 1996).

Contrary to what is normally found among the other great apes and many monkeys, in none of the two above cases is the community size determined by ethological mechanisms and social interaction processes. It appears that the higher sociality of the chimpanzee, as compared with other great apes and monkeys, is an adaptation to his need for a wide diversity of foods (Kortlandt 1984). Following Kortlandt (1984) this finding would also explain the fact that rain forest-dwelling chimpanzees form larger communities than their woodland-, savanna- and mosaic-dwelling conspecifics. This is again contrary to the general rule when comparing (smaller) forest-dwelling with (larger) open-land dwelling mammalian communities (Kortlandt 1984).

Female and male home range patterns

Goodall (1986) states that chimpanzees who live in a relatively lush environment, such as Gombe, have smaller home ranges than chimpanzees inhabiting harsher and more arid parts of Africa. She also mentions that differences exist in home range sizes of individual chimpanzees depending on their age, sex and reproductive status and depending on the year.

The author recorded a distance of 3.0 – 5.0 km travelled per day for an alpha male. A pregnant female travelled a lowest mean of 2.4 km per day in the third week of August 1977, while a female in oestrus travelled a mean of 3.1 km per day. A male and female pair only travelled a mean of 1 km per day during their consortship (Goodall 1986).

Kordtlandt (1984) gives the following examples of community sizes and foraging habitats in mosaic and savannah-woodlands as compared to rain forest habitats:

Table 4.3: *Community sizes and foraging ranges of chimpanzees (following Kortlandt 1984, using his corrections of range sizes)*

Community	Population	Range [km^2]
Mosaic and savannah-woodland habitats		
Gombe, Gombe River	20 - 30	13.0 – 21.0
Mahale Mountains, K-Group	26 - 34	10.5
Kasakati, Group L	40	122.0
Rain forest habitats		
Budongo, Eastern Valley	56	7.5
Bukavu-Walikale	65 - 91	50.0
Pygmy Chimpanzee	45 - 50	22.0

Goodall (1986) defines the *year range* of an individual chimpanzee as "the sum of all areas visited during a given year". As might be expected, her observations showed that the year range of a healthy adult male is larger than that of a healthy anoestrus adult female. For the years 1972/73 she gives the year ranges for adult males between 9 to 12 km^2, with a median of 10.3 km^2; while for three anoestrus females in the same period of time the year ranges where from 5.8 to 7.0 km^2 travelled, with a median of 6.8 km^2 (Goodall 1986).

Goodall (1986) defines the *community range* according to Wrangham (1977) as "the sum of all areas visited by each adult male of the community during a given year". The authors found that the community range of the chimpanzees at Gombe changes over time primarily as a result of changes in the number of adult males in the community from year to year (Goodall 1986).

Goodall (1986) furthermore distinguishes *core areas* and *boundary areas* of a community's home range. While male chimpanzees tend to visit each of the home range's boundary areas about every four days, female chimpanzees, at least when in anoestrus, spend the majority of their time in the core area of the community's home range (Goodall 1986). Additionally, chimpanzees shift their ranges in response to the seasonal fruiting patterns of desired or required species of food (Baldwin *et al.* 1982).

Chimpanzee densities

Teleki (1989) gives general guidelines regarding chimpanzee densities in different habitat types. The author defines *crude density* as a derivative of *population size* and *habitat size* and from his literature study arrives at the conclusion that crude densities of chimpanzees at the most intensely studied sites range from as low as 0.1 to as high as 6.8 chimpanzees per km^2, with an average density far below 1.0 chimpanzee per km^2 (Teleki 1989). As a general rule Teleki (1989) states that in the marginal dry savanna-woodland habitats (e.g. Mt Assirik, Senegal), the average density is about 0.1 chimpanzees per km^2, while for moist mosaic habitats of grassland-woodland forests (e.g. Gombe, western Tanzania) this density is about 0.2 chimpanzees per km^2, and for the rain forest habitat an average density of 0.3 chimpanzees per km^2 might be assumed. However, densities in this habitat show great variations from higher densities of about 4.0 to 6.8 chimpanzees per km^2 (Budongo Forest, Uganda) to lower densities from 0.4 to 2.0 chimpanzees per km^2 (Bwindi and Kibale Forest, Uganda, respectively) (Teleki 1989). Especially, since poaching has become a serious problem the author considers the former high density estimates to be particularly anomalous and therefore decides to adjust the mean density for a rain forest habitat even below the lower estimated values (Teleki 1989). Teleki (1989) thus considers the baselines figures of 0.1, 0.2, and 0.3 chimpanzees per km² to be the best options for projecting wild chimpanzee population numbers across tropical Africa. Table 4.4 lists examples of chimpanzee densities in different habitat types taken from different literature sources.

Table 4.4: *Chimpanzee densities in different habitat types (habitat types according to Teleki 1989)*

Source	Location	Habitat	Density [chimpanzees/km^2]	Range [km^2]
Baldwin *et al.* 1982	Mt Assirik Senegal	Dry savanna-woodland	0.09	239
Tutin & Fernandez 1991	Lopé Reserve Gabon	Primary rain forest	1,00	unknown
Bermejo 1999	Odzala NP* Republic of Congo	Primary & Marantaceae forest	2.20	2 848
Hart & Hall 1996	Maiko NP DRC	Primary rain forest	0.46	10 830
Hart & Hall 1996	Kahuzi-Biega NP DRC	Primary rain forest	0.40	6000
Hart & Hall 1996	Okapi WR** DRC	Primary rain forest	0.89	13 700
Albrecht 1976	Budongo Forest Uganda	Primary rain forest	1.45 – 1.95	Unknown
Ghiglieri 1984	Kibale Forest Uganda	Primary rain forest	1.45 – 2.38	~70
Goodall 1998	Gombe NP Tanzania	Grassland-woodland forest	~2.10	~78

* NP = National Park ** WR = Wildlife Reserve

Chimpanzee nest-building behaviour

According to Fruth & Hohmann (1994) chimpanzees spend at least 50% of their lives on nests. The authors assume therefore that these great apes can be expected to choose their nesting sites carefully (Fruth & Hohmann 1994).

Despite variation related to individual, age or species, all nests constructed by the great apes share three major components constructed by combining plant material: (1) a solid foundation, (2) a central mattress, and (3) a lining made of additional leaves and twigs (Fruth & Hohmann 1994). The technique of nest making entails bending down branches of the surrounding bushes. Though this is not done in a particular order it is still ensured that they criss-cross one another and eventually form a platform on which the ape can sit or stand. Thereafter, all the tops of the branches are bent into a ring resting on the platform (Bolwig 1959).

There are day nests and night nests, the former being much more casually constructed and also used for a much shorter period of time than the latter (Baldwin *et al.* 1981, Fruth & Hohmann 1994, Goodall 1998).

Baldwin *et al.* (1981) compare nests made by different populations of chimpanzees in different habitats – *Pan troglodytes troglodytes* in a forested area in Equatorial Guinea and *Pan troglodytes verus* in a savanna habitat in south eastern Senegal. The authors concluded that all the differences they found in nest-building between populations could be explained by environmental factors (Baldwin *et al.* 1981). It was found that at Mt Assirik, Senegal, the height of nests was highest in the gallery forest, then in grassland and lowest in woodland. The tallest trees occur in the gallery forest, but trees in the grassland are considered lower than in the woodland. When examining the trees chosen for nesting in grassland, it became obvious that the chimpanzees preferred those species which grow along seasonal watercourses, e.g. *Spondas mombin* and *Adansonia digitata*. These species occur only rarely in a grassland habitat, but when they do so, they are exceptionally tall for this type of habitat (Baldwin *et al.* 1981). The average heights for nests were 12.2 m at Ngogo and 10.8 m at Kanyawara, 16.5 m near Fort Portal and in the Ruwenzori (Bolwig 1959, Ghiglieri 1984). Ghiglieri (1984) attributes these differences mainly to "differences in vegetative physiognomies between habitats"

Ghiglieri (1984) found that the chimpanzees in Kibale Forest prefer certain tree species for the construction of their day and night nests. The author concluded that factors influencing this pattern of utilization are "the tensile suitability of the tree's limbs", its "density of foliage" and its proximity to a highly favoured food source (Ghiglieri 1984). Hashimoto (1995) found a similar preference for certain tree species used for nest building among chimpanzees in the Kalinzo Forest, Uganda.

According to Fruth & Hohmann (1994) chimpanzee infants already start at the early age of eight months with their first attempts at nest building. These first attempts are still a long way off from the sophisticated structures an adult chimpanzee will construct. Especially day nest construction increases in frequency and reaches a peak when the infant is about three years old. Therefore, long before weaning, nest building becomes an important part of the behaviour of infant chimpanzees (Fruth & Hohmann 1994).

Chimpanzee feeding behaviour

"The Gombe chimpanzees can be described in summary as omnivorous forager-predators that supplement a basically vegetarian diet in various ways, including the optional practice of hunting other animals, with fellow primates being their most favored prey" (Teleki 1973).

Diet composition

Clutton-Brock & Harvey (1977) divide primates in general into three dietetic groups: insectivores, folivores and frugivores with the chimpanzee being a member of the latter group. The authors found that interspecific differences in the dietetic diversity in primates are positively related to body mass, day range length and home range size. While the proportion of day time spent feeding is positively related to body mass, but negatively related to the proportion of foliage in the diet (Clutton-Brock & Harvey 1977).

Chimpanzees are primarily frugivorous and spend between 46% to 62 % of their time feeding, between 25% to 39% resting, and only between 8% to 20% travelling (Wrangham 1977, Ghiglieri 1984, Isabirye-Basuta 1989, Erwin 1992). The major component (45 – 75%) of their diet is fruits, but, leaves, piths, shoots, seeds, bark, flowers, wood, galls, resin, clay, insects, rodents, suids, bovids, and primates, birds eggs and birds, clay and soil are also consumed (Hladik 1977, Goodall 1986, Erwin 1992). According to Sugiyama & Koman (1987) fruits and seeds (nuts) occupy more than half of the chimpanzees' diet; and leaves, shoots, and twigs (stems) constitute about another third. At Gombe chimpanzees have been observed to eat 184 items of vegetable food from 141 species of trees and plants (Goodall 1986). Also according to Hladik (1973) and Wrangham (1977) fruit and leaves constitute the major part of the chimpanzee's diet. Fruits may form up to 90 % of the daily diet and never less than 40%, with most of the daily fruit consumption being between 55% and 80% (Hladik 1977). At the same time there is a daily intake of animal food of between 2.5% to 6.0%, mainly consisting of ants, some termites, bird eggs and fledglings (Hladik 1977). Newton-Fisher (1999) found that recently habituated chimpanzees of the Sonso community in Budongo Forest, Uganda, spent an average of 64.5% of their time eating fruit and of 19.7% eating arboreal leaves.

A seasonal variation of the diet composition is noticeable and can be explained by the variation of the availability of food stuff over the year (Hladik 1973, 1974 & 1977, Sabater-Pi 1979, Goodall 1986, Tutin *et al.* 1991a, Wrangham *et al.* 1991, Newton-Fischer 1999). Table 4.5 lists the components of the chimpanzees' diet as determined in different study areas and habitats.

Table 4.5: *Composition of chimpanzee diet in different habitats*

Diet Component	Mean percentage of dietary composition [%]							
	1	2	3	4	5	6	7	8
Plant food	93	96	89	91.25	97.5	X	100.9	100
Fruit	(68)*	68	59	59.5	45	X	49.2	57
Leaves	(25)	(28)	17	25.5	32	X	(36.1)	(10)
Blossoms			4	4.75		X	6.3	10
Seeds	(68)		*9*	*1.5*	8	X	3.4	10
Shoot							(36.1)	(10)
Pith						X		
Bark	(25)				12.5	X	(5.9)	7
Stems	(25)	(28)					(36.1)	3
Wood						X	(5.9)	
Resin			X	X		X	(5.9)	
Root						X		3
Bananas (provisioned)	X**	X	X	X				
Animal food	6	4	7	5.75	2.5	X	X	X
Vertebrate prey		(4)	2	1		X	X	X
Mammals		(4)				X	X	X
Birds		(4)				X	X	
Eggs			X	X		X		
Reptiles								X
Fish	6						X	
Insects		(4)	4	4.5	2.5	X	X	X
Galls			1	0.25				
Soil	X	Trace						
Minerals	X					X		
Miscellaneous			4	3		X		

* all diet components in (brackets) contribute to the percentage given.
** an X is made if no percentage of total diet is given in the literature source.

Key:

1 = Hladik 1973, Ipassa, Gabon – *primary rain forest.*
2 = Hladik 1977, Ipassa, Gabon.
3 = Goodall 1986, Gombe, Tanzania, average for 1978 – *mosaic forest, woodland and grassland.*
4 = Goodall 1986, Gombe, Tanzania, average for 1979 – see difference in *seed* consumption to 1978.
5 = Sabater-Pi 1979, Okorobikó Mountains, Equatorial Guinea – *primary and secondary rain forest.*
6 = Nishida & Uehara 1983, Mahale Mountains, Tanzania – *mosaic forest, woodland and riverside.*
7 = Sugiyama & Koman 1987, Bossou, Guinea - *secondary rain forest of different stages.*
8 = McGrew *et al.* 1988, Mount Assirik, Senegal – *heterogeneous Sudanian savannah woodland.*

Factors affecting food choice

Food choice in the chimpanzee is primarily affected by variation in the levels of specific nutrients in different foods rather than by variation in secondary compounds. (Hladik 1977, McGrew 1985, Goodall 1986, Reynolds *et al.* 1998). Hladik (1978) supports the view that plant species are chosen for their nutritional quality. Regarding leaves young leaves are favoured, since they possess a greater amount of proteins and soluble sugars than mature leaves (Hladik 1978). The author concludes that it is therefore mainly the primary compounds of leaves that determine which plants are chosen for food; while the secondary compounds have less influence on vertebrate food choice (Hladik 1978). Hladik (1978) considers the impact of the vertebrate folivorous population on the leaf mass of the primary rain forest of Ipassa, Gabon, as being low, since these consumers do not eat more than one percent of the total leaf production. While the impact of insect folivory on leaf-production in this habitat may reach up to 10% of the total litter fall (Hladik 1978).

The occasionally observed feeding on termite clay by the chimpanzees of Gombe might have the effect of neutralizing tannins (Goodall 1986). However Tutin *et al.* (1991a) conclude that the small number of mature leaves eaten by the chimpanzee suggests a general avoidance of food with high fibre content and/or secondary compounds. Matsumoto-Oda & Hayashi (1999) found that *Pan troglodytes schweinfurthii* at Mahale Mountains, Tanzania, (1) eat fruit that contain significantly more non-fibrous carbohydrates than leaves, (2) of the six most important chimpanzee food items, four are fruits, (3) the important fruits contain significantly more non-fibrous carbohydrates than the unimportant fruits, and (4) fibre and condensed tannin content are negatively correlated with food selection.

According to Sabater-Pi (1979) the chimpanzee mainly chooses his food according to its typology, i.e. taste, smell, texture and abundance. However, Hladik (1977), Matsumoto-Oda & Hayashi (1999) and Wrangham *et al.* (1999a) all agree that chimpanzees choose their food items in such a way as to ensure a maximum yielding of nutrients and calories.

Overall, a diurnal rhythm in food choice can be observed, in that fruits tend to be eaten earlier in the day than leaves (Clutton-Brock 1977, Wrangham 1977, Sabater-Pi 1979, Ghiglieri 1984, Goodall 1986).

Isabirye-Basuta (1989) reports fruit utilization by chimpanzees at Kanyawara, in Kibale Forest, Uganda, was not related to fruit abundance. These apes select certain preferred fruit species which they consume extensively even if their abundance is much lower compared to other fruit species available at the same time (Isabirye-Basuta 1989, Matsumoto-Oda & Hayashi 1999). Based on the number of plant species eaten each month, diet diversity was significantly inversely related to (1) fruit abundance, and (2) the proportion of fruit in the monthly diet (Isabirye-Basuta 1989). The number of plant species used (1) as fruit source, and (2) as food source, was significantly inversely related to the number of fruit species available (Isabirye-Basuta 1989).

According to Baldwin *et al.* (1982) and to Goodall (1986) the availability of water determines to a large extent the seasonal usage of different vegetation types by chimpanzees, especially in a rather arid savanna habitat.

White & Wrangham (1988) compared party size and feeding behaviour in chimpanzees and bonobos. They concluded that party size for both groups was dependent on the size of the food patch (also: Ghiglieri 1984, Isabirye-Basuta 1988); and that party size for feeding chimpanzees was larger in a forest habitat than in a mixed habitat with poorly developed forest (White & Wrangham 1988). Additionally, Isabirye-Basuta (1988) found that large-crowned trees support larger parties of feeding chimpanzees than small-crowned trees. Furthermore, the chimpanzees also feed and stay longer to socialize in the former than in the latter trees (Isabirye-Basuta 1988).

Chapman *et al.* (1994) compared the distribution of chimpanzees and bonobos in the fruiting trees composing a food patch. The authors observed that, while bonobos appeared to feed together in the same tree, the individual members of a chimpanzee party would disperse over several neighbouring trees, thus utilizing and affecting most of the trees in the food patch (Chapman *et al.* 1994).

Protein sources

Chimpanzees compensate for the low protein content of fruits by consuming young leaves with a higher protein content. They select insects for specific amino acids (Hladik 1977). Hladik (1977) gives the average protein content of the pulp of fruits as 5%, which is insufficient to compensate for the loss of nitrogen of an adult chimpanzee. Seeds which have an average protein content of 10.5 % cannot compensate for that. Leaves and stems have a high protein content (mean 24.9%) and are furthermore commonly available. Especially young leaves and shoots may thus be eaten when invertebrates or other animal prey cannot be obtained in sufficient quantity to complement the frugivorous diet (Hladik 1977). The essential amino acids for chimpanzees are cystine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tyrosine and valine (Hladik & Viroben 1974). The chimpanzees of Ipassa consume stems (*Hypselodelphis* species), leaves (*Baphia* species), ant nests (*Macromiscoides*), ants, eggs, larvae and pupae of *Œcophylla* and birds' eggs to replenish their need for essential amino acids (Hladik & Viroben 1974). The main source of protein for chimpanzees released on the island of Ipassa, near Makokou, Gabon, were ants (Hladik 1973).

Nishida & Uehara (1983) have observed the chimpanzees at Mahale Mountains, Tanzania, to feed on mammals, birds and insects as source of animal protein. Their mammal prey mainly consisted of primates and artiodactyles, e.g. *Galago crassicaudatus crassicaudatus*, *Colobus badius tephrosceles*, *Cercopithecus* spp., infant *Pan troglodytes schweinfurthii*, *Cephalophus monticola*, *Tragelaphus scriptus*, and *Potamochoerus porcus*. Other vertebrates come from the taxa Rodentia and Hyracoidea (Nishida & Uehara 1983). Bird prey species include *Francolinus squamatus* and *Gallus gallus*, the latter from neighbouring human settlements (Nishida & Uehara 1983).

Insects from the taxa Hymenoptera, Isoptera, Hemiptera, Coleoptera, Orthoptera, and Lepidoptera are observed prey species and eggs, larvae, pupae, workers, soldiers and reproductives are consumed in varying amounts from the different species (Nishida & Uehara 1983). Mammal prey is in most cases solely hunted and consumed by the male members of a chimpanzee community (Teleki 1973, Goodall 1986).

Sugiyama & Koman (1987) have observed the chimpanzees in Bossou, Equatorial Guinea, to use mammals, birds, fish, crustaceans, and insects as source of animal protein. While McGrew *et al.* (1988) list insects, reptiles and mammals as animal protein source for the chimpanzees at Mt Assirik, Senegal. These chimpanzees are the only population of wild chimpanzees known to concentrate on nocturnal prosimians (*Galago senegalensis* and *Perodicticus potto*) as prey (McGrew *et al.* 1988).

Matsumoto-Oda & Hayashi (1999) state that protein content is positively related with food selection in non-human primates. They examined fruits and leaves composing part of the diet of the Mahale Mountains chimpanzees in Tanzania. Their results showed that leaves contain significantly more protein than fruits, while the lipid content did not differ significantly for the two food items (Matsumoto-Oda & Hayashi 1999). The authors conclude that although fruits composing the natural diet of chimpanzees contain lower levels of protein essential for body building they still are an important resource of ready energy through their high content of non-fibrous carbohydrates (Matsumoto-Oda & Hayashi 1999).

The importance of Ficus species

Wrangham *et al.* (1993a) investigated the differences in nutrient content of pulp and seeds of nine Ugandan *Ficus* species in Kibale Forest, Uganda. Figs are commonly eaten by Ugandan primates and also constitute a major component of the diet of chimpanzees in Kibale Forest (Wrangham *et al.* 1993a). Compared to the seed fraction of figs the authors found that the pulp fraction contains more water-soluble carbohydrates, complex carbohydrates, calories, and ash. The seed fraction, however, possesses more condensed tannins, lipids and fibre (Wrangham *et al.* 1993a). In their analysis the authors assumed that the seed fraction was totally indigestible, a fact that they admit to be an exaggeration (Wrangham *et al.* 1993a). Figs are an energy rich food with adequate protein (Wrangham *et al.* 1993a). The feeding rate of figs increased with increasing fig size, while at the same time, the harvesting rate of figs did not decline sharply with increasing fig size (Wrangham *et al.* 1993a). The feeding rate appears to have a more important effect on the rate of nutrient intake than the nutrient density of the fruit. Thus, even though larger figs have a higher water content than smaller figs, their consumption still leads to a higher nutrient intake per time interval. This higher intake resulted in an intake of more than 167.44 Joule per minute, excluding calories from insoluble fibre, when the chimpanzees harvested larger figs (Wrangham *et al.* 1993a).

A clear tendency was observed among the chimpanzees in Budongo Forest, Uganda, to feed on foods with high sugar content, while tannin content did not affect food choice (Reynolds *et al.* 1998). This latter finding contradicts the observation made by Tutin *et al.* (1991a).

When investigating two different *Ficus* species in Budongo Forest these authors found a significantly higher total sugar content (glucose, fructose, sucrose) and lower tannin content in the pulp compared to the seeds (Reynolds *et al.* 1998). *Ficus vallis-choudae*, has a three times higher tannin content than *F. sansibarica*, and is not eaten as often as *F. sansibarica* (Reynolds *et al.* 1998.)

Newton-Fisher (1999) observed the fig-eating behaviour of chimpanzees in Sonso, Budongo Forest, Uganda. He found that figs were eaten in most or all months of the year and thus considers them to be staple food for chimpanzees since they are so commonly consumed.

Terrestrial herbaceous food

Wrangham *et al.* (1991) distinguish four different plant food categories in the diet of chimpanzees in Kibale Forest, Uganda: (1) non-fig tree fruits, (2) fig tree fruits, (3) herbaceous piths, and (4) terrestrial leaves. The authors observed that chimpanzees eat piths primarily from herbaceous stems in the ground layer and they thus investigated the use of terrestrial fibrous or herbaceous food (THF) by unprovisioned chimpanzees (Wrangham *et al.* 1991). The authors conclude that pith, in time of food scarcity, is an important source of energy for these chimpanzees and thus classify THF as an important fallback food for the chimpanzee community in Kibale Forest (Wrangham *et al.* 1991).

In a second study Wrangham *et al.* (1993b) found a positive correlation between rainfall and pith intake by chimpanzees and baboons in Kibale Forest. They furthermore discovered that a thicker ground cover with THF appears in areas of the forest where (more) logging occurred. However, THF stem density is not positively correlated with the biomass density of edible food and can therefore not be used for predictions (Wrangham *et al.* 1991). The authors conclude that a thicker undergrowth, as the result of selective logging, does not necessarily mean an increase in THF and thus in high food density for apes (Wrangham *et al.* 1991).

Chapman *et al.* (1994) report that chimpanzees spend about 11.8% of their feeding time consuming THF. While doing so, their party sizes are smaller than when feeding in a fruiting-tree patch in the forest (Malenky *et al.* 1994).

Geophagy

According to Hladik (1977) geophagy is a common habit in chimpanzees. Chimpanzees in Gabon and at Gombe, Tanzania, were seen to ingest earth in pieces of about 10 to 20 g up to twice daily. Most of the earth ingested had been moduled by insects beforehand. Especially the cylindric constructions ("chimneys") which are commonly built by Homoptera larvae of the species *Muansa clypealis* were frequently eaten by all members of the observed chimpanzee groups (Hladik 1977). The mineral content of the earth is generally lower than that of common chimpanzee food plants and does not seem to contribute significantly to the mineral nutrition of the chimpanzees. The most likely function of eating clay and other phyllitous material is to act as an absorbent for certain components of the stomach content such as tannins (Hladik 1977, Goodall 1986).

Mahaney *et al.* (1997) examined soil samples eaten by chimpanzees in Kibale Forest, Uganda. They found that the well weathered soils that were ingested had been formed in very fine-grained volcanic deposits (tuffs) and contained an abundance of metahalloysite. This substance is mineralogically and chemically similar to the pharmaceutical Kaopectate™ that alleviates diarrhoea (Mahaney *et al.* 1997). Mahaney *et al.* (1997) thus postulate that chimpanzees ingest soil in the Kibale Forest as a form of treatment for diarrhoea. The only other mineral prominent in these soil samples in any quantity to affect dietary or nutritional intake was iron (Mahaney *et al.* 1997).

Zoopharmacognosy

The observation that chimpanzees consume certain food stuff for therapeutic reasons has opened a new avenue of research called *zoopharmacognosy* (Nishida 1994).

Apart from the ingestion of metahalloysite (Mahaney *et al.* 1997) chimpanzees have been observed to ingest leaves of the genera *Vernonia* and *Aspilia* (Hladik 1977, Wrangham 1977, Wrangham & Nishida 1983, McGrew 1985, Nishida 1994). While a chemical analysis of *Vernonia* leaves showed compounds that are likely to be effective if ingested, an identical analysis for *Aspilia* leaves remained inconclusive (Nishida 1994).

Wrangham & Nishida (1983) describe how chimpanzees mainly consume these leaves early in the morning in contrast to most other foods that are eaten throughout the day. The chimpanzees do not chew these leaves, but one by one slowly suck young leaves in bouts of on average 15 min. The authors suggest that the active ingredient might be a stimulant. Since these leaves are consumed early in the morning they have a layer of moisture on their surface which might contain this ingredient in a soluble form as well as in a pharmacologically active concentration. Furthermore, *Aspilia* leaves are known to be used medicinally by indigenous African people (Wrangham 1977, Wrangham & Nishida 1983, McGrew 1985).

Provisioning

In a number of chimpanzee study sites the provisioning of food, i.e. bananas, has been used to facilitate habituation of wild chimpanzees or to replenish the diet of released chimpanzees (Hladik 1973, 1974, Wrangham 1977, Baldwin *et al.* 1982, Goodall 1986).

Wrangham (1974) observed how the reduction of provisioned food for the chimpanzees in Gombe, Tanzania, increased chimpanzee aggregation size at the feeding site and increased aggression between the chimpanzees waiting for and feeding on the bananas as well as between chimpanzees and baboons also present at the feeding station. The author concludes that this increased aggression might be partly responsible for the fact that chimpanzees hunt and feed on baboons at Gombe (Wrangham 1974).

Furthermore, Wrangham (1974) suggests that the provisioning of food could also affect the area used and the size of the observed chimpanzee population at Gombe. A view that is also supported by Baldwin *et al.* (1982) who believe that the provisioning of food artificially decreases the size of the foraging area used by chimpanzees and leads to overestimated density estimates for chimpanzee populations at such study sites.

Feeding techniques

Nishida & Uehara (1983) summarize the feeding techniques of chimpanzees as follows:

Leaves:

Chimpanzees hold the leafy branch with one hand and strip tiny leaves off with the mouth in a stroke of head movement, or pull them through with fingers and put them into the mouth.

Blossoms:

Blossoms are usually eaten in a similar way as the leaves. For some species chimpanzees break off and hold the flowering branch with one hand and put each blossom into the mouth.

Fruits & Seeds:

Fruits and seeds are mainly taken in the tree. However, for some species chimpanzees prefer to eat fallen fruits, rather than intact ones, these are mostly dry fruit types with sticky pulp available in the dry season.

Some adults remain on the ground picking up and feeding from the fruit-laden branches which are inadvertently discarded by conspecifics climbing on the tree. Chimpanzees usually feed on seeds, pulp and fruit-skin from immature fruits, and only seeds from mature fruits of a few species. Hard-shelled fruit are bitten open with incisors.

Pith:

Herbs of Poaceae and Zingiberaceae are eaten quite reqularly throughout the year. Usually pith of lower parts of immature grass and mature zinger stems are eaten.

Bark:

Outer and inner bark of some species are consumed.

Wood:

Though rarely, chimpanzees earnestly feed on (sometimes lick on) live or dry wood of particular trees. Some of the dry trees are regularly visited by chimpanzees and huge "caves" are thus formed.

Resin:

Resin is available only in small quantities. Usually a chimpanzee stands bipedally on the ground and picks off a small piece of resin.

Root:

A few species of woody roots which emerge on the ground are cut off with incisors and chewed.

Feeding culture

Chimpanzees select their food items mainly according to availability. Interestingly, however, different chimpanzee communities show differences in food choice: some food species, though equally available to both communities are cherished by the one but ignored by the other (Goodall 1986).

There are a number of examples supporting this statement. For example oil-nut palms (*Elais guineensis*) grow at Mahale and at Gombe. While Mahale chimpanzees have never been seen to feed on any part of this plant the chimpanzees at Gombe feed on the fruits, pith, dried flower stems, and dried or rotten wood fibres of oil-nut palms (Nishida *et al.* 1983, Goodall 1986). Furthermore, 16 different foods from nine different plant species, which are present in Mahale and Gombe, are eaten regularly by the Mahale chimpanzees but have not been seen eaten by chimpanzees at Gombe at all or only very seldom (Nishida *et al.* 1983, Goodall 1986). The authors relate these differences in feeding techniques and food choices to different local traditions in the two chimpanzee populations (Nishida *et al.* 1983, Goodall 1986). Table 4.6 gives examples of plants species and fruit eaten by chimpanzees at different study sites.

Table 4.6: *Plant species and fruits eaten by chimpanzees at different study sites*

Plant Family	Plant species	Source & Study Site*
Anacardiaceae	*Pseudospondia microcarpa*	1,2,3
	Lannea velutina	1
Burseraceae	*Canarium schweinfurthii*	2
Caesalpiniaceae	*Cassia* sp.	1
Commelinaceae	*Cyanotis lanata*	1
Euphorbiaceae	*Alchornea cordifolia*	2
Mimosaceae	*Albizia zygia*	2
Moraceae	*Ficus exasperata*	2,3
	Ficus gnaphalocarpa	1,2
	Ficus vallis-choudae	1,3
Ochnaceae	*Lophira alata*	1
Papillionaceae	*Pterocarpus* sp.	2,3
Rubiaceae	*Nauclea latifolia*	1,2
Zingiberaceae	*Aframomum* spp.	2,3

* 1 = Mount Assirik, Senegal, McGrew *et al.* 1988.
2 = Bossou, Equatorial Guinea, Sugiyama & Koman 1987.
3 = Mahale Mountains, Tanzania, Matsumoto-Oda & Hayashi 1999.

Nishida *et al.* (1983) define *culture* as a manner by which animals select one of alternatives. The cultural differences observed in the diet of these non-human primates might originate largely from subtle differences in the environment. Furthermore, a confounding factor in the interpretation of this behaviour might be a difference in the quality of food types, e.g. intraspecific variation in plant chemistry (Nishida *et al.* 1983, Goodall 1986).

It seems that the age class most likely to introduce new feeding habits into a chimpanzee community are the youngsters: they still like to explore and try out different food items, while adult chimpanzees are usually more conservative in their feeding habits (Nishida *et al.* 1983, Goodall 1986).

Chimpanzees as seed dispersers

"Plants of humid tropics depend upon animals for the dispersal of their seeds and fruit is an important food item for many tropical animals" (Estrada & Coates-Estrada 1986). This statement indicates a symbiosis between the tropical rain forest habitat and its frugivorous inhabitants. This mutualism will be elaborated in the following section.

Basic principles of seed dispersal

Hladik & Hladik (1967) distinguish three ways of seed dispersal by trees, namely by water, by wind - which is rare in tropical forests (Janzen 1970) - and by animals. For the latter they define three mechanisms of seed dispersal (Hladik & Hladik 1967):

epizoochory:	a passive transport of seed, e.g. in the fur
synzoochory:	an active transport, e.g. storage of seeds by ants or squirrels
endozoochory:	transport after ingestion, if the seeds which are eventually excreted in the faeces retain their ability to germinate.

Gautier-Hion *et al.* (1985, 1993) divide the "consumer effects on seeds" into three different categories. In their comparison of two African monkeys they define *seed dispersers* as monkeys who eat only the pulp or the aril of seeds and disperse the seeds by epi- or synzoochory. *Predators* are those monkeys who destroy seeds by eating them, and monkeys are regarded as *neutral consumers* when they simply discard the intact seed under the tree where they forage for fruit. However, all seed predators also act as seed dispersers, either for different kinds of seeds or for a certain percentages of the species they prey on (Janzen 1970, Gautier-Hion *et al.* 1985).

Germination success of dispersed seeds

When evaluating the dispersal ability of whole seeds dispersed by endozoochory the main criterion is that the majority of excreted seeds retains its ability to germinate (Hladik & Hladik 1967, Janzen 1969, Takasaki 1983). The germination success of endozoochorous seed is influenced differentially by the passage of the seeds through the gastro-intestinal (GI) tract of seed dispersing animals (Chapman & Chapman 1996): Hladik & Hladik (1967) state a generally favourable influence on the germination of seeds after ingestion and excretion by several primate species in Gabon. The authors also observed a positive effect on seedling growth of *Cercopithecus*-dispersed seeds. These seeds generally germinated earlier and the resulting seedlings grew faster and larger than their controls (Hladik & Hladik 1967).

Takasaki (1983) and Takasaki & Uehara (1984) investigated the fate of chimpanzee (*Pan troglodytes schweinfurthii*)-dispersed seeds in the Mahale Mountains, western Tanzania. The authors collected seeds from chimpanzee faecal samples (faecal seeds) and from ripe fruits fallen to the ground (control) for three tree species and found significantly greater germination for "faecal seeds" than "control seeds". Because of their short study period and other uncertainties Takasaki (1983) and Takasaki & Uehara (1984) simply conclude that seeds of these three tree species "do not lose, and possibly increase germinability through ingestion by chimpanzees" and that "chimpanzees could be their efficient disseminators" (Takasaki 1983, Takasaki & Uehara 1984).

Idani (1986) investigated seed dispersal by pygmy chimpanzees (*Pan paniscus*) at Wamba, Zaïre (now: Democratic Republic of Congo). He used faecal seeds from two bonobo study groups (65 individuals and 80 - 100 individuals) and control seeds from ripe fruits. He found that a number of species showed a significantly higher germination rate for faecal seeds than for control seeds, while other species had a higher germination rate in control seeds than in faecal seeds (Idani 1986).

Wrangham *et al.* (1994a) investigated seed dispersal by forest chimpanzees (*Pan troglodytes*) in the Kibale Forest Reserve, Western Uganda. In the ten fruiting tree species that the authors examined they found that faecal seeds of all species had a higher probability of germinating than control seeds. Control seeds of only two species showed any germination at all (*Tabernaemontana* species and *Ficus* species). Furthermore, the time to germination of faecal seeds was shorter than that of control seeds (Wrangham *et al.* 1994a).

Therefore, seed dispersal by endozoochory in many cases has a positive effect on the onset, speed and success of germination. In some cases it has no effect on the excreted seeds' performance and occasionally it might even prevent or reduce the germination success.

The significance of seed dispersal

Janzen (1969) stresses the "escape component" of seed dispersal. Dispersal can be achieved by gravity, water, wind, but in forests is most effectively achieved by vertebrates. The aim of seed dispersal in this case is to enable the "escape of the offspring of a large sessile organism away from predators and parasites" (Janzen 1969). Janzen (1970) also introduces the concept of *distance-responsive* and *density-responsive predators* for seeds dispersed in close vicinity to the parent tree. While the former predators are mainly parasites on adult trees, they act as predators of the young seedlings (Janzen 1970). Predation by the latter though, is mainly a function of the ecological distance between a certain juvenile and other juveniles of the same species (Janzen 1970).

Augsburger (1984a+b) tested the *escape hypothesis*, i.e. the hypothesis that dispersal increases the offspring's probability to escape density- and/or distant dependent mortality that might be high near the parent tree. She furthermore established and tested the *colonization hypothesis* which states an increased probability that some offspring might end up in a disturbed site as a result of dispersal. It is assumed that such a disturbed site, e.g. a light-gap in a forest, enhances seedling establishment and survival and that the probability for the occurrence of a gap within the dispersal range of a parent tree increases with increasing dispersal distance (Augsburger 1984a+b). She concludes that pathogen activity greatly influenced the location where seeds and seedlings survived and that the survival of offspring to the seedling stage is expected to occur away from the parent tree. Her findings furthermore suggest that the latter is true for distance- and/or density-dependent mortality of seeds of shade-tolerant tree species (escape hypothesis) also in shaded conditions, while in light-gaps (colonization hypothesis) it is valid for all of the tree species studied by her in the semi-deciduous lowland forest on Barro Colorado Island, Panama (Augsburger 1984a+b).

Schupp (1988b) found exactly the opposite in his study of seed and early seedling survival also at Barro Colorado Island, Panama. In his study, seed dispersal to tree fall gaps had no effect on seed survival and actually reduced seedling survival. He suggests that the tangle of limbs, lianas and litter in a tree fall gap offers small terrestrial rodents, known seed and seedling predators, a refuge from their own predators. Their impact on seed and seedling predation for a shade-tolerant tree species would thus be greater in tree fall gaps than in the forest under story (Schupp 1988b). Schupp & Frost (1989) made similar observations in Costa Rica. The results of their study led them to realise that the association between seed dispersal and seed survival is habitat-dependent (Schupp & Frost 1989). Howe (1989) summarizes this effect in a broad sense by saying that "fruit-eating animals deposit viable seeds in patterns that determine the conditions under which seedlings live or die". The post-dispersal fate of a seed indicates whether the fitness of the plant has been raised or lowered through dispersal of the seed by the frugivore (Estrada & Coates-Estrada 1986).

Martinéz-Ramos & Alvarez-Buylla (1986) distinguish two different dispersal syndromes depending on the ecological importance of different plant species. In their study site of a wet tropical forest at Los Tuxtlas, Mexico, they observed the recruitment of (1) pioneer (shade-intolerant) and (2) persistent (shade-tolerant) species, the latter of which they divide into upper-canopy tree species and under storey tree species. They found that pioneer trees have the greatest chance to reach maturity in large forest gaps of a size > 100 m^2 (Martinéz-Ramos & Alvarez-Buylla 1986). Both persistent tree types show a spatially more restricted seed dispersal. Their chance of recruitment to maturity is greatest in smaller tree fall gaps of > 20 m^2. These gaps occur about seven times more often than the larger forest gaps and thus lead to a recruitment wave which is different in time from the one of pioneer tree species (Martinez-Ramos & Alvarez-Buylla 1986).

The authors also formulate a general guideline for the relationship between seed dispersal, gap dependence and fruiting behaviour of tropical trees in that they state that the short-lived and fast growing as well as strongly heliophilic pioneer trees germinate only in forest gaps, have rapidly growing seedlings that mature at an early age and produce fruits which bear a large number of seeds < 5 mm long. Thus, these seeds can easily be dispersed by a number of animals of varying size (*opportunists*). Persistent tree species, on the contrary, generally produce relatively small fruits containing large seeds > 5 mm long in relatively short reproductive periods of ≤ 3 months (Martinéz-Ramos & Alvarez-Buylla 1986). The authors state furthermore that the recruitment of Upper canopy trees depends more on the frequency of gap formation than on the actual gap size. (Martinéz-Ramos & Alvarez-Buylla 1986).

For both persistent tree species the authors state that survival and growth rates of pre-reproductive individuals may be increased in gaps (Martinéz-Ramos & Alvarez-Buylla 1986). Since the frequency of tree fall incidences and thus of gap formation increases during rainfall this climatic factor also plays a role in determining population size and structure of gap-dependent tree species (Martinéz-Ramos & Alvarez-Buylla 1986). Gap formation is also dependent on the time when an area has last suffered a tree fall: the lowest probability for a gap to occur is in areas younger than ten years or older than 60 years. Whereas the maximum probability for gap formation - through rainfall - exists in areas where the trees are between 30 - 45 years old. This corresponds with the maximum age of the most abundant pioneer tree species (Martinéz-Ramos & Alvarez-Buylla 1986).

In summary, for both, pioneer and persistent species the authors conclude that the dispersal pattern found in the adult population is a result of (1) pre-reproductive thinning through mortality due to unfavourable conditions and (2) the spatial pattern of gaps. Thus, the population size of plants is mainly controlled by animal-mediated dispersal patterns and the within and between years, rainfall-induced, tree fall patterns (Martinéz-Ramos & Alvarez-Buylla 1986).

Schupp (1993) concentrates on the animal-mediated aspect of plant recruitment and defines *disperser effectiveness* as a way of ranking the usefulness of an animal disperser for the survival of a certain plant species. He defines *disperser effectiveness* as the contribution a disperser makes to the future reproduction of a plant (Schupp 1993). The two components of disperser effectiveness are (1) the quantity of seed dispersed and (2) the quality of dispersal provided to each seed, resulting in the simple equation of *Effectiveness = (Quantity) x (Quality)* (Schupp 1993). Both, quantity and quality are determined by two factors. The quantity of seed dispersed depends (1) on the number of times a disperser visits a plant and (2) on the number of seeds it disperses subsequent to each visit (Schupp 1993). While the quality of seed dispersal depends (1) on the kind of treatment the seed receives in the mouth and in the gut of a disperser and (2) on the quality of seed disposition, i.e. the probability that the seed will survive and become an adult (Schupp 1993). Schupp (1993) concludes that further studies of effectiveness are necessary and should mainly focus on the consequences of dispersal by different disperser species, which should combine the studies of behaviour, morphology and physiology of disperser species with studies of the demography of plants (Schupp 1993).

Who disperses seeds?

According to White (1994a) frugivores are the dominant group of vertebrates in the forest, while mammals (flying and non-flying) are the most abundant of these frugivores and constitute together with various species of birds an array of dispersers that provides considerable mobility to the seeds they ingest (Martinéz-Ramos & Alvarez-Buylla 1986).

Gautier-Hion *et al.* (1985) distinguish two main classes of seed dispersers, based on the kind of fruits they mainly forage. They determined the existence of a *bird-monkey syndrome* (Coates-Estrada *et al.* 1993) and a *ruminant-rodent syndrome*, combining taxa that feed mainly on a certain type of fruit. They observed a number of fruit consumers, but of those only classified birds and monkeys as true dispersers, while all other species are classified as mainly *seed predators* (Gautier-Hion *et al.* 1985).

Terborgh (1986) calculated that those mammals and birds that mainly feed on the reproductive parts of plants make up a biomass of about 1 400 kg/km^2 of mammals and 160 kg/km^2 of birds in an undisturbed Amazonian locality in south eastern Peru. In their order of importance they could be ranked as primates, rodents and peccaries for the mammals and as cracids, tinamous and toucans for the birds. Furthermore, the group could be divided into *pulp-eaters* which feed mainly in trees and make up two thirds of the biomass, and into *seed predators* which feed mainly on the ground and make up the remaining one third of the biomass (Terborgh 1986). Of the mammalian biomass about 80% is made up by frugivores. And in this ecosystem over half of this biomass is contained in the population of only six species, the two most prominent being monkeys (Terborgh 1986). The major difference between New World and Old World monkeys lies in the action of folivory, since nearly all Old World monkeys include > 10% leaves in their diets (Terborgh 1986). The author describes the importance of primates in tropical forest ecosystems worldwide as follows: "primates occupy a wide range of trophic roles and contribute more to the total biomass of many tropical forest ecosystems than any other taxonomic group" (Terborgh 1986). The validity of this statement is underlined by the number of studies on different species of New and Old World primates and their role as frugivorous seed dispersers (Table 4.7).

Table 4.7: *Primate species and study sites on the trophic role of primates in tropical forest ecosystems*

Species	Locality	Reference
Howling monkey	Mexico	1
Howling monkey & Spider monkey	Peru	2
Spider monkey, Howling monkey & Cebus monkey	Costa Rica	3
Northern bearded saki	Suriname	4
Vervet monkey & Bush baby	Gabon	5
Vervet monkey	Kenya, Uganda & Tanzania	6
Bonobo	Zaïre	7
Vervet monkey	Zaïre	8
Western lowland gorilla	Gabon	9
Western lowland gorilla	Gabon	10

1	Estrada & Coates-Estrada 1986
2	Terborgh 1986
3	Chapman 1989
4	Van Roosmalen *et al.* 1988
5	Hladik & Hladik 1967
6	Struhsaker 1967
7	Idani 1986
8	Gautier-Hion *et al.* 1993
9	Tutin *et al.* 1991a
10	Voysey *et al.* 1999a+b

Concerning chimpanzees as seed dispersers Takasaki (1983) and Takasaki & Uehara (1984) made some observations on the fate of seeds ingested and excreted by *Pan troglodytes schweinfurthii* in the Kasoje area of the Mahale Mountains in western Tanzania. For the majority of the plants studied, viable seeds were passed by the chimpanzees and seed germinability was often increased following their passage through a chimpanzee's gastro-intestinal tract (Takasaki 1983, Takasaki & Uehara 1984). Also important is the fact that many of the fruit plants disseminated by chimpanzees are those utilized by chimpanzees (Takasaki 1983, Takasaki & Uehara 1984). Chimpanzees are efficient disseminators for those seeds and seem to hold a key position in influencing the structure of regional vegetation, especially also since they have a large ranging area and thus defecate part of the seeds far away from the parent plant (Takasaki 1983, Takasaki & Uehara 1984).

Idani (1986) came to a similar conclusion for bonobos and reported on their important role regarding the succession of the vegetation and thus the vegetation structure of the secondary forest as a whole. He assumes that bonobos are probably the most important seed dispersers in his study area (Idani 1986).

In the Kibale Forest Reserve in Western Uganda, Wrangham *et al.* (1994a) found that 98.5% of all chimpanzee faecal samples investigated contained seeds and that the most prominent of those were fig seeds. They observed that in general the passage of seeds through a chimpanzee's gastro-intestinal tract increased the percentage germination and reduced the time to germination for the ten tree species investigated. The authors conclude that these Kibale chimpanzees play a more significant role in the primary dispersal of seeds in this Forest Reserve than their low numbers and biomass might imply, and thus underline the potential importance of great apes, in general, for the maintenance and regeneration of tropical forests (Wrangham *et al.* 1994a).

How plants attract animal dispersers

Janson (1983) distinguished between two fruit types: (a) protected fruits, where the ripe pulp is protected by a husk, e.g. oranges, and (b) unprotected fruits, where the flexible skin is < 10% of external fruit dimension, e.g. cherries (Janson 1983). He found statistically significant correlations between colour and fruit type as well as between fruit size and fruit type, because unprotected fruits are significantly smaller than protected fruits (Janson 1983). *Type A fruits* were therefore defined as: small red, black, white, blue, or mixed-colour fruits without a husk, and *Type B fruits* as: large, orange, yellow, brown, or green fruits with a husk (Janson

1983).

In their study on fruit characters as a basis of fruit choice and seed dispersal in a lowland evergreen forest on the M'passa plateau, Makokou, Gabon, Gautier-Hion *et al.* (1985) established a different classification for fruiting plants and their frugivores. They chose seven parameters to classify the different fruits, namely (1) colour, (2) protective coat, (3) type of edible tissue (by decreasing water content and increasing fibre content), (4) seed protection, (5) seed number, (6) fruit, and (7) seed mass. By means of multivariate analysis the following seven fruit syndromes were distinguished: (1) *bird fruits*: small, red or purple, unprotected, often dehiscent with arillate seeds; (2) *small rodents fruits*: variable, only tendency towards small size; (3) *squirrel fruits*: dull-coloured, dry fibrous flesh and few seeds, mass unimportant; (4) *large rodent fruits*: fibrous, large, few and well-protected seeds; (5) *ruminant fruits*: heavy, rarely red or purple but mainly brown and yellow and fleshy; (6) *elephant fruits*: large; and (7) *monkey fruits*: brightly coloured, mass from 5 to 50 g, either dehiscent with arillate seeds or succulent fleshy fruits (Gautier-Hion *et al.* 1985). The authors classify these fruit-eaters as: (1) *dispersers*, animals dispersing intact seeds by endo- or synzoochory; (2) *neutral consumers*, animals leaving the seeds intact under the parent tree, and (3) *predators*, animals destroying the seeds (Gautier-Hion *et al.* 1985). According to these categories the authors classify only birds and monkeys as true seed dispersers, while all the other consumers are classified mainly as seed *predators*, only occasionally and accidentally functioning as seed *dispersers* or *neutral consumers* for some of the fruits they eat (Gautier-Hion *et al.* 1985).

Howe (1993) looks at the paradigm on "specialization versus generalisation", i.e. the view that some of the tropical trees only produce fruits adapted for use by a small number of species that ensure reliable seed dispersion, e.g. *Cola lizae* and western lowland gorillas (Tutin *et al.* 1991b), while other tree species offer superabundant fruits of lower nutritional value to attract a high number of *opportunists*, who collectively disperse seeds reliable as well, e.g. the potential use of *Type A fruits* by a large number of frugivores from different taxa (Gautier-Hion *et al.* 1985). Howe (1993) argues that there is neither strong evidence for nor against the correctness of this paradigm, especially since not many studies have yet looked into the relative importance of different dispersal agents for seedling recruitment, i.e. which disperser species is the most successful to ensure the long term survival of a certain tropical tree species (Howe 1993).

Herrera (1986) doubts the short-term coevolutionary development of plants and their dispersers. He bases his argument on the fact that often predictions on interactions between vertebrate-dispersed plants and their seed vectors have not been verified by findings in the field, but that those findings revealed patterns that departed significantly from the predictions made. Herrera (1986) distinguishes between *selective agents = non-mutualistic frugivores,* and *non-selective agents = the fruiting environment*. For the former he states an important influence especially for invertebrates and pathogens, since these might often cause up to 60% of damaged fruits on an individual tree. He furthermore mentions that the "*potential* for an interaction between fleshy fruits and damaging invertebrates and pathogens is older than any observed interaction with current legitimate dispersers" (Herrera 1986).

In conclusion, one can say foremost that the knowledge and perception about how plants attract seed dispersers is partly still immature and partly contradictory. It seems that fruiting plants have developed certain characteristics, such as colour, size and morphology, to attract a particular group of disperser species. Whereby some plant species attract a large variety of frugivores, even from different taxa, while others have a more restricted disperser spectrum. The fact that a variety of non-mutualistic frugivores and changing environmental factors also influence the future fate of a fruiting plant's offspring make predictions about plant-disperser mutualism and the resulting distribution in space and time of a particular tree species very difficult, if not impossible.

Predispersal seed predation

"Seed predators are those animals that eat and kill seeds" (Janzen 1970). Arboreal seed predation is a specialised form of seed predation and is a relatively widespread primate dietary strategy found among higher primate species in a variety of forest types on three continents" (Van Roosmalen *et al.* 1988).

Even though the main primate seed predator in the Old World is the black colobus monkey (*Colobus satanas*) from Cameroon (Van Roosmalen *et al.* 1988), Tutin *et al.* (1996) report also about predispersal seed predation by chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) on *Diospyros mannii* in the Lopé Reserve in Gabon. Crunched fragments of seeds were found in chimpanzee and gorilla faeces, while some whole seeds were found only in gorilla faeces, indicating a potential role as *seed disperser* not only as *seed predato*r for this frugivore on *Diospyros mannii* (Tutin *et al.* 1996). Great apes can thus function as *seed dispersers* as well as *seed predators* for the same and different tree species in the same tropical forest environment.

Van Roosmalen *et al.* (1988) observed that many unripe seeds and fruits contain a number of secondary compounds, e.g. tannins, to at least partly prevent predation of unripe seeds. The concentration of these secondary compounds reduces while the ripening of the fruit and seed progresses, thus ensuring palatability of ripe fruit for potential seed dispersers. *Diospyros mannii* uses an outer protection of strong and irritant hair to prevent the predation of its unripe seeds to increase the chance for the survival of its offspring (Tutin *et al.* 1996). Therefore, plants often develop more or less successful defence mechanisms against predispersal predation to ensure a sufficient survival of viable offspring and thus a long term survival of their species.

This finding might underline Herrera's (1986) argument that very often it is the influence of *non-mutualistic frugivores* which is of evolutionary importance for the development of certain plant and fruit characteristics.

Postdispersal seed predation

"The vertebrate-dispersed seed that has survived the voyage through its dispersal agent is usually subject to postdispersal seed predation" (Janzen 1982). This form of seed predation has a major influence on the survival of a tree population (Willson & Whelan 1990).

Janzen (1986) states that the *initial seed shadow* of an individual tree is dependent on the species of large mammal that produces it. This shadow is differentially thinned and trimmed by post-dispersal seed predation into a *final seed shadow*. After germination of the seeds an *initial seedling shadow* is created which might again be thinned and trimmed into a *final seedling shadow* (Janzen 1982, 1986). This process is dependent on what kind of seeds are being dispersed by what kind of animal and where. Eventually, all these processes determine the probability of appearance of a new adult tree at a certain location, since this successful appearance is dependent on the number and the temporal distribution of seedling attempts made at a given site (Janzen 1982, 1986).

Schupp (1988a) looked at factors that influence post-dispersal seed survival of the subcanopy tree *Faramea occidentalis* on Barro Colorado Island, Panama. He observed that for *Faramea occidentalis* the survival of seeds was significantly lower in tree fall gaps than in the forest under story. Furthermore, the size of the nearest adult had a complex effect on seed survival: for seeds directly beneath a parent tree survival decreased with increasing size of the parent tree; while for seeds away from a parent tree the size of the conspecific adult had no influence on seed survival (Schupp 1988a). Schupp (1988a) also found that the distance away from an adult conspecific did not directly influence seed survival; neither did the quantity of leaf litter present, nor the proximity to a tree trunk or log. When Schupp (1988a) compared the data for all four years of his study he found that the above stated pattern repeated itself from year to year, but the location of surviving seeds changed between transects. A transect with a high seed survival in one year did not necessarily show high seed survival also in the following year. It was thus not possible to make predictions about seed survival in a given area for a given year (Schupp 1988a).

Willson & Whelan (1990) evaluated postdispersal seed survival in two habitats (wooded and non-wooded) over three years in Champaign and Vermillion counties, east-central Illinois. The authors found that large depots of seeds were more likely to be discovered by seed predators than small seed depots. Nevertheless, the probability of seed survival was still higher in the larger depots (Willson & Whelan 1990). A finding that is contradictory to the one reported by Janzen (1982, 1986) for guanacaste seeds. Also Willson & Whelan (1990) realized that the spatial and temporal pattern of seed survival is generally unpredictable.

Chapman & Chapman (1996) studied seed and seedling survival of six different tree species over three years in the Kibale National Park, western Uganda. The authors found that, for both, dispersed and non-dispersed seeds there was a bimodal pattern of disappearance that varied between species and locations (Chapman & Chapman 1996). In another study on the fate of dispersed seed in Santa Rosa National Park, Costa Rica, Chapman (1989) found that 51.8% of all seeds disappeared from primate *pseudodefecations* within five days after having been placed in the forest. The seeds were either killed or removed by secondary seed dispersers while the rate of removal varied depending on the seed species (Chapman 1989).

In summary, postdispersal seed predation seems to be an ever changing interaction between the environment (e.g. moonlight patterns, rainfall), the seed predator (e.g. ranging pattern or predator density), the fruiting tree species (e.g. seed size or seed density), and the dispersal agent (e.g. amount of dung, seed density in the dung, dung disperser species).

From the above mentioned studies no definite pattern emerges that would constitute a guideline for the reliable prediction of population dynamics of certain tropical fruiting tree species which are subject to seed dispersal and/or (pre- and/or postdispersal) seed predation.

Seedling survival

"Adult plant dispersion results from an interaction of seed distribution and seed and seedling survival...The varying probabilities of survival for different seed and seedling species, coupled with varying initial seed densities, promote a virtually infinite array of likely relationships between seed and adult distributions" (Howe 1989).

Augspurger (1984b) looked at the light requirements of seedlings from 18 wind-dispersed neotropical tree species on Barro Colorado Island, Panama. The survival in the sun was positively related with survival in the shade, i.e. seedlings with a high mortality rate in the sun also showed a high mortality rate in the shade (Augspurger 1984b). Depending on their light requirements, seedling survival in the shade fitted a negative exponential model thus indicating that a species-specific constant proportion of individuals die during each time period (Augspurger 1984b). Furthermore, shade tolerance and the proportion of seedlings dying from pathogens and disease in the shade were negatively related, with the lowest disease-induced mortality in the most shade tolerant seedling species (Augspurger 1984b). Augspurger (1984b) concluded that for the seeds of the studied tree species dispersal in space is an important strategy to encounter a more favourable light regime. Since the light requirements of the seedlings changed over time for the different species, the encountered light regime also has implications for the size-age structure of the different tree species. While shade-intolerant seeds often build seed banks and stay dormant until a light gap opens, therefore while some seedlings are able to show restricted growth also in the forest under story, other species have to rely on favourable light conditions in light gaps to be able to germinate and grow (Augspurger 1984b).

In a second study on dispersal and light requirements of seeds from tropical trees in Barro Colorado Island, Panama, Augspurger (1984a) found many of her above stated results replicated. She again found a high mortality among seeds and seedlings due to pathogens under shaded conditions. This mortality was mainly due to fungal infection and for most species was distance-dependant. It was higher close to adult conspecifics than further away from them. Mortality in the shade also varied considerably between species which might again have been due to a difference in shade tolerance (Augspurger 1984a+b).

Augspurger (1984b) also measured the one-year survival for the seedlings of her studied tree species in the sun and in the shade. Augspurger (1984a) concludes from her findings that not only the survival probabilities determine in which location a large amount of seedling recruitment will occur. The number of recruited adults also depends on the original distribution of dispersed and germinated seeds and on the relative survival probabilities of seeds and seedlings at various distances away from their parent trees. Furthermore, seedling distributions might start to vary from the originally seed distributions over time, in case of distance- and/or density-dependent mortality (Augspurger 1984a). This finding might be compared to the seed and seedling shadow thinning and trimming suggested by Janzen (1986).

Popma & Bongers (1988) evaluated the effect of canopy gaps on seedling growth and morphology in the tropical rain forest environment around Los Tuxtlas, Vera Cruz, Mexico. Like Augspurger (1984b), Popma & Bongers (1988) found that all species grew faster and larger in light gaps than in the shade with the effect being even more pronounced in large canopy gaps than in small canopy gaps. Furthermore, dry mass and stem diameter for all species were largest in large canopy gaps and smallest in forest under story (Popma & Bongers 1988). The authors observed that all studied plant species showed a complex growth response. In some aspects they resembled the shade tolerant extreme, in other aspects the shade intolerant extreme (Popma & Bongers 1988). The authors state that it might be possible for a plant to change its growth response during its development in so far that juveniles and saplings might be responding to gaps differently than seedlings do (Popma & Bongers 1988). Popma & Bongers (1988) thus conclude that a differentiation in seedling growth in different forest micro habitats might be the reason for a differentiation in distribution patterns (spatial and temporal) of the plant species involved.

Howe (1989) investigated the demographic effects of deposition patterns on seed and seedling survival. He differentiates between *scatter-dispersed plant species* and *clump-dispersed plant species*. The former are dispersed by small-sized frugivores such as birds or bats. These dispersers regurgitate, defecate or drop seeds singly or in pairs, resulting in the recruitment of isolated individuals (Howe 1989). The latter are dispersed by larger terrestrial or arboreal frugivores who defecate seeds in masses thus producing bouquets of seedlings (Howe 1989). Even though *clump-dispersed* seeds occur in large numbers in close spatial proximity Howe (1989) states that in general only one adult plant emerges from each clump, unless some seeds have been scattered by *secondary dispersal* and consequently also reached maturity.

Even though the author gives several examples to consolidate his hypotheses, he eventually also comes to the disappointingly general conclusion that predictions on seed and seedling survival are hardly possible (Howe 1989).

De Steven & Wright (2002) looked into the recruitment pattern and their population consequences for three canopy tree species over a five-year period on Barro Colorado Island, Panama. All three species were shade-tolerant, animal dispersed and had a relatively rapid germination rate. De Steven & Wright (2002) found that for all three species the annual survival rates increased with plant age and plant size. Thus, recruitment probability increased with plant size, i.e. only a few seedlings survived to become saplings, but a greater percentage of saplings survived to proceed to the next size class (De Steven & Wright 2002). The authors also detected that the three, apparently rather similar species, showed large differences in seedling and sapling recruitment which he concludes to be directional and not stochastic and which were consistent with recently-observed population trends (De Steven & Wright 2002).

Chapman & Chapman (1996) evaluated the germination of seeds from six different tree species in the Kibale Forest Reserve, western Uganda. For seeds placed along transects they found that only six out of 3170 seeds (0.2%) germinated, while none of the seeds placed underneath parent trees germinated (Chapman & Chapman 1996). For seedlings planted along transects the authors found an average mortality of 30% with a range from 9 - 38% between the different species. Mortality rates under conspecifics and along transects varied between species (Chapman & Chapman 1996). Chapman & Chapman (1996) also looked at seedling damage over a 24-month period. They found that > 50% of the leaves of seedlings from different tree species showed insect damage. Depending on tree species, between 0 to 11% of seedlings experienced serious damage due to mammal foraging. The authors found that an increasing level of leaf damage was related with a decrease in growth rate (Chapman & Chapman 1996).

The latter two articles indicate that the survival rate for seeds and seedlings is extremely small and that the number of mature trees that a parent tree produces per fruiting period might often be as little as ≤ 1.

After all - how important are chimpanzees as seed dispersers?

"The chimpanzee, which has a diverse food habit and an extraordinary large ranging area, seems to occupy the key position in influencing the regional vegetation" (Takasaki 1983).

Primates in general play an important role in the tropical forest vegetation on three different continents (Janzen 1970, Terborgh 1986). In their remaining Old World habitats chimpanzees, who are foremost frugivores, excrete a high number of seeds, often from different tree species, nearly every time they defecate (Wrangham *et al.* 1994a+b). Since they naturally mainly disperse the seeds of those plants they use chimpanzees continuously perpetuate their own food resources and thus their survival (Takasaki 1983, Takasaki & Uehara 1984). They select fruits from a large array of tree species with rather broad characteristics of fruit size, colour and morphology (Janson 1983, Gautier-Hion *et al.* 1985). They are to a large extent responsible for the spatial distribution of a large number of tree species in their particular habitat since they travel distances of 1.6 - 4.5 km per day, often through different vegetation types (Nishida 1977 in Takasaki 1983).

Idani (1986) estimates that pygmy chimpanzees disperse > 500 seeds per day and presumably between 1,500 to 2,000 on average. With daily travel distances of between 0.4 to 6.0 km a wide spatial distribution of seeds in more or less favourable habitats is ensured (Idani 1986).

For some of the seeds they eat chimpanzees might also act as *seed predators*. Yet, for most seeds they disperse the passage through a chimpanzee's digestive system increases germinability (Takasaki 1983, Takasaki & Uehara 1984, Idani 1986, Wrangham *et al.* 1994a+b)

Even if numbers of seeds dispersed daily by each individual chimpanzee in his natural habitat do look quite impressive they are put into perspective by the very low final recruitment rate for each seed species per dung pile. Post dispersal seed and seedling predation, a number of environmental factors and pathogens cause a tremendously high mortality among dispersed seeds (Janzen 1970, 1982, 1986, Augspurger 1984a+b, Janzen 1986, Estrada & Coates-Estrada 1986, Popma & Bongers 1988, Schupp 1988a, Chapman 1989, Wrangham *et al.* 1994a+b, Chapman & Chapman 1996, De Steven & Wright 2002).

If one hence declares chimpanzees to be their own tropical forest habitat architects one must not forget that this spatial creativity is dependent and based upon an undisturbed artistic development in an unrestricted natural environment over a long period of time.

CHAPTER 5

MATERIALS AND METHODS

DATA COLLECTION ON NGAMBA ISLAND

To assure an even distribution of the sample plots over the island a stratified random sampling method was used. Data and sample collection inside the fenced-off area was conducted while the adult chimpanzees were inside their night enclosure, i.e. in the morning during the time of the infant walks (between 06:45 and 08:30) and in the evening, after the adult chimpanzees had returned to their night enclosure and before the visibility inside the forest became too low (between 18:.00 and 19:00).

Woody vegetation survey

Selecting sample plots

The circumference of the island was measured using a Global Positioning system (Garmin GPS 12XL Personal Navigator^{TM}; Garmin International, 200 East 151st Street, Olathe, Kansas 66062, U.S.A.) while kayaking around the island as close to the shore as possible. A map of the island was drawn using these GPS coordinates. Subsequently, the coordinates of the highest elevation of the island were determined. This point was then used as centre point for a cross that divided the island in four sections (called "quadrats" for the purpose of this study) of slightly different sizes (Figure 6.2) and constituting the sampling strata. Two sample plots (maximum size: 50 x 50 m) were then placed at random in each of the quadrats. Random numbers were used to determine the south/east (S/E) coordinate pair for the centre point of each sample plot. Wherever possible the centre point of a plot was positioned at the crossing of two man-made tracks. Thus, the four tracks extending from this point could be used to mark the four 25 m-long axes necessary to determine the size of the single sample squares, see 'Sampling method for woody vegetation'.

Sampling method

The woody vegetation was sampled and analysed following the "varying quadrat plot method" described by Coetzee and Gertenbach (1977). This method gives the following results per

(a) species, (b) stem growth form and (c) height class:

1. Canopy regime at different height levels;
2. Total projected canopy cover; and
3. Density.

For this study, the woody vegetation was divided into five categories according to Coetzee and Gertenbach (1977):

1. **"Tree growth form" (B)** - an individual with a single stem.
2. **"Sparse shrub growth form" (Y)** - an individual with 2 - 4 stems.
3. **"Shrub growth form" (S)** - an individual with 5 or more stems.
4. **"Standing dead" (D)** - an upright dead individual with a stem diameter > 100 mm.
5. **"Fallen dead" (L)** - a fallen dead individual with a stem diameter > 100 mm.

In the chosen sample plot area a rectangular cross with four equal arms of 25 m and extending from the determined centre point was created using marking poles placed at 5 m intervals: wooden poles were placed at five-meter intervals along the four directions. If the track system did not lend itself to be used in such a way, the necessary trails were created using a *panga*. For each of the height classes described below a total of four test squares is used to determine the size of the quadrat for that height class. One test square is put into each of the quadrants delimited by the cross. "The test square is the smallest, from the following possibilities that would include a rooted portion of a plant of the relevant height class: **5 m x 5 m**; **10 m x 10 m**; **15 m x 15 m**, **20 m x 20 m** and **25 m x 25 m**. The largest of the four [test] squares determines the quadrat size for the height class to be recorded. The quadrat is namely a square with centre at the centre of the cross and divided by the cross into four quarters, each the size of the largest test square" (Coetzee and Gertenbach 1977) (Figure 5.1). This procedure is repeated for each of the following height classes:

1. < 0.75 m recorded as: **0.5 m**
2. 0.75 m - < 1.50 m recorded as: **1.0 m**
3. 1.50 m - < 2.50 m recorded as: **2.0 m**
4. 2.50 m - < 3.50 m recorded as: **3.0 m**
5. 3.50 m - < 5.50 m recorded as: **4.0 - 5.0 m**
6. > 5.50 m recorded as: **> 6.0 m**

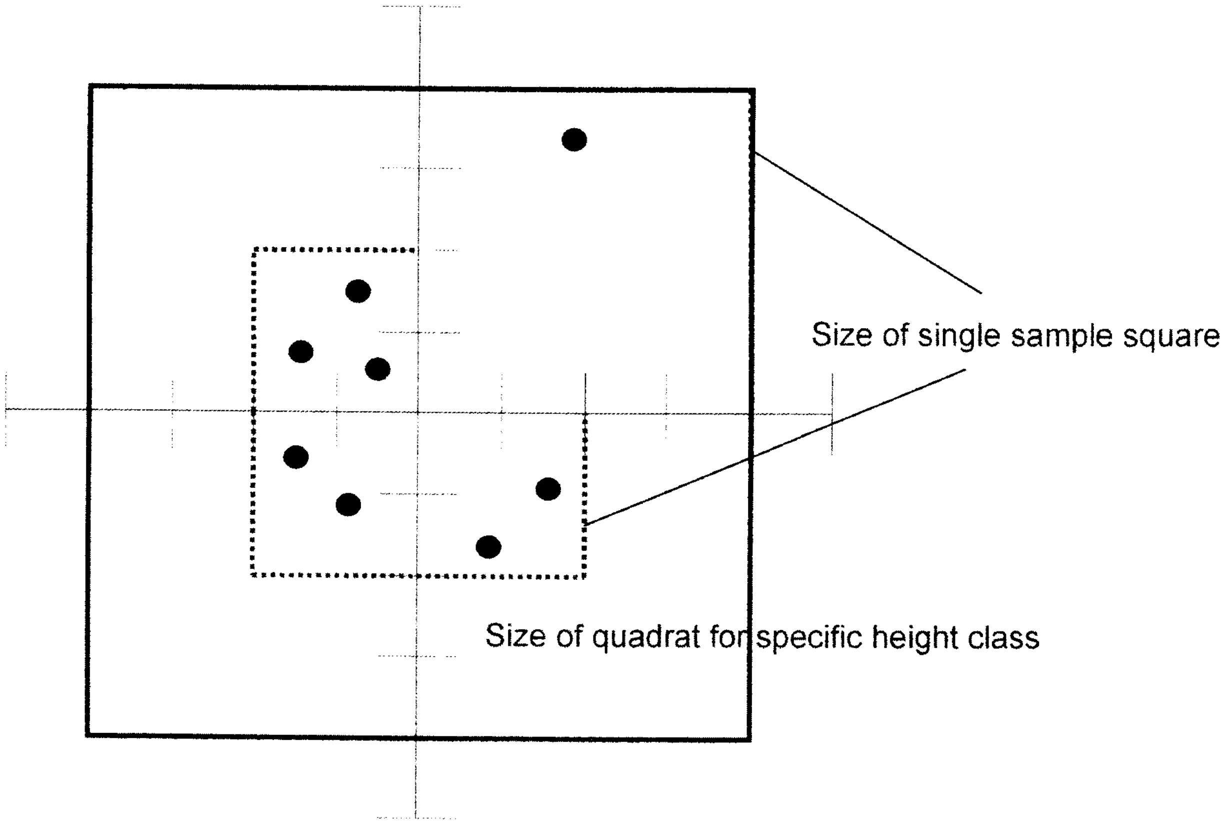

Figure 5.1: Determining quadrat size following the method to analyse woody vegetation structure according to Coetzee and Gertenbach (1977).

Analysis of data

The data thus collected were analysed using the computer programme "Struktuuranalise" available at the Department of Botany at the University of Pretoria. This programme also calculates the Braun-Blanquet cover-abundance value for each species occurring in a plot (Werger 1974):

1. **+** = less than 1% cover
2. **1** = 1- 5% cover
3. **2a** = 6- 12% cover
4. **2b** = 13 - 25% cover
5. **3** = 26 - 50% cover
6. **4** = 51 - 75% cover
7. **5** = 76 - 100% cover

The Braun-Blanquet method estimates the vegetation cover of a given area visually, giving a value for the cover-abundance of every single species present. Since vegetation can be stratified or consist of multiple layers, total cover-abundance values of more than 100% may result (Kent & Coker 1996). "**Cover** is defined as the area of ground within a quadrat which is occupied by the above-ground parts of each species when viewed from above" (Kent & Coker 1996).

Using the Braun-Blanquet values of each species combined with the distribution of species among plant communities the species can then be categorised as either *differential species*, *indifferent species* or *companion species* (Kent & Coker 1996). The *constancy* of a species, i.e. the number of sample plots in which it occurs, determines foremost in which of the before-mentioned categories it will be placed. *Differential species* show medium to low constancy and tend to occur together in a number of sample plots. They can therefore be used to characterise these as a group or plant community (Kent & Coker 1996). *Indifferent species* do not show a definite affinity for any particular plant community (Kent & Coker 1996). *Companion species* only occur in certain sample plots and can be used to place the most similar sample plots of a specified plant community next to each other (Table 6.3) (Kent & Coker 1996).

Slope and Aspect

Using the GPS, altitude measurements were taken from the centre point of each plot and the 25 m endpoints of the four trails. Since these measurements, especially taken underneath a dense vegetation cover, show quite a high variation, a large number of measurements was taken at each point and on different days. Arithmetic mean and standard deviation of the height in meters of each of the points were then calculated. Using these data and the 50 m distance from one endpoint of the sampling cross to the directly opposite one, the slope of each aspect present in the plot area was then calculated. Six 'slope categories' were distinguished and the calculated slopes were then placed in one of the following categories:

Slope categories: 0.0 - 4.5° = **no slope**
4.6 - 9.9° = **slight slope**
10.0 - 27.0° = **moderate slope**
27.1 - 45.0° = **marked slope**
45.1 - 67.5° = **steep slope**
67.6 - 100.0° = **very steep slope**

Herbaceous vegetation survey

Selecting sample plots

The size of the grassland area in the north-eastern corner of the island was determined using a GPS. Three transects were then placed in this area: Two transects (T1+2) ran in an east-west direction parallel to the fence and the visitors' platform and a third one (T3) ran perpendicular to those in a north-south direction.

Sampling method

A square wooden frame was constructed to give a **1 x 1 m** sampling area. Every five meters along the transects the frame was placed on the ground. The vegetation cover inside the frame was estimated using the Braun-Blanquet method as described by Kent and Coker (1996). The following six categories were used to determine the cover of each species in the sample quadrat:

1. **+** = less than 1% cover
2. **1** = 1 - 5% cover
3. **2** = 6 - 25% cover
4. **3** = 26 - 50% cover
5. **4** = 51 - 75% cover
6. **5** = 76 - 100% cover

Analysis of data

The data thus collected were analysed using TWINSPAN (Two Way Indicator Species Analysis) for a classification of the samples by a divisive method (Hill, 1979a) and DECORANA (Detrended Correspondence Analysis) for an ordination of the data (Hill 1973 + 1979b).

Soil samples

Sampling method

Soil samples were collected at the centre point of each sampling plot for the woody vegetation survey to a depth of between 50 – 100 mm. For the herbaceous vegetation three samples were collected for each transect, at the same depth and at either end and in the centre of the transect.

The samples were stored in plastic bags for analysis at the Department of Botany and the Department of Soil Science at the University of Pretoria.

pH determination

20 g of each soil sample were mixed with 50 ml of distilled water, stirred thoroughly and left standing. After 30 minutes this suspension was thoroughly stirred again and left to settle for another 30 minutes. After stirring and leaving the suspension to settle for another 10 minutes the pH was measured using a Crison pH-meter (Crison Instruments S.A. made by Ingold, Dr. W. Ingold AG, Industrie Nord, 8902 Urdorf, SWITZERLAND) (Van der Waals pers. comm.[1]).

Daily temperature, relative humidity and precipitation

Daily temperature and relative humidity were measured in the shade three times a day (at 08:00, 14:00 and 18:00) using a battery driven, digital and combined thermo- and hygrometer (the name and address of the supplier could not be established). Rainfall was measured several times daily if necessary, using a commercially obtainable 'pluvimeter'.

Photographic records

Photographs of the island vegetation were taken from the air, the water, standing on the visitors' platform and on the ground inside the forest.

DATA COLLECTION ON NSADZI ISLAND

Control plots were sampled on neighbouring Nsadzi Island (Figure 6.68) to allow for a long term comparison of changes of the island vegetation on Ngamba Island and to evaluate their possible causes. An area of secondary rainforest was identified on the eastern side of the island. The circumference of this area was measured with the GPS by walking around the forested patch. Using random numbers to select the S/E coordinates for the centre point of each plot, the positions of two plots were determined in the control area. This area will not be part of the area allocated for the new chimpanzee sanctuary on Nsadzi Island.

The woody vegetation was sampled and analysed using the methods employed on Ngamba Island. Soil samples were taken at the centre point of each plot and also analysed by the

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[1] Van der Waals, J. (2001) Department of Soil Science, University of Pretoria, Pretoria, R.S.A.

Departments of Botany and of Soil Science at the University of Pretoria following the above cited method. The data and samples were collected during daylight hours on several consecutive days.

IDENTIFICATION OF COLLECTED VEGETATION SAMPLES

Samples collected of the woody and herbaceous vegetation were identified by Mrs. Olivia Wanyamaganyi and Mrs. Mary Namaganda at the Herbarium of the Department of Botany, Makerere University, Kampala, Uganda.

CHAPTER 6

RESULTS

DESCRIPTION OF SAMPLE PLOTS ON NGAMBA ISLAND

Figure 6.1 shows a map of Ngamba Island based on GPS measurements. The forested areas and those with herbaceous vegetation are indicated. Other landmarks, such as the fence dividing the chimpanzee area from the staff and visitors' area, as well as the centre points of the eight sample plots are also indicated.

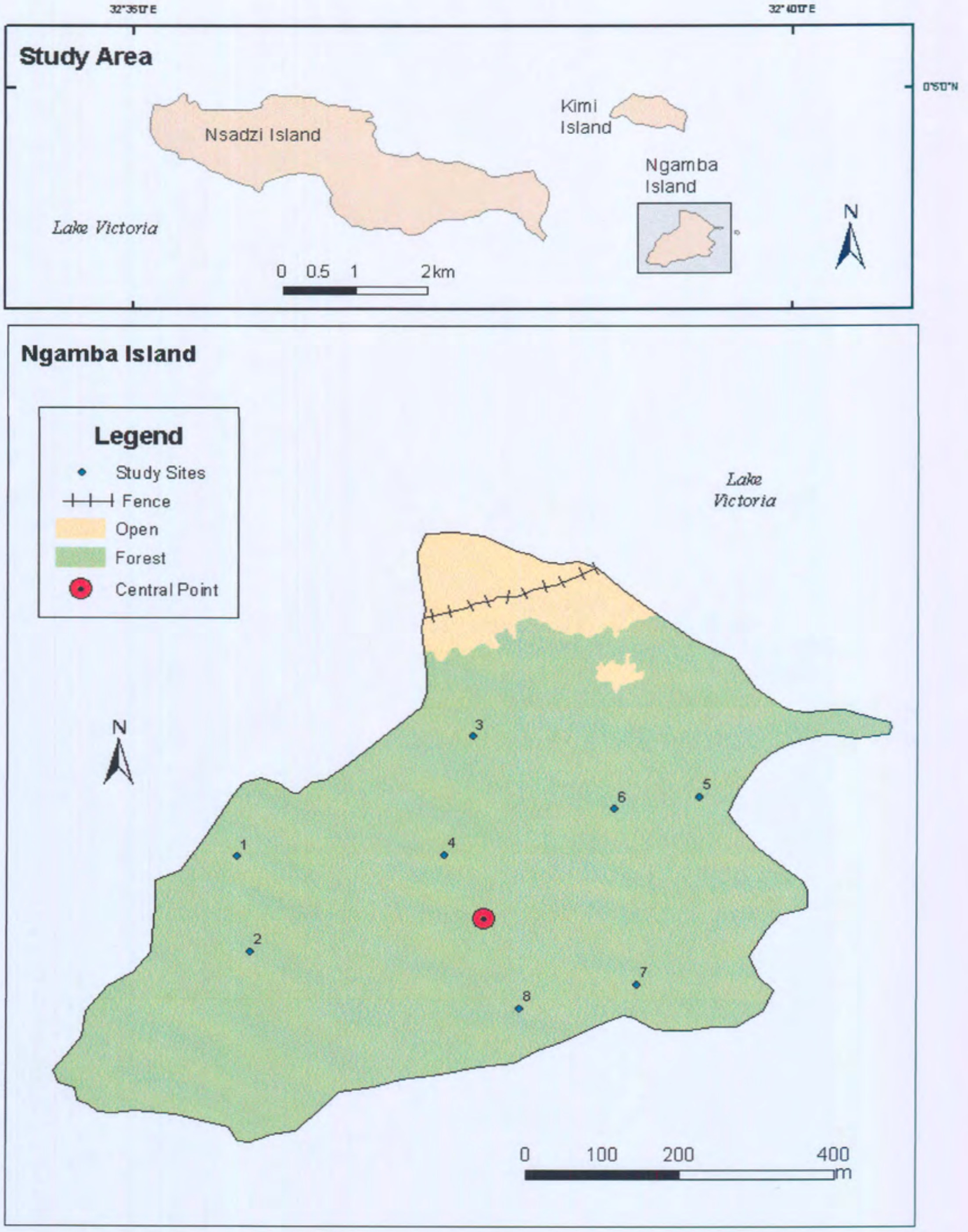

Figure 6.1: Sample plots and vegetation zones on Ngamba Island.

SAMPLE PLOTS ON NGAMBA ISLAND

Using the **highest elevation** of the island **(S 00°06 288 / E 32°39 178; 1195 ± 5 m)** as a **centre point**, four different sampling quadrats were created (Figure 6.2). In each quadrat two sample plots were randomly selected:

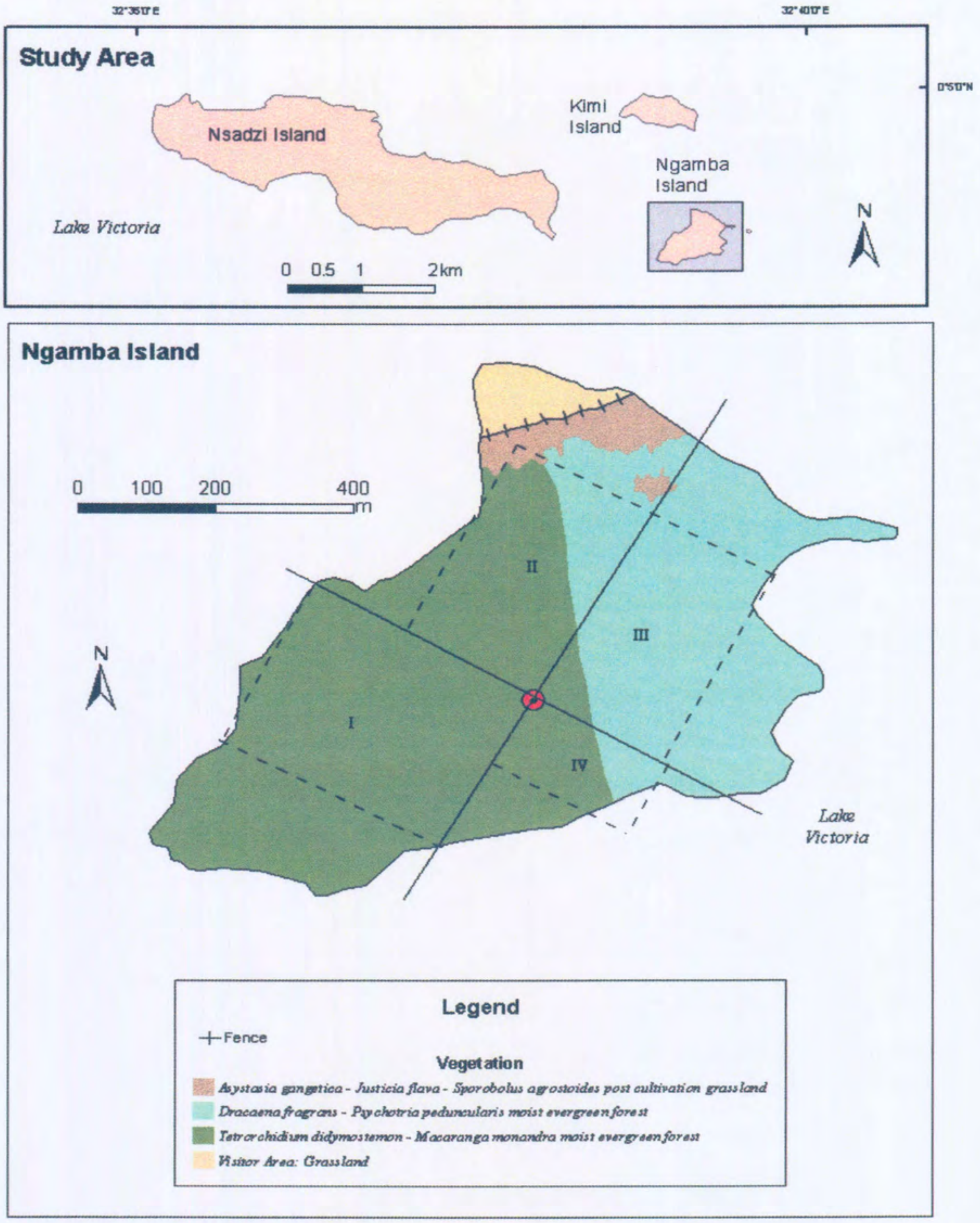

Figure 6.2: Location of the four sample quadrats on Ngamba Island.

Plot 1 - S 00°06 256 / E 32°39 005; 1 160 ± 1 m (Table 6.1)

This plot is close to the western shore of the island and has two slopes: a slight (4.6 – 9.9°) east-westwards slope and a moderate (10.0 – 27.0°) north-southwards slope (Table 6.1). The undergrowth is dense, consisting mainly of *Culcasia falcifolia* - a creeper - and *Commelina capitata*. There are not many trees of > 6.00 m in this plot. The vegetation consists mainly of *Aframomum angustifolium*. Apart from the > 6.00 m height class, trees of all other height classes are present within the five meter squares. Very few dead trees; neither standing nor fallen, are prevalent. This plot seems to receive less wind than those on the eastern side and the vegetation on this side of the island differs from that on the eastern side. There are also fewer spider webs.

Plot 2 - S 00°06 313 / E 32°39 014; 1 172 ± 2 m (Table 6.1)

This plot has a big open space in the centre with fallen dead trees covering part of the area. Almost no tracks are present. The plot has a moderate east-western slope (Table 6.1) and is close to the highest elevation on the island. The ground is covered with *Culcasia falcifolia*. On the northern side of the plot another open space is found where a number of spider webs occur. This plot contains some of the largest trees, many showing very high root buttresses.

Plot 3 - S 00°06 152 / E 32°39 169; 1 170 ± 8 m (Table 6.1)

This plot is close to the northern forest border and to the staff/visitors area. The tracks from east to west and north to south are not particularly straight in this area and could therefore be only partly used to subdivide the plot into sampling squares. There are two slopes: a slight east-western slope and a moderate south-northern slope (Table 6.1). *Albizia gumnifera* and *Aframomum angustifolium* are the most prominent woody species. In general, the vegetation is quite dense but there are also some bare patches.

Plot 4 - S 00°06 240 / E 32°39 150; 1 176 ± 5 m (Table 6.1)

This plot is situated more towards the centre of the island and in close proximity of the highest elevation. There are two slopes: one marked (27.1 – 45.0°) south-northern slope and a second, moderate east-western slope (Table 6.1). Here again, only a few spider webs are seen. The north-southwards running track is almost invisible. Two fallen trees of quite huge dimensions are lying almost in the centre of the plot. The main tree species is *Albizia gumnifera* while fig trees are also quite prominent. The undergrowth is relatively dense.

Plot 5 - S 00°06 197 / E 32°39 328; 1 158 ± 4 m (Table 6.1)

This plot is close to the eastern shore of the island and its eastern 25 m border nearly touches the sandy beach. There is a steep (45.1 -67.5°) west-eastem slope (Table 6.1). The ground is densely covered with *Culcasia falcifolia* and *Commelina capitata*. The south-eastern square of the sample plot mainly contains *Dracaena fragrans* trees of different heights.

The chimpanzees seem to visit this area rather frequently. They seem to follow the existing track system and to diverge from there into the surrounding vegetation at different locations. They mainly pull out creepers and tear down leaves and branches, leaving them lying on the ground without eating them to a large extent. They also pull out the poles, used to mark the 5 m distances inside the plot area, quite frequently. Judging from the damage caused to the adjacent vegetation, the chimpanzees mainly follow the north-southwards running track and to a much lesser extent the west-eastwards running track, while hardly ever approaching the water in this area.

Plot 6 - S 00°06 206 / E 32°39 269; 1 167 ± 6 m (Table 6.1)

This plot is deep inside the forest under a dense vegetation cover with hardly any light penetrating. There is no visible slope (0.0 – 4.5°) present (Table 6.1). The north-western square contains a large number of *Dracaena fragrans* of which many of the taller ones have been bent over towards the ground. Smaller sidebranches spread out from the bent stems. There is a closed ground cover of *Commelina capitata*.

Plot 7 - S 00°06 338 / E 32°39 285; 1 146 ± 5 m (Table 6.1)

This plot is also close to the eastern shore and contains a number of fallen dead trees. There is a moderate north-southern slope (Table 6.1). The foremost species are *Aframomum angustifolium* and *Dracaena fragrans*, many of which are dead or bent to the ground. A large number of spiderwebs and spiders are observed. The area becomes progressively open, i.e. containing less trees, towards the shore (different to plot 5).

The chimpanzees do not seem to frequent this area as regulary as some of the other plots. However, they have broken from the track into the adjacent vegetation in many places and caused a lot of destruction, especially within the *Aframomum angustifolium* and *Dracaena fragrans* stands, many of which have been bent or broken and seem to be dying.

Plot 8 - S 00°06 355 / E 32°39 203; 1 148 ± 6 m (Table 6.1)

This plot is close to the south-eastern shore. There is a moderate north-west to south-eastern slope (Table 6.1). Towards the north-western plot area a number of whitish-grey, solid rocks occur. The vegetation is predominantly made up of *Aframomum angustifolium* while *Dracaena fragrans* is not present at all.

After the chimpanzees have visited the area a lot of destruction is visible: many *Aframomum angustifolium* have been bent and broken and seem to be dying off.

Table 6.1: *S / E-coordinates for woody vegetation on Ngamba and Nsadzi Island: Plot Number, altitude, slope and aspect of sample plots*

	S/E-coordinates	Location	Altitude [m] ± STD		Slope [°]	Category	Aspect
Plot 1	00°06 242/32°39 005	Centre	1160	1			
	00°06 256/32°39 005	South	1162	3	14.4	moderate	N
	00°06 231/32°39 007	North	1154	2	14.4	moderate	N
	00°06 238/32°39 019	East	1161	2	5.4	slight	W
	00°06 237/32°38 990	West	1158	1	5.4	slight	W
Plot2	00°06 313/32°39 014	Centre	1172	2			
	00°06 309/32°39 030	East	1179	4	12.6	moderate	W
	00°06 309/32°39 000	West	1172	5	12.6	moderate	W
Plot 3	00°06 152/32°39 169	Centre	1170	8			
	00°06 161/32°39 166	South	1172	10	23.4	moderate	N
	00°06 138/32°39 168	North	1159	4	23.4	moderate	N
	00°06 150/32°39 181	East	1172	14	5.4	slight	W
	00+06 160/32°39 155	West	1169	10	5.4	slight	W
Plot 4	00°06 240/32°39 150	Centre	1176	5			
	00°06 251/32°39 159	South	1186	9	28.8	marked	N
	00°06 224/32°39 145	North	1170	8	28.8	marked	N
	00°06 236/32°39 162	East	1180	7	10.8	moderate	W
	00°06 240/32°39 136	West	1174	6	10.8	moderate	W
Plot 5	00°06 197/32°39 328	Centre	1158	4			
	00°06 188/32°39 316	West	1173	2	52.4	steep	E
	00°06 205/32°39 333	East	1144	1	52.4	steep	E
Plot 6	00°06 206/32°39 269	Centre	1167	6		no slope	
Plot 7	00°06 338/32°39 285	Centre	1146	5			
	00°06 318/32°39 291	North	1148	7	22.7	moderate	S
	00°06 348/32°39 287	South	1136	9	22.7	moderate	S
Plot 8	00°06 355/32°39 203	Centre	1148	6			
	00°06 341/32°39 207	North	1152	17	18.7	moderate	S
	00°06 368/32°39 213	South	1142	9	18.7	moderate	S
Highest Elevation	00°06 288/32°39 178		1195	5	-	-	-
Nsadzi Plot 1	00°05 731/32°37 252	Centre	1214	32	*	marked	N
	00°05 729/32°37 252	South	1237	0	*	marked	N
	00°05 719/32°37 253	North	1212	2	*	marked	N
Nsadzi Plot 2	00°05 759/32°37 311	Centre	-	-	*	marked	N

* measurements for Nsadszi Island are too inaccurate to determine slope

Slope categories:
0.0 - 4.5° = **no slope**
4.6 - 9.9° = **slight slope**
10.0 - 27.0° = **moderate slope**
27.1 - 45.0° = **marked slope**
45.1 - 67.5° = **steep slope**
67.6 - 100.0° = **very steep slope**

DIMENSIONS OF SAMPLE SQUARES ON NGAMBA ISLAND

The dimensions of the respective sample areas for each height class in the eight sample plots are given in Table 6.2.

Table 6.2: *Size of sample squares for each height class in the eight sample plots on Ngamba Island*

Height class [m]	Plot 1		Plot 2	
	Size [m] of largest square	Area [m^2]	Size [m] of largest square	Area [m^2]
> 6	15 x 15	900	10 x 10	400
4 – 5	5 x 5	100	10 x 10	400
3	5 x 5	100	10 x 10	400
2	5 x 5	100	5 x 5	100
1	5 x 5	100	5 x 5	100
0.5	5 x 5	100	10 x 10	400
Standing dead	25 x 25	2500	25 x 25	2500
Fallen dead	25 x 25	2500	20 x 20	1600

Height class [m]	Plot 3		Plot 4	
	Size [m] of largest square	Area [m^2]	Size [m] of largest square	Area [m^2]
> 6	10 x 10	400	10 x 10	400
4 – 5	5 x 5	100	5 x 5	100
3	5 x 5	100	5 x 5	100
2	5 x 5	100	5 x 5	100
1	5 x 5	100	5 x 5	100
0.5	5 x 5	100	5 x 5	100
Standing dead	25 x 25	2500	25 x 25	2500
Fallen dead	25 x 25	2500	10 x 10	400

Height class [m]	Plot 5		Plot 6	
	Size [m] of largest square	Area [m^2]	Size [m] of largest square	Area [m^2]
> 6	5 x 5	100	5 x 5	100
4 – 5	10 x 10	400	5 x 5	100
3	5 x 5	100	5 x 5	100
2	10 x 10	400	5 x 5	100
1	5 x 5	100	5 x 5	100
0.5	5 x 5	100	5 x 5	100
Standing dead	25 x 25	2500	25 x 25	2500
Fallen dead	25 x 25	2500	15 x 15	900

Height class [m]	Plot 7		Plot 8	
	Size [m] of largest square	Area [m^2]	Size [m] of largest square	Area [m^2]
> 6	10 x 10	400	15 x 15	900
4 – 5	10 x 10	400	10 x 10	400
3	5 x 5	100	5 x 5	100
2	5 x 5	100	5 x 5	100
1	5 x 5	100	5 x 5	100
0.5	5 x 5	100	5 x 5	100
Standing dead	15 x 15	900	20 x 20	1600
Fallen dead	25 x 25	2500	20 x 20	1600

The majority of sample squares has the smallest possible size, i.e. 5 x 5 m (or 100 m^2 for the whole sample area per plot). This indicates a high density of trees in all height classes. In contrast, the sample squares of the two "dead tree" categories tend to be of the largest possible size, i.e. 25 x 25 m (or 2500 m^2 for the whole sample area per plot). Hence, the density of dead trees is on average much lower than that for living trees.

WOODY VEGETATION ON NGAMBA ISLAND

Density

Density of plants over all height classes and growth forms

The density of plants per hectare over all height classes and vegetation types covers quite a wide range from 3 100 plants per hectare in plot 2 to 18 050 plants per hectare in plot 7 (Figure 6.3).

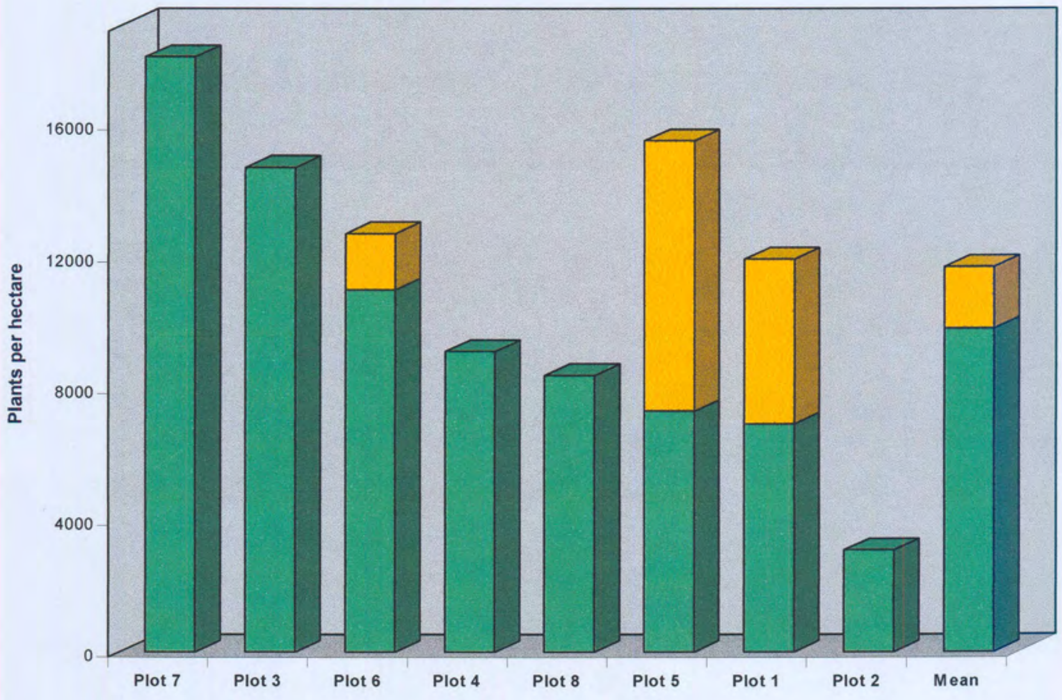

Figure 6.3: Number of plants per hectare over all height classes and vegetation types.

Key:

🟩 Number of plants per hectare without *Commelina capitata*

🟨 Number of *Commelina capitata* per hectare

Even though *Commelina capitata* (COMCAP) is not a woody species but a herb (Lind & Tallantire 1962, Langdale-Brown *et al.* 1964, Lind & Morrison 1974, Blundell 1982, Katende *et al.* 1999), it has been sampled and included under the former since it is very prevalent in three (plot 1, plot 5 & plot 6) of the eight sample plots and is one of the selected food species by Ngamba Island chimpanzees (Marshall, 2000). It increases the number of plants per hectare from 6 922 to 11 922 in plot 1, from 7 300 to 15 500 in plot 5 and from 11 000 to 12 700 in plot 6 (Figure 6.3). For all further calculations *Commelina capitata* is not considered, unless mentioned otherwise.

The mean density of the woody vegetation for the entire Ngamba Island is 9 820 individuals per hectare (Figure 6.3 & 6.4). The lowest densities are found in quadrat I, with 3 100 (plot 2) and 6 922 (plot 1) plants per hectare, respectively (Figure 6.3). Thus, the mean density is 5 011 plants per hectare for the whole of quadrat I, which is far below the mean for the whole island. The difference between the densities of the two plots is 3 822 plants per hectare.

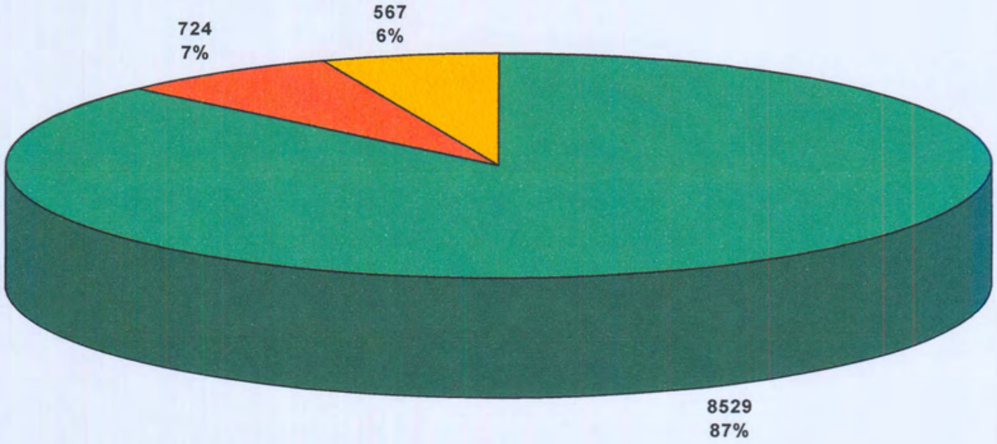

Figure 6.4: Percentage contribution of growth forms to overall density.

Key:
🟩 Tree
🟥 Sparse shrub
🟨 Shrub

Although quadrat I thus has a low density of woody plants per hectare throughout, this density varies widely between areas. With 5 000 plants per hectare plot 1 has the second highest density of *Commelina capitata* (Figure 6.3).

Quadrat II has a mean density of 11 912.5 plants per hectare, with 14 700 (plot 3) and 9 125 (plot 4) plants per hectare, respectively. The difference between the two sample plots is 5 575 plants per hectare and thus varies quite markedly. The two sample plots have the second (plot 3) and fourth (plot 4) highest density of plants and their mean density lies well above the mean for Ngamba Island (Figure 6.3). There is no *Commelina capitata* in this quadrat.

Quadrat III has a mean density of 9 150 plants per hectare which compares well with the mean for the whole island, with 7 300 (plot 5) and 11 000 (plot 7) plants per hectare, respectively. The difference between plots is 3 700 plants per hectare and is thus the most homogenous of all the quadrats. Both plots in this quadrat contain *Commelina capitata* and with 8 200 plants per hectare in plot 5 also the highest number of this species per hectare (Figure 6.3).

Quadrat IV has the highest mean density with 13 218 plants per hectare and thus higher than the mean for the whole island. With 18 050 plants per hectare plot 7 has the highest density of all plots, while plot 8 with 8 386 plants per hectare has the fourth lowest density. The difference between the density in the two plots is 9 664 plants per hectare indicating the highest variation In density of plants per hectare in this quadrat (Figure 6.3).

Density of the different vegetation types

Figure 6.4 compares the mean density of the different growth forms on Ngamba Island. Trees are by far the most prominent growth form with 87% (8 529 plants per hectare), while "sparse shrubs" (individuals with two to four stems) follow with 7% (724 plants per hectare) and then "shrubs" (individuals with five or more stems) which only constitute 6% (567 plants per hectare) of the woody vegetation. This pattern varies slightly between the individual sample plots, although the general trend stays the same (Figure 6.4).

In two of the plots (plot 4 and plot 5) the order of “sparse shrubs“ and “shrubs“ is reversed and with 12.06% respectively 8.22% also markedly above the mean for “shrubs“ per hectare

(Figure 6.5). In both of these plots the percentage of trees is slightly lower than the mean percentage per hectare (Figure 6.4 & 6.5).

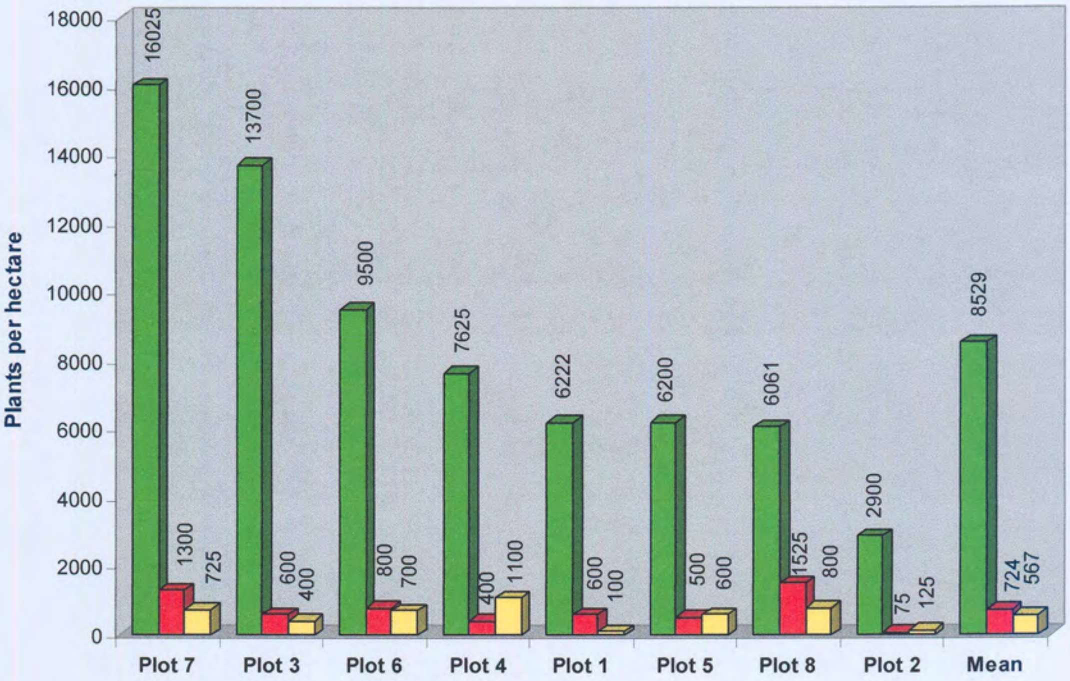

Figure 6.5: Plants per hectare according to growth form.

Key:

🟩 Tree
🟥 Sparse shrub
🟨 Shrub

In plot 8 the shrub component is with 27.72% much higher than in the other sample plots.The percentage of shrubs is about 1.7 times higher than the mean percentage per hectare and the percentage of sparse shrubs about 2.5 times (Figure 6.4 & 6.5).

In contrast to that plot 2 shows a high prevalence of trees (93.55%), while sparse shrubs are hardly present and are with only 2.42% more than three times below the mean percentage per hectare. Similarly, even though shrubs are with 4.03% more prevalent than the former, they are still 1.74% below the mean percentage per hectare for the whole island (Figure 6.4 & 6.5).

Number of plant species

The mean number of different plant species (species richness) per sample plot is 11.63 (Figure 6.6). Plot 5 has the highest number of different species, namely 17, followed by plot 3 with 14 (Figure 6.6). The lowest number of different species occurs in plot 8 with 9, while the remaining five plots all have between ten and eleven different species (Figure 6.6).

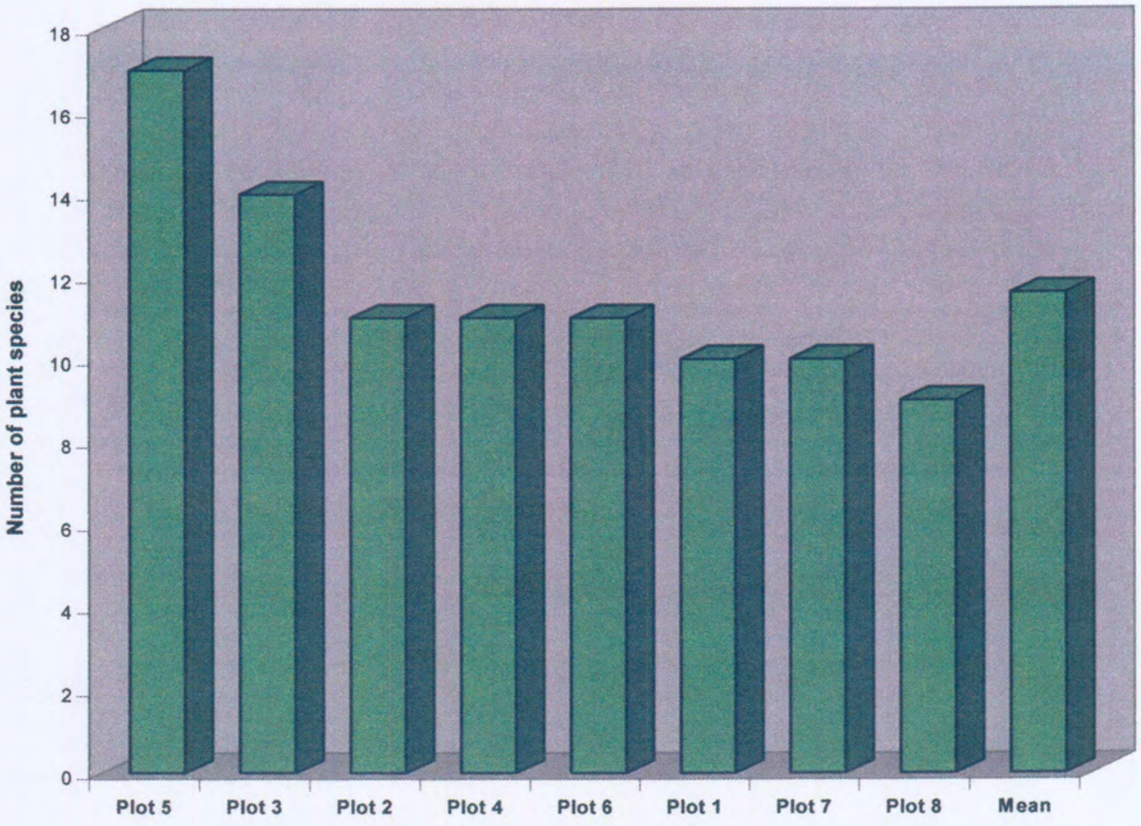

Figure 6.6: Species richness in each of the sample plots.

Key: 🟩 Number of plant species

Braun-Blanquet classification

Using the Braun-Blanquet classification of the vegetation cover (see Chapter 5 – Analysis of data), the single woody species have been categorised as either *differential*, *indifferent* or *companion* species and the eight sample plots have then been combined according to their differential species (Table 6.3).

Table 6.3: *Braun-Blanquet classification of Ngamba Island woody vegetation and combination of plots according to their differential species*

	Community 1					Community 2		
Plot	3	4	8	2	1	6	7	5
Species	Braun-Blanquet Classification							
	Differential species							
Tetrorchidium didymostemon	4	+	3	2A				
Galinera saxifraga	3	2A	1					
Ouratea hiernii		5		2A	1	+		
Macaranga monandra	2A	2B			2A			
Alchornea cordifolia			3	+	1			
Dracaena fragrans	1					2B	4	2A
Psychotria peduncularis						+	+	1
Commelina capitata					1	+		+
Peddiea fischeri						1	1	
	Indifferent species							
Albizia gumnifera	2A	2B	2A	+	2A	+	2A	+
Guarea cedrata	3	1	2B	5	2B	5	2B	2A
Oxyanthus speciosus	2B		3	2B	5	4	+	2B
Aframomum angustifolium	2B		3		2A	2B	2B	+
Palisota mannii	+		1		+		2B	2A
	Companion species							
Pachystela brevipes	1			+				5
Beilschmedia ugandensis		+						1
Dictyandra arborescens					2A			
Clitandra cymulosa				3				
Oxyanthus subpunctatus				1				
Ficus species 1				+				
Nephrolepis biserrata				+				
Canarium schweinfurthii	2A							
Unidentified species 1	2A							
Clitandra species 1	1							
Entandrophragma utile	+							
Ficus ovata		2A						
Coffea canephora		1						
Antiaris toxicara		+						
Trichilia species 1		+						
Eugenia capensis								2B
Rinorea brachipetala								1
Canthium species 1								+
Milettia dura								+
Psychotria mahonii								+
Psychotria species 1								+
Trilepsium madagascariense								+
Clerodendrum formicarum						1		
Palisota schweinfurthii						1		
Oxyanthus speciosus var. stenocarpus							2A	
Ficus species 2							+	
Ficus wildemanniana			1					

Two major plant communities could be established for the whole island (Table 6.3 & Figure 6.7). The first community has *Macaranga monandra*, *Alchornea cordifolia*, *Tetrorchidium didymostemon* and *Galinera saxifraga*, as differential species and contains five of the eight sample plots, namely plot 1, plot 2, plot 3, plot 4 and plot 8 (Figure 6.7). The second community has *Dracaena fragrans*, *Psychotria peduncularis*, *Commelina capitata* and *Peddiea fischeri* as differential species and contains the remaining three sample plots, namely plot 5, plot 6 and plot 7 (Table 6.3 & Figure 6.7). The following two communities can therefore be formed:

Community 1: ***Tetrorchidium didymostemon – Macaranga monandra***
moist evergreen forest

Community 2: ***Dracaena fragrans – Psychotria peduncularis***
moist evergreen forest

Figure 6.2 & 6.7 show the distribution of these plant communities throughout the island. Community 1 occupies, with 25.76 hectare, the larger central and western part of the island, while community 2 occupies, with 16.64 hectare, the remaining smaller and eastern part of the forest-covered island area; community 3 represents the grassland community and covers altogether an area of 1.89 hectare (Figure 6.2 & 6.7).

From observations during the study period it seems that the chimpanzees favour community 2, since they visit (and destroy the vegetation of) the eastern area of Ngamba Island much more frequently

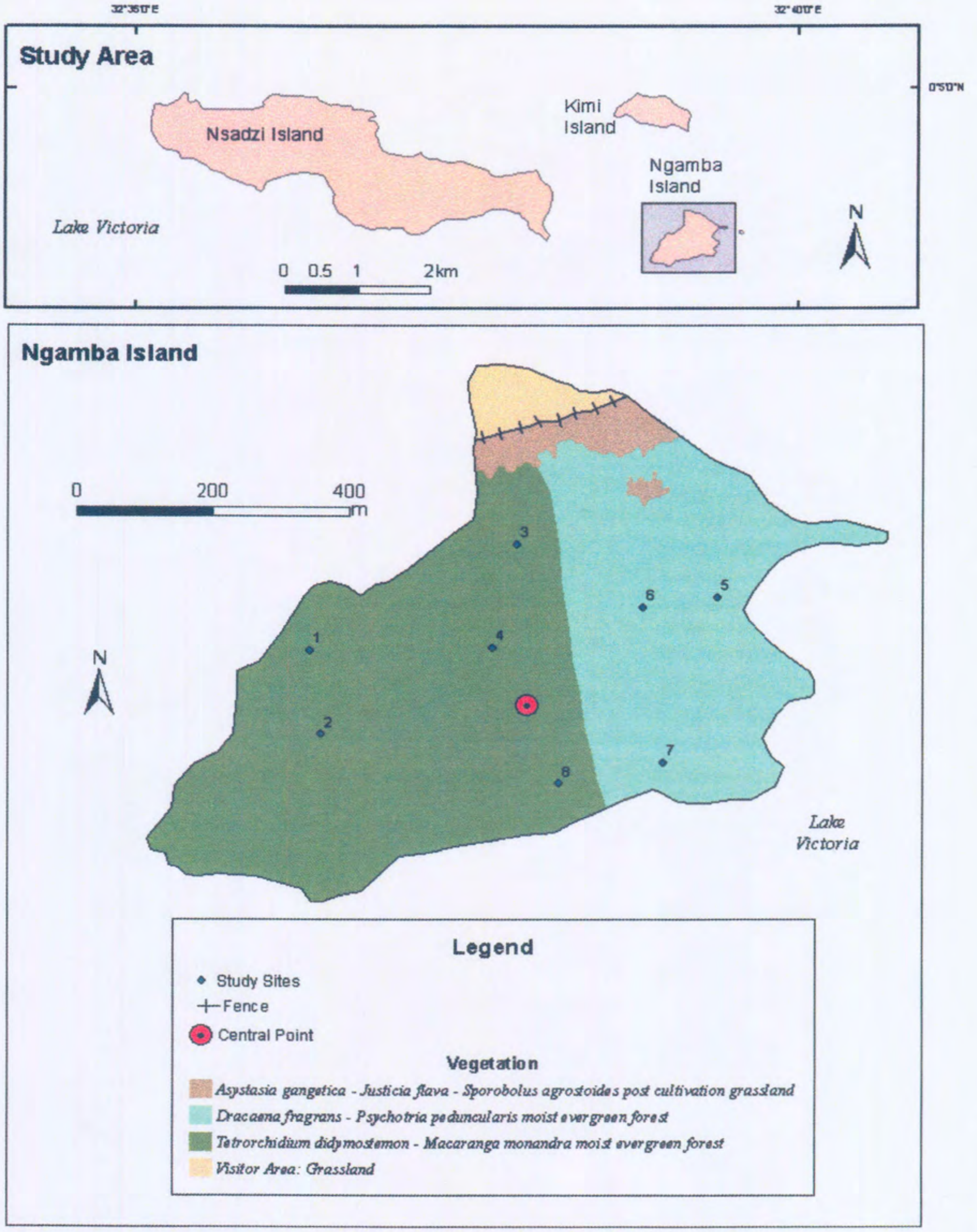

Figure 6.7: Braun-Blanquet classification of Ngamba Island Vegetation.

Density of plants per species and per hectare

Figures 6.8 – 6.11 indicate the mean density of woody species for the whole island. Since there are large differences in plant density, the species have been arranged in four different groups, namely (1) species with > 500 plants per hectare, (2) species with > 100 - 500 plants per hectare, (3) species with > 20 - 100 plants per hectare and (4) species with 1 - 20 plants per hectare (Figures 6.8 – 6.11).

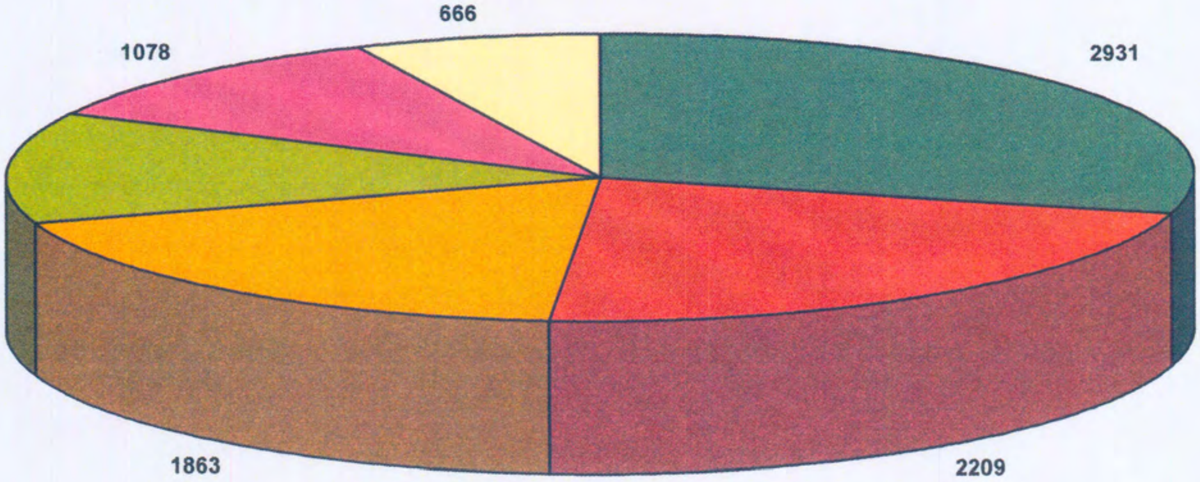

Figure 6.8: Mean density (plants per hectare) for species with > 500 plants per hectare.

Key:
🟩 *Aframomum angustifolium*
🟥 *Dracaena fragrans*
🟧 *Commelina capitata*
🟩 *Albizia gumnifera*
🟥 *Guarea cedrata*
🟨 *Oxyanthus speciosus*

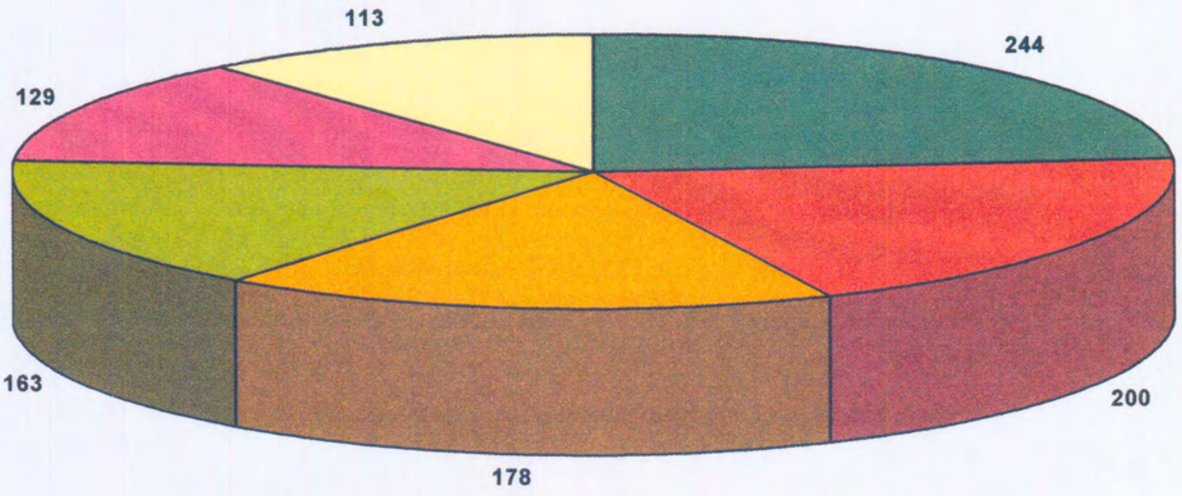

Figure 6.9: Mean density (plants per hectare) for species with > 100 - 500 plants per hectare.

Key:		
	🟩	*Ouratea hiernii*
	🟥	*Palisota mannii*
	🟧	*Galinera saxifraga*
	🟨	*Pachystela brevipes*
	🟪	*Tetrorchidium didymostemon*
	⬜	*Dictyandra arborescens*

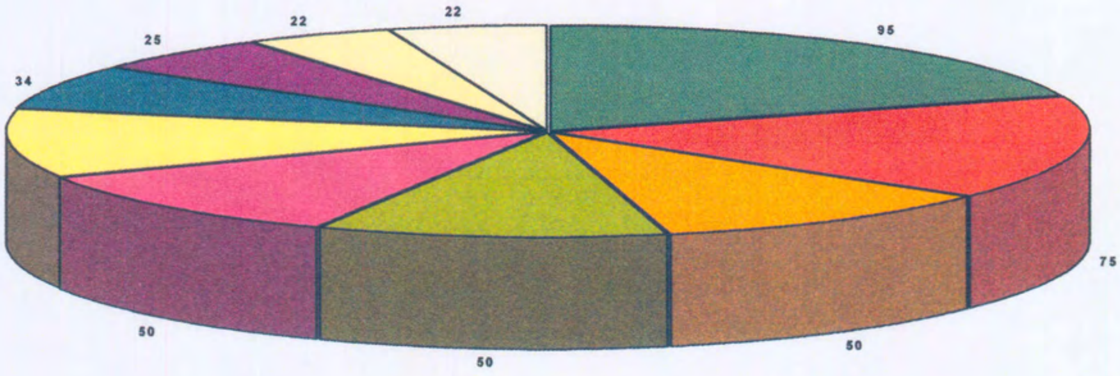

Figure 6.10: Mean density (plants per hectare) for species with > 20 - 100 plants per hectare.

Key:

🟩 *Alchornea cordifolia*
🟥 *Ficus ovata*
🟧 *Macaranga monandra*
🟩 *Coffea canephora*
🟥 *Eugenia capensis*
🟨 *Palisota schweinfurthii*
🟦 *Psychotria peduncularis*
🟪 *Canthium species 1*
🟨 *Beilschmedia ugandensis*
⬜ *Peddiea fischeri*

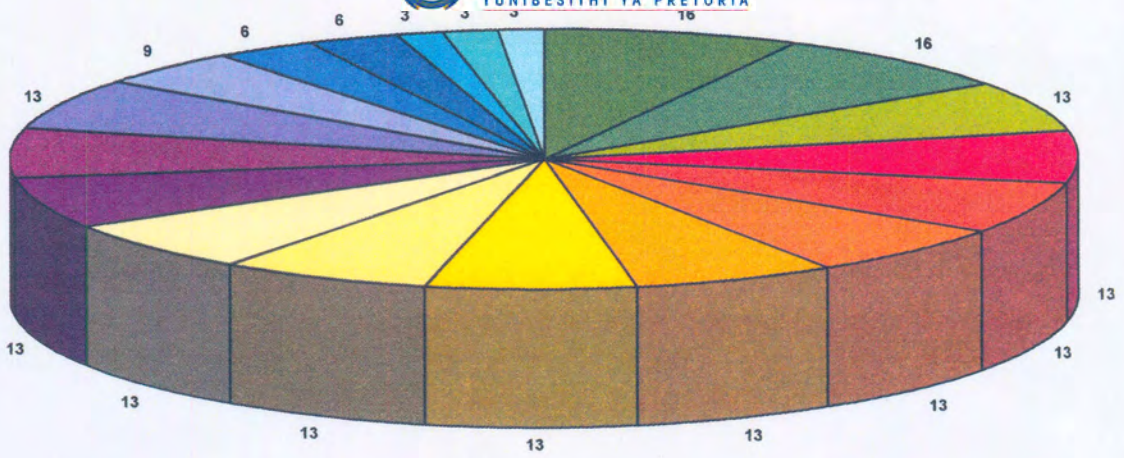

Figure 6.11: Mean density (plants per hectare) for species with 1 - 20 plants per hectare.

- 🟩 *Ficus species 1*
- 🟩 *Nephrolepis biserrata*
- 🟨 *Oxyanthus subpunctatus*
- 🟥 *Canarium schweinfurthii*
- 🟥 *Clitandra species 1*
- 🟧 *Entandrophragma utile*
- 🟧 *Antiaris toxicara*
- 🟨 *Trilepsium species 1*
- 🟨 *Millettia dura*
- 🟨 *Psychotria species 1*
- 🟪 *Clerodendrum formicarum*
- 🟪 *Ficus species 2*
- 🟪 *Oxyanthus speciosus var. stenocarpus*
- 🟪 *Rinorea brachypetala*
- 🟦 *"Unidentified species"*
- 🟦 *Ficus wildemanniana*
- 🟦 *Clitandra cymulosa*
- 🟦 *Psychotria mahonii*
- 🟦 *Trilepsium madagascariense*

There are only six different species in the first group, namely *Aframomum angustifolium*, *Dracaena fragrans*, *Commelina capitata*, *Albizia* gumnifera, *Guarea cedrata* and *Oxyanthus speciosus* (Figure 6.8). Only three of those species, namely *Albizia gumnifera* (1 238 plants per hectare), *Guarea cedrata* (1 078 plants per hectare) and *Oxyanthus speciosus* (666 plants per hectare) are "real" tree species. All three of those species have been classified as *'indifferent species'* in the Braun-Blanquet classification (Table 6.3). They are prevalent to different degrees in all eight sample plots (*Oxyanthus speciosus* only in seven) and hence seem to be distributed ubiquitously throughout the whole island (Table 6.3). They also constitute known food species for the Ngamba Island chimpanzees (Table 6.4).

Table 6.4: *Number of plants per hectare of known Ngamba Island chimpanzees' plant food species*

Species	Plot								Mean
	1	2	3	4	5	6	7	8	
Aframomum angustifolium	2 700		5 700	425	100	3 700	5 200	6 100	2 991
Dracaena fragrans			200		2 300	4 100	11 075		2 209
Commelina capitata	5 000				8 200	1 700			1 863
Albizia gumnifera	133	5 825	2 300		50	100	50	1 022	1 185
Guarea cedrata	344	225	3 350	1 150	1 075	1 700	650	133	1 078
Oxyanthus speciosus	2 333		75	575	1 250	600	300	297	679
Pachystela brevipes			300	100	900				163
Tetrorchidium didymostemon		100	800	100				33	129
Ficus species		125		600			100	50	109
Dictyandra arborescens	900								113
Canthium species 1					100				13
*Culcasia falcifolia**	+	+			+				+
Total	11 410	6 750	12 725	2 475	13 975	11 900	17 375	7 635	10 531

- In this study only the presence (+) or absence of the creeper *Culcasia falcifolia* in a sample plot has been determined.

Aframomum angustifolium (2 931 plants per hectare) has the highest mean density of all plants (Figure 6.8). This underlines the role it plays as a food source for the Ngamba Island chimpanzees (Table 6.10). The same is true for the next two most prominent plants, namely *Dracaena fragrans* (2 209 plants per hectare) and *Commelina capitata* (1 863 plants per hectare) (Table 6.4). Furthermore, all six plant species with the highest mean density per hectare are known potential food species for the Ngamba Island chimpanzees (Marshal 2000).

Six plant species are also represented in the second group, namely *Ouratea hiernii* (244 plants per hectare), *Palisota mannii* (200 plants per hectare), *Galinera saxifraga* (178 plants per hectare), *Pachystela brevipes* (163 plants per hectare), *Tetrorchidium didymostemon* (129 plants per hectare) and *Dictyandra arborescens* (113 plants per hectare) (Figure 6.9). Of those, three are known to be potential food species for Ngamba Island chimpanzees, namely *Pachystela brevipes*, *Tetrorchidium didymostemon* and *Dictyandra arborescens* (Table 6.4) (Marshall 2000). One of these species - namely *Tetrorchidium didymostemon* - has been classified as a *'differential species'* according to the Braun-Blanquet classification (Table 6.3). The other two, *Pachystela brevipes* and *Dictyandra arborescens*, have been classified as *'companion species'* and have a very localized distribution throughout the island, only appearing in three or one sample plot respectively (Table 6.3). Altogether, 75% (9 out of 12) of the known food species of Ngamba Island chimpanzees are represented in the two high density categories of woody plant species (Figure 6.8 & 6.9 & Table 6.4).

Ten species are prevalent in the third group (Figure 6.10). The most prominent species here is *Alchornea cordifolia* with 95 plants per hectare, followed by *Ficus ovata* with 75 plants per hectare (Figure 6.10). Four species are still prominent in this category with 50 plants per hectare, namely *Macaranga monandra*, *Coffea canephora*, *Eugenia capensis* and *Palisota schweinfurthii* (Figure 6.10). The remaining four species, namely *Psychotria peduncularis*, *Canthium sp.1*, *Beilschmedia ugandensis* and *Peddiea fischeri*, all have less than 40 plants per hectare (Figure 6.10). Only *Ficus ovata* and *Canthium sp.1* are known food species of the Ngamba Island chimpanzees (Figure 10 & Table 6.4) (Marshall 2000).

The largest number of species (19) is found in the fourth group (Figure 6.11). The main representatives here are *Ficus sp.1* and *Nephrolepis biserrata* (both with 16 plants per hectare), while 11 species have a mean density of 13 species per hectare each (Figure 6.11). Those are *Oxyanthus subpunctatus*, *Canarium schweinfurthii*, *Clitandra sp.1*, *Entandrophragma utile*, *Antiaris toxicara*, *Trichilia sp.1*, *Millettia dura*, *Psychotria sp.1*, *Clerodendrum formicarum*, *Ficus sp.2* and *Oxyanthus speciosus var. stenocarpus* (Figure 6.11). The remaining six species all have mean densities below 10 plants per hectare (Figure 6.11). The three remaining *Ficus spp.* are part of this last density group (Figure 6.11). All four *Ficus spp.*, namely *Ficus ovata*, *Ficus wildemanniana*, *Ficus sp.1* and *Ficus sp.2*, are collectively called *Ficus spp.* when referring to them as food species for the Ngamba island chimpanzees (Table 6.4).

Density according to height classes and growth form

Trees in all eight sample plots have representatives in each of the six investigated height classes (Table 6.5 - 6.8). Sparse shrub and shrubs are absent in the > 6.0 m height class.

Table 6.5: *Density (plants per hectare) of woody vegetation according to height class and growth form in quadrat I*

Height class	Quadrat I / Plot 1				Quadrat I / Plot 2				Mean Total
	Total	Tree	Sparse shrub	Shrub	Total	Tree	Sparse shrub	Shrub	
> 6 m	122	122			250	250			186
4 – 5 m	1 100	800	300		250	250			675
3 m	1 300	1 200	100		325	325			813
2 m	2 000	1 900	100		600	600			1 300
1 m	1 600	1 600			1 000	1 000			1 300
0.5 m	800	600	100	100	675	475	75	125	737
Total	6 922	6 222	600	100	3 100	2 900	75	125	5 011

Table 6.6: *Density (plants per hectare) of woody vegetation according to height class and growth form in quadrat II*

Height class	Quadrat II / Plot 3				Quadrat II / Plot 4				Mean Total
	Total	Tree	Sparse shrub	Shrub	Total	Tree	Sparse shrub	Shrub	
> 6 m	200	200			125	125			163
4 – 5 m	2 100	2 100			1 200	1 200			1 650
3 m	2 600	2 400	200		2 200	2 100	100		2 400
2 m	3 200	3 000	100	100	2 900	1 700	100	1 100	3 050
1 m	3 800	3 700	100		1 300	1 100	200		2 550
0.5 m	2 800	2 300	200	300	1 400	1 400			2 100
Total	14 700	13 700	600	400	9 125	7 625	400	1 100	11 913

Table 6.7: *Density (plants per hectare) of woody vegetation according to height class and growth form in quadrat III*

Height class	Quadrat III / Plot 5				Quadrat III / Plot 6				Mean Total
	Total	Tree	Sparse shrub	Shrub	Total	Tree	Sparse shrub	Shrub	
> 6 m	700	700			500	500			600
4 – 5 m	275	275			1 000	900	100		638
3 m	700	700			1 800	1 400	200	200	1 250
2 m	925	825	100		1 400	1 100	300		1 162
1 m	1 800	1 400	200	200	3 400	3 100	200	100	2 600
0.5 m	2 900	2 300	200	400	2 900	2 500		400	2 900
Total	7 300	6 200	500	600	11 000	9 500	800	700	9 150

Table 6.8: *Density (plants per hectare) of woody vegetation according to height class and growth form in quadrat IV*

Height class	Quadrat IV / Plot 7				Quadrat IV / Plot 8				Mean Total
	Total	Tree	Sparse shrub	Shrub	Total	Tree	Sparse shrub	Shrub	
> 6 m	425	425			111	111			268
4 – 5 m	425	300		125	375	350	25		400
3 m	600	200	300	100	1 800	800	500	500	1 200
2 m	2 800	2 400	400		3 100	2 100	900	100	2 950
1 m	3 600	3 200	400		1 900	1700	100	100	2 750
0.5 m	10 200	9 500	200	500	1 100	1000		100	5 650
Total	18 050	16 025	1 300	725	8 386	6 061	1 525	800	13 218

Quadrat I

Quadrat I has the lowest incidence of shrubs of all quadrats. Furthermore, these shrubs only occur in the lowest height class of 0.50 m and they are made up solely of *Palisota mannii* (PALMAN) in plot 1 and of *Nephrolepis biserrata* (NEPBIS) in plot 2, respectively (Table 6.5 & Figure 6.12 & 6.13).

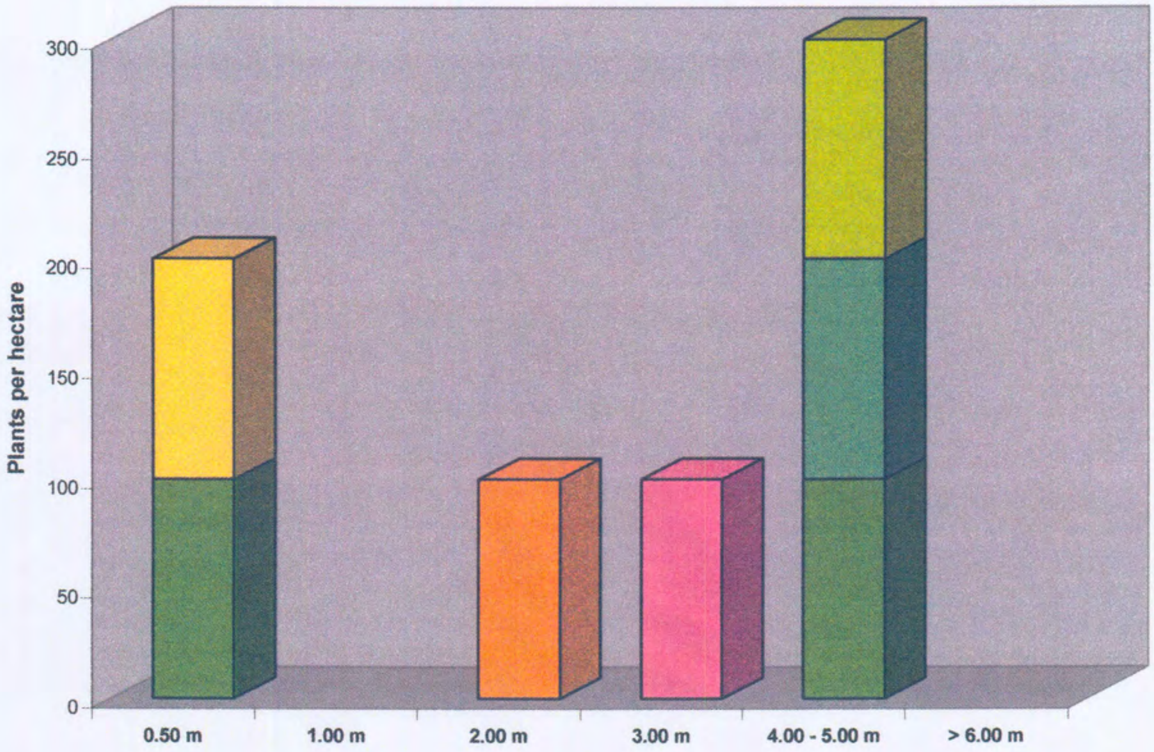

Figure 6.12: Density (plants per hectare) of sparse shrub (full colour) and shrub (chequered colour) according to height class and species in plot 1.

Key:

▨	*Palisota mannii*
🟧	*Ouratea hiernii*
🟥	*Aframomum angustifolium*
🟨	*Macaranga monandra*
🟦	*Dictyandra arborescens*
🟩	*Oxyanthus speciosus*

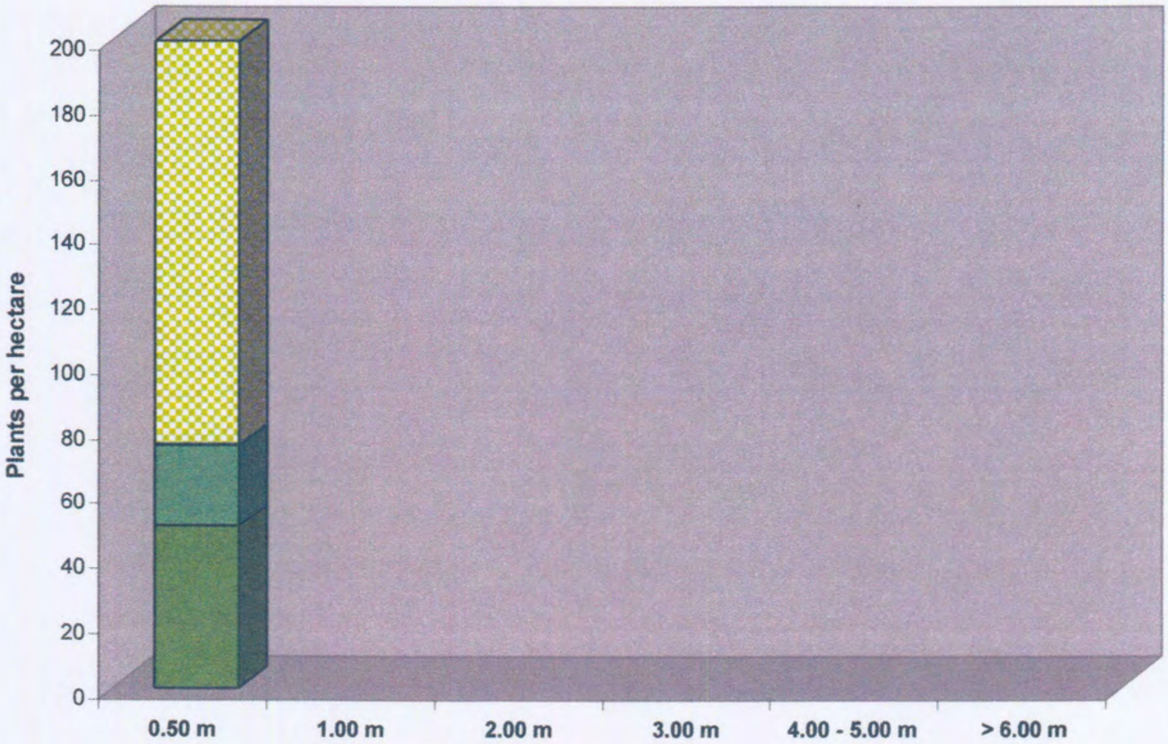

Figure 6.13: Density (plants per hectare) of sparse shrub (full colour) and shrub (chequered colour) according to height class and species in plot 2.

Key:

▨ *Nephrolepis biserrata*
🟩 *Oxyanthus speciosus*
🟩 *Ouratea hiernii*

The sparse shrubs form of *Ouratea hiernii* appears in three height classes (2.0 m, 3.0 m & 4.0 – 5.0 m) in plot 1 and in one height class (0.5 m) in plot 2, which has no sparse shrubs in any other height class. While *Oxyanthus speciosus* appears in both plots, plot 1 additionally contains sparse shrubs of *Aframomum angustifolium*, *Macaranga monandra* and *Dictyandra arborescens* (Table 6.5 & Figure 6.12 & 6.13).

The most widely distributed tree species in plot 1 is *Oxyanthus speciosus* with representatives in all six height classes (Figure 6.14). While *Aframomum angustifolium* is the most prominent species in the three lowest height classes, *Oxyanthus speciosus* is the species with the highest prevalence in the three tallest height classes (Figure 6.14). The number of plants per hectare increases about threefold from the 0.5 m height class, over the 1.0 m height class to the 2.0 m height class (from 600 plants per hectare to 1 900 plants per hectare) (Table 6.5 & Figure 6.14). It decreases again stepwise about 15-fold towards the > 6.0 m height class (from 1 900 plants per hectare to 122 plants per hectare) (Table 6.5 & Figure 6.14). This plot contains seven different tree species with the highest number of species, namely five, in the 4.0 – 5.0 m height class, followed by four different species in the > 6.0 m height class (Table 6.5 & Figure 6.14).

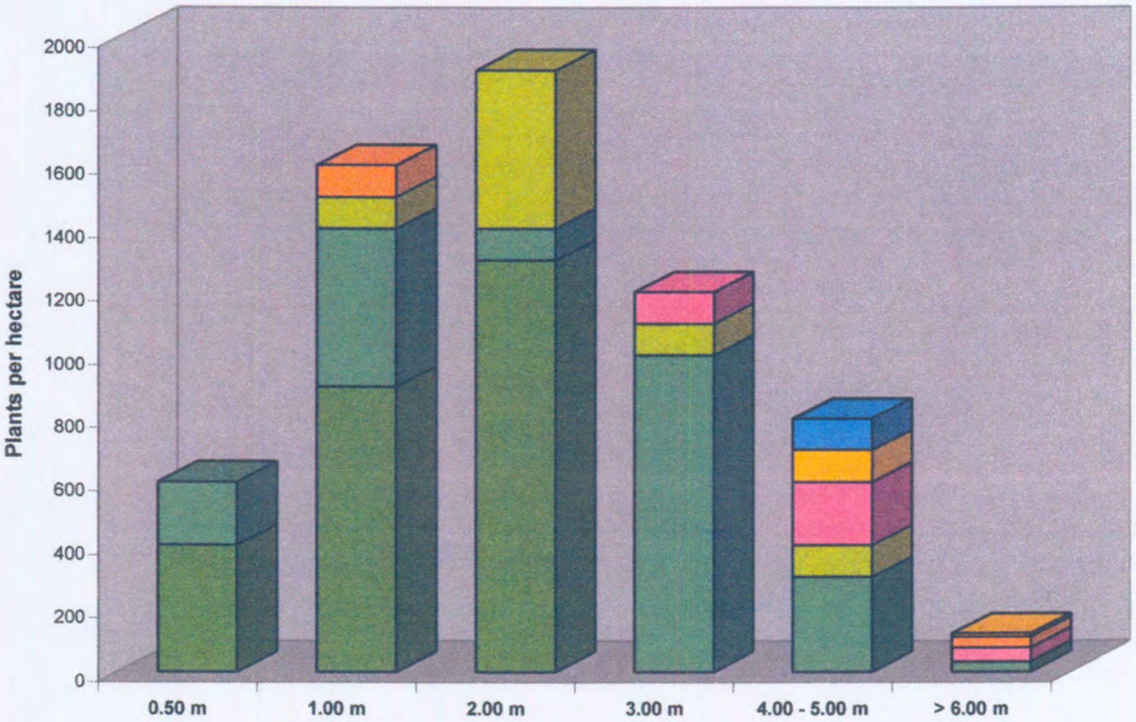

Figure 6.14: Density of trees (plants per hectare) according to height class and species in plot 1.

Key:

🟦	*Macaranga monandra*
🟨	*Alchornea cordifolia*
🟧	*Albizia gumnifera*
🟥	*Guarea cedrata*
🟨	*Dictyandra arborescens*
🟩	*Oxyanthus speciosus*
🟩	*Aframomum angustifolium*

The most widely distributed species in this plot with representatives in all six height classes of the tree category as well as in two of the sparse shrub classes is *Oxyanthus speciosus* with 2 333 plants per hectare (Figure 6.12 – 6.14); while *Aframomum angustifolium* is with 2 600 plants per hectare the most prominent species (Figure 6.12- 6.14).

Altogether ten different tree species are present in plot 2, with the 1.0 m height class showing the highest density per hectare (1 000 plants) (Figure 6.15). The second highest, but 40% lower density of trees is in the 2.0 m height class with 600 plants per hectare. The three tallest height classes all have about half of this plant density per hectare, while the 0.5 m height class lies in between (475 plants per hectare) (Table 6.5 & Figure 6.15). The highest number of different species, namely five, occurs in the 0.5 m height class. The number of species decreases towards the taller height classes with four different species each in the next four height classes and three different species each in the two tallest height classes (Table 6.5 & Figure 6.15).

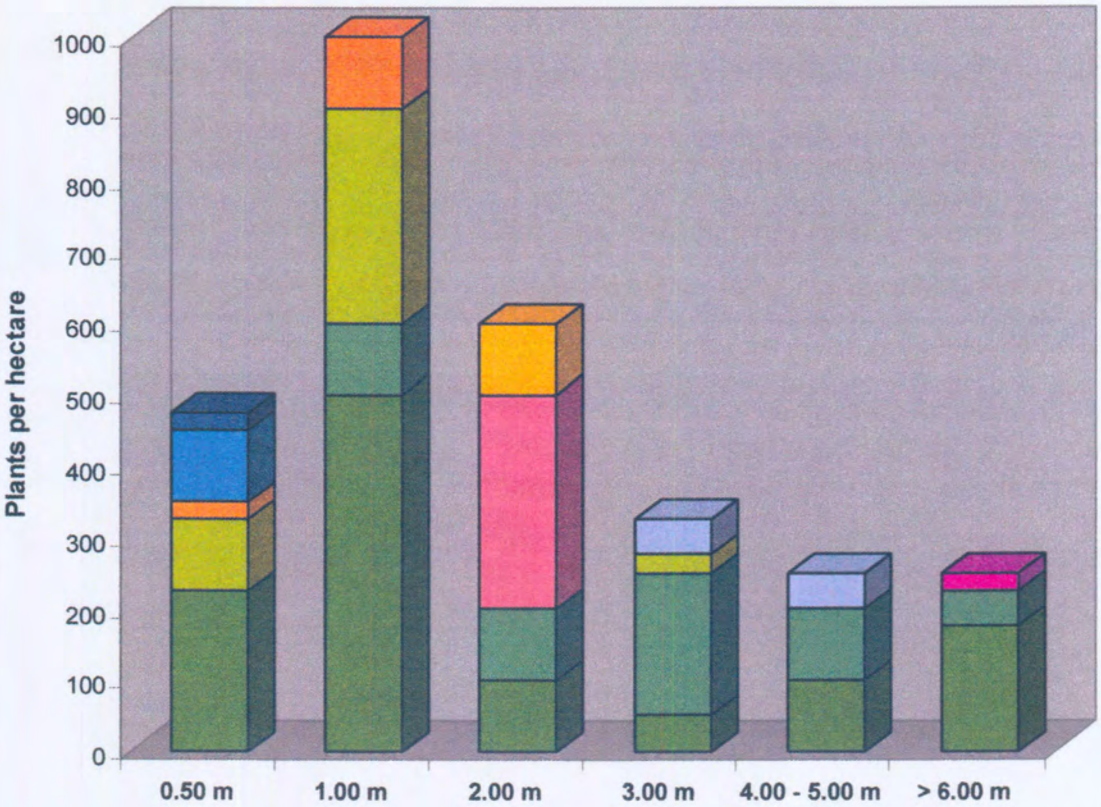

Figure 6.16: Density of trees (plants per hectare) according to height class and species in plot 2.

Key:

🟪 *Clitandra cymulosa*
🟦 *Alchornea cordifolia*
⬜ *Tetrorchidium didymostemon*
🟦 *Pachystela brevipes*
🟨 *Oxyanthus subpunctatus*
🟧 *Ficus species 1*
🟥 *Ouratea hiernii*
🟨 *Albizia gumnifera*
🟩 *Oxyanthus speciosus*
🟩 *Guarea cedrata*

Although *Guarea cedrata* does not contribute to any of the shrub growth forms, it is the most wide spread species with representatives in all six height classes, followed by *Oxyanthus speciosus* with representatives in all but the 0.5 m height class (Figure 6.12, 6.13 & 6.15).

Figure 6.16 summarises the mean number of plants per hectare over all species present, including dead plants, for quadrat I. Species that occur in both sample plots are indicated in a lighter green. Overall, 15 different species occur in quadrat 1 (Figure 6.16). The most prominent species of which is *Oxyanthus speciosus* with a mean of 1 454 plants per hectare. This species is also prevalent in both sample plots and is quite evenly distributed throughout this quadrat. The second most prominent species is *Aframomum angustifolium* with 1 350 plants per hectare. Since this species is only present in plot 1 its distribution throughout quadrat I is patchier. *Guarea cedrata*, as the third most prominent species with 747 plants per hectare, is again prevalent in both sample plots and thus also more evenly distributed in this quadrat. Although *Dictyandra arborescens* is found only in plot 1 it is still the fifth most prominent species with 450 plants per hectare. *Albizia gumnifera* and *Ouratea hiernii* are again prevalent in both sample plots and contribute a mean of 279 and 225 plants per hectare, respectively. The remaining nine species have mean densities of 100 or below plants per hectare and of those only *Alchornea cordifolia* is present in both sample plots. The "Standing dead" (XXXXXX) and "Fallen dead" (YYYYYY) plants account for two and 23 plants per hectare respectively (Figure 6.16).

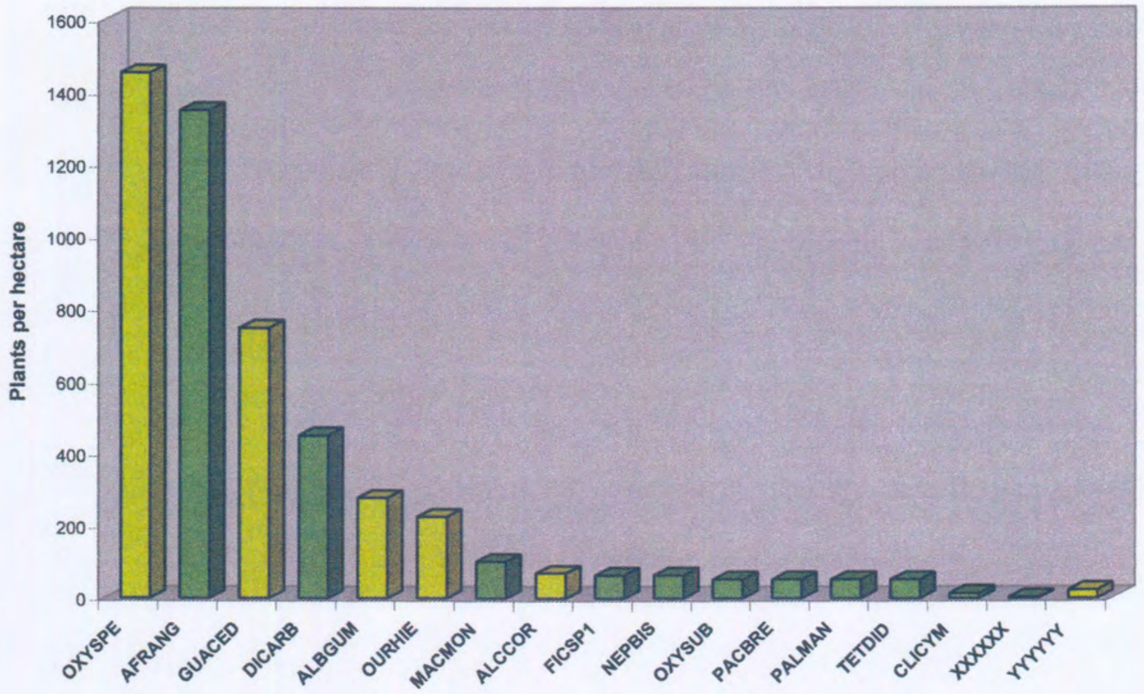

Figure 6.16: Mean density (plants per hectare) per species in quadrat I.

Key: OXYSPE = *Oxyanthus speciosus*
AFRANG = *Aframomum angustifolium*
GUACED = *Guarea cedrata*
DICARB = *Dictyandra arborescens*
ALBGUM = *Albizia gumnifera*
OURHIE = *Ouratea hiernii*
MACMON = *Macaranga monandra*
ALCCOR = *Alchornea cordifolia*
FICSP1 = *Ficus species 1*
NEPBIS = *Nephrolepis biserrata*
OXYSUB = *Oxyanthus subpunctatus*
PACBRE = *Pachystela brevipes*
PALMAN = *Palisota mannii*
TETDID = *Tetrorchidium didymostemon*
CLICYM = *Clitandra cymulosa*
XXXXXX = Standing dead trees
YYYYYY = Fallen dead trees
🟨 = Plant species present in both sample plots
🟩 = Plant species only present in one sample plot

Quadrat II

Quadrat II has shrubs only in two different height classes and each of the height classes is made up of only one species, namely *Palisota mannii* (PALMAN) in the 0.5 m height class of plot 3 (300 plants per hectare); and in the 2.0 m height class of plot 3 and plot 4 *Galinera saxifraga*, (GALSAX) (100 plants per hectare) and *Ouratea hiernii* (1 100 plants per hectare) (Figure 6.17 & 6.18). The mean number of shrubs per hectare for this quadrat is 750 and hence lies about 1.3 times above the mean density for this growth form for all sample plots (Table 6.5 – 6.8 & Figure 6.5). Nearly 75% of this number is contributed by the high density of *Ouratea hiernii* in plot 4 (Figure 6.18).

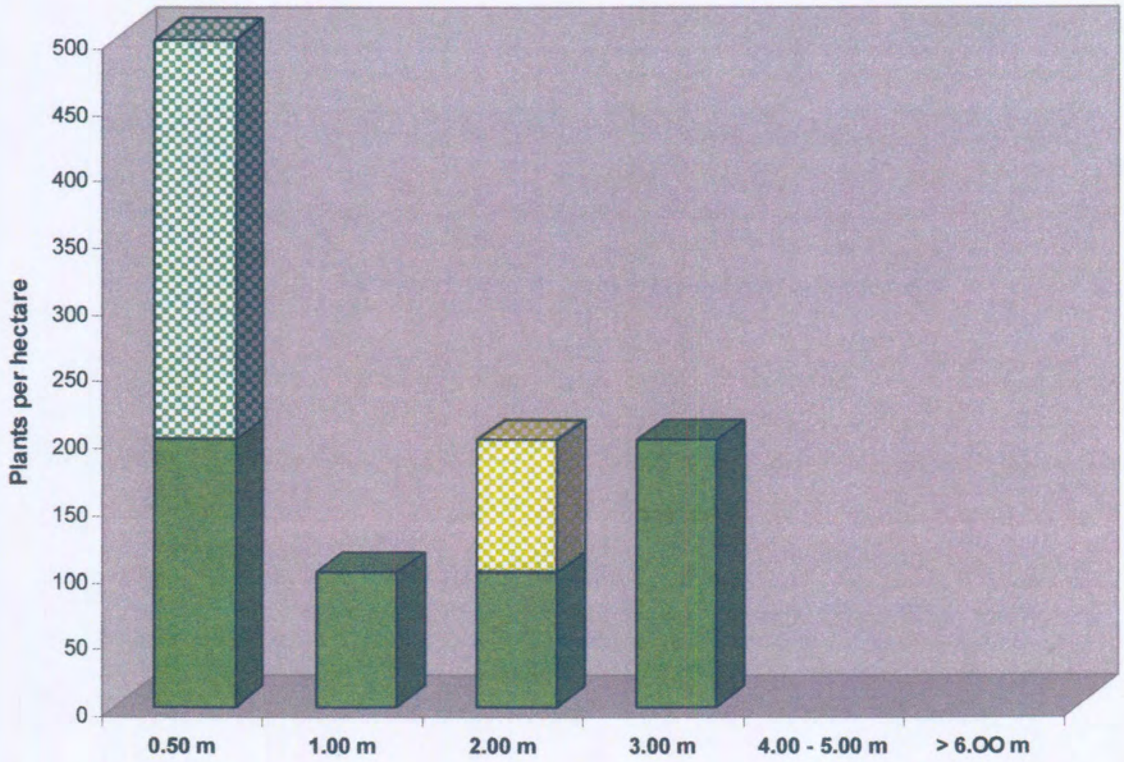

Figure 6.17: Density (plants per hectare) of sparse shrub (full colour) and shrub (chequered colour) according to height class and species in plot 3.

Key:

▦ *Galinera saxifraga*
▦ *Palisota mannii*
🟩 *Aframomum angustifolium*

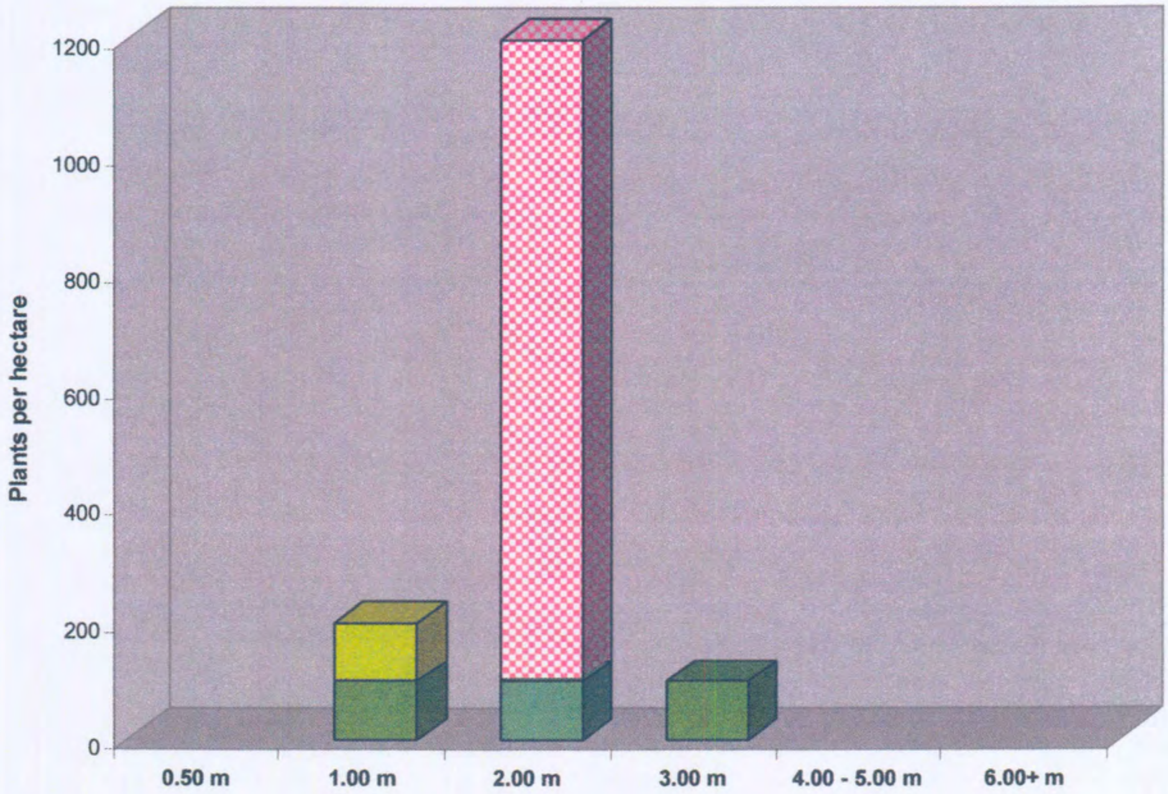

Figure 6.18: Density (plants per hectare) of sparse shrub (full colour) and shrub (chequered colour) according to height class and species in plot 4.

▨ *Ouratea hiernii*

🟨 *Albizia gumnifera*

🟩 *Antiaris toxicara*

🟩 *Coffea canephora*

Sparse shrubs are distributed over the first four height classes in this quadrat (Table 6.6). In plot 3 all these height classes contain only representatives of *Aframomum angustifolium*, namely 200 plants per hectare in the 0.5 m and the 3.0 m height class, respectively, and in the 1.0 m and 2.0 m height classes 100 plants per hectare each (Table 6.6 & Figure 6.17). In plot 4 this growth form has no representatives in the 0.5 m height class (Table 6.6). *Albizia gumnifera* and *Coffea canephora* (COFCAN) are represented in the 1.0 m height class (Figure 6.18), while *Antiaris toxicara* and *Coffea canephora* (100 plants per hectare each) are represented in the 2.0 m and 3.0 m height class, respectively (Figure 6.18).

With 13 700 plants per hectare plot 3 contains the second highest density of trees of all eight sample plots (Table 6.5 – 6.8). *Aframomum angustifolium* (5 100 plants per hectare) is the most prominent tree in this plot, followed by *Guarea cedrata* (3 500 plants per hectare) and *Albizia gumnifera* (2 300 plants per hectare) (Figure 6.19). It also has the second highest number of different tree species, namely 13, of all eight sample plots (Figure 6.14, 6.15, 6.19, 6.20, 6.24, 6.25, 6.29 & 6.30). Like in plot 2 the highest density of plants per hectare is in the 1.00 m height class (3 700 plants per hectare) with a steady decline over the next three taller height classes (to 2 100 plants per hectare in the 4.0 – 5.0 m height class), followed by a more than tenfold decline to the > 6.0 m height class (from 2 100 to 200 plants per hectare) (Table 6.6 & Figure 6.19). The lowest number of different tree species is in the 0.5 m height class, namely three, followed by the > 6.0 m height class with four different tree species, while all other height classes have either six or seven different tree species (Figure 6.19).

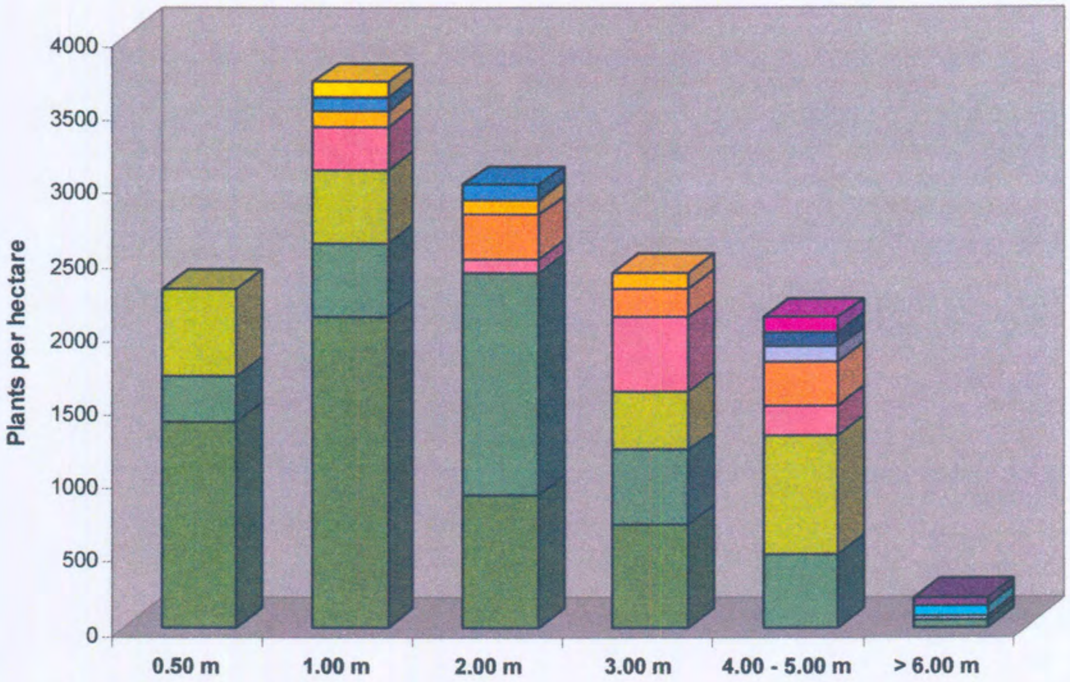

Figure 6.19: Density of trees (plants per hecatre) according to height class and species in plot 3.

🟪 "Unidentified species"
🟦 *Oxyanthus speciosus*
🟨 *Entandrophragma utile*
🟪 *Clitandra species 1*
🟦 *Canarium schweinfurthii*
🟪 *Macaranga monandra*
🟦 *Dracaena fragrans*
🟧 *Pachystela brevipes*
🟧 *Tetrorchidium didymostemon*
🟥 *Galinera saxifraga*
🟨 *Albizia gumnifera*
🟩 *Guarea cedrata*
🟩 *Aframomum angustifolium*

With 7 625 trees per hectare plot 4 lies below the mean number of 8 529 trees per hectare for the whole island and has only the fifth highest density of trees per hectare of the eight sample plots (Table 6.5 -6.8 & Figure 6.5). With ten different tree species this plot has also a species richness below the average of all sample plots (Figure 6.14, 6.15, 6.19, 6.20, 6.24, 6.25, 6.29 & 6.30). With 5 725 plants per hectare *Albizia gumnifera* is the most prominent representative of this growth form and it has representatives in all six height classes (Figure 6.20). *Ficus ovata* (FICOVA) follows far behind with 600 plants per hectare as second most prominent species (Figure 6.20). While *Ouratea hiernii*, *Guarea cedrata*, *Galinera saxifraga* and *Coffea canephora* follow suit with 300, 225, 200 and again 200 plants per hectare each, respectively (Figure 6.20). The remaining four species have between 75 - 100 plants per hectare in this growth form (Figure 6.20). The 3.0 m height class with 2 100 plants per hectare has the highest density of trees, while all other height classes have densities of between 1 000 to 1 700 plants per hectare (Table 6.6 & Figure 6.20). Only the > 6.0 m height class has a more than tenfold lower density with only 125 plants per hectare (Table 6.6 & Figure 6.20). The highest number of different species can be found in the 2.0 m height class, namely five (Figure 6.20).

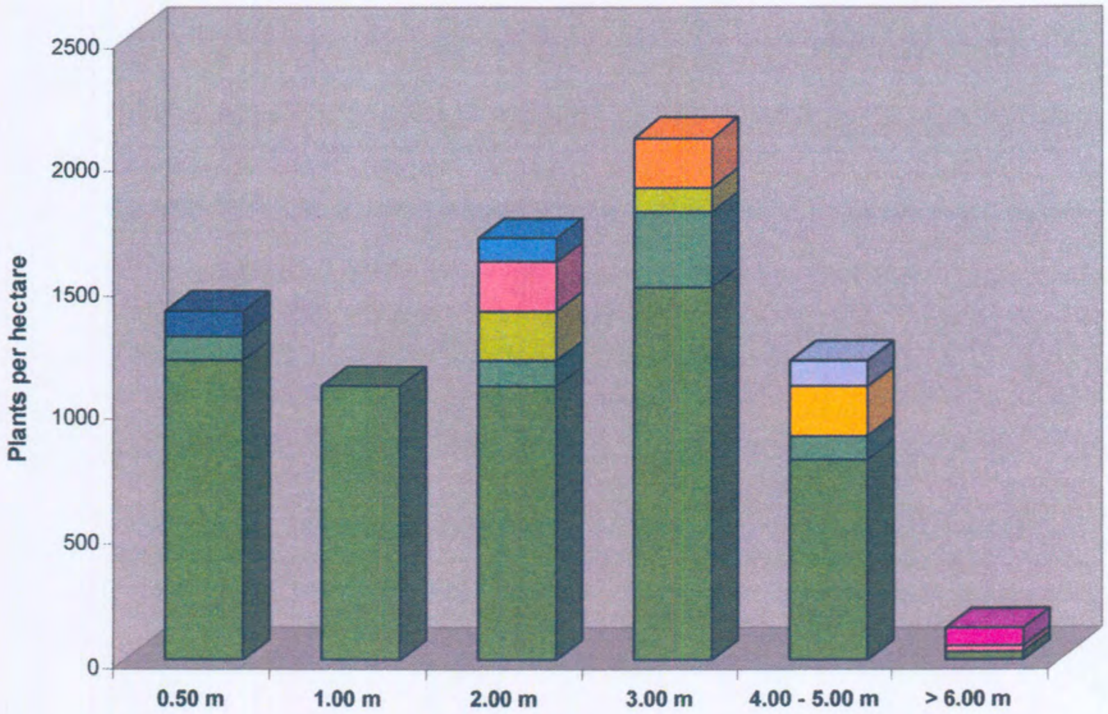

Figure 6.20: Density of trees (plants per hectare) according to height class and species in plot 4.

Key:

🟪 *Macaranga monandra*
🟦 *Trichilia species 1*
⬜ *Tetrorchidium didymostemon*
🟦 *Beilschmedia ugandensis*
🟧 *Galinera saxifraga*
🟧 *Coffea canephora*
🟥 *Guarea cedrata*
🟨 *Ouratea hiernii*
🟩 *Ficus ovata*
🟩 *Albizia gumnifera*

Figure 6.21 summarises the mean number of plants per hectare over all species present, including dead plants, for quadrat II. Twenty different species are present in quadrat II, five of which - *Albizia gumnifera*, *Guarea cedrata*, *Galinera saxifraga*, *Tetrorchidium didymostemon* and *Macaranga monandra* - appear in both sample plots and thus seem to be more evenly distributed throughout the quadrat (Figure 6.21). The mean number of plants for this quadrat is 11 913 per hectare (Table 6.6). The most prominent plant in this quadrat is *Albizia gumnifera* with 4 063 plants per hectare (Figure 6.21), followed by *Aframomum angustifolium* with a density of 2 850 plants per hectare and hence 0.7 times the density of the former species. *Aframomum angustifolium* is also only present in plot 3 indicating a more patchy distribution throughout the quadrat (Figure 6.21). Another prevalent representative is *Guarea cedrata* with 1 788 plants per hectare (Figure 6.21). Also important are *Galinera saxifraga* and *Ouratea hiernii* with 700 plants per hectare each, as well as *Tetrorchidium didymostemon* (450 plants per hectare), *Ficus ovata* (300 plants per hectare) and *Coffea canephora* (200 plants per hectare) (Figure 6.21). All remaining species contribute between 12 - 150 plants per hectare (Figure 6.21). An important feature in this quadrat is the high mean number of "Fallen dead" trees with 79 plants per hectare which occur mainly in plot 4 (Figure 6.21).

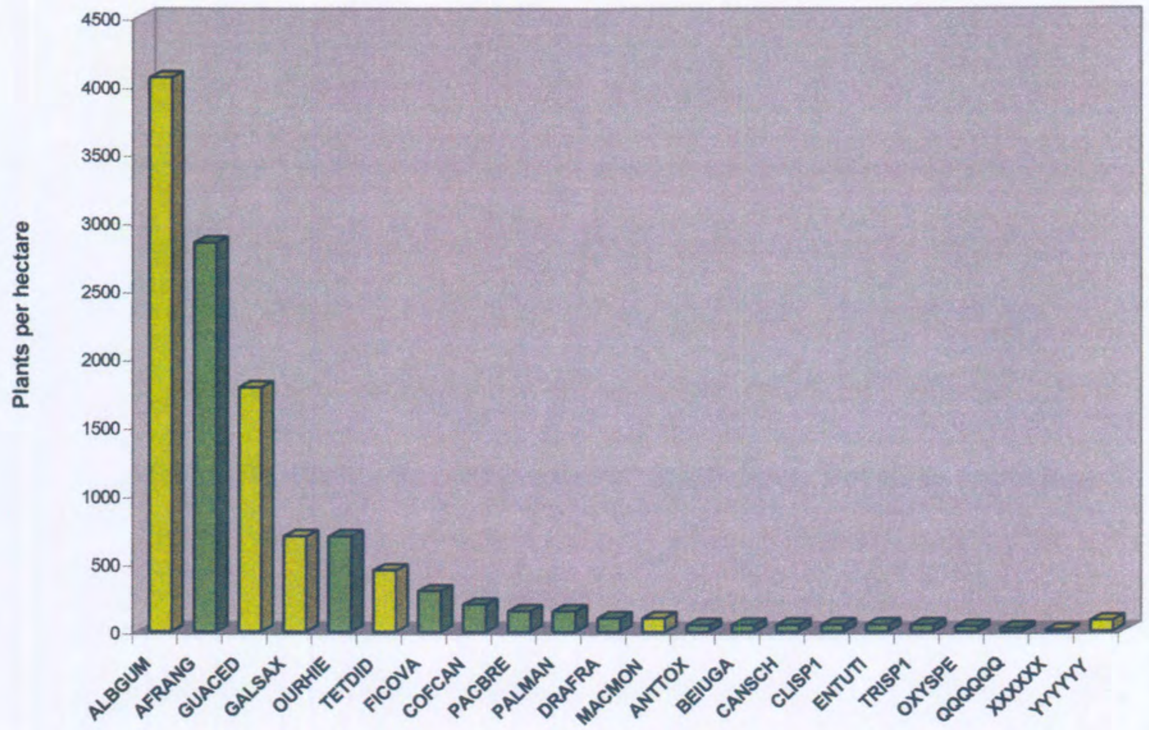

Figure 6.21: Mean density (plants per hectare) per species in quadrat II.

ALBGUM = *Albizia gumnifera*
AFRANG = *Aframomum angustifolium*
GUACED = *Guarea cedrata*
GALSAX = *Galinera saxifraga*
OURHIE = *Ouratea hiernii*
TETDID = *Tetrorchidium didymostemon*
FICOVA = *Ficus ovata*
COFCAN = *Coffea canephora*
PACBRE = *Pachystela brevipes*
PALMAN = *Palisota mannii*
DRAFRA = *Dracaena fragrans*
MACMON = *Macaranga monandra*
ANTTOX = *Antiaris toxicara*
BEIUGA = *Beilschmedia ugandensis*
CANSCH = *Canarium schweinfurthii*
CLISP1 = *Clitandra species 1*

ENTUTI = *Entandrophragma utile*
TRISP1 = *Trichilia species 1*
OXYSPE = *Oxyanthus speciosus*
QQQQQQ = Unidentified species
XXXXXX = Standing dead tree
YYYYYY = Fallen dead tree
🟨 = Plant species present in both sample plots
🟩 = Plant species only present in one sample plot

Quadrat III

The only representative of the shrubs growth form in plot 5 is *Palisota mannii* in the two lowest height classes (400 and 200 plants per hectare, respectively). In plot 6 three species constribute to the shrub growth form, each of them in a different height class, namely *Palisota schweinfurthii* (0.5 m), *Oxyanthus speciosus* (1.0 m) and *Aframomum angustifolium* (3.0 m) (Table 6.7 & Figure 6.22 & 6.23).

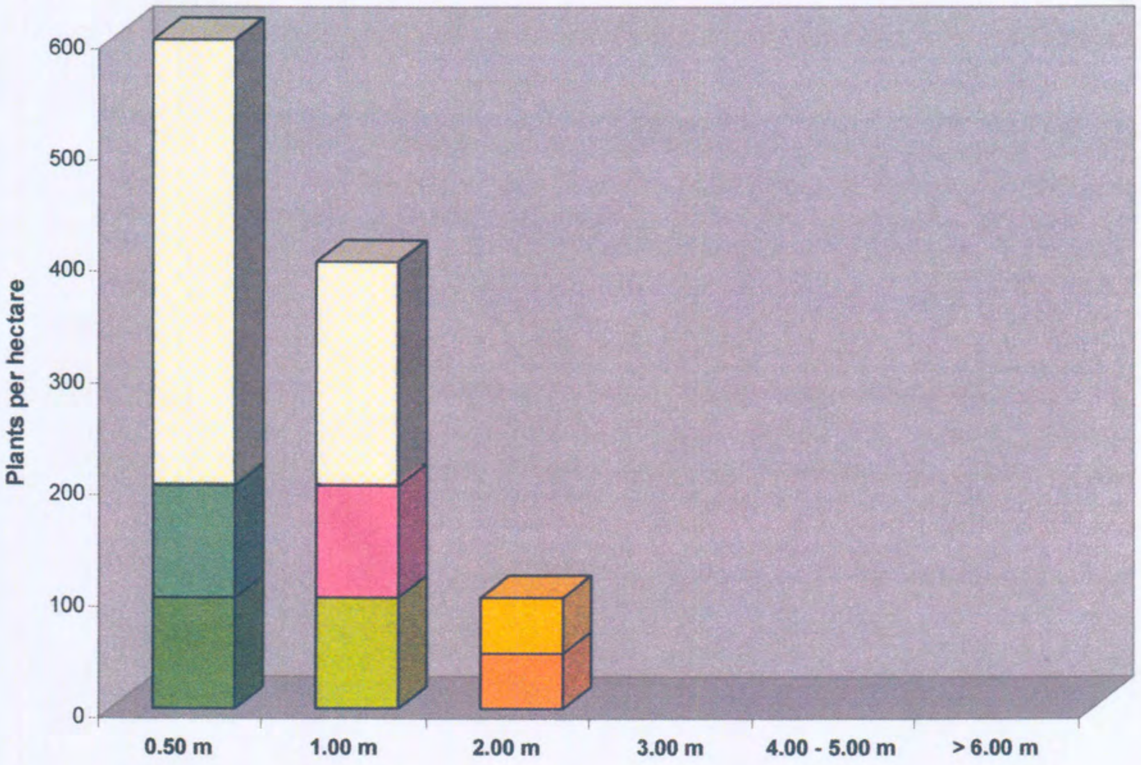

Figure 6.22: Density (plants per hectare) of sparse shrub ((full colour) and shrub (chequered colour) according to height class and species in plot 5.

Key:

⬜ *Palisota mannii*
🟧 *Dracaena fragrans*
🟧 *Aframomum angustifolium*
🟥 *Oxyanthus speciosus*
🟨 *Eugenia capensis*
🟩 *Millettia dura*
🟩 *Guarea cedrata*

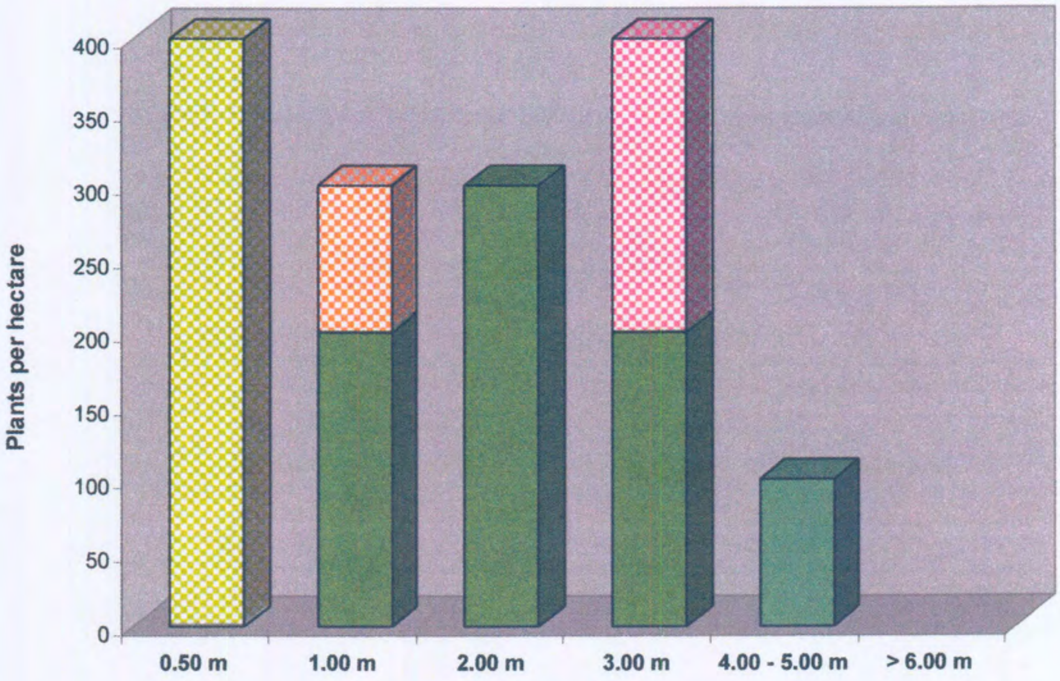

Figure 6.23: Density (plants per hectare) of sparse shrub (full colour) and shrub (chequered colour) according to height class and species in plot 6.

Key:

🟧 *Oxyanthus speciosus*
🟥 *Aframomum angustifolium*
🟨 *Palisota schweinfurthii*
🟩 *Peddiea fischeri*
🟩 *Aframomum angustifolium*

While plot 5 has representatives of the sparse shrub growth form in the three lowest height classes, this growth form is represented in plot 6 in the four height classes from 1.0 m to 4.0 - 5.0 m (Figure 6.22 & 6.23). There are six different species in plot 5, each of them only represented in one height class, namely *Guarea cedrata*, *Millettia dura* (both in the 0.5 m height class), *Eugenia capensis*, *Oxyanthus speciosus* (both in the 1.0 m height class), *Aframomum angustifolium* and *Dracaena fragrans* (both in the 2.0 m height class) (Figure 6.22). In plot 6 only two species are present in the sparse shrub growth form, namely *Aframomum angustifolium* and *Peddiea fischeri*, the latter of which only occurs in the 4.0 – 5.0 m height class (Figure 6.23).

Thirteen different tree species are present in plot 5 (Figure 6.24). The number of plants declines steadily from the 0.5 m height class to the 4.0 – 5.0 m height class (from 2 300 to 275 plants per hectare), the latter of which contains only one-tenth of the number of trees of the former (Table 6.7 & Figure 6.24). Even though plot 5 has the highest number of different tree species it is with only 6 200 trees per hectare far below the mean number for all sample plots (Table 6.5 – 6.8 & Figure 6.14, 6.15, 6.19, 6.20, 6.24, 6.25, 6.29 & 6.30). The > 6.0 m height class of plot 5 is represented by *Pachystela brevipes* (600 plants per hectare) and *Eugenia capensis* (100 plants per hectare). Both of these species occur again only once in any of the lower height classes (Figure 6.24). The most prominent tree species in this plot is *Dracaena fragrans* (2 250 plants per hectare) followed by *Oxyanthus speciosus* (1 150 plants per hectare). The 2.0 m height class with nine different tree species contains the greatest species richness in this plot (Figure 6.24).

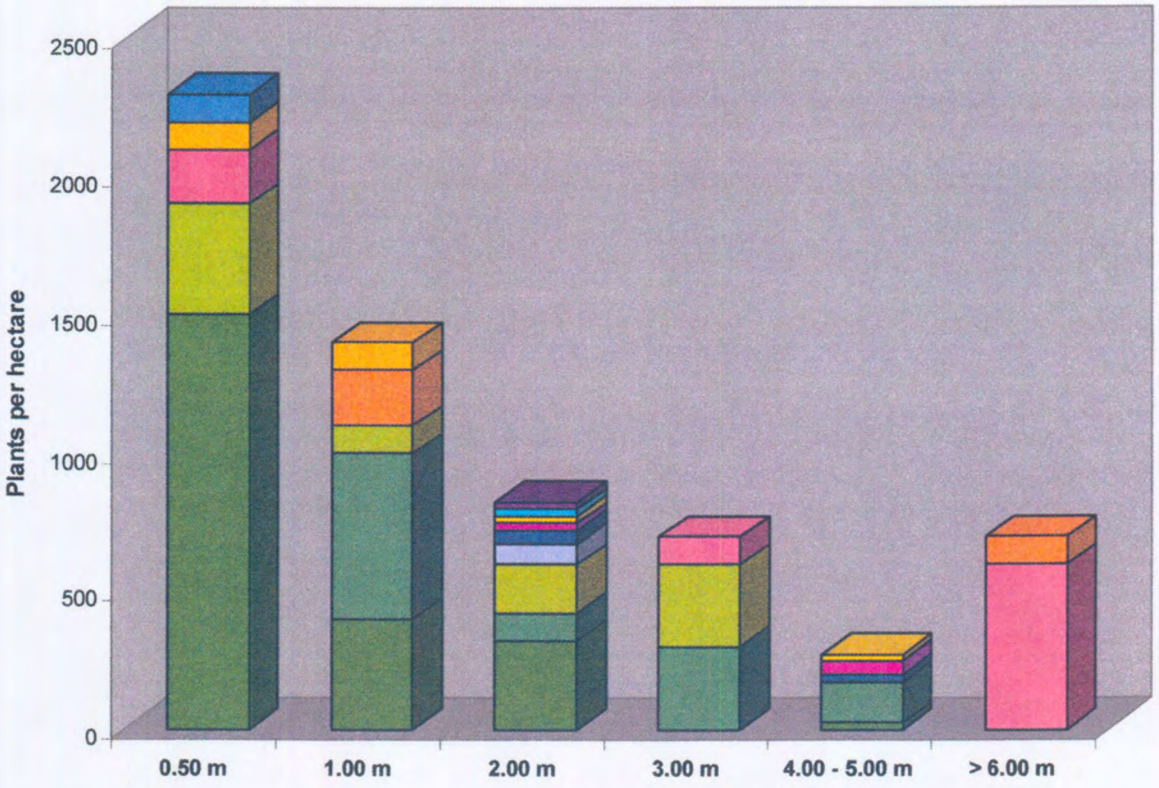

Figure 6.24: Density of trees (plants per hectare) according to height class and species in plot 5.

Key:

🟪	*Trilepsium madagascariense*
🟦	*Psychotria mannii*
🟨	*Albizia gumnifera*
🟪	*Rinorea brachypetala*
🟦	*Beilschmedia ugandensis*
⬜	*Psychotria peduncularis*
🟦	*Psychotria species 1*
🟧	*Canthium species 1*
🟧	*Eugenia capensis*
🟥	*Pachystela brevipes*
🟨	*Guarea cedrata*
🟩	*Oxyanthus speciosus*
🟩	*Dracaena fragrans*

In contrast to plot 5, plot 6 has with 9 500 trees per hectare a density which is higher than the mean density of all sample plots (Table 6.5 – 6.8 & Figure 6.14, 6.15, 6.19, 6.20, 6.24, 6.25, 6.29 & 6.30). Even though, this plot only contains eight different tree species (Figure 6.25). Here again *Dracaena fragrans* is the most prominent tree species with 4 100 plants per hectare, followed by *Aframomum angustifolium* with 2 800 plants per hectare. All but the > 6.0 m height class contain either three or four different tree species (Figure 6.25). The highest tree density with 3 100 plants per hectare is in the 1.0 m height class, followed by 2 500 plants per hectare in the 0.5 m height class. All other height classes have a density below 1 500 trees per hectare. The > 6.0 m height class has, with 500 plants per hectare, the lowest density of all height classes and consists of only one species, *Guarea cedrata* (Table 6.7 & Figure 6.25).

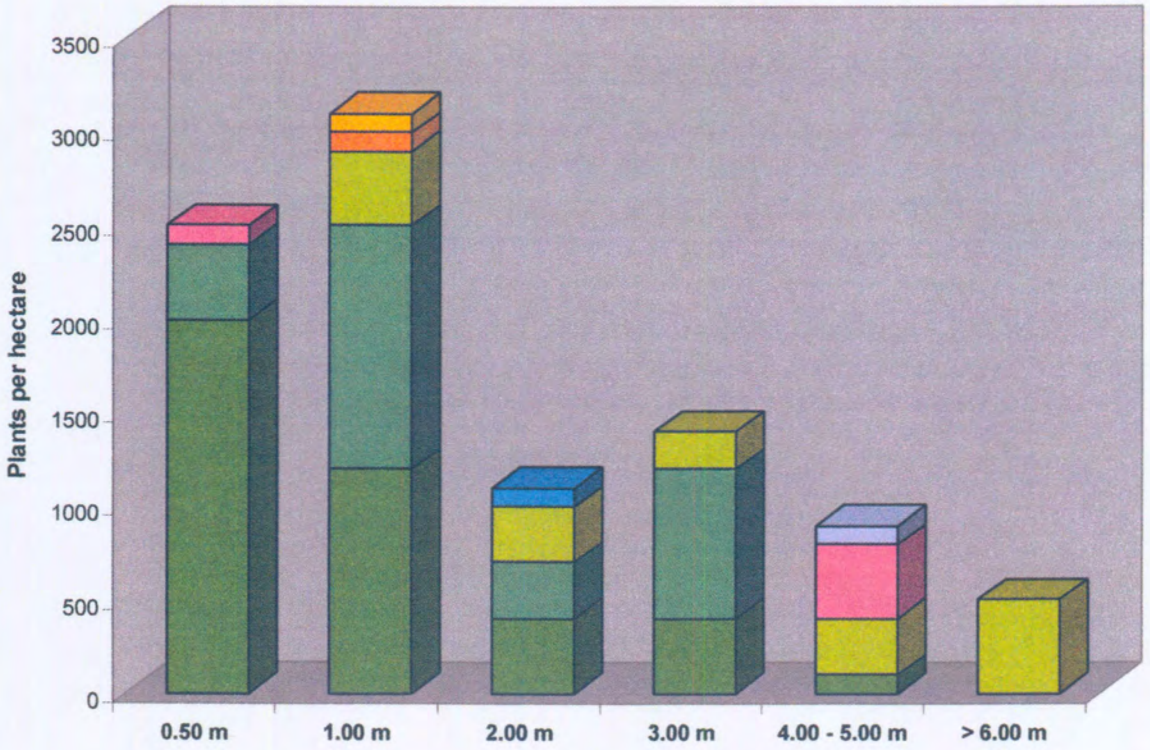

Figure 6.25: Density of trees (plants per hectare) according to height class and species in plot 6.

Key:

🟪 *Albizia gumnifera*
🟦 *Psychotria peduncularis*
🟨 *Ouratea hiernii*
🟧 *Clerodendrum formicarum*
🟥 *Oxyanthus speciosus*
🟨 *Guarea cedrata*
🟩 *Aframomum angustifolium*
🟩 *Dracaena fragrans*

Figure 6.26 summarises the mean number of plants per hectare over all species present, including dead plants, for quadrat III. There are 20 different species present in this quadrat and the mean number of plants per hectare over all live vegetation types is 9 150 (Table 6.7 & Figure 6.26). The four most prominent species, which also occur in both sample plots and are thus rather evenly distributed throughout the quadrat, are *Dracaena fragrans* (3 200 plants per hectare), *Aframomum angustifolium* (1 775 plants per hectare), *Guarea cedrata* (1 388 plants per hectare) and *Oxyanthus speciosus* (925 plants per hectare) (Figure 6.26). Four less prominent species, which are present in only one sample plot and hence show a more patchy distribution throughout quadrat III, are *Pachystela brevipes* (450 plants per hectare), *Palisota mannii* (300 plants per hectare), *Eugenia capensis* (200 plants per hectare) and *Palisota schweinfurthii* (200 plants per hectare) (Figure 6.26). All remaining species have a density of only 100 plants per hectare or below (Figure 6.26). "Fallen dead" trees are conspicuous with 46 plants per hectare (Figure 6.26).

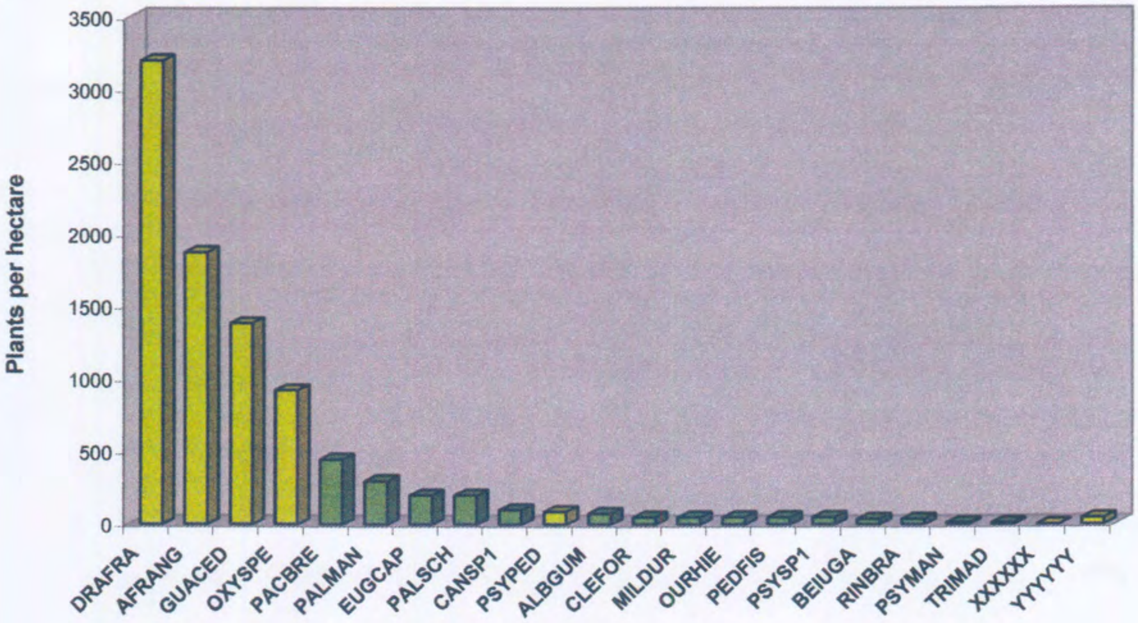

Figure 6.26: Mean density (plants per hectare) per species in quadrat III.

DRAFRA = *Dracaena fragrans*
AFRANG = *Aframomum angustifolium*
GUACED = *Guarea cedrata*
OXYSPE = *Oxyanthus speciosus*
PACBRE = *Pachystela brevipes*
PALMAN = *Palisota mannii*
EUGCAP = *Eugenia capensis*
PALSCH = *Palisota schweinfurthii*
CANSP1 = *Canthium species 1*
PSYPED = *Psychotria peduncularis*
ALBGUM = *Albizia gumnifera*
CLEFOR = *Clerodendrum formicarum*
MILDUR = *Millettia dura*
OURHIE = *Ouratea hiernii*
PEDFIS = *Peddiea fischeri*
PSYSP1 = *Psychotria species 1*
BEIUGA = *Beilschmedia ugandensis*
RINBRA = *Rinorea brachypetala*
PSYMAN = *Psychotria mannii*
TRIMAD = *Trilepsium madagascariense*
XXXXXX = Standing dead trees
YYYYYY = Fallen dead trees
🟨 = Plant species present in both sample plots
🟩 = Plant species only present in one sample plot

Quadrat IV

The shrub growth form in plot 7 is restricted to the 0.5 m, 3.0 m and 4.0 – 5.0 m height class. While the former is solely occupied by *Palisota mannii* (500 plants per hectare), *Aframomum angustifolium* is represented in both of the taller height classes, both times with 100 plants per hectare. *Dracaena fragrans* (25 plants per hectare) is the second representative in the 4.0 – 5.0 m height class (Table 6.8 & Figure 6.27). In plot 8 *Palisota mannii* and *Aframomum angustifolium* are the only representatives of the shrub growth form, the former only in the 0.5 m height class, the latter in the 1.0 m, 2.0 m and 3.0 m height class, contributing 500 plants per hectare to the tallest height class (Table 6.8 & Figure 6.28).

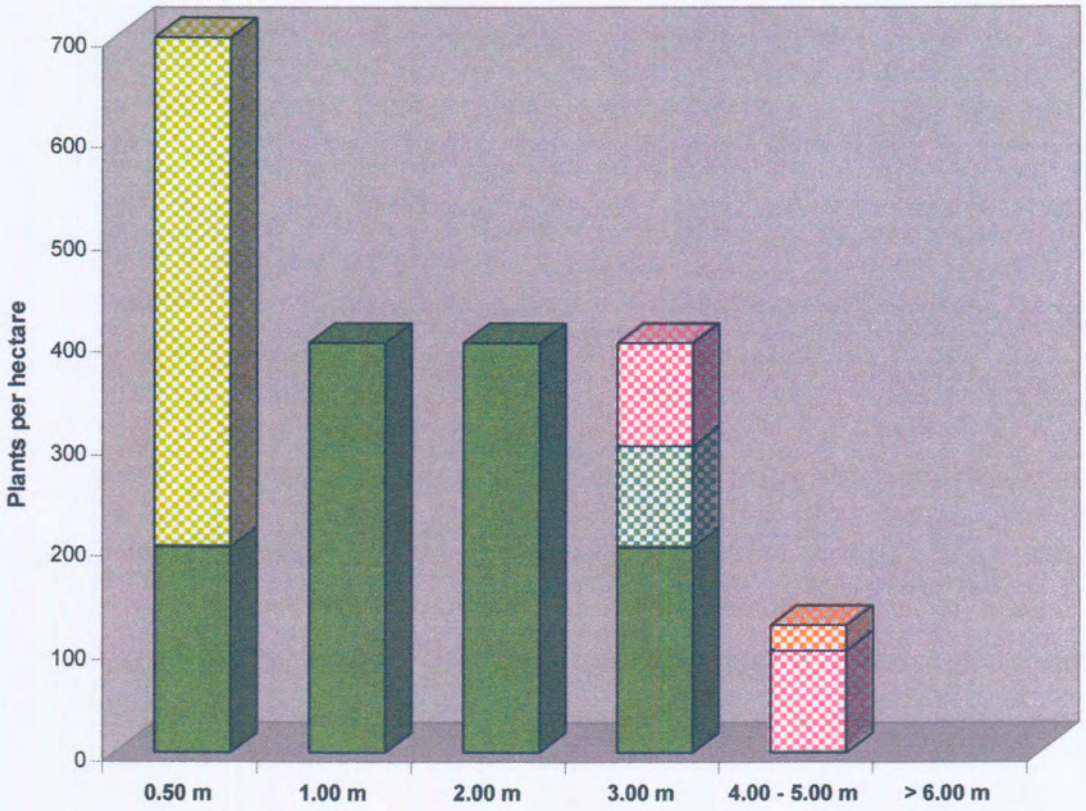

Figure 6.27: Density (plants per hectare) of sparse shrub (full colour) and shrub (chequered colour) according to height class and species in plot 7.

Key:

▦ *Dracaena fragrans*
▦ *Aframomum angustifolium*
▦ *Palisota mannii*
▦ *Dracaena fragrans*
■ *Aframomum angustifolium*

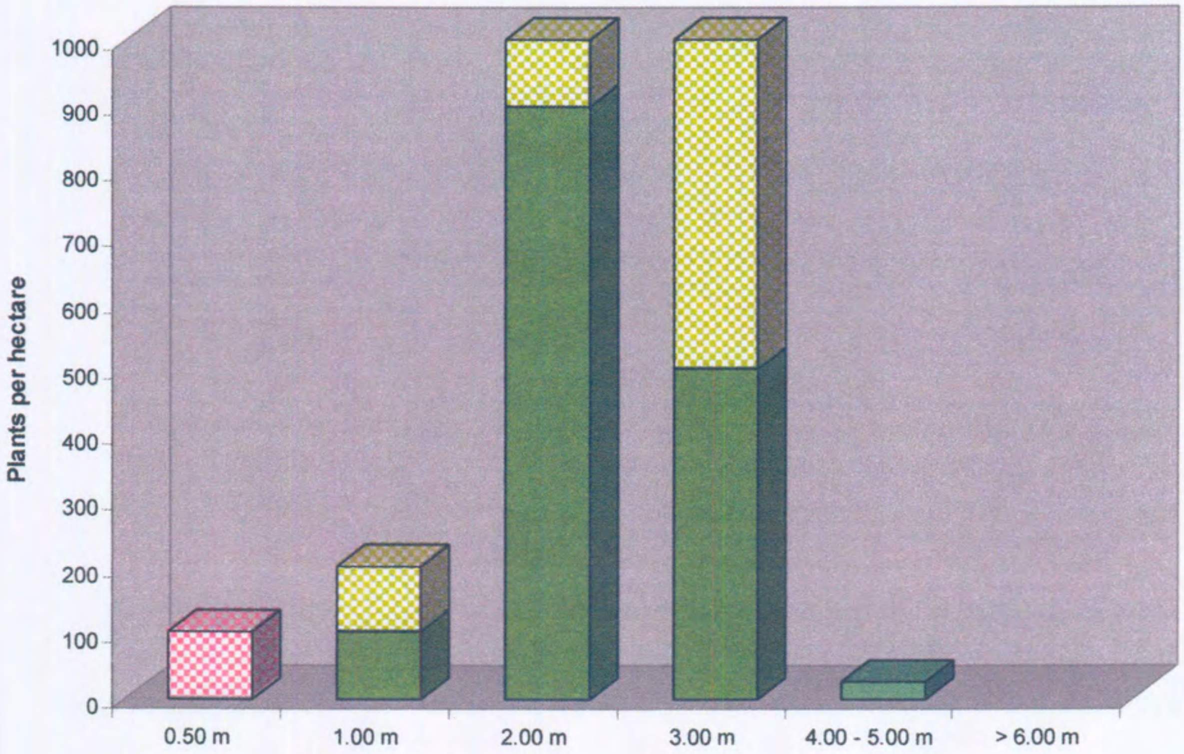

Figure 6.28: Density (plants per hectare) of sparse shrub (full colour) and shrub (chequered colour) according to height class and species in plot 8.

Key:

▨ *Palisota mannii*
▨ *Aframomum angustifolium*
🟩 *Oxyanthus speciosus*
🟩 *Aframomum angustifolium*

The sparse shrub growth form is represented in plot 7 in the first four height classes with *Dracaena fragrans* only occurring in the 3.0 m height class, while *Aframomum angustifolium* is represented in all of these height classes (Table 6.8 & Figure 6.27). In plot 8 *Aframomum angustifolium* is again the dominant sparse shrub with representatives in the 1.0 m up to the 3.0 m height class, and being most prominent in the 2.0 m height class with 900 plants per hectare (Table 6.8 & Figure 6.28). In the 4.0 – 5.0 m height class only *Oxyanthus speciosus* is represented as a sparse shrub, with 25 plants per hectare (Figure 6.28).

With nine different tree species, which altogether contribute 16 050 plants per hectare, plot 7 is the sample plot with the highest density for this growth form, having nearly twice as many trees per hectare as the mean for all sample plots (Table 6.8 & Figure 6.14, 6.15, 6.19, 6.20, 6.24, 6.25, 6.29 & 6.30). The highest number of trees occurs in the 0.5 m height class with 9 500 plants per hectare or 59% of the 16 050 trees. Of those 7 700 trees are represented by *Dracaena fragrans* alone (Figure 6.29). There is a decline to about one-third of this density to the 1.0 m height class, with 3 200 plants per hectare and *Dracaena fragrans* again being the most prominent representative (2 100 plants per hectare) (Table 6.8 & Figure 6.29). The 2.0 m height class has a similar density (2 400 plants per hectare) but now with *Aframomum angustifolium* as main representative (1 500 plants per hectare) (Figure 6.29). The three remaining height classes all have below 500 trees per hectare, with the > 6.0 m height class being the most prominent (425 plants per hectare). In this height class *Guarea cedrata* is the most prominent representative (350 plants per hectare), which occurs otherwise only in the 0.5 m height class (300 plants per hectare) (Figure 6.29).

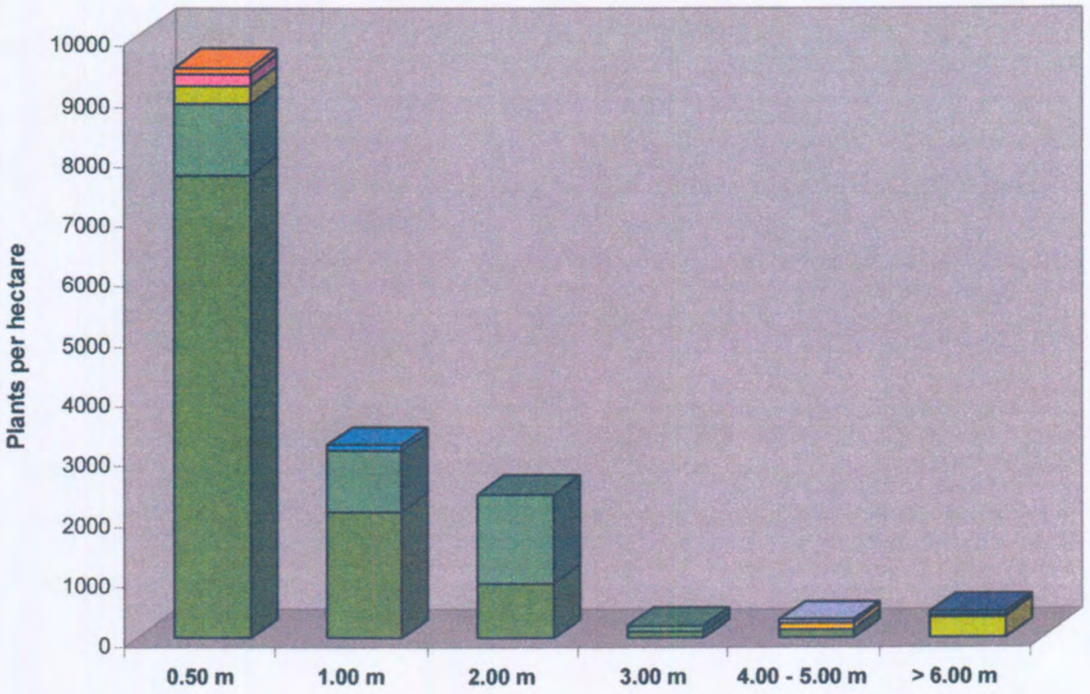

Figure 6.29: Density of trees (plants per hectare) according to height class and species in plot 7.

Key:

🟦 *Albizia gumnifera*
🟪 *Peddiea fischeri*
🟦 *Psychotria peduncularis*
🟨 *Oxyanthus speciosus var. stenocarpus*
🟧 *Ficus species 2*
🟥 *Oxyanthus speciosus*
🟨 *Guarea cedrata*
🟩 *Aframomum angustifolium*
🟩 *Dracaena fragrans*

In plot 8 *Aframomum angustifolium* is the most prominent of all eight represented tree species. It is mainly represented in the three lowest height classes, being most prominent in the 2.0 m height class (1 800 plants per hectare). There is a more than two-fold increase in density from the 0.5 m to the 2.0 m height class (from 1 000 to 2 100 plants per hectare) (Table 6.8 & Figure 6.30). This is followed by a sharp drop to the 3.0 m height class (800 plants per hectare) caused mainly by the sharp decline in density of *Aframomum angustifolium* (from 1 800 to 100 plants per hectare) (Figure 6.30). The two tallest height classes have below 400 plants per hectare each, with the > 6.0 m height class having the lowest density of this height class of all sample plots, i.e. 111 trees per hectare (Table 6.8 & Figure 6.30). This small number is still represented by four different species, namely *Guarea cedrata*, *Tetrorchidium didymostemon*, *Albizia gumnifera* and *Oxyanthus speciosus* (Figure 6.30). This plot has a tree density of only 6 061 plants per hectare, i.e. the second lowest number of trees per hectare of all sample plots, and hence below the mean density for trees per hectare (Table 6.8 & Figure 6.5).

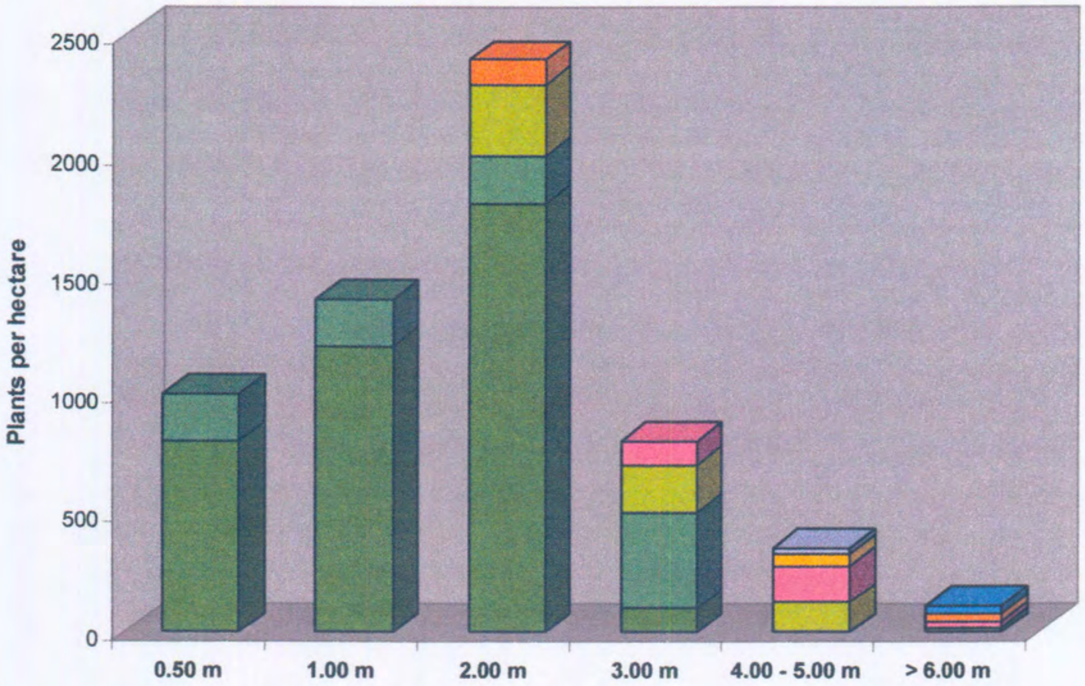

Figure 6.30: Density of trees (plants per hectare) according to height class and species in plot 8.

Key:

🟪 *Galinera saxifraga*
🟦 *Tetrorchidium didymostemon*
🟨 *Ficus wildemanniana*
🟧 *Guarea cedrata*
🟥 *Oxyanthus speciosus*
🟨 *Alchornea cordifolia*
🟩 *Albizia gumnifera*
🟩 *Aframomum angustifolium*

Figure 6.31 summarises the mean number of plants per hectare over all species present, including dead plants, for quadrat IV. There are 14 different species present in this quadrat and the mean number of plants per hectare over all live vegetation types is 13 218 plants per hectare (Table 6.8).The two most prominent species are *Aframomum angustifolium* with 5 650 plants per hectare and *Dracaena fragrans* with 5 538 plants per hectare (Figure 6.31). The former occurs in both sample plots and hence, again seems to be more evenly distributed throughout this quadrat (Figure 6.31); while the latter only occurs in plot 7, which indicates a more patchy distribution throughout the quadrat but at the same time a particularly high density of plants per hectare where it occurs (Figure 6.27 - 6.30). All other species have far lower densities in this quadrat. The next five important species are *Albizia gumnifera* (536 plants per hectare), *Guarea cedrata* (392 plants per hectare), *Alchornea cordifolia* (313 plants per hectare), *Palisota mannii* (300 plants per hectare) and *Oxyanthus speciosus* (249 plants per hectare) (Figure 6.31). Of those, only *Alchornea cordifolia* and *Oxyanthus speciosus* occur just in one of the sample plots (Figure 6.31). The remaining seven species all have densities of 50 plants per hectare or below (Figure 6.31). The number of "Dead Trees" is rather prominent in both categories with 41 "Fallen dead" trees per hectare and 44 "Standing dead" trees per hectare, and a more or less equal distribution of those trees in both sample plots (Figure 6.31).

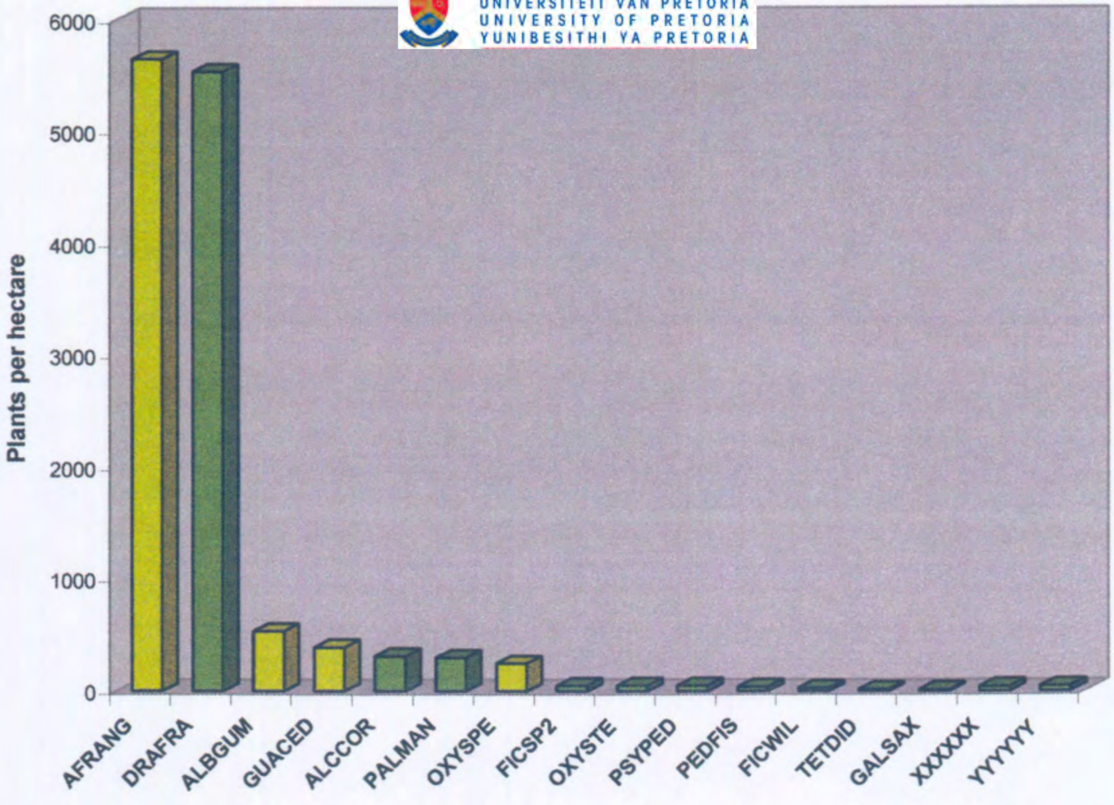

Figure 6.31: Mean density (plants per hectare) per species in quadrat IV.

AFRANG = *Aframomum angustifolium*
DRAFRA = *Dracaena fragrans*
ALBGUM = *Albizia gumnifera*
GUACED = *Guarea cedrata*
ALCCOR = *Alchornea cordifolia*
PALMAN = *Palisota mannii*
OXYSPE = *Oxyanthus speciosus*
FICSP2 = *Ficus species 2*
OXYSTE = *Oxyanthus speciosus var. stenocarpus*
PSYPED = *Psychotria peduncularis*
PEDFIS = *Peddiea fischeri*
FICWIL = *Ficus wildemanniana*
TETDID = *Tetrorchidium didymostemon*
GALSAX = *Galinera saxifraga*
XXXXXX = Standing dead trees
YYYYYY = Fallen dead trees
🟨 = Plant species present in both sample plots
🟩 = Plant species only present in one sample plot

"Tree" density corrected for Aframomum angustifolium

Although, *Aframomum angustifolium* is classified as a herb (Lind & Tallantire 1962, Langdale-Brown *et al.* 1964, Katende *et al.* 1999) for the purpose of this study its single-stem representatives were listed under "Trees". Figure 6.32 shows the number of trees in each sample plot without single-stem *Aframomum angustifolium*.

Compared to Figure 6.5 the sequence of plots according to tree density changes as follows: from plot 7 — plot 3 – plot 6 – plot 4 – plot 1 – plot 5 – plot 8 – plot 2 to plot 7 – plot 3 – plot 4 – plot 6 – plot 5 – plot 1 – plot 2 – plot 8.

While the first two plots – both containing *Aframomum angustifolium* – hence keep their respective ranks the sequence of the next six plots changes pair wise. The following three pairs, e.g. plot 6 and plot 4, change places among each other since, after subtracting the plants per hectare of *Aframomum angustifolium*, the remaining tree density falls below the one of the plot directly following, i.e. plot 4 is now ahead of plot 6.

The three plots (2, 4, 5) not containing *Aframomum angustifolium* are distributed more or less on a straight line from the west to the east of the island (Figure 6.1).

While plot 2 and plot 4 are both characterised by wide-open spaces (see this Chapter - Description of sample plots) and are therefore also more exposed to wind, plot 5 has a dense and closed tree cover adjacent to the eastern shore of the island (Figure 6.1)

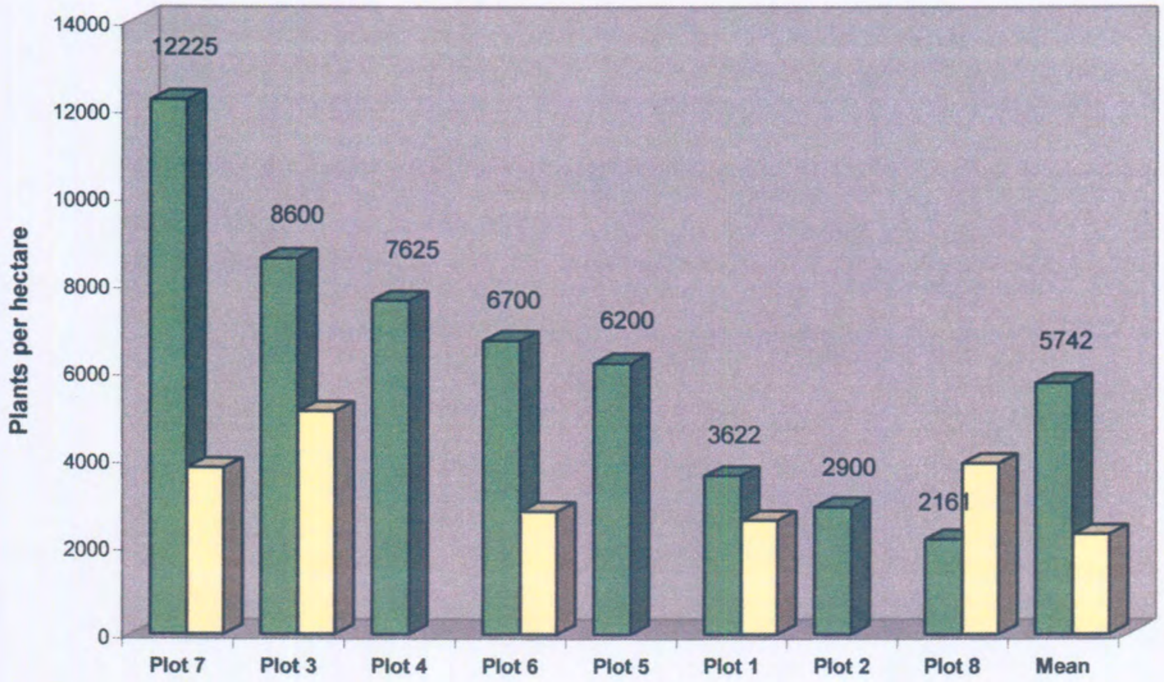

Figure 6.32: Number of woody "Trees" in each sample plot after correcting for *Aframomum angustifolium*.

Key:

🟨	Number of subtracted *Aframomum angustifolium*
🟩	Number of "Real Trees"

Distribution of plant species according to growth form

Shrub

From the eight different plant species which are represented in this growth form *Palisota mannii* is the most prevalent species in the 0.5 m and the 1.0 m height classes (Figure 6.33). *Aframomum angustifolium* is the most widely distributed species occurring in four of the five represented height classes, while missing in the 0.5 m height class (Figure 6.33). The shrub growth form has no representatives in the > 6.0 m height class (Figure 6.33). The 0.5 m height class has the highest density of shrub with a mean of 241 plants per hectare. The 1.0 m and 4.0 - 5.0 m height class both have a density equal to or below 50 plants per hectare, with the latter height class having the lowest mean density with 16 plants per hectare (Figure 6.33). *Nephrolepis biserrata*, *Palisota mannii and Palisota schweinfurthii* are only represented in the shrub growth form (Figure 6.33 – 6.38).

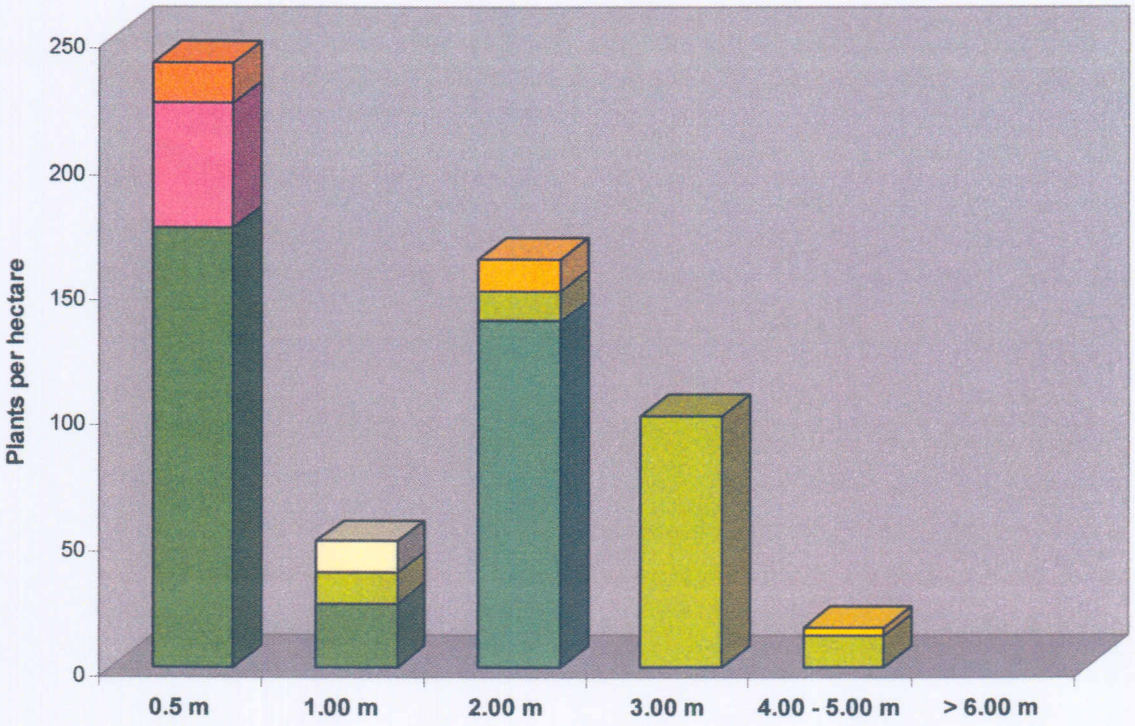

Figure 6.33: Mean density (plants per hectare) of shrub according to plant species and height class.

Key:

🟨 *Dracaena fragrans*
⬜ *Oxyanthus speciosus*
🟧 *Galinera saxifraga*
🟧 *Nephrolepis biserrata*
🟥 *Palisota schweinfurthii*
🟩 *Aframomum angustifolium*
🟩 *Ouratea hiernii*
🟩 *Palisota mannii*

Sparse shrub

This growth form is represented by 13 different plants species, while only four of the species contributing to the shrub growth form are also represented here, namely *Aframomum angustifolium*, *Dracaena fragrans*, *Ouratea hiernii* and *Oxyanthus speciosus* (Figure 6.34). *Aframomum angustifolium* is again the most widely distributed and also the most abundant species (Figure 6.34). It occurs in the first four height classes, but not in the 4.0 - 5.0 m height class. There are no representatives of this growth form in the > 6.0 m height class (Figure 6.34). The height class with the highest density of plants is the 2.0 m height class with 250 sparse shrub per hectare, while the 4.0 -5.0 m height class has the lowest density with 54 plants per hectare. Both of these height classes contain four different plant species (Figure 6.34). *Antiaris toxicara* and *Millettia dura* are the only two species which have representatives solely in the sparse shrubs growth form but in no other growth form (Figure 6.33 – 6.38).

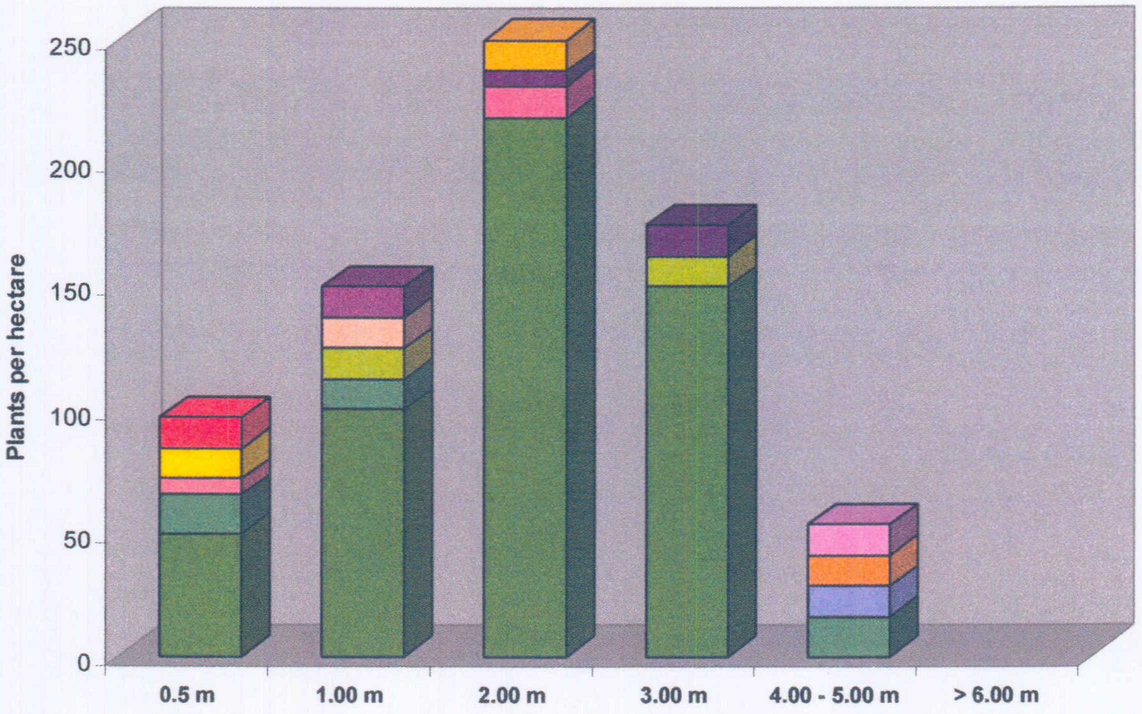

Figure 6.34: Mean density (plants per hectare) of sparse shrub according to plant species and height class.

Key:

🟪 *Peddiea fischeri*
🟪 *Eugenia capensis*
🟥 *Milettia dura*
🟨 *Guarea cedrata*
🟧 *Albizia gumnifera*
🟧 *Antiaris toxicara*
🟧 *Macaranga monandra*
🟦 *Dictyandra arborescens*
🟪 *Dracaena fragrans*
🟨 *Ouratea hiernii*
🟨 *Coffea canephora*
🟩 *Oxyanthus speciosus*
🟩 *Aframomum angustifolium*

Tree

Trees are present in all six of the investigated height classes and 35 of the identified 41 woody species contribute to this growth form. Of those, twelve species also have representatives in either one or both of the shrub vegetation types, i.e. *Aframomum angustifolium, Albizia gumnifera, Coffea canephora, Dictyandra arborescens, Dracaena fragrans, Eugenia capensis, Galinera saxifraga, Guarea cedrata, Macaranga monandra, Ouratea hiernii, Oxyanthus speciosus* and *Peddiea fischeri*. On the basis of their density the 35 species have been assembled into four different groups (Figures 6.35 – 6.39).

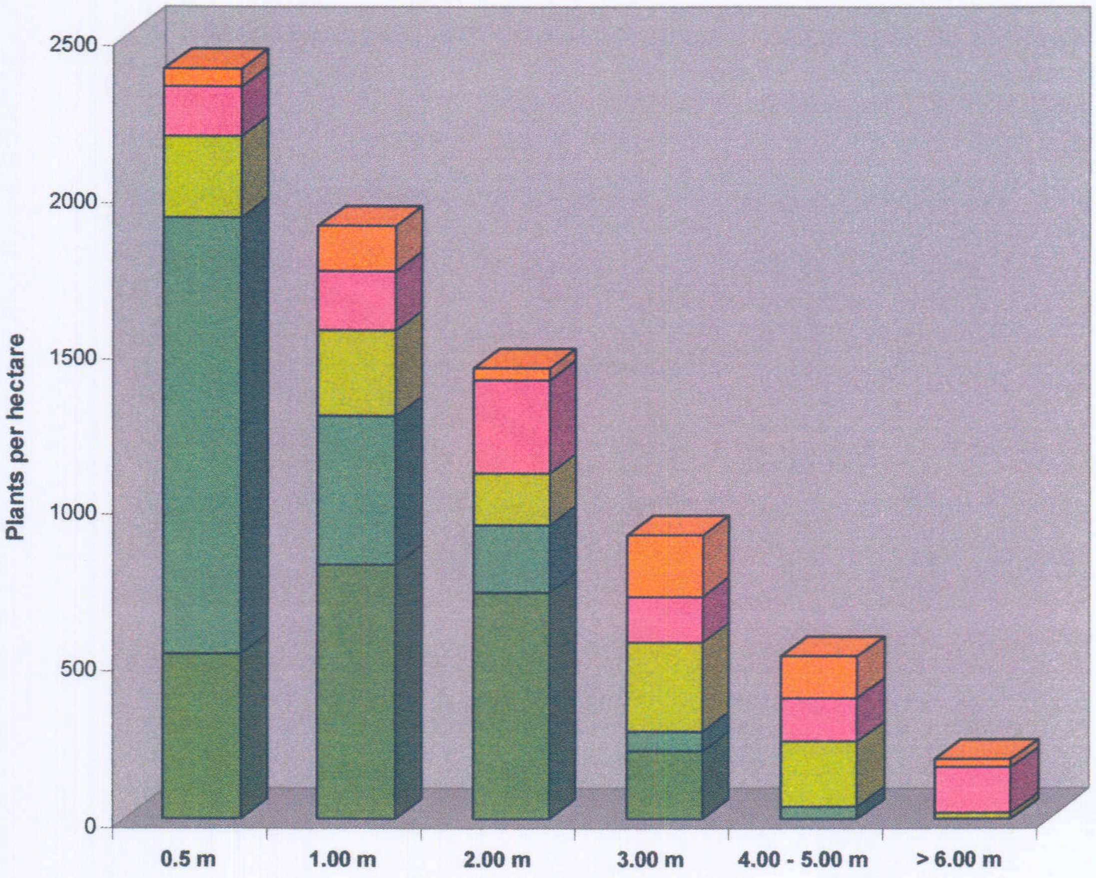

Figure 6.35: Mean density (plants per hectare) of trees of species reaching densities of > 500 plants per hectare.

Key:

🟧 *Oxyanthus speciosus*
🟥 *Guarea cedrata*
🟨 *Albizia gumnifera*
🟩 *Dracaena fragrans*
🟩 *Aframomum angustifolium*

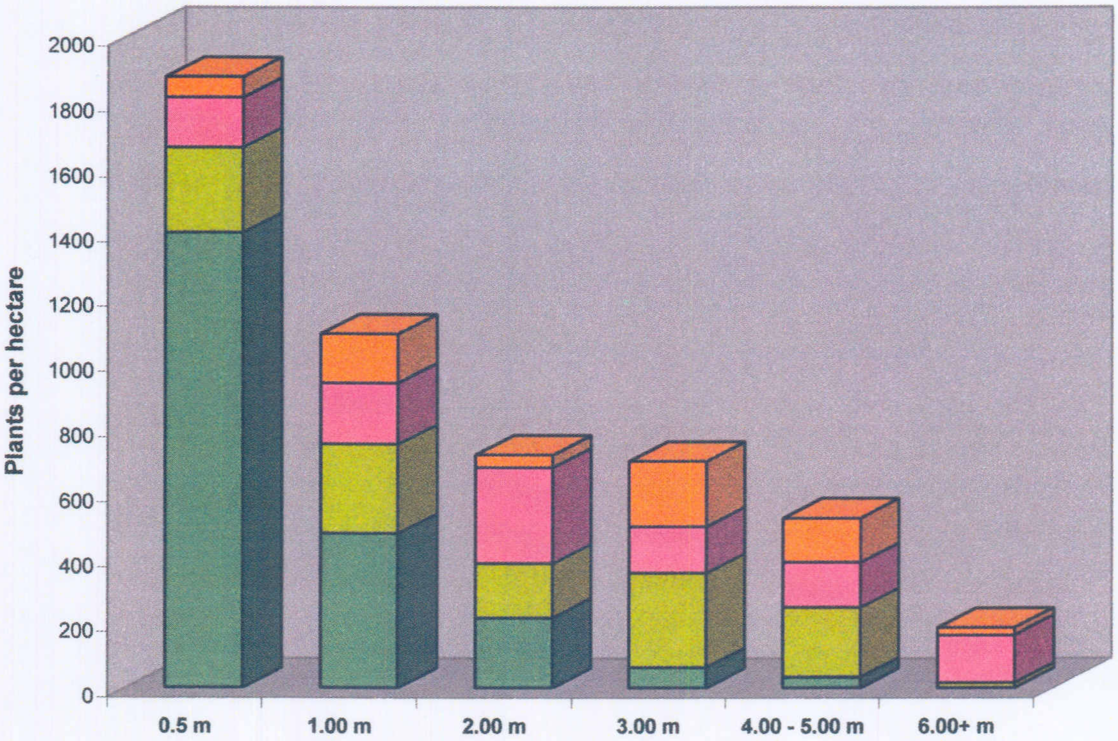

Figure 6.36: Mean density (plants per hectare) of trees of species reaching densities of > 500 plants per hectare. Contributions of *Aframomum angustifolium* are not taken into consideration.

Key:		
	🟧	*Oxyanthus speciosus*
	🟥	*Guarea cedrata*
	🟨	*Albizia gumnifera*
	🟩	*Dracaena fragrans*

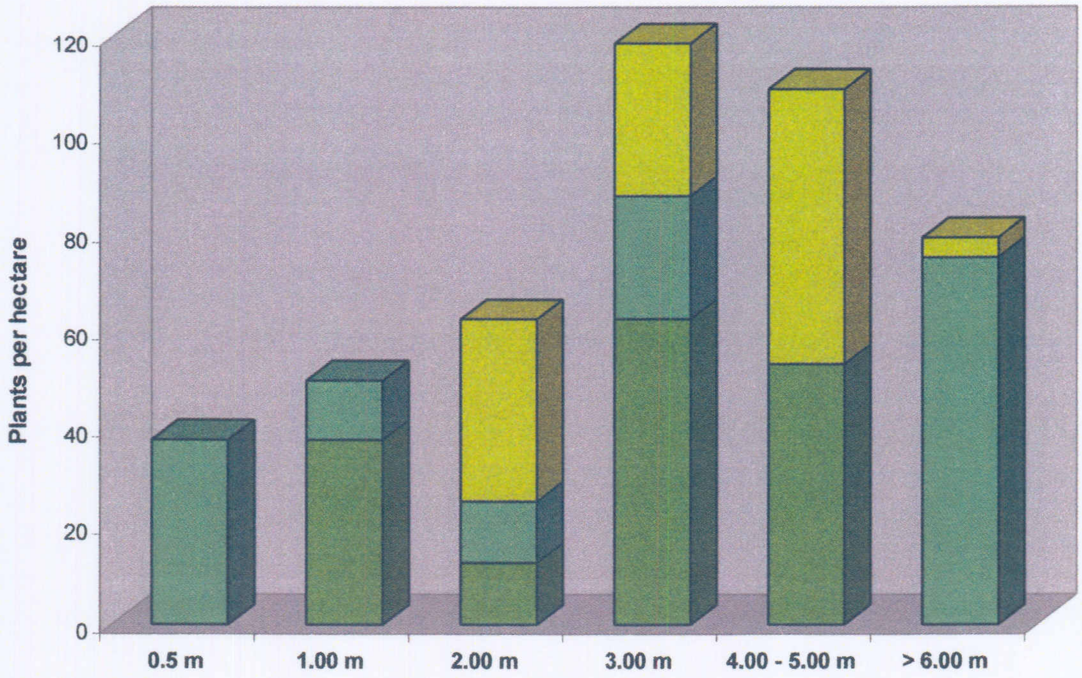

Figure 6.37: Mean density (plants per hectare) of trees of species reaching densities of > 100 to 500 plants per hectare.

Key:

🟨 *Tetrorchidium didymostemon*

🟩 *Pachystela brevipes*

🟩 *Galinera saxifraga*

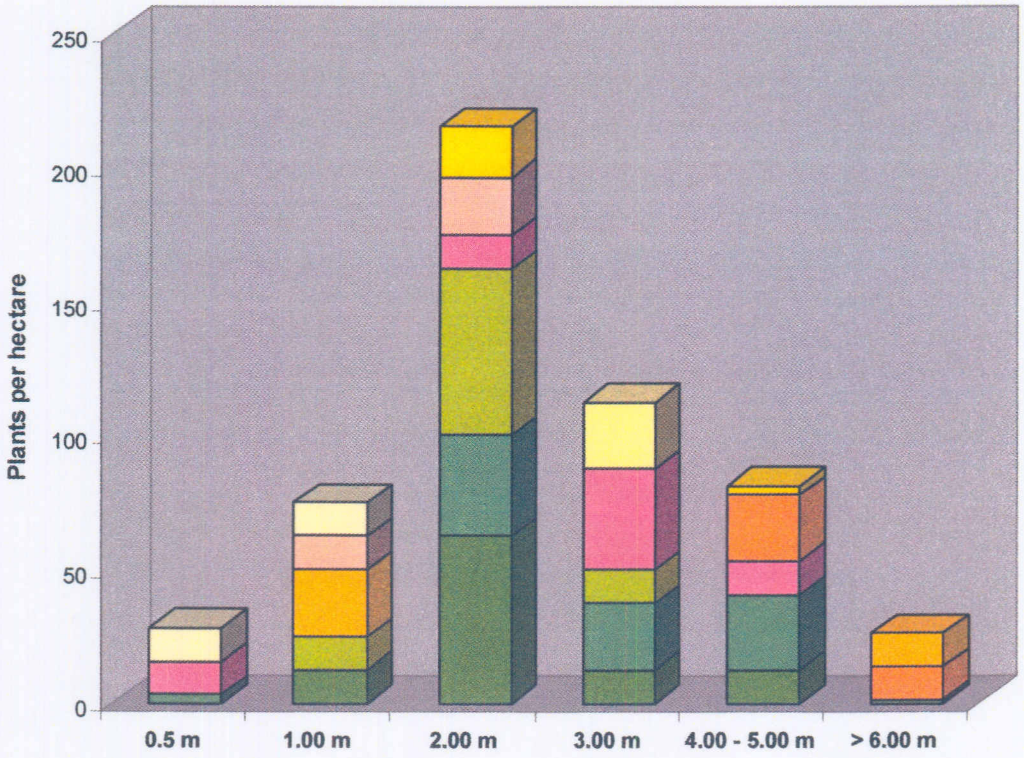

Figure 3.38: Mean density (plants per hectare) of trees of species reaching densities of > 20 to 100 plants per hectare.

Key:

🟨 *Beilschmedia ugandensis*
⬜ *Canthium species 1*
🟨 *Coffea canephora*
🟧 *Psychotria peduncularis*
🟧 *Eugenia capensis*
🟧 *Macaranga monandra*
🟥 *Ficus ovata*
🟩 *Ouratea hiernii*
🟩 *Alchornea cordifolia*
🟩 *Dictyandra arborescens*

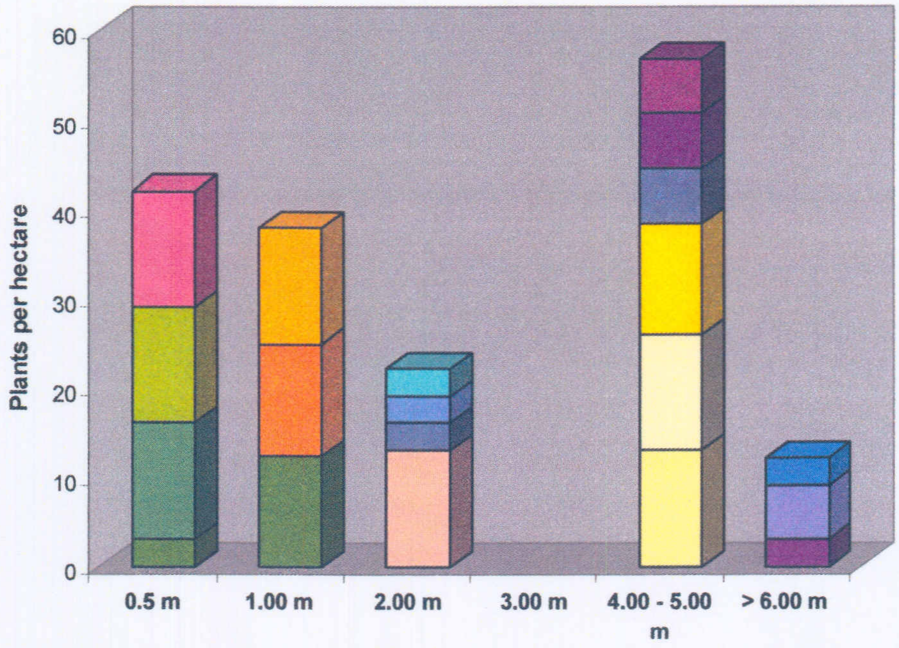

Figure 6.39: Mean density (plants per hectare) of trees of species reaching densities of >1 to 20 plants per hectare.

Key:

🟦	*Clitandra cymulosa*
🟦	*Trilepsium madagascariense*
🟪	*Psychotria mannii*
🟪	*"Unidentified species"*
🟪	*Ficus wildemanniana*
🟪	*Peddiea fischeri*
🟦	*Ronorea brachipetala*
🟨	*Oxyanthus speciosus* var. *stenocarpus*
⬜	*Clitandra species 1*
🟨	*Canarium schweinfurthii*
🟧	*Oxyanthus subpunctatus*
🟧	*Clerodendrum formicarum*
🟧	*Entandophragma utile*
🟥	*Psychotria species 1*
🟩	*Trichilia species 1*
🟩	*Ficus species 2*
🟩	*Ficus species 1*

The first group with mean tree densities of > 500 plants per hectare comprises five different species (Figure 6.35). The tree density in this group declines stepwise from the 0.5 m (2 403 plants per hectare) to the > 6.0 m height class (186 plants per hectare) (Figure 6.35). This is mainly due to the high density of *Dracaena fragrans* and *Aframomum angustifolium* in the three lowest height classes (Figure 6.35). Without *Aframomum angustifolium* the sequence of densities remains the same (Figure 6.36). There is a ten-fold, but stepwise decrease in tree density from the 0.5 m (1 879 plants per hectare) to the > 6.0 m (186 plants per hectare) height class (Figure 6.36). The highest contribution of *Aframomum angustifolium* is to the 2.0 m height class to which it contributes 50% of plants per hectare, followed by the 1.0 m height class with 43% of plants per hectare (Figure 6.35). *Aframomum angustifolium* contributes about one-fifth of the plants per hectare in the 0.5 m (22%) and the 3.0 m (23%) height class (Figure 6.35).

The second group with mean tree densities of > 100 to 500 plants per hectare comprises only three different plant species (Figure 6.37). The highest density of trees per hectare is in the 3.0 m height class (119 plants per hectare), mainly due to a high density of *Galinera saxifraga* (63 plants per hectare) (Figure 6.37). There is a slight decline in density towards the two taller height classes and a nearly two-fold decline towards the 2.0 m height class (64 plants per hectare), with tree density further decreasing towards the 0.5 m height class (38 plants per hectare), only representing *Pachystela brevipes* (Figure 6.37).

The third group with mean tree densities of > 20 to 100 plants per hectare comprises ten different species (Figure 6.38). The highest density of trees per hectare is in the 2.0 m height class (218 plants per hectare) (Figure 6.38). The density decreases towards the three taller height classes, beginning with a more than two-fold decrease in density to the 3.0 m height class (Figure 6.38). It also decreases towards the two smaller height classes, beginning with a nearly three-fold decrease towards the 1.0 m height class. The smallest and tallest height class have nearly the same tree density, namely 27 and 29 plants per hectare, respectively (Figure 6.38). In this group *Dictyandra arborescens* is the most prominent species with 100 trees per hectare, but with no representatives in the 0.5 m height class and the > 6.0 m height class (Figure 6.38).

The final group with mean tree densities of > 1 to 20 plants per hectare contains 17 different species, but has no representatives in the 3.0 m height class (Figure 6.39). Only two species represented in the three smallest height classes also have representatives in the two tallest height classes, namely *Oxyanthus speciosus var. stenocarpus* (1.0 m and 4.0 - 5.0 m height class) and *Rinorea brachipetala* (2.0 m and 4.0 - 5.0 m height class) (Figure 6.39). The highest tree density is in the 4.0 - 5.0 m height class with 57 plants per hectare and representing also the greatest species richness, namely six different species (Figure 6.39).

Overall, this group has the greatest species richness of all four groups, followed by the third group with ten different species (Figure 6.38 & 6.39). The first and second group, showing the highest tree densities, have the smallest species richness with four, respectively three different species each – if *Aframomum angustifolium* is not considered (Figure 6.36 & 6.37).

Density of "Dead Trees"

Tables 6.9 & 6.10 show the number of "Standing dead" and "Fallen dead" trees per hectare for each sample plot and stem diameter classes, while Figure 6.40 classifies the sample plots according to their density of the total number of dead trees per hectare and Figure 6.41 shows the percentage of dead trees in each sample plot. To calculate these percentages the number of trees per hectare in each sample plot corrected for *Aframomum angustifolium* have been used (Figure 6.32).

Table 6.9: *Number of "Fallen dead" trees per hectare in each sample plot according to stem diameter categories*

Number of "Fallen dead" trees												
Plot		1	2	3	4	5	6	7	8	Mean	Σ	%
Stem diameter [cm]	10-15	4	6	4	75	20	11	8	25	19.1	153	40.13
	> 15-20	4				8	33		6	6.4	51	13.45
	> 20-25	8	6	4	25	8		4	13	8.5	68	17.86
	> 25-30		6		25		11	8	6	7	56	14.71
	> 30-50	4	6					12	6	3.5	28	7.35
	> 75-100				25					3.1	25	6.51
Total		20	24	8	150	36	55	32	56	47.6	381	100

Table 6.10: *Number of "Standing dead" trees per hectare in each sample plot according to stem diameter categories*

Number of "Standing dead" trees												
Plot		1	2	3	4	5	6	7	8	Mean	Σ	%
Stem diameter [cm]	10-15			8				44		6.5	52	46.43
	> 15-20						4			0.5	4	3.57
	> 20-25	4		4	4				19	3.9	31	27.86
	> 25-30			4					6	1.3	10	9.29
	> 30-50			4				11		1.9	15	13.57
Total		4	0	20	4	0	4	55	25	14	112	100

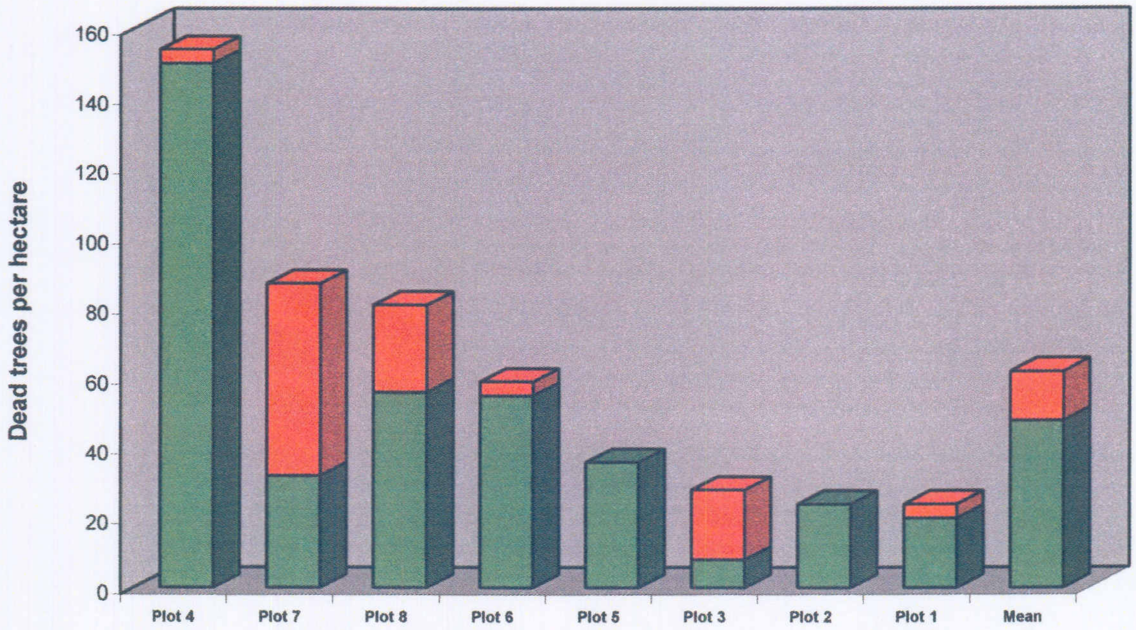

Figure 6.40: Number of dead trees per hectare.

Key: 🟥 Number of standing dead trees
🟩 Number of fallen dead trees

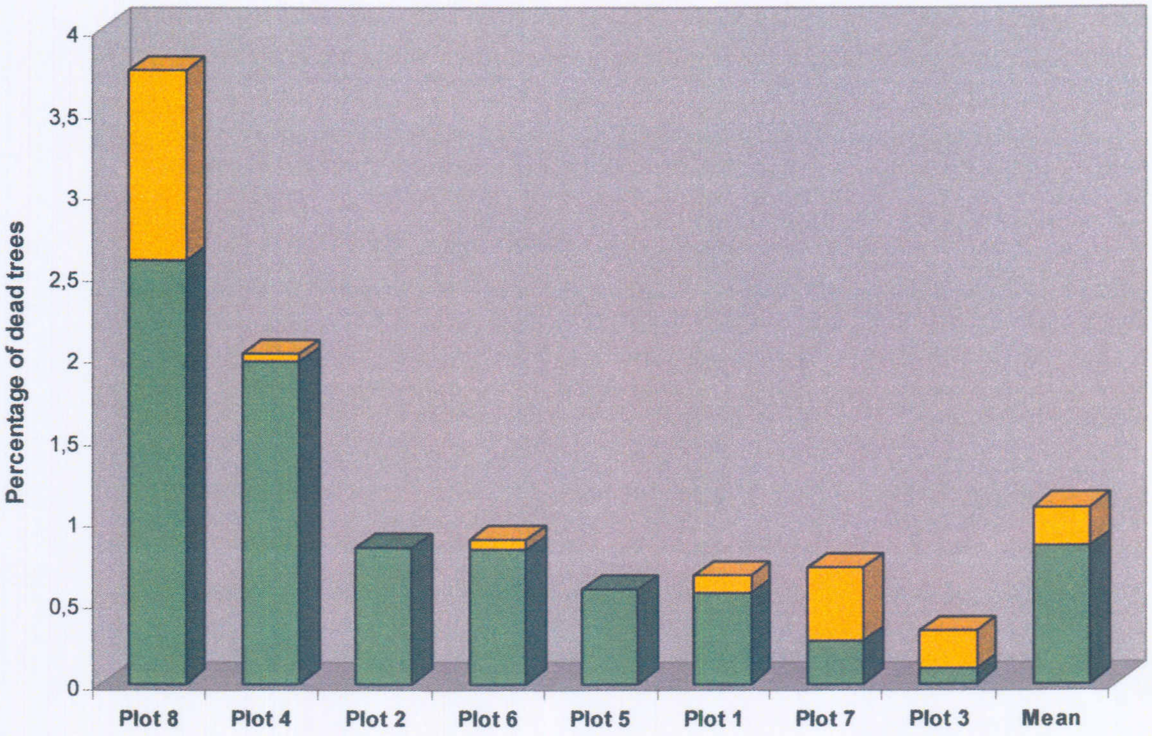

Figure 6.41: Percentage of total density made up by dead trees.

Key:
🟧 Percentage of standing dead trees
🟩 Percentage of fallen dead trees

The mean density of dead trees for the whole island is 62 plants per hectare, composed of a mean of 14 "Standing dead" and 48 "Fallen dead" (Figure 6.40). The mean percentage contribution to the mean total density made by dead trees is 1.08% for the whole island with 0.24% "Standing dead" and 0.84% "Fallen dead" trees (Figure 6.41).

The highest density of "Fallen dead" trees occurs in plot 4 (150 plants per hectare), followed by plot 8 (56 plants per hectare) and plot 6 (55 plants per hectare) (Table 6.9 & Figure 6.40). The highest percentage of "Fallen dead" trees though occurs in plot 8 (2.59%), followed by plot 4 (1.97%) and plot 2 (0.83%) (Figure 6.41). Considering the stem diameter a mean of 40.13%, i.e. 19.1 plants per hectare of "Fallen dead" trees occurs in the lowest diameter class of 10-15 cm (Table 6.9), followed by the third diameter class of > 20-25 cm, with a mean of 8.5 plants per hectare or 17.86% (Table 6.9).

The highest density of "Standing dead" trees occurs in plot 7 (55 plants per hectare), followed by plot 8 (25 plants per hectare) and plot 3 (20 plants per hectare) (Table 6.10 & Figure 6.40). The highest percentage of "Standing dead" trees though occurs in plot 8 (1.16%), followed by plot 7 (0.45%) and plot 3 (0.23%) (Figure 6.41). Considering the stem diameter a mean of nearly 50% (46.43%), i.e. 6.5 plants per hectare of "Standing dead" trees occurs in the lowest diameter class of 10-15 cm (Table 6.10), followed by the third diameter class of > 20-25 cm with a mean of 3.9 plants per hectare or 27.86% (Table 6.10).

The highest percentage of "Fallen dead" and "Standing dead" hence occurs in plot 8, while the stem diameter classes with the highest mean percentages of "Dead trees" per hectare are the lowest (10-15 cm) and third (> 20-25 cm) class for both "Dead tree" categories (Table 6.9 & 6.10 & Figure 6.40 & 6.41).

Ngamba Island chimpanzees' plant food species

When comparing Marshall's (2000) list of known Ngamba Island chimpanzees' plant food species (see Annex - Table 2) with the distribution and densities of these species throughout the eight sample plots, the following picture emerges:

The plot with the highest density of food plants is plot 7 (17 375 plants per hectare), followed by plot 5 (13 975 plants per hectare), plot 3 (12 725 plants per hectare) and plot 6 (11 900 plants per hectare). Three of these plots (5, 6 & 7) are part of the *Dracaena fragrans*-

Psychotria peduncularis moist evergreen forest community in the eastern part of the island, while plot 3 represents the highest density of *Aframomum angustifolium* (5 700 plants per hectare) (Table 6.3 & 6.4). All four plots are concentrated in the central and eastern part of the island (Figure 6.1). The plant species with the highest mean density is *Aframomum angustifolium* (2 991 plants per hectare), followed by *Dracaena fragrans* (2 209 plants per hectare), *Commelina capitata* (1 863 plants per hecatre), *Albizia gumnifera* (1 185 plants per hectare) and *Guarea cedrata* (1 078 plants per hectare). Apart from *Oxyanthus speciosus* (679 plants per hectare) all remaining food plant species have a mean density below 200 plants per hectare (Table 6.4).

Distribution and density of* Ficus *species

Only four of the eight sample plots comprise any *Ficus* spp. (Figure 6.42). The highest density of fig trees is represented in plot 4 (600 plants per hectare) which is also the plot with its centre point at the highest altitude (1 176 ± 5 m) (Table 6.1). Three of the four plots (2, 4, & 8) are part of the *Tetrorchidium didymostemon-Macaranga monandra moist evergreen forest community* and all plots are concentrated more in the south-western part of Ngamba Island (Table 6.3 & Figure 6.1 & 6.2).

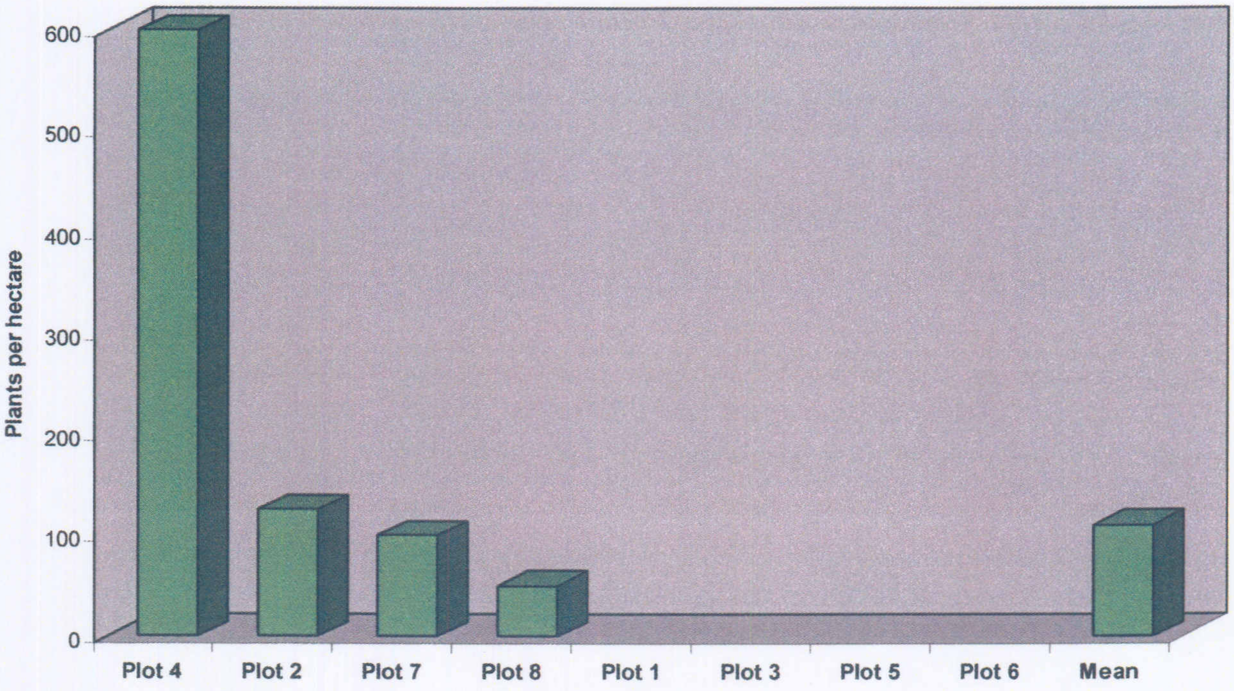

Figure 6.42: Number of individual Fig trees (*Ficus* species) per hectare.

Key: 🟩 Number of *Ficus* trees

Total projected canopy cover

Total projected canopy cover at different height classes

The projected canopy cover was calculated using the method as described by Coetzee and Gertenbach (1977). In the > 6.0 m height class plot 2 has the highest percentage of total projected canopy cover (363.59%), followed by plot 5 (304.27%) and plot 6 (233.59%). In all these plots the> 6.0 m height class contributes the highest percentage of all height classes to the total projected canopy cover (Figures 6.43 – 6.47). For the remaining five plots this is not the case and the total projected canopy cover for all these is below 75% in the > 6.00 m height class (Figure 6.43 – 6.47). Considering the density of plants plot 2 has the lowest number of trees (2 900) as well as plants (3 100) per hectare of all plots (Figure 6.5). While plot 5 represents the third lowest density of trees (6 200) and plants (7 300), respecftively, plot 6 possesses the third highest density of trees (9 500) and plants (11 000) per hectare (Figure 6.5).

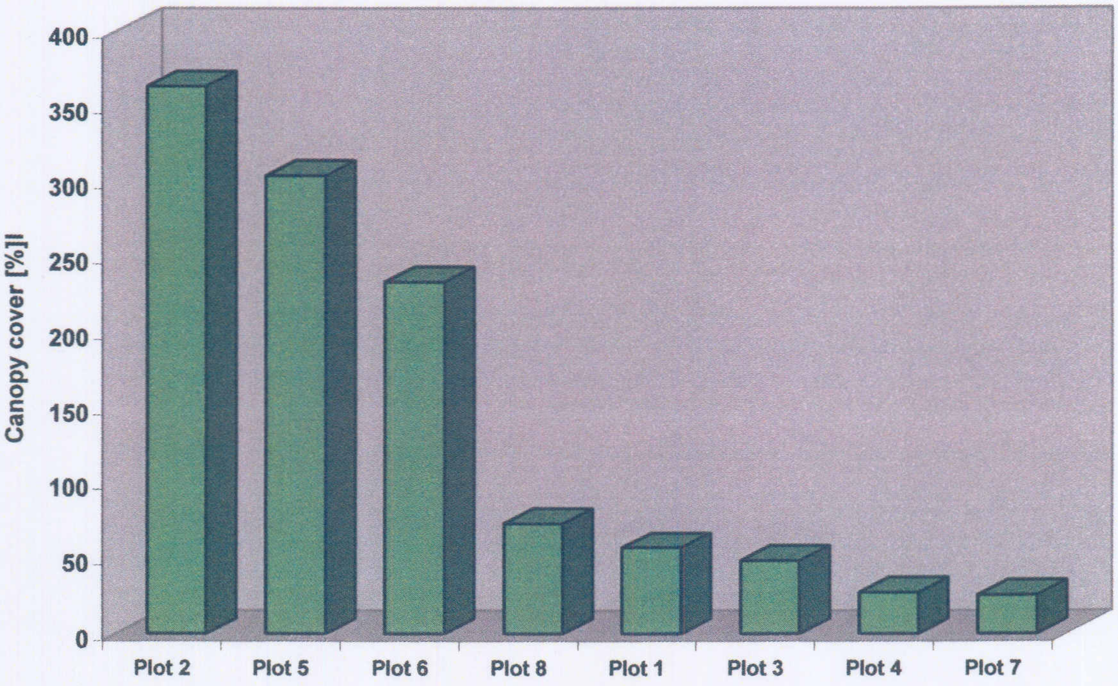

Figure 6.43: Total projected canopy cover of the > 6.0 m height class for all sample plots.

Key: 🟩 Percentage canopy cover

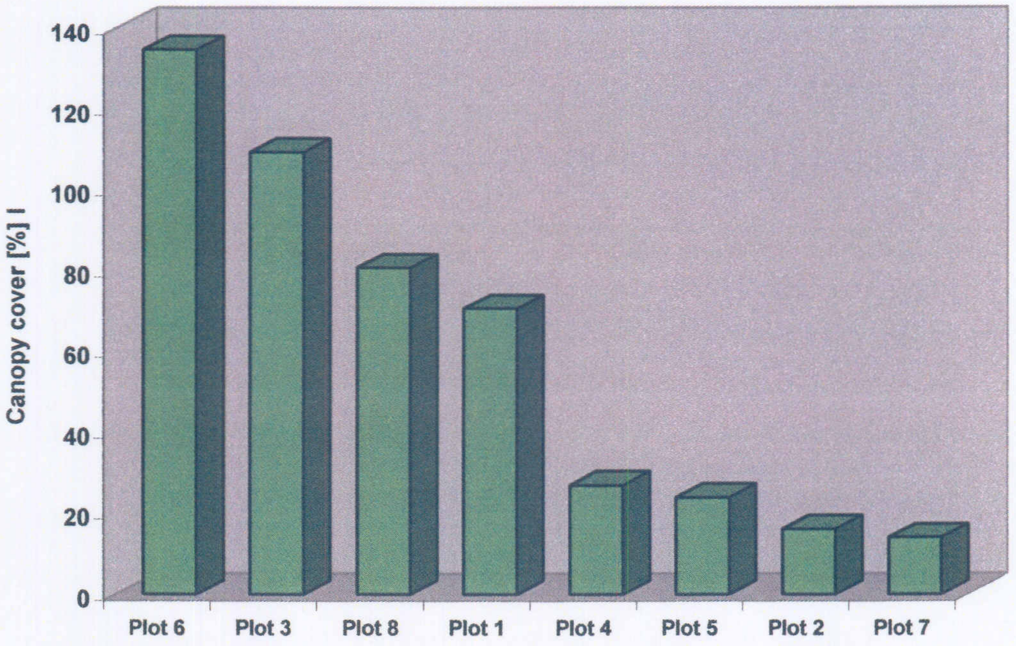

Figure 6.44: Total projected canopy cover of the 4.0 - 5.0 m height class for all sample plots.

Key: 🟩 Percentage canopy cover

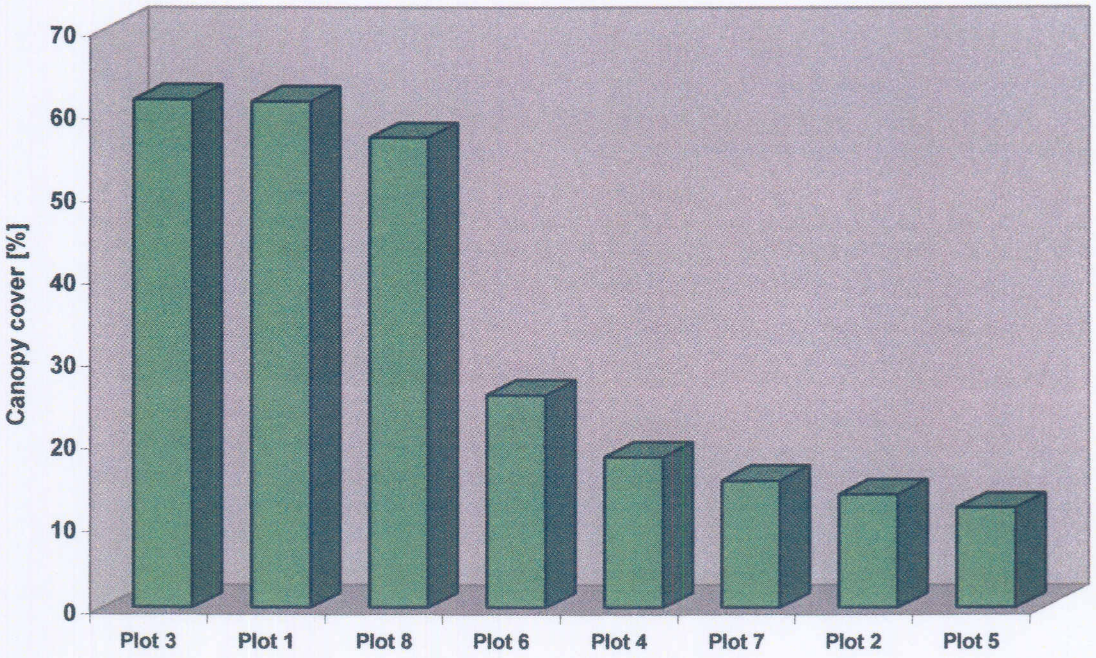

Figure 6.45: Total projected canopy cover of the 3.0 m height class for all sample plots.

Key: 🟩 Percentage canopy cover

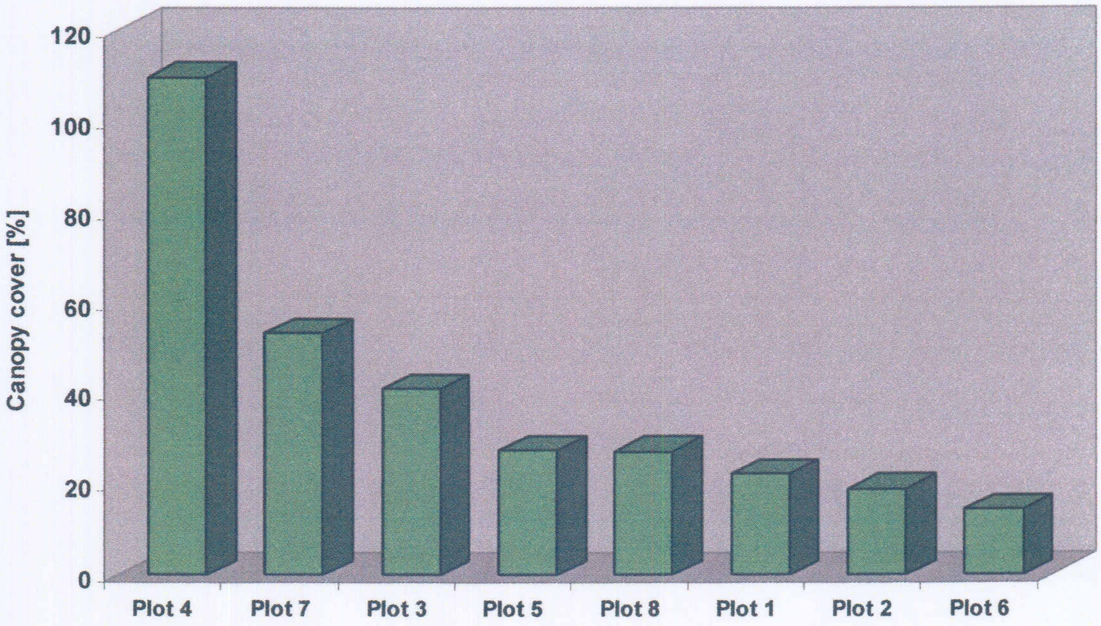

Figure 6.46: Total projected canopy cover of the 2.0 m height class for all sample plots.

Key: 🟩 Percentage canopy cover

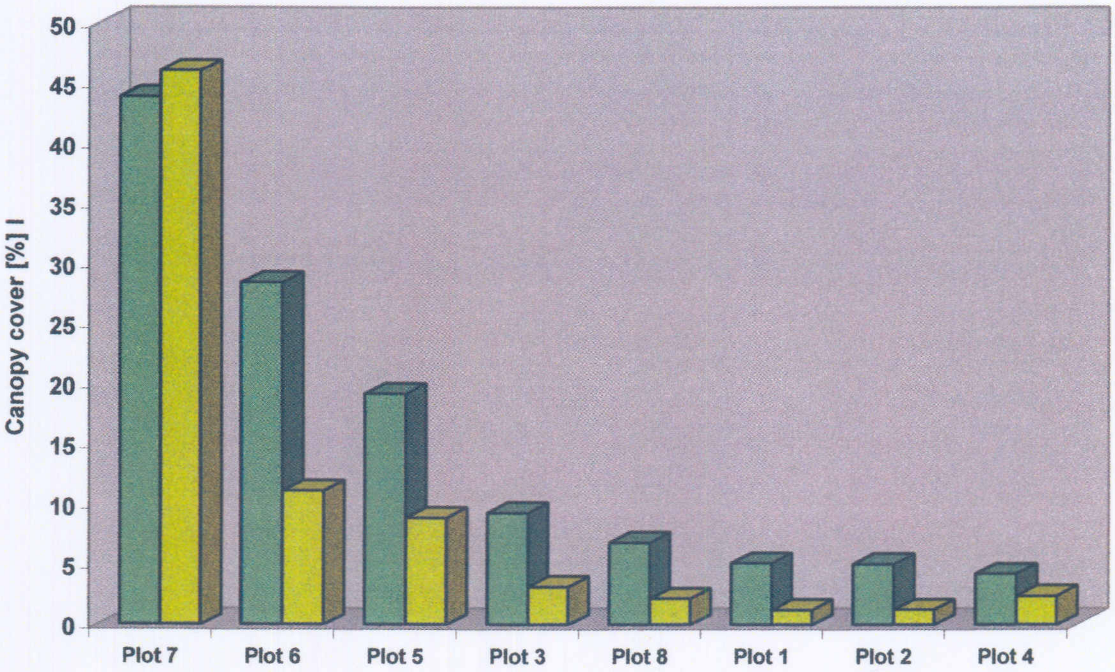

Figure 6.47: Total projected canopy cover of the 1.0 m and 0.5 m height classes for all sample plots.

Key:

🟨	Percentage canopy cover of the 0.5 m height class
🟩	Percentage canopy cover of the 1.0 m height class

In the 4.0 – 5.0 m height class plot 6 has the highest percentage of total projected canopy cover (134.81%), followed by plot 3 (109.39%) and plot 8 (80.73%). While plot 1 still contributes a high percentage in this height class (70.72%), the total projected canopy cover for all the remaining plots is below 30% (Figure 6.44). Considering the density of plants plot 3 possesses the second highest density of trees (13 700) as well as of plants (14 700) per hectare, while plot 8, though only representing the second lowest density of trees per hectare (6 061), ranges fifth with its overall density of plants per hectare (9 386) (Figure 6.5).

In the 3.0 m height class the percentages of total projected canopy cover are below 65% for all plots, with plot 3 (61.59%), plot 1 (61.35%) and plot 8 (56.94%) being the most prominent plots and contributing nearly the same percentage of total projected canopy cover in this height class (Figure 6.45). Considering the density of plants plot 1 ranges fifth in the density of trees (6 222) and seventh in the density of plants (6 922) per hectare (Figure 6.5).

In the 2.0 m height class plot 4 has the highest percentage of total projected canopy cover (104.66%), followed by plot 7 (53.16%) and plot 3 (40.95%). In plot 4 the 2.00 m height class contributes the highest percentage of all height classes to the total projected canopy cover (Figure 6.46). Considering the density of plants plot 4 ranges fourth in the density of trees (7 625) as well as in the density of plants (9 125) per hectare. While plot 7 has the highest density of trees (16 025) and plants (18 050) per hectare of all plots (Figure 6.5).

The 1.0 m and 0.5 m height classes are of minor importance in their contributions to the total projected canopy cover. In the 1.00 m height class all contributions are below 30% (plot 5 & 6) or 10% (plot 3, 1, 2, & 4), respectively. In the 0.5 m height class all contributions are below 12% of total projected canopy cover (Figure 6.47). The exception in both height classes is plot 7 which represents 43.95% of total projected canopy cover in the 1.0 m height class and 46.12% in the 0.5 m height class. It is therefore far above the contributions of the other plots to the total projected canopy cover in these height classes (Figure 6.47).

Considering the overall percentage of total projected canopy cover for each sample plot the three most prominent plots are plot 6 (448.30%), plot 2 (418.69%) and plot 5 (369.05%) (Table 6.10). The remaining plots represent an overal total canopy cover of below 300% (plot 3, 8, & 1) and 200% (plot 7 & 4), respectively (Table 6.10). Tree density and percent canopy cover do not seem to correlate with each other since e.g. plot 7 with the highest plant density represents with 198.15% the second lowest overall percentage of total projected canopy cover (Table 6.11 & Figure 6.3).

Table 6.11: *Total projected canopy cover over all height classes for all sample plots*

Total projected canopy cover over all height classes [%] for all sample plot							
6	2	5	3	8	1	7	4
448.30	418.69	396.05	272.52	247.36	217.63	198.15	188.67

Mean total projected canopy cover at different height classes

The > 6.0 m height class contributes overall by far the highest percentage to the total projected canopy cover (141.57%) with the contribution by the > 6.0 m height level nearly four times higher (105.17%) than that of the second prominent 4.0 – 5.0 m height level (27.26%). It is the only height class which does not contribute at the 0.5 m height level (Figure 6.48). All other height classes contribute on average only one quarter or less of the percentage of the > 6.0 m height class to the total projected canopy cover. Every height class contributes the largest percentage of total projected canopy cover in its highest height level (Figure 6.48).

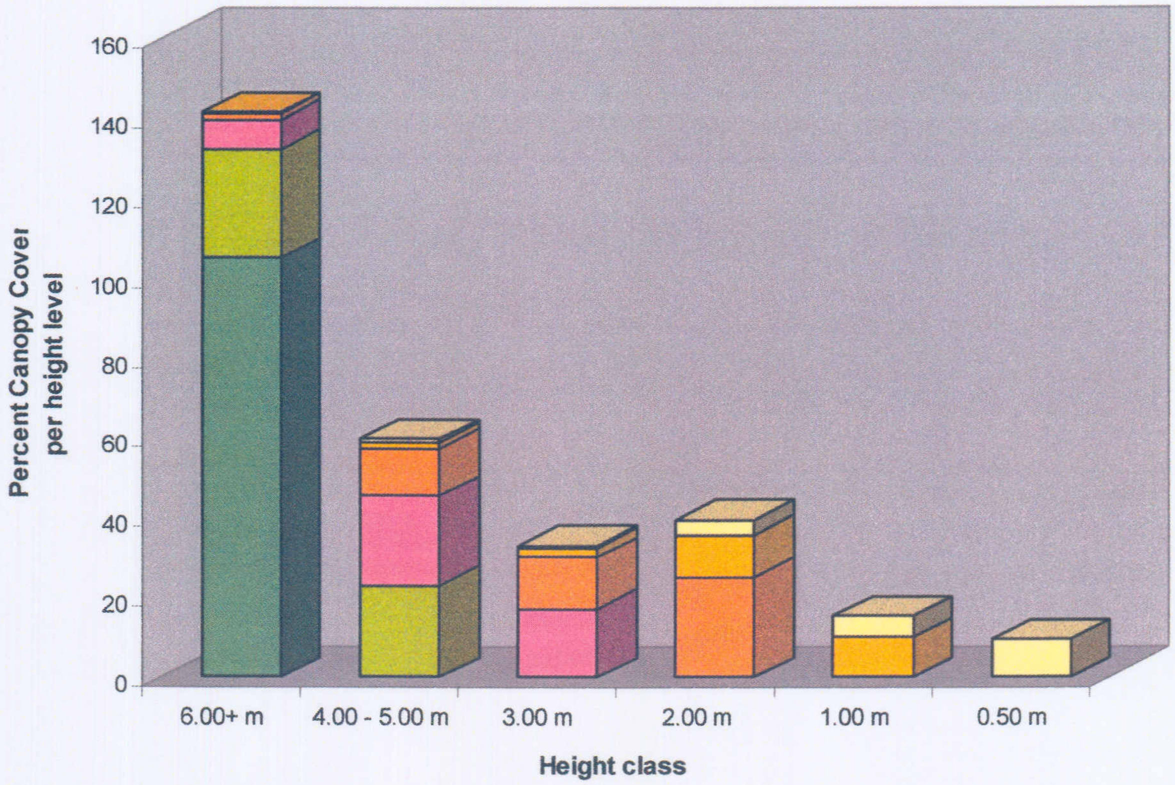

Figure 6.48: Mean total projected canopy cover at different height classes.

Key:

- 🟨 0.5 m height class
- 🟧 1.0 m height class
- 🟧 2.0 m height class
- 🟥 3.0 m height class
- 🟩 4.0 – 5.0 m height class
- 🟩 > 6.0 m height class

Total projected canopy cover at different height levels

There are three plots where the > 6.0 m height level contributes the highest percentage of total projected canopy cover (Figure 6.49 – 6.56). In plot 2 all the other height levels contribute less than 20% each to the total projected canopy cover, with the 361.04% of the > 6.0 m height level therefore being much more prominent. In contrast in plot 5 and plot 6 the 4.0 – 5.0 m height level (115.59% and 74.62%) and the 3.0 m height level (53.34% and 97.02%) also contribute a high percentage to the total projected canopy cover compared to the respective covers at the > 6. 0 m height level (150.86% and 146.34%). Overall, the > 6.0 m height level in plot 2 contributes a more than two-fold higher percentage to the total projected canopy cover than in plot 5 and 6 (Figure 6.50, 6.53 & 6.54).

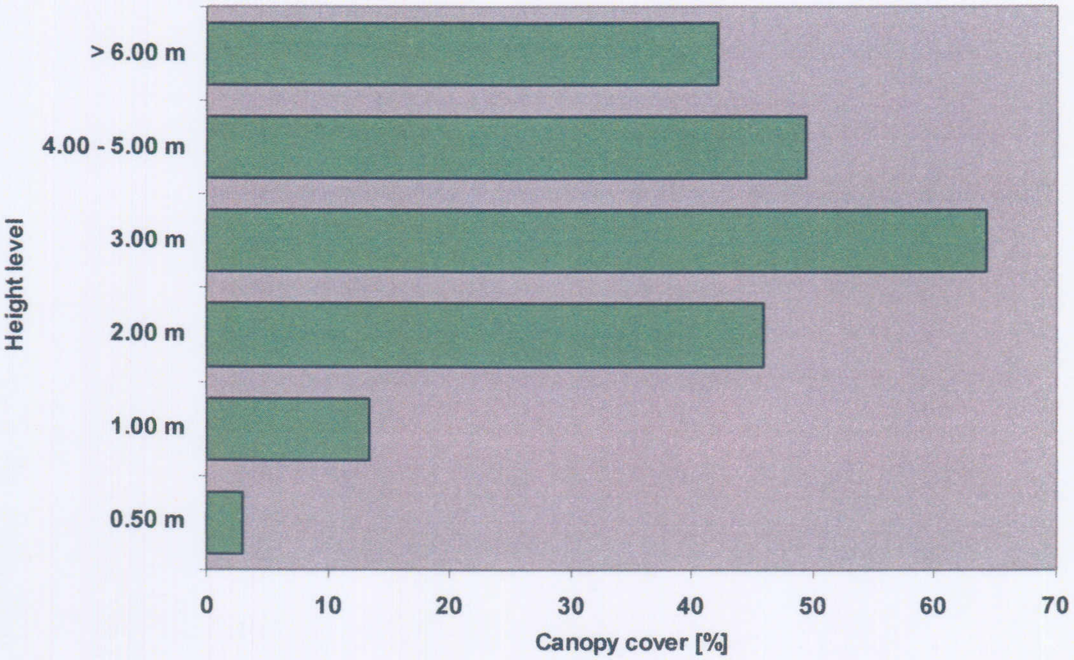

Figure 6.49: Total projected canopy cover at all height levels for plot 1.

Key: 🟩 Canopy cover [%]

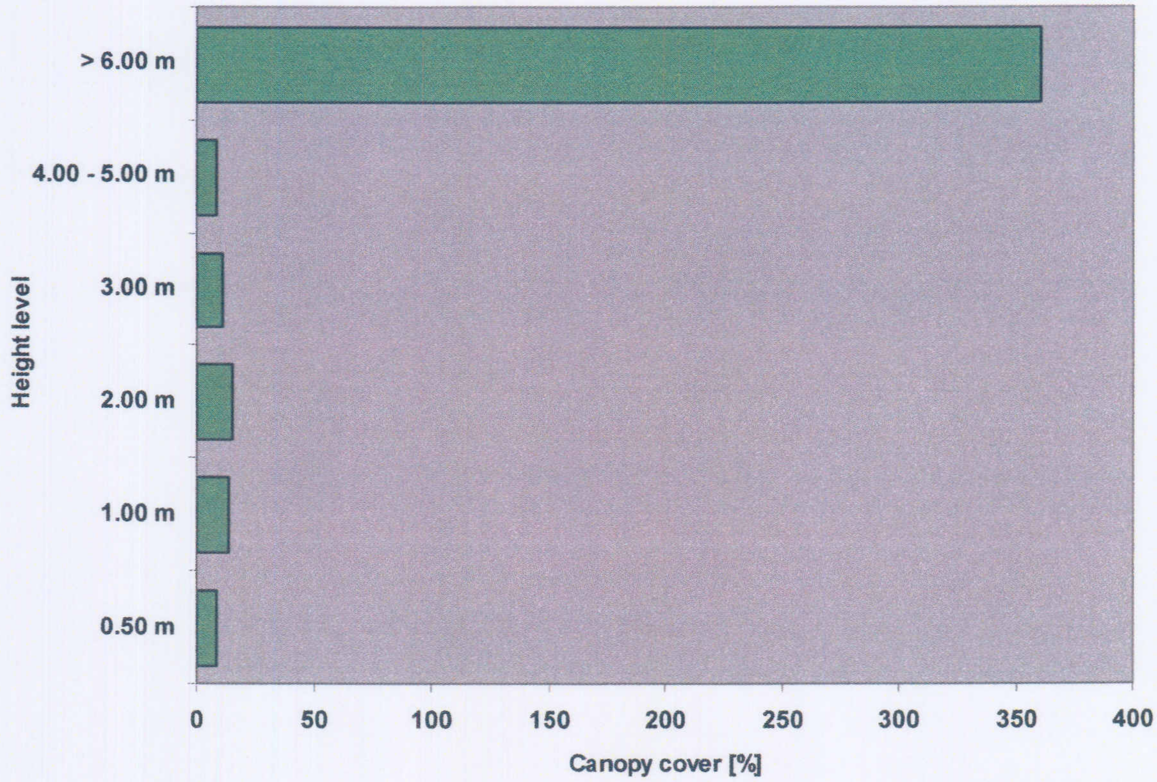

Figure 6.50: Total projected canopy cover at all height levels for plot 2.

Key: 🟩 Canopy cover [%]

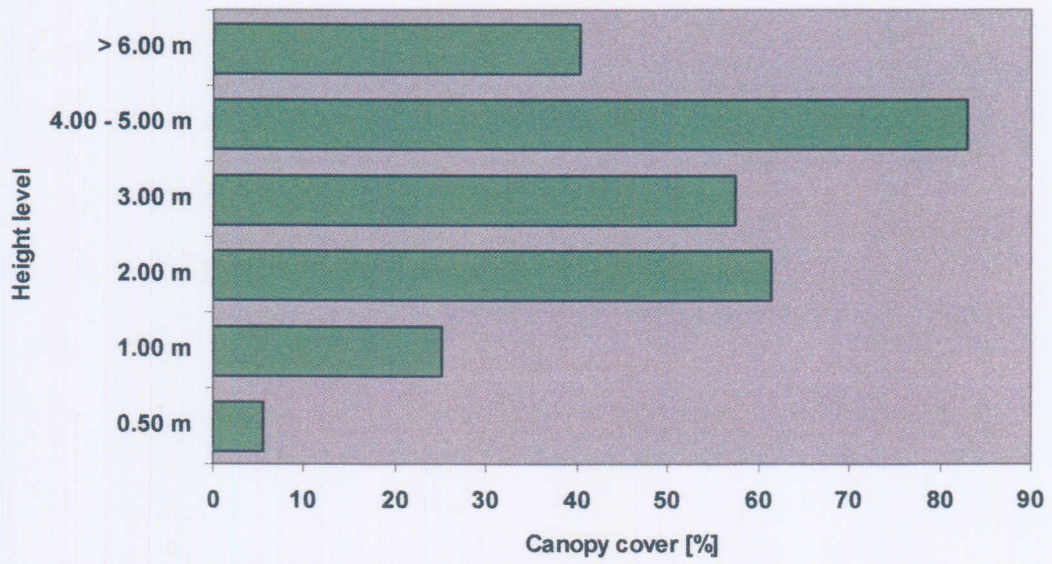

Figure 6.51: Total projected canopy cover at all height levels for plot 3.

Key: 🟩 Canopy cover [%]

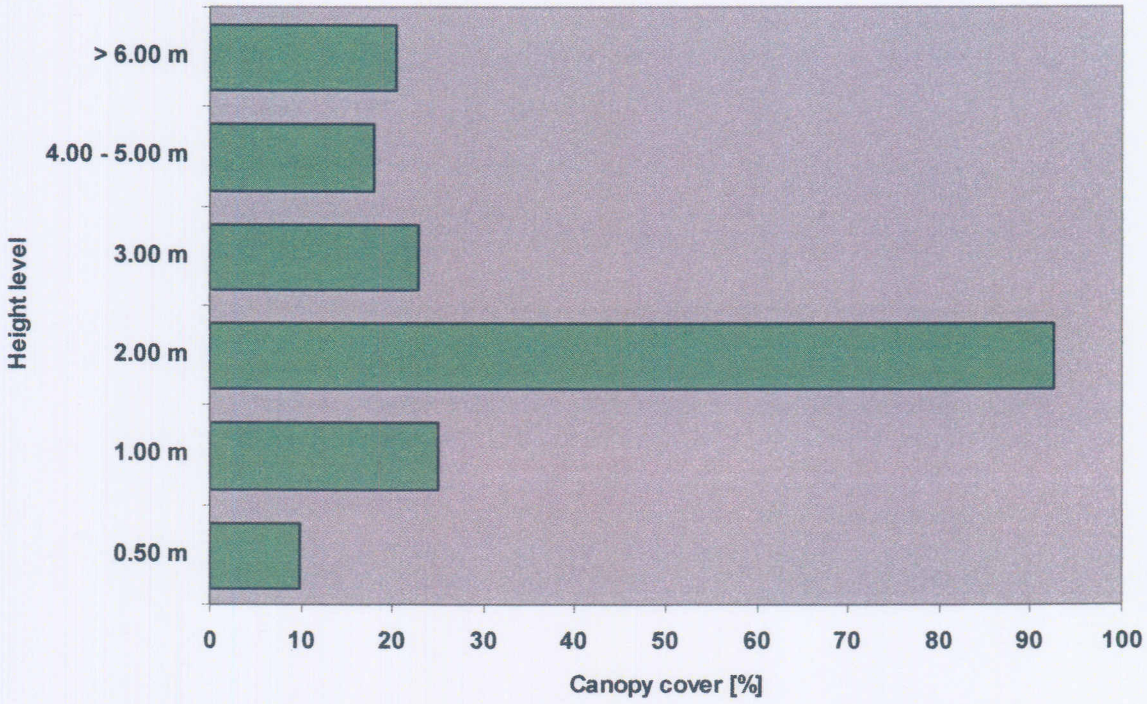

Figure 6.52: Total projected canopy cover at all height levels for plot 4.

Key:	🟩	Canopy cover [%]

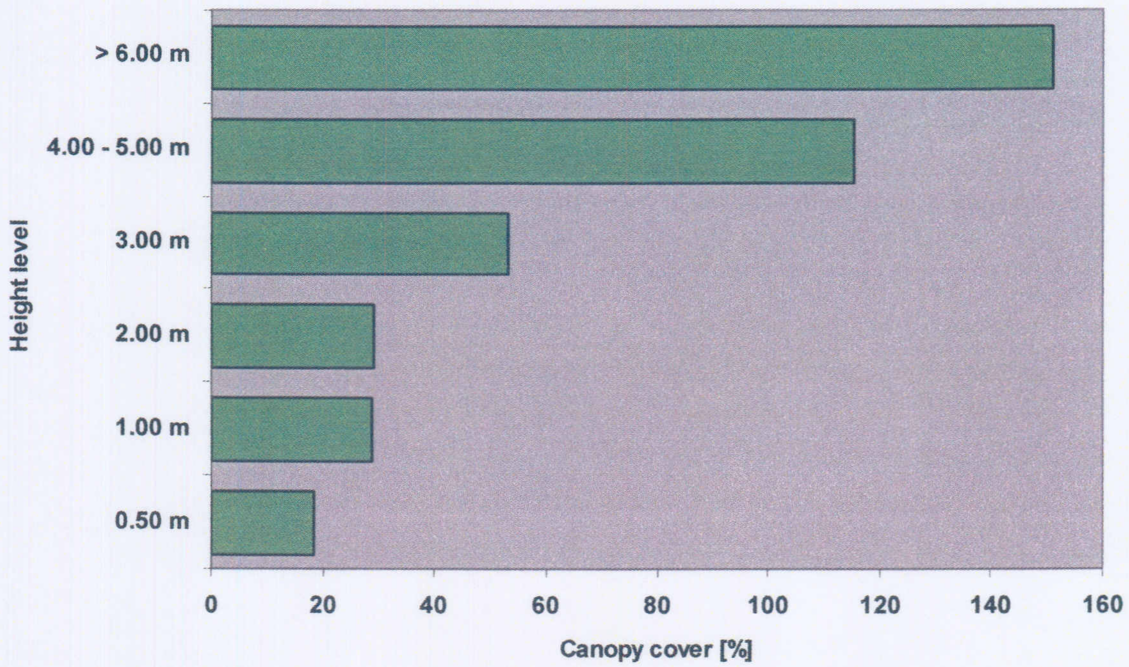

Figure 6.53: Total projected canopy cover at all height levels for plot 5.

Key: 🟩 Canopy cover [%]

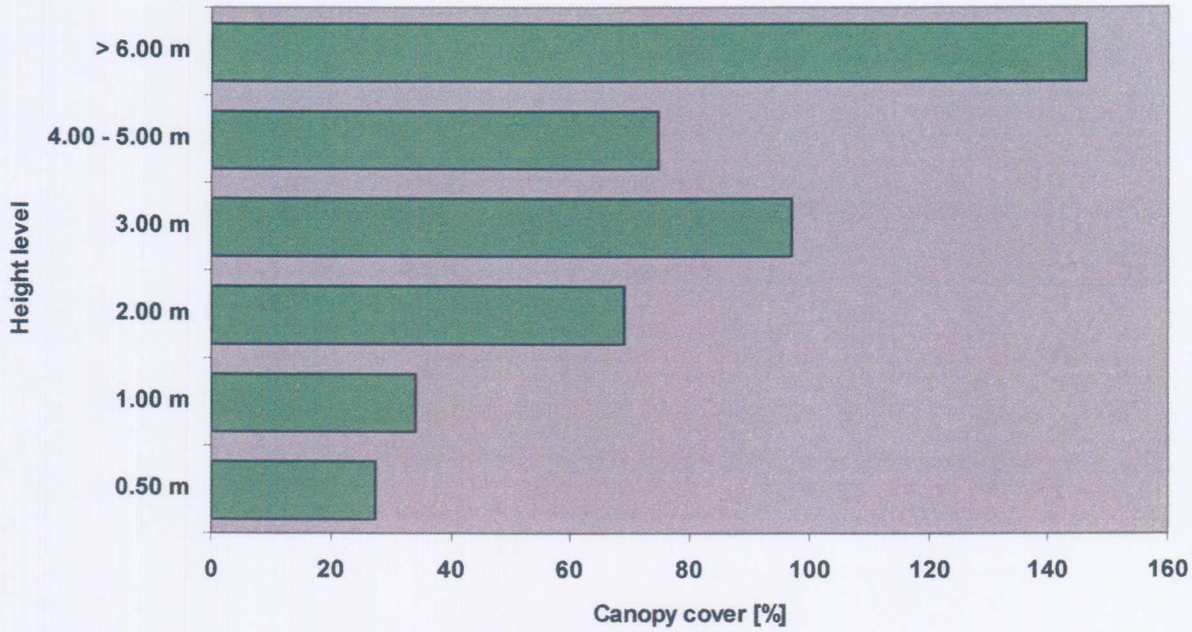

Figure 6.54: Total projected canopy cover at all height levels for plot 6.

Key: 🟩 Canopy cover [%]

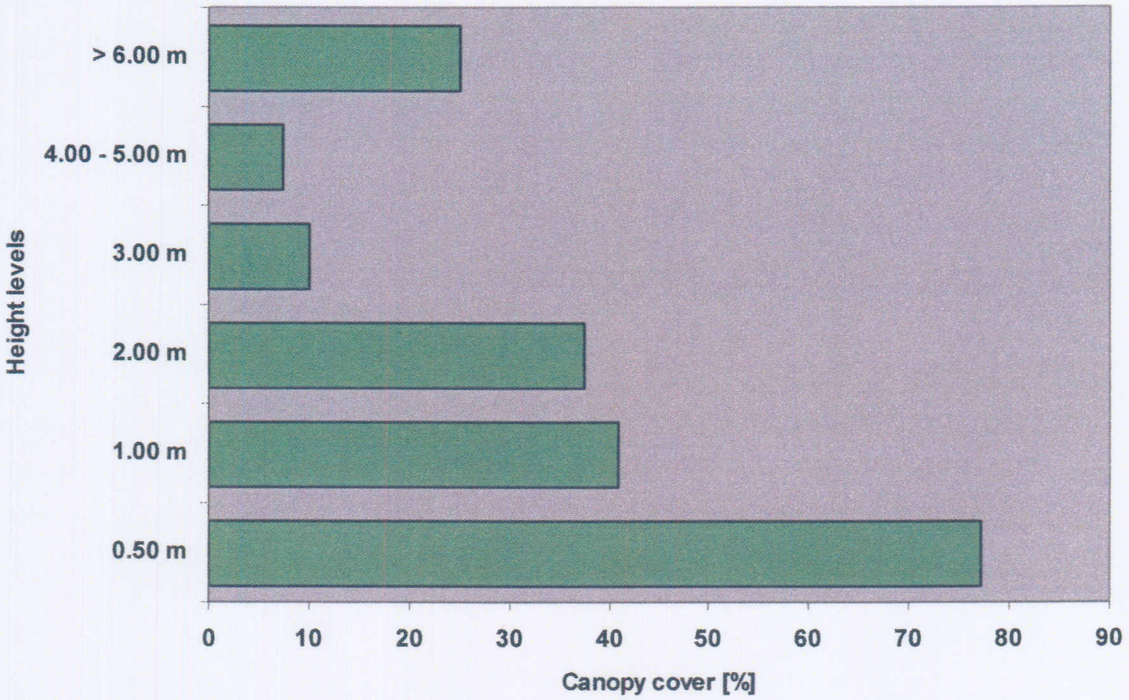

Figure 6.55: Total projected canopy cover at all height levels for plot 7.

Key: 🟩 Canopy cover [%]

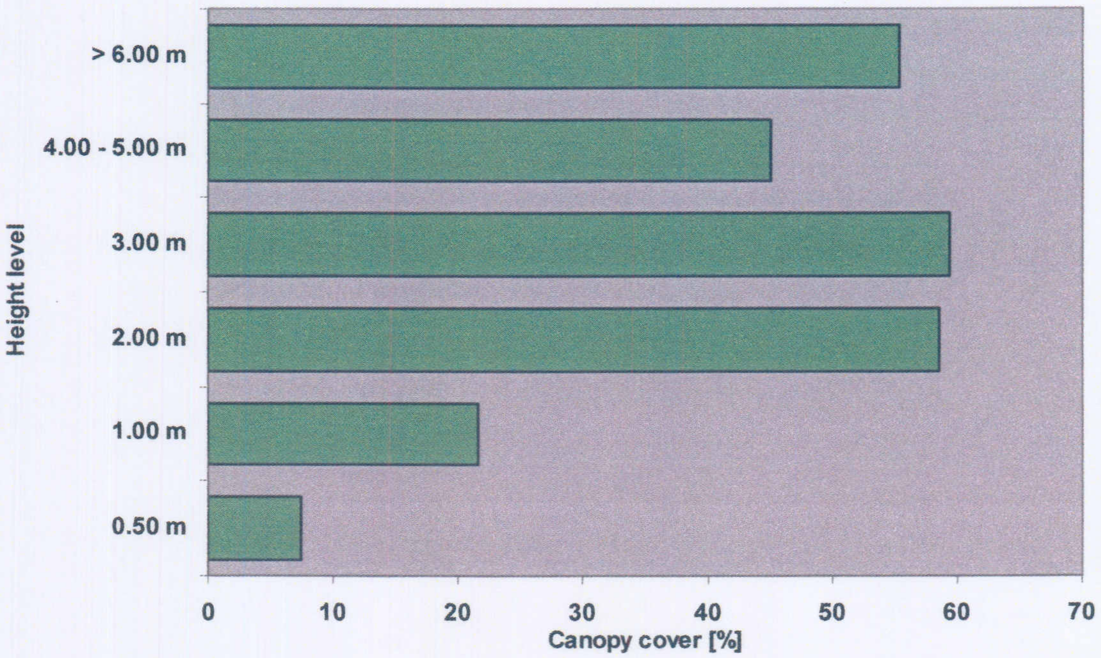

Figure 6.56: Total projected canopy cover at all height levels for plot 8.

Key: 🟩 Canopy cover [%]

Only in plot 3 does the 4.0 – 5.0 m height level represent the highest percentage of total projected canopy cover (82.95%) (Figure 6.49 – 6.56) with all remaining but the 1.0 m and 0.5 m height levels also contributing over 40% of total projected canopy cover (Figure 6.51).

There are two plots where the 3.0 m height level contributes the highest percentage of total projected canopy cover (Figure 6.49 – 6.56). In plot 1 and plot 8 also all remaining but the 1.0 m and 0.5 m height levels contribute a high percentage of total projected canopy cover. In plot 1 the 3.0 m height level (64.14%) contributes a slightly higher percentage than in plot 8 (59.37%). The former height level is also more prominent compared to the > 6.0 m (42.07%), 4.0 – 5.0 m (49.29%) and 2.00 m (45.94%) height level, while in plot 8 the contributed percentage is nearly equal for these three (55.35%, 45.02% and 58.65%) and the 3.0 m height level (Figure 6.49 & 6.56).

The only plot in which the 2.0 m height level represents the highest percentage of total projected canopy cover (92.61%) is in plot 4 (Figure 6.49 – 6.56), while all remaining but the 0.50 m height level (9.95%) contribute only around 20% of total projected canopy cover per hectare (Figure 6.52).

Only in plot 7 does the 0.5 m height level represent the highest percentage of total projected canopy cover (77.21%), with the 1.0 m height level following second (40.84%) but contributing only about half as much (Figure 6.55). In all other plots the 0.5 m height level contributes the lowest percentage of total projected canopy cover (Figure 6.49 – 6.56). In plot 7 the three lowest height levels contribute the highest percentages while the three highest height levels contribute the lowest percentages of total projected canopy cover per hectare. This trend is reversed in all other seven sample plots (Figure 6.49 - 6.56).

Mean total projected canopy cover at different height levels

The > 6.0 m height level with 105.17% contributes the highest mean percentage of total projected canopy cover. The three following height levels all contribute about half that percentage. While the two lowest height levels contribute about one-fifth of this percentage of mean total projected canopy cover (Figure 6.57).

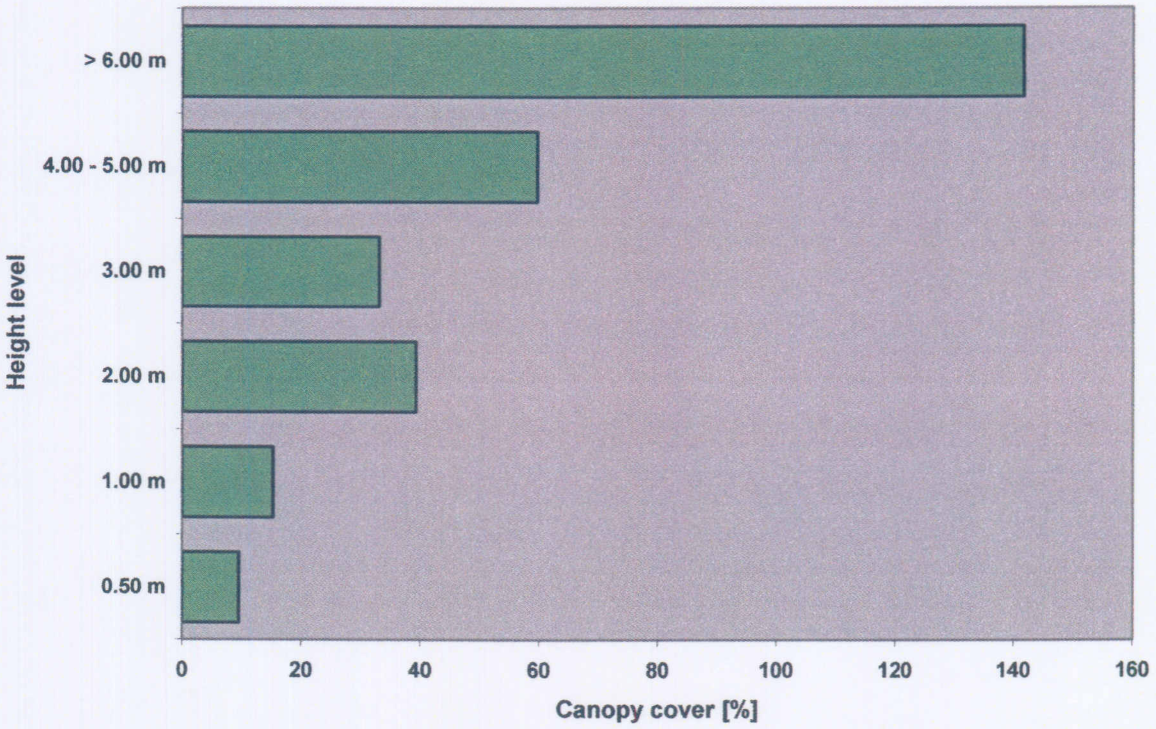

Figure 6.57: Mean total projected canopy cover at different height levels.

Key: 🟩 Canopy cover [%]

Total projected canopy cover according to growth form

In seven of the eight plots the tree growth form is the most prominent one. Only in plot 4 is this place taken over by the shrub growth form (Figure 6.58). The sparse shrub growth form contributes below 30% of total projected canopy cover in plot 1 and 8, below 20% in plot 7 and 6, and below 5% in plot 4, 3, 5, and 2 (Figure 6.58). Apart from plot 4 (93.73%) the shrub growth form is even less prominent, contributing 23.61% of total projected canopy cover in plot 7, 12.78% in plot 8 and below 6% (plot 5, 6, & 3), respectively below 1% (plot 1 & 2) in the remaining plots (Figure 6.58).

Plot 4 has its centre point at the highest altitude of all sample plots (Table 6.1) and has by far the highest number, though not the highest percentage, of fallen dead trees per hectare (Figure 6.40 & 6.41).

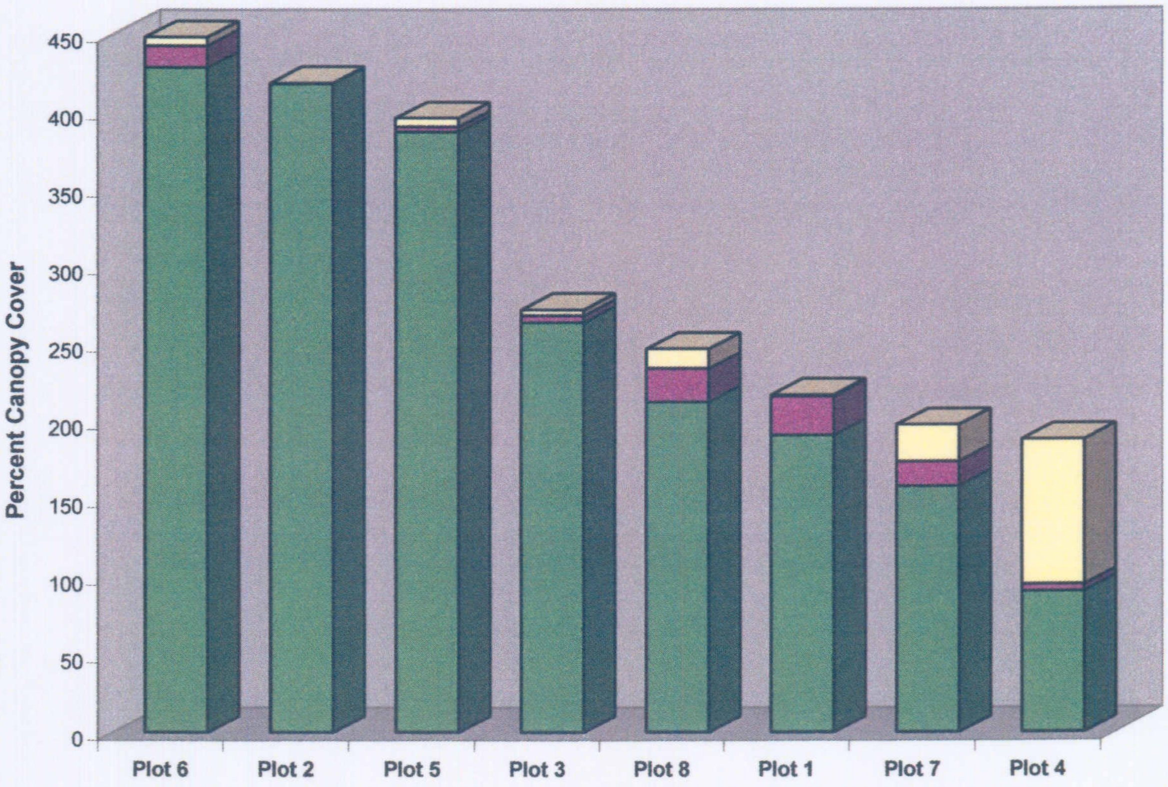

Figure 6.58: Total projected canopy cover for all sample plots according to growth form.

Key:

🟨 Shrub

🟪 Sparse shrub

🟩 Tree

Mean total projected canopy cover at different height levels according to growth form

The total projected canopy cover at the > 6.0 m height level is solely represented by the tree growth form, which is also overall the most prominent growth form in the percentage contribution of total projected canopy cover (Figure 6.59). At the three following height levels trees contribute about half of the percentage total projected canopy cover compared to the > 6.0 m height level; at the two lowest height levels less than a fifth of that (Figure 6.59). The shrub growth form becomes more prominent at the three lowest height levels, showing its highest contribution of total projected canopy cover at the 2.0 m height level (10.24%). The sparse shrub growth form has the lowest overall contribution of total projected canopy cover. Only at the 3.0 m and 4.0 – 5.0 m height level does it show a greater contribution than the shrub growth form (1.00%) (Figure 6.59).

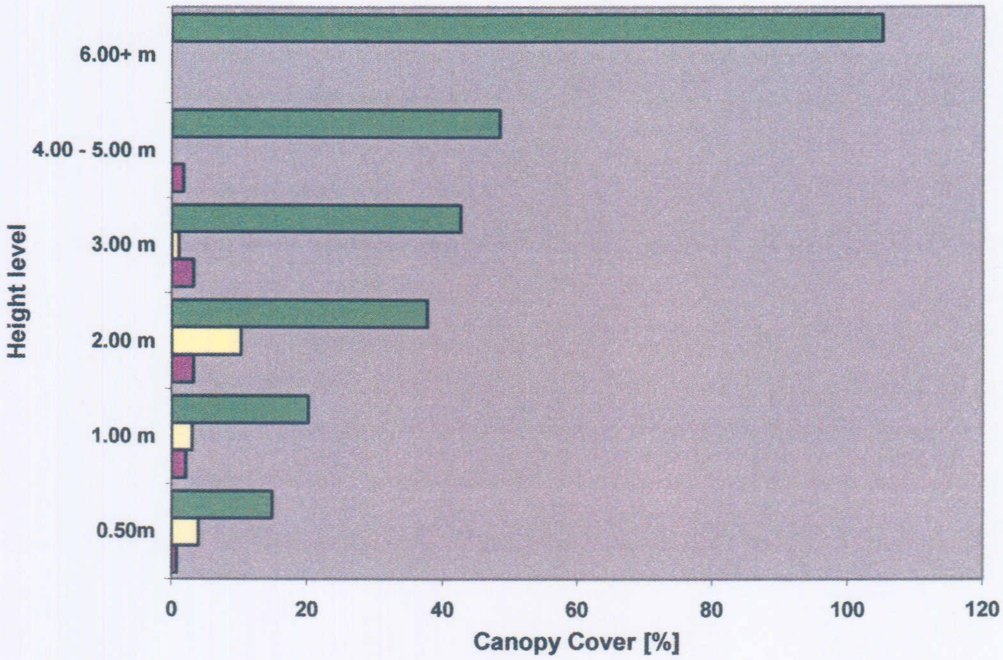

Figure 6.59: Mean total projected canopy cover at different height levels according to growth form.

Key:
🟨 Shrub
🟪 Sparse shrub
🟩 Tree

Canopy regime at different height levels

Mean percentage canopy cover of selected plant species

Figures 6.60 to 6.66 show the canopy regime at different height levels for seven selected plant species on Ngamba and Nsadzi Island. The selected plant species are those species which occur on both of the islands in the determined sample plots. Three of those seven species are known Ngamba Island chimpanzees' food plant species, namely *Dictyandra arborescens*, *Oxyanthus speciosus*, and *Tetrorchidium didymostemon* (Figure 6.60, 6.63 & 6.65). The remaining four species, i.e. *Eugenia capensis*, *Ouratea hiernii*, *Peddiea fischeri*, and *Trichilia species 1*, do not fall under this category (Figure 6.61, 6.62, 6.64 & 6.66). Four of the seven species do not show many similarities in their mean percentage canopy cover at different height levels. While *Dictyandra arborescens*, *Eugenia capensis*, *Peddiea fischeri*, and *Tetrorchidium didymostemon* show the highest mean percentage canopy cover in the three to four higher height levels of woody vegetation on Ngamba Island, the same woody vegetation on Nsadzi Island only shows any canopy cover at the two to three lowest height levels (Figure 6.60, 6.62, 6.63 & 6.65). *Oxyanthus speciosus* and *Trichilia species 1* show a similar pattern in their mean percentage canopy cover at different height levels for woody vegetation on either island (Figure 6.63 & 6.66). In general though the woody vegetation on Ngamba Island possesses a higher mean percentage canopy cover at each of the height levels compared to the one on Nsadzi Island. *Ouratea hiernii* shows a different pattern again in so far that its woody vegetation on Ngamba Island shows a low mean percentage canopy cover and only at the three lowest height levels while its woody vegetation on Nsadzi Island shows a high mean percentage canopy cover over all height levels (Figure 6.62).

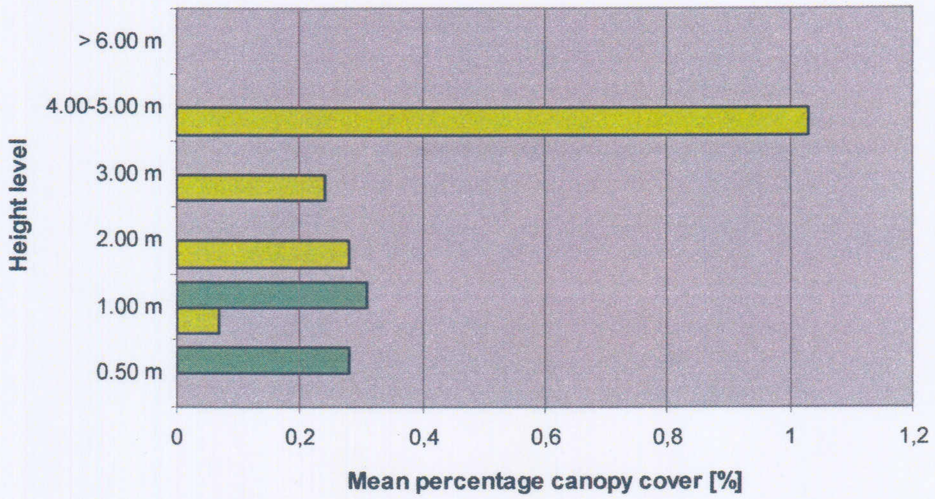

Figure 6.60: Mean percentage canopy cover of *Dictyandra arborescens* at different height levels on Ngamba and Nsadzi Island.

Key:
🟨 Ngamba Island
🟩 Nsadzi Island

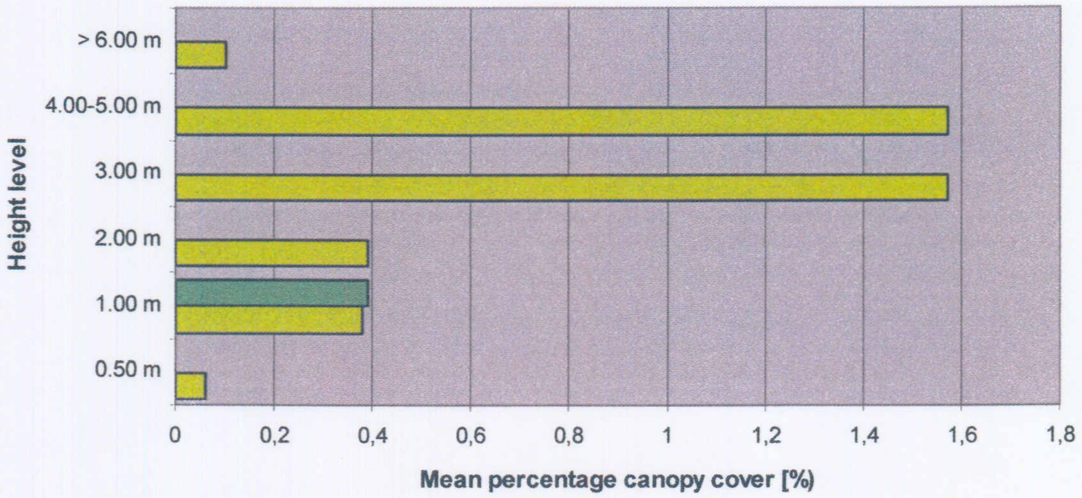

Figure 6.61: Mean percentage canopy cover of *Eugenia capensis* at different height levels on Ngamba and Nsadzi Island.

Key:

🟨	Ngamba Island
🟩	Nsadzi Island

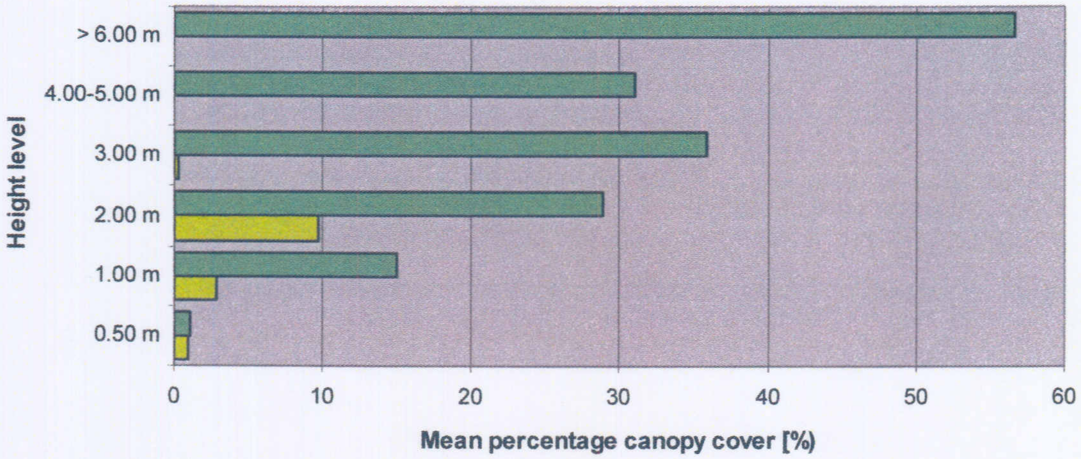

Figure 6.62: Mean percentage canopy cover of *Ouratea hiernii* at different height levels on Ngamba and Nsadzi Island.

Key:

🟨	Ngamba Island
🟩	Nsadzi Island

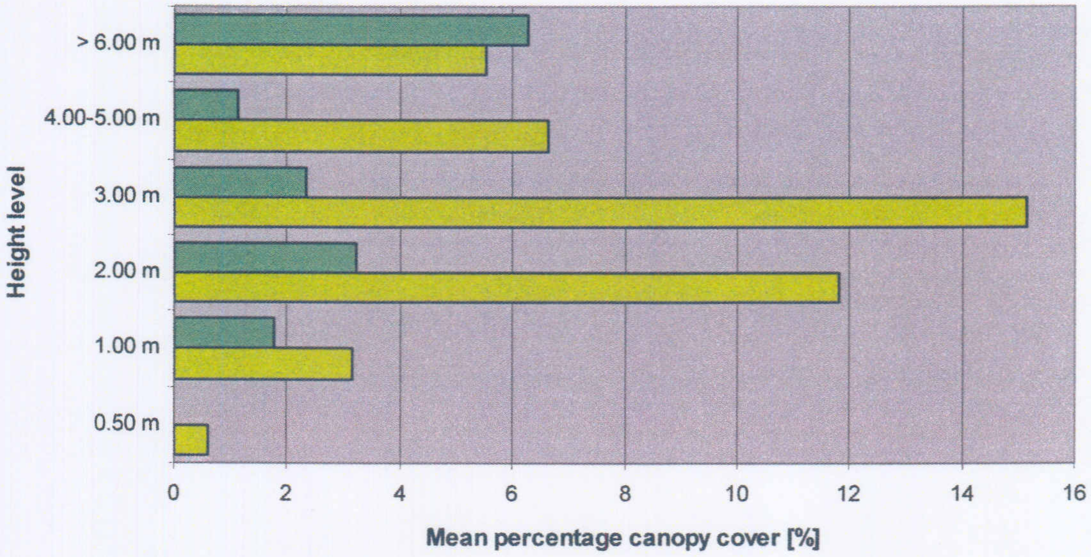

Figure 6.63: Mean percentage canopy cover of *Oxyanthus speciosus* at different height levels on Ngamba and Nsadzi Island.

Key:

🟨 Ngamba Island

🟩 Nsadzi Island

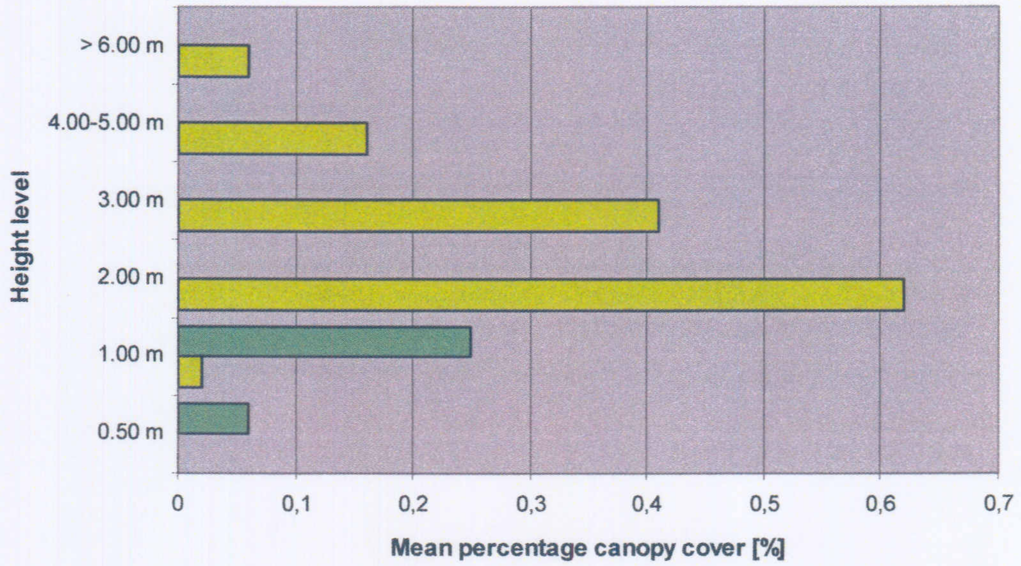

Figure 6.64 Mean percentage canopy cover of *Peddiea fischeri* at different height levels on Ngamba and Nsadzi Island.

Key:
🟨 Ngamba Island
🟩 Nsadzi Island

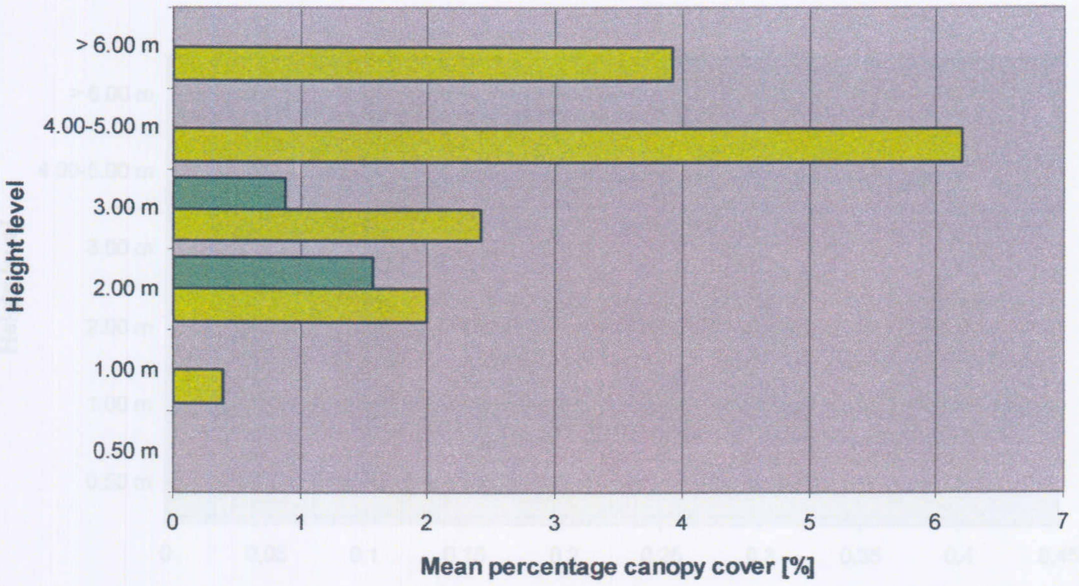

Figure 6.65: Mean percentage canopy cover of *Tetrorchidium didymostemon* at different height levels on Ngamba and Nsadzi Island.

Key:
🟨 Ngamba Island
🟩 Nsadzi Island

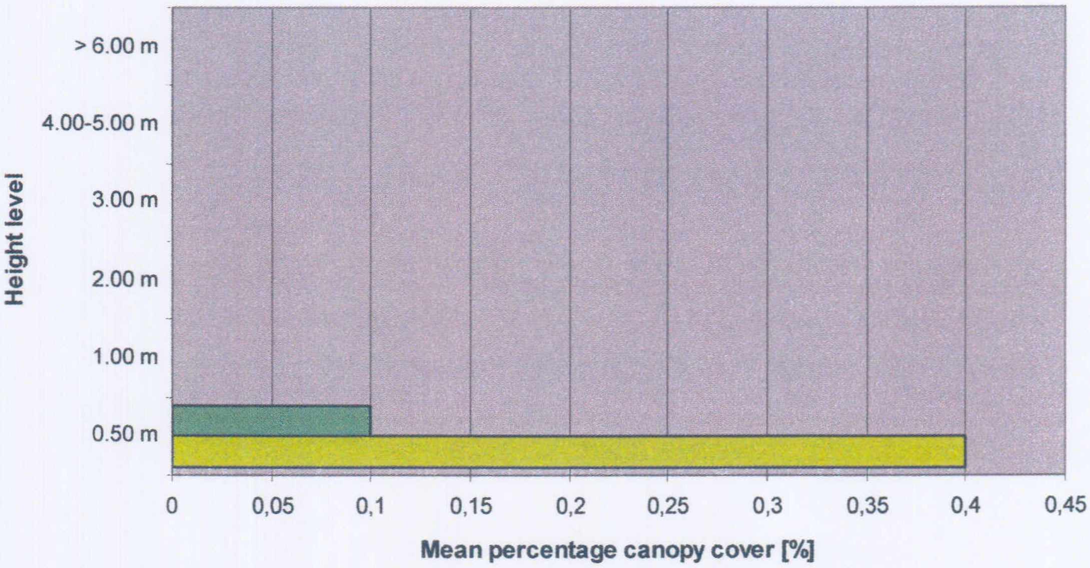

Figure 6.66: Mean percentage canopy cover of Trichilia species 1 at different height levels on Ngamba and Nsadzi Island.

Key:

🟨 Ngamba Island

🟩 Nsadzi Island

Mean total projected canopy cover of Ngamba Island chimpanzees' food plant species

From the four food plant species with the highest mean percentage canopy cover (*Guarea cedrata* = 94.52%, *Oxyanthus speciosus* = 42.85%, *Pachystela brevipes* = 35.33 %, *Dracaena fragrans* = 22.18%) it is *Guarea cedrata* which has by far the highest mean percentage canopy cover in the > 6.0 m height level (64.27%, i.e. 67.38% of all food plant species contributing to the > 6.0 m height level) (Figure 6.67). The 4.0 - 5.0 m height level is dominated by *Pachystela brevipes* (12.28%, i.e. 30.98%), while the 3.0 m and 2.0 m height levels are dominated by *Oxyanthus speciosus* (15.15%, i.e. 49.94% & 11.81%, i.e. 35.03) (Figure 6.67). The representative with the highest mean percentage canopy cover in the 1.0 m and 0.5 m height level is *Dracaena fragrans* (6.13%, i.e. 31.66% & 10.89%, i.e.74.69%) (Figure 6.67).

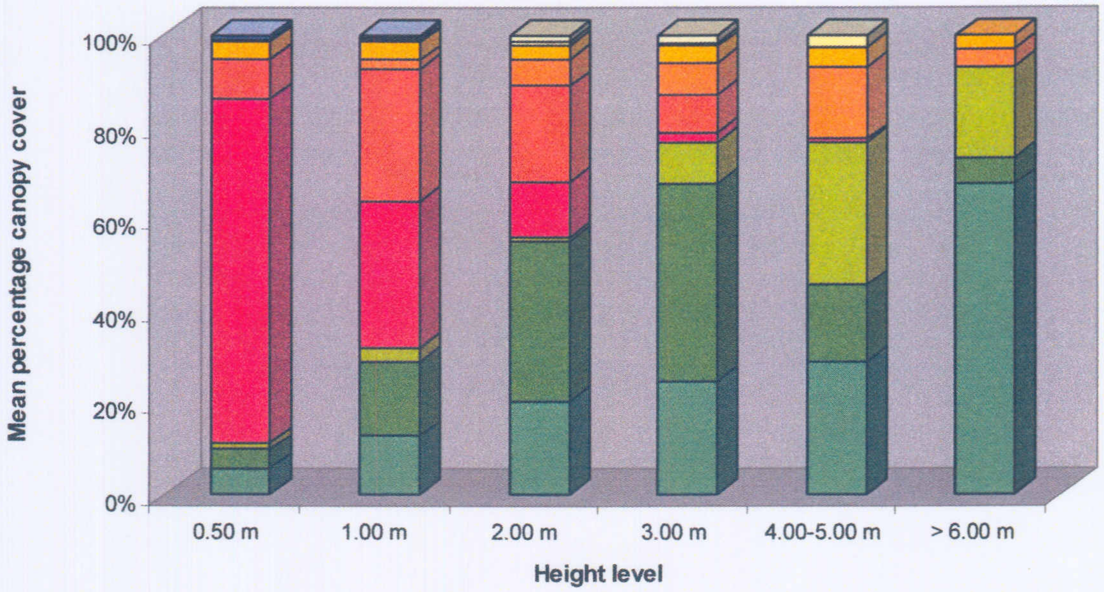

Figure 6.67: Mean percentage canopy cover of known Ngamba Island chimpanzees' food plant species.

Key:

🟪 Canthium species
🟦 Commelina capitata
⬜ Ficus species
🟨 Dictyandra arborescens
🟨 Albizia gumnifera
🟧 Tetrorchidium didymostemon
🟥 Aframomum angustifolium
🟥 Dracaena fragrans
🟩 Pachystela brevipes
🟩 Oxyanthus speciosus
🟩 Guarea cedrata

HERBACEOUS VEGETATION ON NGAMBA ISLAND

TWINSPAN and DECORANA classification

Analysis of the herbaceous vegetation using TWINSPAN and DECORANA did not show any definite pattern. It was decided that the area of herbaceous vegetation on Ngamba Island was with a size of 1.89 hectare too small and its physical condition too uniform to show distinctive features using these two methods of vegetation analysis. The herbaceous vegetation is not expected to be affected by the chimpanzees in the way the woody vegetation may be. Furthermore, no control plot for herbaceous vegetation had been established on Nsadzi Island. It was therefore decided to subjectively name the prevalent herbaceous community on Ngamba Island using the Braun-Blanquet principles, as the ***Asystasia gangetica – Justicia flava – Sporobolus agrostoides post-cultivation grassland*** (Annex - Table 6 & Figure 6.2) (Langdale-Brown *et al*. 1964).

Transect surveys

Altogether, three transects with a total of 65 different 1 m x 1 m sample plots have been evaluated (Annex - Table 6).

A total of 47.7% (31) of all sample plots show patches of bare soil ranging from 10% to 60% cover per plot. The median percentage of bare soil is 20% (10 times) (Annex - Table 6). Patches of volcanic soil appear in 6.2% (4) of the sample plots; while gravel occurs in only 4.7% (3) of the plots (Annex -Table 6). Dead branches are part of the vegetation cover in 15.4% (10) of the sample plots representing a maximum of 40% of the total area covered (Annex - Table 6).

The herbaceous vegetation covers a total area of 1.89 hectare. This area consists of one small patch of herbaceous vegetation the size of 0.17 hectare and with a perimeter of 240.54 m inside the eastern edge of the secondary rain forest cover (Figure 6.2 & 3.34). The remaining area of 1.72 hectares and a perimeter of 834.27 m is situated between the fence and the fringe of the secondary rain forest cover and can be overlooked from the visitors' platform (Figure 6.2 & 3.27 – 3.30).

SOIL SAMPLES FROM NGAMBA AND NSADZI ISLAND

A total of 19 soil samples in triplets were collected. The samples were taken from the centre of each woody vegetation plot, i.e. eight times three samples from Ngamba Island and two times three samples from Nsadzi Island (Table 6.12). Three times three samples were taken from each herbaceous vegetation transect, one at the beginning, one in the middle and one at the end of each transect (Table 6.12). Table 6.12 lists the samples taken, their location, their X,Y-coordinates and their pH value.

Table 6.12: *Location, S/E-coordinates and pH values of collected soil samples from Ngamba and Nsadzi Island*

Sample Plot	S/E-coordinates	Location	Vegetation type	pH
1	00°06 242 / 32°39 005	Ngamba Island	woody	2.78
2	00°06 313/32°39 014	Ngamba Island	woody	2.61
3	00°06 152/32°39 169	Ngamba Island	woody	2.74
4	00°06 240/32°39 150	Ngamba Island	woody	2.81
5	00°06 194/32°39 325	Ngamba Island	woody	3.51
6	00°06 206/32°39 269	Ngamba Island	woody	2.78
7	00°06 338/32°39 285	Ngamba Island	woody	2.50
8	00°06 355/32°39 203	Ngamba Island	woody	2.45
1	00°05 731/32°37 252	Nsadzi Island	woody	3.15
2	00°05 759/32°37 311	Nsadzi Island	woody	2.99
T1/S1*	00°06 056/32°39 152	Ngamba Island	herbaceous	4.69
T1/S2	00°06 049/32°39 182	Ngamba Island	herbaceous	4.97
T1/S3	00°06 029/32°39 234	Ngamba Island	herbaceous	4.21
T2/S1	00°06 076/32°39 163	Ngamba Island	herbaceous	4.20
T2/S2	00°06 065/32°39 195	Ngamba Island	herbaceous	3.60
T2/S3	00°06 036/32°39 242	Ngamba Island	herbaceous	4.09
T3/S1	00°06 050/32°39 237	Ngamba Island	herbaceous	4.37
T3/S2	00°06 056/32°39 249	Ngamba Island	herbaceous	4.10
T3/S3	00°06 077/32°39 275	Ngamba Island	herbaceous	3.56

* T = Transect S = Sample

pH of collected soil samples

The mean pH of collected soil samples is lowest in the woody vegetation plots on Ngamba Island (pH 2.77 ± 0.33) compared to that on Nsadzi Island (pH 3.07 ± 0.11) and that for the samples of herbaceous vegetation on Ngamba Island (pH 4.2 ± 0.46) (Table 6.12). The pH for soil samples of woody vegetation sample plots ranges from between pH 2.45 (plot 8) to pH 3.51 (plot 7) on Ngamba Island, and from pH 2.99 to pH 3.15 on Nsadzi Island. The pH for the samples of herbaceous vegetation ranges from pH 3.56 (T3/S3) to pH 4.97 (T2/S2) (Table 6.12).

SLOPE AND ASPECT OF SAMPLE PLOTS ON NGAMBA AND NSADZI ISLAND

Table 6.1 lists slope and aspect of the woody vegetation sample plots on Ngamba and Nsadzi Island. Since the dense vegetation on Nsadzi Island did not allow reliable altitude measurements the degree of slope was estimated subjectively by comparison with the classification of slopes on Ngamba Island (Table 6.1). The majority of slopes on Ngamba Island show moderate steepness while the two sample plots on Nsadzi Island possess marked slopes (Table 6.1).

DESCRIPTION OF SAMPLE PLOTS ON NSADZI ISLAND

Figure 6.68 shows a map of Nsadzi Island based on a topographic map of the British aerial survey from 1952. Nsadzi Island covers an area of about 574.1 hectare (5.74 km²) with a perimeter of 15 100.70 m. It is partly inhabited and is to a large extent covered by herbaceous vegetation and cultivated fields. The sample area was selected according to 1. continuous vegetation cover with moist evergreen secondary rain forest and 2. closest proximity to Ngamba Island.

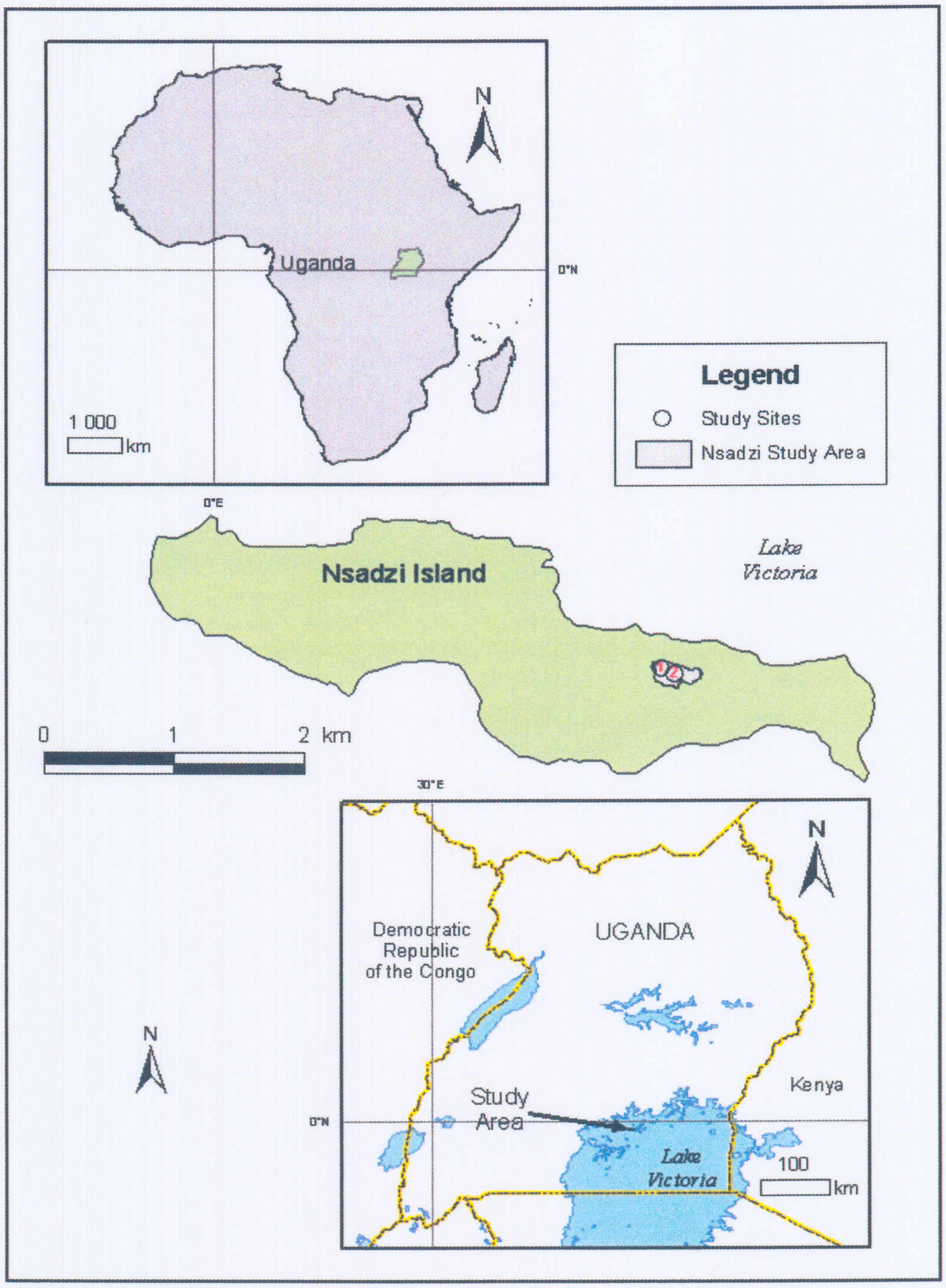

Figure 6.68: Nsadzi Island and location of study area and sample plots.

SAMPLE PLOTS ON NSADZI ISLAND

Figure 6.68 shows the sample area on Nsadzi Island based on GPS measurements. The size of the sample area is 5.27 hectare with a perimeter of 1 233.76 m. The location of the two sample plots was determined by random number selection of south / east coordinates.

Plot 1 - S 00°05 731 / E 32°37 252; 1214 ± 32 m (Table 6.1)

The forest in this plot is quite dense. The vegetation differs from that on Ngamba Island. There is widespread thorny undergrowth. A number of termite mounds and extensive termite activity can be noticed.

Plot 2 – S 00°05 759 / E 32°37 311; > 1 212 m (Table 6.1)

Here, the forest is even denser than in plot 1. Accurate GPS measurements of the coordinates for the four endpoints of the sample rectangle are not possible due to too dense vegetation. Attempts to determine altitude and slope via GPS measurements are futile on several occasions.

DIMENSIONS OF SAMPLE SQUARES ON NSADZI ISLAND

The dimensions of the respective sample areas for each height class in the two sample plots are given in Table 6.13. The majority has the smallest possible size of 5 x 5 m, like on Ngamba Island. Just as on the latter island the sample squares of the two "dead tree" categories tend to be of the largest possible size (Table 6.2 & 6.13). On Nsadzi Island therefore the density of dead trees is also on average much lower than that of the other growth form categories.

Table 6.13: *Size of sample squares for each height class in the two sample plots on Nsadzi Island*

Height class [m]	Plot 1		Plot 2	
	Size [m] of largest square	Area [m^2]	Size [m] of largest square	Area [m^2]
> 6	5 x 5	100	5 x 5	100
4 – 5	5 x 5	100	5 x 5	100
3	5 x 5	100	5 x 5	100
2	5 x 5	100	5 x 5	100
1	5 x 5	100	5 x 5	100
0.5	5 x 5	100	5 x 5	100
Standing dead	25 x 25	2500	25 x 25	2500
Fallen dead	10 x 10	400	25 x 25	2500

WOODY VEGETATION ON NSADZI ISLAND

Density

Mean density of plants over all height classes and growth forms

The mean density of plants per hectare over all height classes and vegetation types is 7 800 plants per hectare for the two sample plots on Nsadzi Island (Figure 6.69).

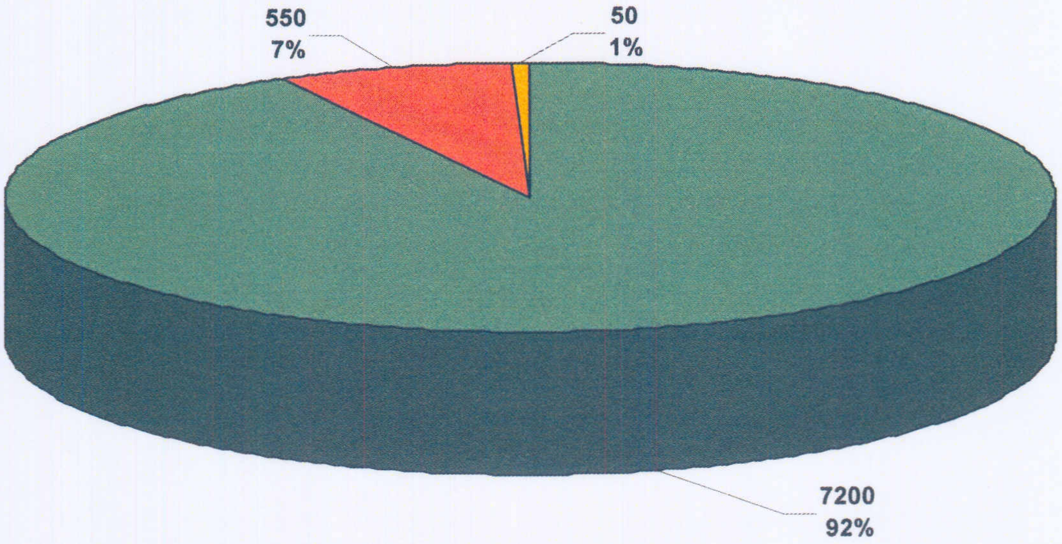

Figure 6.69: Mean number of plants per hectare and percentage per growth form.

Key:
🟨 Shrub
🟥 Sparse shrub
🟩 Tree

Mean density of different growth forms

Figure 6.69 compares the mean density of different growth forms on Nsadzi Island. Trees are by far the most prominent growth form with 92% (7 200 plants per hectare), while sparse shrubs follow with 7% (550 plants per hectare). Shrubs contribute with only 1% (50 plants per hectare) the smallest number of plants per hectare (Figure 6.69).

Mean number of plant species

The mean number of different plants species per sample plot is 16 (Table 6.14). There are a total of 24 different plant species in the two sample plots on Nsadzi Island (Annex – Table 7). Only seven of those species (*Dictyandra arborescens*, *Eugenia capensis*, *Ouratea hiernii*, *Oxyanthus speciosus var. stenocarpus*, *Peddiea fischeri*, *Tetrorchidium didymostemon* and *Trichilia species 1*) are also present in the sample plot areas on Ngamba Island (Annex – Table 1). Three of the seven plant species present in sample plots on both islands are also Ngamba island chimpanzees' food plant species, namely *Dictyandra arborescens*, *Oxyanthus speciosus var. stenocarpus* and *Tetrorchidium didymostemon* (Table 6.4).

Table 6.14: *Braun-Blanquet cover abundance classes of Nsadzi Island woody vegetation*

Species	Plot 1	Plot 2
	Braun-Blanquet classification	
*Ouratea hiernii**	4	5
Rhytigynia species 1	2A	4
Uvaria angolensis	5	+
Turrea vogellioides	1	3
*Oxyanthus speciosus***	1	2B
Calycosiphonia spathicalyx	2A	+
Coffea eugenioides	+	+
Menisorus pauciflorus	+	+
Funtumia africana	5	
Olinea rochetiana		5
Argomuellera macrophylla		2A
*Dictyandra arborescens***	1	
Oncinotis species 1	1	
*Tetrorchidium didymostemon***		1
Eugenia capensis	+	
Monanthotaxis species 1	+	
Ouratea bukobensis	+	
Peddiea fischeri	+	
Turrea species 1	+	
Olea africana		+
Unidentified species 1		+
Unidentified species 2		+
Unidentified species 3		+
Trichilia species 1		+

☐ Plant species present in both sample plots on Nsadzi Island.

* Plant species also present on Ngamba Island.

** Ngamba Island chimpanzees' food plants species on Nsadzi Island.

Braun-Blanquet cover abundance classes

Table 6.14 lists the Braun-Blanquet cover abundance classes for the different plants species of woody vegetation on Nsadzi Island. Eight species are present in both sample plots, namely *Calycosiphonia spathicalyx, Coffea eugenioides Menisorus pauciflorus*, *Ouratea hiernii Oxyanthus speciosus var. stenocarpus*, *Rhytigynia species 1, Turrea vogellioides,* and *Uvaria angolensis* (Table 6.14). *Ouratea hiernii* is the most prominent species with scores of 5 and 4 in plot 1 and 2, followed by *Rhytigynia species 1* (2A, 4) and *Uvaria angolensis* (5, +) (Table 6.14). Of the 16 plant species which are only present in one of the two sample plots *Funtumia africana* (5), *Olinea rochetiana* (5) and *Argomuellera macrophylla* (2A) are the most prevalent (Table 6.14).

Mean number of plants per species and per hectare

Figures 6.70 – 6.72 indicate the mean density of woody species for the sample area on Nsadzi Island. Since there are large differences in plant density, the species have been arranged in three different groups, namely (1) species with > 500 plants per hectare, (2) species with > 100 to 500 plants per hectare, and (3) species with 1 to 100 plants per hectare (Figures 6.70 – 6.72).

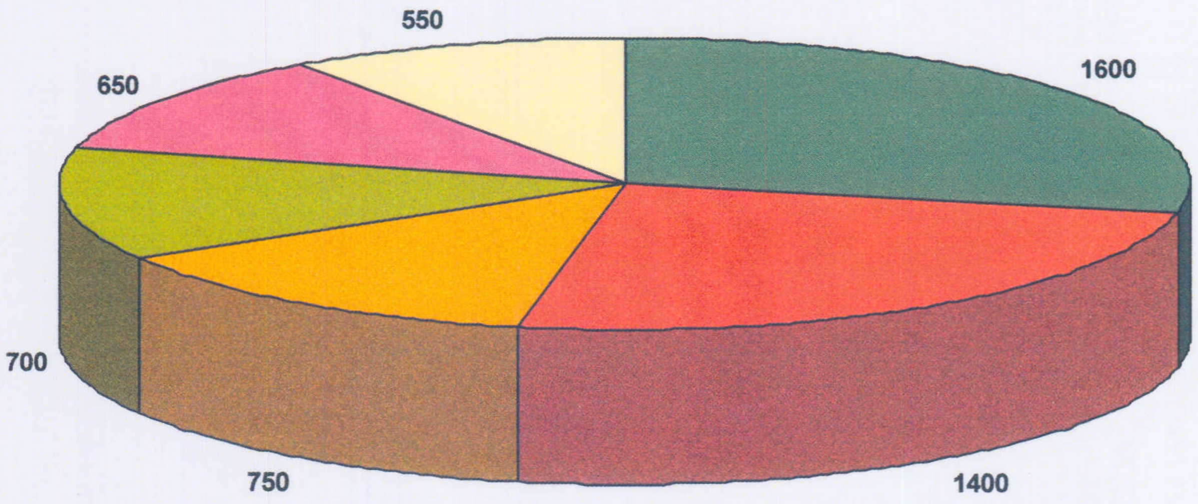

Figure 6.70: Mean density (plants per hectare) for species with > 500 plants per hectare.

Key:

- 🟨 *Uvaria angolensis*
- 🟥 *Oncinotis species 1*
- 🟩 *Menisorus pauciflorus*
- 🟧 *Turrea vogellioides*
- 🟧 *Ouratea hiernii*
- 🟩 *Rhytigynia species 1*

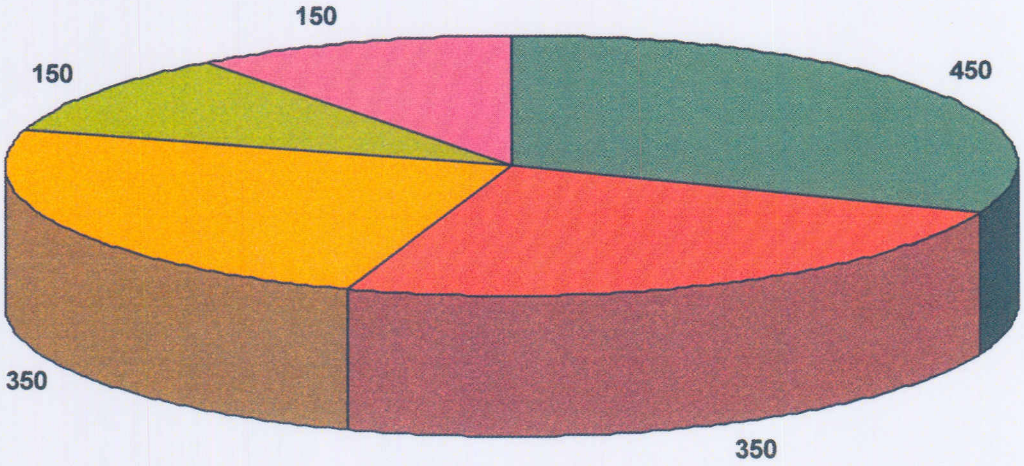

Figure 6.71: Mean density (plants per hectare) for species with > 100 - 500 plants per hectare.

Key:

🟪	*Oxyanthus speciosus var. stenocarpus*
🟩	*Calycosiphonia spathicalyx*
🟨	*Funtumia africana*
🟧	*Dictyandra arborescens*
■	*Coffea eugenioides*

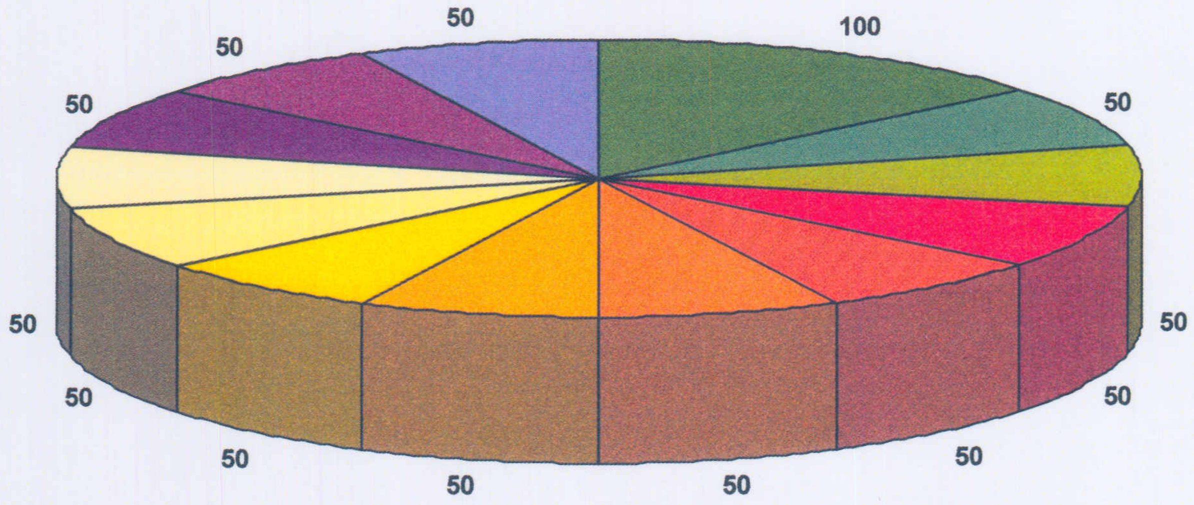

Figure 6.72: Mean density (plants per hectare) for species with 1 - 100 plants per hectare.

Key:

🟪 *Turrea species 1*
🟪 *Trichilia species 1*
🟪 *Tetrorchidium didymostemon*
🟨 *"Unidentified species 3"*
🟨 *"Unidentified species 2"*
🟨 *"Unidentified species 1"*
🟧 *Peddiea fischeri*
🟧 *Ouratea bukabiensis*
🟥 *Olinea rochetiana*
🟥 *Olea africana*
🟩 *Monanthotaxis species 1*
🟩 *Eugenia capensis*
🟩 *Argomuellera macrophylla*

There are only six species in the first group, namely *Rhytigynia species 1*, *Ouratea hiernii*, *Turrea vogellioides*, *Menisorus pauciflorus*, *Oncinotis species 1*, and *Uvaria angolensis* (Figure 6.70). Of those six species only *Oncinotis species 1* is solely present in one sample plot. The other five species are present in both sample plots and thus seem to be rather ubiquitously distributed throughout the whole sample area on Nsadzi Island (Table 6.12 & Figure 6.70).

Five plant species are present in the second group with between > 100 – 500 plants per hectare (Figure 6.71). *Coffea eugenioides* is the most prevalent plant species in this category (450 plants per hectare) and also the only species present in both sample plots on Nsadzi Island (Table 6.11 Figure 6.71). Two Ngamba Island chimpanzees' food plant species are represented in this group, namely *Dictyandra arborescens* (350 plants per hectare) and *Oxyanthus speciosus var. stenocarpus* (150 plants per hectare).

The remaining 13 plant species are all part of the last group of 1 – 100 plants per hectare (Figure 6.72). Only one species, i.e. *Argomuellera macrophylla* is represented with 100 plants per hectare. All other species have a density of 50 plants per hectare (Figure 6.72). This group also contains the third Ngamba Island chimpanzees' food plant species present on Nsadzi Island, namely *Tetrorchidium didymostemon* (50 plants per hectare) (Table 6.4 & Figure 6.72).

Mean density according to height class and growth form and mean distribution of plant species present on both islands according to growth form

Figure 6.73 and Table 6.15 show the mean distribution of height class and growth form for the plant species present on Nsadzi Island. For the plant species present on both islands, namely *Dictyandra arborescens*, *Eugenia capensis*, *Ouratea hiernii*, *Oxyanthus speciosus var. stenocarpus*, *Peddiea fischeri*, *Tetrorchidium didymostemon* and *Trichilia species 1*, the following pattern is observed on Nsadzi island: The sparse shrub growth form is only represented through *Peddiea fischeri* and here only in the 1.0 m height class (50 plants per hectare) (Figure 6.73). The shrub growth form is not represented at all between these seven species. The remaining six plant species are all represented by the tree growth form. *Ouratea hiernii* is the most abundant species and the only species present in all height classes and the most prominent species in the 2.0 m (300 plants per hectare), 3.0 m (250 plants per hectare) and 4.0 – 5.0 m (450 plants per hectare) height class (Figure 6.73).

Dictyandra arborescens is the most prominent species in the 0.5 m (200 plants per hectare) and 1.0 m (500 plants per hectare) height class (Figure 6.73). The overall mean density of woody vegetation is highest for the 1.0 m height class of trees (3 000 per hectare), followed by the 0.5 m height class (1 350 plants per hectare). The remaining height classes contribute about half or less than this number of plants. The two shrub classes only contribute to the two lowest height classes (Figure 6.73). In Comparison with the remaining plant species *Ouratea hiernii* and *Dictyandra arborescens* belong to the most abundant plant species on Nsadzi Island, while the other five species are of minor importance (Table 6.15 & Figure 6.73).

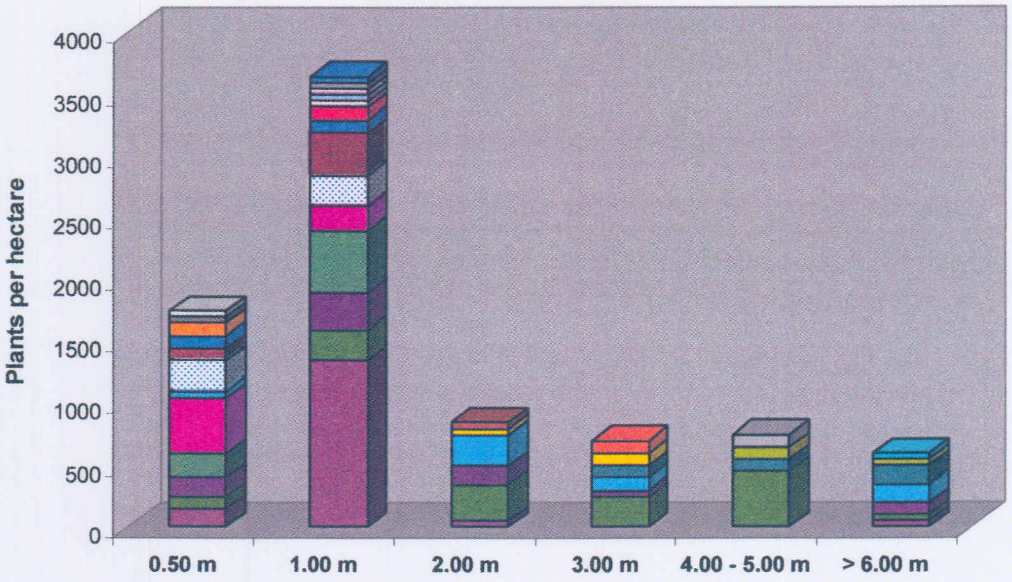

Figure 6.73: Mean density (plants per hectare) of tree (full colour), sparse shrub (points) and shrub (lines) according to height class and species.

Key:
■ *Turrea species 1*
■ *Unidentified species 3*
□ *Unidentified species 2*
■ *Unidentified species 1*
▤ *Ouratea bukobensis*
■ *Olinea rochetiana*
■ *Olea africana*
Monanthotaxis species 1
■ *Peddiea fischeri*
░ *Argomuellera macrophylla*
■ *Trichilia species 1*
■ *Tetrorchidium didymostemon*
■ *Eugenia capensis*
■ *Calycosiphonia spathicalyx*
■ *Oxyanthus speciosus var. stenocarpus*
■ *Funtumia africana*
■ *Menisorus pauciflorus*

■ *Coffea eugenioides*
░ *Menisorus pauciflorus*
■ *Uvaria angolensis*
■ *Oncinotis species 1*
■ *Dictyandra arborescens*
■ *Turrea vogellioides*
■ *Ouratea hiernii*
■ *Rhytigynia species 1*

Table 6.14: *Mean density of woody vegetation according to height class and growth form*

Height class	Mean density of woody vegetation			
	Tree	Sparse shrub	Shrub	TOTAL
> 6.00m	600			600
4.00 – 5.00 m	750			750
3.00 m	650			650
2.00 m	850			850
1.00 m	3 000	300	50	3 350
0.50 m	1 350	250		1 600
TOTAL	7 200	550	50	7 800

Mean density of "Dead Trees"

Table 6.16 shows the mean number of "Standing dead" and "Fallen dead" trees per stem diameter and hectare for the sample area, while Figure 6.74 classifies the sample area according to its mean density of total number of dead trees per hectare and Figure 6.75 according to its mean percentage of total density contributed by dead trees.

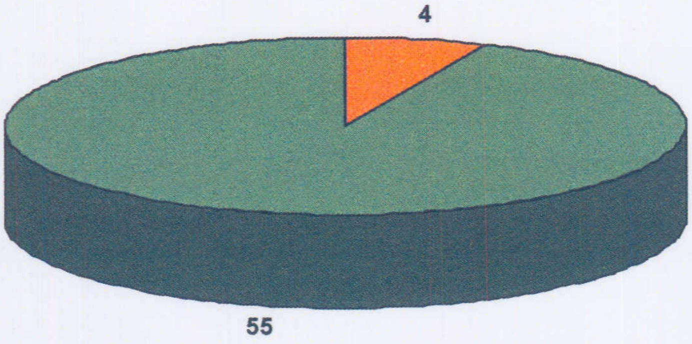

Figure 6.74: Mean number of dead trees per hectare.

Key:
🟧 Standing dead tress
🟩 Fallen dead trees

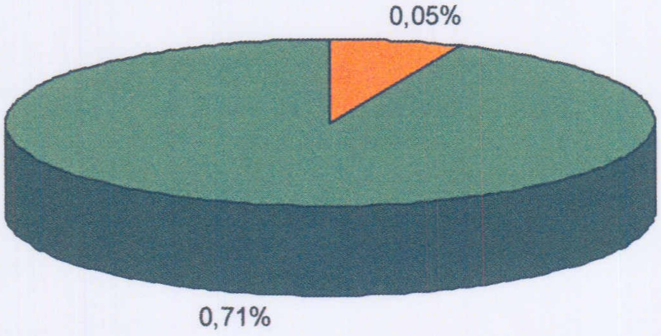

Figure 6.75: Mean percentage of total density contributed by dead trees.

Key:
🟧 Standing dead tress
🟩 Fallen dead trees

Table 6.16: *Mean number per hectare and percentage of total density contributed by "Fallen dead" and "Standing dead" trees per hectare according to stem diameter*

	Stem diameter [cm]					
	10 - 15	> 15 - 20	> 20 - 25	> 25 - 30	> 30 - 50	Total
Number (and percentage) of "Fallen dead" trees	40 (72.73)		2 (3.64)	13 (23.64)		55 (100)
Number (and percentage) of "Standing dead" trees	2 (50)		2 (50)			4 (100)

The mean density of dead trees for the sample area on Nsadzi Island is 59 plants per hectare, composed of a mean of 4 "Standing dead" and 55 "Fallen dead" trees per hectare (Figure 6.74). The mean percentage contribution to the total density made by dead trees is 0.76% for the whole sample area with 0.05% "Standing dead" and 0.71% "Fallen dead" trees per hectare (Figure 6.75).

Most of the "Fallen dead" trees, i.e. 72.73% (40 plants per hectare) of all "Fallen dead" trees, have a stem diameter of 10 – 15 cm, followed by the > 25 – 30 cm class (23.64%) (Table 6.16). Only two stem diameter classes with furthermore the same number and percentage, i.e. 2, respectively 50% of all "Standing dead" trees, occur, namely the 10 – 15 cm class and the 20 – 25 cm class (Table 6.16).

Ngamba Island chimpanzees' food plant species present on Nsadzi Island

Three food plant species are present in the sample area on Nsadzi Island (Table 6.14). With a mean number of 350 plants per hectare *Dictyandra arborescens* is the most prominent species (Figure 6.71), followed by *Oxyanthus speciosus* (150 plants per hectare) (Figure 6.71), and finally *Tetrorchidium didymostemon* (50 plants per hectare) (Figure 6.72). Only *Oxyanthus speciosus* occurs in both sample plots on Nsadzi Island (Table 6.14).

Total projected canopy cover and canopy regime at different height levels

Mean total projected canopy cover at different height classes

Figure 6.76 shows the mean total projected canopy cover for all height classes on Nsadzi Island. The > 6.0 m height class with 325.68% contributes the highest percentage of canopy cover (Figure 6.76). The percentage canopy cover declines sharply over the following height classes and only the 1.0 m height class (9.51%) has a slightly higher mean percentage canopy cover compared to the 2.0 m height class (7.93%) (Figure 6.76). The overall mean canopy cover is 491.12% per hectare for the sample area on Nsadzi Island.

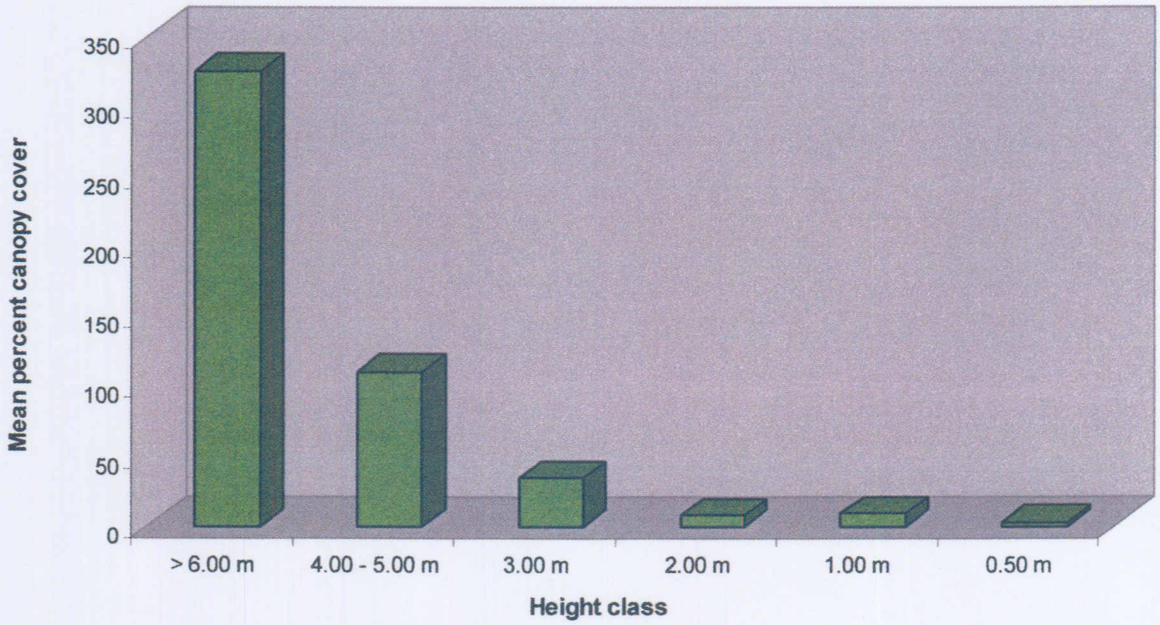

Figure 6.76: Mean total projected canopy cover of all height classes for the sample area.

Key: 🟩 Percent canopy cover

Mean total projected canopy cover at different height classes for all height levels

The > 6.0 m height class only contributes any canopy cover, namely 325.68%, at the > 6.0 m height level (Figure 6.77). The 4.00 – 5.00 m height class contributes about one-third of the percentage of the > 6.0 m height class to the total projected canopy cover (Figure 6.77). The remaining height classes contribute on average only 10% or less of the percentage of the > 6.0 m height class to the total projected canopy cover. Only the 1.0 m and 0.5 m height class contribute any canopy cover (2.48% and 2.68%) to the 0.5 m height level (Figure 6.77). Every other height class also contributes the largest percentage of mean total projected canopy cover in its highest height level (Figure 6.77).

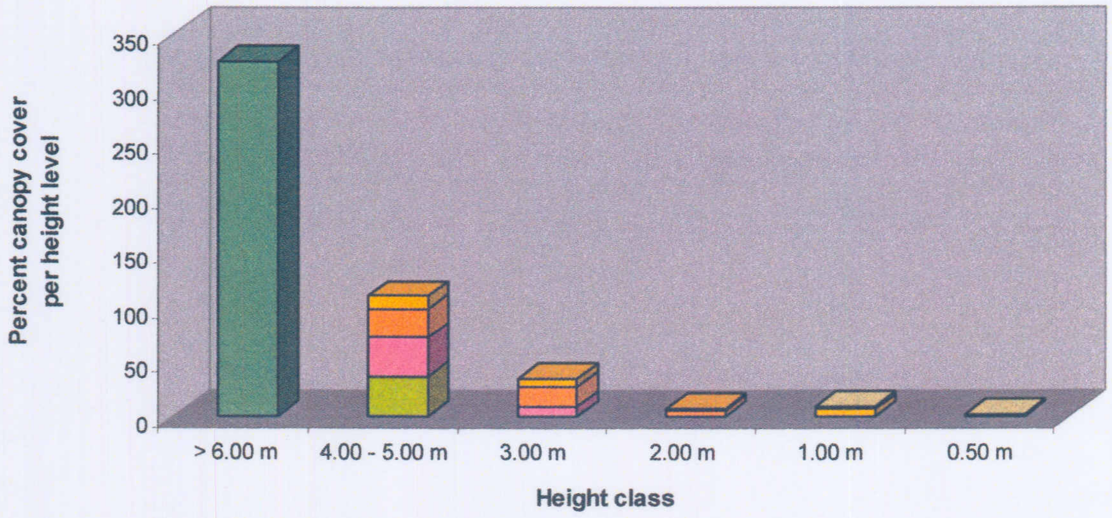

Figure 6.77: Mean total projected canopy cover at different height classes for all height levels.

Key:

🟨 0.5 m height class
🟧 1.0 m height class
🟧 2.0 m height class
🟥 3.0 m height class
🟩 4.0 – 5.0 m height class
🟩 > 6.0 m height class

Mean total projected canopy cover at different height levels

The > 6.0 m height level contributes by far the highest percentage of mean total projected canopy cover, namely 325.68% (Figure 6.78). All other height levels contribute around 15% or less of this percentage to the mean total projected canopy cover (Figure 6.78).

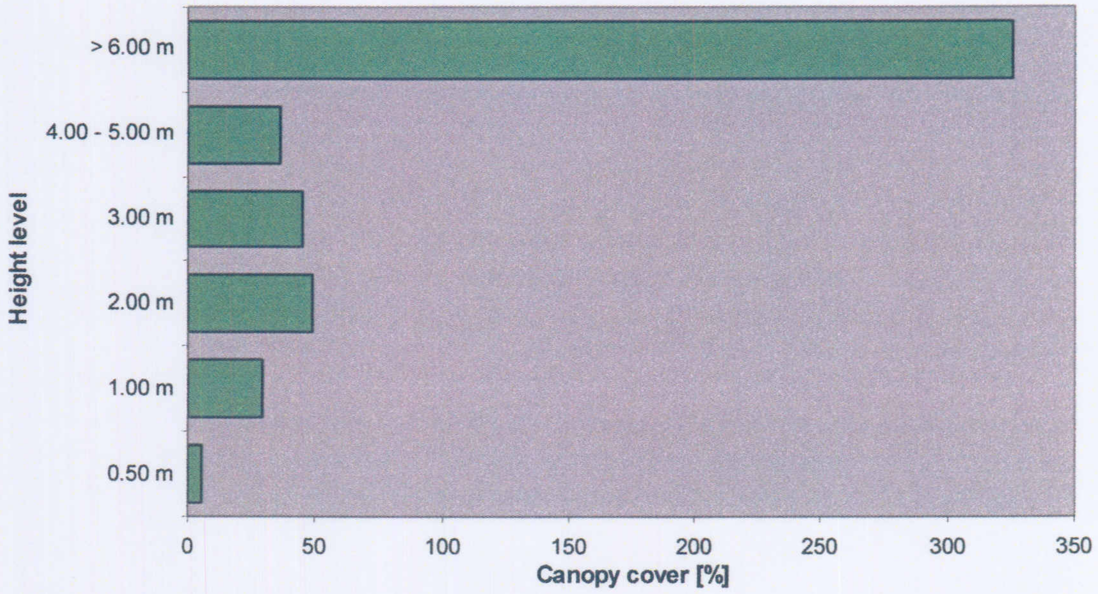

Figure 6.78: Mean total projected canopy cover at different height levels for the sample area.

Key: 🟩 Percent canopy cover

Mean total projected canopy cover according to growth form

The sparse shrub and shrub growth form contribute less than one percent (0.47% and 0.38%) to the mean total projected canopy cover according to growth form for the sample area on Nsadzi Island (Table 6.17 & Figure 6.79). The tree growth form contributes nearly all of the 491.12% of mean total canopy cover, i.e. 490.27% (Table 6.17 & Figure 6.79). The two shrub growth forms only contribute any canopy cover in the two lowest height classes, and here only 0.33% or less per growth form and height level (Table 6.17).

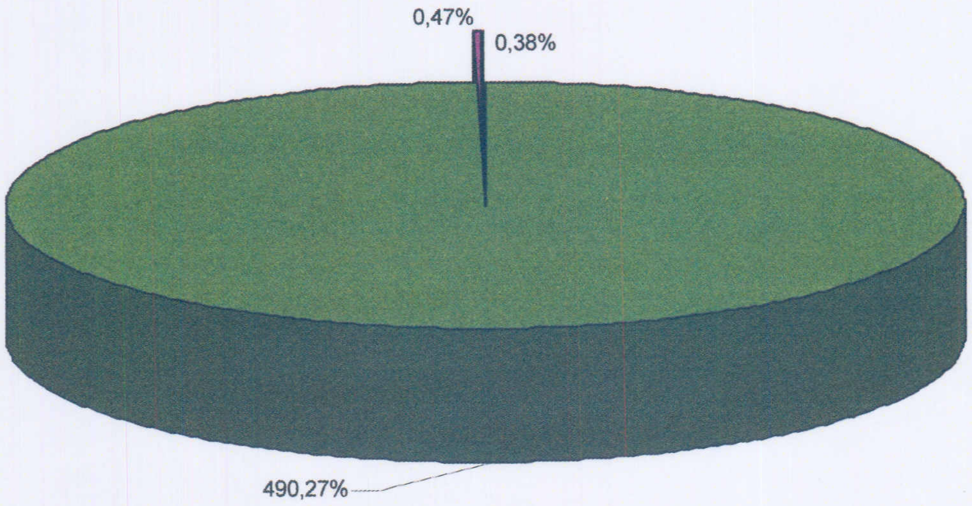

Figure 6.79: Mean total projected canopy cover according to growth form.

Key:
🟨 Shrub
🟪 Sparse shrub
🟩 Tree

Table 6.17: *Mean total projected canopy cover at different height levels according to growth form*

Height level	Canopy cover [%]			
	Tree	Sparse shrub	Shrub	TOTAL
> 6.00 m	325.68			325.68
4.00 - 5.00 m	36.61			36.61
3.00 m	45.27			45.27
2.00 m	49.30			49.30
1.00 m	28.58	0.33	0.19	29.10
0.50 m	4.83	0.14	0.19	5.16
TOTAL	490.27	0.47	0.38	491.12

CHAPTER 7

DISCUSSION AND VEGETATION MONITORING RECOMMENDATIONS

THE SECONDARY RAIN FOREST IN THE STUDY AREA

Following Langdale-Brown *et al.* (1964) the secondary rain forest cover of Ngamba Island (and the Ugandan Islands in Lake Victoria in general) constitutes or at least approaches the final stage of reforestation. The authors characterize such forests as *Piptadenestrum-Albizia-Celtis* Forest (Langdale-Brown *et al.* 1964) (Figure 3.21). The secondary rain forest cover on Ngamba Island represents a young to intermediate stage of this forest: *Albizia* spp. are still quite prominent and also a number of *Antiaris toxicara* trees are present (Figure 6.8 & 6.11). While those two species are indicators of the younger stages of this medium altitude moist evergreen forest type, the occurrence of *Entandrophragma utile* indicates that this forest approaches the middle stages of its development (Langdale-Brown *et al.* 1964) (Figure 6.11). Furthermore, the presence of *Dracaena fragrans* as prominent representative of the shrub layer and of *Commelina capitata* as the typical ground herb are additional indicators for the classification as *Piptadenestrum-Albizia-Celtis* Forest (Langdale-Brown *et al.* 1964). The mean annual rainfall of 1 457 mm for Ngamba Island (Figure 3.4) falls well between the limits of annual rainfall of 1 270 – 1 524 mm (50 to 60 inches) given by Langdale-Brown *et al.* (1964) for this forest type in Uganda. With 1 160 m Ngamba Island's altitude above sea level (see Chapter 3 – Study sites) also fulfils the observation made by those authors that the *Piptadenestrum-Albizia-Celtis* Forest occurs at an altitude of between 1 128 – 1 280 m (3 700 – 4 200 feet) above sea level at the north-west shores of Lake Victoria (Langdale-Brown *et al.* 1964).

Status of the forest edge on Ngamba Island

Using Langdale-Brown's *et al.* (1964) classification of tropical forest edges (Figure 7.1) the woody vegetation cover on Ngamba Island can be classified as possessing a 'retreating secondary rain forest edge' (compare Figure 7.1 with Figure 3.27 – 3.30). This indicates that while the forest as a whole is still advancing towards the final stage of its climax vegetation a disturbance at the northern forest edge adjacent to the herbaceous vegetation cover is already occurring (Figure 7.1). This disturbance will partly have been caused by the little fishing community which inhabited Ngamba Island before it became a chimpanzee sanctuary (see Chapter 2 – The History of Ngamba Island Chimpanzee Sanctuary). However, part of this disturbance might be caused by the newly introduced chimpanzees who frequent the edge area between forest and herbaceous vegetation quite regularly, especially during the morning and afternoon feeding (see Chapter 2 – The History of Ngamba Island Chimpanzee Sanctuary & Figure 3.27 – 3.30). At the same time they also frequently use the trees at the forest edge for resting, feeding and playing and have caused substantial damage already through the continuing defoliation of branches (Figure 4.8 & 4.12).

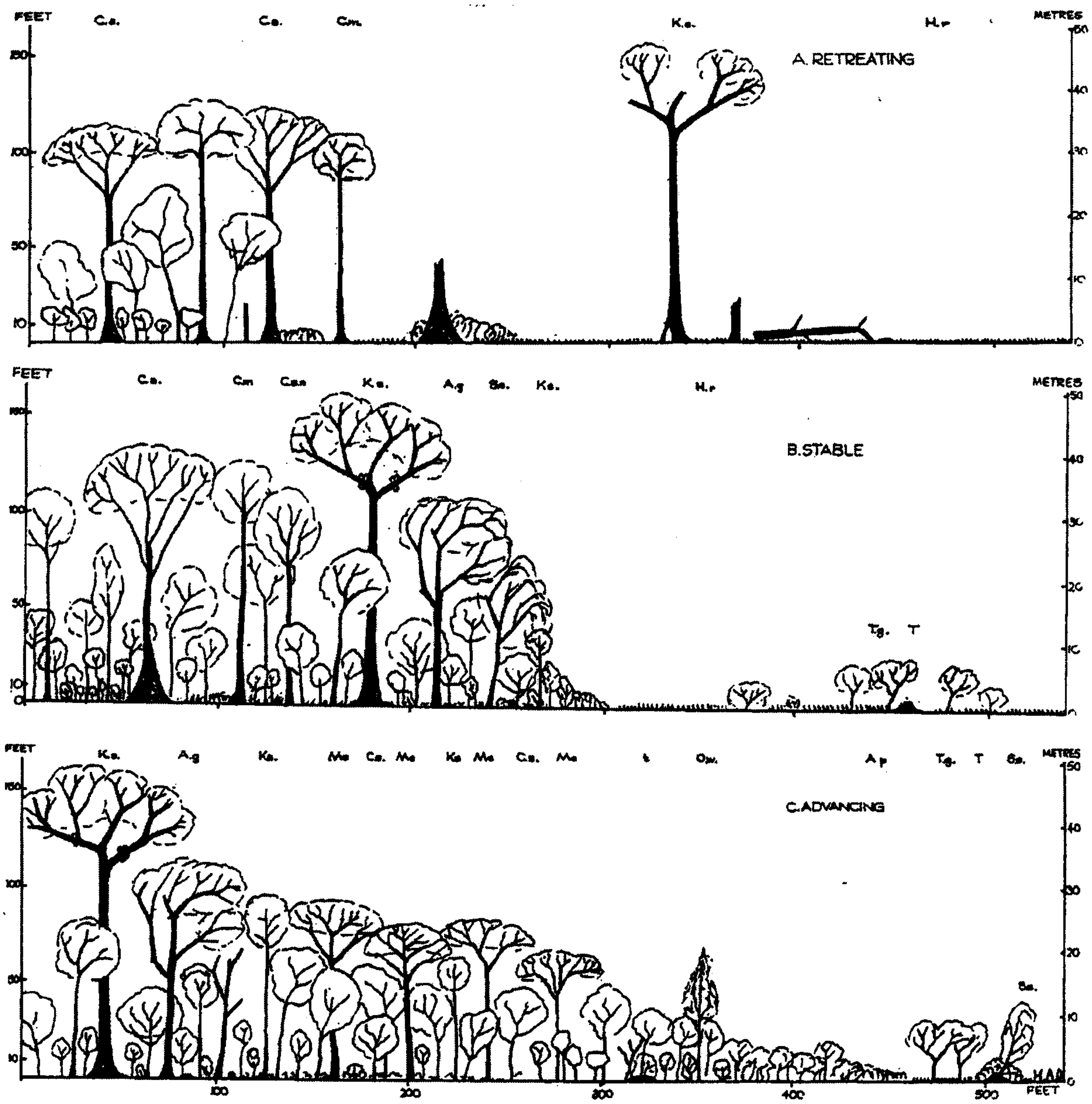

Fig. 4. The forest edge: examples from semi-deciduous forest.

Key

C.a. = Cynometra alexandri
C.m. = Celtis mildbraedii
C.sn. = Chrysophyllum sp. nov.
C. = Celtis zenkeri
K.a. = Khaya anthotheca
A.g. = Albizia grandibracteata
S.e. = Sapium ellipticum
T.g. = Terminalia glaucescens
T = live termite mound
t = dead termite mound
H.r. = Hyparrhenia rufa
M.e. = Maesopsis eminii
C.s. = Caloncoba schweinfurthii
O.w. = Olea welwitschii
A.p. = Acanthus pubescens

Figure 7.1: The three possible forms of forest edges of tropical rain forest (following Langdale-Brown *et al.* 1964).

Recommendation: To evaluate the effect the chimpanzees have on the vegetation cover of the forest edge over time photographs of this area should be taken at regular intervals and compared to any such previous documentation. The GPS coordinates of the forest edge should be regularly checked and compared with previous data as well. A southwards shift of this limit will be a sure indication of a continuing disturbance (Figure 6.1). Comparison with the location of the limits of the control area on Nsadzi Island over time (Figure 6.68) will allow an assessment of how much of the cause of this development might be attributed to the presence of chimpanzees on Ngamba Island. However, the human impact on the vegetation on Nsadzi Island will always have to be considered as well.

Pioneer and persistent woody vegetation species on Ngamba Island

When applying Martinéz-Ramos & Alvarez-Buylla's (1986) classification of pioneer and persistent tree species (see Chapter 4 – The significance of seed dispersal) the tree species on Ngamba Island with an abundance of ≥ 100 plants per hectare (Figure 6.8 & 6.9) can be classified as outlined in Table 7.1 (*Commelina capitata* has not been considered).

Table 7.1: *Classification of tree species on Ngamba Island with an abundance of ≥ 100 plants per hectare into pioneer and persistent species*[1] *and giving their mean abundance as plants per hectare*

Species [plants per hectare]	Pioneer tree (many seeds < 50 mm)	Persistent tree (few seed > 50 mm)
Aframomum angustifolium	2 931	
Albizia gumnifera	1 238	
Dracaena fragrans	2 209	
Dictyandra arborescens	113	
Galinera saxifraga		178
Guarea cedrata		1 078
Ouratea hiernii	244	
Oxyanthus speciosus		666
Pachystela brevipes		163
Palisota mannii	200	
Tetrorchidium didymostemon		129
Total	6 935	2 214

[1] Sources: Eggeling 1951, Lind & Tallantire 1962, Langdale-Brown *et al.* 1964, Lind & Morrison 1974, Katende *et al.* 1995, Katende *et al.* 1999.

There is nearly equilibrium between the number of pioneer (6) and persistent (5) tree species on the Island (Table 7.1). It is hence shown by the high number of pioneer species present that this forest is still in its young to intermediate stage of climax vegetation. This finding furthermore supports the observation by Langdale-Brown *et al.* (1964) that the *Piptadenestrum-Albizia-Celtis* Forest is characterized by a mixture of genera usually represented by only one species. Here 11 species represent nine different genera (Table 7.1 & Annex – Table 1). The pioneer species are about three times as abundant as the persistent species – another indication for the young to intermediate age of the forest successional stage (Table 7.1).

Recommendation: As part of the monitoring programme on Ngamba Island the ratio and abundance of these single pioneer and persistent tree species should be determined regularly. A steady increase in the number and abundance of persistent species would indicate that the forest cover progresses undisturbed towards its mature climax stage. Major disturbances, such as tree fall gaps, might eventually lead to an increase in the number and ratio of pioneer species to persistent species when over the years the gaps are covered again by woody vegetation. These gaps might be caused by wind as well as by the destructive influence of the chimpanzees (Figure 4.8 – 4.17).

Pioneer and persistent woody vegetation species on Nsadzi Island

When classifying tree species on Nsadzi Island with abundance ≥ 100 plants per hectare into pioneer and persistent species a picture different to that of Ngamba Island emerges. Only two species in these groups are the same on both islands, namely *Dictyandra arborescens* and *Ouratea hiernii* (Table 7.1 & 7.2). Also on Nsadzi Island 11 different species representing 6 different genera belong to this category of abundance (Table 7.2), but the ratio of pioneer species to persistent species is 9:2, i.e. higher than on Ngamba Island (Table 7.1 & 7.2).

Table 7.2: *Classification of tree species on Nsadzi Island with an abundance of ≥ 100 plants per hectare into pioneer and persistent species*[1] *and giving their mean abundance as plants per hectare*

Species [plants per hectare]	Pioneer tree (many seeds < 50 mm)	Persistent tree (few seed > 50 mm)
Calycosiphonia spathicalyx	150	
Coffea eugenioides	450	
Dictyandra arborescens	350	
Funtumia africana	350	
Menisorus pauciflorus	700	
Oncinotis species 1		650
Ouratea hiernii	1 400	
Oxyanthus speciosus var. *stenocarpus*		150
Rhytigynia species 1	1 600	
Turrea vogellioides	750	
Uvaria angolensis	550	
Total	6 300	800

[1] Sources: Eggeling 1951, Lind & Tallantire 1962, Langdale-Brown *et al.* 1964, Lind & Morrison 1974, Katende *et al.* 1995, Katende *et al.* 1999.

Recommendation: This rather pronounced difference between the two islands forecloses a meaningful comparison of the future fate of their pioneer and persistent tree species as a result of the impact of chimpanzees. When monitoring the future development of pioneer and persistent tree species on Ngamba Island it will therefore only be possible to make an assessment of the impact the chimpanzees might have on them, since a direct comparison with a similarly structured control forest is not possible.

COMPARISON OF CANOPY COVER AND HEIGHT CLASS DISTRIBUTION OF PLANT SPECIES PRESENT ON NGAMBA AND NSADZI ISLAND

A comparison of the mean number of trees per hectare according to height class on both Ngamba and Nsadzi Island also shows a rather different forest structure (Table 7.3). While the number of trees on Ngamba Islands declines fractionally from the lowest to the highest height class, as predicted by Langdale-Brown *et al.* (1964) for tropical rain forest vegetation, no such pattern is visible on Nsadzi Island (Table 7.3). Here, the 1.0 m height class shows the highest number of trees followed by the 0.5 m height class, while the remaining four height classes show about the same mean number of trees per hectare (Table 7.3). The mean total number of trees is higher on Ngamba Island than on Nsadzi Island (Table 7.3). At this stage therefore the forest structure on Ngamba Island still looks healthy, but it does not look like it is healthy on Nsadzi Island (Table 7.3).

Table 7.3: *Mean number of trees per hectare according to height class on Ngamba and Nsadzi Island*

Height class	Mean number of trees per hectare	
	Ngamba Island	Nsadzi Island
> 6 m	304	600
4 – 5 m	772	750
3 m	1 141	650
2 m	1 703	850
1 m	2 100	3 000
0.5 m	2 509	1 350
Total	8 529	7 200

Recommendation: It is postulated that the chimpanzees' impact on the forest structure will in the short to medium term mainly be evident on the density of the lower height classes. Here, younger saplings and trees will be bent and broken and uprooted by displaying male adults and by youngsters during their infant walks (see Chapter 2 - The History of Ngamba Island Chimpanzee Sanctuary, Chapter 4 – Destructive behaviour & Figures 4.8 – 4.11). To evaluate this impact and the above hypothesis the sample plots on Ngamba Island should regularly be monitored using the "Varying quadrat plot method".

Comparison of growth form abundance and species richness on Ngamba and Nsadzi Island

Growth form abundance

The main difference between the percentage contribution of growth forms to overall density on Ngamba and Nsadzi Island is the more or less complete absence of a shrub layer on Nsadzi Island (1%), while it shows about the same abundance as the sparse shrub (6%, 7%) layer on Ngamba Island (Figure 6.4 & 6.69). With a mean total number of 7 800 plants per hectare (Table 6.15 & Figure 6.69) Nsadzi Island also possesses a lower density of woody vegetation than the secondary rain forest cover on Ngamba Island with a mean total of 9 820 plants per hectare (Figure 6.69).

Recommendation: The regular monitoring of the mean density of woody vegetation of the sample areas on both islands will indicate a possible impact of the chimpanzees on the Ngamba Island woody vegetation density. This density will decrease over time through the destructive behaviour of the chimpanzees (see Chapter 4 - Island chimpanzees + - Destructive behaviour). Should a decrease of density also occur on Nsadzi Island a comparison of the degree of decline on both islands will allow a conclusion on the percentage of decline attributable to the chimpanzees' impact on the woody vegetation on Ngamba Island. This percentage can then be used to make and adjust predictions for the future development of forest density over time according to number of chimpanzees present on Ngamba Island.

Importance of Aframomum angustifolium *and* Dracaena fragrans

The contribution of the shrub layer to overall woody vegetation density on Ngamba Island is mainly caused by high mean densities of *Aframomum angustifolium* and *Dracaena fragrans* (see Chapter 6 - Tree density corrected for *Aframomum angustifolium*,

- Distribution of plant species according to growth form & Figure 6.8, 612, 6.17, 6.22, 6.23, 6.27, 6.28, & 6.32). Both of those species are also Ngamba Island chimpanzees' food plant species (see Chapter 4 – Terrestrial herbaceous food + Feeding techniques, Chapter 6 – Ngamba Island chimpanzees' food plant species & Table 6.4).

Recommendation: Regular monitoring of the density of these two species will show whether the use by the chimpanzees - while also acting as possible seed dispersers - will increase or decrease the abundance of those two plant species on the island. The chimpanzees have also quite a destructive influence on those two plant species simply through bending and uprooting of stems (see Chapter 6 - Sample plots on Ngamba Island).

Species richness

In the eight sample plots on Ngamba Island a total of 41 different woody vegetation species has been found (Annex – Table 1). Species richness in the sample plots on Ngamba Island varies from 9 to 17 different species (Figure 6.6), while it is 16 for the two plots on Nsadzi Island (Table 6.14). The two sample plots on Nsadzi Island contain altogether 24 different species (Annex – Table 7). Some of the plots on Ngamba Island are species poor with a high density of a selected number of species, e.g. plot 7 and 8 which show a high abundance of *Dracaena fragrans* and *Aframomum angustifolium*, respectively (see Chapter 6 – Density according to height class and growth form).

Recommendation: Regular monitoring of the eight sample plots on Ngamba Island will indicate whether a change in the species richness and species diversity in the eight plots on the island occurs. Special emphasis should be put on the monitoring of *Aframomum angustifolium* and *Dracaena fragrans* (see above) as well as on the other Ngamba Island chimpanzees' food plant species (see below).

Height class and mean percentage canopy cover of tree species on Ngamba Island with an abundance of ≥ 100 plants per hectare

When comparing the mean number of plants per hectare with the mean percentage canopy cover it becomes obvious that the three most abundant tree species are pioneer species or typical representatives of the shrub layer of the *Piptadenestrum-Albizia-Celtis* Forest (Langdale-Brown *et al.* 1964) (Table 7.1 & 7.4), while the three tree species with the highest mean percentage canopy cover are persistent tree species (Table 7.1 & 7.5). The former tree species have their highest abundance in the lower and younger height classes which still possess a limited degree of foliage (Table 7.4 & 7.5). The latter tree species have their highest abundance of plants and canopy cover in the higher height classes (Table 7.4 & 7.5).

Table 7.4: *Mean number of plants per hectare according to height class for species with an abundance of ≥ 100 plants per hectare*

Species [plants per hectare]	Height class						
	0.50m	1.00 m	2.00 m	3.00 m	4.00 – 5.00 m	> 6.00 m	Total
Aframomum angustifolium F	575	900	956	463	13		2 907
Dracaena fragrans F	1 400	475	225	75	38		2 213
Albizia gumnifera F	263	438	166	291	216	16	1 390
Guarea cedrata F	166	188	284	144	138	147	1 067
Oxyanthus speciosus F	78	175	38	200	153	23	667
Ouratea hiernii	6	13	213	13			245
Palisota mannii	175	25					200
Galinera saxifraga		38	25	63	53		179
Pachystela brevipes F	38	13	13	25		75	164
Tetrorchidium didymostemon F			38	31	56	4	129
Dictyandra arborescens F		25	63	13	25		126

□	Pioneer tree species
■	Persistent tree species
F	Ngamba island chimpanzees' food plant species

Table 7.5: *Mean percentage canopy cover for species with an abundance of ≥ 100 plants per hectare*

Species [Percentage canopy cover]	Height class						
	0.50m	1.00 m	2.00 m	3.00 m	4.00 – 5.00 m	> 6.00 m	Total
Guarea cedrata F	0.84	2.48	6.82	8.69	11.42	64.27	94.52
Oxyanthus speciosus F	0.60	3.14	11.81	15.15	6.63	5.52	42.85
Pachystela brevipes F	0.23	0.58	0.23	3.25	12.28	18.76	35.33
Dracaena fragrans F	10.89	6.13	4.13	0.73	0.30		22.18
Aframomum angustifolium F	1.23	5.75	6.96	2.91	0.01		16.86
Terorchidium didymostemon F	0.02	0.39	2.00	2.41	6.20	3.93	14.95
Ouratea hiernii	0.95	2.87	9.74	0.22			13.78
Albizia gumnifera F	0.55	0.76	0.96	1.27	1.71	2.90	8.15
Galinera saxifraga F	0.03	0.32	2.37	3.63	1.54		7.89
Palisota mannii	2.80	0.50					3.3
Dictyandra arborescens F		0.07	0.28	0.24	1.03		1.62

□	Pioneer tree species
🟩	Persistent tree species
F	Ngamba island chimpanzees' food plant species

Tetrorchidium didymostemon is a persistent tree species which seems the one most likely to disappear from Ngamba Island over time. It has no more young seedlings and saplings which could eventually replace old dying trees (Table 7.4). Other persistent tree species which might follow at a later stage are *Galinera saxifraga* and *Oxyanthus speciosus* (Table 7.4). Overall, all persistent tree species seem to be having a problem recruiting new trees. Those being food species for chimpanzees will face an additional pressure – apart from *Galinera saxifraga* that are all of them (Table 7.4). The pioneer species most likely to disappear seems to be *Dictyandra arborescens*, followed by *Ouratea hiernii* (Table 7.4).

Two of the three species with the highest mean percentage canopy cover, namely *Guarea cedrata* and *Oxyanthus speciosus*, have been classified as *indifferent species* using the Braun-Blanquet classification (Table 6.3). This indicates that they are distributed ubiquitously throughout the island (see Chapter 5 – Analysis of woody vegetation data). *Pachystela brevipes* is a companion species (Table 6.3) and occurs only in confined areas throughout Ngamba Island (see Chapter 5 – Analysis of woody vegetation). This species belongs to the family Sapotaceae, members of which characterize, according to Langdale-Brown *et al.* (1964), the final stages of the climax vegetation in a *Piptadenestrum-Albizia-Celtis* Forest. This climax vegetation can be compared to the 'tree stage of succession' of secondary rain forest succession described by Richards (1966) and Ewel (1980) and can again be divided into three different phases.

Based on the canopy cover values it is currently definitely the group of persistent tree species which is giving the character and appearance of the woody vegetation cover on Ngamba Island (Table 7.5).

Recommendation: As part of the vegetation monitoring programme possible changes in these patterns should be determined and evaluated. The forest cover on Ngamba Island seems to be in a transition period from the young to the intermediate stage of climax vegetation (Langdale-Brown *et al.* 1964). It will be interesting to see whether and if so to which extent the impact of the newly introduced species of chimpanzees onto the island will interfere with this natural progress in forest development. It is postulated that through continuing destruction of the existing vegetation cover and simultaneous destruction of upcoming plant seedlings and saplings the chimpanzee population on Ngamba Island will eventually bring this development to a complete standstill.

Comparison of the seven tree species present on both Ngamba and Nsadzi Island

Figures 6.60 – 6.66 summarize the mean percentage canopy cover of the seven tree species, namely *Dictyandra arborescens*, *Eugenia capensis*, *Ouratea hiernii*, *Oxyanthus speciosus*, *Peddiea fischeri*, *Tetrorchidium didymostemon and Trichilia species 1*, present on both, Ngamba and Nsadzi Island (Table 6.14). Of those seven species only *Oxyanthus speciosus* and *Trichilia species 1* show a similar pattern in their mean percentage canopy cover at different height levels (see Chapter 6 – Mean percentage canopy cover of selected plant species) with it still being considerably higher for both species and at all height levels on Ngamba Island (Figure 6.63 & 6.66).

Because of these varying patterns in mean percentage canopy cover a direct comparison of the seven tree species on both islands over time will be inconclusive. It will be worthwhile, though, to compare trends in the development of the canopy cover of the single species. It is predicted that the mean canopy cover of the individual species on Nsadzi Island will increase over time, while that of the same species on Ngamba Island will decrease.

Recommendation: As part of the regular vegetation monitoring special emphasis should be put on the evaluation of the development of the mean canopy cover of the seven plant species present on both, Ngamba and Nsadzi Island. If an opposite trend in the mean percentage canopy cover on both islands can be detected, as predicted above, the destructive impact of the chimpanzees on the woody vegetation of Ngamba Island will be directly demonstrated.

Food plant species

There are only three Ngamba Island chimpanzees' food plant species present on both, Ngamba and Nsadzi Island, namely *Dictyandra arborescens*, *Oxyanthus speciosus var. stenocarpus* and *Tetrorchidium didymostemon* (see Chapter 6 – Woody vegetation on Nsadzi Island, Table 6.14). Being part of the seven species present on both islands they will be especially monitored as outlined already above.

The mean total projected canopy cover of Ngamba Island chimpanzees' food plant species is presented in Figure 6.67. It is predicted that this canopy cover will decrease over time in all 11 species shown through the destructive feeding techniques applied by the chimpanzees (see Chapter 4 – Chimpanzee feeding behaviour). Since the chimpanzees and their destructive impact are confined to a limited fenced-off area the trees may have no chance to recover. Especially, as long as the tree is fruiting, each individual tree will be regularly exposed to visiting chimpanzees. The animals have no other chance but to return over and over again to the same fruiting trees in their limited forest refuge.

Recommendation: Regular monitoring of the mean percentage canopy cover of these species, especially in comparison with the three chimpanzees' food plant species also present on Nsadzi Island, will allow this prediction to be tested, and to assess the degree of destruction caused by the Ngamba Island chimpanzees on the canopy cover of those selected species.

EVALUATION OF "DEAD TREE" ABUNDANCE ON NGAMBA ISLAND

When applying Skorupa & Kasenene's (1984) 1.3% to 1.4% annual rate of natural tree fall for mature tropical forests (see Chapter 4 – Logging and natural tree mortality) the mean percentage of 0.84% of "Fallen dead" trees for Ngamba Island (Figure 6.41) falls well below this threshold. The mean percentage of 0.71% of "Fallen dead" trees on Nsadzi Island (Figure 6.75) hence also falls below this threshold. The mean percentage fallen trees determined for both islands is (incorrectly) assumed here to be an *annual* tree fall rate. The real value of the latter will therefore be even lower for both islands. It can therefore be concluded that the mean annual natural tree fall rate for Ngamba and Nsadzi Island falls well below the mean rate determined by Skorupa & Kasenene (1984). There need therefore not be any concern for the long term survival of the secondary rain forest cover on either of the islands when considering the natural tree fall rate alone.

There are two sample plots on Ngamba Island (plot 4 & 8) with a significantly higher density of "Fallen dead" trees. The highest percentage occurs in plot 8 and with 2.59% exceeds the annual natural tree fall rate by more than one percent. The second highest percentage occurs in plot 4 with 1.97% and hence lies about 0.5% above the annual natural tree fall rate. In both plots the 10 – 15 cm stem diameter class contributes between two to three times the number of trees compared to any other stem diameter class (Table 6.8). It therefore seems evident that it is the youngest group of trees which mainly falls victim to influences preventing them from maturing. The main cause of uprooting trees might be wind as postulated by Skorupa and Kasenene (1984). Plot 8 is the southernmost of the sample plots (Table 6.1 & Figure 6.1). Furthermore, with 8 386 plants per hectare it has the fourth lowest density of woody vegetation of all eight sample plots (Figure 6.3). It has also though more than 150% of canopy cover in the 3.0 m height level and above (Figure 6.56), which would indicate a canopy cover sufficiently closed to act as an efficient wind brake (Fons 1940). Considering though the moderate slope of the plot combined with the rather open stand of trees the canopy does not form a closed and uniform cover and is hence not efficient enough to brake the incoming partly high winds sufficiently (Fons 1940) to prevent them from damaging weak and young, feeble trees. Plot 4 on the other hand is the plot with the highest elevation (Table 6.1). With 9 150 plants per hectare (Figure 6.3) it has a similarly low density of woody vegetation as plot 8 and is dominated by a canopy cover in the 2.0 m height level (Figure 6.52). It furthermore has a marked northern slope (Table 6.1). Its woody vegetation will therefore be fairly unprotected (Fons 1940) from the heavy storms which occur about twice-yearly, coming from the north (Figure 3.16) and hitting this fairly high and unprotected plot situated north of the highest elevation on Ngamba Island (Table 6.1 & Figure 6.1).

A second influence causing tree mortality especially in young, slim trees might be the destruction through displaying chimpanzees (see Chapter 4 – Destructive behaviour + Feeding techniques & Figures 4.8 – 4.11). They might not necessarily uproot these trees but might bend them and shake them and even defoliate them when sitting, resting, playing and building nests in them (Figure 4.8). This might result in a rather high number of “Standing dead” trees present in a confined area inhabited by chimpanzees. The mean percentage of “Standing dead” trees is 0.24% for Ngamba Island (Figure 6.41) and 0.05% for Nsadzi Island (Figure 6.75). This difference between the two islands is marked and might be an indicator of a disturbance and destruction of the woody vegetation cover caused by the chimpanzee inhabitants of Ngamba Island. The trend of this development will in future have to be measured and compared between the sample plots of the two islands. It will then become possible to assess and furthermore predict the impact per chimpanzee and per year on defoliation followed by destruction of the woody vegetation cover of Ngamba Island. Three (plot 3, 7 + 8) of the eight plots on Ngamba Island show an above average percentage of “standing dead” trees: plot 8 shows with 1.16% the highest percentage followed by plot 7 (0.45%) and plot 3 (0.23%) (Figure 6.40).

The high percentage of standing dead trees in plot 8 might partly again simply be caused by the constant impact of southerly winds on the rather open stand of trees on a moderate slope defoliating and subsequently killing a number of standing trees (Fons 1940, Figure 3.12 – 3.16). It is assumed that the trees might be defoliated partly by the often moderate to strong southerly winds as well as partly also by adult chimpanzees who might use the exposed trees as lookouts and at the same time defoliate them as shown in Figure 4.12. Plot 7 and plot 8 have a very different woody vegetation structure (Figure 6.27 – 6.30). While plot 7 has a high abundance of trees in the three lower height classes (Figure 6.29) and a high percentage of “Standing dead” trees in the 10 – 15 cm stem diameter class mainly representing young trees (Table 6.9); plot 8 has the highest abundance of trees in the 2.0 m height class (Figure 6.30) while its high percentage of "Standing dead" trees is recruited only from the > 20 – 25 cm and the > 25 – 30 cm stem diameter classes mainly representing more mature trees (Table 6.9). Also the distribution of total projected canopy cover shows a concentration in the 0.50 m height level for plot 7 (Figure 6.55) and in the four highest height levels in plot 8 (Figure 6.56).

There seems to be no correlation between the distribution and abundance of Ngamba Island chimpanzees' food species (Table 6.4) and the percentage of "Standing dead" trees (Table 6.10) in the sample plots.

Recommendation: To assess whether there is an impact by the chimpanzees additionally to wind on the occurrence and hence percentage of "Standing dead" trees (on the sample plots) on Ngamba Island the following should be observed in the future:

1. Does the mean percentage of "Standing dead" trees increase over time?
2. Does the mean percentage of "Standing dead" trees increase in comparison with that on Nsadzi Island?
3. Does the percentage of "Standing dead" trees increase in the single sample plots?
4. Does the percentage of "Standing dead" trees change between sample plots?
5. Is the percentage of "Standing dead" trees in the different sample plots correlated with the movement patterns of the chimpanzees on the Island and with the "time-spent" by (certain) chimpanzees in different areas of the island?

THE ROLE OF WIND ON NGAMBA ISLAND

As outlined above and in Chapter 3 – Wind, the wind on Ngamba Island mainly originates from the south. Heavy storms however, mainly come from the north and occur about twice a year (Figure 3.12 – 3.16).

A major impact chimpanzees have on the woody vegetation cover of Ngamba Island is that they defoliate trees of all height classes (see Chapter 4 – Island chimpanzees, Destructive behaviour + Feeding techniques & Figure 4.8 & 4.12 – 4.16). An intact tree canopy is of major importance in reducing the impact of wind velocity and hence the destruction caused by wind in a forest habitat (Fons 1940).

With increasing defoliation the destructive effect especially of heavy storms on the woody vegetation cover of Ngamba Island is likely to increase. This will result in an increase of the number of "Fallen dead" trees over a period of time. It is therefore postulated that the number of "Fallen dead" trees will increase firstly in the northern part of the Island where the impact through heavy storms is greatest. This effect will though only become noticeable after a number of years. Monitoring the woody vegetation cover following the recommendations given above (see Evaluation of "Dead tree" abundance on Ngamba Island) will eventually allow this hypothesis to be tested (and hopefully substantiate it).

ASSESSMENT OF THE IMPACT OF NGAMBA ISLAND CHIMPANZEES ON THE VEGETATION COVER OF THEIR FOREST REFUGE

Using different approaches and calculations to estimate the necessary home ranges for chimpanzees in a confined habitat the results given in Table 7.6 vary considerably. These areas are calculated under the condition that the chimpanzees have to live self sustainable on the area available to them (see Chapter 4 – Island chimpanzees + Chimpanzee ranging pattern & Figure 4.6). For a confined habitat in a sanctuary or zoo, where food is often provided for chimpanzees, their required home range would be smaller (see Chapter 4 – Factors affecting food choice + Provisioning). Only regular monitoring of the vegetation cover of a confined habitat, like on Ngamba Island, will show, which of the calculated home ranges (Table 7.6) comes closest to the area required by chimpanzees under such circumstances. At present it is therefore postulated that the required home range for each chimpanzee lies in between the areas calculated using Jenkins' (pers. comm.)[1] and Ghiglieri's (1984) estimates (Table 7.6). Since there is an 11.2-fold difference between these estimates they can only be considered to be rather broad guidelines. They indicate nevertheless, that Ngamba Island with an area of 42.40 ha of secondary rain forest cover and 16 adult and 17 juvenile chimpanzees is already highly overstocked (Table 7.6 & Figure 4.6).

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[1] Jenkins, P. 2001. Pandrillus, Calabar, Nigeria.

Table 7.6: *Chimpanzee home ranges in a tropical rain forest habitat*

Home ranges for self sustainability required by chimpanzees in a confined tropical rain forest habitat / sanctuary [ha]					
Number of Chimpanzees[1]	**McNab (1963)**[2] **Food hunters**	**Milton & May (1976)**[3] **Primate hunters**	**Ghiglieri (1984)**[4] **Ngogo chimpanzees**	**Jenkins (2001)**[5] Boki Ogi Chimpanzees	**Destruction / year [ha]**
1	🟥 70	🟥 34	🟥 56	5	0.05
5	350	170	280	25	0.25
10	700	340	560	🟥 50	0.50
15	1 050	510	840	75	0.75
16	1 120	544	896	80	0.80
17	1 190	578	952	85	0.85
18	1 260	612	1 008	90	0.90
19	1 330	646	1 064	95	0.95
20	1 400	680	1 120	100	1.00
25	1 750	850	1 400	125	1.25
30	2 100	1 020	1 680	150	1.50
35	2 450	1 190	1 960	175	1.75

1. For the mean body mass of an individual chimpanzee 28.7 kg is used as estimated by Ghiglieri (1984).
2. McNab (1963) uses the equation: $R_h = 0.20$ M for Food hunters, with M = basal metabolic rate [Kcal/day.), Rh = Home range [acres].
3. Milton & May (1976) use the equation: Log $HR_i = 0.83$ Log BW – 2.17, with HR_i = size of home range [ha] of the individual, BW = body mass [g].
4. Ghiglieri (1984) calculates a mean home range of 30.5 km² for the 55 chimpanzees in Ngogo, Kibale Forest, Uganda, i.e. 0.56 km² / Chimpanzee.
5. Jenkins (*pers. comm. 2001*) estimates an area of at least 4 – 5 ha of tropical rain forest habitat per chimpanzee for self sustainability.

🟥 Cut-off limit for stocking density of chimpanzees on Ngamba Island.

Table 7.6 also gives an indication of the destruction caused by chimpanzees in a confined habitat depending on their density. When using Jenkins' (pers. comm.) description of the destruction of the secondary rain forest cover by chimpanzees kept in a confined habitat as a guideline a mean destruction of 0.05 ha (= 500 m^2) of rain forest cover per chimpanzee per year can be calculated (see Chapter 4 – Destructive behaviour). Applying this value Table 7.7 gives an overview of the future destruction of the secondary rain forest cover on Ngamba Island depending on chimpanzee stocking density.

Table 7.7: Destruction of the secondary rain forest cover on Ngamba Island depending on chimpanzee stocking density

Number of Chimpanzees	Time until destruction [Years]	Destruction per year [%]
1	844	0.12
5	169	0.59
10	84	1.19
15	56	1.78
16	53	1.90
17	50	2.01
18	47	2.13
19	44	2.25
20	42	2.37
25	34	2.96
30	28	3.55
35	24	4.15

Considering the maximum life span of a chimpanzee to be about 50 years it becomes obvious that only a stocking density ≤ 17 chimpanzees can, while not being sustainable, ensure a safe habitat for one generation of sanctuary chimpanzees while still resulting in the complete destruction of the secondary rain forest cover of the island. This would also mean that breeding by individual chimpanzees confined in any sanctuary should be controlled or prohibited completely, at least as soon as the maximum stocking density has been reached (see Chapter 2 – Origin of the Ngamba Island chimpanzees & Cox *et al.* 2000).

There will be a "cut-off" limit for stocking density where the destruction caused by a number of chimpanzees in a confined habitat can still be restored by natural forest regeneration and hence allow sustainable use of such a refuge. Using Jenkins' (pers. comm.) values this density lies between 5 to 10 chimpanzees for Ngamba Island (Table 7.6). When applying Ghiglieri's estimate it would be about 1 chimpanzee (Table 7.6).

Might this dark picture of the continuing and unavoidable destruction of the secondary rain forest cover of Ngamba Island perhaps be enlightened by the fact that chimpanzees also act as efficient seed dispersers (see Chapter 4 – Chimpanzees as seed dispersers)? Sadly, the answer here also seems to be "no". Following De Steven & Wright (2002) and Chapman & Chapman (1996) the number of mature trees that a parent tree produces per fruiting period might often be as little as ≤ 1. As stated by a number of authors the impressive number of seeds dispersed by each individual chimpanzee is put into perspective by the very low final recruitment rate (Janzen 1970, 1982, 1986, Augspurger 1984a+b, Janzen 1986, Estrada & Coates-Estrada 1986, Popma & Bongers 1988, Schupp 1988a, Chapman 1989, Wrangham *et al.* 1994a+b, Chapman & Chapman 1996, De Steven & Wright 2002). It is therefore also doubted that the presence of the chimpanzees on the island will increase the number of fig trees over time, even though they are an important food source for this species (see Chapter 4 – The importance of *Ficus* species & Chapter 6 – Distribution and density of *Ficus* spp.).

In consequence of the above it is postulated that the impact of the Ngamba Island chimpanzees as seed dispersers for selected woody vegetation species is of low importance if not negligible. It is by far outweighed by the destruction caused to the secondary rain forest cover of the island by this newly introduced species.

CONCLUSION

In summary, the impact the newly introduced species of chimpanzee will over time have on the secondary rain forest cover of their forest refuge on Ngamba Island is that of continuing destruction. Using a rate of destruction of about 0.05 ha per chimpanzee per year the secondary rain forest cover of Ngamba Island will be completely destroyed in 53 years with a stocking density of 16 adult chimpanzees, in 39 years with a stocking density of 22 adult chimpanzees and in 26 years with a stocking density of 33 adult chimpanzees. Regular and intensive monitoring of the vegetation cover will allow the evaluation and, if necessary, the adjustment of these values predicting the rate of destruction.

Overall, increasing stocking density - also through maturing of the juvenile chimpanzees currently present on the island into adulthood - will increase the rate of destruction of the woody vegetation cover of Ngamba Island proportionally.

CHAPTER 8

MANAGEMENT RECOMMENDATIONS

A number of management recommendations are proposed for Ngamba Island Chimpanzee Sanctuary. As outlined in detail below they can be divided into three broad categories, namely (1) chimpanzee management, (2) vegetation monitoring, and (3) climate monitoring.

CHIMPANZEE MANAGEMENT

The following seven major recommendations for the management of the chimpanzees on Ngamba Island are proposed (Table 8.1):

Abandon the track system inside the forest

The track system inside the forest should be reduced to a minimum or better, be abandoned completely (see Chapter 5 – Selecting sample plots for the woody vegetation survey). The woody vegetation cover is already rather small. A constantly maintained grid system of man-made tracks covering the island additionally opens up the vegetation. It hence facilitates access for the chimpanzees also into the denser areas of the rain forest cover (see Chapter 6 – Sample plots on Ngamba Island). Furthermore, the chimpanzees create their own track system which adds further to the destruction of woody vegetation. Letting the vegetation on the tracks recover will increase the density of and the area covered with woody vegetation inside the secondary rain forest cover (Table 8.1).

Restrict area of infant walks

The chimpanzee infants cause a considerable destruction of selected trees during their infant walks inside the forest area in the morning and the evening (see Chapter 2 – Previous research on flora and fauna of Ngamba Island, Chapter 3 – Data collection on Ngamba Island & Chapter 4 – Destructive behaviour). The tree in Figure 4.8 was a healthy young plant in May 2000. In November 2000, after only six months, it had been completely defoliated and destroyed by the playing infant chimpanzees during their forest walks. By reducing the area of the infant walks to the small open grassland area in the east of the island (Figure 6.1 & 3.34 - arrow) the destruction caused by these infants is also limited to a rather small area (Table 8.1).

Provide “Playground”

To further reduce the destructive impact of the infants, some playground-like structures should also be erected in this open grassland area. Those can also be used by the adult chimpanzees during their ventures inside the fenced off area (Figure 8.1 & 8.2). This will give them the chance to test their - mainly unintended - destructive strength also on other features besides healthy woody vegetation (Table 8.1).

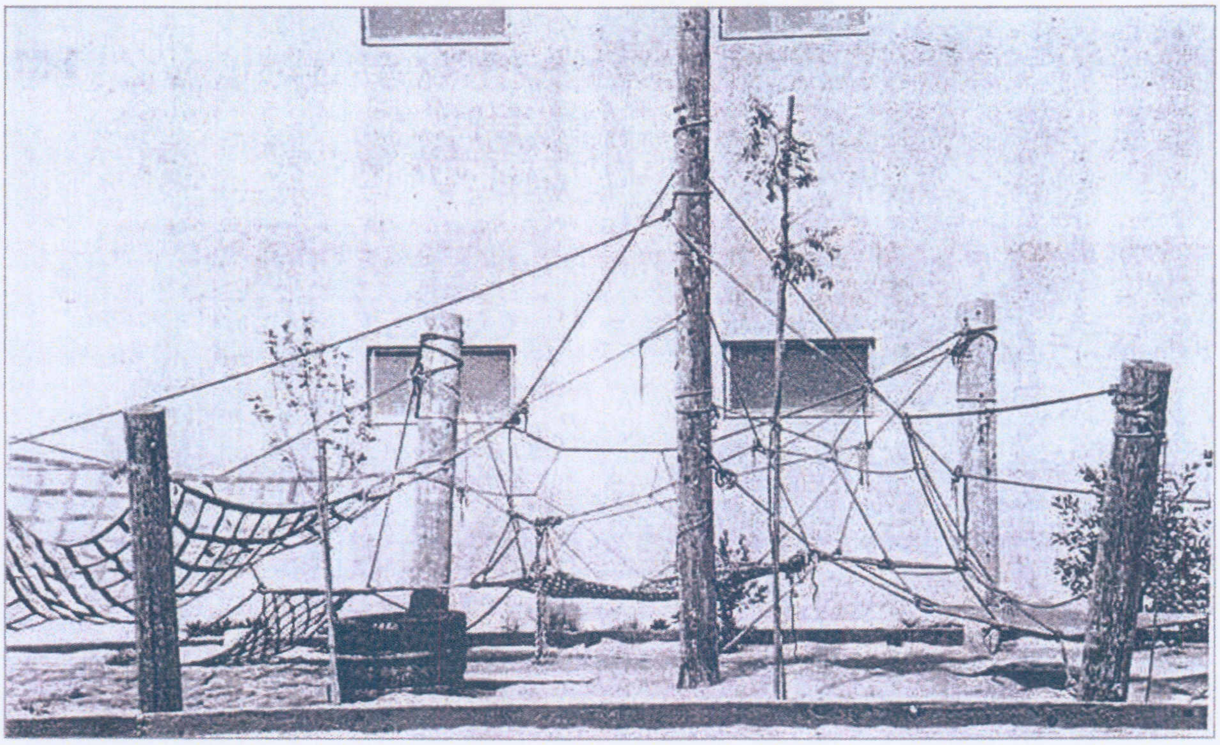

Figure 8.1: Example of a playground structure which could be erected on Ngamba Island (following Hewes 1975).

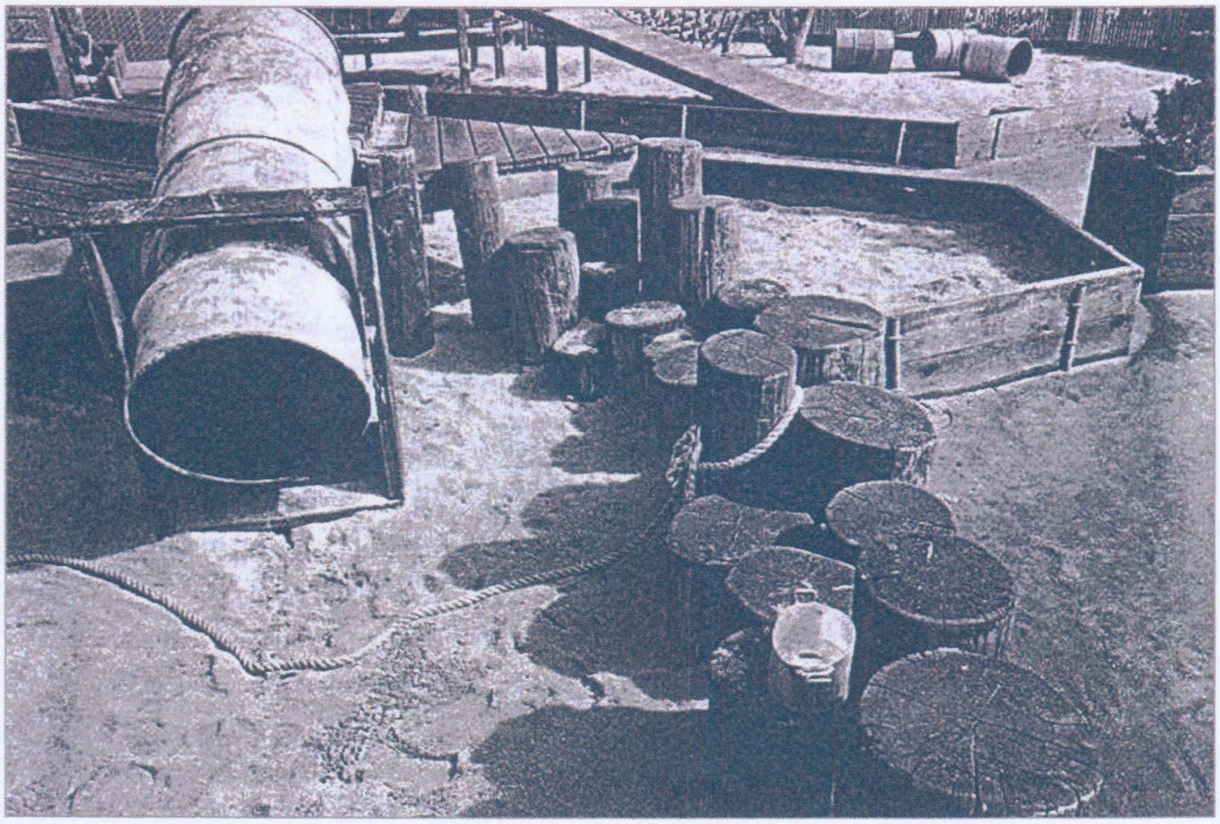

Figure 8.2: Example of a playground structure which could be erected on Ngamba Island (following Hewes 1975).

A separate playground area only for infant chimpanzees (Montgomery pers. comm.)[1] could be constructed outside the fenced-off area close to the landing area (Figure 2.2). This would allow reducing the number of infant walks and their destruction inside the forest (Table 8.1).

Provide toys

Toys like tyres, different sized boxes, sticks, etc., could be distributed throughout the Island (and also in the holding facility) to offer further entertainment and distraction from the use of the woody vegetation cover as toy and display material (Table 8.1).

Keep chimpanzees in enclosure during the night

To prevent destruction through the building of night nests (see Chapter 4 – Destructive behaviour + Chimpanzee nest-building behaviour) the chimpanzees should generally be kept inside the enclosure during the night (Table 8.1).

Provide hammocks in trees inside the forest

To reduce the number of day nests that are built (see Chapter 4 – Chimpanzee nest-building behaviour) by the Ngamba Island chimpanzees during their time spent in the forest hammocks like those used in the enclosure (Figure 8.3) could be provided in a number of trees inside the fenced-off area (Table 8.1).

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[1] Montgomery, C. 2002. Jane Goodall Institute Uganda, Entebbe, Uganda.

Figure 8.3: Type of hammock provided for Ngamba Island chimpanzees inside the holding facility. The same type could also be provided in a number of trees inside the forest area.

Rotate chimpanzees between “used” and “empty” island

All management recommendations suggested above cannot sustainable and successfully reduce the destructive influence of the current number of chimpanzees on the secondary rain forest cover of Ngamba Island in the long run. They can only assist in reducing this impact and hence prolonging the time until complete destruction of the woody vegetation cover occurs.

It is therefore postulated that the only way how Ngamba Island can be sustainable managed as a chimpanzee sanctuary without finally destroying the vital habitat for the species at the same time is through the introduction of a rotation system. The chimpanzees have to be rotated between two or three islands (see Chapter 2 – Future plans) one of which is always kept void of chimpanzees at any given time.

This surely is a cost- and labour-intensive exercise and brings with it a number of risks also for the health and well being of the chimpanzees. The latter is mainly caused by the fact that at least all adult chimpanzees will have to be immobilized before they can be transported. Since all anaesthesia also always carry a fatal risk, though minimal, the possibility that an immobilized chimpanzee might not survive such anaesthesia always needs to be considered.

On the other hand the introduction of such a rotation system is the only chance to give the rain forest vegetation a chance to recover and hence to use Ngamba Island sustainable as a chimpanzee sanctuary. It furthermore gives the chance for thorough health checks of all individuals and to implant hormone contraceptives at regular intervals. Without chimpanzees on the island thorough vegetation monitoring can be performed as well in a short period of time.

The rotation should take place about every two to four years considering actual chimpanzee density and destruction caused per year (Table 7.7). Evaluation of the results of the intense vegetation monitoring will allow adjusting this interval if necessary (Table 8.1).

VEGETATION MONITORING

The management recommendations for the regular monitoring of the vegetation cover of Ngamba and Nsadzi Island have been outlined in detail in Chapter 7 – *Recommendations* (Table 8.1).

CLIMATE MONITORING

The following two major recommendations for the monitoring of climate on Ngamba Island are suggested:

Continue measuring daily temperature, relative humidity and precipitation

All necessary equipment for such measurements has been put in place on Ngamba Island (see Chapter 5 – Daily temperature, relative humidity and precipitation). Furthermore, respective data can be collected from the Meteorological Department based in Entebbe. It should be assured that at least monthly daily minimum and maximum values as well as the monthly mean for temperature and relative humidity can be obtained and compared to previously collected data. Precipitation should be measured several times daily at the same time of the day if appropriate (Table 8.1).

Determine wind direction and wind velocity

This information also has to be obtained from the Meteorological Department in Entebbe. It should be collected once per month and also compared to data previously collected.

Table 8.1: Management Recommendations for Ngamba Island Chimpanzee Sanctuary

Management recommendation	**Time period**	**Comments**
	Chimpanzee Management	
Abandon the track system inside the forest.	Immediately & Constantly	Reduce the track system inside the forest to two parallel tracks from north to south and west to east, or better: abandon completely.
Restrict area of infant walks.	Immediately & Constantly	Use only the open grassland area and forest edge in the east of the Island.
Provide "Playground".	Immediately & Constantly	Inside the fenced-off area in the open grassland area in the east of the Island. Outside the fenced-off area in a confinement next to the landing area, to be used only by infant chimpanzees.
Provide toys.	Immediately & Constantly	Distribute tyres, different sized boxes, sticks, etc., throughout the forest, especially to give adult males a chance and tools to display without destroying the woody vegetation cover.
Keep chimpanzees in enclosure during the night.	Immediately & Constantly	To prevent further destruction through the building of night nests.
Provide hammocks in trees inside the forest.	Immediately & Constantly	To prevent chimpanzees from building day nests in trees.
Rotate chimpanzees between "used" and "empty" island.	Every two to four years (Adjust time span according to results of vegetation monitoring.)	Though tedious and expensive this is the only chance to give the vegetation a chance to recover and to use Ngamba Island sustainably as a chimpanzee sanctuary. It furthermore gives the chance for thorough health checks of all individuals and to implant hormone contraceptives. Without chimpanzees on the island thorough vegetation monitoring can be performed in a short period of time.

Table 9.1: Management Recommendations for Ngamba Island Chimpanzee Sanctuary (continued)

Management recommendation	**Time period**	**Comments**
Vegetation Monitoring		
Monitor woody vegetation on Ngamba and Nsadzi Island using the "Varying quadrat plot" method.	Every two years at the end of the long rainy season in June / July	Concentrate especially on dead tree density, plant species with a density ≥ 100 plants per hectare, the seven plant species present on both islands and Ngamba Island chimpanzees' food plant species (as outlined in Chapter 7 and 8).
Monitor forest edge.	Yearly at the end of the long rainy season	Take photographs and GPS readings of the forest edge and compare to previous data to evaluate if edge keeps retreating.
Climate Monitoring		
Continue measuring daily temperature, relative humidity and precipitation.	8:00 14:00 18:00	Compare regularly with historical data to detect possible climate changes.
Determine wind direction and wind velocity.	Daily	Collect data from Entebbe Meteorological Station.

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ANNEX

Table 1: *List of woody and herbaceous plant species on Ngamba Island*

Woody Vegetation			
Number	**Species**	**Family**	**Code**
1	*Aframomum angustifolium*	Zingiberaceae	AFRANG
2	*Albizia gumnifera*	Mimosaceae	ALBGUM
3	*Alchornea cordifolia*	Euphorbiaceae	ALCCOR
4	*Antiaris toxicara*	Moraceae	ANTTOX
5	*Beilschmedia ugandensis*	Lauraceae	BEIUGA
6	*Canarium schweinfurthii*	Burseraceae	CANSCH
7	*Canthium species 1*	Rubiaceae	CANSP1
8	*Clerodendrum formicarum*	Verbenaceae	CLEFOR
9	*Clitandra cymulosa*	Apocynaceae	CLICYM
10	*Clitandra species 1*	Apocynaceae	CLISP1
11	*Coffea canephora*	Rubiaceae	COFCAN
12	*Commelina capitata*	Commelinaceae	COMCAP
13	*Culcasia falcifolia*	Araceae	CULFAL
14	*Dictyandra arborescens*	Rubiaceae	DICARB
15	*Dracaena fragrans*	Dracaenaceae	DRAFRA
16	*Entandrophragma utile*	Meliaceae	ENTUTI
17	*Eugenia capensis*	Myrtaceae	EUGCAP
18	*Ficus cf. wildemanniana*	Moraceae	FICWIL
19	*Ficus ovata*	Moraceae	FICOVA
20	*Ficus species 1*	Moraceae	FICSP1
21	*Ficus species 2*	Moraceae	FICSP2
22	*Galinera saxifraga*	Rubiaceae	GALSAX
23	*Guarea cedrata*	Meliaceae	GUACED
24	*Macaranga monandra*	Euphorbiaceae	MACMON
25	*Millettia dura*	Papilionaceae	MILDUR
26	*Nephrolepis biserrata*	Davalliaceae	NEPBIS
27	*Ouratea hiernii*	Ochnaceae	OURHIE
28	*Oxyanthus speciosus*	Rubiaceae	OXYSPE
29	*Oxyanthus speciosus* var. *stenocarpus*	Rubiaceae	OXYSTE
30	*Oxyanthus subpunctatus*	Rubiaceae	OXYSUB
31	*Pachystela brevipes*	Sapotaceae	PACBRE
32	*Palisota mannii*	Commelinaceae	PALMAN
33	*Palisota schweinfurthii*	Commelinaceae	PALSCH
34	*Peddiea fischeri*	Thymelaeaceae	PEDFIS
35	*Psychotria mahonii* var. *puberula*	Rubiaceae	PSYMAN
36	*Psychotria peduncularis*	Rubiaceae	PSYPED
37	*Psychotria species 1*	Rubiaceae	PSYSP1
38	*Rinorea brachypetala*	Violaceae	RINBRA
39	*Tetrorchidium didymostemon*	Euphorbiaceae	TETDID
40	*Trichilia species 1*	Meliaceae	TRISP1
41	*Trilepsium madagascariense*	Moraceae	TRIMAD

Table 1: *List of woody and herbaceous plant species on Ngamba Island - continued*

Herbaceous Vegetation		
Number	**Species**	**Family**
1	*Asystasia gangetica*	Acanthaceae
2	*Bidens pilosa*	Asteraceae
3	*Cassia occidentalis*	Caesalpiniaceae
4	*Cassia species*	Caesalpiniaceae
5	*Coccinea mildbraedii*	Cucurbitaceae
6	*Cynodon nienfuensis*	Poaceae
7	*Cyperus species*	Cyperaceae
8	*Justicia flava*	Acanthaceae
9	*Panicum species*	Poaceae
10	*Paspalum notatum*	Poaceae
11	*Pavonia patens*	Malvaceae
12	*Phyllanthus pseudo-niruri*	Euphorbiaceae
13	*Sida ovata*	Malvaceae
14	*Sporobolus agrostoides*	Poaceae
15	*Triumfetta rhombifolia*	Tiliaceae

Table 2: *List of Ngamba Island chimpanzees' food plant species (following Marshall 2000)*

	October 1998	December 1999 - May 2000
Family	**Species**	**Species**
Acanthaceae	Asystacia gangetica	
	Justicia flava	Justicia flava
Amaryllidaceae	Scandoxus cinnaberinus	
Anacardiaceae	Pseudospondias microcarpa	
Araceae	Culcasia falcifolia	Culcasia falcifolia
Asclepiadaceae	Mondia whitei	
Asteraceae	Crassocephalum crepidioides	
	Erlangea tomentosa	Erlangea tomentosa
Basellaceae		Basella alba
Caesalpinaceae	Senna occidentalis	
Commelinaceae		Commelina africana
	Commelina capitata	
		Pollia condensata
Convolvulaceae	Ipomoea cairica	
Cucurbitaceae	Cucumis sp.	
	Lagenaria sphaerica	
Cyperaceae	Cyperus latifolius	
Dracaenaceae	Dracaena fragans	
Euphorbiaceae	Tetrorchidium didymostemon	Tetrorchidium didymostemon
Lamiaceae	Solenostemon latifolius	
Loganiaceae	Anthocleista vogelii	
Malvaceae	Hibiscus physaleides	
	Hibiscus rivularis	
	Hisbiscus sp.	
	Sida rhombifolia	
Melastomataceae		Guarea cedrata
	Iristemma mauritianum	
Meliaceae		Melastomastrum capitatum
Mimosaceae		Albizia gumnifera
Moraceae	Ficus cyathistipula	
	Ficus ottoniifolia	
		Ficus saussureana
		Ficus trichopoda
	Myrianthus holstii	
Papilionaceae		Abrus pulchellus
	Crotalania pallida	Crotalania pallida
	Sesbania dummeri	
Passifloraceae	Passiflora edulis	
Phytolaccaceae	Phytolacca dodecandra	
Poaceae		Cyrtococaum multirode

Table 2: *List of Ngamba Island chimpanzees' food plant species - continued (following Marshall 2000)*

	October 1998	**December 1999 - May 2000**
Family	**Species**	**Species**
Rubiaceae	Oxyanthus speciosus	
		Canthium species 1
		Canthium species 2
		Dictyandra arborescens
		Morinda Lucida
		Tarrena pavettoides
Sapindaceae		Cardiosperum herbaceum
Sapotaceae	Pachystela brevipes	Pachystela brevipes
Solanaceae	Capscum frutescens	
	Solanum macrocapon	
	Solanum nigrum	
	Solanum terminate	
Tiliaceae	Triumfetta annua	
	Triumfetta tomentosa	
Verbenaceae	Curodendrum silvanum	
Zingeraceae	Aframomum angustifolium	Aframomum angustifolium

Table 3: *List of plant species from previous surveys (following Kityo 1998)*

Transect 1	
Species	**Abundance***
Antiaris toxicara	4
Aframomum angustifolium	5%
Aframomum malanthacloa	30%
Annonaceae	1
Anthocleista vogeli	2
Barteria fisculosa	5
Beilschmedia ugandensis	2
Canarium schweinfurthii	4
Canthium vulgare	many
Clitandra oweriensis	6
Coffea eugenioides	5
Culcasia scandens	70%
Dictyandra arborescens	2
Dracaena fragrans	many
Eugenia bukobensis	3
Ficus asperifolia	3
Ficus cyastipula	6
Ficus dawei	4
Ficus ovata	7
Geophilia hirsuta	10%
Guarea cedrata	many
Maesopsis eminii	3
Milicia excelsea	2
Musanga scrope	4
Oxyanthus speciosus	many
Pachystela brevipes	2
Palisota manii	5
Saba comorensis	3
Tristema species	10+
Vangueria apiculata	1

Transect 2	
Species	**Abundance***
Aframomum angustifolium	10%
Aframomum malanthacloa	30%
Alafia ugandensis	1
Anthocleista vogeli	4
Barteria fisculosa	2
Beilschmedia ugandensis	1
Canthium vulgare	3+
Clitandra oweriensis	1
Culcasia scandens	70%
Dictyandra arborescens	1
Dracaena fragrans	2
Eugenia Bukobensis	1
Ficus cyastipula	1
Ficus dawei	many
Ficus percifolia	1
Geophilia hirsuta	30%
Guarea cedrata	2
Oxyanthus speciosus	
Pachystela brevipes	1
Palisota manii	many
Rytigenia beniensis	3

Transect 3	
Species	**Abundance***
Aframomum angustifolium	2%
Aframomum malanthacloa	30%
Anthocleista vogeli	2
Canarium schweinfurthii	1
Dracaena fragrans	many
Eugenia bukobensis	2
Ficus dawei	many
Ficus ovata	2
Ficus percifolia	1
Ficus sur	1
Ficus thonningii	2
Milicia excelsea	1
Musanga scnepoides	3
Pachystela brevipes	2
Passiflora edulis	1
Rytigenia beniensis	many

* Results from three one-quarter acre plots: frequencies above three (3) show common plants, while percentages were entered for plants that were very many and constituting a considerable plant cover.

Table 4: *List of plant species from previous surveys (following Zwick & Lloyd 1998b)*

Species	Abundance*
Family Aspleniaceae	
Asplenum aethiopicum	
Family Lomariopsidaceae	
Bolbitis auriculata	
Bolbitis gemnifera	
Lomariopsis warneckii	
Family Acanthaceae	
Asystasia gangetica	
Barleria stuhlmanii	
Dyschoriste sp.	
Justicia flava	
Family Agavaceae	W
Dracaena fragans	
Family Amaranthaceae	W
Celosia globosa	
Cyathula prostrata	
Family Apiaceae	
Centella asiatica	
Family Apocynaceae	W
Tabernaemontana pachysiphora	
Family Araceae	O
Culcasia angolensis	
Culcasia falcifolia	DW
Family Asclepiadaceae	OW
Cynanchum oldolinow	
Family Asteraceae	
Erlangea tomentosa	
Melanthera scandens	
Synedrella nodiflora	
Family Balsaminaceae	W
Impatiens sp.	
Family Basellaceae	
Basella alba	
Family Commelinaceae	W
Bufforestia imperforata	
Commelina africana	
Commelina capitata	
Pollia condensata	W
Family Cucurbitaceae	
Diplocyclos palmatus	
Family Cyperaceae	
Cyperus cyperoides	
Cyperus sp.	
Family Euphorbiaceae	
Alchornea cordifolia	
Argomuellera macropylla	W
Croton macrostachus	
Macaranga monandra	
Tetrorchidium didymostemon	W
Family Leguminosae	W
Aeschynomene elaphroxylon	
Albizia zygia	
Piptadeniastrum africanum	W
Family Loganiaceae	
Anthocleista schweinfurthii	
Family Melastomataceae	
Melastomastrum capitatum	
Family Moraceae	
Ficus thonningii	
Family Ochnaceae	
Ouratea densiflora	
Ouratea hiernii	
Family Oleaceae	
Jasminium pauciflorum	W
Family Piperaceae	
Piper guineense	
Family Poaceae	
Cynodon aethiopicus	
Megastachya mucronata	
Panicum heterostachyum	W
Paspalum conjugatum	
Family Polygonaceae	
Polygonum salcifolium	
Family Pontederiaceae	
Eichhornia crassipes	O
Family Rhamnaceae	
Maesopsis eminii	
Family Rubiaceae	
Coffea eugenoides	W
Dictyandra arborescens	
Geophila repens	W
Oldenlandia corymbosa	
Oxyanthus speciosus	
Pentas pubiflora	
Family Sapotaceae	
Aningeria altissima	
Family Thymelaeaceae	
Peddiea fischeri	
Family Verbenaceae	
Clerodendrum formicarum	W
Family Zingiberaceae	
Aframomum angustifolium	A
Aframomum luteolatum	W
Aframomum mildbraedii	
Aframomum sp.	F

***Abundance**

D	dominant
A	abundant
F	frequent
O	occasional
W	widespread

Table 5: *List of Ngamba Island Fauna - Mammals (following Zwick & Lloyd 1998b)*

		Small rodents and shrews	
		Species	**Common name**
Order	Insectivora		
Family	Soricidae	*Crocidura olivieri*	Northern giant musk shrew
		Crocidura turba	Southern woodland musk
Order	Rodentia		
Family	Muridae	*Grammomys dolichurus*	Common thicket rat
		Rattus rattus	Black rat
		Bats	
		Species	**Common name**
Order	Macrochiroptera		
Family	Pteropodidae		
Subfamily	Pteropodinae	*Eidolon helvum*	Straw-coloured fruit bat
		Micropteropus pusillus	Dwarf-epauletted fruit bat
Order	Microchiroptera		
Family	Nycteridae	*Nycteris hispida*	Hairy slit-faced bat
	Hipposideridae	*Hipposideros ruber*	Noack's leaf-nosed bat
	Molossidae	*Chaerophon major*	Lappet-eared free-tailed bat
		Larger Mammals	
		Species	**Common Name**
Order	Artiodactyla		
Family	Hippopotamidae	*Hippopotamus amphibius*	Hippopotamus

Table 5: *List of Ngamba Island Fauna - Reptiles & Amphibians (following Zwick & Lloyd 1998b)*

Reptiles

		Species	**Common name**
Order	Sauria		
Family	Gekkonidae	*Hemidactylus brookii*	House gecko
	Scincidae		
Subfamily	Feylininae	*Feylinia currori*	Western forest limbless skink
	Lygosomatinae	*Mabuya mabuya maculilabris*	Speckle-lipped skink
Family	Varanidae	*Varanus niloticus*	Nile monitor lizard
Order	Serpentes		
Family	Typhloidae	*Typhlos angolensis*	Angolan blind snake

Amphibians

		Species	**Common name**
Order	Anura		
Family	Bufonidae	*Bufo regularis*	Square-marked toad
	Hyperoliidae		
Subfamily	Hyperoliinae	*Hyperolius kivuensis*	Kivu reed frog
		Hyperolius nasutus	Gunther's sharp-nosed reed frog
		Hyperolius viridiflavus	Reed frog
Family	Ranidae		
Subfamily	Raninae	*Rana occipitalis*	Grooved-crowned bullfrog

Table 5: *List of Ngamba Island Fauna - Butterflies following Zwick & Lloyd 1998b)*

Butterflies		
		Species
Order	Lepidoptera	
Family	Pieridae	
Subfamily	Colladinae	*Catopsila florella*
		Eurema hecabe
Subfamily	Pierinae	*Belenois gidica abyssinica*
Family	Lycaenidae	
Subfamily	Polyommatinae	*Anthenae schoutedeni*
		Zizinia antanossa
Family	Nymphalidae	
Subfamily	Danainae	*Danaus chrysippus*
Subfamily	Satyrinae	*Melanitis leda*
Subfamily	Nymphalinae	*Hypolimnas misippus*
		Junonia o. oenone
Subfamily	Acraeinae	*Acrea n. neobule*

Table 5: *List of Ngamba Island Fauna - Birds - continued (following Wilson & Schipper 2002)*

Birds

Species	**Common name**
	Osprey
	Family - Pandionidae
Pandion haliaetus	Osprey
	Owls
	Family - Tytonidae
Tyto alba	Barn Owl
	Parrots & Cockatoos
	Family - Psittacidae
Psittacus erithacus	Grey Parrot
	Pelicans
	Family - Pelecanidae
Pelecanus onocrotalus	Great White Pelican
Pelecanus rufescens	Pink-backed Pelican
	Pigeons & Doves
	Family - Columbidae
Treron calva	African Grey Pigeon
Turtur afer	Blue-spotted Wood Dove
Turtur tympanistria	*Tambourine Dove*
Streptopelia semitorquata	Red-eyed Dove
	Plovers & Lapwings
	Family - Charadriidae
Charadrius hiaticula	Ringeed Plover
Vanellus lugubris	senegal lapwing
Vanellus spinosus	Spur-winged Lapwing
Burhinus vermiculatus	Water Thicknee
	Robin Chats
	Family - Turdidae
Cossypha heuglini	Heuglin's Robin Chat
Cossypha niveicapilla	Snowy-headed Robin Chat
	Sandpipers & Snipes
	Family - Scolopacidae
Limosa limosa	Black-tailed Godwit
Actitis hypoleucos	Common Sandpiper
Calidirs ferruginea	Curlew Sandpiper
Tringa ochropus	Green Sandpiper
Tringa nebularia	Green Shank
Tringa stagnatilis	Marsh Sandpiper
Philomachus pugna	Ruff
	Shrikes
	Family - Lanidae
Lanius collurio	Red-backed Shrike
	Stilts
	Family - Recurvirostridae
Himantopus himantopus	Common Stilt
	Storks
	Family - Ciconiidae
Anastomus lamelligerus	Open-billed Stork
Leptoptilos crumeniferus	Marabou Stork
Mycteria ibis	Yellow-billed Stork
Ciconia abdimii	Abdim's Stork

Species	**Common name**
	Sunbirds
	Family - Nectariniidae
Anthreptes collaris	Collard Sunbird
Nectarinia chloropygia	Olive-bellied Sunbird
Nectarinia olivacea	Olive Sunbird
Nectarinia erhythrocerca	Red-chested Sunbird
	Swallows & Martins
	Family - Hirundinidae
Hirundo angolensis	Angola Swallow
Hirundo rustica	Barn Swallow
Riparia paludicola	Brown-throated Sand-Martin
Riparia riparia	Common Sand-martin
Hirundo abyssinica	Lesser Striped Swallow
	Swifts
	Family - Apodidae
Apus affinus	Little Swift
Cypsiurus parvus	Palm Swift
	Turacos
	Family - Musophagidae
Crinifer zonurust	Eastern Grey Plaintain-eater
	Wagtails
	Family - Motacillidae
Motacilla aguimp	African Pied Wagtail
Motacilla flava	Yellow wagtail
	Warblers & Cisticolas
	Family - Sylviidae
Sylvia communis	Common Whitethroat
Acrocephalus scirpaceus	Eurasian Reed Warbler
Camaroptera brachyura	Grey-backed Camaroptera
Acrocephalus schoenobeanus	Sedge Warbler
Phylloscopus trochilus	Willow Warbler
Zosterops senegalensis	Yellow White-eye
	Weavers & Sparrows
	Family - Ploceidae
Ploceus cucullatus	Black-headed Weaver
Passer griseus	Grey-headed Sparrow
Ploceus castanops	Northern-brown-thorated Weaver
Ploceus aurantius	Orange Weaver
Ploceus pelzelni	Slender-billed Weaver
Ploceus ocularis	Spectacled Weaver

Table 6: *Braun-Blanquet classification of herbaceus vegetation on Ngamba Island*

Sample #	**45**	**14**	**15**	**16**	**11**	**13**	**63**	**34**	**57**	**62**	**25**	**31**	**64**	**32**	**36**	**29**	**65**	**2**	**47**	**46**	**48**	**4**	**3**	**5**	**17**	**20**	**21**	**19**	**43**
Plant species																													
Asystasia gangetica	4	+	1	1	1	+	5	5	5	4	3	3	3	2	+	+	+	4	4	4	2	3	2	2	5	5	5	3	
Justicia flava	2	3	2	1	1	1	1	+	+	1	3	3	3	2	5	4	2												5
Sporobolus agrostoides																		2	2	1	4	1	2	1					
Sida ovata	1	1																				2	1	2	3	+	+	+	
Cynodon nienfuensis					2																								
Parnicum sp.																													+
Coccinea mildbraedii			2	5																									
Cassia sp.						1																							
Microglossa angolensis					1																								
Kyllinga alba																													
Phyllanthus pseudo-niruri		1	+																										
Cyperus sp.		2																											
Paspalum notatum																							2						
Phytolacca dodecandra																													
Pavonia patens					1																								
Triumfetta rhombifolia																									1				
Bidens pilosa																													
Cassia occidentalis			+																										
Commelina africana													+																
Erlangea tomentosa																													
Bare soil [%]					*20*	*20*				*10*	*10*			*50*		*20*	*40*	*20*	*20*	*40*		*10*	*20*	*50*				*20*	
Vulcanic rock [%]		*20*	*75*	*75*																									
Gravel [%]																													
Dead branches [%]									*5*	*10*							*40*												

Table 6: *Braun-Blanquet classification of herbaceus vegetation on Ngamba Island - continued*

Sample #	**6**	**8**	**53**	**54**	**22**	**59**	**60**	**23**	**50**	**18**	**56**	**24**	**58**	**51**	**52**	**1**	**49**	**61**	**26**	**55**	**33**	**35**	**40**	**44**	**28**	**12**	**10**	**7**	**9**
Plant species																													
Asystasia gangetica			3	3	5	4	3	5	5	5	5	5	4	4	4	4	4	4	3	3									
Justicia flava																					5	5	5	5	4				
Sporobolus agrostoides	5	+																								5	5	3	
Sida ovata																													
Cynodon nienfuensis	1	5																											5
Parnicum sp.																													
Coccinea mildbraedii																													
Cassia sp.																													
Microglossa angolensis							2																						
Kyllinga alba			1	1																									
Phyllanthus pseudo-niruri																													
Cyperus sp.																													
Paspalum notatum																													
Phytolacca dodecandra						2																							
Pavonia patens																													
Triumfetta rhombifolia																													
Bidens pilosa					+																								
Cassia occidentalis																													
Commelina africana																													
Erlangea tomentosa						+																							
Bare soil [%]			*60*	*60*		*15*						*20*		*20*	*20*	*25*	*40*	*60*	*30*	*30*					*40*		*10*	*50*	
Vulcanic rock [%]				*5*																									
Gravel [%]			+				*70*											+											
Dead branches [%]						*15*				+	+		*40*							*30*									

Table 7: *List of woody plant species on Nsadzi Island*

Number	Species	Family	Code
1	*Argomuellera macrophylla*	Euphorbiaceae	ARGMAC
2	*Calycosiphonia spathicalyx*	Rubiaceae	CALSPA
3	*Coffea eugonioides*	Rubiaceae	COFEUG
4	*Dictyandra arborescens*	Rubiaceae	DICARB
5	*Eugenia capensis ssp. nyassensis*	Myrtaceae	EUGCAP
6	*Funtumia africana*	Apocynaceae	FUNAFR
7	*Menisorus pauciflorus*	Thelypteridaceae	MENPAU
8	*Monanthotaxis species 1*	Annonaceae	MONSP1
9	*Olea africana*	Oleaceae	OLEAFR
10	*Olinea rochetiana*	Olineaceae	OLIROC
11	*Oncinotis species 1*	Apocynaceae	ONCSP1
12	*Ouratea bukobensis*	Ochnaceae	OURBUK
13	*Ouratea hiernii*	Ochnaceae	OURHIE
14	*Oxyanthus speciosus var. stenocarpus*	Rubiaceae	OXYSTE
15	*Peddiea fischeri*	Thymeliaceae	PEDFIS
16	*Rytigynia species cf. bagshawei*	Rubiaceae	RHYSP1
17	*Tetrorchidium didymostemon*	Euphorbiaceae	TETDID
18	*Trichilia species 1*	Meliaceae	TRISP1
19	*Turrea species 1*	Meliaceae	TURSP1
20	*Turrea vogellioides*	Meliaceae	TURVOG
21	*Uvaria angolensis*	Annonaceae	UVAANG
22	*Unknown species 1*		QQQSP1
23	*Unknown species 2*		QQQSP2
24	*Unknown species 3*		QQQSP3