

Fire regimes, floristics, diversity, life forms and biomass in wooded grassland, woodland and dry forest at Gambella, western Ethiopia

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The Gambella Region contains examples of most Sudanian vegetation types found in Ethiopia. Five sites up to 85 km from Gambella town and subject to different fire regimes in wooded grassland, deciduous woodland and dry forest were investigated with regard to the floristic composition, diversity, life forms and biomass of the vascular plants. Exact quantification of the fire pressure is difficult, but it seems likely that fires occur at least once a year in nearly all vegetation, dry forest excepted. Severe fires are found to be associated with low plant diversity. A total of 50 plant families, 94 genera and 135 species were observed in the studied sites (14000 m²); families represented with more than 2 species are Gramineae (Poaceae), Fabaceae (Papilionaceae), Acanthaceae, Combretaceae, Tiliaceae, Convolvulaceae, Cucurbitaceae, Euphorbiaceae, Rubiaceae, Verbenaceae, Vitaceae, Capparaceae, Malvaceae, Mimosaceae, Asteraceae, and Rhamnaceae. The life form spectra of woodlands and wooded grasslands have high frequencies of phanerophytes, hemicryptophytes and geophytes; the frequency of hemicryptophytes, geophytes and therophytes seems to increase with decreasing severity of burning, but low frequencies of all life forms except phanerophytes are found in dry forest. The biomass of the tree and shrub strata seems to be inversely related to the severity of the burning, which is positively correlated with the grass biomass. Size class studies show that large-size trees are almost entirely absent from the most severely burnt sites. Differences in soil conditions, apart from the marked distinction between vertisols and ferralsols, do not seem to play a major role in the determination of the vegetation types. Total protection from fire seems to lead to the development of dry forest and shading out of almost all the grasses, and most of the herbs are replaced with a low number of shade tolerant forest species.

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Introduction

This paper is part of a series dealing with studies of fire susceptible ecosystems across Africa from Senegal to Ethiopia. The field and laboratory work behind these papers has been carried out

during 1996-1999. The project was part of a collaborative research programme involving scientists at a number of institutes at the Faculty of Science, University of Copenhagen (the Geographical Institute, the Botanical Institute, the

Botanical Museum and Library, the Institute of Molecular Biology, and the Zoological Institute), biologists and geographers at the Centre de Suivi Écologique (CSE), Dakar, Senegal, the University of Ouagadougou, Burkina Faso, the University of Ghana, Legon, Ghana, and the Addis Ababa University, Ethiopia. This collaborative programme, called FITES (Fire in Tropical Ecosystems) has been supported by a joint grant for all the groups from the Danish Council for Development Research. The present paper reports on our studies of fire susceptible vegetation in the western Ethiopian lowlands, and the results are seen in a wider African context wherever available material for comparison makes this possible. Other related papers deal with the soil seed bank and above-ground cover of a dominant grass, *Hyparrhenia confinis*, in the area (Menassie Gashaw & Michelsen 2001), and with the effects of experimental fire on plant, soil and microbial biomass and nutrient pools (Jensen *et al.* 2001).

Wooded grasslands, woodlands and forests in the Sudanian Region: definitions

The study sites, situated between 10 and 85 km from Gambella town in the western Ethiopian lowlands fall within the eastern part of the Sudanian phytogeographical region, and the vegetation can be referred to as dry forest, woodland, wooded grassland and various kinds of thicket (White 1983: 102-109). These vegetation types experience pronounced drought for more than three months in each year. In reviews, Menaut (1983) and Menaut *et al.* (1995) have distinguished three principal vegetation types within the Sudanian and Zambezan regions: (1) savanna (in the present paper termed wooded grassland in agreement with White 1983), which has a very open canopy of scattered trees (<70% canopy cover) and large biomass in the stratum of suffrutices, herbs and grasses, enough to allow annual burning during the dry season; (2) woodland, which

has an upper stratum of small or medium sized deciduous trees with a relatively species-poor canopy that covers 70-90% of a sparse woody understorey, a ground cover of grasses, herbs and suffrutescent plants in sufficient density to allow for annual burning; and (3) dry forest, which has a closed or almost closed canopy (cover 90-100%) with several woody strata of more numerous deciduous species and a weak, discontinuous and species-poor grass- and herb-stratum only allowing accidental and rare fires. The trees of the upper stratum of the dry forest proper are typically deciduous (although a facies with predominantly evergreen trees has also been described from other parts of lowland Africa by Menaut (1983)), while the lower woody strata may contain a mixture of evergreen and deciduous species. The canopy of the dry forest proper is often devoid of the dominant canopy species of the woodlands, and the species of the upper and the lower strata of dry forest are often different.

Menaut *et al.* (1995) do not discuss in detail savanna-like vegetation types with very low percentage of canopy cover (savanna grasslands), or types dominated by shrubs (thickets), but such vegetation types almost devoid of trees are described from parts of lowland Africa in Menaut's review of African savannas (Menaut 1983). They exist as edaphic vegetation types in the lowlands, and are also prominent in Afromontane vegetation (White 1983). However, our studies in the Gambella Region do not include these vegetation types, and in the following account we will therefore apply the combined definitions of Menaut *et al.* (1995) and White (1983) for the three terms of the vegetation we have studied: wooded grassland, woodland and dry forest.

Previous descriptions of vegetation types in the western Ethiopian lowlands

On the vegetation map of Ethiopia by Pichi-Sermolli (1957) the vegetation of western

Ethiopia on and below the western escarpment of the Ethiopian highlands consists of “deciduous woodland,” with a mosaic of patches of “bamboo thicket (*Oxytenanthera*)” scattered in the woodland. The areas in the lowlands north and south of the Gambella Region are characterised as “savanna (various types),” while approximately the whole of the Gambella Region is referred to as “xerophilous open woodland.” According to Pichi-Sermolli, the latter is a vegetation type with its main distribution on the eastern side of the Ethiopian highlands, where it refers to a fairly dense type of *Acacia-Commiphora* bushland, especially in Sidamo, Bale, Harar, Somalia and eastern Kenya. In Breitenbach’s elaborate system of Ethiopian vegetation types (Breitenbach 1963), discussed by Friis *et al.* (1982) and Friis & Sebsebe Demissew (2001), the dominant vegetation in the western part of the Ethiopian highlands is referred to as “Lowland-Woodlands”; in the western lowlands north of the town of Asosa (Gonder and Gojam regions) and south-west of the town of Maji (Kefa region) as “Lowland-Savannahs”, while in western Welega, Ilubabor (incl. the Gambella Region), and in western Kefa south west of Maji, as “Lowland Steppe.” We do not find that either of these two systems described the Gambella vegetation adequately.

Friis *et al.* (1982) followed the system for descriptive classification of African vegetation by Greenway (1973) when they referred to the vegetation of the western Ethiopian escarpment and the deep river valleys in Kefa and Ilubabor as “deciduous woodland,” a characterisation also used by White (1983), although the trees in some of these sites are rather widely spaced in relation to the strict definition of woodland. Some of White’s vegetation types are grasslands, which occupy only very small and marginal areas along the border with the Sudan, such as his no. 61, “Edaphic grasslands in the Upper Nile basin”, or his no. 62,

“Edaphic grassland mosaics with *Acacia* wooded grassland”, and his no. 64, “Edaphic grassland mosaics with semi-aquatic vegetation.” The western escarpments and lowlands of Ethiopia on White’s vegetation map are referred to as a fairly uniform 100-200 km broad zone of (no. 29a) “Undifferentiated woodland (Ethiopian type)” which borders almost the whole of the western Ethiopian escarpment from Eritrea in the north to the Boma Plateau south west of the town of Maji, penetrating into the highlands along the major rivers. This zone is widest in the Gambella Region. The westernmost part of the Gambella Region is considered a transition zone indicated as White’s no. 35b “Transition from undifferentiated woodland to *Acacia* deciduous bushland (Ethiopian type)”. The “Undifferentiated woodland (Ethiopian type)” contains according to the descriptive memoir (White 1983: 107) *Anogeissus leiocarpus*, *Balanites aegyptiaca*, *Boswellia papyrifera*, *Combretum collinum*, *C. hartmannianum*, *Commiphora africana*, *Dalbergia melanoxyton*, *Erythrina abyssinica*, *Gardenia ternifolia* (lutea), *Lannea schimperii*, *Lonchocarpus laxiflorus*, *Piliostigma thonningii*, *Stereospermum kunthianum* and *Terminalia brownii*. A note (White 1983: 62) describes the “Transition from undifferentiated woodland to *Acacia* deciduous bushland (Ethiopian type)” as “transition from the edaphic grasslands of the Flood Region of the Nile to the *Anogeissus-Combretum hartmannianum* woodland flanking the Ethiopian Highlands to the east. *Acacia seyal* and *Balanites aegyptiaca* occur throughout except for patches of thornless woodland dominated by *Combretum hartmannianum*, *Sterculia setigera*, *Stereospermum kunthianum* and *Adansonia digitata*.” The few marginal vegetation types (White’s no. 61, 62 & 64) mentioned above are in Ethiopia, as far as we have been able to see, basically only localised vegetation patches, not extensive habitats. But it is quite possible that more extensive areas with such grassland or mosaics

exist further away from Gambella town towards the Nile plains.

Sebsebe Demissew *et al.* (1996) has published a vegetation map of Ethiopia and Eritrea on a small scale. This map attempts to show formations, of which 8 are recognised on the map and described in the text (see Friis & Sebsebe Demissew 2001). The map shows a zone of *Combretum-Terminalia* deciduous woodland throughout the western Ethiopian escarpments and lowlands from approximately the Boma Plateau in the south through the Gambella Region to the western escarpment of Eritrea in the north. Sebsebe Demissew *et al.* (1996) also mentions the dense semi-deciduous lowland forest south of Gambella town, particularly between Abobo and Gog, and refers to the description by Friis (1992).

The broad outline of White's and Sebsebe Demissew *et al.*'s characterisations of the Ilubabor lowland agree well with observations from field trips to areas near the Ethiopia-Sudan border, partly undertaken with Sally Bidgood, Royal Botanic Gardens, Kew, Menassie Gashaw and staff members from the Ethiopian National Herbarium of Addis Ababa from 1973 and onwards. These trips went to the Humera area (northwestern Gonder), the Galabat-Matemma area (western Gonder), the Guba region (western Gojam), the Asosa-Kurmuk-Gizen area (western Welega), and the Dima area (southwestern Kefa), and the Gambella area (western Ilubabor). Indeed, these observations form a small part of the background material for both White's and Edward's maps and descriptions, as appears from acknowledgements in the two works.

Own observations on vegetation in western Ethiopian sites

According to the observations made on these field trips, a mosaic of various types of evergreen and deciduous forest, riverine forest, deciduous woodland, wooded grassland and

grassland covers the western lowlands of Ethiopia. These vegetation types, especially the deciduous woodlands and wooded grasslands, penetrate deeply into the Ethiopian highlands along the deep river gorges. The physiognomy of the vegetation and the floristic composition vary considerably within the lowlands, but patches of vegetation which are floristically very similar can be found on comparable sites throughout the area from the border with Eritrea to the Boma Plateau south west of the town of Maji in south western Kefa. The variation seems to be caused by differences in altitude, local edaphic variation, drainage conditions and fire regimes, rather than a south-north gradient, which runs parallel with increasing latitude, as in West Africa. A complex study of wooded grasslands on rocky slopes and adjacent lowlands in Sudanian vegetation in Northern Nigeria was carried out by Ramsay & de Leeuw (1964, 1965a, 1965b). They found *Combretum*-dominated woodland and wooded grassland on basaltic rocky slopes, together with the following species also found in our area: *Acacia hockii*, *Annona senegalensis*, *Balanites aegyptiaca*, *Crossopteryx febrifuga*, *Zizyphus mauritiana*, *Terminalia laxiflora*, *Anogeissus leiocarpus*, *Maytenus senegalensis*, *Stereospermum kunthianum*, and *Entada africana*. In some cases vicariant species were found in Nigeria and Ethiopia, e.g. *Boswellia dalzielii* (*B. papyrifera* further to the north on the western Ethiopian escarpment, but not in our site), and *Sterculia setigera* (*S. africana* in our site, but *S. setigera* also occurs on the western Ethiopian escarpment). Furthermore, the following species were both found in the Nigerian plots and occur on the western Ethiopian escarpment, but were not found in our sites: *Securidaca longipedunculata*, *Sclerocaria birrea*, and *Pseudocedrela kotschyi*. *Azelia africana* was found in the Nigerian plots and occurs in southern Sudan, but is not known from Ethiopia. On the alluvia clays and sands, Ramsay & de Leeuw (*l.c.*) found the fol-

lowing species also found in our sites: *Acacia senegal*, *Annona senegalensis*, *Anogeissus leiocarpus*, *Balanites aegyptiaca*, *Combretum molle*, *Crossopteryx febrifuga*, *Grewia mollis*, *Lonchocarpus laxiflora*, *Terminalia laxiflora*, and *Zizyphus mauritiana*. Thus, there is great floristic and ecological similarity between the two study areas.

The chief variation in the vegetation of the western Ethiopian lowland is between rocky sites, sites with sandy soils, and sites with impeded drainage and dark vertisols. These major types are covered in the analyses from the Gambella Region in the parts of this paper termed "Description of the five study sites ..." and "Analysis of vegetation data."

There seems to be no striking difference between regularly burned woodland on basaltic rocks and regularly burnt woodland on rocks formed by the basement complex. Dominant in these woodlands are all the trees mentioned above by White (1983: 107) as characteristic of the "Undifferentiated woodland (Ethiopian type):" Open *Balanites aegyptiaca* or *Acacia seyal* wooded grassland is characteristic of large areas in the lowlands along the Barka River (western Eritrea) and in the northern part of the lowlands around the Anghrib River (western Gonder), both areas with seasonal water-logging and the development of vertisols. In Uganda and eastern Sudan such woodlands are typically found in seasonally waterlogged sites (White 1983). Throughout Africa, seasonal waterlogging tends to reduce tree growth and promote the development of grasslands (Michelmore 1939). The Baro Lowlands, which cover the whole of the Gambella Region, carry a mosaic of broad-leaved Sudanian woodlands and wooded grassland with *Terminalia spp.*, local patches of dry semi-evergreen or deciduous forest, and along the rivers narrow bands or patches of riverine forest, riparian scrub and areas of seasonally flooded grassland which locally may be treeless. Thus, a classification of the western Ethiopian lowlands in the

broad categories (29b and 35b) of White (1983), leaving no. 61, 62 and 64 as local variants not shown on the vegetation maps, as Sebsebe Demissew *et al.* (1996) has done, seems to agree best with our observations.

The area around Gambella town studied in more detail in this paper was chosen because it contains a large mosaic of the most extensive examples of fire-prone woodlands and wooded grasslands in western Ethiopia. It is, according to our surveys, typical of comparable lowland vegetation from the Eritrean border to the Boma Plateau south west of the town of Maji, that is the whole of the Ethiopian lowlands within the Sudanian phytogeographical region.

Fire as an ecological factor

For thousands of years, fire has been an important factor in vegetation development in many dry tropical areas, including the Sudanian vegetation zone of Africa. Natural fires have probably always existed. It is likely that natural phenomena like lightning and volcanic activity were the cause of fires in the past, and the general fire frequency was probably considerably lower than now. Lock (1998) has assumed that "... it seems a reasonable hypothesis that the frequency of fire increased when man first began to use fire in Africa (probably 1.0-1.5 Myr BP ...), again when fire could be made, and yet again with the introduction of the safety match." It has been shown that the African wooded grassland flora has characteristic adaptations to burning, for example that awned grass propagules like those of *Themeda triandra*, capable of burying themselves in the soil and hence perhaps an adaptation to grass fires, are a distinctive feature of African grasslands and wooded grasslands (Lock & Milburn 1971). In fact, it can be demonstrated that the frequency of awned species of grasses in the African grassland is higher than in the grassland flora of South America (Lock 1998). It is tempting to

see the effect of increased fire frequency during the evolution of the African grasslands and wooded grasslands in such trends, but much more work is of course still needed to illustrate the fire adaptation in the African savanna flora. Today increasing population pressure and human activity are no doubt the main reasons why fires have become much more frequent, often being an annual occurrence in many places.

Also in the wooded grasslands and woodlands of south-western Ethiopia there has apparently been a general trend towards more frequent fires, presumably causing a more open canopy in the woody vegetation and a more lush ground cover, but this information is only obtained from local informants and our personal general observations and judgement of the development of the area. There are no exact records of fire frequency and extent available, even from recent years. In the years from 1996 to 1999 when this project has been in operation, the tall grass was burnt annually at all study sites situated around the regional capital Gambella, except the dry forest inside the Airport area. However, it was not always 100% of the surface that was burnt in a single fire. According to observations from residents as well as researchers visiting the area on earlier occasions, this pattern has probably been in existence for some time before the beginning of the study period. The following analysis will attempt to point out the effect of fire as one of several factors causing the variation between the sites selected for study in different habitats around Gambella town.

Study sites and methods

Five sites were selected for detailed study in the Gambella Region (Fig. 1). The sites were selected in such a way that they sampled a cline from almost closed dry lowland forests with fine loamy soil through vegetation on the

floodplains near the Alwero and Baro Rivers with a mosaic of finer and coarser loams to open woodland on flat ground far away from the western Ethiopian escarpment with dark brown vertisols to a somewhat sloping woodlands near the western Ethiopian escarpment with a very stony fine loam. The observations of the sites were carried out from October 1996 until December 1998.

The location of the sites was determined with a GARMIN 45 GPS navigator. At each of the five different sites (situated 10 to 85 km from Gambella town), which we believed to have differing severity of fire, 3 replicate plots were established, except at site X where it was only possible to establish two replicates. This location, situated within the area of the local airport, was used as control site for a number of other studies mentioned in the introduction to this paper, since this area was found to be the only one that had enjoyed some protection from fire. This protection was estimated to have lasted for at least 10 years and probably much longer, as suggested by $^{13}\text{C}/^{12}\text{C}$ measurements, because C-3- (mainly trees) and C-4- plants (mainly grasses) discriminate differently against these two isotopes during carbon assimilation. The analysis is further described by Michelsen, Friis, Jensen & Andersson (in prep.). The other 4 sites were judged from a number of subjective indicators (fire scars on trees, charcoal remains, etc.) to suffer increasing fire severity in terms of intensity and/or frequency in the following order: B, A, D and C. Each plot measured 20 by 50 meters. In each plot, all trees and shrubs were identified, mapped and DBH and stem and total height were measured. All grasses and herbs were identified either in the field or collected as voucher specimens and subsequently identified at the National Herbarium in Addis Ababa or at the Royal Botanic Gardens at Kew, England. Plant collection was carried out continuously over the three fire seasons covered by the

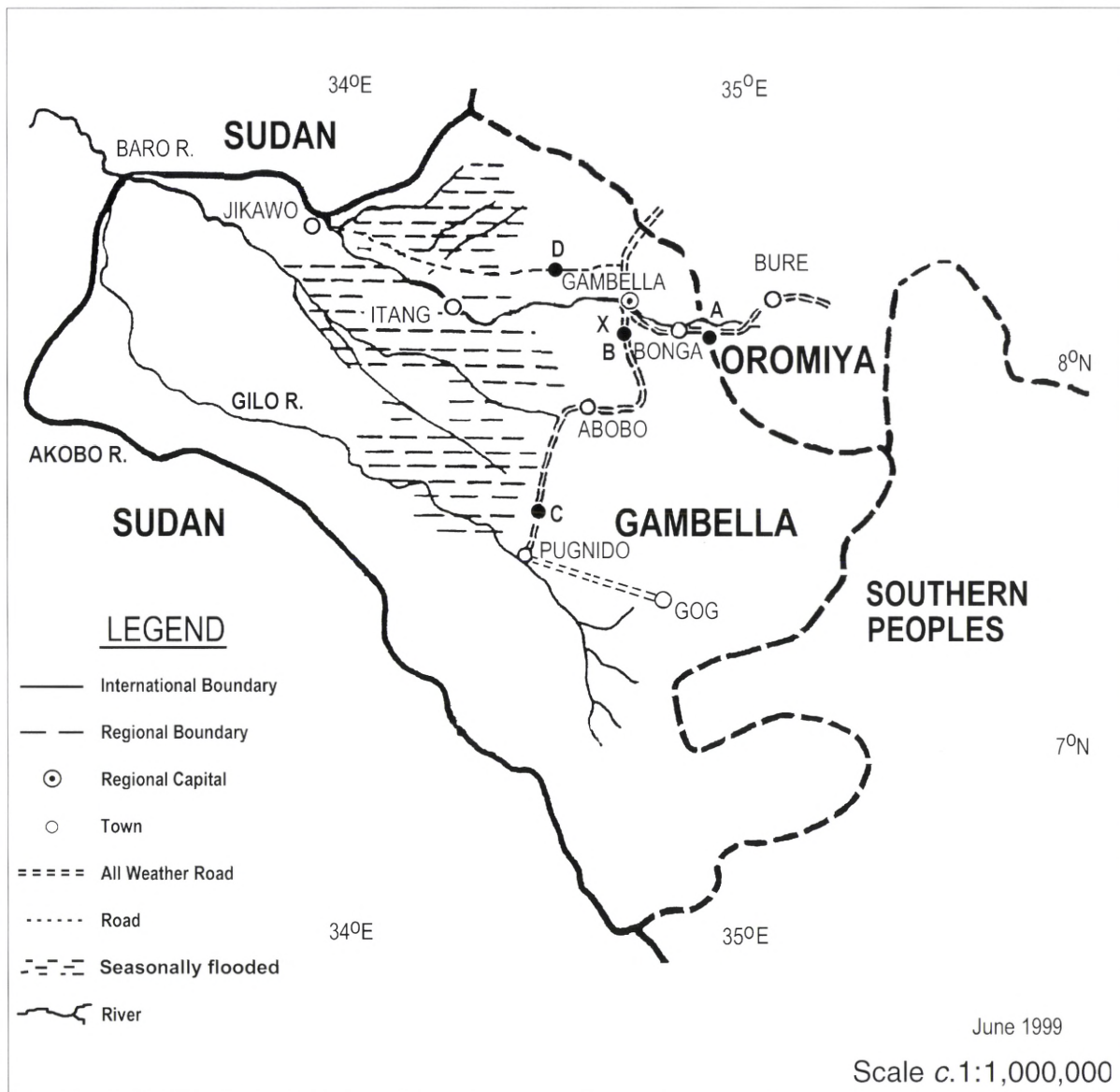


Fig. 1. Map of the Gambella Region. The region borders to the Sudan (west), the Oromiya Region (north-east) and the Southern Nation, Nationalities and Peoples' Region (south east). Redrawn and modified from Solomon Tilahun et al. (eds.), Ethiopian Wildlife and Natural History Society: Important Bird Areas of Ethiopia. A first inventory. Addis Ababa. (1996).

project, and at different times of year, since there was a number of species only occurring during distinct seasons, especially among the geophytes and therophytes.

At the end of the wet season, tree canopy cover was estimated and at the same time plus in the dry season as well as at the beginning of the rainy season, the grass and broad-leaved

herb cover was estimated. In both cases a method of pinpointing with a long stick along 4 lines in the plot was used. The lines and 100 points were applied in a "stratified random" manner. If plants touched the stick when this was put down vertically in the vegetation, this was recorded as one hit. Multiple hits were not recorded. Canopy cover was estimated by recording whether the vertical projection of the stick hit the canopy above. Initial testing of this modified standard method gave very good replicability with variations as low as 1-2%.

Grass and herb biomass was sampled in November 1997 at the end of the rainy season at peak biomass. In each plot 8 randomly located squares measuring 1 x 1 m were harvested, and biomass divided into grasses and broad-leaved herbs. All herb biomass was kept, and the grass biomass harvested was weighed in the field. After finely cutting and mixing of the grass biomass 5 subsamples were taken, weighed and pooled into one. Samples were then air- and sun-dried in the field and later in the oven at 80° C, and the dry weight determined. From these findings, the original total dry weight of the grass samples could be calculated.

Processed satellite data on fire densities were obtained from the archive files of the Global Vegetation Monitoring Unit's FIRE project at Space Application Institute, Ispra. Input data came from AVHRR-sensors on-board the NOAA-11 polar orbiting satellite. This satellite performs 14 complete orbits per day, and maps the entire globe in five visible and infrared bands at a resolution of about 1.1 km at nadir. Data was collected and archived, and image segments from different receiving stations are "stitched" together to produce 14 separate images per day. The fire detection took place during a total of 21 months from April 1992 to December 1993. The product files were produced with the application of a contextual algorithm used for the fire detection, because

such an algorithm can be applied to a global data set without having to be adjusted for different geographical regions. The algorithm chosen is based on work by Prins & Menzel (1992) and Flasse & Ceccato (1996), as reported in Justice & Dowty (1993). The product gives a global picture of vegetation fire densities at a relative scale. The fire data set from Ispra was interpreted in the GIS-programmes ARC-Info and ARC-view at the Institute of Geography, University of Copenhagen.

Data on temperature and rainfall in the study area was obtained from the Ethiopian National Meteorological Institute in Addis Ababa.

The nomenclature and classification of genera and species follow as far as possible the published volumes of the *Flora of Ethiopia and Eritrea* (Edwards & Hedberg 1989; Edwards, Mesfin Tadesse & Hedberg 1995; Hedberg & Edwards 1995; Edwards, Sebsebe Demissew & Hedberg 1997).

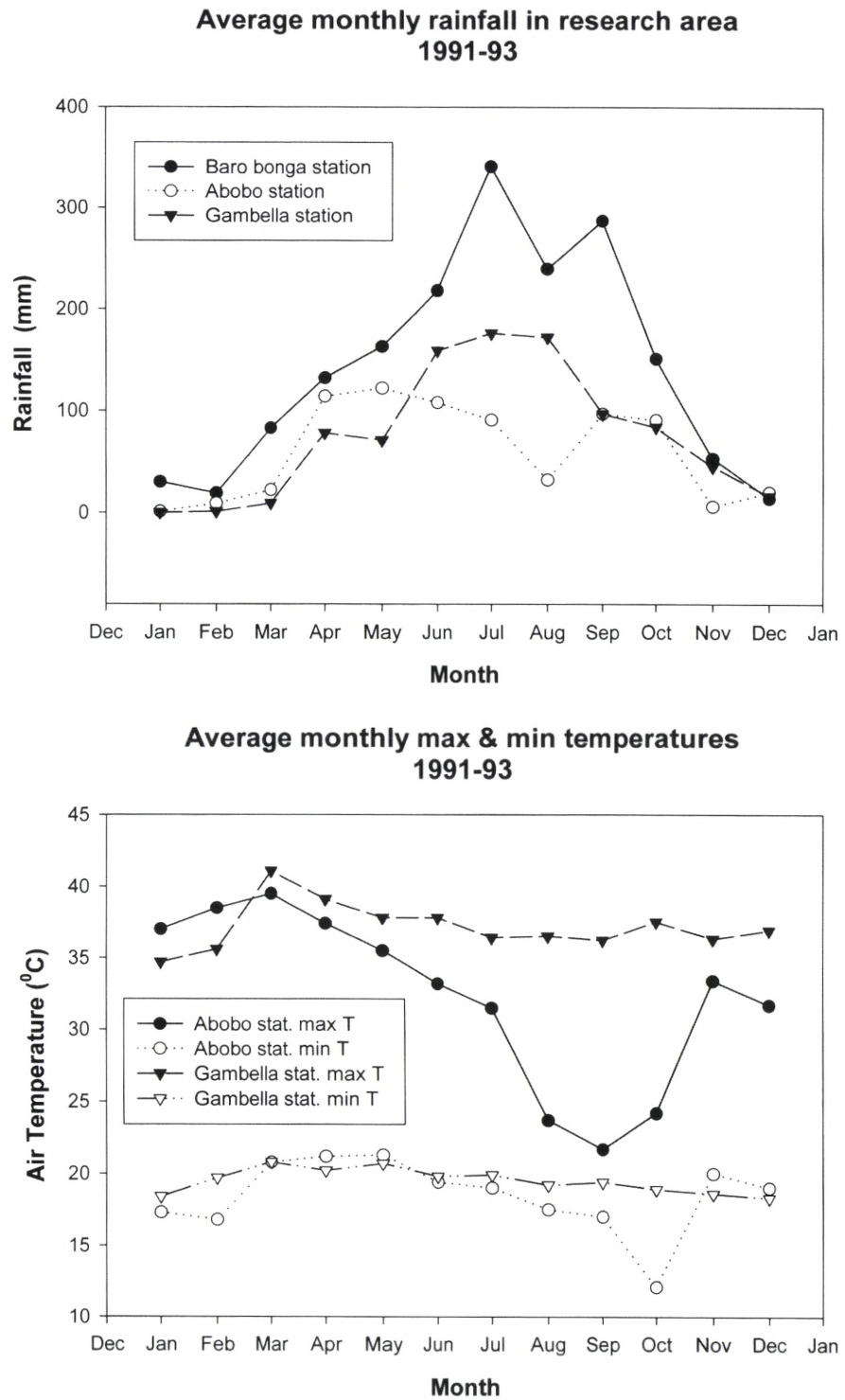
Description of the five study sites: climate, soil and fire

This section of the paper presents an overview of the general observations we have made in the study area, including both our own data and data on climate and fire obtained from elsewhere and analysed here. It also presents descriptions and some general observations on each of the five study sites.

Climate

The altitude of the study area varies between 550 and 650 m a.s.l. It receives an approximate average of 1100 mm rain annually, concentrated in the main rainy season from late May to October, but the variation between sites is considerable (see below). The average monthly rainfall at Gambella town (between site B and X and site D), at Abobo (between site B and site C) and at Baro Bonga (near site A) during the years 1991-1993 is shown in Fig.

Fig. 2. Annual monthly rainfall and maximum and minimum temperatures in the research area 1991-1993. The diagram is based on results from the Ethiopian Meteorological Office in Addis Ababa. Data from the period of our studies was not available.



2, which also demonstrates the considerable variation between the sites. The lowest annual rainfall is recorded at Abobo with approximately 700 mm. The rainfall here shows a tendency to be bimodal, with the highest rainfall in April-June and in September-October. The dry season lasts approximately for 5 months, from November to March. This rainfall distribution is reminiscent of the bimodal rainfall of southern Ethiopia within the Somalia-Masai region (Ethiopian Mapping Agency 1988, map 16). The Gambella station has an annual rainfall of approximately 900 mm. The rainfall is unimodal, with early rain in April and May, high rainfall in June to August, and late rain in September-October. The dry season lasts approximately 5 months, from November to March. By far the highest rainfall is found at Baro Bonga at the foot of the southwestern escarpment of the Ethiopian highlands, with an average annual rainfall of 1730 mm. The rain starts in March-April, reaches its highest values in July-September, and is low again from November. The dry season is therefore approximately 4 months, from November to February. The high rainfall here agrees well with the rainfall higher on the western escarpment, where the highest rainfall in Ethiopia, raising to figures between 2400 and 2600 mm/year, is found in the zone from Gore to Gecha and Mezan Tefari (Ethiopian Mapping Agency 1981, map 21). The latter area at the top of the escarpment also has a different rainfall distribution, with rain in nearly all months of the year.

Observations of monthly minimum and maximum temperatures from the same period exist only from the stations at Gambella town and Abobo, also shown in Fig. 2. The recordings from the Gambella station are very constant throughout the year. The average annual maximum is 37° C, and the average monthly figures vary between 35° and 40° C. The average annual minimum is 19° C, and the average

monthly figures vary between 18° and 21° C. At Abobo the average annual maximum is 32° C, but there is a very notable drop in the average monthly maximum during August, September and October, where the average maximum is below 25° C. The average annual minimum is 18° C, but also here there is a seasonal drop which reach down to 12° C in October.

Geology and soils

The soils are ultimately derived from parental material in the highlands to the east, or from underlying rocks. The tertiary volcanic rocks are restricted to the highlands east of Bure. The western escarpment of the highlands consists of Precambrian granitoids (the basement complex). These rocks can be seen as outcrops (inselbergs) in the lowlands as far west as Gambella town, or even a few isolated hills between Gambella town and Itang (Ethiopian Mapping Agency 1981, Map 6 & 1988, Map 7; personal observations). At altitudes below the escarpment and the inselbergs, the surface geology is indicated as Quaternary or Pleistocene sediments on all the geological maps we have consulted.

The published soil maps of Ethiopia indicate the soil types near the western escarpment in different ways. According to Ethiopian Mapping Agency (1981, Map 13) the soils in the Baro Valley as far as Gambella town are humic cambisols (including site A), while the soils of the plains to the west and south-west are chromic vertisols (including site B, C, D and X). Also according to the Ethiopian Mapping Agency (1988, Map 8) the soils of the sites B, C, D and X are vertisols, while the soil of site A is an orthic Acrisol. We think that this part of the map may be overly simplified, and based on our field observations of soil profiles combined with the chemical analysis recorded in Table 1 we characterise the sites X, A, B and C as more or less similar weathered ferralsols, while the soils of the plains at site D are in fact a vertisol.

Table 1. The soil profile characteristics of the 5 study sites (SOM: soil organic matter)

	X	B	A	C	D
Classification (FAO/UNESCO)	Ferralsol. Surface brown, deeper strata yellowish brown to red	Ferralsol. Brown red to yellow	Ferralsol. Brown to yellowish red	Ferralsol. Yellowish brown	Vertisol. Dark brown to reddish brown
Texture group	Fine/coarse loamy	Fine/coarse loamy	Fine loamy (stony)	Coarse loamy	Fine clayey
Density (g/cm ³)	–				
Top		1.42	1.38	1.56	1.34
Medium		1.56	1.56	1.65	1.74
Deep		1.66	1.69	1.58	1.74
pH (H ₂ O)					
Top	7.0	6.5 ±0.4	6.9 ±0.2	6.8 ±0.3	7.0 ±0.5
SOM (%)					
Top	5.1	3.5 ±0.8	6.2 ±0.9	2.7 ±0.3	16.5 ±0.9
Medium	1.9 ±0.11	1.8	5.8	3.1	16.0
Deep	2.4 ±0.07	2.5	5.4	5.2	15.3
Carbon (%)	–	1.3 ±0.4	1.9 ±0.5	0.9 ±0.2	4.6 ±0.9
Total N (%)					
Top	0.16	0.11	0.16	0.04	0.20
Medium		0.02	0.05	0.02	0.05
Deep		0.02	0.03	0.03	0.06
Total P (%)	0.02	0.01	0.01	0.09	0.09

The latter has the characteristic dark colour of vertisols and is shrinking and cracking during the dry season, as well as being relatively more fertile than the soils at the remaining sites. All the ferralsols are rather sandy, poor in nutrients, and neutral to weakly acid. The soil at site A does not have the very acid reaction characteristic of acrisols. The total nitrogen varies from 0.04% in site C up to 0.2% in the vertisol in site D, and the phosphorus varies from 0.01% in site A and B up to 0.09% in site C and D shortly after fires. The latter two sites are those assumed to have the most severe fires, and the higher P-values here are derived from the ash input, and are seasonal (Jensen, Michelsen & Menassie, in prep.). These N- and P-figures are comparable to those indicated from Zambian woodlands (Trapnell *et al.*

1976). The soil organic matter (SOM) contents varies from 2.7% in the poorest ferralsol in site C to 16.5% in the vertisol of site D. The high organic content here is probably due to the periodic flooding inhibiting decomposition. The annual variation in the soil nutrients is dealt with in further detail by Jensen *et al.* (2001). The field experiments in the area have shown that fire plays a major role in redistributing nutrients between standing dead biomass, soil, soil microbes and plants emerging after fire (Jensen *et al.* 2001).

Fire

In the beginning of the dry season, most of the grass biomass in the vegetation around Gambella town is burned by the local population in a non-systematic way in order to gain access to

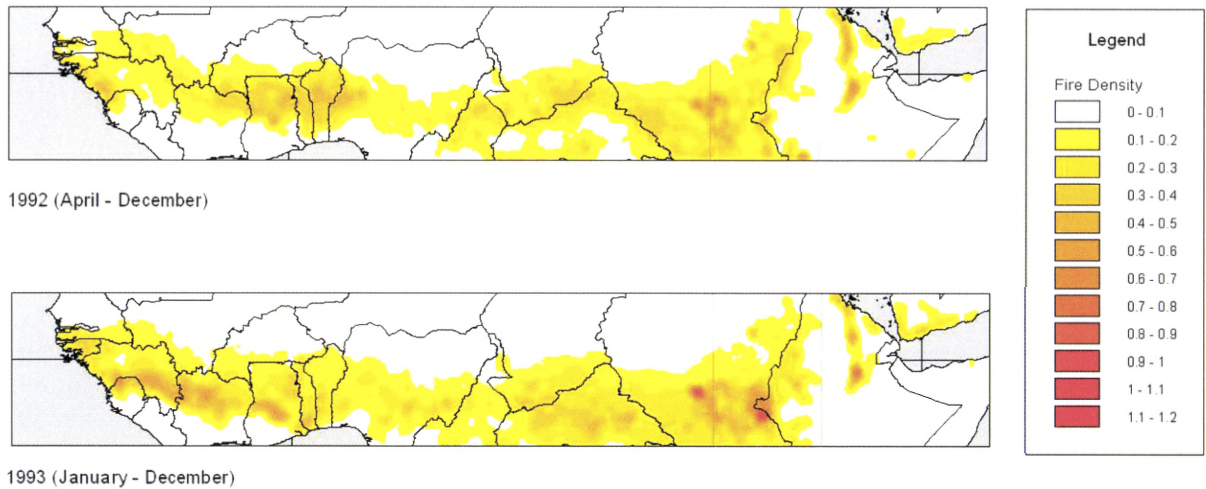


Fig. 3. Fire density across Africa in April-December 1992 and January-December 1993. Fires have been recorded within an area 50 km across; the scores have been marked on the map with a grid size of 0.1 degree. Based on data from the archive files of the Global Vegetation Monitoring Unit's FIRE project at Space Application Institute, Ispra. Produced by Thomas Theis Nielsen, Institute of Geography, University of Copenhagen, under the FITES project. The density scale is relative, and not necessarily comparable between the subsets of data represented in Fig. 3-6.

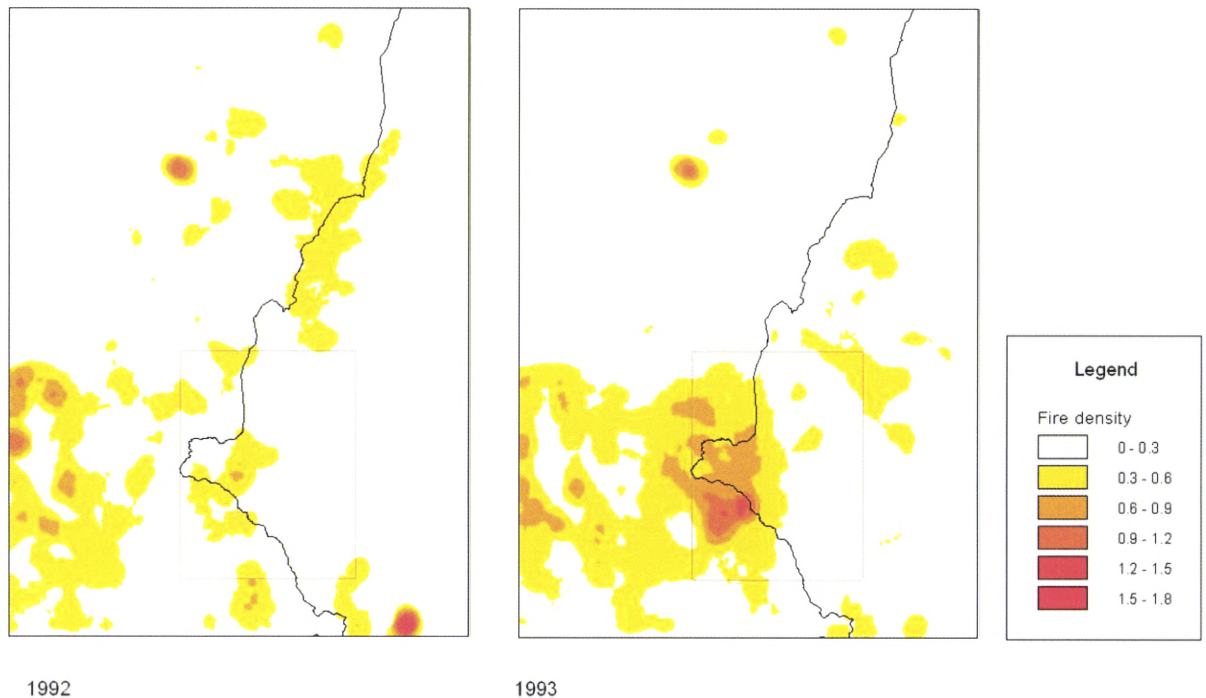


Fig. 4. Fire density of western Ethiopia in April-December 1992 and January-December 1993. Fires have been recorded within an area 25 km across; the scores have been marked on the map with a grid size of 0.01 degree. (Source etc. as for Fig. 3).

the woodland for hunting and for honey and firewood collection. Burning, which can be induced for a wide range of reasons, is done right across Africa from the Atlantic coast to Ethiopia; Fig. 3 shows that the density of fires in various areas in the fire zone across Africa may change somewhat from year to year, but generally the continental pattern is very constant, and the extent of this pattern agrees well with the Sudanian region of White (1983), especially when allowance is made for some overlap with the transition zone between the Guineo-Congolian and the Sudanian regions. This is the zone where the grass biomass is large enough and dries out well enough to produce fierce fires. Fig. 3 also demonstrates that the whole of the western lowlands of Ethiopia have fire densities comparable to the general situation across Africa, and that the areas with intense fires agree with the areas referred to the vegetation types no. 29b and 35b of White (1983), but that the highest densities in Western Ethiopia are found in the Gambella Region. Fig. 4 shows that there is high fire density in the Gambella Region in both the observed years, whereas in the lowlands to the north in the Oromia and Beni-Shangul Regions densities are lower, and it is not necessarily the same areas which burn every year. Fig. 5 has zoomed in on the Gambella Region with increasing resolution of the recording of fire density. Even within the Gambella Region, there seems to be marked variation in distribution and density of fires, although areas along major roads and around towns seem to burn annually. This is particularly notable from the figure to the left, showing the fires recorded from April to December, 1992, in a pattern that is strikingly similar to the location of roads and towns shown on Fig. 1.

Fig. 6 shows the yearly variation in fire density from April 1992 to December 1993. There are already fires in December, both in the Gambella Region and in the deep river valleys

of the adjacent Ethiopian Highlands. The number and density of fires increase during January, February, March and April, whereas the density of fires in May is probably highly dependent on the onset of the rainy season. From July to October, no fires in the Gambella Region have been detected in the data shown in Fig. 6. Also in this illustration of the yearly variation, we can note that fires are most frequent along major transport routes, stressing the anthropogenic nature of most fires. In March and April fires seem to be most frequent along the rivers, probably reflecting a high frequency of people travelling by river in those months.

Description of edaphic conditions and vegetation of the sites

Dry forest: Site X

The densest and most developed vegetation was studied in site X, used as a control site with no signs of recent burning, and located inside the fence surrounding the Gambella Airport (*c.* 8° 08' N, 34° 34' E; *c.* 600 m altitude). The two replica plots were established about 500 m apart. The vegetation formed a dense woody cover with an almost continuous canopy covering 92% or more. The site had, at least according to local verbal reports from the airport staff, not been burnt recently, and it did not burn during the three years of the study; there was rotten wood on the forest floor, and no signs of charcoal or ashes were found during our studies. The soil type was a fine to coarse loamy, brown or yellowish brown to red ferralsol. The highest trees in the canopy were 20-25 m high, with one or two tree strata below and a fairly dense shrub stratum. The canopy contained *Anogeissus leiocarpus*, *Diospyros mespiliiformis*, *Tamarindus indica*, and *Vangueria apiculata*. *Allophylus rubifolius*, *Erythroxylum fischeri*, *Maerua triphylla*, *Meyna tetraphylla*, and *Zizyphus*

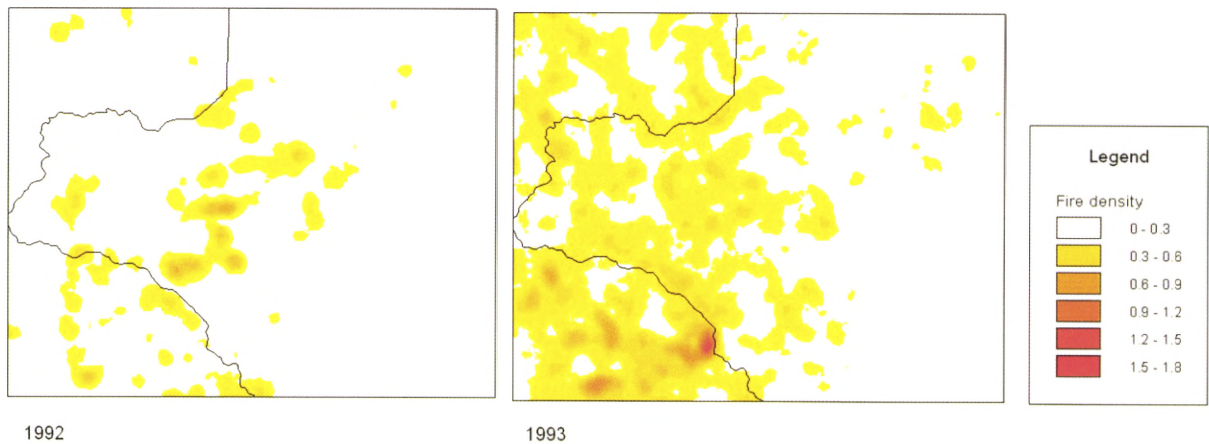


Fig. 5. Fire density of Gambella Region in April-December 1992 and January-December 1993. Fires have been recorded within an area 5 km across; the scores have been marked on the map with a grid size of 0.0025 degree. (Source etc. as for Fig. 3). For position of roads and rivers, compare with Fig. 1.

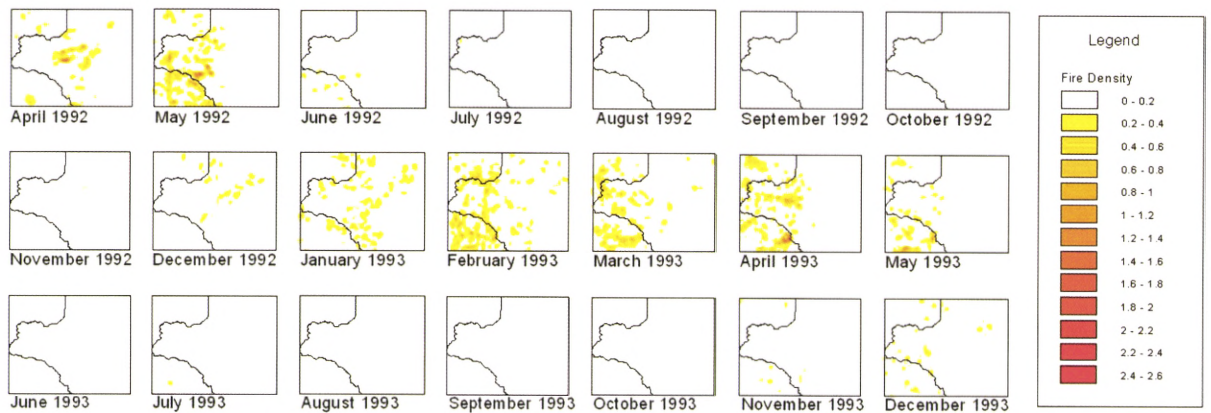


Fig. 6. Monthly fire density of Gambella Region from April 1992 to December 1993. (Source etc. Fig. 3). For position of roads and rivers, compare with Fig. 1.

pubescens occurred in the lower strata. Common shrubs were *Flueggea virosa* and *Harrisonia abyssinica*. Climbers were fairly prominent: *Abrus precatorius*, *Ampelocissus schimperianus*, *Periploca linearifolia*, *Plumbago zeylanica*, *Pyrenacantha kaurabassana*, *Opilia amentacea* and *Dioscorea prehensilis*. There were a number of herbs, but hardly any grasses on the forest floor (the grasses that are present have prostrate rhizomes and are not tufted as in the open vegetation): *Psilotrichum* sp. cf. *P. elliotii*, *Barleria* sp. cf.

B. ventricosa, *Justicia diclipteroides*, *Blepharis maderaspatensis*, *Cyperus subumbellatus* and *Panicum comorense*. The standing volume of the tree trunks and other woody stems was on average 185 m³/ha. The tree stem density was on average 329 stems/ha. The biomass of the ground cover was negligible. The vegetation can be characterised as dry deciduous forest.

Physiognomically, the forest in site X resembles the *Baphia abyssinica*-dominated semi-deciduous forest described by Friis (1992: 28-

29) from the area between Abobo and Gog, but *Baphia* and the emergent, very tall trees are absent from site X. Floristically, the forest in site X is poorer than the *Baphia abyssinica* forest, and would appear to be a transition type between the *Baphia* forest and the dense *Anogeissus* woodland.

Woodland: Site B

The second densest vegetation was studied in site B between 10 and 12 km south of the bridge across the Baro River at Gambella town on the road to Akobo and Pugnido (c. 8° 10' N, 34° 35' E; c. 550 m altitude). Three replica plots were established with two next to each other, one to the east and one to the west of the road, and the last one two kilometres to the south on the east side of the road. The landscape is slightly undulating, with faint shifts between low ridges with coarser sandy soils and lower ground with finer soils in between. The soils can be generally characterised as coarse to fine loamy, brown to red yellow ferralsols. The vegetation forms a fairly dense canopy with approximately 60% canopy cover or occasionally more, with poorly defined and very discontinuous lower woody strata. The grass cover of the site burnt in patches between late November 1996 and the end of January 1997, burnt very early during August-September 1997 and again in November-December 1997. The highest trees in the canopy were 17-20 m high. The tree stratum consisted of *Anogeissus leiocarpus*, *Bridelia scleroneura*, *Combretum collinum* subsp. *binderianum*, *Combretum molle*, *Pterocarpus lucens*, *Terminalia laxiflora*, *Strychnos innocua*, and *Zizyphus abyssinica*. A shrub stratum contained: *Grewia mollis*, *Maytenus senegalensis*, *Acacia senegal*, *Flueggea virosa*, *Gardenia ternata* subsp. *jovistonantis*, and on termite mounds *Harrisonia abyssinica*. The climbers included: *Jasminum streptopus* (which did not develop much beyond a low, climbing shrub in the plots), *Tylosema fassoglensis*, *Vigna ambacensis*, *Ampelocissus schimpe-*

rianus, *Cyphostemma adenocaulis* and *Neorautanenia mitis*. More than 15 species of herbs, partly with woody base, were observed. The grasses were *Pennisetum polystachia*, *Sporobolus pyramidalis*, *Loudetia spp.* and *Hyparrhenia spp.*, especially *Hyparrhenia confinis* var. *nudiglumis*. All these grass species appeared to be tufted perennials, but *Hyparrhenia confinis* var. *nudiglumis* is according to Phillips (1995) a tufted annual. The standing volume of the tree trunks and other woody stems was on average 93 m³/ha. The tree stem density was on average 240 stems/ha. The biomass of the grasses was 4.8 t/ha and of the herbs c. 150 kg/ha. The vegetation can be characterised as woodland.

Woodland and wooded grassland intermediate: Site A

The third densest vegetation was studied in site A located near the western Ethiopian escarpment just west of the foothills (8° 12' N, 34° 57' E; c. 650 m altitude) along the road from Bure to Gambella town about 8 km east of Baro Bonga. Three replica plots were established less than 500 m apart, two north of the road, and one south of the road. The landscape is gently sloping, with much loose coarse gravel or stones on the surface and in between a fine loamy brown to yellowish red ferralsol. The woody vegetation forms an open canopy with 29% cover or more, very variable from place to place. The grass cover of the site burnt before November 1996, and again before January 1997. It burnt again very early during August-September 1997, and again between December 1997 and February 1998. The tree stratum consisted of *Lonchocarpus laxiflorus*, *Pterocarpus lucens*, *Balanites aegyptiaca*, *Combretum collinum* subsp. *binderianum*, *Entada africana*, *Lannea barteri*, *Lannea fruticosa*, *Stereospermum kunthianum*, *Acacia senegal*, and *Zizyphus abyssinica*. The highest trees in the canopy were 10-15 m high. Among these, large individuals of *Sterculia africana* stood out as very large, isolated trees

with a very broad crown which locally could increase the canopy cover well above average. A shrub stratum contained: *Cadaba farinosa*, *Ximenia americana*, *Acacia senegal* and *Flueggea virosa*, and in somewhat protected sites *Harrisonia abyssinica*. The climbers included: *Tylosema fassoglensis*, *Cyphostemma adenocaulis*, *Pyrenacantha kaurabassana*, and *Asparagus scaberulus*. About 5 species of herbs, partly with woody base, were observed. The grasses were *Sporobolus festivus*, *Loudetia* spp. and *Hyparrhenia* spp., especially *Hyparrhenia confinis* var. *nudiglumis*. The standing volume of the tree trunks and other woody stems was on average (a single large individual of *Sterculia africana* excepted) 24 m³/ha; if the single, large *Sterculia* is included, the figure is raised to 56 m³/ha. The tree stem density was on average 160 stems/ha. The biomass of the grasses was 7.0 t/ha and of the herbs c. 30 kg/ha. The vegetation can be characterised as intermediate between woodland and wooded grassland, as the canopy cover is comparatively low for woodland vegetation, and the biomass of the ground cover is comparatively low for wooded grassland.

Wooded grassland: Site C

The fourth densest vegetation was studied in site C located c. 85 km south of the bridge across the Baro River at Gambella town on the road from Akobo towards Pugnido (c. 7° 48' N, 34° 17' E; c. 550 m altitude). All three replica plots were established less than 200 m from each other to the west of the road. The landscape is slightly undulating, with shifts between low ridges with coarser and lower ground with finer loams. The soils can be generally characterised as coarse loamy yellowish brown ferralsol. The vegetation forms a rather open canopy with less than 30% cover. The grass cover of the site was partly burnt between November 1996 and early February 1997, it burnt again more completely in early February 1997, and again between December 1997 and February 1998,

but many of the culms of the grasses remained unburned. The highest trees in the canopy were 8-11 m high. The discontinuous tree stratum consisted of *Annona senegalensis*, *Lonchocarpus laxiflorus*, *Bridelia scleroneura*, *Combretum collinum* subsp. *collinum*, *C. adenogonum*, *Crossopteryx febrifuga*, *Lannea barteri*, *Maytenus senegalensis*, *Ochna leucophloeos*, *Strychnos innocua* and *Terminalia laxiflora*. Shrubs were not prominent, noted were *Grewia mollis*, *G. cf. velutina* and *Harrisonia abyssinica*. Among the herbs were noted *Clerodendrum alatum*, *C. cordifolium*, *Hoslundia opposita* and *Indigofera garckeana*. Climbers were *Ipomoea blepharophylla*, *I. heterotricha*, *Jasminum streptopus* (which did not develop much beyond a low, climbing shrub in the plots) and *Neorautanenia mitis*. The most important grasses were *Hyparrhenia confinis* var. *nudiglumis*, *Andropogon gayanus*, *Hyperthelia dissoluta*, *Loudetia arundinacea* and *L. simplex*. The standing volume of the tree trunks and other woody stems was on average 15 m³/ha. The tree stem density was on average 160 stems/ha. The biomass of the grasses was 14.9 t/ha and of the herbs 230 kg/ha. (In this figure is included young herbaceous parts of plants that might later develop a shrubby habit). The vegetation can be characterised as wooded grassland.

Wooded grassland: Site D

Similarly open vegetation was studied in site D located c. 22 km west of Gambella town along the road to Itang and Jicawo (c. 8° 17' N, 34° 28' E; c. 550 m altitude). Three replica plots were established less than 500 m from each other, two south of the road, and one north of the road. The landscape is very flat, and the soil is a rather uniform dark brown to reddish brown fine clayey vertisol. The site is probably occasionally flooded during the rainy season. The vegetation forms a very open canopy with an average of 25% cover, which varies because of the local presence of large specimens of *Ficus sycomorus*. The grass cover of the site was

burnt between November 1996 and early February 1997, and again before mid November 1997, probably most of it during an unusual, short dry spell in August-September where some burning did occur (local informant). The highest trees in the canopy were 12-15 m high. The tree stratum consisted of *Annona senegalensis*, *Bridelia scleroneura*, *Terminalia laxiflora*, *Ficus sycomorus*, *Lannea fruticosa*, *Lonchocarpus laxiflorus*, and *Stereospermum kunthianum*. In the shrub stratum was: *Maytenus senegalensis*, *Harrisonia abyssinica*, *Flueggea virosa*, *Grewia* sp. There were a few mainly herbaceous climbers: *Asparagus* sp., *Cissus petiolata* (or *C. populnea*), *Coccinia grandis*, *Teramnus labialis*. The herbs were: *Astripomoea malvacea*, *Echinops longifolius*, *Lippia* sp., *Indigofera* sp. cf. *I. spicata*, *Vernonia turbinata*. The grasses were *Andropogon gyanus*, *Loudetia* spp. and *Hyparrhenia* spp.,

especially *Hyparrhenia filipendula*. The standing volume of the tree trunks and other woody stems was on average 36 m³/ha. The tree stem density was on average 250 stems/ha. The biomass of the grasses was 16.9 t/ha and that of the herbs negligible. The vegetation can be characterised as wooded grassland.

Analyses of vegetation data

A number of analyses of diversity, life forms, size class distribution of woody species and biomass and annual growth of the herbaceous stratum were made on the vegetation data from the five sites. Although there now exist several studies of the Sudanian woodlands between Senegal and Ethiopia there is no comparable study recorded in the literature from other sites in the Sudanian region emphasising

Table 2. Number of species per family ranked according to size. No. of sp. = number of species.

Family	No. of sp.	Family	No. of sp.	Family	No. of sp.
Gramineae	12	Anacardiaceae	2	Ebenaceae	1
Fabaceae	11	Asparagaceae	2	Erythroxylaceae	1
Acanthaceae	7	Commelinaceae	2	Icacinaceae	1
Combretaceae	7	Hyacinthaceae	2	Lamiaceae	1
Tiliaceae	6	Nyctaginaceae	2	Loganiaceae	1
Convolvulaceae	5	Zingiberaceae	2	Meliaceae	1
Cucurbitaceae	5	Agavaceae	1	Moraceae	1
Euphorbiaceae	5	Annonaceae	1	Ochnaceae	1
Rubiaceae	5	Anthericaceae	1	Oleaceae	1
Verbenaceae	5	Araceae	1	Opiliaceae	1
Vitaceae	5	Asclepiadaceae	1	Oxalidaceae	1
Capparaceae	4	Balanitaceae	1	Plumbaginaceae	1
Malvaceae	4	Bignoniaceae	1	Sapindaceae	1
Mimosaceae	4	Caesalpinjiaceae	1	Simaroubaceae	1
Compositae	3	Celastraceae	1	Solanaceae	1
Rhamnaceae	3	Cyperaceae	1	Sterculiaceae	1
Amaranthaceae	2	Dioscoreaceae	1	Taccaceae	1

the same details and using the same methods. The presentation of the observations is therefore divided into a number of themes, each of which is then compared with other available observations, which vary from subject to subject.

Family, genus and species diversity

A total of 50 families, 94 genera and 135 species were observed from the sites during our field work; see the list of species in the Appendix, the list of families in Table 2, and the list of genera in Table 3. Each plot was 20 x 50 m (1000 m²), so our 4 sites with 3 replicate

plots cover 3000 m² each, and the fifth site with two replicate plots covers 2000 m², giving a total coverage of 14,000 m².

A list of the number of species in each family is shown here as Table 2. The distribution of species on families is shown in a graphic form in Fig. 7, where a curve expressing an inverse second order polynomial curve has been fitted, using the statistic functions of Sigma-Plot Version 4.0 Curve Fitting function ($r = 0.967$). A list of the number of species in each genus represented in our plots is shown here as Table 3, and the distribution of species on genera is shown in a graphic form in Fig. 8, where an

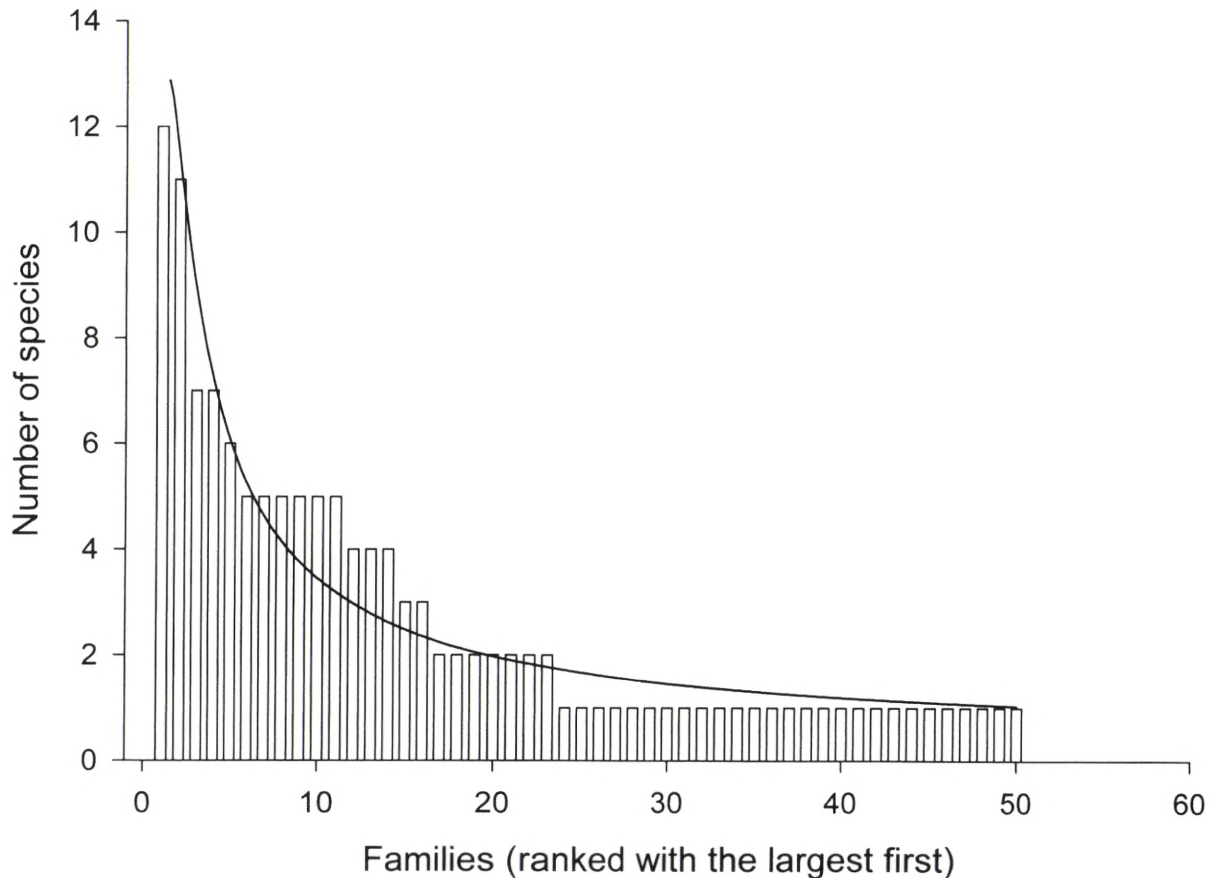


Fig. 7. Species distribution on families. The fitted inverse second order polynomial curve has the formula $y = 0.389 + 32.74/x - 21.37/x^2$. (x = number of family in ranking). $r = 0.967$.

Table 3. Number of species and subspecies per genus ranked according to size. (*gen. indet.*) = unidentified genus.

Genus	No. sp.	Genus	No. sp.	Genus	No. sp.
<i>Combretum</i>	5	<i>Andropogon</i>	1	<i>Jasminum</i>	1
<i>Clerodendrum</i>	4	<i>Annona</i>	1	<i>Lippia</i>	1
<i>Ipomoea</i>	4	<i>Anogeissus</i>	1	<i>Lonchocarpus</i>	1
<i>Grewia</i>	4	<i>Aspilia</i>	1	<i>Maytenus</i>	1
<i>Coccinia</i>	3	<i>Astripomoea</i>	1	<i>Meyna</i>	1
<i>Hibiscus</i>	3	<i>Azadirachta</i>	1	<i>Neorautanenia</i>	1
<i>Hyparrhenia</i>	3	<i>Balanites</i>	1	<i>Ochna</i>	1
<i>Indigofera</i>	3	<i>Biophytum</i>	1	<i>Opilia</i>	1
<i>Loudetia</i>	3	<i>Blepharis</i>	1	<i>Panicum</i>	1
<i>Zizyphus</i>	3	<i>Bridelia</i>	1	<i>Pennisetum</i>	1
<i>Abrus</i>	2	<i>Chlorophytum</i>	1	<i>Periploca</i>	1
<i>Acacia</i>	2	<i>Corchorus</i>	1	<i>Plumbago</i>	1
<i>Acalypha</i>	2	<i>Crossopteryx</i>	1	<i>Psilotrichum</i>	1
<i>Ampelocissus</i>	2	<i>Cucumis</i>	1	<i>Pterocarpus</i>	1
<i>Asparagus</i>	2	<i>Cucurbitaceae (gen. indet.)</i>	1	<i>Pyrenacantha</i>	1
<i>Barleria</i>	2	<i>Cyperus</i>	1	<i>Sansevieria</i>	1
<i>Boerhavia</i>	2	<i>Cyphostemma</i>	1	<i>Siphonochilus</i>	1
<i>Cadaba</i>	2	<i>Dichrostachys</i>	1	<i>Solanum</i>	1
<i>Cissus</i>	2	<i>Dioscorea</i>	1	<i>Spermacoce</i>	1
<i>Commelina</i>	2	<i>Diospyros</i>	1	<i>Sterculia</i>	1
<i>Justicia</i>	2	<i>Echinops</i>	1	<i>Stereospermum</i>	1
<i>Lannea</i>	2	<i>Entada</i>	1	<i>Strychnos</i>	1
<i>Ledebouria</i>	2	<i>Erythrococca</i>	1	<i>Tacca</i>	1
<i>Maerua</i>	2	<i>Erythroxyllum</i>	1	<i>Tamarindus</i>	1
<i>Sporobolus</i>	2	<i>Ficus</i>	1	<i>Teramnus</i>	1
<i>Vigna</i>	2	<i>Flueggea</i>	1	<i>Terminalia</i>	1
<i>Abutilon</i>	1	<i>Gardenia</i>	1	<i>Triumfetta</i>	1
<i>Acanthaceae (gen. indet.)</i>	1	<i>Harrisonia</i>	1	<i>Tylosema</i>	1
<i>Achyranthes</i>	1	<i>Hoslundia</i>	1	<i>Vangueria</i>	1
<i>Aframomum</i>	1	<i>Hyperthelia</i>	1	<i>Vernonia</i>	1
<i>Allophylus</i>	1	<i>Hypoestes</i>	1	<i>Ximenia</i>	1
<i>Amorphophallus</i>	1				

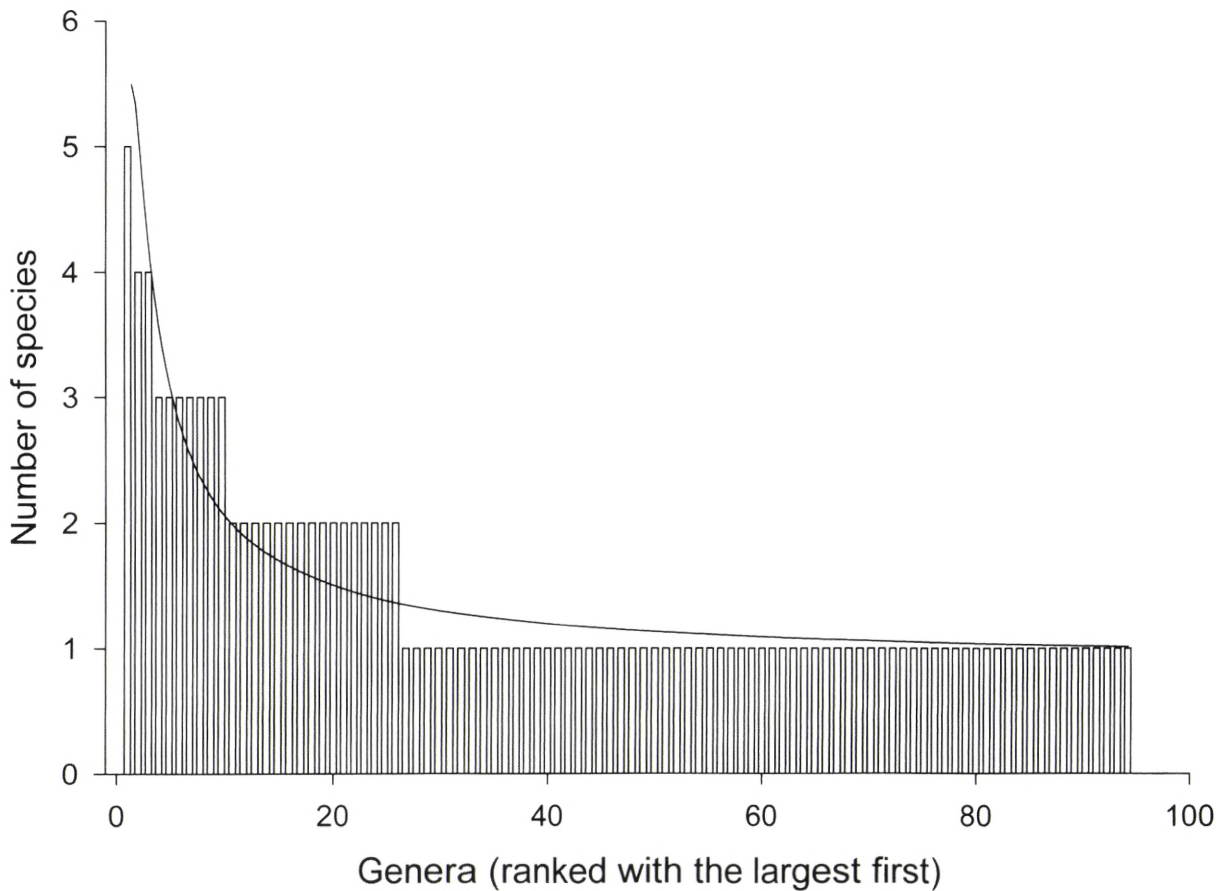


Fig. 8. Species distributions on genera. The fitted inverse second order polynomial curve has the formula $y = 0,874 + 13.04/x - 9.19/x^2$. (x = number of genus in ranking). $r = 0.929$.

inverse second order polynomial has again been fitted ($r = 0.929$).

The distribution of family- and genus-sizes agree with established knowledge about the size-distribution of families and genera on a world scale, and the fit with an inverse second order polynomial is acceptable for both families and genera ($r > 0.9$). The fact that few families have a high number of species and strikingly many families have only a few species is well known from the total flora of the world. This has for example been described by Clayton (1974) for the distribution of genera on

families and species on genera on a global basis. This characteristic frequency distribution has been summed up in the colloquial sentence: *It is rare to be common and common to be rare.*

However, an excess of families represented by one or two species only, and a deficiency of families represented by a large number of species here modify the general pattern. Our sample does therefore not represent a completely random selection of the world flora. It has been suggested that disturbance at some intermediate level acts to maintain high divers-

ity (Connell 1978), and patterns like this are often found where the flora has been subjected to fluctuations over comparatively short time. In such cases, many families are represented by a single or a few widespread species each, and very few families have formed local species in the area. Also the distribution of genera size agrees with this deviation from the world pattern. However, the number of large genera is even more restricted in relation to the number of genera represented by one species only; the explanation may be as mentioned above for the family level.

The variation between the species richness in the plots is shown in Table 4. It is seen that the highest species diversity (average 32.7) is found in site B, the dense *Anogeissus* woodland south of Gambella town. The second highest value (average 26.0) is found in the dry forest (site X) at the airport south of Gambella. Slightly lower diversity (total 19.7) is found in site C, the open grass-rich site between Abobo and Pugnido. This is followed by a lower value (average 16.7) in the vegetation intermediate between woodland and wooded grassland at Baro Bonga near the western Ethiopian escarpment. The lowest diversity value (average 14.0) was found in the vegetation characterised as wooded grassland on vertisol between Gambella town and Itang (site D).

The number of studies available for comparison from other localities in the Sudanian zone is limited. Oteng-Yeboah (1985) studied 8 plots of 2500 m², or a total of 20000 m² in the savanna region of Sokoto State, Northern Nigeria. The area studied is thus comparable to our total study site, but our sites cover a somewhat wider range of habitats. In Oteng-Yeboah's sites were observed a total of 30 families, 50 genera and 66 species, or 62.5% of the number of families we have observed, 54% of genera, and 52% of the species. Without more detailed knowledge of the variation between Oteng-Yeboah's study sites it is difficult to draw

conclusions from these figures about differences in the influence of fire. Oteng-Yeboah found that the most diverse families with regard to species in his sites were Mimosaceae and Combretaceae, while Caesalpiniaceae had the highest number of genera. Hence, Combretaceae scores high on both Oteng-Yeboah's list and our Table 2, whereas both Mimosaceae and particularly Caesalpiniaceae come lower down in our results. This agrees well with the known floristic composition of the "Undifferentiated woodland (Ethiopian type)" which has a very low component of Caesalpiniaceae in comparison with the Sudanian woodlands in West Africa (White 1983).

Floristic similarity between the sites

The species composition of the sites has been compared by the use of the software NTSYSpc Version 2.0 (Rohlf 1998). Species lists from the sites have been extracted from the appendix and compared. Similarity coefficients between the species lists were calculated by the use of Jaccard's coefficient, using the procedure SIMQUAL (SIMQUAL – Similarity for qualitative data). The resulting similarity matrix was analysed by the use of the module SAHN (Sequential, Agglomerative, Hierarchical, and Nested clustering methods), using the clustering procedure UPGMA (SAHN – Sequential agglomerative hierarchical nested cluster analysis). The resulting cluster is shown in Fig. 9. It can be seen that the dry forest (site X) is floristically the most isolated, joining the cluster of the other four sites at the level of similarity less than 0.1. The four fire prone clusters all group together, but are divided into two groups, consisting of site A and D and site B and C respectively. A and D are located far apart and on different soil types, although both have high organic content; we must also assume that rainfall is different, certainly high at A, and probably much lower at D. B and C are also far

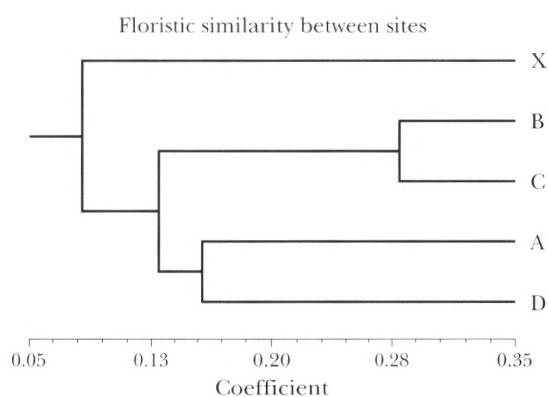


Fig. 9. Cluster showing floristic similarity between the sites. (Jaccard's coefficient of similarity and UPGM has been used). There is clear distinction between dry forest in site X and the woodlands and wooded grasslands in the other sites (B, C, A, D).

Table 4. Number of species of trees, shrubs and herbs (grasses shown separately) in the plots (each plot was 20 x 50 m). *Az* = average. st.dev = standard deviation.

	trees	shrubs	tree+shrub	herbs	grasses	total
X1	10	3	13	14	2	29
X2	8	1	9	13	1	23
<i>Az</i>	9.0	2.0	11.0	13.5	1.5	26.0
st.dev.	1.4	1.4	2.8	0.7	0.7	4.2
B1	10	4	14	24	2	40
B2	8	4	12	22	2	36
B3	4	8	12	8	2	22
<i>Az</i>	7.3	5.3	12.7	18.0	2.0	32.7
st.dev.	3.1	2.3	1.2	8.7	0.0	9.5
A1	8	4	12	6	2	20
A2	9	2	11	2	2	15
A3	6	3	9	3	3	15
<i>Az</i>	7.7	3.0	10.7	3.7	2.3	16.7
st.dev.	1.5	1.0	1.5	2.1	0.6	2.9
C1	12	2	14	11	4	29
C2	5	1	6	7	3	16
C3	7	1	8	4	2	14
<i>Az</i>	8.0	1.3	9.3	7.3	3.0	19.7
st.dev.	3.6	0.6	4.2	3.5	1.0	8.1
D1	6	0	6	1	3	10
D2	6	1	7	9	2	18
D3	7	2	9	3	2	14
<i>Az</i>	6.3	1.0	7.3	4.3	2.3	14.0
st.dev.	0.6	1.0	1.5	4.2	0.6	4.0

apart, but share rather similar edaphic conditions, and probably also very similar rainfall. The floristic similarities between the sites A, B, C, and D can thus probably be explained without invoking explanations from fire intensity. In contrast, the great differences between these sites on one hand and the dry forest in site X on the other, must be assumed to be due to the protection of site X from burning, as the edaphic and climatic conditions in site X and B are very similar.

Life forms

In this paper, two evaluations of life forms have been made. One that compares the number of species of three basic life forms (trees, shrubs, and herbs) in all plots analysed in this study and calculating the interplot variation (Table 4). Another evaluation applied here attempts

at a more sophisticated subdivision of the species in the life form system of Raunkiaer (1934) (Table 5). Some comments are necessary on the problems encountered when the species are classified into life forms. The distinction between the three basic life forms (trees, shrubs, herbs) is only apparently simple; there is no clear distinction between trees and shrubs, and the border between shrubs and what is often colloquially referred to as “woody herbs” is not easily determined: many species are woody at the base and herbaceous in the younger parts of the stems. The classification does also force us to place lianas either into the shrub or the herb life form; we chose to classify lianas with woody stems as shrubs in Table 4, and as phanerophytes in Table 5, and lianas that shoot from underground tubers as herbs in Table 4, and as geophytes (geophytic lianas) in Table 5. The problem was not a large one in

Table 5. The frequency of Raunkiaer life forms in the sites. G = grass-habit. L = liana-habit.

Life form	All sites	Site X	Site B	Site A	Site C	Site D
Mesophanerophytes (MEP)	16	5	8	4	8	3
Microphanerophytes (MIP)	35	14	11	11	12	8
(Of which lianas (MIP(L)))	(6)	(4)	(0)	0	(2)	(1)
Nanophanerophytes (NAP)	15	3	7	3	4	3
Of which lianas (NAP(L))	(3)	(0)	(1)	(1)	(1)	(1)
Chamaephytes (CHP)	2	1	0	0	0	1
Hemicryptophytes (HEC)	23	9	8	3	6	7
HEC that are grasses (HEC(G))	(9)	(1)	(3)	(3)	(5)	(5)
HEC that are lianas (HEC(L))	(2)	(2)	(0)	(0)	(0)	(0)
Geophytes (GEP)	23	6	14	6	5	4
Of which geophytic lianas (GEP(L))	(13)	(3)	(10)	(4)	(2)	(2)
Therophytes (THP)	16	1	13	3	4	0
Of which annual lianas (THP(L))	(1)	(0)	(1)	(0)	(0)	(0)
Succulents (SUC)	1	1	0	0	0	0
Life form not ascertainable	5	1	2	0	2	
Total no. of species (all life forms)	136	41	63	30	41	26

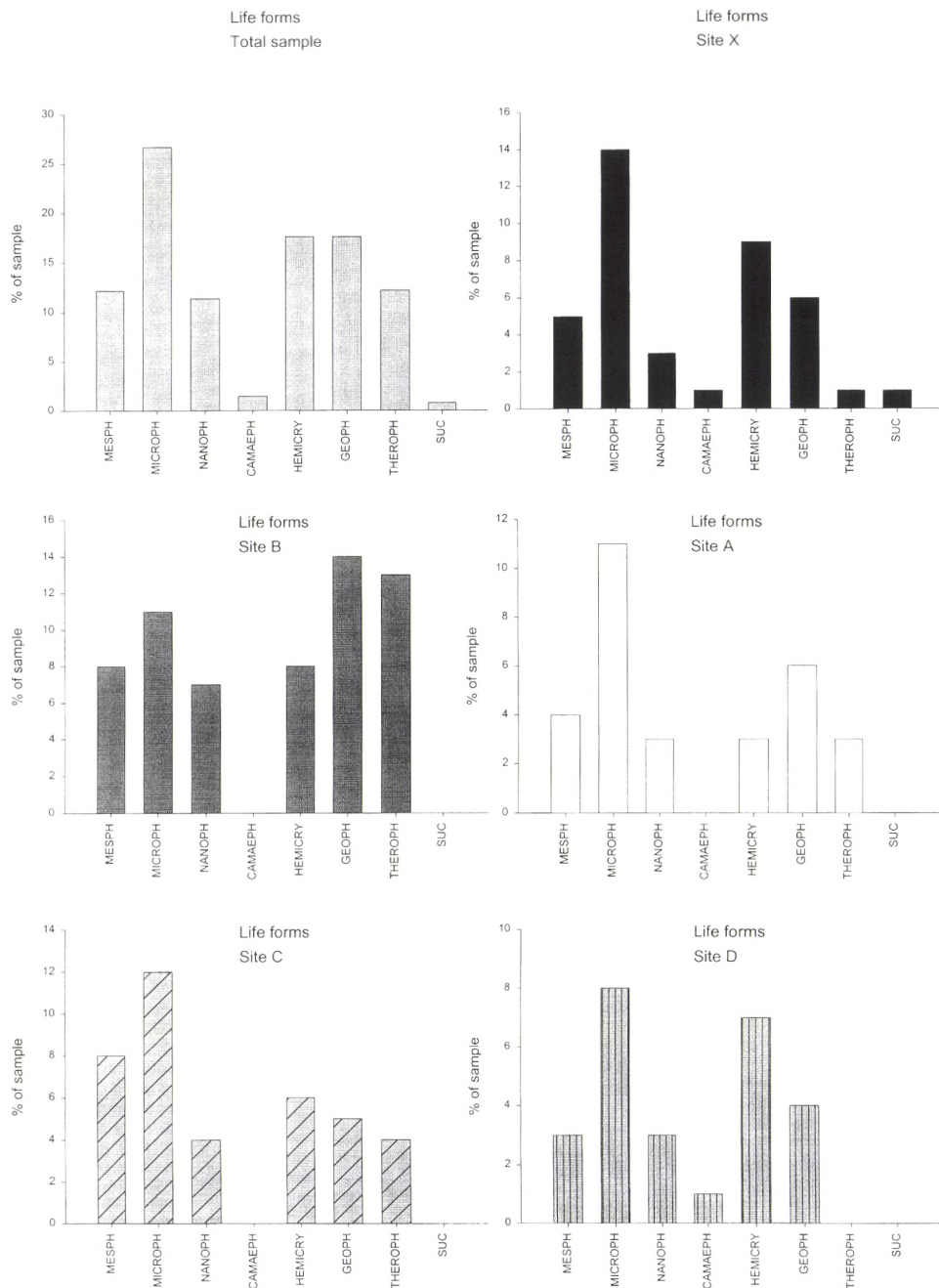


Fig. 10. Distribution on Raunkiaer's life forms shown as the accumulated figures in percent of samples from all sites, and for the individual sites. MESPH: Mesophanerophytes. MICROPH: Microphanerophytes. NANOPH: Nanophanerophytes. CHAMAEPH: Chamaephytes. HEMICRY: Hemicryptophytes. GEOPH: Geophytes. THEROPH: Therophytes. SUC: Succulents. While all sites have a rather similar pattern with regard to the classes Meso-, Micro- and Nanophanerophytes, there is considerable variation in frequencies of the other life form classes. However, Hemicryptophytes and Geophytes remain frequent in all sites.

our case, as only very few phanerophytic lianas existed in the sites.

The categories of trees and shrubs are according to Raunkiaer's system classified by the height above ground where the buds are found that shoot after the unfavourable season. This height is fairly easy to establish with the accuracy required. There were no megaphanerophytes in the plots. Mesophanerophytes have buds up to 8 to 30 m above ground; microphanerophytes have buds up to 2 to 8 m above ground; nanophanerophytes have buds up to 0.25 to 2 m above ground; all these are, as could be expected, reasonably well represented in our sites, but with a declining frequency as the buds become more and more exposed to fire in woody plants of small stature. Chamaephytes have buds between 0 and 0.25 m above ground, but only two species in this category were found in the plots, and one of those occurred in closed forest. The hemicryptophytes were nearly all grasses, where the buds are placed in the dense grass tufts, which act as protection against fire. Species have been considered geophytes if they have large, tuberous underground rootstocks from which they sprout after fire. Usually these tubers are located completely underground. The geoxyllic suffrutices so characteristic of wooded grassland elsewhere in Africa, especially in the Zambezian region (Lock 1998), were not noted in our plots; they would have been classified as hemicryptophytes. Very thin and semi-woody stems of perennials are assumed to burn, and these plants must shoot from buds near the surface of the soil; such plants are rather frequent in our sites and are considered as hemicryptophytes, rather than chamaephytes. Therophytes are annual and reproduce from seeds. True stem-succulents were not recorded, but one species of *Sansevieria* was scored as a leaf succulent.

Fig. 10 shows the distribution on life forms as the accumulated percentages of life forms

for all sites, and for the individual sites (A-D and X). It can be seen that the figures for phanerophytes are more stable than the figures for geophytes and therophytes, where especially site B, the woodland stands out because of high numbers of geophytes and therophytes. This is surprising, as one would expect the site with severe fires to have the highest number of these life forms, but the high numbers in site B must be seen in relation to the fact that that site has the highest species diversity of all in the study.

Comparison with other areas

We have been able to trace only relatively few studies of life forms in vegetation types comparable to those of the Gambella Region. One of the comparisons possible is with data from dry savanna in Botswana (Cole & Brown 1976). An additional number of possibilities for comparison is a summary table (Table 6.2) in Menaut (1983). Table 6 shows a compilation of all these results, most of which are found in rare publications, which we have not been able to trace, and they are therefore here cited from Menaut (1983).

Menaut (1983) points out that the Raunkiaer life form system has been widely used by botanists studying African savannas, but that it has also been criticised for not being very suitable for that purpose. He further mentions that the variability between sites of the life form "typical" of a given species is one of the characteristics of savanna plants; the life form for the same species may change from a site with regular burning to a protected site, *etc.* Tchoumé (1966) describes how species of *Cissus* may in protected forest sites be classified as lianescent phanerophytes and as geophytes in frequently burnt savanna. As pointed out by Sarmiento & Monasterio (1983), the savanna ecosystem in its many modifications probably provides the most marked example of a tropical seasonal ecosystem, and yet there seems to

Table 6. Comparison of life forms at Gambella with life forms in other savanna or woodland sites

Other authors did not record succulents, of which we had a frequency of 1%.

	Oteng-Yeboah (1985)	Our data: All sites	Our data: Savanna and woodland sites	César (1971) Humid savanna Ivory Coast	Makany (1976) Humid savanna Congo	Hopkins (1962) Humid savanna Nigeria	Sillans (1958) Mesic savanna Central African Republic	Troupin (1966) Mesic savanna Rwanda	Lebrun (1947) Mesic savanna Zaïre	Boudet & Duverger (1961) Dry savanna South Mauritania	Cornet & Poupon (1977) Dry savanna Northern Senegal	Gillet (1961) Dry savanna Northern Chad	Cole & Brown (1976) Dry savanna Botswana
Phanerophytes	50-77%	50%	51%	28%	14%	30%	13%	29%	38.2%	24%	19%	14%	18.0%
Chamaephytes		2%	1%	–	25%	–	24%	30%	43.6%	–	2%	2%	16.5%
Hemicryptophytes		18%	14%	42%	26%	23%	8%	12%	9.1%	6%	2%	12%	28.2%
Geophytes		18%	18%	6%	16%	21%	11%	7%	3.6%	2%	2%	5%	7.6%
Therophytes		12%	12%	24%	19%	25%	40%	20%	5.4%	61%	75%	67%	1.7%

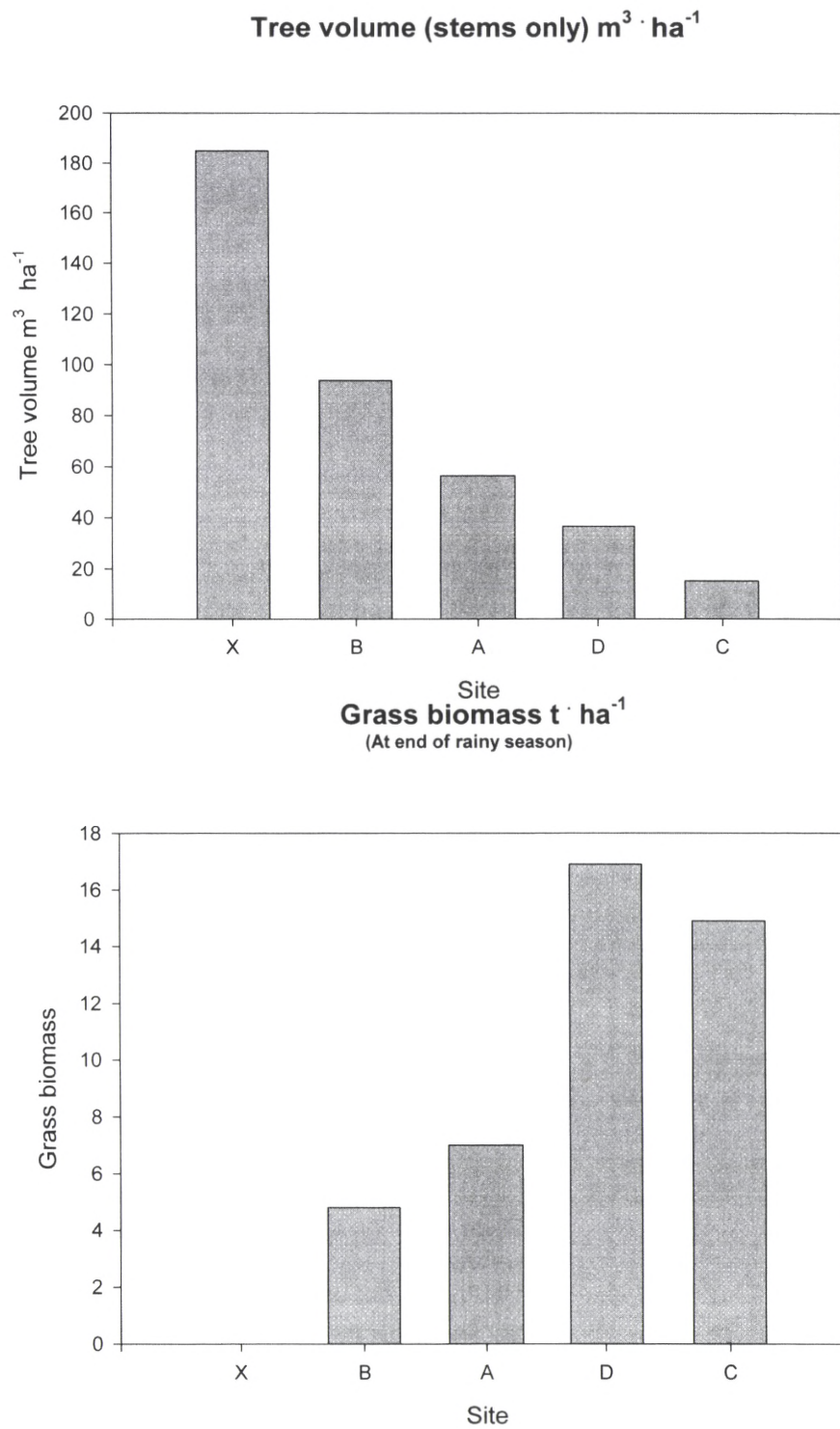
be no characteristic life form spectrum in common for it. This is quite different from the temperate deciduous forest and the typical tropical lowland rain forest (Richards 1964: 9, Fig. 1), for which it is possible to establish generalised life form spectra. The reasons for the considerable variation in savanna life form spectra are, as pointed out by Menaut (1983) and Sarmiento & Monasterio (1983), that the types of environmental stress on the species in tropical savanna vary considerably and have allowed a wider spectrum of individual or evolutionary responses to the characteristic stress factors: seasonal drought, flood, and periodic burning. Resource allocation in all species except the tall trees may be compatible with the periodic consumption of almost the whole aerial standing crop by fire, but it is not a priori dictated by this consumption by fire whether the herbaceous plants should be annuals, geophytes or hemicryptophytes. It is therefore hardly surprising that the comparison of the representation of Raunkiaer's life forms in seven African, Malagasy and South American savannas by

Sarmiento & Monasterio (1983, Table 5.1) shows at least as strongly fluctuating spectra as those shown by Menaut (1983) for African savannas.

Biomass

The biomass of trees and grasses at the end of the rainy season in November 1997 is shown in Fig. 11. As illustrated, there is a clear inverse relationship between tree trunk volume and grass biomass. No tree biomass regressions for this type of vegetation exist in the literature, and it is therefore not possible to give a more precise estimate of the total tree biomass. However, assuming an average wood density of 0.6 t/m³ and that trunks constitute about 50% of total tree biomass one would get a very rough estimate of the total tree biomass at site X, B, A, D and C, respectively, of: 222, 112, 67, 43 and 18 t/ha, which is probably an under-estimate for all sites, since the below-ground biomass can be considerable in these habitats (Menaut *et al.* 1995). Our values agree reasonably well

Fig. 11. The biomass of trees and grasses at the end of the rainy season in November 1997 in the sites X, B, A, D and C. The values of tree stem volume for each site represent an average of three plots (two for site X). The values of grass biomass for each site represent the average of the unburned plots at time of measurement.



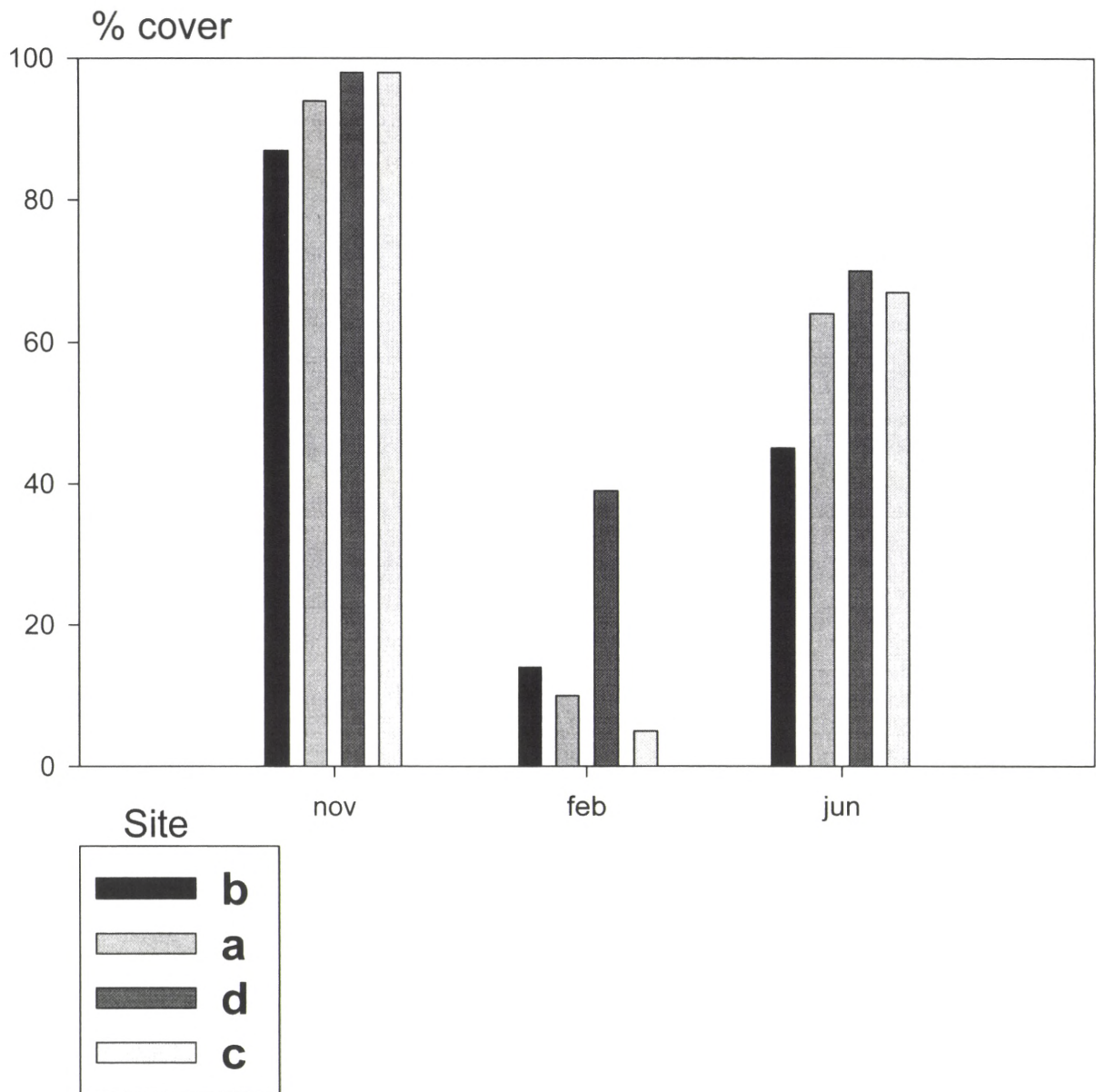


Fig. 12. Seasonal ground cover by grass, in November (end of rainy season), February (peak of dry season) and June (beginning of rainy season), in site B, A, D and C (the values for each site represent an average of three plots). Site X contained negligible to no grass cover.

with those reported from SE Zaire of 10, 150 and 320 t ha⁻¹ for savanna, woodland and dry forest respectively except that our estimate of

the dry forest is lower than that in Zaire (Menaut *et al.* 1995). But, according to these authors dry forests of northern Africa has con-

siderable lower biomass than southern dry forests. The northern dry forest has according to Menaut *et al.* (1995) characteristically a biomass around 140 t ha⁻¹, which in fact is lower than our estimate.

The canopy cover ranged from 25-29% in the wooded grassland and open woodland in site A, C and D, over 60% in the woodland in site B, and reached 92 % in the dry forest. Menaut *et al.* (1995) listed slightly lower ranges for savanna and higher for woodland and dry forest.

We measured a peak aboveground grass biomass of 4.8 t ha⁻¹ in the woodland site (site B), whereas the wooded grassland sites (site A, C and D) ranged from 7 to 16.9 t ha⁻¹. Our values are considerably larger than those reported from SE Zaire, but falls fairly close to or a little higher than the general range for Africa of 4-10 t ha⁻¹. We can assume an additional below-ground biomass of at least the same size, as this has been demonstrated in several other studies (Menaut *et al.* 1995; Kinyamario & Imbamba 1992).

Seasonal ground cover by (green) grass in woodland and woodland savanna varied considerably at all sites, as shown in Fig. 12. Values peaked at the end of the rainy season in November, dropped dramatically from above 90% cover at the end of the rainy season to around 10% or less at the height of the dry season in February, following drying and burning. Values were intermediate in June after the rains had started again in May, stimulating new growth. The seasonal pattern was more or less similar at all sites. For more details of the seasonal changes of the above-ground cover of the dominant grass, *Hyparrhenia confinis*, see Menassie & Michelsen (2001).

Although we have not aimed directly at measurements of productivity of the grass and herb layer, it is reasonable to assume that our figures for peak biomass of herbs and grasses give a very close estimate of the annual productivity

in this stratum. Because of the annual burning there is an almost complete replacement of the above-ground grass and herb biomass. Our figures vary from nearly nil in dry forest (site X) to the sites with wooded grassland (site C: 1513 g/m², and site D: 1690 g/m²). These latter figures are high compared with measured annual productivity in a range of African woodlands, wooded grasslands and grasslands, which according to Kinyamario & Imbamba (1992) range from 220 to 1880 g/m² (the latter including root production).

Size class distribution of trees

Our observations of the dimensions of trees have for all sites been divided into size classes of 10 cm DBH each (5-15 cm, 15-25 cm, etc.). We have then scored the number of individuals/ha in each size class (Fig. 13), and the sites have been arranged in order of increasing fire severity. Not all individuals could be identified to species level, especially the *Combretum* species, and size class diagrams are therefore not made for individual species. In all cases there are approximations to the logarithmic decreasing curve, which should be expected in vegetation with regular or natural turnover. However, there are deviations from this distribution, most prominently in the sites X, B and A.

The relative peak in the size classes 25-35 cm DBH in Site A (transition between woodland and wooded grassland) makes the size class distribution of this site resemble that of the forest and woodland vegetation in Site X and B. This perhaps indicates that the number of trees in site A is in the process of declining. The variation in the ¹³C/¹²C isotope ratio with soil depth also suggests that site A has experienced a change from a vegetation cover with a high frequency of C-3-plants (trees and shrubs) to a more open one dominated by C-4-plants, mainly grasses (see further in the coming work

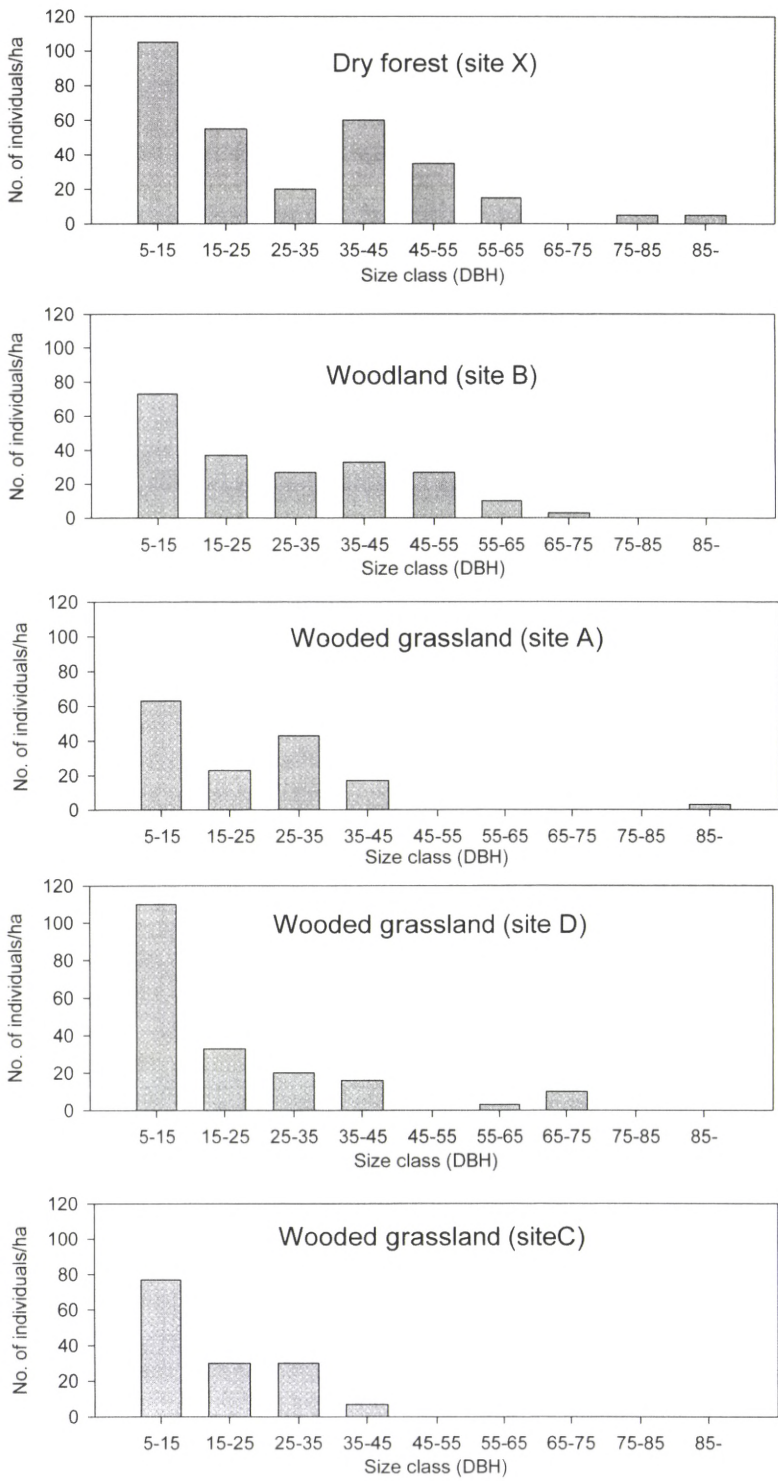


Fig. 13. Size class distribution of trees per ha in the study sites. The sites are arranged according to increasing fire severity from site X (no fires) to site C.

by Michelsen, Friis, Jensen & Andersson, in prep.). The time scale of this change is not known. The improved road conditions between the Ethiopian highlands and Gambella have much improved the access to the area in which site A is located, and there is an increasing number of Sudanian refugees in camps below the escarpment where site A is located; both of these two human factors may have some influence on this change. The tendency to a secondary peak between 35-55 cm DBH in the histograms for site X and B are not correlated with a similar change in the C isotope ratio in the soil, so it is difficult to explain this pattern. However, we noted that fuel wood cutting around Gambella town mainly affected trees in our lowest size class (5-15 cm DBH). A fairly recent increase in removal of trees in this size class could disrupt the usual size class distribution in a way similar to what we see in site X and B.

Greig-Smith (1991) has pointed out the high mortality of small woody stems in a fire-influenced derived savanna in Nigeria, resulting in a certain shift in the size structure from the usual distribution with the highest number in the smallest size-classes (< 10 cm DBH); his size class curve also shows the odd very large trees. Our examples do not show the shift away from the very small size classes clearly, partly because we have not included trees under 5 cm DBH (Greig-Smith's intervals are also smaller than ours). The largest size classes in site X and A are above 85 cm DBH, while in site B it is one individual in the class 65-75 cm DBH. Although the sites D and C also have the highest number of individuals in the smallest size class, the secondary peak found in X, B and A is not prominent, and large trees in size classes above 45 cm DBH are rare or absent, in fact restricted to 3 specimens of *Ficus sycomorus* in site D.

The high number of individuals in the small size classes may have different explanations in different sites. In the infrequently burnt sites,

such as site X and B, these size classes consist partly of young individuals of species which grow to a larger size, and partly of shade-tolerant, but not fire-resistant understorey trees (e.g. *Allophylus rubifolius*, *Erythroxylum fischeri*, *Vangueria madagascariensis*, and *Meyna tetraphylla*) that do not grow to a large size. In contrast, the small size classes in the frequently burnt sites (A, C and D) consist chiefly of small, fire-adapted species such as *Grewia mollis*, *G. bicolor* and *Bridelia scleroneura*, which all have thick bark which do not grow to large size, whereas young individuals of the large trees were comparatively rare or absent. The presence of very large trees in two of the wooded grassland-sites (A and D) can partly be explained by their special adaptations to fire, e.g. through thick and peeling bark, as seemed to be the case with the isolated individual of *Sterculia africana* in site A, partly by clumped distribution, as was probably the case with the three large specimens of *Ficus sycomorus* in site D. The fire resistance of *Ficus sycomorus* is further enhanced by the fact that the shade of the broad canopy of this species reduces the growth of grasses beneath it and thus also the effect of fire. A similar phenomenon is seen on the termite mounds, where the shade of evergreen shrubs partly excludes the growth of grass. The large individuals of trees, such as *Ficus sycomorus*, can develop on termite mounds. In contrast, the large trees in site X and B (2 individuals in size classes above 75 cm DBH in site X, one in site B) are all *Anogeissus leiocarpus* that have grown beyond the common size due to the absence or low severity of fire in these sites.

Conclusion

Our study of the distribution of fires as shown by remote sensing shows that there is good agreement between high fire density and the distribution of Sudanian woodlands as defined

by White (1983), especially when allowance is made for White's transition zone between the Sudanian and the Guineo-Congolian region in West Africa. Within this broadly defined Sudanian zone fire seems to affect nearly all vegetation types, except closed forest. This is also clearly the case in western Ethiopia, from the border region with western Eritrea in the north to the Boma Plateau south west of the town of Maji in the south. Unlike what has been shown on early vegetation maps of Ethiopia, this western zone of Ethiopia has many features in common, and all parts are affected by high fire density. Within this part of Ethiopia, especially in the Gambella Region, we have noted that there is a clear association between towns and routes of transportation on one hand and density of fires on the other, indicating that man starts most fires. Within the fire-prone zone, there is a mosaic of areas with high and low fire severity, but the location of this mosaic seems to vary from year to year. There is also a mosaic of vegetation types, but this may be as much influenced by edaphic and climatic factors as by burning. Flooding is an important factor in Gambella, influencing both soil and vegetation. The effect of severe flooding and development of vertisols may influence the floristic composition as much as severe fires. There seems to be no sharp boundaries between these types with regard to floristic characteristics, again with exception of the fairly sharp distinction between forest on one hand and woodland, wooded grassland and grassland on the other. A cluster analysis of the floras of the sites showed a sharp distinction between dry forest flora on one side and all fire-influenced sites on the other. The sites have comparatively many families and genera, but a low number of species per family and genus, which is believed to be indicating disturbance.

Increasing fire severity seems to be somewhat negatively correlated with species rich-

ness, but the number of species also declines in the shaded situation of the dry forest. A clear association has been observed between severe fires and high grass biomass, whereas the tree biomass, and the number of large trees, was negatively correlated to increasing fire severity. The life forms of savanna and woodland species have evolved under the influence of fire, and apparently fire-adapted hemicryptophytes, geophytes and therophytes were prominent in the burned sites, but we found no marked difference with regard to frequency of life forms between sites in our study area.

The current situation seems to indicate a decline in the extent of dry forest, which near Gambella town only persists in protected sites. With the current population pressure and fire intensity the process of change from dry forest and dense woodland to open woodland and wooded grassland is likely to continue, and this process may ultimately lead to the destruction of dry forest and dense woodland in the region. The time scale of this process will undoubtedly be largely dependent on the demographic development in the region. Where dry forest or dense woodland has been replaced with wooded grassland, as it may probably have happened in sites C and D in our study area, the vegetation and soil seems to have reached a somewhat stable level of fertility, structure and floristics, characterised by an impoverished tree flora and a very tall and abundant grass stratum which has its peak biomass at the end of the rainy season. The burning of this very large biomass is critical. Too late, and hence very severe fires will result in a further degradation of the tree stratum.

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Appendix

Species list of the Gambella woodland savanna research sites

Includes species encountered and identified between Nov 1996 and Dec 1998. The following life forms have been recorded: MEP: Mesophanerophyte (8-30 m). MIP: Microphanerophyte (2-8 m). NAP: Nanophaneropytes (0.25-2 m). CHP: Chamaephytes (0-0.25 m). HEC: Hemicryptophytes (including the tufted grass-life form [HEC(G)]). GEP: Geophytes. THP: Therophytes. SUC: Succulent. Where the life form of a species represents lianas or vines, this has been separately indicated with "(L)".

Species	Family	Life form	Site X	Site B	Site A	Site C	Site D
<i>Abrus schimperi</i> Hochst. ex Bak.	Fabaceae	NAP	•	•		•	
<i>Abrus praecatorius</i> Linn.	Fabaceae	MIP(L)	•				
<i>Abutilon</i> sp.	Malvaceae	NAP	•				
<i>Acalypha ciliata</i> Forssk.	Euphorbiaceae	THP		•			
<i>Acalypha villicaulis</i> Hochst. ex A. Rich.	Euphorbiaceae	NAP		•			
<i>Achyranthes</i> sp.	Amaranthaceae	?	•				
<i>Acacia senegal</i> Willd.	Mimosaceae	MIP		•	•	•	
<i>Acacia</i> sp.	Mimosaceae	MIP			•		
<i>Acanthaceae</i> (gen et sp. indet.)	Acanthaceae	HEC	•				
<i>Aframomum</i> sp.	Zingiberaceae	GEP		•		•	
<i>Allophylus rubifolius</i> Engl.	Sapindaceae	MIP	•	•			
<i>Amorphophallus abyssinicus</i> (A. Rich.) N.E. Br.	Araceae	GEP	•				
<i>Ampelocissus abyssinica</i> (A. Rich.) Planch.	Vitaceae	GEP(L)		•			
<i>Ampelocissus schimperia</i> Planch.	Vitaceae	GEP(L)	•	•			
<i>Andropogon gayanus</i> Kunth	Gramineae	HEC(G)				•	•
<i>Annona senegalensis</i> Pers.	Annonaceae	MIP					•
<i>Anogeissus leiocarpa</i> Guill. & Perr.	Combretaceae	MEP	•	•		•	
<i>Asparagus scaberulus</i> A. Rich.	Asparagaceae	NAP(L)			•		
<i>Asparagus</i> sp.	Asparagaceae	NAP(L)					•
<i>Aspilia kotschyi</i> (Sch. Bip ex Hochst.) Oliv.	Compositae	THP		•		•	
<i>Astripomoea malvacea</i> A. Meeuse	Convolvulaceae	NAP (?)					•
<i>Azadirachta indica</i> A. Juss.	Meliaceae	MIP				•	
<i>Balanites aegyptiaca</i> Wall.	Balanitaceae	MIP			•		
<i>Barleria grandicalyx</i> Lindau	Acanthaceae	HEC(?)		•			
<i>Barleria ventricosa</i> Hochst. ex Nees	Acanthaceae	HEC(?)	•				
<i>Biophytum umbraculum</i> Welw.	Oxalidaceae	THP		•			
<i>Blepharis maderaspatensis</i> Heyne ex Roth.	Acanthaceae	HEC	•				
<i>Boerhavia coccinea</i> Mill.	Nyctaginaceae	THP		•	•		

Species	Family	Life form	Site X	Site B	Site A	Site C	Site D
<i>Boerhavia repens</i> Rojas	Nyctaginaceae	THP			•		
<i>Bridelia scleroneura</i> Muell. Arg.	Euphorbiaceae	MIP		•		•	•
<i>Cadaba farinosa</i> Forssk.	Capparaceae	NAP		•			
<i>Cadaba</i> sp.	Capparaceae	NAP			•		•
<i>Chlorophytum tordense</i> Chiov.	Anthericaceae	GEP		•		•	
<i>Cissus petiolata</i> Hook. f. (or <i>C. populnea</i> Guill. & Perr.)	Vitaceae	MIP(L)/ MEP(L)					•
<i>Cissus</i> sp.	Vitaceae	MIP(L)	•			•	
<i>Clerodendrum alatum</i> Gürke	Verbenaceae	GEP		•		•	
<i>Clerodendrum capitatum</i> Hook.	Verbenaceae	MIP(L)	•				
<i>Clerodendrum cordifolium</i> A. Rich	Verbenaceae	MIP(L)				•	
<i>Clerodendrum</i> sp.	Verbenaceae	?		•			
<i>Coccinia adoensis</i> (Hochst. ex A. Rich.) Cogn.	Cucurbitaceae	GEP(L)		•			
<i>Coccinia grandis</i> Voigt.	Cucurbitaceae	GEP(L)			•		•
<i>Coccinia megarrhiza</i> C. Jeffrey	Cucurbitaceae	GEP(L)					•
<i>Combretum adenogonium</i> Steud. ex A. Rich.	Combretaceae	MEP				•	
<i>Combretum collinum</i> Fresen. subsp. <i>binderianum</i> (Kotschy) Okafor	Combretaceae	MEP		•	•		
<i>Combretum collinum</i> Fresen. subsp. <i>collinum</i>	Combretaceae	MEP				•	
<i>Combretum molle</i> Engl. & Diels.	Combretaceae	MEP		•			
<i>Combretum</i> sp.	Combretaceae	MEP		•		•	•
<i>Commelina benghalensis</i> Linn.	Commelinaceae	HEC		•			
<i>Commelina</i> sp.	Commelinaceae	HEC	•			•	
<i>Corchorus tridens</i> Linn.	Tiliaceae	THP		•			
<i>Crossopteryx febrifuga</i> Benth.	Rubiaceae	MIP				•	
<i>Cucumis metuliferus</i> E. Mey. ex Naud.	Cucurbitaceae	THP(L)		•			
<i>Cucurbitaceae</i>	Cucurbitaceae	?				•	
<i>Cyperus subumbellatus</i> Kukenth.	Cyperaceae	HEC	•				
<i>Cyphostemma adenocaula</i> (A. Rich) Wild & R.B. Drumm.	Vitaceae	GEP(L)/ HEC(L)		•	•		
<i>Dichrostachys cinerea</i> (Linn.) Wight. & Arn.	Mimosaceae	MIP		•			
<i>Dioscorea praehensilis</i> Benth.	Dioscoreaceae	GEP(L)	•	•			
<i>Diospyros mespiliformis</i> Hochst. ex A. DC.	Ebenaceae	MEP	•				
<i>Echinops longifolius</i> A. Rich.	Compositae	HEC					•
<i>Entada africana</i> Guill. & Perr.	Mimosaceae	MIP			•		

Species	Family	Life form	Site X	Site B	Site A	Site C	Site D
<i>Erythrococca</i> <i>cf.</i> <i>abyssinica</i> Pax	Euphorbiaceae	MIP	•				
<i>Erythroxyllum fischeri</i> Engl.	Erythroxyllaceae	MIP	•				
<i>Ficus sycomorus</i> L.	Moraceae	MEP				•	•
<i>Flueggea virosa</i> (Willd.) Voigt	Euphorbiaceae	MIP	•	•	•		
<i>Gardenia ternifolia</i> Schum. & Thonn.	Rubiaceae	MIP		•			
<i>Grewia mollis</i> Juss.	Tiliaceae	MIP		•	•	•	•
<i>Grewia tenax</i> Aschers. & Schweinf. ex E. Christ.	Tiliaceae	MIP	•				
<i>Grewia</i> <i>cf.</i> <i>velutina</i> (Forssk.) Vahl	Tiliaceae	MIP				•	
<i>Grewia</i> <i>sp.</i>	Tiliaceae	MIP					•
<i>Harrisonia abyssinica</i> Oliver	Simaroubaceae	MIP	•	•	•	•	•
<i>Hibiscus calyphyllus</i> Cav.	Malvaceae	NAP	•				
<i>Hibiscus cannabinus</i> Linn.	Malvaceae	THP		•			
<i>Hibiscus</i> <i>sp.</i>	Malvaceae	?		•			
<i>Hoslundia opposita</i> Vahl	Labiataeae	NAP		•		•	
<i>Hypparrhenia confinis</i> (A. Rich.) Stapf var. <i>nudiglumis</i> (Hackl.) W.D. Clayton	Gramineae	THP		•	•	•	
<i>Hypparrhenia filipendula</i> Stapf.	Gramineae	HEC(G)					•
<i>Hypparrhenia</i> <i>sp.</i>	Gramineae	HEC(G)		•	•	•	•
<i>Hyperthelia dissoluta</i> (Nees ex Steud.) W.D. Clayton	Gramineae	HEC(G)				•	
<i>Hypoestes forskalii</i> (Vahl) R. Br.	Acanthaceae	HEC	•	•			
<i>Indigofera garckenana</i> Vatke	Fabaceae	NAP		•		•	
<i>Indigofera</i> <i>sp.</i> <i>aff.</i> <i>I. spicata</i> Forsk.	Fabaceae	HEC		•			•
<i>Indigofera trita</i> L.f. var. <i>scabra</i> (Roth) Ali	Fabaceae	NAP		•			
<i>Ipomoea blepharophylla</i> Hallier f. ex Engl.	Convolvulaceae	GEP(L)				•	
<i>Ipomoea eriocarpa</i> R.Br.	Convolvulaceae	THP		•			
<i>Ipomoea heterotricha</i> F. Didr.	Convolvulaceae	THP				•	
<i>Ipomoea</i> <i>sp.</i>	Convolvulaceae	?				•	
<i>Jasminum streptopus</i> E. Mey. ex DC.	Oleaceae	NAP(L)		•		•	
<i>Justicia ladanoides</i> Lam.	Acanthaceae	HEC		•			
<i>Justicia diclipteroides</i> Lindau	Acanthaceae	HEC	•				
<i>Lannea barteri</i> Engl.	Anacardiaceae	MEP			•	•	
<i>Lannea fruticosa</i> Engl.	Anacardiaceae	MIP			•		•
<i>Ledebouria revoluta</i> (L.f.) J.P. Jessop	Hyacinthaceae	GEP			•		
<i>Ledebouria</i> <i>sp.</i>	Hyacinthaceae	GEP			•		

Species	Family	Life form	Site X	Site B	Site A	Site C	Site D
<i>Lippia</i> sp.	Verbenaceae	NAP					•
<i>Lonchocarpus laxiflorus</i> Guill. & Perr.	Fabaceae	MEP		•		•	•
<i>Loudetia arundinaceae</i> Hochst. ex Steud.	Gramineae	HEC(G)				•	
<i>Loudetia</i> sp.	Gramineae	HEC(G)	•	•	•	•	•
<i>Loudetia simplex</i> (Nees) C. E. Hubbard	Gramineae	HEC(G)					•
<i>Maytenus senegalensis</i> (Lam.) Exell	Celastraceae	MIP		•		•	•
<i>Maerua oblongifolia</i> A. Rich.	Capparaceae	NAP/ (MIP)		•			
<i>Maerua triphylla</i> A. Rich.	Capparaceae	MIP	•				
<i>Meyna tetraphylla</i> Robyns	Rubiaceae	MIP	•				
<i>Neorautanenia mitis</i> (A. Rich.) Verdc.	Fabaceae	GEP(L)		•		•	
<i>Ochna leucophloeos</i> A. Rich.	Ochnaceae	MIP				•	
<i>Opilia amentacea</i> Roxb.	Opiliaceae	MIP(L)	•				
<i>Panicum comorense</i> Mez	Gramineae	THP	•				
<i>Pennisetum polystachion</i> Schult.	Gramineae	THP		•			
<i>Periploca linearifolia</i> A. Rich.	Asclepiadaceae	HEC(L)	•				
<i>Plumbago zeylanica</i> Linn.	Plumbaginaceae	HEC(L)	•				
<i>Psilotrichum</i> sp. <i>cf.</i> <i>P. elliotii</i> Bak.	Amaranthaceae	CHP	•				
<i>Pterocarpus lucens</i> Lepr. ex Guill. & Perr.	Fabaceae	MEP	•	•			
<i>Pyrenacantha kawabassana</i> Baill.	Icacinaceae	GEP(L)	•	•	•		
<i>Sansevieria</i> sp.	Agavaceae	SUC	•				
<i>Siphonochilus aethiopicus</i> (Schweinf.) B.L. Burt	Zingiberaceae	GEP	•				
<i>Solanum incanum</i> Linn.	Solanaceae	NAP			•		
<i>Spermacoce sphaerostigma</i> Oliver	Rubiaceae	THP		•		•	
<i>Sporobolus festivus</i> A. Rich.	Gramineae	GEP(G)			•		
<i>Sporobolus pyramidalis</i> Beauv.	Gramineae	GEP(G)		•			
<i>Sterculia africana</i> (Lour.) Fiori	Sterculiaceae	MEP			•		
<i>Stereospermum kunthianum</i> Cham.	Bignoniaceae	MIP			•		•
<i>Strychnos innocua</i> Delile	Loganiaceae	MIP	•	•		•	
<i>Tacca leontopetalodes</i> Kuntze	Taccaceae	GEP	•	•			
<i>Tamarindus indica</i> Linn.	Leguminosae	MEP	•	•			
<i>Terminalia laxiflora</i> Engl.	Combretaceae	MEP		•		•	
<i>Teramnus labialis</i> Spreng.	Fabaceae	GEP					•
<i>Tylosema fassoglensis</i> (Schweinf.) Torre & Hillc.	Caesalpinaceae	GEP(L)		•	•		

Species	Family	Life form	Site X	Site B	Site A	Site C	Site D
<i>Triumfetta pentandra</i> A. Rich.	Tiliaceae	THP		•			
<i>Vangueria madagascariensis</i> J. F. Gmel	Rubiaceae	MIP	•				
<i>Vernonia turbinata</i> Oliver	Compositae	GEP					•
<i>Vigna ambacensis</i> Welw. ex Bak.	Fabaceae	GEP(L)/ THP(L)		•			
<i>Vigna unguiculata</i> Savi	Fabaceae	GEP(L)/ THP(L)		•			
<i>Zizyphus abyssinica</i> Hochst. ex A. Rich.	Rhamnaceae	MIP		•	•		
<i>Zizyphus mauritiana</i> Lam.	Rhamnaceae	MEP			•		
<i>Zizyphus pubescens</i> Oliver	Rhamnaceae	MEP	•				
<i>Ximenia americana</i> Linn.	Olacaceae	MIP			•		

