# Herbaceous vegetation in different forest types in the Lopé Reserve, Gabon: implications for keystone food availability

L. J. T. WHITE[1,2], M. E. ROGERS[1], C. E. G. TUTIN[3,4], E. A. WILLIAMSON[5] and M. FERNANDEZ[3,4]

[1]*Institute of Cell, Animal & Population Biology, Scottish Primate Research Group, University of Edinburgh, Edinburgh EH9 3JT, UK,* [2]*NYZS—The Wildlife Conservation Society,* [3]*Centre International de Recherches Médicales de Franceville, BP 769, Franceville, Gabon,* [4]*SPRG, Department of Biological & Medical Sciences, University of Stirling, UK,* [5]*SPRG, Department of Psychology, University of Stirling, UK*

## Summary

The density of herbaceous plants in the families Marantaceae and Zingiberaceae was measured in different forest types within the Lopé Reserve, Gabon, to ascertain their distribution and availability as food for primates and elephants. Stem densities were measured in five sites with different logging histories and tree species composition. Data from a permanent five-kilometre transect at each site showed that densities varied widely between sites. It was also found that the phenology of fruit and leaf production varied both in different seasons and different forest types. It is suggested that differences in the stem densities of these plants can be explained in the Lopé Reserve by a model involving progressive savanna recolonization, and that the wide variations found must have profound implications for the past and present ranging behaviour of the animals which use them as keystone foods.

*Key words:* elephants, gorillas, herb density, Marantaceae, Zingiberaceae

## Résumé

Dans différents types forestiers de la Réserve de Lopé, au Gabon, on a mesuré la densité des plantes herbacées de la famille des Zingiberaceae et de celle des Marantaceae pour déterminer leur distribution et la disponibilité de nourriture pour les primates et les éléphants. On a mesuré la densité des pousses à cinq endroits où les coupes d'arbres et la composition des espèces d'arbres sont différentes. Les données provenant de transects permanents de 5 kilomètres, à chaque emplacement, ont montré que la densité varie fortement entre les sites. On a aussi trouvé que la phénologie de la production de fruits et de feuilles varie en fonction et des saisons et des différents types forestiers. On suggère que les différences de densité des pousses de ces plantes pourraient s'expliquer, dans la Réserve de Lopé, par un modèle qui implique une recolonisation progressive de la savane, et que les grandes variations constatées devraient avoir de profondes implications dans la distribution passée et présente des animaux qui les utilisent comme nourriture de base.

Correspondence address: Dr E. Rogers, ICAPB, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK.

**Introduction**

Plants belonging to the families Marantaceae (arrowroot) and Zingiberaceae (gingers) are a major component of the understorey in certain tropical African forests, to the extent that 'Marantaceae Forest' is a recognized forest type in some areas (e.g. Koechlin, 1964; Letouzey, 1968; Rogers & Williamson, 1987; de Foresta, 1990; Maley, 1990; Swaine, 1992; White, 1992).

Several species of Marantaceae and Zingiberaceae provide important food items for apes (*Gorilla gorilla* Geoffroy and *Pan troglodytes* (Blumenbach) (L.), mandrills (*Mandrillus sphinx* (L.)) and elephants (*Loxodonta africana* (Blumenbach)) in the forests of Central Africa (Jones & Sabater-Pi, 1971; Kano, 1983; Badrian & Malenky, 1984; Kano & Mulavwa, 1984; Hoshino, 1986; Rogers & Williamson, 1987; Carroll, 1988; Malenky & Stiles, 1991; Wrangham *et al.*, 1991 and 1993; White, Tutin & Fernandez, 1993). In the Lopé Reserve in Gabon, young leaves and pith of five species, *Aframomum* sp.? nov. (Zingiberaceae), *Haumania liebrechtsiana*, *Megaphrynium velutinum*, *M. macrostachyum* and *Hypselodelphys violacea* (Marantaceae) were eaten throughout the year by lowland gorillas (*Gorilla g. gorilla* (Savage & Wyman)) and chimpanzees (*Pan t. troglodytes* (Blumenbach)) (Rogers *et al.*, 1990; Williamson *et al.*, 1990; Tutin & Fernandez, 1993a). When fruit was scarce, both species of ape at Lopé increased their consumption of these foods. In addition, gorillas ate large quantities of the aquatic Marantaceae, *Marantochloa cordifolia*, but only during the annual dry season when fruit was scarce (Rogers *et al.*, 1988; Tutin *et al.*, 1991). Parts of 14 other species of Marantaceae and Zingiberaceae were eaten less frequently (Williamson *et al.*, 1990; Tutin & Fernandez, 1993a), but the five species named above were amongst the keystone foods of the apes at Lopé; that is, they play prominent roles in sustaining apes through periods of food (i.e. fruit) scarcity, and are reliably available all year (Terborgh, 1986). As well as providing crucial foods, 62% of gorilla night nests (*N*=2435) were built using one or more of these species as nesting materials (Tutin *et al.*, in press).

Other authors have cited species of Marantaceae and Zingiberaceae as keystone foods for bonobos (*Pan paniscus* Schwarz) (Kano, 1983; Badrian & Malenky, 1984; Kano & Mulavwa, 1984; Malenky & Stiles, 1991), chimpanzees (Wrangham *et al.*, 1991) and mandrills (Hoshino, 1986). At Lopé, Marantaceae are an important component of forest elephant diet (*Loxodonta african cyclotis* (Matschie); White *et al.*, 1993), and high elephant densities have been recorded (White, 1992) in comparison to other sites (Fay, 1991). In a study of the density and distribution of western lowland gorillas and forest elephants in southwestern Central African Republic, Carroll (1988) found that densities of both species were particularly high in a forest type characterized by dense herbaceous vegetation, especially plants of the genus *Aframomum* (Zingiberaceae). It has been suggested that the availability of 'abundant' herbaceous foods may have influenced the evolution of social organization in the great apes (Wrangham, 1986) and of terrestriality in African apes (Wrangham *et al.*, 1991); however, because of highly selective feeding behaviour, 'abundance' may be deceptive (Malenky & Stiles, 1991). More information is needed about these plants and their consumers, before their inter-relationships can be understood. In particular, relatively little is known about local variations in the density of herbaceous food

plants and their productivity, and of how this might be related to the ranges of resident mammals.

This paper presents data on the distribution of Marantaceae and Zingiberaceae species in five sites in the Lopé Reserve, Gabon. These data are related to the different forest types in this area (White, 1992), and the implications of variations in densities of arrowroots and gingers are discussed in the context of the diet of browsing mammals, particularly lowland gorillas. Opportunistic data on forest elephant diet are reported elsewhere (White et al., 1993). Other plant families in the understorey vegetation are not considered here, because it is only the arrowroots and gingers which combine dominance in the habitat with importance as food for apes. For convenience the term 'herbs' is used to refer collectively to all species of Marantaceae and Zingiberaceae [others have referred to these plants as 'THV' (terrestrial herbaceous vegetation) e.g. Wrangham, 1986; Rogers & Williamson, 1987].

**Study site**

Research was carried out in the Lopé Reserve, central Gabon, at the Station d'Etudes des Gorilles et Chimpanzés (SEGC) at 0°10′S, 11°35′E and the Société Forestier du Gabon (SOFORGA) logging concession (0°25′S, 11°25′E). Most of the reserve is covered by semi-evergreen lowland tropical rain forest, but there are 300 km$^2$ of savanna and forest–savanna mosaic along its northern and eastern limits (Fig. 1). About 2500–3000 km$^2$ of the forest have been selectively logged at low intensity (1–2 trees ha$^{-1}$; c. 10 m$^3$ ha$^{-1}$ timber), principally for one species, *Aucoumea klaineana* (Burseraceae).

Lopé lies in an area of low rainfall compared to much of Gabon (EDICEF, 1983). Mean annual rainfall at SEGC is 1506 mm (1984–92), although there is considerable inter-annual variation in the amount and distribution of rainfall (Tutin & Fernandez, 1993b). A feature of the annual cycle is a 'major dry season' in July/August, but the timing of its onset and duration vary between years. December–February is generally relatively dry, but a second dry season is not well-defined. Mean relative humidity does not drop below 70%. Temperatures vary little over the year, but both mean monthly minima and maxima are lowest during the major dry season, with a range of 20–23°C and 26–33°C, respectively, over nine years (Tutin & Fernandez, 1993b).

Vegetation in Lopé is a complex mosaic of plant associations. Twenty forest types have been identified in the reserve on the basis of differences in vegetation structure and composition (White, 1992). For the purposes of this paper, these were grouped into the following categories, defined in terms of structure and commonest tree species:

1   **Colonizing forest** (recently colonized savanna), adjacent to savannas, dominated principally by *Aucoumea klaineana* (Burseraceae), *Lophira alata* (Ochnaceae) and *Sacoglottis gabonensis* (Humiriaceae), species which are able to colonize savanna, with *Xylopia* spp. (Annonaceae), *Klainedoxa gabonensis* (Irvingiaceae), *Barteria fistulosa* (Passifloraceae), *Eriocoelum macrocarpum* (Sapindaceae), *Uvariastrum pierreanum* (Annonaceae) and *Elaeis guineensis* (Palmae) also relatively common. The dominant species, which can be tall
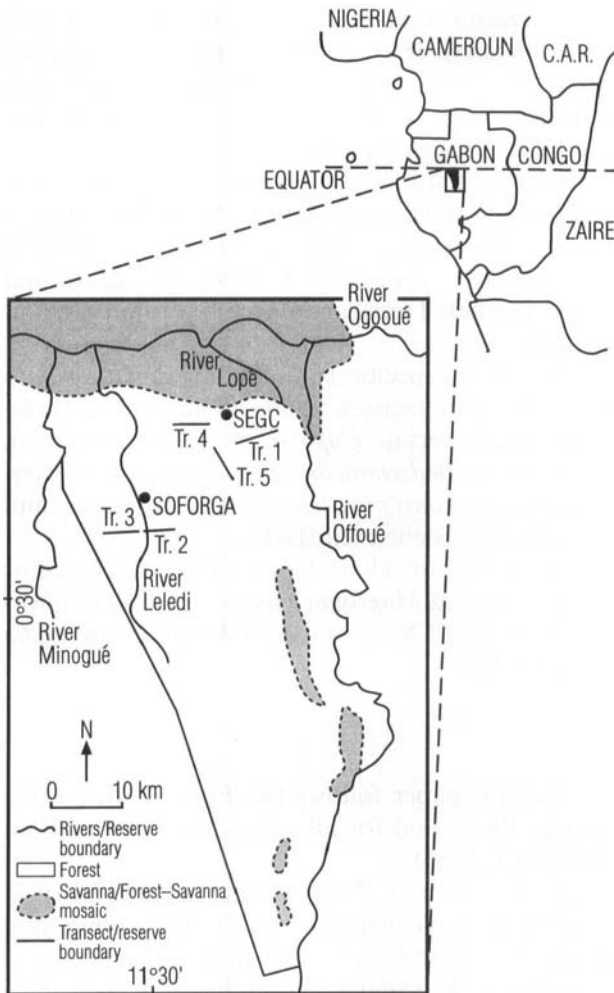
**Fig. 1.** Map of the Lopé Reserve showing the positions of each 5 km transect, and of the Station d'Etudes des Gorilles et Chimpanzés (SEGC) and the Chantier of the Société Forestier du Gabon (SOFORGA).

rain forest trees elsewhere, tend to be relatively short and branch low down. Canopy cover is discontinuous at 30–70%.

2   **Marantaceae forest**, in which the canopy remains discontinuous at about 85%, and consequently light penetrates to the forest floor. Canopy cover is particularly low in the middle storey. The dominant tree species are *Cola lizae* (Sterculiaceae) and *Aucoumea klaineana*, with *Xylopia* spp., *Diospyros* spp. (Ebenaceae), *Pentaclethra* spp. (Mimosaceae) and *Pycnanthus angolensis* (Myristicaceae) relatively common.

3   **Mixed forest**, with increased canopy cover (95%) and species diversity and evenness in comparison to **2**. *Cola lizae* and *Aucoumea klaineana* decrease in dominance and *Scyphocephalium ochocoa* (Myristicaceae), *Santiria trimera* (Burseraceae), *Irvingia* spp. (Irvingiaceae), *Dacryodes* spp. (Burseraceae), *Desbordesia glaucescens* (Irvingiaceae), and *Strombosiopsis tetrandra* (Olacaceae) are characteristic species.

4   **Mature closed canopy forest**, with even greater diversity in comparison to **3**, particularly trees in the families Caesalpiniaceae (e.g. *Paraberlinia bifoliolata*,

*Sindoropsis letestui, Augouardia letestui, Dialium* spp.), Olacaceae (e.g. *Coula edulis, Strombosia* spp., *Strombosiopsis tetrandra* and *Tetrastylidium* sp. nov.), Myristicaceae (e.g. *Staudtia* spp., *Scyphocephalium ochocoa, Coelocaryon preusii*), Sapotaceae (e.g. *Baillonella toxisperma, Gambeya africana*,) and Euphorbiaceae (e.g. *Conceveiba africana*).

5  **Rocky forest** (with rock outcrops and thin soils): dominated by *Diospyros* spp. (Ebenaceae), *Dichapetalum* sp. (Dichapetalaceae), *Scottellia coriacea* (Flacourtiaceae), *Hylodendron gabonense* (Caesalpiniaceae), *Trichilia prieureana* (Meliaceae), *Cassipourea congensis* (Rhizophoraceae) and *Monanthotaxis congensis* (Annonaceae). Trees rarely exceed 30 cm dbh, and their canopies are 10–20 m high.

6  **Marshes and streams** (water), where species such as *Mitragyna ciliata* (Rubiaceae), *Nauclea vanderguchtii* (Rubiaceae), *Anthocleista* spp. (Loganiaceae), *Berlinia* spp. (Caesalpiniaceae), certain *Uapaca* spp. (Euphorbiaceae), some *Rinoria* spp. (Violaceae), certain *Beilschmiedia* spp. (Lauraceae), *Myrianthus arboreus* (Moraceae), *Pseudospondias microcarpa* (Anacardiaceae) and *Marquesia excelsa* (Dipterocarpaceae) occur exclusively.

7  **Disturbed areas:** associated with light gaps along logging roads and tractor trails, dominated by *Macaranga* spp. and *Maprounea membranacea* (Euphorbiaceae), *Xylopia* spp. (Annonaceae), and *Nauclea diderrichii* and *Porterandia cladantha* (Rubiaceae), amongst others.

## Methods

Botanical nomenclature throughout this paper follows the *Flore du Gabon* for families treated to date (Aubréville, 1964), and for all others the *Flora of West Tropical Africa* (Hutchinson & Dalziel, 1954).

A preliminary survey of Marantaceae and Zingiberaceae stem density at Lopé was undertaken in 1984 (Rogers & Williamson, 1987). The commonest species at Lopé were: Zingiberaceae—*Aframomum* sp.? nov., *Aframomum* ? *leptolepis* (J. M. Lock, pers. comm.), *Renealmia cincinnata* and *Renealmia macrocolea*; Marantaceae—*Ataenidia conferta, Halopegia azurea, Haumania liebrechtsiana, Hypselodelphys violacea, Marantochloa cordifolia, Marantochloa filipes, Marantochloa purpurea, Megaphrynium velutinum* and *Megaphrynium macrostachyum*. Collections of botanical specimens have been made and are at the Royal Botanic Garden, Edinburgh, UK (E), and Missouri Botanical Garden (MO), USA. The voucher specimen for *Aframomum* sp.? nov. is Rogers 152 (E). Figure 2 shows a schematic drawing of the life forms of all species encountered. All are free standing, with the exception of *Hypselodelphys violacea* and *Trachyphrynium braunianum*, which trail over and through low-lying vegetation, and *Haumania liebrechtsiana*, which has two growth forms (see below).

During an investigation of the effects of commercial selective logging on rain forest vegetation and wildlife from 1989–91 (White, 1992), data were collected on herbs along five 5-km line transects (fig. 1). Five study sites were established in areas with different logging histories. A 5-km line-transect was cut in each study site, starting from a randomly selected point on the periphery, following a compass bearing crossing the major drainage pattern (cf. Norton-Griffiths, 1978).
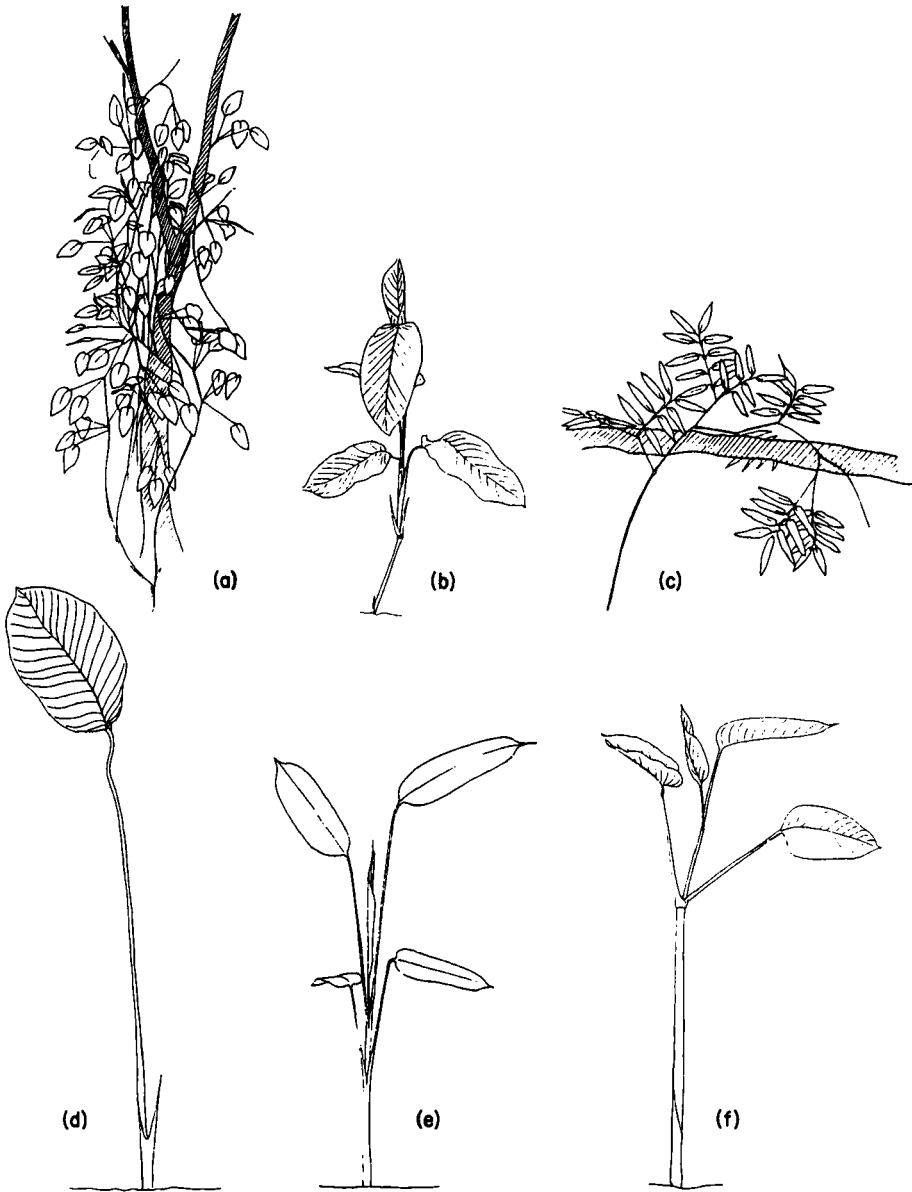
**Fig. 2.** Life forms of Marantaceae and Zingiberaceae at Lopé (a) *Haumania liebrechtsiana* vine tower as found in Marantaceae forest; (b) *H. liebrechtsiana* as it often occurs in Mature forest; *Ataenidia conferta*; (c) *Hypselodelphys* and *Trachyphrynium* spp.; (d) *Megaphrynium* spp.; (e) *Halopegia azurea*; (f) *Marantochloa* spp.; (next page) (g) *Aframomum* spp.; (h) *Renealmia* spp.; (i) *Costus* spp.

Herb density was assessed by counting stems of each species present in 1 m$^2$ quadrats, displaced one metre off the transect, at five metre intervals along each transect, giving a sample of 0·1 ha in each site (cf. Rogers & Williamson, 1987). Each stem was identified at least to generic level, usually from vegetative characteristics.
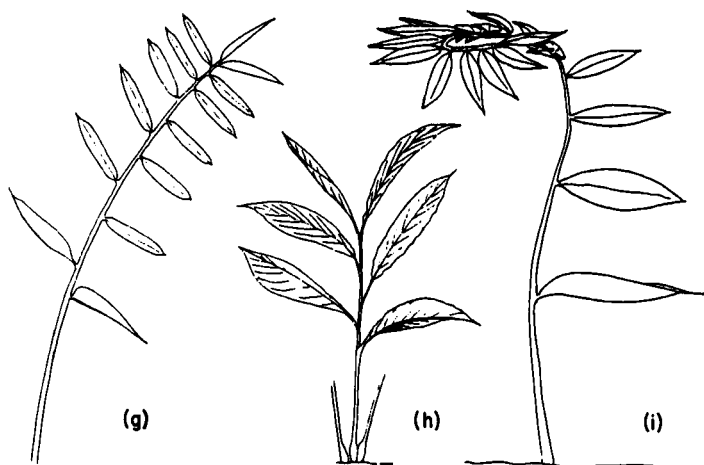
**Fig. 2.** (g)–(i).

Each 50-m section of all five transects was classified by forest type, using the categories described above. Some sections were difficult to assign to a single category since, for example, they might be principally located in Marantaceae forest, but include a stream, a rocky outcrop, or both. In such cases, any 50 m sections containing a perennial stream or swamp were classified as 'Water'. Any area with rocky outcrops, or close enough to be visibly affected, was classified as 'Rocky'. Any section at least part-affected by logging damage was classified as 'Disturbed'. Sections which were intermediate between two or more categories were eliminated from the analysis.

In addition to differences in density, *Haumania liebrechtsiana* exhibited different growth forms in different forest types (Fig. 2a, b). This was most marked between Marantaceae and Closed-canopy forest. To analyse the effect of this on food availability, a sample of 32 plants was collected in Marantaceae forest, by selecting the closest stem at 5-m intervals on Transect 1, and cutting it at the base. These were compared to a sample of 57 stems collected in Closed-canopy forest by scanning a strip about 20 m wide and selecting the stem closest to the centre of the strip from each clump encountered (different sampling methods were chosen due to the large differences in densities between these two vegetation types). The number of leaves on each stem was counted, individual leaves were weighed, and the weight of the remaining stem was recorded.

The phenology of *Aframomum* sp.? nov. and *Megaphrynium* spp. was studied bimonthly on 16 strip transects (50 × 1 m) distributed at random through Marantaceae forest in Site 1. All stems, shoots, young leaves (*Megaphrynium*), flowers and fruits were counted each time. Young leaf production in Site 1 was also monitored bimonthly for 14 months in a separate study on 10 stems of *Haumania liebrechtsiana* and 10 clumps of *Megaphrynium* spp. selected at random in each 100 m along a 1 km transect (Rogers *et al.*, 1988; Williamson, 1988). To compare production in Marantaceae forest with that in Mature forest, young leaves were counted on the nearest clump (*Megaphrynium*) or stem (*Haumania*) to a point 2 m off Transect 1 at 5-m intervals in stretches of Marantaceae forest until 100 *Megaphrynium* clumps (*N*=891 stems) or

**Table 1.** Stem densities of herbs in different forest types

| Family/species<br>[No. 1 m² quadrats.] | Stem density (stems ha⁻¹)/Vegetation category | | | | | | |
|---|---|---|---|---|---|---|---|
| | Colonizing [440] | Marantaceae [390] | Mixed [1180] | Mature [660] | Rocky [90] | Water [470] | Disturbance [370] |
| Marantaceae | | | | | | | |
| *Ataenidia conferta* | 2159 | 2077 | 0 | 0 | 333 | 1915 | 514 |
| *Halopegia azurea* | 0 | 0 | 0 | 0 | 0 | 10,617 | 0 |
| *Haumania liebrechtsiana* | 8159 | 25,179 | 5915 | 3364 | 8889 | 7553 | 13,865 |
| *Hypselodelphys violacea* | 455 | 1641 | 254 | 121 | 0 | 1383 | 1297 |
| *Marantochloa cordifolia* | 0 | 0 | 0 | 0 | 0 | 9532 | 0 |
| *Marantochloa filipes* | 0 | 820 | 51 | 0 | 333 | 2128 | 1270 |
| *Marantochloa purpurea* | 0 | 0 | 0 | 0 | 0 | 476 | 0 |
| *Megaphrynium* spp.[1] | 15,886 | 25,282 | 772 | 0 | 11,000 | 5574 | 6919 |
| Zingiberaceae | | | | | | | |
| *Aframomum ? leptolepis* | 159 | 26 | 246 | 15 | 0 | 43 | 2649 |
| *Aframomum* sp.? nov | 1182 | 2744 | 0 | 0 | 556 | 681 | 3459 |
| *Renealmia cincinnata* | 341 | 77 | 35 | 106 | 0 | 383 | 378 |
| *Renealmia macrocolea* | 227 | 1718 | 0 | 0 | 1222 | 953 | 270 |

[1]Principally *M. velutinum* and *M. macrostachyum*. Nomenclature follows Koechlin (1964) and J.M. Lock (pers. comm.).

100 *Haumania* stems had been sampled. Closed-canopy forest was sampled on Transect 4, and contained no *Megaphrynium* spp. *Haumania* young leaves were counted on the nearest 100 stems as they were encountered along the transect, since their density is far lower in this forest type.

Consumption of the fruits of these herbs by gorillas and chimpanzees has been monitored continuously since 1984 by means of faecal analysis (Tutin & Fernandez, 1993a; Williamson *et al.*, 1990); and consumption of young leaves and pith by gorillas has been studied by counting feeding remains on trails (Rogers *et al.*, 1990). Herb parts referred to below as 'important' foods are those that dominate the diet on a regular or irregular basis and influence ranging patterns (Tutin & Fernandez, 1993a). Weights of leaf and pith consumed were estimated by comparison between items processed by gorillas and whole items of similar size. Techniques used for the nutritional analysis of food items were described in Rogers *et al.* (1990). Consumption of herbs by elephants has not been quantified, but qualitative data are given in White *et al.* (1993).

## Results

### Stem densities at different sites

Dramatic differences in the densities of different herb species were found between habitat types. Table 1 gives the densities of common Marantaceae and Zingiberaceae species in each vegetation type. Marantaceae forest had the greatest herb densities (hence the assigned name), particularly of *Haumania liebrechtsiana*, *Hypselodelphys violacea*, *Megaphrynium* spp., *Aframomum* sp.? nov. and *Renealmia macrocolea*. *Haumania liebrechtsiana* and *Megaphrynium*

| Table 2. Characteristics of *Haumania liebrechtsiana* in Marantaceae and Closed canopy forest | Habitat type | Mean stem weight (g) | Mean no. leaves/stem | Mean leaf weight (g) |
|---|---|---|---|---|
| [1]All differences statistically significant: Mann–Whitney U-test, P<0·0001 in all cases. | Marantaceae Forest[1] | 190·8 (N=32) | 25 | 2·5 (N=789) |
| | Closed canopy forest | 30·4 (N=57) | 9 | 1·4 (N=522) |

spp. both reach densities of over 25,000 stems ha$^{-1}$, although when comparing the relative abundance of these species it should be remembered that they have different growth forms: *Haumania liebrechtsiana* stems may have over 100 leaves, whilst each *Megaphrynium* stem is tipped by a single leaf (see Fig. 2). Colonizing forest had intermediate herb densities, whilst Mixed and Mature closed canopy forest, which had increased canopy cover, had progressively fewer herbs.

Halopegia azurea, Marantochloa cordifolia and Marantochloa purpurea were restricted to sections containing permanent water, and Marantochloa filipes was more commonly found close to water, although it did not occur in water. Actual densities for the three aquatic species in marshes or along streams were higher, since not all 10 quadrats in a 50-m section in this vegetation category were necessarily affected. If only individual quadrats located in marshes are considered, localized densities for *Halopegia azurea* and *Marantochloa cordifolia* were up to 635,000 and 340,000 stems ha$^{-1}$ respectively (see also Rogers & Williamson 1987). *Trachyphrynium braunianum* (Marantaceae) was locally common along the banks of some larger streams in Marantaceae forest, but was not recorded on transects. *Aframomum* sp.? nov. and particularly *Aframomum* ? *leptolepis* were found at elevated densities in areas affected by logging (roads, skidder trails and gaps). Rocky forest was located exclusively within Colonizing and Marantaceae forest, and therefore herb densities in this vegetation type should be compared to those habitats only, and are well below densities in Marantaceae forest.

In Marantaceae forest, *Haumania liebrechtsiana* stems were often lianescent, forming dense tangles and vine towers. In Closed-canopy forest it tended to be smaller and free-standing. Table 2 illustrates this difference (see also Fig. 2), showing that *Haumania liebrechtsiana* stems in Marantaceae forest were significantly heavier, had significantly more leaves and that the leaves were heavier (larger). In fact, the largest individual stem collected in Marantaceae forest weighed as much as all stems (N=57) from Closed-canopy forest combined.

### Herb density and food density

*Aframomum* sp.? nov. fruit is an 'important' food (see Methods) of both gorillas and chimpanzees, while fruit of other *Aframomum* and *Megaphrynium* species and immature seeds of *Haumania liebrechstiana* and *Hypselodelphys violacea* are eaten less frequently (Williamson et al., 1990; Tutin & Fernandez, 1993a). Peak fruiting periods corresponded to the annual peak in overall fruit availability in Lopé in February–March (see Tutin et al., 1991).

Vegetative parts (stem pith and/or developing leaves) of *Aframomum* spp., *Megaphrynium* spp., *Haumania liebrechstiana* and *Hypselodelphys violacea* were

eaten throughout the year by gorillas and chimpanzees at Lopé (Rogers *et al.*, 1990) and are 'important' foods. The pith and developing leaves of *Marantochloa cordifolia* are an 'important' food for gorillas during the annual dry season but are eaten rarely at other times of year (Williamson *et al.*, 1990; Tutin *et al.*, 1991). Vegetative parts of *Marantochloa purpurea* and *Halopegia azurea* are also eaten by gorillas during the dry season but infrequently and in small amounts. None of the aquatic Marantaceae are eaten by chimpanzees, perhaps because of their general avoidance of water (Tutin *et al.*, 1991). The pith of *Renealmia* spp. is eaten occasionally by both species of ape, and gorillas eat it more frequently during the dry season.

Feeding on the vegetative parts of all of these herbs is highly selective. Hands, teeth and lips are used to extract the tender pith, or non-emerged developing leaves, from the tough outer sheath which is discarded. Young leaves of Marantaceae are plucked and only the pale-coloured basal portion of the leaf with the petiole, or in the case of more-developed leaves, only the pale base of the petiole, are eaten. This selective feeding results in an average of only 18% ($N=30$) of the wet weight of *Aframomum* stems being ingested, and 14% ($N=65$) of the wet weight of young *Haumania* leaves. Rogers *et al.* (1990) found that eaten parts of both stems and leaves contained significantly more protein and less fibre than the rejected parts. Processing is rapid and hundreds of stems and leaf parts can be consumed when apes feed in dense thickets of herbs. These herbaceous foods are also harvested opportunistically during movement through the forest and are processed without interrupting travel.

Phenological data on *Aframomum* sp.? nov., *Megaphrynium* spp. and *H. liebrechtsiana* have shown that availability of fruit and young leaves varies through the year and between years. Productivity of young leaves of the two Marantaceae species in Marantaceae forest peaked in November and May (wet seasons) (Rogers *et al.*, 1988; Williamson, 1988). Maximum fruit and young leaf production so-far recorded in a peak month was 247 *Aframomum* fruit, and 1354 *Megaphrynium* young leaves ha$^{-1}$. In terms of wet weight of food, this represents about 8 g seeds+aril per fruit, and about 1·1 g leaf base per young leaf (the distal leaf blade is discarded), totalling 3·4 kg ha$^{-1}$ for these two items. Much the largest bulk of herb food is provided by *Aframomum* pith. The mean wet weight consumed per stem was found to be 13·7 g ($N=30$), which represents about 37·6 kg ha$^{-1}$ extrapolated from stem counts in Marantaceae forest (Table 1). Thus, approximately 41 kg ha$^{-1}$ of fruit, pith and young leaves from these two species of herb were available in Marantaceae forest where they occurred at the highest recorded densities. Other parts of these plants were eaten less frequently, but would add to this figure—for example, *Aframomum* shoots and *Megaphrynium* fruit, mature leaf petioles and pith. Also, stem densities were averaged over a large area, and local densities may be much higher as, for example, for *Aframomum* in light gaps. Leaf production by *Haumania* was less easy to quantify, because of its climbing habit, but although more young leaves were produced per plant than by *Megaphrynium*, each leaf weighed less [mean weight was 2·9 g ($N=65$) cf. 6·8 g ($N=54$) for *Megaphrynium*]. At peak production, an average of 1·76 young leaves/*Haumania* stem were counted, which represents about 18 kg ha$^{-1}$ wet weight of food from young leaf bases in Marantaceae forest. Thus, our calculations suggest that 59 kg ha$^{-1}$ of food may

**Table 3.** Marantaceae young leaf production (kg ha$^{-1}$)

| Year | Dry season | | | Wet season | | |
|------|-----------|----------|------|-----------|----------|------|
| | YL ha$^{-1}$ | kg ha$^{-1}$ | | YL ha$^{-1}$ | kg ha$^{-1}$ | |
| 1984/85 | | | | | | |
| Megaphrynium | 328·7 | 2·2 | | 1264 | 8·6 | |
| Haumania | 8309·1 | 15·3 | | 44,315 | 81·5 | |
| 1989 | | | | | | |
| Megaphrynium | 126·4 | 0·86 | | 707·9 | 4·8 | |
| 1993 | | | | | | |
| Megaphrynium | 225 | 1·53 | (MF) | 1354·4 | 9·2 | (MF) |
| | 0 | 0 | (CCF) | 0 | 0 | (CCF) |
| Haumania | 7050 | 12·97 | (MF) | 25,179 | 46·3 | (MF) |
| | 168·2 | 0·22 | (CCF) | 590·2 | 0·76 | (CFF) |

Abbreviations: YL, young leaves; MF, Marantaceae forest; CCF, mature closed canopy forest. Data collected in 1984/85 and 1989 were all from Marantaceae forest.

be available at any one time from the most eaten parts of three of the commonest herb species in Marantaceae forest during the most productive times of year. This figure will increase as more data are collected on the amounts of other herbaceaous foods eaten by gorillas, particularly from *Marantochloa* spp. in marshes distributed through Marantaceae forest.

During the dry season, production of fruit and young leaves decreases dramatically. *Aframomum* sp.? nov. fruit production is negligible, whereas the production of young leaves of *Megaphrynium* and *Haumania* has been measured at 17% to 25% of peak levels (Table 3). Given this situation, it is not surprising that gorillas turn to items from other locally common species such as *Marantochloa cordifolia*. Production of young leaves also varies considerably between forest types. In 1993, production (kg ha$^{-1}$) of *Haumania* young leaves in Marantaceae forest was found to be 16·7 times greater than in Closed-canopy forest (Table 3), which was due not only to the difference in *Haumania* stem density, but also to a lower number of young leaves per stem and a lower average weight per leaf.

### Nutritional analysis of herb foods

Herb foods provide water, fibre, sugars and protein (Table 4, derived from data in Rogers *et al.*, 1990). In the dry season, when gorillas eat mostly herbs, sugars and hemicellulose may be particularly important as sources of carbohydrate, because the succulent fruits eaten during the rest of the year are not available. *Aframomum* clumps vary in the sugar content of their pith (Rogers, unpublished data), but initial analyses have suggested that pith has a higher sugar content in the dry season. In June, the mean % dry weight water-soluble carbohydrate was 16·6% ($N=4$ clumps), compared to 8% ($N=5$ clumps) in January. Another significant feature of herb foods may be that they generally have low concentrations of tannin in stems and young leaves, which thus might dilute the effects of eating high-tannin fruits (Table 4; Rogers *et al.*, 1990). Zingibers contain

**Table 4.** Nutritional analysis of herbaceous foods

| Food item | H₂O | CP | WSC | CL | ADF | TP | CT |
|---|---|---|---|---|---|---|---|
| Fruit | | | | | | | |
| *Aframomum* aril | 88·9 | 3·8 | 36·4 | 2·1 | 4·8 | 0·3 | 0·0 |
| *Megaphrynium* aril | ND | 12·8 | 28·3 | 9·7 | 16·2 | 0·0 | 1·3 |
| *Haumania* seed | 77·0 | 10·0 | 3·3 | 1·3 | 25·1 | 3·1 | 11·0 |
| *Hypselodelphys* seed | 43·1 | 13·1 | 2·3 | 1·1 | 23·8 | 2·2 | 6·8 |
| Leaves | | | | | | | |
| *Haumania* YL | 87·3 | 22·2 | 0·2 | ND | 35·6 | 1·2 | 0·0 |
| *Megaphrynium* YL | 88·5 | 17·7 | 0·4 | 1·3 | 33·8 | 0·4 | 0·0 |
| Pith | | | | | | | |
| *Aframomum* | 82·5 | 7·1 | 10·6 | 0·8 | 34·8 | 1·4 | 5·7 |
| *Renealmia* | 59·6 | 3·1 | 20·3 | 1·3 | 54·4 | 0·4 | 0·1 |
| *Marantochloa* | 89·6 | 5·8 | 4·0 | 0·8 | 44·9 | 0·8 | 1·8 |

Abbreviations: CP, crude protein; WSC, water-soluble carbohydrate; CL, crude lipid; ADF, acid-detergent fibre; TP, total phenols; CT, condensed tannins; ND, not done.

terpenes, but these do not apparently deter feeding by mammals, and, if human consumption is any guide, may add to their attractiveness as food. Ginger terpenes may incidentally provide protection against helminth infections (Sofowora, 1982).

## Discussion

### Forest composition

Occurrence of dense stands of plants in the families Marantaceae and Zingiberaceae in African rain forests has been variously attributed to: association with permanent water (e.g. Rogers & Williamson, 1987; Wrangham *et al.*, 1993); forest disturbance (Calvert, 1985; Carroll, 1988); savanna recolonization (Letouzey, 1968; de Foresta, 1990; White, 1992); fire (Swaine, 1992; Hawthorne, in press); and elephants (Calvert, 1985; Guillaumet, 1967); although in some central African forests there is no obvious explanation for their occurrence (D. Harris, Central African Republic, pers. comm.). In Lopé some species of Marantaceae occurred exclusively or were more often found close to water, whilst *Aframomum* spp. were more abundant in areas where logging had opened up the canopy.

None of these factors, however, can account for the marked differences in herb density between other vegetation types. White (1992) discussed the history of vegetation in Lopé with respect to prehistoric climatic changes, and concluded that differences in forest structure and composition could be explained by a model involving savanna colonization. According to this model, much of the Lopé Reserve was covered by savanna vegetation during previous arid climatic phases (e.g. Hamilton, 1982; Maley, 1991 & 1992). When more humid conditions returned, forest vegetation recolonized the savannas. Tree species such as *Lophira alata, Aucoumea klaineana* and *Sacoglottis gabonensis* are able to establish in savanna edge conditions. They form colonizing forest extension that

provides shade, moderating the extremes of temperature and humidity experienced in open savanna. Early colonizing individuals have low, round canopies and branch low down, but successive generations of seedling grow taller and branch higher to escape from the shadow of their predecessors. As more individuals become established, canopy cover increases, and there is a corresponding increase in relative humidity and rates of organic deposition, whilst soil temperatures come to resemble those found within the forest. Soil quality improves, and new species establish themselves in a post-colonizing formation. Increased shade reduces the competitive advantage of grasses and new species of herbs and shrubs appear.

As the process continues and more species establish, conditions become favourable for the growth of herbs such as *Haumania liebrechtsiana, Megaphrynium* spp. and *Aframomum* spp, i.e. Marantaceae forest, characteristic of many savanna/forest areas (Letouzey, 1968; de Foresta, 1990). *Haumania liebrechtsiana* densities increase until it forms a tangled carpet smothering the ground and climbing up to 10 m or more in dense towers that can engulf small trees. This formation may persist for long periods, as the ground cover interferes with establishment of the next generations of trees. Marantaceae forests have characteristic low stocking densities of trees, especially medium-sized trees whose crowns form the middle canopy (Letouzey, 1968; de Foresta, 1990), giving them an open appearance (see photographs in: Letouzey 1968, p. 225; de Foresta 1990, pp. 335) and there are sometimes extensive areas (up to about 1 ha) with few or no trees at all (de Foresta, 1990).

There is a gradual build-up of canopy cover in Marantaceae forest, which results in decreased light levels and a decrease in herb densities, and new tree species invade which are characteristic of Mixed forest. As these become established the succession proceeds towards Mature closed-canopy forest, characterized by increased dominance of the Caesalpiniaceae, Olacaceae and Myristicaceae, and further decreased herb densities. This succession is described in detail in White (1994a).

Areas of Rocky forest were almost exclusively found within Colonizing and Marantaceae forest and were perhaps a product of erosion when savanna vegetation dominated these areas in the relatively recent past (cf. Schwartz *et al.*, 1990). This vegetation type had lower herb densities than Marantaceae forest, and higher densities than Mixed and Mature forest (Table 1), probably due to 'contamination' from surrounding vegetation.

*Herb density and biomass of food available*
The data presented here show that many factors can affect herb density, and significant differences can occur in nearby study sites in response to changes in forest structure and composition. It is Marantaceae forest which provides much larger quantities of essential herbaceous food plants all year at Lopé than any other forest type (Table 1). However, the standing crop biomass of these plants is much greater than the biomass of food available from them, because apes feed selectively and consume only a small proportion by weight of any plant. This reinforces the conclusion of Malenky & Stiles (1992) that apparent abundance of herbaceous food plants may not convert into an equivalent abundance of food, as is more nearly the case for mountain gorilla food plants in the Virungas

(Watts, 1984). There may also be a size effect, in that smaller individuals may not be used as a food source (Malenky & Stiles, 1992; Wrangham *et al.*, 1993). Current data from Lopé suggest that all size classes of developing Marantaceae leaves are used as food by apes, but pith may be selected from a particular size range of stems in both arrowroots and gingers. This, and morphological variation of the sort reported here for *H. liebrechtsiana* (Table 2), will reduce further the actual amount of food available from herbs. Estimates of herbaceous food biomass at Lopé are now lower than those obtained earlier after a limited survey at Site 1 (Rogers & Williamson, 1987), because the latter were based on data from a smaller area where herb densities were relatively high, and because we now have more accurate information on ape feeding habits.

Further reasons for revising our overview of food availability from herbs in lowland forest derive from seasonal and annual variations in productivity. This is well documented for fruit and leaves of trees in primate habitats (e.g. Terborgh 1986), but less attention has been devoted to herbaceous foods of forest primates. It has been shown here that production of new leaves in two species of Marantaceae, both important ape foods, also varies between seasons and years (Table 3). Thus, not only do consumers have to contend with spatial variation in herb food availability in a forest mosaic habitat, but also with temporal variation in food production. Minimal production of new leaves from herbs at Lopé coincides with minimal tree fruit production (Rogers *et al.*, 1988; Williamson, 1988). Nevertheless, high densities of herbs do provide a food source which is particularly important for apes at times of low fruit availability, as experienced annually in the major dry season, or during years with unusually low fruit production (Tutin *et al.*, 1991). Fluctuations in availability of edible parts from herbs must be a key factor in determining ranging at these times. Furthermore, browsing on herbs by mammals may itself affect productivity (Bullock, 1981; Watts, 1987).

Researchers working on the ecology of apes in Africa plan to collect comparative data to assess availability of herbaceous foods in different study sites (Malenky & Chapman, 1992; Wrangham *et al.*, 1993). The data presented here suggest that comparisons between forests in different parts of Africa should be made with caution, for even if comparable techniques are used, the area of forest surveyed may give a limited idea of the extent of habitat variation within the range of a group of apes or elephants, as was the case with the present authors' preliminary data (Rogers & Williamson, 1987). It is now known that all the forest types described here occurred within the known annual range of a group of gorillas (Tutin *et al.*, in press). In Kibale forest, Uganda, herb densities were about an order of magnitude less than those measured at Lopé in 1984, and it was concluded that overall they could not support even one breeding group of gorillas (Wrangham *et al.*, 1993). This paper demonstrates that there are forest types within the Lopé Reserve with a biomass of herbaceous foods as low as or lower than those found in Kibale forest, even though the Reserve as a whole supports many groups of gorillas. This means that future judgements about which habitats might be or have been optimal for apes or elephants should be based on detailed background knowledge of vegetation history and composition covering the whole area under consideration, which should in turn be related to known ranging behaviour.

*Animal densities*

White (1992, 1994b) estimated mammalian biomass along the line-transects used to sample herb density in this study. There were statistically significant differences in encounter rates for several species in two or more sites. The two sites in which Marantaceae forest was the dominant vegetation type had higher densities of both gorillas and elephants, although no statistical differences in mandrill densities could be detected.

Due to the fine mosaic of vegetation types in Lopé, in relation to the comparatively large daily ranges of apes, mandrills and elephants, it is not presently possible to compare densities between habitat types. Ranging patterns of large-bodied mammals, which are able to travel long distances, may be adapted to take advantage of complex vegetation mosaics as found in Lopé, and it may be important that these ranges include a habitat such as Marantaceae forest, containing reliable fallback foods. For example, encounters with mandrills in the SEGC study area, which is dominated by Marantaceae forest, have been noted systematically since 1984 (SEGC, unpubl. data). Mandrills have large annual ranges (Jouventin, 1975) and no groups are entirely resident in the SEGC study area, but over 50% of days when mandrills were known to be present were in July and August, during the major dry season.

If Marantaceae forest is indeed a product of savanna colonization, as is suggested here and by White (1992, 1994a), this vegetation type would have been much more widespread following arid periods in Africa's climatic history, when forests were spreading out from small refugia (cf. Maley, 1990). Today this formation is found principally in central Africa (Letouzey, 1968; de Foresta, 1990; Maley, 1990; White, 1992) and corresponds to the main range of western lowland gorillas (Groves, 1971) and forests in which elephants are, or have been, particularly abundant (e.g. Carroll, 1988; Fay, 1991; Barnes *et al.*, 1993). This suggests that foods provided year round by herbs in Marantaceae forest may have influenced the geographical distribution and densities of these species.

Due to its structure and dense undergrowth, Marantaceae forest is often mis-classified as secondary vegetation, and as such, tends to be assigned low conservation priority. It is, in fact, a vegetation type of great importance to several mammalian 'flagship' species, providing a dependable year-round supply of vegetative foods which may be vital during periods of low fruit availability. Future research and conservation initiatives should consider this vegetation type as a priority.

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