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Vegetation and Chimpanzee Ranging in the Mahale Mountains National Park, Tanzania

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Abstract Ranging behavior and habitat use by chimpanzees were studied for ten months in the Kasoje area of the Mahale Mountains National Park, Tanzania. The line transect method was used to estimate the density and diversity of trees, lianas and herbaceous plants in the families Marantaceae and Zingiberaceae to determine their distribution and availability as food for chimpanzees. A principal components analysis of the transect plots using species presence and absence and species frequency data identified seven distinct vegetation types including five types of lowland forest and two types of woodland. Moisture was the variable best correlated with the distribution of forest and woodland. Chimpanzees utilized both forest and woodland, ingesting 70 food items which included 59 species of plants, 6 species of animals, termite earth and water. Fruits were preferred in the diet but other plant parts such as leaves and pith were consumed to meet nutritional requirements and to offsets periods when fruit was scarce. Chimpanzee foods were classified as "major" or "minor" based on their relative proportion in the diet. The density of major food plants was highest in lowland forest while woodland contained a relatively higher proportion of "minor" foods. Therefore, forest was determined to be the vegetation type most important to the chimpanzees in Mahale. Ranging patterns were explained by the distribution of vegetation types and the density of seasonally available foods. Chimpanzees used forested areas intensively when fruits were available, and ranged over a wider area and made less frequent visits to individual areas of the home range when fruits were less abundant. Differences in the density and distribution of some food species were explained by the presence of the exotic tree *Senna spectabilis*. Quantification of the occurrence of *Senna* relative to native vegetation revealed that this tree is a poor competitor under established secondary forest but a successful invader of areas previously cleared for farmland.

Key words Chimpanzee, Diet, Food availability, Mahale, Ranging pattern, Vegetation

Introduction

The Kasoje area is the site of long-term investigations into the behavior and socioecology of the eastern subspecies of chimpanzee, *Pan troglodytes schweinfurthii* (Nishida 1990). A number of descriptions of the chimpanzee habitat have been published (Nishida 1968; Nishida & Uehara 1981; Collins & McGrew 1988; Itani 1990) and scientists have collected and catalogued many of the plants in the area including those used by the chimpanzees as food (Nishida & Uehara 1983). Nishida & Uehara (1981) listed more than 600 species of plants found at Kasoje and surrounding areas. Lovett (1994) estimated that there may be in excess of 2000 vascular plant species in the Park and among these are probably numerous rare plants and endemics.

It has been noted that chimpanzees have an "affinity for forests" (Massawe 1992). Kasoje has a higher proportion of forest relative to other vegetation types when compared to sites to the north such as Bilenge and Gombe (Collins & McGrew 1988). However, no data have thus far been available on the relative densities of resources or differential use of these vegetation types by chimpanzees.

Some studies have attempted to relate differences in the behavior of chimpanzees at different sites to differences in their habitat (e.g. Suzuki 1969). Studies have shown that chimpanzees living in lowland forests are mainly frugivorous (Nishida & Uehara 1983; Goodall 1986; Isabirye-Basuta 1989 and others) while fruit constitutes a much smaller proportion of their diet in montane areas (Yamagiwa *et al.* 1996). Variation in the spatial and temporal availability of resources would be expected to have an impact on such characteristics as population density, group movement and home range size, however until recently comparable measures across most chimpanzee populations have been lacking (Collins & McGrew 1988). This paper provides a quantitative description of the chimpanzee habitat at Kasoje, and explores their ranging behavior and habitat use in relation to food availability.

The park lies within the transition zone between the chief West African and East African subdivisions of the Ethiopian region. White (1981) classified the vegetation of this area as "wetter Zambezian miombo woodland" dominated by *Brachystegia*, *Julbernardia* and *Isoberlinia* which extends over western Tanzania, Zambia and Angola. There are also patches of riverine, lowland, submontane and montane forest which are mostly Guineo-Congolian in origin (Lovett 1994). Kasoje has been described as a "forest island" in the midst of the miombo (Nishida 1990). Evaporative cooling of lake air supports extensive forest development on the western slopes of the mountains and permits the existence of a number of moist forest species, many of which link the area to the Guineo-Congolian forests to the west. In drier areas of the coastal plain there are expansive woodlands with affinities to the Zambezian region of endemism (White 1981).

The general goals of the study was to analyze the structure and composition of vegetation in the habitat and quantification of the spatial availability of chimpanzee food trees and lianas and to collect data on the ranging and feeding behavior of M group chimpanzees.

Methods

A total of 10 months were spent in the field, from 23 July 1994 to 30 May 1995. Days were divided between botanical sampling and following chimpanzees. The year was divided into wet and dry seasons based on the amount of rainfall in each month. A "dry" month was one in which total rainfall amounted to less than 100 mm and a "wet" month one in which total rainfall exceeded 100 mm (Myers 1980). Total rainfall for the study period (1586.8 mm; Fig. 1) was below normal (mean of 1975-1988 was 1835.5 mm;

Takasaki *et al.* 1990). The monthly mean daily minimum and maximum temperatures were 18.3°C and 29.0°C respectively. There was little variation between months (< 4°C) (Fig. 1). Humidity was high throughout the year, and usually ranges from 85-100% at 0800 hours.

Transect studies

Forest composition was studied by line transect. Transects were located within vegetation types previously classified by Nishida on the basis of physiognomy (Nishida 1977; Nishida & Uehara 1981) at altitudes from 780 m to 1300 m. The vegetation of different areas of the habitat including features such as slopes, valley bottoms, riverbanks and ridge tops were sampled in a total of 140 plots (18 transects with a combined area of 7 hectares). Straight lines were cut through the vegetation on predetermined compass bearings and distance markers were positioned every 50 m. All trees within 5 m of the transect's main line with a diameter of 10 cm or greater (measured at 1.3 m above the ground or above buttresses) and all lianas with a diameter of 3 cm or greater (measured 1.3 m from where the stem emerged from the ground; if there were several stems they were measured individually and an average taken) were identified assigned identification numbers. The forest ground cover was sampled by recording the densities of herbs, shrubs, seedlings and saplings within six hundreds 1 m^2 plots nested within the transect plots. Altitude was recorded and soil type and canopy cover were described. Trees were identified by reference to a list of plant names for Mahale (Nishida & Uehara 1981). The identification of many species was confirmed on site by Mr. CK Ruffo of the National Tree Seed Programme, Morogoro, Tanzania. Additional identification of botanical specimens was done by Dr. K Vollesen of the Royal Botanic Gardens at Kew. For some trees which could not be identified during the study fertile voucher specimens were collected and identified with the assistance of Dr. N Itoh.

The following characteristics were considered to be indicators of vegetation structure: densities and basal areas of trees, liana density, canopy cover and density of the ground cover. The density and basal area of tree and liana species considered to be impor-

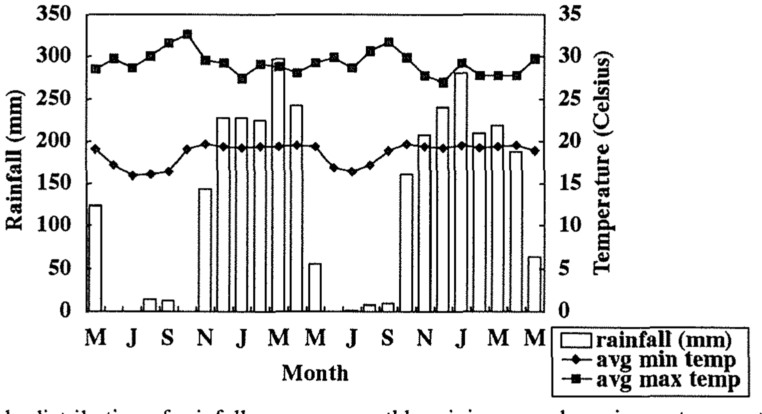

Fig. 1. Monthly distribution of rainfall, average monthly minimum and maximum temperature at Kasoje during study period.

tant sources of food for chimpanzees were used as measures of resource abundance in each vegetation type.

Herbaceous vegetation

To examine the availability of the herbaceous vegetation, *Aframomum mala, Aframomum alboviolaceum, Costus afer* (Zingiberaceae) and *Marantochloa leucantha* (Marantaceae) and one shrub, *Psychotria peduncularis* (Rubiaceae) were counted in 1 m^2 plots (n=300) randomly located on transects in forest.

Diversity measures

The measures used to evaluate diversity at Kasoje were chosen because they are widely used and relatively easy to calculate and understand. Ordination techniques such as principal components analysis are useful for identifying the characteristic communities and species present in a sample; however they do not directly measure β diversity per se (β diversity is the difference or similarity of a range of habitats or samples in terms of the variety and sometimes the abundance of species in them (Magurran 1988)). Measures of β diversity can thus be used to compare the diversity of different communities. One widely used index is the Sorensen quantitative index ($2Nj$ / (Na+Nb)) where Na=the total number of individuals in site *a*; Nb=the total number of individuals in site *b*; Nj=the sum of the lower of the two abundances recorded for species found in both). The disadvantage of qualitative similarity indices is that all species count equally in the equation whether they are abundant or rare (Magurran 1988). The Sorensen index takes into account the relative abundance of all species in the sample and is thus considered a better representation of the true diversity of the sample. The index is designed to equal 1 in cases of complete similarity.

Shannon's measure, $H' = -\Sigma i \rho_i \log p_i$ where p_i is the proportion of the *i*th out of S species is also commonly used as an indicator of species diversity (Grieg-Smith 1983).

Vegetation map

A preliminary map of the vegetation in the study site (Appx. 1) was prepared using an existing Tanzanian-Canadian government map of the area (Ministry of Lands series Y742 sheet 150/2 edition 1-TSD) and results of the transect studies supplemented by aerial photographs (provided by T. Nishida) and a Landsat TM image of Mahale taken in 1984.

Chimpanzee behavior

The M group numbered approximately 60 individuals (8-9 adult males and 22-25 adult females) in 1994-1995. The data were collected during 460 hours of direct observation during 207 days from August to April. Once the main study group (the alpha male and his followers) was located they were followed as long as possible, until they were lost or made their night nests. Follows which lasted less than 1 hour were excluded from the analysis. Feeding and ranging behavior of the group were sampled continuously. The position and movement of the group were plotted on an existing map of the study site and trail system divided into 250 m x 250 m quadrats. The length of a day journey was the distance traveled by the study group from the time they left their nests from the previous night or were located to the time they made their new night nests or were lost. Home range use was measured by counting the number of quadrats visited and revisited each day and the cumulative number of different quadrats visited each month. Home range size was measured by counting the cumulative number of different quadrats entered during the entire study. To study differential use of the vegetation by chimpanzees, the quadrat use map was superimposed over the vegetation map and the numbers and vegetation types of each quadrat entered were recorded. This information was used to calculate the percent use and seasonality of use of each vegetation type.

Definitions

In this paper "forest" means a continuous stand of trees at least 10 m tall consisting of several layer or storeys. The crowns of individual trees interdigitate or overlap (White 1981) and "woodland" means a stand of "small to medium-sized trees (8-20 m), with a canopy cover of 70-90%, light foliage of compound leaves, sparse woody undergrowth and a more or less continuous cover of sun-loving grasses" (Menaut *et al.* 1995). The term "semi-evergreen forest" is used to signify that some canopy species are briefly deciduous although not all at the same time, while most members of the understorey are evergreen. The term "mature" is used instead of "primary" which have been used to describe the vegetation at Kasoje (Takasaki 1983; Itani 1990; Lovett 1994).

Statistics

Transect plots were compared by developing matrices based on 1) Jaccard's similarity coefficient for presence/absence data (j / (a+b-j), j = the number of species found in both plots; a = the number of species in plot a; b = the number of species in plot b) and 2) Euclidean normalized distance measure for frequency data and the matrices was ordinated at the Environment Department, University of York, England using the principal coordinates analysis (PCA) R-package written by Pierre Legendre, University of Montreal, Canada. Ordination is a multivariate statistical method used to arrange samples (species) on axes by order of the amount of variation they contain. PCA rotates the data points such that maximum variability in the data is visible, thus identifying important gradients such as moisture or altitude. The results can be displayed graphically where sites with similar species compositions are nearby and dissimilar sites are far apart. Each axis has an associated eigenvalue (also known as latent root) related to the amount of variation explained by the axis. With a complex data set each axis will not contain a large amount of the variation, therefore multiple axes are used in the biological interpretation of the data.

Results

Ordination

The ordination using presence absence data (see Methods) shows separation of data points representing 3 distinct plant communities. Communities were distinguished as either "forest" or "woodland" based on the presence or absence of indicator species, a welldefined set of species nearly restricted to those formations (Lind & Morrison 1974; Palgrave 1977; White 1981; Beentje 1994). Woodland and forest are clustered and separated along the positive and negative parts, respectively, of Axis 1 (Fig. 2). The environmental gradients most closely associated with this separation are 1) moisture, i.e. formations containing moist forest species are well-developed on the lower slopes of the mountains and around permanent streams and 2) disturbance, with forest predominated by colonizing species (such as *Senna spectabilis* and *Croton sylvaticus* found in areas of abandoned farmland on the coastal plain.

Axes 1 and 3 of PCA using species frequency data reveals dissimilarities in the composition of transect plots in woodland. Plots where *Brachystegia bussei* was abundant are grouped on the negative part of axis 3 and the positive part of axis 1, and separated from plots where trees of the *Combretum* genera were abundant. The plots containing *B. bussei* are classified as "miombo woodland" (Fig. 3). On this set of axes riverine forest dominated by *Ficus vallis-choudae* also appears as a distinct cluster of data points high on the positive part of axis 3.

The ordination of species frequency data separated two forest communities which were classified on the basis of the predominant tree species found in them: *Erythrophleum suaveolens*) forest appears as a cluster on the positive parts of Axis 3 and Axis 2 with *Xylopia-Pycnanthus* forest below it on the negative part of Axis 3 and the positive part of

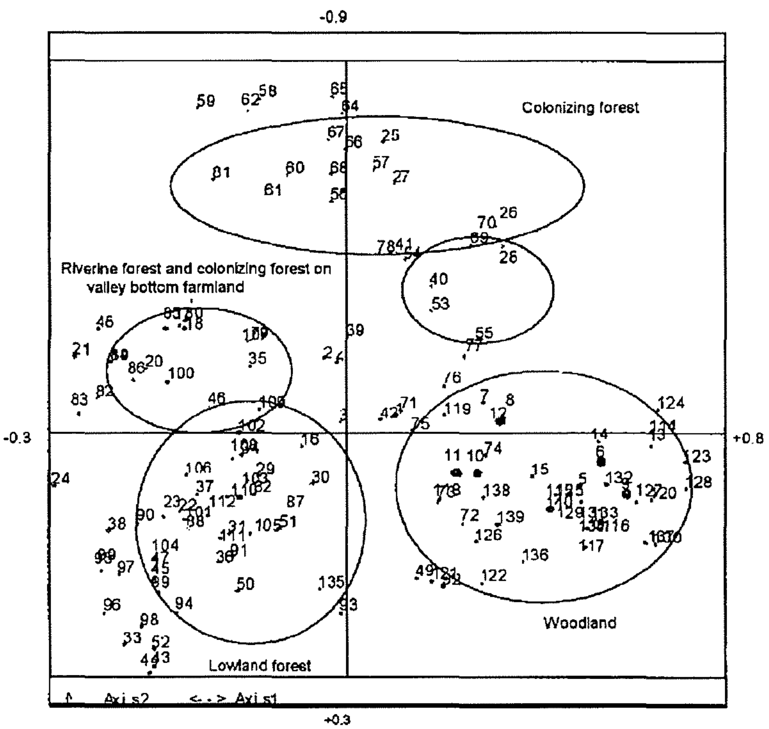

Fig. 2. Axes 1 and 2 of PCA ordination based on species presence and absence.

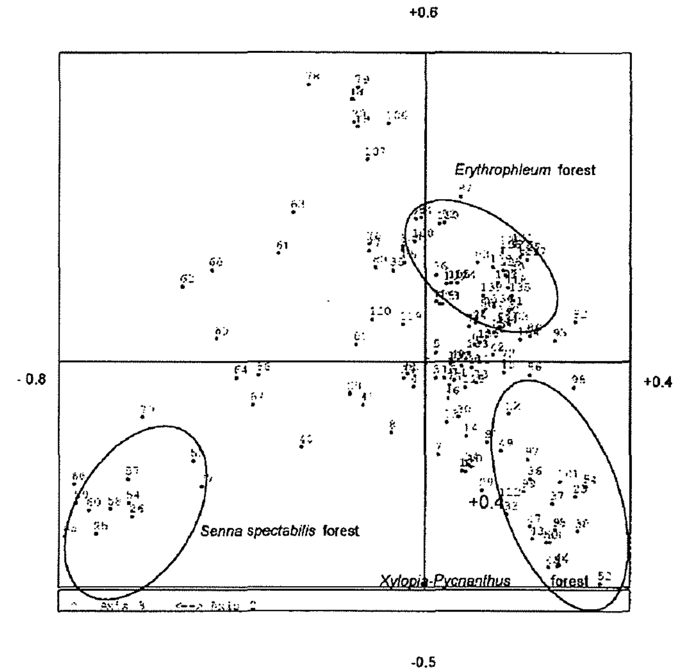

Fig. 3. Axes 1 and 3 of PCA ordination based on species frequency.

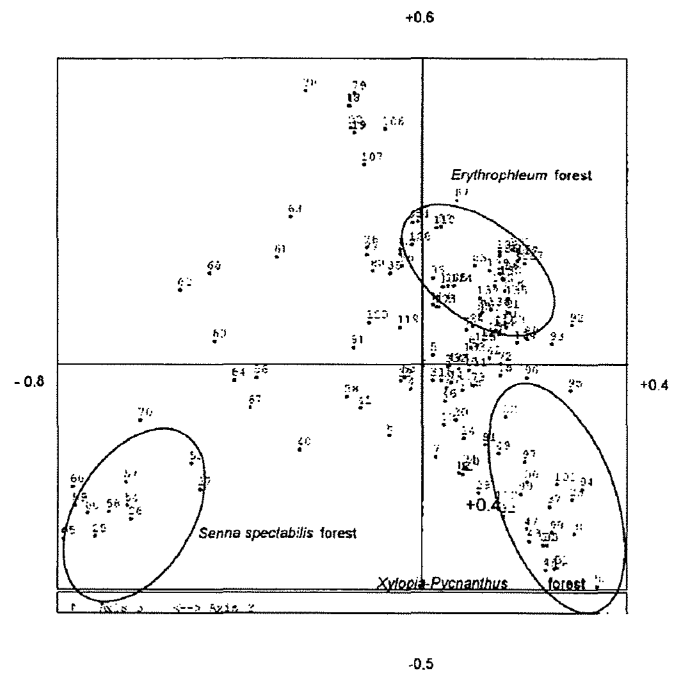

Fig. 4. Axes 2 and 3 of the PCA ordination based on species frequencies.

Axis 2 (Fig. 4). Forest dominated by the exotic tree *S. spectabilis* also appears as a distinct cluster of data points separated low on the negative part of axis 3. The major vegetation types and the percent cover of each type are as follows: lowland forest (*Xylopia-Pycnanthus* and *Erythrophleum*) (61.5%); forest on abandoned farmland (*S. spectabilis*, *C. sylvaticus* and other spp.) (11.5%); woodland (*Combretum* and other spp.) (19.2%); Miombo (*B. bussei*) woodland (3.8%); and swamp (3.8%). For tree species representing these vegetation types, see Appx. 2.

Forest and woodland structure

a. Tree basal area and diameters

Basal area of trees calculated from diameters have been used as a measure of forest maturity (Williamson 1988). The pan-tropical mean for mature forest is 32 m^2/ha (Dawkins 1958, 1959 cited in Mabberly 1992). At Kasoje, basal area is very close to or at the mean at 33.2 m^2/ha in *Xylopia-Pycnanthus* forest and 31.7 m^2/ha in *Erythrophleum* forest.

The frequency distributions of tree diameters in forest (Figs. 5 and 6) and woodland (Fig. 7) show that overall there are large numbers of trees in the small diameter classes and fewer large trees with a declining tendency from small to large diameters.

b. Tree densities

Tree densities in forest at Kasoje varied among vegetation types: The highest density was in *Erythrophleum* forest (473 stems/ha) followed by *C. sylvaticus* forest (451 stems/ha), *Xylopia-Pycnanthus* forest (437 stems/ha) and *S. spectabilis* forest (239 stems/ha). Biochemical studies have revealed that *S. spectabilis* produces allelochemicals which may interfere with the growth of other plant life (H. Ohigashi pers. comm.) but it is not understood whether that plays a factor in the very low density of trees in that vegetation type compared to other types of forest at Kasoje. Tree density in *Combretum* woodland was 572 stems/ha., while density in miombo woodland was estimated at 480 stems/ha.

c. Lianas

Erythrophleum forest had the greatest numbers and species of lianas: 11 species (9 families) of woody climbers formed 26% of the total density and approximately 1% of the total basal area in plots. Several species of woody climbers sometimes formed "vine towers" on isolated trees, totally covering the canopy. The same species of lianas found in *Erythrophleum* forest were present in *Xylopia-Pycnanthus* forest but they comprised a much smaller proportion of the density (7%) and basal area (0.3%). Twenty eight lianas of 6 species and 5 families were recorded in riverine forest. Large lianas such as *S. comorensis* sometimes spanned the crowns of several trees. Lianas formed a very small proportion of the total basal area (< 1%) in *C. sylvaticus* and *S. spectabilis* forest and were absent or nearly absent in miombo and *Combretum* woodland.

Diversity of tree species and vegetation types

Diversity has two components: the variety and the abundance of species. Species richness (abundance) can be measured by a straightforward count of the number of spe-

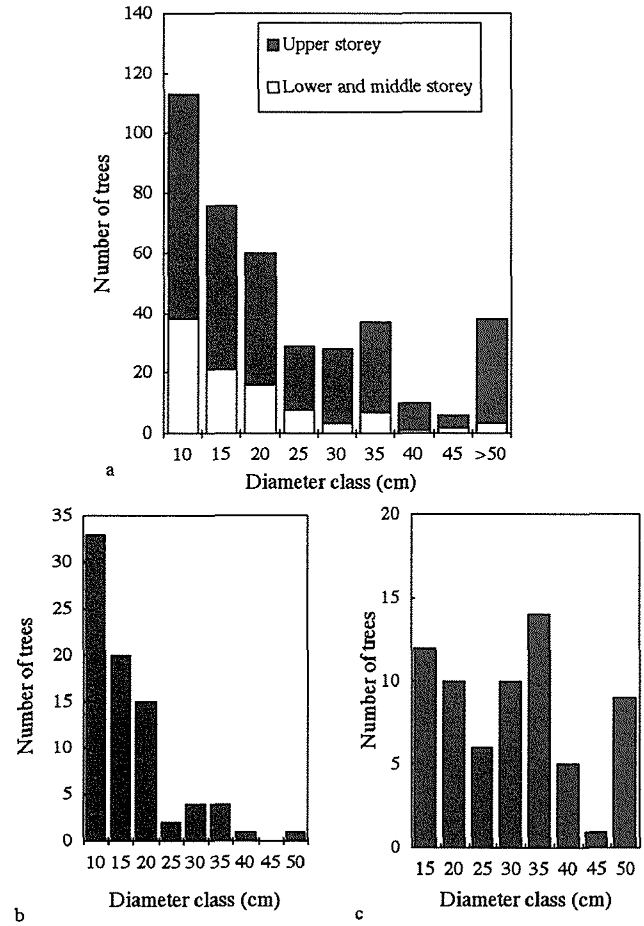

Fig. 5. (a) Frequencies of overall tree diameters, (b) Frequencies of diameters of *Xylopia parviflora*, and (c) Frequencies of diameters of *Pycnanthus angolensis* trees in *Xylopia-Pycnanthus* forest. A diameter class of "10" includes trees which measured 10 to 14 cm at breast height (dbh), a class of "15" means 15 to 19 cm dbh etc.

cies present. 2268 individuals of 129 species of trees and lianas representing 41 families were identified on transects. Caesalpiniaceae was represented by the highest number of trees (Table 1). Together the Leguminosae (Caesalpiniaceae, Mimosaceae and Papilionaceae) accounted for 20% of the total density and 44% of the diversity (20 species). A plot of cumulative species diversity against the area sampled (Fig. 8) shows that the number of new species encountered on transects began to level off at about 4 hectares, so it is possible to make some reasonable estimates about the diversity of trees and large lianas at Kasoje.

Diversity of tree species in *S. spectabilis* forest was slightly lower than other types of forest but not extremely low at 36 spp./ha. The highest diversity was found in *Erythrophleum* forest and *Combretum* woodland, both estimated at 48 spp./ha.

A number of factors contribute to the diversity of the habitat at Kasoje. Fundamental

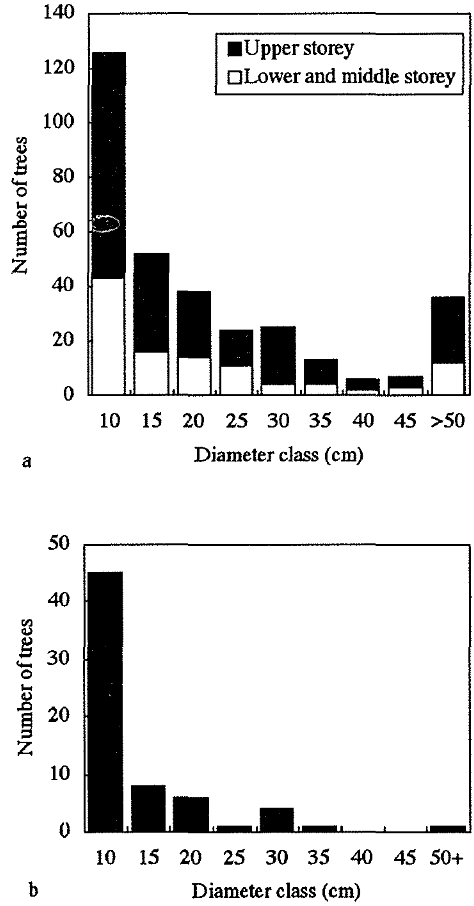

Fig. 6. (a) Frequencies of overall tree diameters, and (b) frequencies of diameters of *Erythrophleum suaveolens* trees in *Erythrophleum* forest (see Fig. 5 for explanation of diameter classes).

variations in forest structure are further modified by seasonal, orographic, topographic, edaphic and human influences. The Sorenson quantitative index was used to assess whether there were significant differences between vegetation types. The Sorenson index for *Xylopia-Pyncnanthus* forest and *Combretum* woodland was 0.013, showing that these two vegetation types are very dissimilar in species composition and abundances. The index for *Xylopia-Pycnanthus* and *Erythrophleum* forest was 0.324, which indicates dissimilarity even within forest types.

Shannon's measure also revealed significant differences in the diversity of vegetation types (Table 2). A t-test showed that there were significant differences in diversity between most vegetation types ($p < 0.01$). Again, *Erythrophleum* forest was the most diverse of the vegetation types. Shannon measures calculated for two other types of lowland forest indicated that they were less diverse than *Erythrophleum* forest (*C. sylvaticus* for-

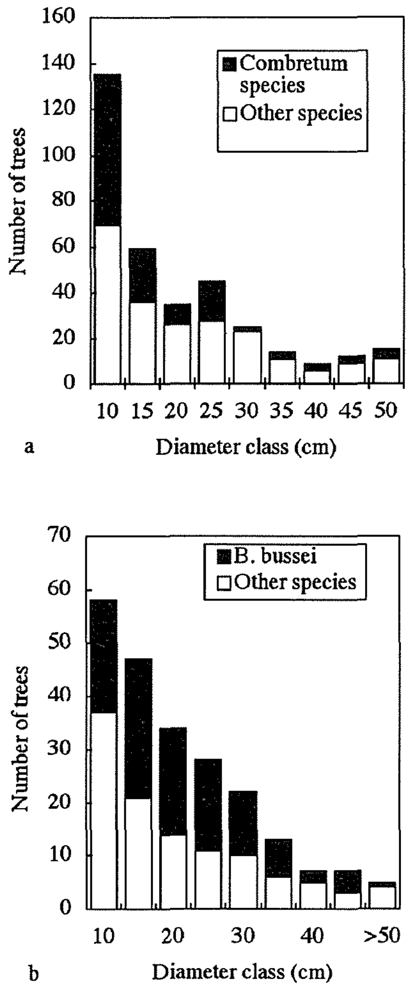

Fig. 7. (a) Frequencies of tree diameters in *Combretum* woodland, and (b) in miombo woodland (see Fig. 5 for explanation of diameter classes).

est: H' = 2.906; *S. spectabilis* forest: H' = 2.643). Diversity was lower in miombo woodland, where one species, *B. bussei*, made up a large proportion of the density. Diversity in *Xylopia-Pycnanthus* forest and *Combretum* woodland were slightly lower but similar to *Erythrophleum* forest.

Chimpanzee food availability

a. Density of food trees and lianas

The proportion of food trees in the population was used as an indicator of chimpanzee food availability in different vegetation types. Some studies have used Importance Values (IVs; Williamson 1988) which combine measurements of relative density, basal area and frequency into one value; however they are open to criticism in that the mode of combining is arbitrary and different situations can give rise to the same combined value (Grieg-Smith 1983). When detailed information on e.g. species abundance and biomass is available it is considered more straightforward to report the proportional abundance of species in the habitat rather than possibly masking diversity in IVs (E.C. Pielou pers. comm.). Food species have been classified as "major" (eaten for more than 30% of feeding time in a given month) or "minor" according to their relative importance in the chimpanzee diet based on long-term feeding records (Nishida 1991). Table 2 shows the relative density and basal area of major and minor food trees and lianas in all vegetation types. *Xylopia-Pycnanthus* and *Erythrophleum* forests are particularly rich in foods considered key components of the chimpanzee diet, while *C. sylvaticus* forest and *Combretum* woodland have higher proportions of minor foods. Miombo woodland contains the lowest density of chimpanzee foods (Table 2) due to the fact that one species, *B. bussei*, makes up a large portion of the total density and basal area in this vegetation type. Chimpanzees have been noted to occasionally eat the seeds and bark of *B. bussei*, however this species is not considered an important source of food for chimpanzees (Nishida pers. comm.).

b. Distribution of food trees

Many fruit trees occurred in clumps or patches as opposed to being more regular in their distribution (Appx. 3). Complex analyses of pattern were beyond the scope of this study, however some observations can be made. The widespread or "hyperdispersion" of species such as *S. comorensis* and *P. angolensis* may be due to the high density of these species and heterogeneity of forest composition in some areas. *F. vallis-choudae*, however, is fairly restricted, occurring along rivers or in moist valley bottoms and therefore can be considered "patchy" or "contagious" in its distribution.

Table 1 Dominant families of trees and lianas in Kasoje as a proportion of the total density (2268 individuals) and the total basal

Family	No. of Species	Density (%)	Basal area (%)
Caesalpiniaceae	8	14.9	4.5
Combretaceae	4	10.0	2.2
Apocynaceae	5	8.2	1.6
Euphorbiaceae	11	8.1	4.7
Annonaceae	5	6.6	1.7
Moraceae	6	6.2	8.5
Bignoniaceae	4	5.4	1.5
Myristicaceae	1	4.5	3.9
Anacardiaceae	4	4.0	4.3
Papilionaceae	7	3.4	0.5
Mimosaceae	5	1.6	2.4
Total	60	72.9	35.8

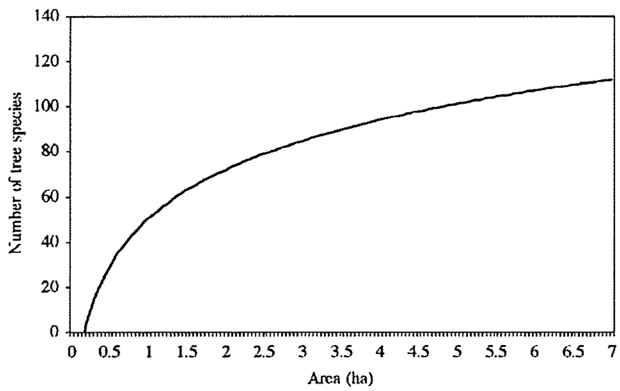

Fig. 8. Species/area curve for tree species in vegetation types in Kasoje area of Mahale Mountains National Park.

Table 2 Diversity of vegetation types and percentages of major and minor foods at Kasoje.

Vegitation type	Shannon index of diversity (H')	No. of spp/ha	Density		Total basal area (%)	
			Major	Minor	Major	Minor
Xylopia-Pycnanthus forest	2.88		38	17	63	14
Erythrophleum forest	3.65	48	29	34	43	37
Riverine forest	2.25					
Croton sylvaticus forest	2.91		22	66	20	71
Senna spectabilis forest	2.64	36	17	39	24	39
Combretum woodland	2.89	48	4	57	10	53
Miombo woodland	2.08		0	30	0	21

c. Herbaceous vegetation

The distribution of *P. peduncularis*, the fruits of which are consumed by chimpanzees during the latter part of the rainy season and early dry season, was ubiquitous (75% of plots) in *Xylopia-Pycnanthus* and *Erythrophleum* forest with densities ranging from one to 20 stems per plot (mean density 4.1 stems/m^2) while stems of *M. leucantha* were patchy in their distribution (16% of total density; mean density 5.6 stems/m^2). The relative density of *Costus afer* was low (4% of total density) with stems concentrated in two small patches of a few plots each. Although not common on transects, this herb was observed to form dense stands up to 2 meters tall in marshy areas along streams. Species of *Aframomum* were rare on transects, with only one or two stems in a small number of plots.

The density and distribution of herbaceous foods in *S. spectabilis* forest differed markedly between secondary and other types of forest. Thirty seven species of herbs, lianas, shrubs and tree seedlings (<1 m tall) and saplings (>1 m tall) were identified in 1842 m^2 plots placed randomly on a transect in *S. spectabilis* forest. Seedlings and saplings of *S. spectabilis* occurred in 43% of plots and formed 73% of the total density. *P. peduncularis* was the second most frequent and second most common species (29% of plots; 14% of total density). The two species showed little overlap in their distribution (Fig. 9). Other species of chimpanzee foods, i.e. *M. leucantha* and *Aframomum* spp. were rare.

The pith of *Pennisetum purpureum* (Gramineae) is eaten by chimpanzees regularly throughout the year (Nishida & Uehara 1983). This species did not occur in any plots in either mature or secondary forest but rather is abundant in monodominant stands of several hectares in what was formerly farmland.

Diet composition and diversity

At least 70 different items including parts from 59 plant species, 6 animal species (2 mammal, 1 bird and 2 insect), soil from termite mounds and water were ingested during the study period (Appx. 4). Fruit accounted for over 50% of the diet in all months of the study based on time spent feeding (Fig. 10). Chimpanzees ate the leaves and piths of 7 herbs and the fruit of one herb. Piths were harvested on the ground from large herbs of Zingiberaceae and *Pennisetum purpureum* (Graminae) and small lianas; the pith of 1 large liana, *S. comorensis* (Apocynaceae) was eaten once. They also ate the leaves, flowers, fruit, seeds, resin and bark of 52 species of trees, shrubs and lianas (see Appx. 4). Chimpanzees consumed the fruits of 28 trees, 6 lianas, 2 shrubs and 1 herb. Fruits were harvested in the canopy, while foraging on the ground or collected from where they had fallen and eaten either aloft or on the ground.

Consumption of animal prey was highly seasonal. Chimpanzees hunted more in the late dry and early rainy season (August to November) and ate ants of *Crematogaster* spp., especially in September and October. In August to October they also ate insects (species unknown) which formed galls on the leaves of the forest tree, *Milicia excelsa.*

Chimpanzees fed on a larger number of food items during months of the late dry season (August and September) when many trees in lowland forest did not bear fruit. The proportion of fruit in the diet during those months remained high (Fig. 11). Diet diversity based on food items was not significantly correlated with the proportion of fruit or leaves in the diet.

During most months chimpanzees depended heavily on only a few, key items. Except for August and September, more than 50% of feeding was concentrated on only 3 to 4 food items. A food item was determined to be important based on its proportional abundance in the diet, the number of months it was eaten and its relative availability in the habitat.

Foods which were especially important to chimpanzees are as follows. Fruits and or leaves of trees of the genus *Ficus* were eaten in 9 months during the study although the overall importance in the diet varied from month-to month. The fruit of the liana species *S. comorensis* was eaten extensively in 9 months during the early to mid rainy season when it comprised more than 20% of all feeding in each month. Large ground herbs of the genus *Aframomum* were eaten in all months except October. Chimpanzees ate the fruit of *P. angolensis* from September to January. The pith of *Pennisetum purpureum* was eaten in 8 months but was especially important in February (13% of feeding). The ripe berries of *P. peduncularis* were eaten in 3 months but became especially important in April (18.6% of feeding) as the availability of fruit in forest declined.

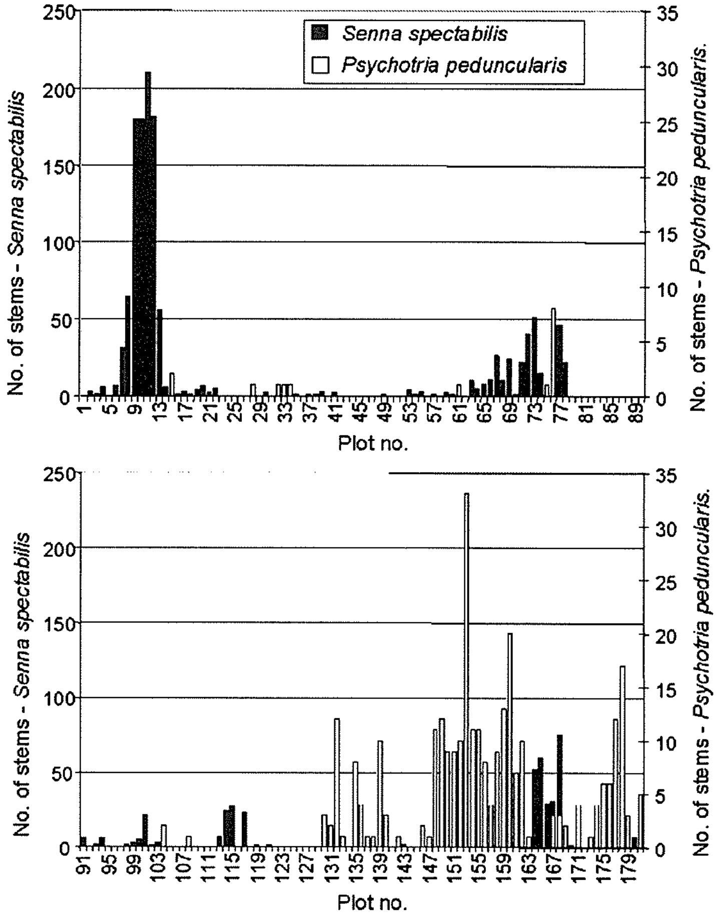

Fig. 9. Densities of *Senna spectabilis* and *Psychotria peduncularis* in plots in lowland forest on abandoned farmland.

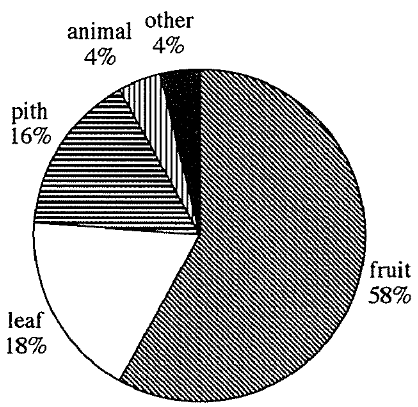

Fig. 10. Proportional abundance of items in the chimpanzee diet during the entire study.

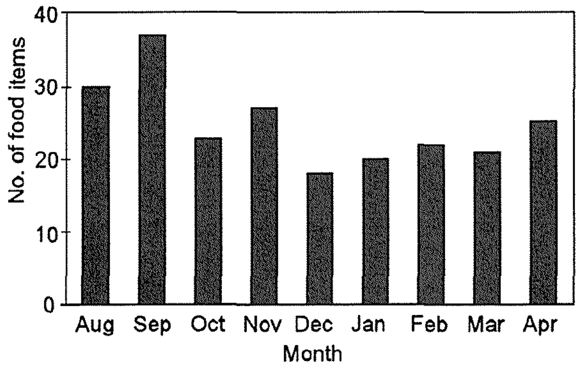

Fig. 11. Number of food items eaten by chimpanzees during months of the study.

Chimpanzee home range size

During a fourteen-month period chimpanzees visited a total of 281 quadrats. A further 31 quadrats not visited but bordered on at least two sides by ones which had been were included in the final home range total of 312 quadrats. Home range size was estimated to be 19.5 km^2. This is smaller than Nishida's (1990) estimate of 21 km^2 which is based on long-term observations but very close to Hasegawa's (1990) estimate of 19.4 km^2. The number of individuals in M group has declined from more than 100 in 1989 to less than 50 in 1998. Changes in group demographics no doubt have an affect on the size of the territory the group needs and is able to defend (T. Nishida pers. comm.).

Day journey length

The total range of day journeys for the study group was 500 m to 5000 m (Fig. 13; mean 1811 m, s.d. 916, n = 208). When day journey length was compared on a month to month basis (t-test) the following observations could be made: 1) Mean day journey values were low in May, increased in June and decreased in July (no significant differences between months); 2) Day journey length increased August and continued to increase in September. The September monthly mean was significantly higher than the mean in all months except August (April, May, July and November $p < 0.005$; January and June $p < 0.05$; December $p < 0.02$); 3) Day journey length decreased significantly in October ($p < 0.05$) and continued to decrease in November; 4) Day journeys increased in December and January. Chimpanzees were rarely sighted and no observations were possible for those months.

When dry and wet seasons were compared there was no significant difference in mean monthly day journey length (mean dry = 1734 m; mean wet = 1886 m).

Home range utilization

An analysis of chimpanzee range use showed that they used different areas of their home range at different rates and times during the study period (χ^2-test, $p < 0.001$). The 281 quadrats in which chimpanzees were observed received a total of 2021 visits. The

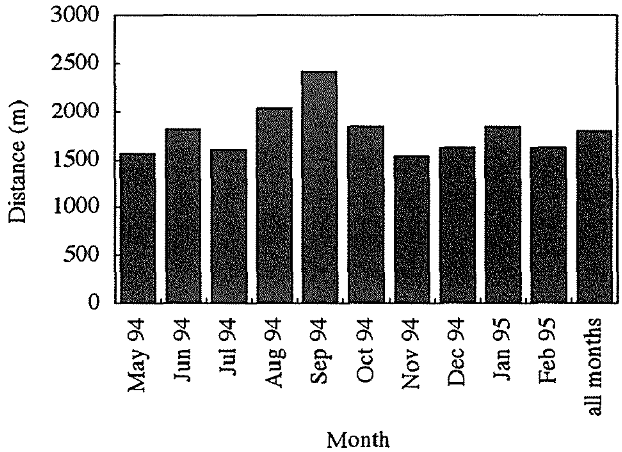

Fig. 13. Mean day journeys by chimpanzees. Data not available for March 1995 due to infrequent sightings of the main study group.

frequency and location of visits are shown in Fig. 14 and the distribution of visits is shown in Fig. 15. The highest number of visits recorded to a single quadrat was 38. This quadrat was in the area of the research camp which had been located on a travel route often used by the chimpanzees. Fifty-four (19.2%) quadrats accounted for more than 50% of total visits.

The total number of quadrats of each vegetation type in the home range, number of quadrats and the intensity of use by chimpanzees are shown in Table 3. A comparison of vegetation in quadrats which were frequently visited (more than ten times) and those which were not showed the following: Of the 31 quadrats in which chimps were not observed two were in the permanently flooded delta of a large river and one was in a seasonally flooded area where the vegetation was dominated by dense *Pennisetum purpureum* and bamboo. Twenty three quadrats were in areas of hilly, forested terrain above research trails. It is due perhaps more to the inaccessibility of these areas to researchers than any other factor that chimpanzees were not directly observed in them; in fact chimpanzee calls were heard coming from some mountainous areas that could not be reached from the roads. Four quadrats which were not visited were on wooded hillsides dominated by *B. bussei* and a final quadrat was in an area of forest at the northern boundary of the home range. Forty one quadrats received 10 or more visits. All of these were located in lowland forest where the densities of fruit trees which are an important source of food for chimpanzees are high.

There were significant differences in the monthly totals of visits and revisits per quadrat (χ^2-test, $p < .001$). The months having the lowest total number of visits to all quadrats were April 1994 and February and March 1995. These months have been noted as periods of fruit scarcity when chimpanzees do not form large parties and feed mostly on terrestrial

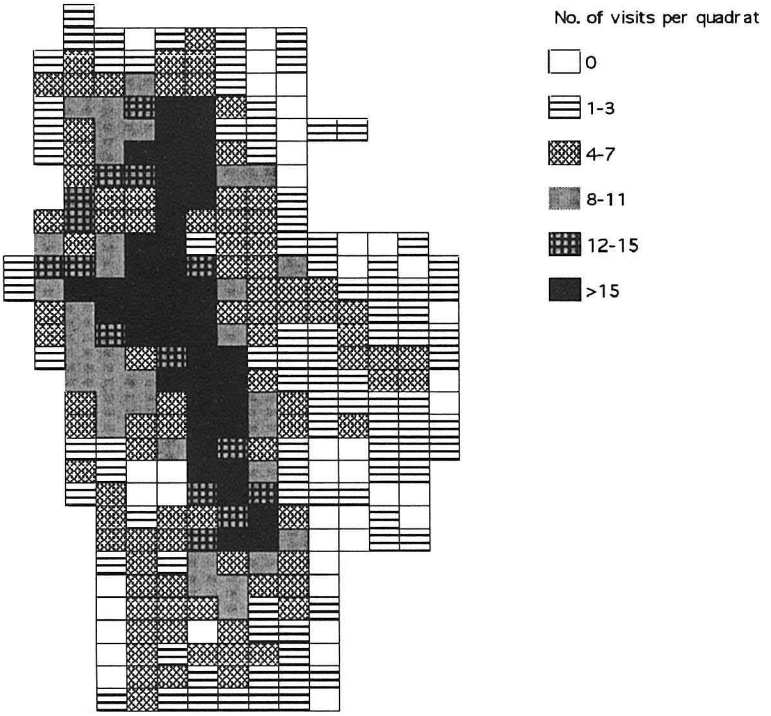

Fig. 14. Numbers of visits to quadrats in the home range during all months of the study.

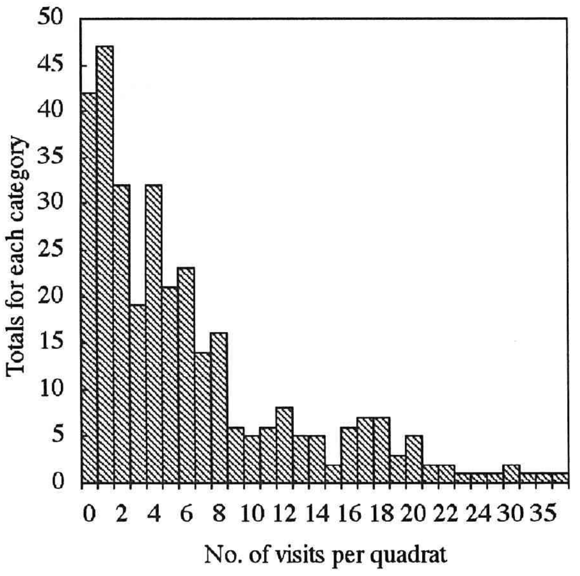

Fig. 15. Frequency distribution of visits to quadrats during the study period.

Table 3 Vegetation types and percent use of quadrats in vegetation types by chimpanzees during the study.

Vegetation type	Total no. of quadrates	% use	Relative use (%) High	Low to moderate	Not used
Lowland forest (*Xylopia-Pycnanthus* and *Erythrophleum*)	199	87.9	20.6	57.3	0.0
Forest on abandoned farmland (*Senna spectabilis, Croton sylvaticus* and other spp)	62	100.0	45.2	54.8	0.0
Woodland (*Combretum* and *Brachystegia bussei*)	42	90.5	4.8	85.7	9.5
Swamp	9	66.7	0.0	66.7	33.3
Total	312	90.1			

Each quadrat measures approximately 250 x 250 m. "High" use indicates chimpanzees were seen in the quadrat 10 times or more; "low to moderate" use indicates less than 10 visits to a quadrat.

herbaceous vegetation. April 1994 and March 1995 were also months in which the total number of different quadrats visited was low. However, because of the infrequent sightings of chimpanzees during these months it is not possible to draw conclusions about their ranging behavior during these months.

Sightings of chimpanzees in lowland areas increased significantly in May 1994 when fruits of *H. madagascariensis* became available in secondary forest and wooded grassland. Although the total number of quadrats visited was high, many quadrats were only visited a few times. In June and July 1994 chimpanzees were observed in the eastern, hilly part of their home range feeding on fruits of *Afrosersalisia cerasifera* (Fig. 16). After *A. cerasifera* trees finished fruiting and fruits of the forest tree *P. angolensis* became available, the number of visits and revisits to quadrats in lowland forest increased, particularly in September and October. During this time chimpanzees concentrated their search for food in lowland areas, visiting and revisiting forest where the density of *P. angolensis* is high. The total number of visits and revisits to quadrats remained high in January and February 1995 when fruits of *C. millenii* and *S. comorensis* were also available in the forest.

Discussion

Structure and composition of the vegetation

The Kasoje habitat is composed of a number of different forest and woodland types which vary in structure and composition. Most of the grassland and various successional stages of forest are the result of earlier forest clearing for agriculture. Nishida (1990) theorized that forest succession at Kasoje proceeded in the following manner: abandoned field was replaced by *Pennisetum purpureum* (elephant grass) bush which would then be colonized by pioneering trees such as *H. madagascariensis* and *Ficus* spp., followed by *P.*

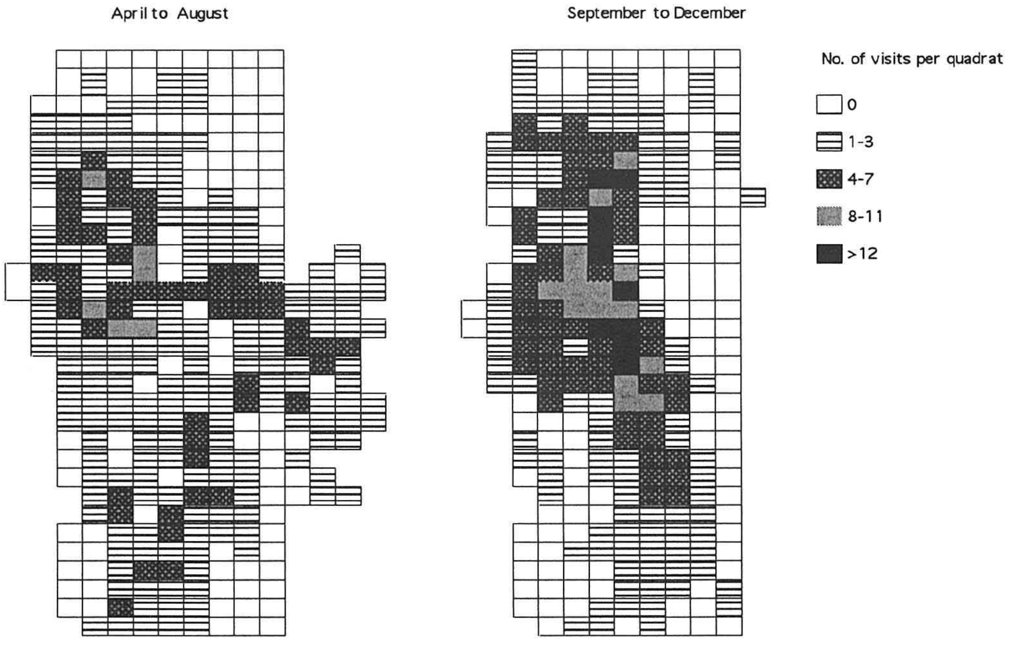

Fig. 16. Numbers of visits to quadrats from April to August and from September to December 1994. Chimpanzees ranged widely in the home range from April to August. Visits to quadrats were concentrated in forest when fruits of *Pycnanthus angolensis* and *Cordia millenii* were available.

angolensis dominated forest, and then a "climax" forest in which *Albizia glaberrima*, *Xylopia parviflora* and *Julbernardia seretti* were characteristic tree species. Although this pattern has been observed to occur in some areas of lowland forest it has not occurred in others (S Uehara pers. comm.). Some areas on the coastal plain which were disturbed over a long period of time have been replaced by *Imperata* grassland (T Nishida pers. comm.). The path that succession takes after forest has been cleared is likely to be influenced by a number of factors. Ewel (1980) has pointed out that tropical succession seems to be a nonlinear process that proceeds by "manifold routes" from pioneer phase to maturity. Differences in the pattern of succession at Kasoje may reflect local differences in climate, soil, drainage and/or differences in the history of land use by humans. The composition of the initial regrowth also may depend on species present in the pre-disturbance soil seed bank, the timing of disturbance in relation to the availability of wind-dispersed seeds and the initial immigration of shade tolerant primary species (Swaine & Hall 1983). The composition of forest on abandoned agricultural land at Kasoje is quite varied; where the exotic tree *S. spectabilis* was introduced that species has spread to form large, nearly monodominant stands while in other areas *C. sylvaticus* and other pioneering species predominate.

The density of trees in lowland forest at Kasoje (*Xylopia-Pycnanthus* and *Erythrophleum* forest) was similar to that reported for forest at Gombe, while density in *Combretum* woodland was higher than in vegetation types of similar composition at Gombe

Table 4 Density and diversity of trees in miombo woodland in Kasoje and other sites in Africa.

Location	Sample area (ha)	No. of trees (ha)	No. of spp/ha
Kasoje area, Mahale Mts.	0.55	452	62
Simbo Forest Reserve Plot no. 25, Tabora region, Tanzania[1]	3.3	1244	32
Simbo Forest Reserve Plot no. 26, Tabora region, Tanzania[1]	4.2	131	?
Shaba region, Democratic Republic of Congo[2]	?	447	?
Geita region, Tanzania[1]	0.1	1340	160

1: Borota, 1991; 2: Malaisse, 1978.

(Clutton-Brock & Gillett 1979). The number of trees per unit area in miombo forest shows considerable variation according to the different localities in which it occurs (Borota 1991). The density of miombo in lowland areas of Kasoje approximates that of forest in the Shaba region in the southeastern part of the Democratic Republic of the Congo (Table 4) and is intermediate to areas of miombo in other regions of Tanzania. Differences in tree density between Kasoje and other areas in Tanzania may be related to local difference in soil, temperature and rainfall.

Profiles of diameter classes of trees showed that there were overall large numbers of trees in the smaller diameter classes with the numbers of trees in each class declining from small to large. This may be due to a previous history of forest clearing at Kasoje, however the biological interpretation of stand tables is problematic (Brunig 1983) and the same patterns of tree diameter distribution can be seen in mature as well as young forest (Hallé *et al.* 1978 cited in Swaine & Hall 1983). In the absence of successive measurements on sample plots, the size of a tropical tree is not a reliable indicator of its age (Longman & Jeník 1987). One very comprehensive investigation in a forest in Southern Nigeria (Jones 1955;1956 cited in Longman & Jeník 1987) found that numbers of shade-tolerant species of the lower storeys decreased logarithmically, while light-demanding emergents were deficient in some of the middle size-classes with sometimes no individuals of smaller sizes. Frequency distributions of diameter classes in *Xylopia-Pycnanthus* and *Erythrophleum* forest do not follow this pattern: there are large numbers of upper storey as well as lower-storey trees in the smaller diameter classes. Much more information about tree growth and underlying environmental factors would be needed to understand forest succession and the patterns of density and diameter that are seen at Kasoje.

Tree and liana diversity

It has been suggested that sampling is likely never to be comprehensive in terms of the total number of species recorded from an area unless almost the whole area is used as the sample (Mabberly 1992). This is reflected by the fact that although it began to level

Table 5 Density and diversity of trees in forest in Kasoje and other African forests.

Location	No. of trees/ha	Basal area (m^2/ha)	No. of spp/ha
Tanzania			
Mahale Mountains National Park (Kasoje)[1]	456	33	39
Gombe National Park[2]	437		41
Cameroon			
Southern Bakundu Forest Reserve[3]	368		109
Gabon			
Lopé Reserve[4]	384	40	35
Nigeria			
Okumo Forest Reserve[5]	390		70
Uganda			
Budongo Forest[3]			39
Kibale National Park (Kanyawara)[6]		35	36
Democratic Republic of Congo			
Kahuzi-Biega National Park	186-248		

1: This study; comparisons are for *Xylopia-Pycnanthus* and *Erythrophleum* forest; 2: Clutton-Brock and Gillett, 1979; 3: Mabberly, 1992; 4: Williamson, 1988; 5: Longman and Jenik, 1987; 6: Struhsaker, 1975; 7: Yamagiwa, et al., 1996.

off, the area species curve did not reach a plateau even after 7 hectares of sampling. Additionally, the chimpanzee habitat includes areas of montane forest which have yet to be studied in detail; further research will undoubtedly contribute more to knowledge about species diversity and vegetation types in Mahale.

Estimates of the number of tree species in African forest range from 25 to 60 species per hectare with the exception of particularly species-rich forests such as that of Korup in Cameroon (Whitmore 1990). Table 5 presents comparisons of forest diversity, tree density and basal area in Kasoje with other African forests. Diversity of *Xylopia-Pycnanthus* forest at Kasoje falls in the middle of this continuum at 39 species/ha. This equals the estimate for Budongo (Eggeling 1947) and is similar to estimates for Kibale (Struhsaker 1975) and Lopé (Williamson 1988).

The proportion of the population formed by the ten most common species is sometimes used as a measure of diversity. Comparisons to forests in other areas shows that diversity at Kasoje is similar in this respect to sites such as Kahuzi-Biega in Zaire and Kibale in Uganda. A list of all tree and liana species identified on transects and floral overlap between the study site and other sites where chimpanzees and gorillas are studied is given in Appx. 5. The greatest overlap was with Gombe (64.5%), followed by Budongo (51.1%). Less overlap (24.4%) was seen with the Ugalla, a much drier chimpanzee habitat east of Mahale. The central and West African sites of Wamba (16.0%), Kahuzi-Biega (11.4%), the Lopé (13.7%) and Ndoki (8.4%) showed the least similarity to Kasoje.

The level of diversity in lowland forest was similar to that calculated for the Lopé forest (H' = 3.34; Williamson 1988). The Shannon measure showed a level of diversity for *Xylopia-Pycnanthus* forest and *Combretum* woodland (H' = 2.882 and H' = 2.893, respectively) which is similar to that found at Kibale in unlogged forest compartments (H' = 2.819; Struhsaker 1997).

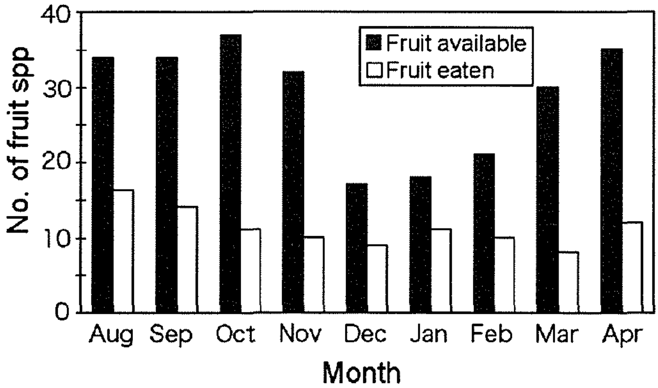

Fig. 12. Number of fruit species potentially available in the habitat compared to the number of fruit species eaten by chimpanzees during months of the study.

Density and diversity of chimpanzee foods

Although food appears to be abundant in all vegetation types seasonal rhythms in food production must be considered. Temporal variation in fruit bearing by tropical trees is well known (Lieberman 1982; Struhsaker 1997; Tutin & Fernandez 1993). In 1994 at Kasoje, for example, chimpanzees fed intensively on the fruit of *Afrosersalisia cerasifera* trees in one part of their home range. In 1995, however, eight out of ten trees in the same patch produced no fruit, and the amount of fruit produced by the remaining two trees was small.

P. peduncularis, a shrub noted to be an important source of fruit for chimpanzees when other fruits are scarce, was found to be common in forest. The mean density of one large forest herb, *M. leucantha*, was higher than the overall density reported for the Kanyawara community of Kibale (Wrangham *et al.* 1993) where it was noted to be an important part of the chimpanzee diet. The sample area at Kanyawara was larger (900 m^2) and took into account differences in logging intensities in forest compartments and this may account for the differences in densities. At the Lopé where both gorillas and chimpanzees live, *Aframomum* and Marantaceae were reported to be common throughout the study area with a basal area of 7.7 m^2/ha (Williamson 1988). Chimpanzees at Lopé eat the fruit and pith of *Aframomum* but not *Marantachloa*; both are considered important in the gorilla diet (Tutin & Fernandez 1993). It was suggested that the high biomass of herbaceous foods at that site and of Visoke, Rwanda (8.8 m^2/ha) is an important structural component of the gorilla habitat (Williamson *et al.* 1990).

Diet of chimpanzees

Although chimpanzees fed on a variety of foods most of their feeding was concentrated on a relatively small number of food items, and the availability of these resources may be critical to their survival. Long-term records show that chimpanzees at Mahale eat the fruit of a large number of plant species (Nishida & Uehara 1983). The number of species which may bear fruit in any given month, however, was not correlated with the number of species actually eaten by chimpanzees in the 1994-1995 study season (r=0.467) (Fig. 12). Chimpanzee foraging was not strictly optimal. Isabirye-Basuta (1989) found that diet diversity in terms of the number of food items eaten by chimpanzees at Kibale was heavily negatively correlated with the proportion of fruit in the diet. During the 1994-1995 study period, however, the number of items in the diet and proportion of fruit were actually positively correlated, although not significantly so.

Availability of a potential food alone does not necessarily determine behavior. A survey of plant food use by groups of chimpanzees at Kasoje and Gombe revealed that of 143 plant food species available in both areas, only 85 (59.4%) species were noted to be eaten in both areas (Nishida *et al.* 1983). Such differences in feeding have been attributed to differences in plant densities between the two sites or interpreted as examples of local tradition or "culture".

The reliance by chimpanzees on a few key food items is undoubtedly influenced by the availability of these items in the habitat. Use of a particular species, however, may not be solely related to its abundance; nutritional content and even feeding preferences may also play a role in a chimpanzee's choice of food. Indices of fruit abundance based on feeding alone are unreliable; chimpanzees living elsewhere have been observed to continue to exploit diminishing patches of fruit when other, more abundant fruit foods are available (Isabirye-Basuta 1989). Fluctuation in the abundance of plant reproductive parts in tropical forest is known to be seasonal to markedly seasonal (e.g. Medway 1972; Terborgh 1983), with the greatest scarcity of ripe fruit in forest occurring at the end of the wet and beginning of the dry season. The results of this study support previous findings by Matsumoto-Oda & Sprague (1999) that chimpanzees do not exist within a habitat where the amount of resources at any given time can be simply characterized as "abundant" or "scarce". Chimpanzees must respond rather to an environment where change in the level and availability of resources is a more-or-less continuous process.

Chimpanzee ranging

Patterns of food distribution may be the key element determining how chimpanzees utilize their home range. An analysis of range use showed that in months of fruit scarcity chimpanzees traveled widely throughout the habitat in search of food, visiting many different areas infrequently, while in months when major fruit foods such as *P. angolensis*, *C. millenii* and *S. comorensis* were available visits to areas of forest where the density of those species is relatively high increased in frequency.

The size of the Kasoje chimpanzees' home range was similar to that calculated by Hasegawa (1990) although this estimate reflects only the area that the chimpanzees were actually observed to use. On many occasions when the chimpanzees could not be visually located their calls were heard coming from remote and inaccessible areas of the habitat, particularly areas of hilly terrain. Therefore, the actual size of the home range is probably much larger. Kawanaka (1982) estimated that M group may use an area as large as 33 km^2.

The length of day journeys by Kasoje chimpanzees (range 2-6 km) was similar to chimpanzees at Gombe (Goodall 1968; Wrangham 1975). Comparisons of monthly mean day journey lengths showed no obvious effect of climate on daily travel distance, although chimpanzees were observed to halt travel when it poured rain. When the chimps were feeding on *P. angolensis* fruits (September-December) the distance between crops affected the distance traveled in a day. This species can occur in large patches of 30 or more trees with distances of 0.5-2 km between patches, and chimpanzees may feed at more than one patch in a day.

Chimpanzees in forest habitats such as Kasoje and Gombe (Wrangham 1975) utilize a relatively smaller home range than chimpanzees living in dry habitats, which have been observed to travel longer distances and range over a much larger area (Suzuki 1969; Izawa 1970; Kano 1972; McGrew *et al.* 1981). Matsumoto-Oda & Sprague (1999) found that feeding and grouping behavior of Kasoje chimpanzees showed similarities to chimpanzees living in lowland rain forest, while activity budgets in the dry season were similar to those of Mt. Assirik chimpanzees which live in a savanna habitat where it is dry year-round (Baldwin *et al.* 1982). Chimpanzees show a great deal of flexibility in their ranging behavior and grouping patterns (Reynolds & Reynolds 1965; Nishida 1979; Goodall 1968) and each habitat most likely presents a variety of challenges including seasonal differences in the availability of food to which they respond behaviourally (Chapman *et al.* 1995).

One of the main goals of the study was to provide information on the diversity and spatial availability of food in vegetation types at Kasoje. Magurran (1998) notes that "Classifications of habitat type and resource use are often devised afresh for each study. Such unique classifications will usually preclude a direct comparison between investigations." Efforts are being made to standardize methods for describing the habitats of all great apes (Williamson 1988; Malenky *et al.* 1993). It is hoped that the methods used and information provided in this paper will further the understanding of the socioecology of chimpanzees living in tropical forest habitats.

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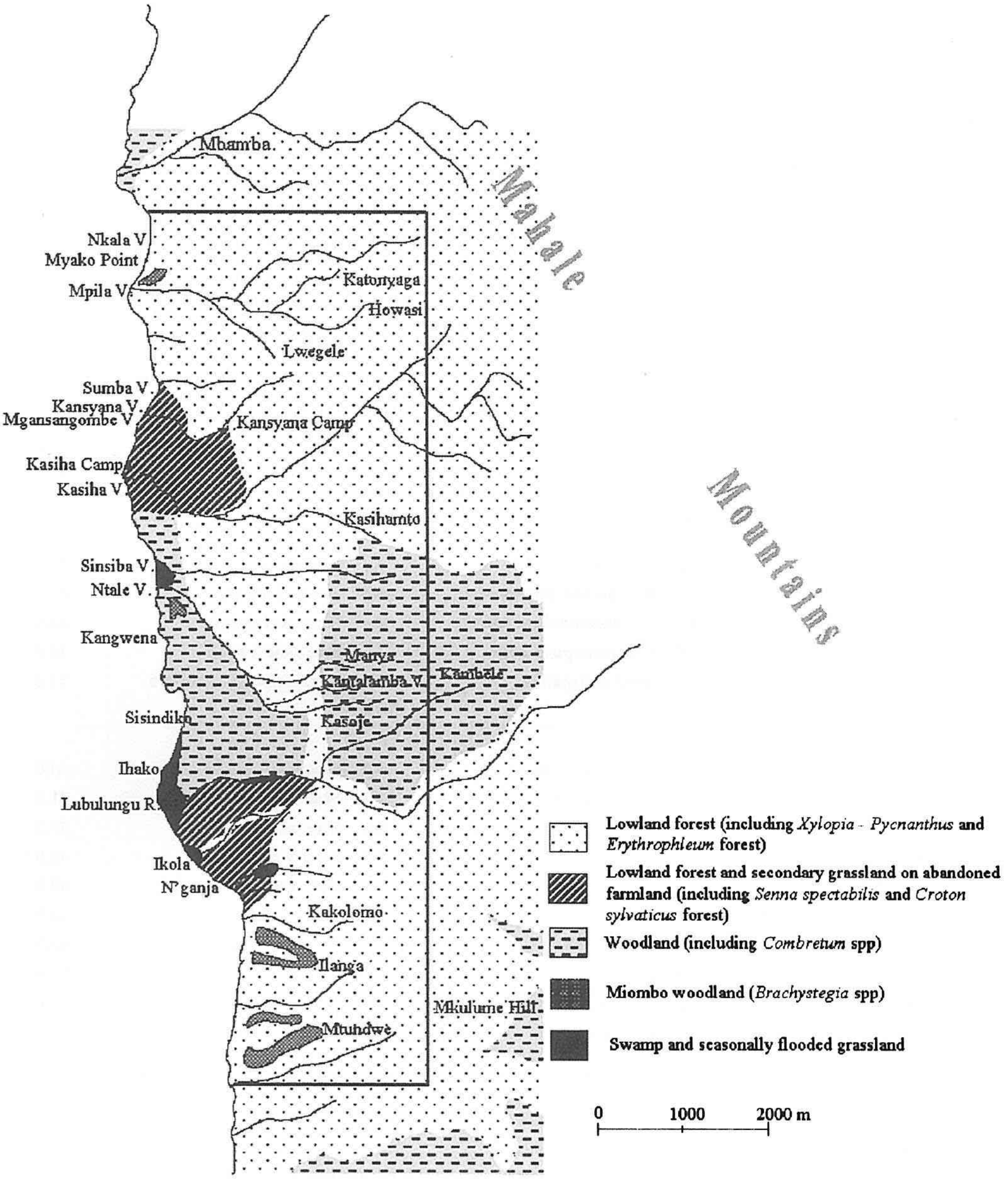
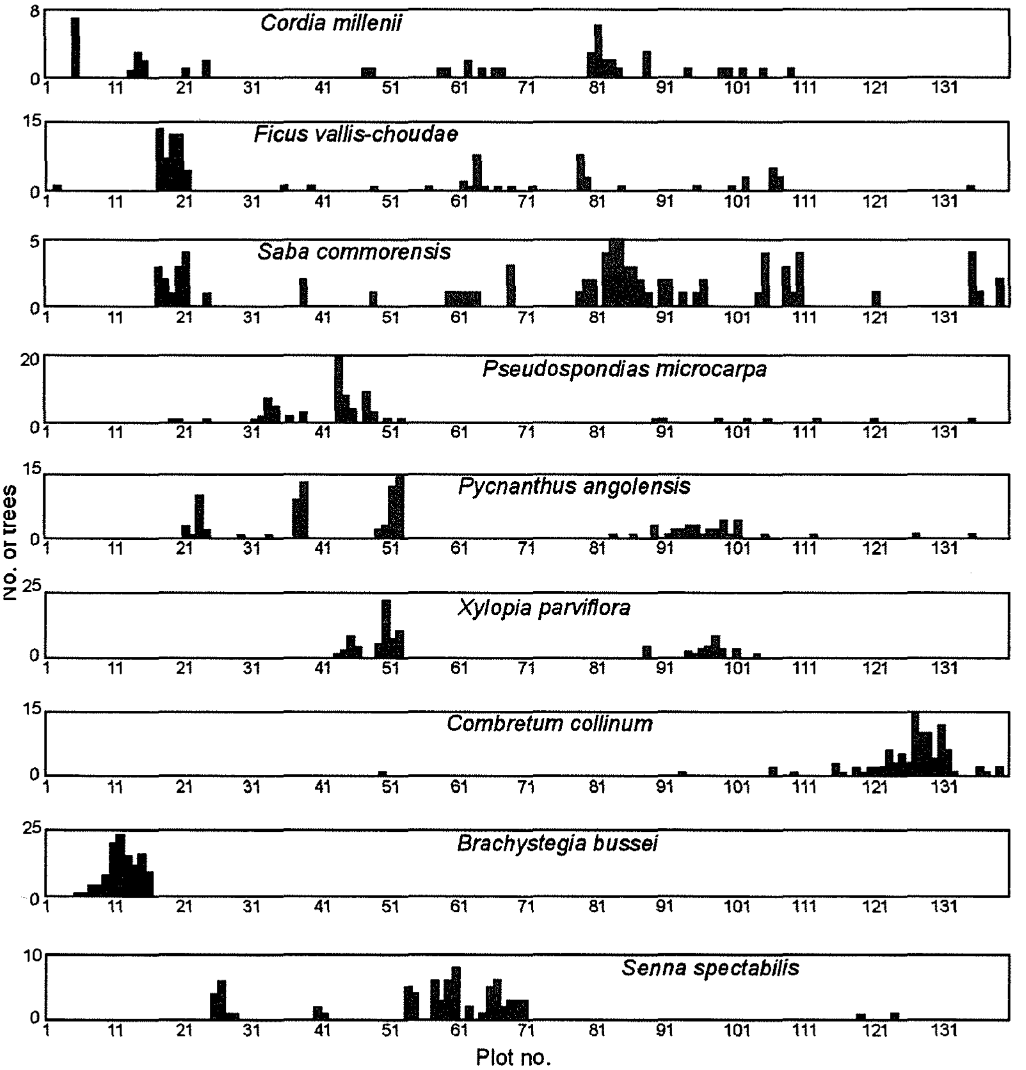


Appx. 1. Major vegetation types of the Kasoje area of the Mahale Mountains National Park. The home range of the M group chimpanzees is outlined.

Appx 2 The ten species which are the most frequent, greatest contributors to basal area and greatest density in plots in each vegetation type. The most frequent species occurs in the greatest number of plots. The species which contributes the greatest area has the greatest cumulative basal area. The percentage contribution of each species is given in parentheses following the species name.

Density	% of Total	Basal area	% of Total	Most frequent	% of Plots
***Xylopia – Pycnanthus* forest**					
Xylopia parviflora	19.3	*Pycnanthus angolensis*	28	*Pycnanthus angolensis*	75
Pycnanthus angolensis	17.6	*Pseudospondias microcarpa*	27.7	*Xylopia parviflora*	70
Pseudospondias microcarpa	11.8	*Xylopia parviflora*	6.6	*Anthocleista schweinfurthii*	50
Tabernaemontana holstii	7.5	*Cordia millenii*	5.7	*Pseudospondias microcarpa*	50
Oxyanthus sp	4.6	*Tabernaemontana holstii*	4.4	*Dracaena mannii*	40
Syzygium guineense	4.3	*Anthocleista schweinfurthii*	4.1	*Erythrophleum suaveolens*	30
Anthocleista schweinfurthii	2.9	*Canarium schweinfurthii*	3.7	*Landolphia* sp	30
Dracaena mannii	2.7	*Syzygium guineense*	3.5	*unk mtwentwe*	30
Erythrophleum suaveolens	2.4	*Albizia glaberrima*	2.9	*Cissus* sp	25
Stereospermum kunthianum	2.4	*Dracaena mannii*	1.7	*Cordia millenii*	25
Total	75.5		88.3		
***Erythrophleum* forest**					
Erythrophleum suaveolens	14.7	*Cordia millenii*	15.6	*Erythrophleum suaveolens*	68.4
Saba comorensis	8	*Myrianthus arboreus*	11.3	*Saba comorensis*	68.4
Cissus sp	6.2	*Milicia excelsa*	8.1	*Cissus* sp	63.2
Croton sylvaticus	5.8	*Albizia glaberrima*	7.9	*Croton sylvaticus*	47.4
Spathodea campanulata	4.5	*Erythrophleum suaveolens*	6.7	*Dalbergia malangensis*	47.4
Ficus capensis	4.2	*Croton sylvaticus*	6.7	*Spathodea campanulata*	47.4
Myrianthus arboreus	3.1	*Pycnanthus angolensis*	5.8	*Ficus capensis*	42.1
Bridelia micrantha	2.9	*Tabernaemontana holstii*	4.4	*Ficus exasperata*	42.1
Afrosersalisia cerasifera	2.7	*Syzygium guineense*	4.1	*Dracaena mannii*	36.8
Dalbergia malangensis	2.7	*Ficus exasperata*	3.8	*Afrosersalisia cerasifera*	31.6
Total	54.8		74.4		
***Croton sylvaticus* forest**					
Croton sylvaticus	25.9	*Croton sylvaticus*	14.6	*Croton sylvaticus*	100
Stereospermum kunthianum	9.5	*Albizia glaberrima*	10.1	*Stereospermum kunthianum*	71.4
Cissus sp	7	*Stereospermum kunthianum*	8.5	*Sterculia tragacantha*	57.1
Cordia millenii	7	*Senna spectabilis*	6.2	*Albizia glaberrima*	42.9
Senna spectabilis	5.1	*Piliostigma thonningii*	6.2	*Cordia millenii*	42.9
Antidesma membranaceum	4.4	*Sterculia tragacantha*	5.8	*Grewia mollis*	42.9
Saba comorensis	3.8	*Cordia millenii*	5.7	*Saba comorensis*	42.9
Sterculia tragacantha	3.8	*Lecaniodiscus fraxinifolius*	5.3	*Senna spectabilis*	42.9
Harungana madagascariensis	3.2	*Annona senegalensis*	4.7	*Annona senegalensis*	28.6
Piliostigma thonningii	3.2	*Acacia albida*	4.6	*Antidesma membranaceum*	28.6
Total	72.9		71.7		
***Senna spectabilis* forest**					
Senna spectabilis	34.2	*Elaeis guineensis*	18.5	*Senna spectabilis*	100
Voacanga africana	7.2	*Senna spectabilis*	15.6	*Azanza garckeana*	42.9
Annona senegalensis	5.9	*Albizia glaberrima*	9.1	*Annona senegalensis*	35.7
Azanza garckeana	5.9	*Acacia albida*	7.3	*Stereospermum kunthianum*	35.7
Trema orientalis	5.3	*Voacanga africana*	7	*Trema orientalis*	35.7
Antidesma membranaceum	4.6	*Ficus vallis-choudae*	5.7	*Voacanga africana*	35.7

Lecaniodiscus fraxinifolius	3.9	*Myrianthus arboreus*	5.3	*Albizia glaberrima*	28.6
Harungana madagascariensis	3.3	*Azanza garckeana*	5	*Antidesma membranaceum*	28.6
Acacia albida	2.6	*Ficus exasperata*	3.4	*Harungana madagascariensis*	28.6
Stereospermum kunthianum	2.6	*Lecaniodiscus fraxinifolius*	3.1	*Cordia millenii*	21.4
Total	75.5		80		
Riverine forest					
Ficus vallis-choudae	48.5	*Ficus vallis-choudae*	73.4	*Ficus vallis-choudae*	100
Saba comorensis	9.2	*Myrianthus arboreus*	11.9	*Saba comorensis*	77.8
Croton sylvaticus	5.4	*Milicia excelsa*	3.3	*Myrianthus arboreus*	44.4
Myrianthus arboreus	4.6	*Sterculia tragacantha*	2.6	*Cissus* sp	33.3
Cissus sp	3.8	*Spathodea campanulata*	1.2	*Croton sylvaticus*	33.3
Mucuna gigantea	3.1	*Combretum molle*	1.2	*Mucuna gigantea*	33.3
Spathodea campanulata	2.3	*Croton sylvaticus*	1.1	*Combretum molle*	22.2
Combretum molle	1.5	*Pseudospondias microcarpa*	1.1	*Dracaena mannii*	22.2
Keetia venosa	1.5	*Stereospermum kunthianum*	0.9	*Keetia venosa*	22.2
Phytolacca dodecandra	1.5	*Bridelia atroviridis*	0.5	*Pseudospondias microcarpa*	22.2
Total	81.4		97.1		
***Combretum* woodland**					
Combretum collinum	10.8	*Uapaca nitida*	8.5	*Combretum molle*	75
Uapaca nitida	9.8	*Uapaca sansibarica*	7.9	*Antidesma membranaceum*	71
Antidesma membranaceum	9.5	*Parinari curatellifolia*	7.7	*Annona senegalensis*	64
Combretum molle	8.2	*Combretum collinum*	6.9	*Bridelia micrantha*	57
Margaritaria discoidea	4.2	*Antidesma membranaceum*	5.7	*Combretum collinum*	57
Combretum sp	4	*Bridelia micrantha*	5.1	*Margaritaria discoidea*	57
Annona senegalensis	3.6	*Combretum molle*	4.9	*Stereospermum kunthianum*	43
unk *lujongololo*	3.6	*Combretum sp*	4.8	*Bauhinia petersiana*	36
Parinari curatellifolia	3.3	*Afzelia* sp	4.8	*Uapaca nitida*	36
Stereospermum kunthianum	3.2	*Annona senegalensis*	4.5	*Grewia mollis*	29
Total	60.2		60.8		
Miombo woodland					
Brachystegia bussei	38.3	*Brachystegia bussei*	42.8	*Brachystegia bussei*	80
Brachystegia spiciformis	12.5	*Diplorhynchus condylocarpon*	13.7	*Diplorhynchus condylocarpon*	70
Diplorhynchus condylocarpon	6.8	*Brachystegia spiciformis*	11.3	*Uapaca nitida*	60
Uapaca nitida	4.9	*Annona senegalensis*	4.9	*Annona senegalensis*	50
Stereospermum kunthianum	4.2	*Uapaca nitida*	3.8	*Antidesma membranaceum*	50
Annona senegalensis	3.8	*Antidesma membranaceum*	3.5	*Stereospermum kunthianum*	50
Combretum molle	3.8	*Stereospermum kunthianum*	2.3	*Combretum molle*	40
Antidesma membranaceum	3	*Parinari curatellifolia*	1.8	*Lannea schimperi*	40
Lannea schimperi	2.3	*Sterculia quinqueloba*	1.6	*Bauhinia petersiana*	30
Margaritaria discoidea	2.3	*Combretum* sp	1.6	*Brachystegia spiciformis*	30
Total	81.9		87.3		



Appx. 3. Distribution of some common tree and 1 liana species on 7 ha of transects in the Kasoje area of Mahale National Park.

Appx 4. List of plant speices eaten by chimpanzees, life form and part eaten. H: herb, L: Liana or other climber, S: shrub, T: tree

Botanical name	Life form	Part eaten
MONOCOTYLEDONEAE		
Acanthaceae		
Asystasia gangetica (l.) T. Anders.	H	leaf
Blepharis buchneri Lindau	H	leaf
Dyschoriste trichocalyx (Oliv.) Lindau	T	
Asclepiadiaceae		
Ceropegia sp.	L	leaf
Convolvulaceae		
Ipomoea rubens Choisy	L	leaf
Dennstaedtiaceae		
Pteridum aquilinum (L.) Kuhn subsp. *Centrali Africanum Hieron.*	H	leaf
Graminae		
Pennisetum purpureum Schumach.	H	pith
Marantaceae		
Marantochloa leucantha (K. Schum.) Milne-Redh	S	pith
Smilacaceae		
Smilax kraussiana Meisn.	L	leaf
Zingiberaceae		
Aframomum alboviolaceum (Ridley) K. Schum.	H	pith
Aframomum mala (K. Schum.)	H	fruit, pith
Costus afer Ker-Gawl	H	pith
ANGIOSPERMAE		
DICOTYLEDONEAE		
Anacardiaceae		
Mangifera indica L (alien)	T	fruit
Pseudospondias microcarpa (A. Rich.) Engl.	T	fruit
Annonaceae		
Artabotrys monteiroea Oliv.	L	fruit
Apocynaceae		
Diplorhynchus condylocarpon (Muell. Arg.) Pichon	T	seed
Landolphia owariensis P. Beauv.	L	fruit
Saba comorensis (Bojer) Pichon = *Saba florida* (Benth) Bullock	L	fruit, pith
Tabernaemontana pachysiphon Stapf = *T. holstii* K. Schum	T	fruit
Boraginaceae		
Cordia africana Lam = *C. abyssinica*	T	fruit
Cordia millenii Bak.	T	fruit, flower
Caesalpiniaceae		
Julbernardia sp.	T	fruit
Piliostigma thonningii (Schumach.) Milne-Redh.	T	seed
Dioscoreaceae		
Discorea odoratisima Pax	L	flower
Euphorbiaceae		
Antidesma membranaceum Muell. Arg.	T	fruit
Guttiferae		
Garcinia buchananii Bak. = *G. huillensis* Oliv.	T	fruit
Harungana madagascariensis Poir.	T	fruit
Malvaceae		
Azanza garckeana (F. Hoffm.) Exell & Hillcoat		fruit
Hibiscus sp.		leaf
Meliaceae		
Trichilia pleuriana		leaf
Menispermaceae		
Tinospora caffra (Miers) Troupin		leaf
Mimosaceae		

Albizia glaberrima (Schum. & Thonn.) Benth. var. *glabrescens* (Oliv.) Brenan	resin
Moraceae	
Ficus sur Forssk. = *F. capensis* Thunb.	fruit, leaf
Ficus congensis Engl.	fruit
Ficus exasperata Vahl.	fruit, leaf
Ficus vallis-choudae Del.	fruit
Ficus urceolaris Welw. ex. Hiern.	fruit, leaf
Ficus glumosa	fruit
Ficus thonningii Blume	fruit
Ficus sp	fruit
Ficus sp	fruit
Myrianthus holstii Engl.	fruit
Myristicaceae	
Pycnanthus angolensis (Welw.) Warb.	fruit, bark
Myrtaceae	
Psidium guajava L. (alien)	fruit
Syzygium guineense (Wild.) DC.	fruit
Papilionaceae	
Baphia capparidifolia Bak. subsp. *Multiflora* (Harms) Brummitt	fruit, leaf
Erythrina abyssinica DC	flower
Pterocarpus tinctorius Welw. var *tinctorius*	leaf
Rubiaceae	
Keetia venosa (Oliv.) Bridson = *Canthium venosum* (Oliv.) Hiern	fruit
Psychotria peduncularis (Salisb.) Steyerm.	fruit
Rothmannia manganjae (Hiern.)	fruit
Rutaceae	
Citrus limon L. N.L. Burm. (alien)	fruit
Citrus aurantium (alien)	fruit
Clausena anisata (Willd.) Hook. f. ex Benth.	leaf
Sapotaceae	
Afrosersalisia cerasifera (Welw.) Aubrev.	fruit
Mimusops bagshawei S. Moore	fruit
Sterculiaceae	
Sterculia quinqueloba (Garcke) K. Schum.	leaf
Vitaceae	
Ampelocissus cavicaulis (Bak.) Planch	fruit

Appx 5. List of all species identified on transects and overlap with other sites where chimpanzees and gorillas are studied. A checkmark indicates the same species occured at both sites. An asterisk indicates the same genus occured at both site. G: Gombe; B: Budongo; L: Lope; N: Ndoki, K: Kahuzi; W: Wamba; U: Ugalla.

Botanical name	G	B	L	N	K	W	U	Notes
ANGIOSPERMAE								
DICOTYLEDONEAE								
Anacardiaceae								
Lannea schimperi (A. Rich.) Engl.	✓	✓	*	*		*	*	Woodland and wooded grassland
Mangifera indica L (alien)	✓		✓					Cultigen along the lakeshore and rare in secondary forest
Ozoroa obovata (Oliv.) R. & A. Fernandes (*Heeria mucronata*)		*		*			✓	Drier forest and woodland
Pseudospondias microcarpa (A. Rich.) Engl.	✓	✓	✓	✓	✓			Forest tree usually in wet areas
Annonaceae								
Annona senegalensis Pers.	✓	✓					✓	Tree in woodland, wooded grassland and colonizing forest
Artabotrys monteiroea Oliv.		*	*		*	*	✓	Climbing shrub in forest
Monanthotaxis poggei Engl. & Diels	✓		*		*		✓	Climbing shrub in forest
Uvaria angolensis Oliv.	✓	✓	*	*		*		Climbing shrub in forest
Xylopia parviflora A. Rich. Benth.			✓	*	*	*		Tall tree in closed forest
Apocynaceae								
Diplorhynchus condylocarpon (Muell. Arg.) Pichon	✓						✓	Tree in woodland
Landolphia owariensis P. Beauv.		*	*	✓	*	✓	*	Large woody liana in forest
Saba comorensis (Bojer) Pichon = *Saba florida* (Benth) Bullock	✓	✓		✓	*	✓	*	Large woody liana in riverine forest
Tabernaemontana pachysiphon Stapf = *T. holstii* K. Schum	✓	✓	*	*	✓	*	*	Forest in moist areas
Voacanga africana Stapf = V. *lutescens* Stapf		*			*		✓	Small tree in secondary forest
Bignoniaceae								
Markhamia lutea (Benth.) K. Schum. = M. Hildebrandtii (Baker) Sprague	✓	✓	*	*				Forest tree
Markhamia obtusifolia (Baker) Sprague	✓						✓	Drier forest and woodland tree
Spathodea campanulata P. Beauv. = *S. nilotica* Seem.	✓	✓	✓					Tree in colonizing and secondary forest
Stereospermum kunthianum Cham.	✓	✓						Woodland and wooded grassland
Boraginaceae								
Cordia africana Lam = *C. abyssinica*	✓	✓					✓	Tree in woodland and colonizing forest
Cordia millenii Bak.	✓	✓	✓					Forest tree
Burseraceae								
Canarium schweinfurthii Engl.		✓	✓		✓	✓		Rare, large, deciduous forest tree
Caesalpiniaceae								
Afzelia quanzensis Welw.	✓					*		Tree in woodland
Bauhinia petersiana Bolle								Small tree in woodland
Brachystegia bussei Harms	✓						✓	Tree in miombo woodland
Brachystegia spiciformis Benth.							✓	Tree in woodland
Erythrophleum suaveolens Guill. & Perr. Brenan		✓				✓	*	Small tree in colonizing forest; canopy tree in closed forest
Julbernardia unijugata					*		*	Tree in forest
Piliostigma thonningii (Schumach.) Milne-Redh.	✓	✓					✓	Small tree in wooded grassland
Senna spectabilis (DC) Irwin & Barneby = *Cassia spectabilis*		✓						Tree planted for shade and fences now naturalized widely in colonizing forest
Celastraceae								
Salacia cerasifera Oliv.	*		*		*	*		Climber frequent in riverine forest
Chrysobalanaceae								
Parinari curatellifolia Benth. subsp. *curatellifolia*	✓	*		*	*	✓	✓	Wooded grassland and forest edge

Combretaceae

Botanical name	G	B	L	N	K	W	U	Notes
Combretum apiculatum Sond.			*	*		*		
Combretum collinum Fresen.	✓							Frequent tree in woodland and wooded grassland
Combretum molle G. Don	✓						✓	Frequent tree in woodland and wooded grassland
Terminalia sericea DC	*			*			✓	Woodland tree
Compositae								
Vernonia amygdalina Del.	*	✓			*	*		Forest edges
Vernonia subuligera O. Hoffm.								Forest edges
Dilleniaceae								
Tetracera potatoria G. Don		✓	*	*	*	*		Small woody climber in colonizing forest
Dipterocarpaceae								
Monotes elegans Gilg	✓						✓	A small to medium-sized tree in woodland
Euphorbiaceae								
Acalypha sp.	*	*			*			Shrub in riverine forest or woodland
Antidesma venosum Tul. = *A. membranaceum* Muell. Arg.	✓	✓	*	*				Shrub or tree in forest or wooded grassland
Bridelia atroviridis Müll. Arg.	✓	✓			*	✓		Shrub or tree in forest
Bridelia micrantha (Hochst.) Baill.	✓	✓	*		✓		✓	Shrub or tree in forest or at forest margins
Croton sylvaticus Hochst. ex Krauss	✓	✓	*	*		*		Colonizing forest; also in older forest
Hymenocardia acida Tul.	✓	✓				*		Shrub or tree in woodland and wooded grassland
Margaritaria discoidea (Baill.) Webster	✓	✓						Tree in forest and at forest margins
Phyllanthus muelleranus (O. Kuntze) Exell	✓	*	*		*	✓		Forest shrub with spines at base of leaves
Phyllanthus reticulatis Poir.								Shrub in forest and riverine areas
Uapaca nitida Muell. Arg.	✓		*	*	*	*	✓	Tree in woodland
Uapaca sansibarica Pax	✓							Tree in woodland
Flacourtiaceae								
Flacourtia indica (Burm. f.) Merrill	✓	✓						Tree in wooded grassland or woodland
Oncoba spinosa Forsk.	✓		*				✓	Shrub or small tree in forest
Phylloclinium paradoxum								Shrub in forest
Scolopia sp								Small tree in (riverine) forest
Guttiferae								
Garcinia buchananii Bak. = *G. huillensis* Oliv.	✓		*	*		*	✓	Forest tree
Harungana madagascariensis Poir.	✓	✓	*	✓	✓	✓	✓	Small tree on forest edges, in wooded grassland and colonizing forest
Psorospermum febrifugum Spach var. febrifugum	✓	✓	✓					Small to medium tree in woodland and wooded grassland
Loganiaceae								
Anthocleista schweinfurthii Gilg.	✓		✓	*		*		Large tree in closed and colonizing forest
Strychnos cocculoides Bak.	✓	*	*	*		*	✓	Wooded grassland or woodland
Strychnos innocua Del.	✓							Wooded grassland or woodland
Malvaceae								
Azanza garckeana (F. Hoffm.) Exell & Hillcoat	✓						✓	Woodland or wooded grassland
Hibiscus sp.	*	*	*	*		*		Shrub along trailsides and in colonizing forest
Meliaceae								
Trichilia emetica Vahl.		*	*	*		*		Riverine forest
Menispermaceae								
Tinospora caffra	✓							Secondary forest or wooded grassland
Mimosaceae								
Acacia albida Del.							✓	Tree in woodland and wooded grassland
Acacia sieberiana DC.	✓	✓						Tree in wooded grassland
Albizia glaberrima (Schum. & Thonn.) Benth. var. *glabrescens* (Oliv.) Brenan	✓	✓	*	*		*	✓	Tree in forest and at forest edges

Botanical name	G	B	L	N	K	W	U	Notes
Mimosaceae, cont.								
Newtonia buchananii (Bak.) Gilb. & Bout.	✓	✓	*		✓			Tree in forest
Parkia filicoidea Oliv.		✓	✓		✓	✓		Tree in forest
Moraceae								
Ficus sur Forssk. = *F. capensis* Thunb.	✓	✓					✓	Tree in forest
Ficus congensis Engl.	✓							Tree in forest
Ficus exasperata Vahl.	✓	✓			✓	✓		Tree in forest
Ficus vallis-choudae Del.	✓	✓					✓	Large tree in (riverine) forest
Milicia excelsa (Welw.) C.C. Berg = *Chlorophora excelsa* (Welw.) Benth. & Hook. f.	✓	✓	✓		✓	✓		Tree with stilt roots in forest
Myrianthus arboreus Engl.	✓	✓	✓	✓				Tree with stilt roots in forest
Myrsinaceae								
Maesa lanceolata Forsk.		✓			✓			Small tree in colonizing forest
Myristicaceae								
Pycnanthus angolensis (Welw.) Warb.		✓	✓	✓	✓	✓	✓	Common tree in closed forest
Myrtaceae								
Psidium guajava L. (alien)			✓			✓		Small tree common on roadsides near the research camp.
Syzygium guineense (Willd.) DC.	✓	✓	*		*			Large tree in closed forest.
Oleaceae								
Schrebera alata (Hochst.) Welw.	✓	✓						Small tree in forest or woodland
Papilionaceae								
Craibia grandiflora		*						Small shrub or tree in forest
Dalbergia boehmii Taub.		*	*	*		*		Tree in forest or woodland
Dalbergia malangensis E.P. Sousa	✓							Climber in forest
Erythrina abyssinica DC	✓	✓	*					Woodland and scattered tree grassland
Mucuna gigantea (Willd.) DC.	*	*						Large woody climber in forest
Pericopsis angolensis	✓			*			✓	Tree in woodland
Pterocarpus tinctorius Welw. var *tinctorius*	✓	*	*	*		*	✓	Tree in woodland
Phytolaccaceae								
Phytolacca dodecandra L'Herit.				*		✓		Riverine or forest edge
Polyglaceae								
Carpolobia alba G. Don	✓			*		✓		Shrub or small tree in forest
Proteaceae								
Faurea speciosa Welw.	*							Small woodland tree
Rubiaceae								
Tarenna pavettoides (Harv.) Sim.		✓						Shrub or small tree in colonizing forest and forest edge
Keetia venosa (Oliv.) Bridson = *Canthium venosum* (Oliv.) Hiern	✓	*	*	*	*	*	✓	Shrub or climber in forest
Multidentia crassa Hiern								Shrub or small tree in woodland or wooded grassland
Mussaenda arcuata Lam. ex Poir.	✓	*	*	*				Shrub or climber in wooded grassland or at forest edges
Oxyanthus sp.		*	*		*	*		Forest or woodland shrub
Pavetta tarennoides S. Moore		*	*		*			Shrub or small tree in forest
Psychotria peduncularis (Salisb.) Steyerm.	*	✓	✓					Understorey shrub in closed and colonizing forest.
Rothmannia manganjae (Hiern.)	*	*	*	*	*	*	*	Shrub in forest.
Rytigynia sp.	*	*				*		Shrub or small tree in colonizing forest or wooded grassland near forest
Rutaceae								
Citrus limon L. N.L. Burm. (alien)								Exotic tree in the area of the research camp; rare in colonizing forest
Clausena anisata (Willd.) Hook. f. ex Benth.		✓						Shrub or small tree in colonizing forest
Toddalia asiatica (L.) Lam.	✓	✓						Thorny climber or scrambling shrub in colonizing forest

Botanical name	G	B	L	N	K	W	U	Notes
Sapindaceae								
Allophylus congolanus Gilg.	✓	*		*		*	✓	Forest climber
Blighia unijugata Bak.	✓	✓	*	*	*	*		Forest tree
Lecaniodiscus fraxinifolius Bak.	✓		*			*		Tree in secondary forest and woodland
Paullinia pinnata L.				*				Climbing shrub in colonizing forest and forest edge
Zanha golungensis Hiern.	✓	✓						Tree in forest
Sapotaceae								
Afrosersalisia cerasifera (Welw.) Aubrev.	✓	✓			*			Tree in closed forest
Mimusops bagshawei S. Moore		✓						Tree in forest, often in moist areas
Sterculiaceae								
Dombeya rotundifolia (Hochst.) Planch.	✓	*						Tree in wooded grassland
Pterygota macrocarpa K. Schum.								Forest tree
Sterculia quinqueloba (Garcke) K. Schum.	✓	*	*					Medium to large tree in woodland
Sterculia tragacantha Lindl.	✓			✓	✓	✓		Tree in forest
Tiliaceae								
Grewia forbesii Harv. ex Mast.				*	*	*	*	Shrub, small tree or climber
Grewia mollis Juss.	✓	✓						Large shrub or small tree
Grewia platyclada K. Schum.	✓							Shrub or climber
Ulmaceae								
Trema orientalis (L.) Blume	✓	✓		*	✓	✓		Tree in colonizing and secondaryforest
Verbenaceae								
Clerodendrum umbellatum	*	*		*		*		Forest shrub or small tree
Clerodendrum schweinfurthii Guerke								Forest shrub or small tree
Vitex doniana Sweet	✓	✓	*	✓		*	✓	Deciduous woodland tree
Vitaceae								
Cissus petiolata Hook. f.	✓	✓	*	*	*	*		Climber in (riverine) forest
Rhamnaceae								
Ziziphys mucronata Willd.	*							Shrub or small tree in wooded grassland
MONOCOTYLEDONEAE								
Agavaceae								
Dracaena reflexa Lam. var. *nitens* Bak.	✓	*	*	*	*	✓		Evergreen forest shrub
Araceae								
Culcasia falcifolia Engl.		*		*	*			Herbaceous climber in closed forest; seen in wet areas
Marantaceae								
Marantochloa leucantha (K. Schum.) Milne-Redh	✓			✓	✓	*		Forest herb, widespread in colonizing and most secondary forest
Palmae								
Elaeis guineensis Jacq. (alien)	✓		✓	✓				Cultigen; numerous in areas of old homesteads
Phoenix reclinata Jacq.								Forest palm, frequent along streams
Smilacaceae								
Smilax kraussiana Meisn.	✓	*	✓	✓		✓		Thorny climber in colonizing forest
Zingiberaceae								
Aframomum alboviolaceum (Ridley) K. Schum.	*	✓	*	✓	*	*		Herb in wooded grassland
Aframomum mala (K. Schum.)		✓	*					Herb in colonizing and secondary forest
Costus afer Ker-Gawl	✓		✓	✓	✓	✓		Herb on river banks