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A reconnaissance survey of the vegetation of the North Luangwa National Park, Zambia

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ABSTRACT

A comprehensive survey of the vegetation of the North Luangwa National Park (NLNP) was carried out over a period of two years. The main aims of the survey were to describe the major vegetation communities in the park and to produce a vegetation map of the NLNP.

Initial differentiation of vegetation units was established by the appearance of the vegetation on aerial photographs. Further information was derived from 353 ground plots in which > 20 000 woody plants were identified and measured. Thirteen broad vegetation types were recognised in the NLNP. Details of their physiognomy, species composition, distribution, topography and edaphic associations are given.

INTRODUCTION

Until the present study, no detailed vegetation survey of Zambia's North Luangwa National Park (NLNP) had been carried out. Naylor *et al.* (1973) and Phiri (1989) have described the vegetation of the Luangwa valley, but in both of these surveys, the area covered is too large and the classification too broad to be useful to park managers. The most detailed study of the region available is that of Astle *et al.* (1969), who surveyed the South Luangwa National Park, the North Luangwa National Park east of the Muchinga Escarpment, and surrounding areas. Habitat classification in this study was based on physiognomic units recognised in a series of landsystems representing all of the topographic units present in the survey area.

The close relationship between vegetation, climate, landsystems, edaphic factors is well established (Cole 1982; Bell 1984), and the rationale for producing a vegetation-based habitat classification of the NLNP was founded on the premise that vegetation is a readily identifiable and measurable facet of habitat (Timberlake *et al.* 1993). In the long term, the vegetation boundaries designated in this study will form part of a geographical information system for the NLNP, together with soil, geological, hydrological, topographical and other information which, combined, will help define habitats for individual species. Justification for studying the vegetation component of habitat as a first step is that a vegetation type is readily discernable to managers and park personnel, people who are not necessarily plant ecologists. Descriptions based on vegetation physiognomy (e.g. woodland, wooded grassland, thicket) and four or five characteristic species should be recognisable to all.

As well as providing a valuable basis for habitat description and monitoring, floristic data are a useful measure of biological diversity. Conservation resources are scarce in Zambia, as in most developing countries, and as a signatory to the Convention on Biological Diversity, Zambia is committed to conserving as much of her biological resource as possible. Clearly, a rational approach to conservation needs to be devised in which limited financial and technical resources can be used to maximum benefit. An essential first step is to carry out a biological resource assessment (Article 7a of the Convention) with the aim of identifying areas of high biodiversity for priority protection. Zambia has set aside 63 585 km^2 (8.5%) of its total land mass as national park and a further 10% is designated as forest reserve. All of these areas require protection, but only a fraction have been subjected to biological inventory. Without such basic inventory, monitoring (Article 7b), identification of adverse processes (7c) and maintenance or management (7d) of the biodiversity resource is impossible. Due to its great topographical diversity, North Luangwa National Park is potentially one of the most biologically diverse of Zambia's protected areas. The results of the present study will help to confirm this and will form baseline data against which future trends in plant diversity can be measured.

This paper describes the major vegetation types present in the NLNP, and presents a vegetation map of the park. A comprehensive checklist of the plants collected during this study is published elsewhere (Smith 1998).

STUDY AREA

The North Luangwa National Park (NLNP) is the most northerly national park in Zambia's Luangwa Valley (Figure 1). It covers an area of 4 636 km^2 (between 11°25' S to 12°20' S and 31°45' E to 32°40' E) and is situated entirely on the west bank of the Luangwa River, which forms its eastern boundary. In the west, the park boundary incorporates part of the Muchinga Escarpment which constitutes approximately 24% (1 113 km^2) of the park's area. The northern boundary of the park is formed by the Lufila River, while in the south, the NLNP is bordered by the Munyamadzi corridor.

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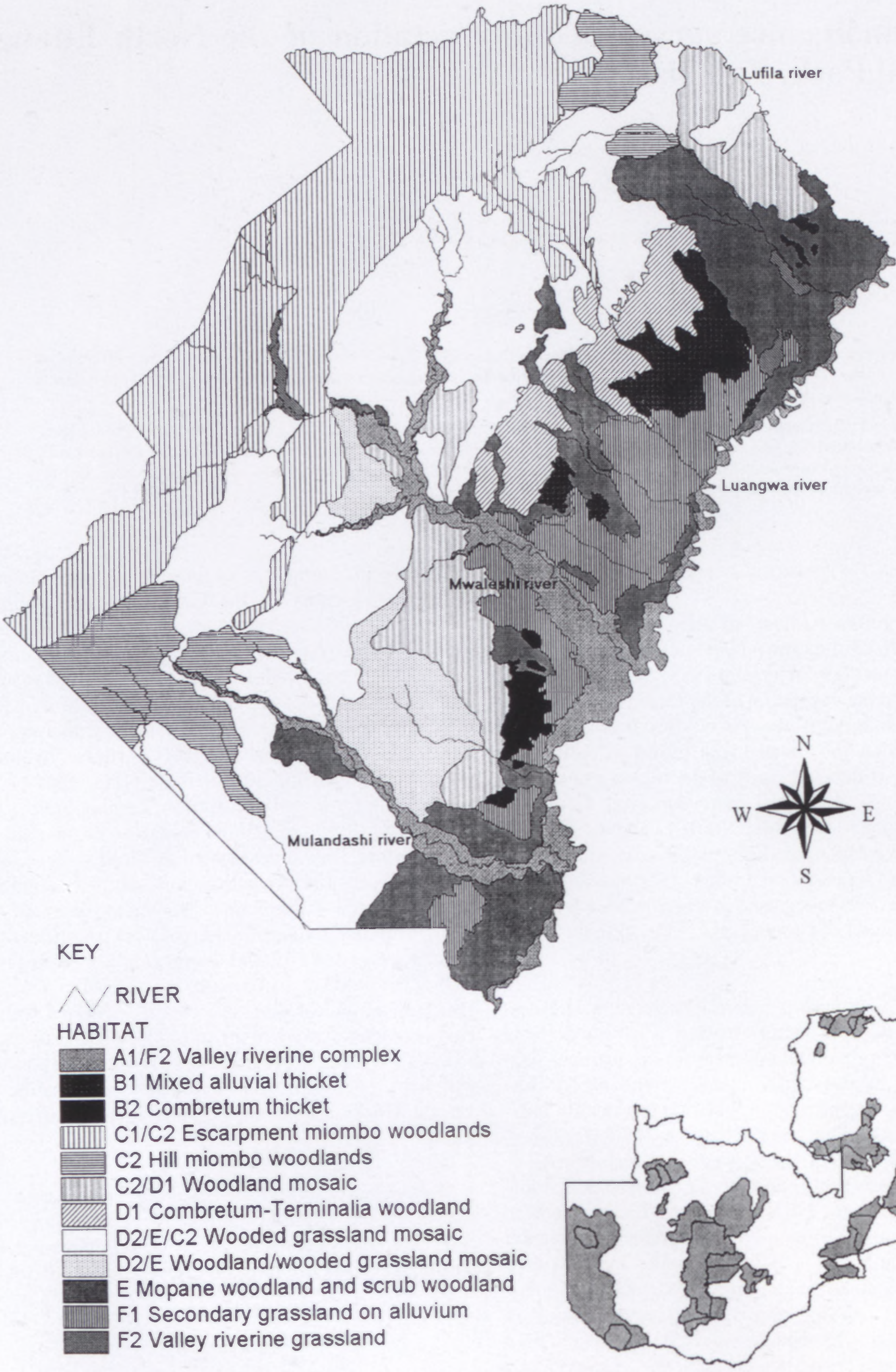

FIGURE 1.—The vegetation of the North Luangwa National Park, Zambia. Scale approx. 1 : 900 000.

Karoo System (Permian) sedimentary rocks form the dominant strata of the valley floor while the escarpments to the east and west of the Luangwa valley are made up of igneous (e.g. granite) and/or metamorphic (e.g. gneiss and quartzite) rocks (Utting 1976). In the NLNP, the elevation of the Luangwa River and its adjacent floodplain is ± 600 m. Topographical relief in this region is only a few metres. Further west, but still on the valley floor, the terrain becomes more dissected (relief 5–50 m) and the elevation rises to between 700 and 800 m. In the far western areas of the park the Muchinga Mountains rise 600–700 m above the valley floor, with the highest peaks within the National Park reaching between 1 200 and 1 300 m. In this area the terrain is deeply dissected with a relief of 500–600 m.

The valley receives a moderate rainfall of between 700 mm and 900 mm per annum, the wet season extending from November through to April. At higher altitudes, on the Muchinga Escarpment and plateau, rainfall is correspondingly higher [mean for the plateau (Mpika), 1 065 mm].

No comprehensive study of the soils of the Luangwa valley has yet been carried out. However, in their land classification study of the South Luangwa National Park (SLNP), Astle *et al.* (1969) described and mapped the heterogeneous soil types of the park according to their association with the vegetation. Soil types range from the deep, red sandy loams of the upper escarpment to the alluvial sands and clays of the Luangwa floodplain.

The NLNP forms part of the Zambezian Regional Centre of Endemism (White 1983) and, due to its great topographical diversity, it probably possesses a greater range of habitats than any other park in Zambia. In the higher (800–1 200 m) deeply dissected terrain of the Muchinga Mountains, miombo woodland predominates, while in the lower (600–700 m) nearly flat valley regions, mopane woodland is the dominant vegetation type. Fire (Naylor *et al.* 1973) and elephant damage (Caughley 1976) have been the most influential factors affecting vegetation in the NLNP in recent years.

METHODS

Site selection and data collection

The approach employed for this survey was essentially inductive, with the primary aim being vegetation description rather than analysis (Kent & Coker 1992). As a first step, the vegetation of the park was stratified according to its macroscopic appearance, and subsequently systematic ground survey was used to provide descriptive detail.

Initial differentiation of vegetation units was carried out using aerial photographs and aerial survey. In this procedure, panchromatic aerial photographs of the NLNP (1983, scale 1 : 34 000) were used to delineate natural vegetation boundaries. Interpretation of the air-photo mosaic was carried out in order to define areas homogeneous in tone and texture, corresponding to homogeneous vegetation types. Thus, physiognomic units (woodland, bushland, grassland etc.) were differentiated and marked on the aerial photographs. Air-photo information was validated and augmented by aerial survey. Homogeneous areas of vegetation (and to a certain extent, their composition) were identified by an observer and positions were recorded using a Garmin inboard Geographical Positioning System (GPS). A total of 116 points were recorded in a systematic transect survey and a further 105 points were recorded on other aeroplane and helicopter flights over the park.

In the second part of the survey, floristic and physiognomic vegetation data were collected in ground studies. Physiognomic classification followed White (1983) (Table 1). A total of 353 belt transects were located within the vegetation types defined in the air-photo mosaic. Placement of transects was not random as an effort was made to cover as many vegetation units (homogeneous areas defined on the aerial photographs) as possible. Other considerations were accessibility and avoidance of ecotones and atypical landscape features e.g. termite mounds, tracks, roads (Walker 1976). Transect positions were determined using a portable GPS (Magellan 5000). Standard transects measured 50 × 5 m (= 250 m^2), rectangular plots being chosen for ease of sampling and to maximise species diversity (Brown 1954; Condit *et al.* 1996). Transects incorporated a minimum of 50 trees/shrubs or at least 15 specimens of a dominant species. Where these criteria were not met, transects were broadened or lengthened accordingly (Taylor & Walker 1978). Within each transect, woody plants (> 1 m in height) were identified, counted and measured (diameter at breast height and estimated height). Herbs and grasses were collected and/or noted at all transect sites.

Samples of all plant species recorded were collected, pressed and dried. Identifications were carried out in herbaria in Lusaka, Kitwe, Harare and Kew. Nomenclature follows *Flora zambesiaca*, *Flora of tropical East Africa* and Lebrun & Stork (1991–1997). Voucher specimens are lodged at the Kew, Missouri and Mount Makulu herbaria. A full checklist of the plants collected in the NLNP is published elsewhere (Smith 1998).

In addition to the vegetation survey, a limited soil survey of the NLNP was carried out and the resulting soil types were related to the plant communities defined above. In order to include the main vegetation types, soil pits were dug beside a vehicle track which transects the park, from Mano Game Scout Camp (11°37' S, 32°02' E) on the Muchinga Escarpment in the west, to the Luangwa River (11°51' S, 32°26' E) in the east. Additional pits were dug between 11°37' S, 32°30' E and 11°33' S, 32°25' E along a cutline parallel to the Lufila River. Soil pits (2 m deep) were dug at ± 2 km intervals within 5–10 m of the track. Soil profiles were measured and photographed and a soil sample (200 g) from each horizon was placed in a plastic bag and retained for further analysis. The displaced soil was returned to the pit and the surface levelled in an attempt to minimise disturbance to the site. Retained soil samples were measured for colour, texture and pH. Colour was determined using Munsell Soil Colour Charts (1949). Soil texture (stoniness, shape of peds, structure, consistency and roots) was described according to Courtney & Trudgill (1988); sand, silt and

TABLE 1.—Physiognomic classification of vegetation from White (1983)

Forest	continuous stand of trees at least 10 m tall, crowns interlocking
Woodland	open stand of trees at least 8 m tall; canopy cover 40% or more; field layer dominated by grasses
Bushland	open stand of bushes, 3–7 m tall; canopy cover of 40% or more
Thicket	closed stand of bushes and climbers, 3–7 m tall
Grassland	land covered with grasses and other herbs; with woody plant cover 10% or less
Wooded grassland	land covered with grasses and other herbs, woody plant cover 10–40%
Scrub woodland	stunted woodland < 8 m tall, or vegetation intermediate between woodland and bushland

clay content of the soil was determined using the hydrometer method (Pramer & Schmidt 1964). Finally, the pH of the soil was recorded using a Kel soil tester (for acidity and soil moisture).

Data analysis and interpretation

Ground study provided detailed information on vegetation structure and composition. Thus, for each vegetation unit delineated from the aerial photographs, it was possible to: 1, list plant species; 2, calculate tree/shrub density, expressed as n ha^{-1} (Brown 1954); 3, calculate woody biomass, expressed as t ha^{-1} using the following formulae developed in similar habitats in Sengwa, Zimbabwe by Guy (1981):

$$\text{Tree biomass (Kg)} = 0.0549 \times (\text{diameter at breast height})^{2.5101}$$
$$\text{Shrub biomass (Kg)} = 1.2102 \times (\text{canopy volume})^{0.9138}$$

4, determine dominant species by calculation of importance values (Curtis & McIntosh 1951) for each species according to the formula:

$$\text{Importance value} = \text{relative frequency} + \text{relative density} + \text{relative dominance}$$

Ground study data permitted further division of vegetation units according to the floristic criteria above and the environmental information collected from each plot (altitude, soil type, topography).

Vegetation types were described in terms of their typical vegetation structure, characteristic woody species, associated grass and herb species, soils, geology, topography, distribution and area covered.

Map production

A preliminary working vegetation map of the NLNP was derived from the 1983 panchromatic aerial photographs. Transparent overlays marked with the vegetation boundaries delineated on the aerial photographs were reduced from a scale of 1 : 34 000 to a scale of 1 : 250 000 on a photocopier (Xerox U.K. Ltd). This reduction was then superimposed onto the 1 : 250 000 UTM Ordnance Survey maps of the NLNP (no. SD-36-2 and SC-36-14) and redrawn. This rough map was used as a working image upon which ground survey could be based.

A second more accurate, more detailed and up to date vegetation map (scale 1:100 000) was produced from a partial scene (90 × 90 km) LANDSAT TM satellite image (Band 4, 7th July 1995), georeferenced and geocoded to UTM map projection (Satellite Applications Centre, Pretoria). The image was supplied by SAC as digital data (EOSAT Fast Format) on CD-ROM, which was processed into a photographic image (Hunting Technical Services, UK) upon which vegetation boundaries could be marked by hand. The vegetation types delineated on this image were assigned according to the aerial and ground survey results presented below and the end result is a map incorporating 11 broad vegetation types and in which vegetation mosaics are indicated (Figure 1). This map was digitised using PC ARC/INFO (Kent Cassells, DICE, UK) and incorporated into the beginnings of a Geographical Information System (GIS) for the NLNP. More detailed vegetation data, as well as information about geology, topography, water relations, plant-animal interactions, etc. can all be incorporated into this database in the future in order to build up a more complete picture of the park ecosystem.

RESULTS AND DISCUSSION

During this study, the vegetation of the NLNP was stratified into six floristic classes, divided into 13 distinct vegetation types. Vegetation type distributions are shown in Figure 1, with the exception of types A2 and F3, the areas of which are too small to be shown at this scale.

The vegetation descriptions below are largely based upon quantitative tree/shrub data from sample sites. The herbaceous component is described from qualitative data and collection material. Further division of vegetation types into subtypes is based on substrate. A detailed description of all vegetation types and subtypes is given below. Key characteristics of woody vegetation types are given in Table 2.

A. RIPARIAN FORESTS, WOODLANDS AND THICKET

This vegetation class comprises moist forests to woodlands and thicket fringing perennial and seasonal watercourses. At lower altitudes (600–700 m) valley riverine fringe vegetation takes the form of woodland (usually with a well-developed shrub layer), and thicket. It should be noted that even on the valley's perennial rivers (Luangwa, Lufila and Mwaleshi), fringe woodland and thicket is discontinuous, being interspersed with other vegetation types such as riverine grassland (F2) and/or non-riverine vegetation types. This is even more noticeable on seasonal watercourses where fringe riverine trees are usually mingled with trees and shrubs characteristic of adjacent vegetation types. At higher altitudes (800–1 300 m), on the Muchinga Escarpment, riverine fringe vegetation takes the form of dense evergreen forest which, on the larger watercourses, may extend to adjacent swampy areas. This vegetation type tends to be well developed and distinctive (although narrow) even on the smaller, seasonal watercourses.

Valley riverine woodland (A1), as described in the present study, is readily recognisable in the Luangwa valley surveys of Astle *et al.* (1969), Naylor *et al.* (1973) and Phiri (1989) (Table 3). Escarpment riverine forest (A2) however, is not described in detail in any of the above studies but is covered thoroughly by Fanshawe (1971). Vegetation type A2 contains elements of Fanshawe's 'Riparian forest' (p. 34) and 'Swamp forest' (p. 32).

A1. **Valley riverine woodland and thicket**

The Luangwa River lies at an altitude of ± 600 m and topographical relief is only a few metres. The large tributaries of the Luangwa in the NLNP are the Lufila, Mwaleshi and Mulandashi Rivers. These rivers emerge from the Muchinga Escarpment in the west at an altitude of between 700 and 800 m. Topographical relief along

TABLE 2.—Summary of woody vegetation data in the NLNP from aerial and ground survey results

Vegetation type	Description	Mean no trees/ha	Mean woody biomass T/ha	Soil type	Terrain	Elevation (m)	Ground survey dominant species (importance values)
A1	Valley riverine woodland and thicket	*	*	recent alluvium	flat	600–800	*Combretum obovatum* (49.0) *Combretum fragrans* (48.0) *Kigelia africana* (39.8) *Feretia aeruginescens* (30.2)
A2	Escarpment riverine forest	5 492	275.3	alluvial/ colluvial	deeply dissected	800–1 300	*Syzygium cordatum* (53.9) *Rothmannia whitfieldii* (43.2) *Craterispermum schweinfurthii* (30.4)
B1	Mixed alluvial thicket	2 023	157.9	alluvium	flat	600–650	*Vangueria infausta* (57.8) *Diospyros quiloensis* (49.6)
B2	*Combretum* thicket	2 112	74.3	alluvium	flat	600–650	*Combretum elaeagnoides* (126.7) *Combretum celastroides* (37.0)
C1	Upper escarpment miombo woodland	2 444	95.2	laterite, deep	deeply dissected	1 000–1 300	*Brachystegia stipulata* (70.3) *Memecylon flavovirens* (37.4) *Brachystegia utilis* (36.3)
C2	Lower escarpment and hill miombo woodland	s1: 3 649 s2: 1 065	39.3 98.9	stony, shallow or deep	dissected	700–1 000	*Julbernardia globiflora* (84.6) *Brachystegia allenii* (34.0) *Diplorhynchus condylocarpon* (33.7)
D1	*Combretum-Terminalia* woodland	1 841	52.5	sandy, deep	flat	650–700	*Terminalia sericea* (91.2) *Combretum zeyheri* (52.9) *Combretum molle* (39.4)
D2	*Combretum-Terminalia-Diospyros* wooded grassland	1 722	8.9	variable, shallow	undulate	650–800	*Diospyros kirkii* (68.7) *Terminalia stenostachya* (66.1) *Combretum apiculatum* (33.9)
E1	*Colophospermum* woodland	781	219.3	cracking clays	flat	600–800	*Colophospermum mopane*
E2	*Colophospermum* scrub woodland	3 437	77.1	cracking clays	flat	600–1 000	*Colophospermum mopane*

* Data not available, due to the discontinuous nature of A1 Valley riverine woodland and thicket.

these watercourses varies from as much as 5–50 m near the escarpment to only a few metres at the Luangwa confluences.

Valley riverine woodland and thicket is associated with the rich, recently deposited alluvial soils which lie adjacent to the rivers of the valley floor. This alluvial belt may only be a few metres wide or, along the Luangwa and its major tributaries, may extend many hundreds of metres from the river. Riverine valley soils show considerable diversity and cannot be assigned to any one soil class. In general, these are deep, stoneless, clearly stratified soils which vary in texture from sands to clays (see vegetation type F2). Soil pH is usually around neutral but ranges from pH 5.6 to pH 6.9. Soil colour varies from light yellow brown to dark grey.

The fringe woodland of the valley's perennial and seasonal rivers is generally two-storeyed in structure, with canopy trees reaching 20 m or higher and a well-developed shrub layer, which may extend to form areas of bushland or thicket. Characteristic tall trees include *Kigelia africana, Diospyros mespiliformis, Trichilia emetica, Lonchocarpus capassa, Colophospermum mopane, Combretum imberbe, Faidherbia albida, Sclerocarya birrea* and *Tamarindus indica* (invariably associated with termitaria). Other less frequent but typical large trees include *Breonadia salicina* and *Khaya nyasica*. Commonly occurring small trees and shrubs are *Piliostigma thonningii, Ziziphus abyssinica, Oncoba spinosa, Feretia aeruginescens, Flueggea virosa, Antidesma venosum, Phyllanthus reticulatus, Acacia sieberiana* and *A. polyacantha* subsp. *campylacantha*. Amongst the thicket-forming shrubs, the genus *Combretum* is well represented: *C. obovatum* (on clay), *C. fragrans* and *C. imberbe* (as a shrub) are all common. *C. fragrans* may form areas of bushland in which it is the single dominant species. Other frequent thicket-forming species are *Diospyros senensis* (on sand), *Keetia zanzibarica* and *Friesodielsia obovata*. Climbers in this vegetation type include *Jasminum fluminense, Abrus precatorius* and *Dregea macrantha*. The grass layer associated with well-developed fringe woodland or thicket is sparse and confined to shade-loving species such as *Panicum maximum, Phyllorachis sagittata* and *Setaria homonyma*. Herbs typical of the stratified soils of the larger rivers of the valley floor include *Senna obtusifolia, Indigofera tinctoria, Sida alba, Vernonia glabra* and spp., *Duosperma* spp., *Corchorus* spp. and *Ocimum* spp.

On the major rivers such as the Luangwa, Lufila, Mwaleshi and Mulandashi, vegetation type A1 occurs in a substrate-dependent mosaic with the riverine herbaceous habitats described in vegetation type F2.

A2. Escarpment riverine forest

This forest is found fringing the rivers and streams of the Muchinga Mountains in the west of the NLNP. Elevation ranges from 800–1 300 m and the terrain is deeply dissected with relief measured in hundreds of metres. The igneous/metamorphic geology of the Mu-

TABLE 3.—Comparison of vegetation classifications of the Luangwa valley in past and present surveys

Present survey	Astle *et al.* 1969	Naylor 1973	Phiri 1989
A1 Valley riverine woodland	Riparian forest landsystem 1: facets 1–4 landsystem 3: facets 3–4	1. Riparian forest	1. Riparian woodland
A2 Escarpment riverine forest	Riparian forest landsystem 8: facet 2	*	1. Riparian woodland
B1 Mixed alluvial thicket B2 *Combretum* thicket	Thicket on freely draining alluvium landsystem 2: facet 4	2. *Kigelia–Combretum* type e. thicket	8. Thickets
C1 *Brachystegia–Julbernardia–Isoberlinia* upper escarpment and plateau miombo woodland	*	4. Miombo type a. miombo woodland	7. Miombo woodland
C2 *Julbernardia–Brachystegia* lower escarpment and hill miombo		4. Miombo type a. miombo woodland	7. Miombo woodland
Subtype 1: scrub woodland	Miombo woodland and scrub on shallow soils landsystem 4: facet 2 landsystem 8: facet 1		
Subtype 2: woodland	Miombo woodland on deep soils landsystem 4: facet 1 landsystem 7: facet 1 landsystem 9: facet 1		
D1 *Combretum–Terminalia* woodland	*Terminalia–Erythrophleum* woodland savanna landsystem 2: facet 3	3. *Combretum–Terminalia* type a. Com–Term woodland	4. *Erythrophleum* woodland
D2 *Combretum–Terminalia–Diospyros* wooded grassland	Miombo scrub on shallow soils landsystem 3: facet 1 landsystem 5: facet 1	4. Miombo type b. scrub miombo woodland c. mopane	11. Savanna?
E1 *Colophospermum* woodland	Mopane woodland landsystem 2: facets 2,5a	2. *Kigelia–Combretum* type d. mopane	6. Mopane woodland
E2 *Colophospermum* scrub woodland	Mopane woodland landsystem 2: facet 5b	3. Com–Term type c. mopane	6. Mopane woodland
F1 *Chloris–Dactyloctenium–Echinochloa* secondary grassland	*Echinochloa* grassland landsystem 1: facet 7	*	9. Grasslands
F2 Valley riverine grassland	Floodplain grassland landsystem 1: facets 1b, 5a Woodland savanna landsystem 1: facet 4b	*Kigelia–Combretum* type a. Kig–Com woodland b. dambos c. mudflats g. pointbar grasses	9. Grasslands
F3 *Loudetia simplex–Hyparrhenia* dambo grassland	*	*	*

* not applicable.

chinga Escarpment means that many of its rivers pass through rocky terrain (granite, quartzite) and waterfalls are common.

Soils associated with this vegetation type are very variable in texture and tend to be alluvial on the valley bottoms and colluvial on the valley sides.

On the Muchinga Escarpment, rivers and streams are bounded by dense, usually 3-storeyed evergreen forest (known as *Mushitu* in CiBemba) which may extend to adjacent swampy areas. The canopy is closed and the trees from which it is formed may be 20 m or more in height. Characteristic tall trees in this vegetation type include *Syzygium cordatum, Breonadia salicina, Cleistanthus polystachyus, S. guineense* subsp. *afromontanum, Uapaca lissopyrena, U. sansibarica* and *Apodytes dimidiata*. Other less frequent, but characteristic large trees include *Parkia filicoidea, Sapium ellipticum, Tabernaemontana pachysiphon* and *Xylopia rubescens. Monopetalanthus trapnellii* is locally common on the Mwaleshi River and can form extensive stands of forest in which it is the single dominant species. Characteristic understorey species are *Antidesma vogelianum, Englerophytum magalismontanum, Craterispermum schweinfurthii, Faurea saligna, Garcinia smeathmannii* and *Bersama abyssinica*. Shrubs include *Diospyros natalensis, Rothmannia whitfieldii, Cremaspora triflora, Rhus longipes, Tricalysia coriacea, Lasianthus kilimandscharicus* and *Erythroxylum emarginatum*. Climbers typical of this habitat are *Carissa edulis, Sabicea laurentii, Smilax anceps, Phyllanthus muelleranus, Clematis welwitschii, Artabotrys* spp. and *Strychnos* spp. *Oxytenanthera* bamboo is locally common on escarpment streams and rivers. Where A2 fringing forest is a narrow belt of riparian trees, grasses and herbs associated with dambo margins occur (see F3). Common grass species include *Loudetia simplex, Trachypogon spicatus, Cleistachne sorghoides,* *Hyparrhenia* spp., *Pennisetum* spp. and *Setaria* spp. Characteristic subshrubs and herbs are *Acalypha chirindica, Urena lobata, Polygala exelliana, Phaulopsis imbricata, Droogmansia pteropus, Helichrysum* spp., *Tinnea* spp. and *Dissotis* spp. Where riparian forest extends into seasonally flooded swamp forest, or *Monopetalanthus* forest, the forest floor is carpeted with moss, and ferns are common (*Asplenium, Adiantum, Pellaea*). Epiphytes may also occur. Herbs in this habitat include *Geophila obvallata, Schwartzkopffia lastii, Leptactina benguellensis* and *Biophytum* spp. *Sclerochiton vogellii* is locally common in *Monopetalanthus* forest.

B. BUSHLANDS AND THICKET

Both vegetation types described below are characterised by thicket species which form closed stands. However, in some places more open stands occur and therefore vegetation types B1 and B2 are best regarded as mosaics of bushland and thicket. Both Mixed alluvial thicket (B1) and *Combretum* thicket (B2) are confined to the alluvial areas adjacent to the valley's larger rivers (Luangwa, Mwaleshi). Together, vegetation types B1 and B2 cover an area of approximately 180 km^2, and seem to occupy a niche on soils of an intermediate nature between the low, poorly drained clays of vegetation type F1 and the higher, sandy soils of vegetation type D1. Mixed alluvial thicket is the characteristic thicket vegetation type north of the Mwaleshi River, while *Combretum* thicket largely occurs to the south of the Mwaleshi. Both types are dominated by different species of thicket-forming shrubs, but share many species in common. The absence of *C. elaeagnoides* and *C. celastroides* in large areas of Mixed alluvial thicket, north of the Mwaleshi River, which led to the distinction being made in the present survey, is apparently a local phenomenon because these two species do occur further north, on the Lufila River. The reason for their absence in the middle of the park is unknown, and requires further study.

Astle *et al.* (1969) make no distinction between Mixed alluvial thicket (B1) and *Combretum* thicket (B2), referring to this vegetation type as 'Thicket on freely draining alluvium'. Their species list for this vegetation type contains the dominant elements of both B1 and B2.

B1. **Mixed alluvial thicket**

This vegetation type is found on the alluvial soils associated with the Luangwa River in the east of the park and is the characteristic thicket vegetation type north of the Mwaleshi River. Elevation in this area is between 600 m and 625 m and the terrain undulates slightly with a relief of only a few metres. This vegetation type is frequently found in mosaic with *Chloris–Dactyloctenium–Echinochloa* secondary grassland (F1) but occupies higher ground and better drained, sandy soils so that while the surrounding grassland becomes waterlogged during the wet season, the areas of thicket remain comparatively dry.

Soils associated with this vegetation type are freely draining and are typically pale brown to orange, stoneless, sandy clay loams (60–75% sand) of slightly acid to neutral pH (pH 6.5–7.0).

Vegetation type B1 comprises closed and open stands of bushes 2–7 m high with occasional tall trees. *Colophospermum mopane* is present to a greater or lesser extent. It is found in clumps on patches of calcareous or sodic clay soil but also as individual, usually tall trees dotted throughout the habitat. Other occasional tall trees include *Xeroderris stuhlmannii, Pseudolachnostylis maprouneifolia, Stereospermum kunthianum* and *Adansonia digitata*. Common smaller trees are *Boscia angustifolia, Excoecaria bussei* (also a shrub) *Schrebera trichoclada* and *Diospyros quiloensis* (occasionally a large tree). Vegetation type B1 is dominated by the shrubs *Croton gratissimus, Friesodielsia obovata, Mundulea sericea, Combretum obovatum, Vangueria infausta, Markhamia obtusifolia* and *M. zanzibarica*. *Baphia massaiensis* is locally common. The grass and herb layer is not well developed in Mixed alluvial thicket but contains elements of vegetation types D1, E1 and F1. Grasses include *Digitaria acuminatissima, Sporobolus cordofanus, Urochloa mossambicensis, Dactyloctenium* spp. and *Chloris* spp. In the wetter sump areas, *Brachiaria deflexa, Sporobolus pyramidalis* and *Setaria* spp. are characteristic. Common herbs are *Hibiscus cannabinus, H. calyphyllus, Cleome monophylla, C. hirta, Senna absus, Blepharis tenniramea, Clerodendrum* spp. and *Duosperma* spp.

B2. ***Combretum* thicket**

This is the characteristic thicket type south of the Mwaleshi River. Elevation is ± 600–620 m and the terrain is flat with a relief of only a few metres. As with Mixed alluvial thicket (B1), *Combretum* thicket is found on alluvial, sandy soils close to the Luangwa and Mwaleshi Rivers.

Vegetation type B2 is comprised of thicket-forming shrubs, 2–7 m in height, which grow in a mosaic of closed and open stands. The grass layer is not well developed. Tall trees are rare but species such as *Manilkara mochisia* and *Diospyros quiloensis* may occur infrequently. Small trees found in *Combretum* thicket include *Schrebera trichoclada* and *Combretum collinum* subsp. *gazense*. The dominant shrubs are *Combretum elaeagnoides, C. celastroides, C. obovatum, Holarrhena pubescens, Vangueria infausta* and *Markhamia* spp. Grasses and herbs associated with this habitat are the same as those in vegetation type B1.

C. MIOMBO WOODLANDS

The miombo woodlands of North Luangwa National Park cover an area of approximately 1 300 km^2. This is the dominant vegetation type of the Muchinga Escarpment and its attendant foothills, Chinshenda, Soma and the Mvumvwe range. The vegetation described under the umbrella of miombo woodlands is physiognomically diverse, ranging from closed woodland to open woodland to scrub woodland. For the purposes of this classification, miombo woodland in the NLNP has been divided into two types, C1 Upper escarpment and C2 Lower escarpment/hill miombo woodland, a division largely based on floristic composition. Further division into subtypes is dependent on substrate.

Miombo woodland is clearly recognised in all three of the previous valley surveys (Table 3). Further descriptions are available from Trapnell (1953) and from Fanshawe (1971).

C1. *Brachystegia–Julbernardia–Isoberlinia* upper escarpment and plateau miombo woodland

At elevations over 1 000 m, this is the most important and extensive vegetation type of the Muchinga Escarpment. It can be separated into three distinct vegetation subtypes dictated by substrate. Subtype 1 occurs over most of the upper escarpment, on deep laterite soils. Subtype 2 is rare in the NLNP and is found in isolated patches on shallower plateau soils. Subtype 3 is associated with the granite outcrops dotted throughout the escarpment terrain.

Vegetation type C1 (subtype 1) corresponds to Trapnell's E and E1 types (Trapnell *et al.* 1950), which occur on the deep soils of the escarpment, as evidenced by the dominance of *Brachystegia utilis* and *B. spiciformis*, species which cannot tolerate shallow soils (Fanshawe 1971). The tall trees and comparatively sparse grass layer seen in this vegetation type are probably due to the improved drainage and better soils associated with the dissected terrain (Cole 1963). In this vegetation type, laterite was more commonly found as nodules in the B horizon rather than the impermeable layer characteristic of the pediplain plateau soils (C1 subtype 2). Subtype 2 corresponds to Trapnell's P4 type (Trapnell *et al.* 1950), and Subtype 3 is described by White (1983) as 'Zambezian rupicolous bushland and thicket'.

Subtype 1. *Upper escarpment miombo woodland*: is the dominant vegetation type of the upper Muchinga Escarpment in the west of the NLNP, and is found at elevations ranging from 1 000 to > 1 300 m over deeply dissected terrain where relief is measured in hundreds of metres.

Subtype 1 is associated with deep, red, stoneless sandy loams or sandy clays. These soils are slightly acid (pH 6.6–7.0) and usually contain laterite nodules and mica aggregates in the B horizon.

This woodland takes the form of a clearly two-storeyed woodland with an open to lightly closed canopy of semi-evergreen trees 15–20 m high. Characteristic canopy trees include *Julbernardia paniculata, Brachystegia spiciformis, B. utilis, Isoberlinia angolensis, Marquesia macroura, Parinari curatellifolia, B. manga* and *Pericopsis angolensis*. Common lower storey trees are *Brachystegia stipulata, Uapaca kirkiana* and spp., *Craterosiphon quarrei, Phyllocosmos lemaireanus, Memecylon flavovirens, Dalbergia nitidula, Combretum zeyheri, B. longifolia, Anisophyllea pomifera, Diplorhynchus condylocarpon* and *Pseudolachnostylis maprouneifolia*. Frequent shrubs are *Keetia gueinzii, K. venosa, Rothmannia engleriana, Landolphia parvifolia* and *Protea* spp. Climbers are infrequent in this vegetation type, *Strophanthus welwitschii* being a notable exception. In upper escarpment miombo woodland, the grass layer is sparse and generally restricted to scattered clumps of predominantly tall grasses. Common species are *Andropogon chinensis, A. schirensis, Anthephora elongata, Heteropholis sulcata, Loudetia simplex, Sporobolus sanguineus* and *Trichopteryx fruticulosa*. The herb layer is sparse but varied. *Pteridium aquilinum* subsp. *centrali-africanum* is locally common, and sedges such as *Ascolepis elata, Carex echinochloe* subsp. *nyasensis, Bulbostylis* spp., *Cyperus* spp. and *Scleria* spp. are found in poorly drained areas. Frequent subshrubs are *Psychotria spithamea, P. eminiana, Indigofera emarginelloides, Tapiphyllum cinerascens, Desmodium barbatum* and *Kotschya* spp. Typical herbs include *Costus spectabilis* and *Siphonochilus rhodesicus* at the beginning of the rains, followed by *Thunbergia kirkiana, Endostemon dissitifolius, Hybanthus enneaspermus, Otiophora scabra, Nidorella spartioides, Rhynchotropis poggei, Aspilia* spp., *Becium* spp., *Spermacoce* spp., *Tephrosia* spp. and *Triumfetta* spp.

Subtype 2. *Plateau miombo woodland*: occurs in isolated patches in the far west of the NLNP, and is associated with flat terrain. Plateau soils tend to be shallow, poor in nutrients and humus, slightly acid, and are typically leached, with a laterite or gley horizon near the surface. In contrast to upper escarpment miombo woodland, plateau miombo woodland is of single storey structure and is characterised by stunted *Brachystegia–Julbernardia*, interspersed with *Uapaca, Protea, Faurea* and *Monotes* species. In addition, the shrub and grass layers are comparatively well developed, with *Hyparrhenia* and *Andropogon* spp. predominant. This subtype occurs on the comparatively shallow, infertile soils of the plateau peneplain and over large areas of Zambia appears to be secondary miombo woodland which has been subjected to repeated fires and cultivation (Fanshawe 1971).

Subtype 3. *Rupicolous miombo woodland*: the rocky outcrops and granite kopjes of the Muchinga Escarpment support a distinctive vegetation type and although many of the taxa listed above may occur, additional species such as *Brachystegia microphylla, Pterocarpus rotundifolius, Schrebera trichoclada, Kirkia acuminata, Landolphia parvifolia* and *Tarenna neurophylla* are typical. *Carphalea pubescens* is a characteristic subshrub.

C2. *Julbernardia–Brachystegia* lower escarpment and hill miombo woodland and scrub woodland

This woodland covers much of the lower Muchinga Escarpment and its attendant foothills, Chinshenda, Soma and the Mvumvwe range. It is also found on the upper valley floor where it may intergrade with vegetation types D1 and D2.

Vegetation type C2 can be separated into two subtypes according to substrate and vegetation physiognomy. Subtype 1 is miombo scrub woodland, associated with the thin, eroded, stony soils of the hill slopes. Subtype 2 is open woodland, found on the deeper soils of the interfluves and flatter sites.

Vegetation type C2, subtype 1 (scrub woodland) is recognised by Astle *et al.* (1969) who refer to it as 'Miombo scrub on shallow soils'. This type is also described by White (1983), in a direct reference to the Luangwa valley (p. 99). Fanshawe (1971), Naylor *et al.* (1973) and Phiri (1989) all refer to this distinctive form of miombo as 'Scrub miombo woodland'. Vegetation type C2, subtype 2 (woodland) is designated 'Miombo woodland on deep soil' by Astle *et al.* (1969). Phiri (1989) cites *Brachystegia boehmii, B. bussei, B. manga* and *Julbernardia globiflora* as common taxa in this habitat.

Subtype 1. *Brachystegia stipulata–Julbernardia globiflora miombo scrub woodland*: occurs at elevations ranging from 700–1 000 m and is the most extensive vegetation type of the lower Muchinga Escarpment, where it occurs in mosaic with subtype 2. It also intergrades with vegetation types D1 and D2 on the upper valley floor.

Subtype 1 occurs on the shallow, slightly acid (pH 6.6–6.9) light grey to yellowish brown, generally stony sandy clay loam soils (lithosols and shallow fersiallitic soils) associated with the hill slopes of the lower escarpment and foothills.

The vegetation takes the form of 3–5 m tall scrub woodland, in which there are very few tall trees, *Brachystegia bussei* being an infrequent exception. In this habitat the vegetation is dominated by *Julbernardia globiflora, Brachystegia allenii* and *B. stipulata* in stunted form. *B. manga* is locally dominant on Chinshenda hill. Other common small trees and shrubs are *B. boehmii, Diplorhynchus condylocarpon, Combretum zeyheri, Pseudolachnostylis maprouneifolia* and *Monotes africanus*. The grass layer is sparse, but similar in composition to that found in vegetation types C1 and D2. Typical grasses are *Trichopteryx fruticulosa, Tristachya bequaertii, Diheteropogon amplectens, Sporobolus myrianthus, Andropogon* spp. and *Melinis* spp. Common subshrubs include *Ochna leptoclada, O. richardsiae* and *Cyphostemma* spp. Characteristic herbs are *Chlorophytum rubribracteatum, Ectadiopsis producta, Endostemon dissitifolius, Indigofera sutherlandoides, Justicia striata, Zygotritonia nyassana, Becium* spp. and *Commelina* spp.

Subtype 2. *Julbernardia–Brachystegia open miombo woodland*: is found in the deeply dissected terrain of the lower Muchinga Escarpment and its foothills, where it occurs in mosaic with miombo scrub woodland (Subtype 1). It also intergrades with the Combretaceae woodlands and wooded grasslands, D1 and D2, on the upper valley floor.

Subtype 2 is found on the deep, yellowish brown slightly acid, sandy soils associated with the hill tops and ridges of the lower escarpment and foothills.

The vegetation takes the form of open woodland with scattered tall trees (15–20 m) and a well-developed grass layer, dominated by tall species. Shrub patches are occasional. Characteristic tall trees include *Burkea africana, Julbernardia globiflora, Pericopsis angolensis* and *Brachystegia allenii*. Common small trees include *Brachystegia stipulata, Combretum zeyheri, C. psidioides, Terminalia sericea,* and *Oldfieldia dactylophylla*. The shrub layer is reduced but includes *Ozoroa insignis, Diplorhynchus condylocarpon, Vernonia glaberrima* and *Lannea discolor* (also a small tree). Common grasses are *Andropogon chinensis, A. gayanus, A. schirensis, Hyparrhenia anemopaegma, H. filipendula, Hyperthelia dissoluta* and *Tristachya superba*. Like the grasses, the herb component is related to that of vegetation types D1 and D2 (below); typical species include *Acalypha allenii, A. villicaulis, Barleria fulvostellata, Dicoma anomala,* and *Agathisanthemum* spp.

D. COMBRETACEAE WOODLAND AND WOODED GRASSLAND

This vegetation class is dominated by (distinct) species of the genera *Combretum* and *Terminalia*. Both vegetation types described below have well-developed grass layers.

Vegetation type D1, *Combretum–Terminalia* woodland, closely resembles the '*Terminalia sericea* tree savanna' of Wild & Barbosa (1967). White (1983) refers to it as 'North Zambezian undifferentiated woodland', comprising miombo associates but not *Brachystegia/Julbernardia* species. Fanshawe (1971) groups this vegetation type together with the miombo woodlands of the valley floor, but refers to it as '*Erythrophleum* woodland'. The classification of the present survey is largely based on floristic composition and our ground survey data strongly indicates that vegetation type D1 does not fall into the miombo class. *Brachystegia/Julbernardia* species do occur in the ecotones where vegetation type C2 intergrades with *Combretum–Terminalia* woodland, but elsewhere they are never dominant and over large areas of this woodland, particularly in the east, they do not occur at all. Astle *et al.* (1969) and Phiri (1989) refer to this vegetation type as '*Terminalia sericea–Erythrophleum africanum* woodland savanna' and '*Erythrophleum* woodland' respectively (Table 3). This nomenclature can be related to our results in that *E. africanum* is an important component of this vegetation type. However, in the NLNP at least, *Combretum/ Terminalia* species are more frequent, more abundant and account for more woody biomass than *E. africanum*. Like us, Naylor *et al.* (1973) refer to this vegetation type as '*Combretum–Terminalia* woodland'.

Astle *et al.* (1969) classify vegetation type D2, *Combretum–Terminalia–Diospyros* wooded grassland, under 'Miombo scrub on shallow soils', although they do make a topographic distinction between this habitat (3;1 and 5;1) and vegetation type C2 subtype 1 (4;2 and 8;1). In Astle's updated landsystem/vegetation map (Astle 1989) a further land facet is added (landsystem 7; facet 6) in which this vegetation type is described as: 'semi-deciduous scrubland with local variation in species composition. A mopane and *Terminalia stenostachya* association on the flatter sites. *Brachystegia stipulata, Combretum apiculatum, Julbernardia globiflora* association in areas of greater relief.' This is a landsystem description incorporating the floristic mosaic described below, of which vegetation type D2 is the non-miombo component.

D1. *Combretum–Terminalia* woodland

Vegetation type D1 is characterised by fire-tolerant, sandy soil species (e.g. *Terminalia sericea*) and bears a close resemblance to other high grass-woodland vegetation types such as the *Burkea–Erythrophleum* woodlands of western Zambia and the *Chipya* woodlands of the Bangweulu region (Trapnell *et al.* 1950). The common herbaceous indicators of lake basin *Chipya*, *Aframomum alboviolaceum*, *Smilax anceps* and *Pteridium aquilinum* are not a feature of this habitat, but like *Chipya* woodland (Lawton 1978), it is probable that vegetation type D1 is maintained by the fierce dry season fires which sweep through the NLNP every year. *Combretum–Terminalia* woodland is found in close association with thicket (B1/B2), both vegetation types occupying a belt of deep, sandy soil running parallel to the Luangwa River. The relationship between thicket and woodland is not clear, but it is possible that the two vegetation types are determined by edaphic factors. In certain (western) areas of the park, this woodland intergrades with hill miombo woodland (C2). It covers large areas of the valley floor (180 km^2 in addition to 313 km^2 in mosaic with vegetation type C2) over elevations ranging from 650 m to 700 m. It is generally associated with flat terrain where relief is only up to 10 m.

Soils associated with this vegetation type are deep, light brown to orange and are mildly acidic to neutral (pH 6.4–7.0). These soils are characterised by a very high sand content (70–90%) and are probably colluvial (or old alluvial) and derived from Karoo sandstone.

Combretum–Terminalia woodland takes the form of open 1- or 2-storeyed deciduous woodland. Canopy species may be up to 20 m tall. The grass layer is tall and well developed. The tall trees found in this habitat are dominated by *Terminalia sericea* (up to and above 15 m high), *Pseudolachnostylis maprouneifolia*, *Pericopsis angolensis*, *Burkea africana*, *Erythrophleum africanum* and *Amblygonocarpus andongensis*. Common small trees and shrubs are *Combretum molle*, *C. collinum* subsp. *gazense*, *C. zeyheri*, *Bridelia cathartica*, *Crossopteryx febrifuga* and *Baphia massaiensis*. On the deep soils of this type, the grass layer is well developed with both tall and short grasses. Common tall grasses are *Andropogon schirensis*, *A. gayanus*, *A. chinensis*, *Hyparrhenia anemopaegma*, *H. filipendula*, *Pogonarthria squarrosa* and *Tristachya superba*. Shorter species are *Aristida scabrivalvis*, *Digitaria gayana*, *D. acuminatissima*, *Heteropogon contortus* and *Sporobolus festivus*. Characteristic subshrubs include *Senna petersiana*, *Cissus cornifolia* and *Euphorbia matabelensis*. The herb component is dominated by ground creepers of the family Vitaceae and includes *Cyphostemma gigantophyllum*, *C. hermannioides*, *C. viscosum* and *Cissus nigropilosa*. Other typical herbs are *Polycarpaea corymbosa*, *Hypoestes forskaolii*, *Tricliceras* spp. and *Phyllanthus* spp.

D2. *Combretum–Terminalia–Diospyros* wooded grassland

In the NLNP, vegetation type D2 occurs in mosaic with mopane (E1/E2) and hill miombo (C2) throughout its range (see map, Figure 1). The *Combretum apiculatum/Terminalia stenostachya/Diospyros kirkii* association (vegetation type D2) is the most extensive vegetation type in this mosaic, as it occurs on the shallow, stony fersiallitic soils which cover the gentler slopes and flatter regions of the upper valley floor. Hill miombo (C2 subtype 2) occurs in isolated patches on the deeper soils of the ridge tops, while scrub miombo (C2 subtype 1) occurs on the thin rocky soils of the steeper slopes. Mopane woodland and scrub woodland (E1 and E2) occur on sodic or calcareous patches of soil dotted throughout the upper valley floor. This grassland, in mosaic with vegetation types E1, E2 and C2, covers an area of approximately 1200 km^2 in the NLNP and occurs on the upper valley floor and in the foothills of the Muchinga Mountains. Throughout its range this vegetation type is associated with gently sloping terrain with relief measured in tens of metres.

The soils associated with D2 wooded grassland are stoneless to very stony soils, over siltstone and grits, which may or may not be covered with a surface mantle of quartzoze stones. They are highly variable in texture but tend to be shallow, grey to reddish brown and moderately acid (pH 5.4–6.6).

Combretum–Terminalia–Diospyros wooded grassland is defined by a well-developed grass/herb layer scattered with small trees and shrubs covering 10% to 40% of the surface. It is heterogeneous in composition and form, grading into woodland in some areas and pure grassland in others. Dominant small trees are *Diospyros kirkii*, *Terminalia stenostachya*, *T. stuhlmannii*, *Combretum apiculatum*, *C. fragrans*, *C. zeyheri*, *Crossopteryx febrifuga* and *Pseudolachnostylis maprouneifolia*. Shrub species include *Bauhinia petersiana*, *Acacia hockii*, *A. gerrardii* and *Ximenia caffra* subsp. *caffra*. On the shallow, stony soils of this habitat, the grass layer is well developed and dominated by medium to tall, coarse grasses. Common species are *Andropogon gayanus*, *A. schirensis*, *A. fastigiatus*, *Aristida scabrivalvis*, *Diheteropogon amplectens*, *Heteropogon contortus*, *Hyparrhenia anemopaegma*, *Loudetia flavida*, *Monocymbium ceresiiforme*, *Sorghum versicolor* and *Zonotriche amoena*. *Bothriochloa bladhii*, *Sporobolus pyramidalis*, *Heteropogon contortus*, *Echinochloa colona* and *Setaria* spp. are locally common in poorly drained areas. Subshrubs typical of this habitat are *Xerophyta suaveolens*, *Pachycarpus lineolatus*, *Cissus cornifolia* and *Cyphostemma* spp. Characteristic herbs include *Ipomoea welwitschii*, *Pterodiscus elliottii*, *Chlorophytum sylvaticum*, *Lapeirousia eryantha*, *Raphionacme longituba*, *Neorautanenia mitis*, *Vernonia melleri*, *Tephrosia* spp. and *Gladiolus* spp. Common ground herbs are *Crotalaria cephalotes*, *Euphorbia oatesii*, *Gardenia subacaulis* and *Torennia spicata*. Sumps and wet areas are characterised by *Cycnium tubulosum* and sedges including *Ascolepis protea* var. *splendida*, *Kyllinga alba*, *Scleria bulbifera*, *Cyperus margaritaceus* and *C. macrostachys*.

Trapnell believes that this vegetation mosaic is the result of sheet erosion. He suggests that the colluvial soils of the escarpment were more extensive in the past, covering much of the upper valley floor in the NLNP. Evidence for this is to be found outside the park, north of the Lufila river, where miombo woodland covers a large area of the upper valley floor (Trapnell *et al.* 1950; Edmonds 1976) and is found on soils of a colluvial nature containing laterite nodules. It is postulated that, in the NLNP and further south, much of this escarpment soil has been washed away, leaving a dissected, undulating terrain, the slopes of which are characterised by a thin, stony soil cover. This niche is occupied by vegetation type D2 in the areas of gentler relief and miombo scrub woodland (C2 subtype 1) on the steeper slopes. Hill miombo woodland (C2, subtype 2) occupies the ridge tops, where remnants of the deep escarpment soil cover remain. The patches of sodic or calcareous soil, associated with the mopane vegetation (E1/E2) of the upper valley floor, are almost certainly derived from ancient, and in some cases recent, termite activity (Trapnell *et al.* 1976).

E. *COLOPHOSPERMUM MOPANE* WOODLAND AND SCRUB WOODLAND

Colophospermum mopane is the single dominant tree species in this vegetation class. In the NLNP, mopane may grow as a tall tree of up to 15 m, or it may take the form of a multistemmed, stunted shrub < 3 m tall. The tall form is typical of *Colophospermum mopane* woodland (E1) and the shrub form is characteristic of *Colophospermum mopane* scrub woodland (E2). These two vegetation types may occur in discrete areas or they may grow together in mosaic. The difference between the two types is largely the physiognomy of *C. mopane*, which can be related to browsing damage and substrate as described below. Together, the two mopane habitats cover an area of approximately 600 km^2 in the NLNP.

Mopane woodland and scrub woodland are recognised by all of the authors referred to above (Trapnell 1953; Wild & Barbosa 1967; Astle *et al.* 1969; Fanshawe 1971; Naylor *et al.* 1973; Edmonds 1976; Phiri 1989).

E1. *Colophospermum mopane* woodland

This woodland occurs on the alluvial soils associated with the Luangwa River and its tributaries in the east of the park. The terrain is flat, but due to the sparse herbaceous layer and the impermeable nature of the soil, mopane woodland is usually dissected with drainage channels and erosion gullies.

Mopane woodland soils typically consist of a shallow (sandy loam) A horizon over an impermeable B horizon of brown or grey, cracking, slightly acid (pH 6.0–6.5) clay. These soils are poorly drained and as a result, are waterlogged during the rainy season. Continual sheet erosion has the effect of removing the topsoil, and the roots of mopane trees in this habitat are frequently exposed or undermined.

In this vegetation type, *Colophospermum mopane* grows as the single dominant species in an open two-storeyed woodland comprising a canopy layer of mature trees (10–15 m tall) and an understorey of trees in various stages of development. Trees and shrubs associated with *C. mopane* are comparatively few, mainly species found in the thicket habitats B1 and B2. Other associated species are *Afzelia quanzensis, Balanites aegyptiaca,* and *Ximenia americana.* The herbaceous component is dependent on substrate. On soils with a sandy A horizon, the herbaceous layer is sparse and largely composed of grasses, particularly those associated with vegetation type F1 (e.g. *Urochloa mossambicensis, Chloris* spp., *Dactyloctenium* spp.). Other characteristic species are *Alloteropsis cimicina, Aristida rhiniochloa, A. scabrivalvis, Eragrostis viscosa, Microchloa indica, Sporobolus cordofanus* and *S. panicoides*. In the sumps and wetter areas typical grasses are *Brachiaria deflexa, Echinochloa colona* and *Setaria pumila*. On alluvial black and brown clay soils, dicotyledons make up a larger proportion of the herbaceous component with the family Acanthaceae particularly well represented (see vegetation type F2 subtype 2). Common species are *Duosperma crenatum, D. quadrangulare, Hygrophila auriculata, Blepharis tenniramea, Barleria prionitis* and *Monechma debile*. Other common herbs are *Kalanchoe lanceolata, Senna absus, Cyphostemma* spp. and *Ocimum* spp.

The tall 'cathedral mopane' woodland associated with deep alluvial soils east of the Luangwa, outside the NLNP, is not common in the park. Instead, this two-storeyed form of woodland has arisen due to browsing pressure, which prevents recruitment into taller size classes (Caughley 1976). The most influential browsers in mopane woodland are elephants, which tend to browse destructively, pollarding the trees as they feed (Anderson & Walker 1974; Caughley 1976; Lewis 1991; Styles 1993). However, in the past ten years the elephant population of the Luangwa valley has been severely reduced due to ivory poaching (Leader-Williams *et al.* 1990) and if elephants are responsible for the maintenance of this scrub mopane, it is to be expected that without their browsing pressure, scrub mopane trees will grow into tall trees and set seed. In the mopane plots laid down in this study, individual tree heights, extent of damage and seed status were recorded. Measurements in 1993, and 1994 suggest that, in many cases, height recruitment is occurring. Further visits to these plots will be necessary to confirm this trend.

E2. *Colophospermum mopane* scrub woodland

This woodland occurs in discrete patches throughout all the habitats of the valley floor forming distinct islands of vegetation, which are clearly visible as white patches on aerial photographs. They appear to arise due to local soil conditions.

The soils are typically compacted pinkish grey to light grey sandy silt loams over an impermeable calcareous or sodic clay loam B horizon. The xerophytic conditions created by the impermeability of the soil, and the relative alkalinity of the B horizon produce a hostile environment for herbaceous plant species. The resulting paucity of herbaceous ground cover exacerbates the erosion problems in this habitat and, as with vegetation type E1, scrub mopane soils are dissected by numerous drainage channels and erosion ditches.

As in E1, *Colophospermum mopane* is dominant in this vegetation type, but here its growth is stunted, and it rarely exceeds 3 m in height. Characteristic associated shrubs are *Commiphora* spp., *Maerua angolensis* (as a shrub) and *Lannea humilis*. Climbers include *Maerua juncea*, *Hippocratea indica* and *Cissus* spp. The herbaceous layer is sparse. Typical grasses are *Aristida* spp., *Sporobolus cordofanus*, *S. panicoides* and *Eragrostis viscosa*. Characteristic subshrubs and herbs include *Zanthoxylum chalybeum*, *Cadaba kirkii*, *Jasminum stenolobum* (as a ground herb or suffrutex), *Decorsea schlechteri*, *Scadoxus multiflorus*, *Plectranthus tettensis* and *Cyphostemma* spp. *Ipomoea kituiensis* is locally common.

There are two major factors which cause the shrub growth form of *Colophospermum mopane* in the NLNP: browser damage (see above) and/or soil conditions. Where scrub mopane trees are intimately associated with tall mopane trees, as in vegetation type E1 on the alluvial soils in the east of the park, stunted growth appears to be largely due to browser-pollarding. Elsewhere, both near the river and throughout the rest of the park, comparatively large, discrete areas of scrub woodland occur. This is a distinct vegetation type in which edaphic factors are more important than browsing pressure in influencing vegetation physiognomy (Dye & Walker 1980).

F. GRASSLANDS

The grasslands of the NLNP, defined as areas of herbaceous vegetation with less than 10% woody vegetation cover, are all associated with water. Vegetation Type F1 is seasonally waterlogged, while types F2 and F3 are associated with the rivers and dambos of the valley and escarpment respectively.

Vegetation type F1 is referred to by Phiri (1989) as 'Floodplain grassland' with *Echinochloa colona* cited as the dominant species. Astle *et al.* (1969) describe this vegetation type (landsystem 1; facet 7; photo 4) as 'Short *Echinochloa* grassland with *Combretum obovatum* shrubs on dark cracking clays'.

Vegetation type F2 is readily recognisable in the previous valley surveys. The sandbar grassland (landsystem 1; facet 1b) and pointbar deposit grassland (1; 5a) of Astle *et al.* (1969) are synonymous with vegetation types F2 subtype 1 and subtype 3, respectively, of the present survey. Similarly, the dambos, mudflats and pointbar grass habitats (2b, 2c and 2g, respectively) of Naylor *et al.* (1973) are directly referable to vegetation type F2.

Vegetation type F3 is not dealt with by any of the valley surveys, as it is an upper escarpment and plateau habitat. However, Vesey-Fitzgerald (1963) gives a detailed account of this vegetation type which he calls 'Headwater valley grasslands (dambos)'. *Loudetia simplex* and *Hyparrhenia* spp. are named as characteristic species. White (1983) and Fanshawe (1971) also describe this vegetation type, referring to it as 'Dambo grassland' and 'Bush-group grassland' respectively.

F1. ***Chloris–Dactyloctenium–Echinochloa* secondary grassland**

This type takes the form of short, annual grassland punctuated with occasional clumps of *Combretum obovatum* thicket. It is found on degraded mopane woodland and, as a result, is often scattered with the skeletons of dead mopane trees. Vegetation type F1 covers a large area of the NLNP (approximately 335 km^2) and is found on recently deposited alluvial soils adjacent to the Luangwa River. The terrain is flat and low lying, and is seasonally waterlogged during the rainy season.

Soils associated with this habitat tend to be shallow, poorly drained, light grey, compacted neutral sandy clays or sandy loams.

The important grasses in this habitat are short to medium-sized, nutritional species such as *Chloris virgata*, *Dactyloctenium aegyptium*, *D. giganteum*, *Urochloa mossambicensis*, *Digitaria acuminatissima* and *Eragrostis gangetica*. *Echinochloa colona*, *Brachiaria deflexa* and *Sporobolus pyramidalis* favour the wetter sites in this habitat. Typical herbs are *Ammocharis tinneana*, *Crinum minimum*, *Leonotis nepetifolia*, *Senna absus*, *Indigofera gairdnerae* (ground herb), and in the wetter areas, *Heliotropium* spp., *Cycnium tubulosum* and sedges such as *Ascolepis protea* var. *splendida* and *Cyperus macrostachyos*.

This grassland (F1) is clearly part of a dynamic succession. The extensive areas of F1 grassland present in the NLNP today were not recorded by Astle in 1965. At that time, these areas were largely covered by mopane woodland. It is probable that this succession has arisen due to extensive browsing damage in mopane woodlands, concomitant with the well documented increase in elephant numbers recorded in the valley during the 1970's (Caughley 1976). Additional factors such as waterlogging and fire may have been involved in maintaining the grassland state. Recent observations made by the author suggest that mopane seedlings are starting to re-invade the F1 grasslands in certain areas of the park. This reversion to mopane woodland would be consistent with the hypothesis that these grasslands are created and maintained by elephants because, as stated above, elephant numbers in the Luangwa valley have declined drastically in the past ten years (Leader-Williams *et al.* 1990). Furthermore, recent anti-poaching efforts have greatly reduced the incidence of man-made fires in the park. The mechanics of this succession need to be understood because this grassland is a particularly productive habitat, which aerial survey has shown is utilised by large numbers of grazers (NLCP census 1994). If these grasslands revert back to mopane woodlands, an important grazing habitat will be lost from the NLNP. Further research is needed to investigate the grassland-mopane succession, and the factors which influence it.

F2. **Valley riverine grasslands**

These grasslands are associated with the larger rivers of the valley floor. The Mwaleshi, Mulandashi and Luangwa Rivers all have extensive floodplains within their meander belts as well as numerous attendant drainage channels, oxbow lagoons and dambos.

Various soils are associated with this vegetation type, but all are based on the recently deposited alluvium of the large rivers. All tend to be deep and stratified, with soil textures ranging from the well-drained sandy soils of the sandbars to the cracking black clays of the floodplains. Each substrate supports a distinctive grass and herb component.

Subtype 1. *Cynodon-Eragrostis grassland on sandy soils*: on the sand bars and sandy deposits of the inside curves of the valley's rivers and streams, common tall grasses are *Andropogon gayanus, Cymbopogon excavatus, Digitaria milanjiana, Hyparrhenia filipendula, Hyperthelia dissoluta, Pennisetum purpureum, Phragmites mauritianus, Setaria sphacelata* and *Themeda triandra*. Common medium-sized grasses include *Dactyloctenium giganteum, Eragrostis cylindriflora, E. cilianensis, Heteropogon contortus, Perotis patens* and *Sporobolus pyramidalis*. Smaller grasses include the stoloniferous perennial *Cynodon dactylon*, which frequently carpets sand bars and abandoned river channels or 'wafwas' on compacted sands. Other short grass species found on sandy alluvial soils are *Chloris* spp., *Dactyloctenium* spp., *Eleusine indica, Eragrostis ciliaris, Perotis leptopus, Sporobolus festivus* and *Urochloa mossambicensis*. Herbs associated with the sandy riverine soils of the valley floor include *Waltheria indica, Trichodesma zeylanicum, Tridax procumbens, Sesamum* spp. and *Striga* spp.

Subtype 2. *Setaria-Hyparrhenia grasslands and wooded grassland on clay*: the brown and black clay loams associated with the floodplains of the valley's larger rivers support distinctive tall grassland. An important species on brown clay loam soils is *Hyparrhenia rufa*, whereas on black (black cotton) clays, *Setaria incrassata* (Kasense) grows in pure stands. Interspersed with stands of *Hyparrhenia* and *Setaria*, riverine clay soils support areas of herbaceous vegetation dominated by the family Acanthaceae. *Hygrophila auriculata, Duosperma quadrangulare* and *D. crenatum* are common in these areas, together with species such as *Senna obtusifolia, Indigofera tinctoria, Sida alba, Ocimum* spp. and *Corchorus* spp. *Sesbania greenwayii* is locally common.

Setaria-Hyparrhenia riverine grassland frequently grades into wooded grassland, with scattered trees from vegetation type A1 (e.g. *Kigelia africana, Acacia* spp., *Combretum* spp.) or *Colophospermum mopane* forming the woody component.

Subtype 3. *Aquatic associations*: water grass associations are found on the seasonally waterlogged clays of the Luangwa River's oxbow lagoons and dambos. In these areas, which remain under water for most of the rainy season, water-loving grasses such as *Oryza barthii, Echinochloa colona, Sporobolus pyramidalis* and *Setaria* spp. dominate. Common sedges in this habitat include *Cyperus esculentus, C. articulatus, C. distans* and *Kyllinga alba*. Characteristic water-associated herbs are *Polygonum setulosum, Lindernia oliveriana, Sphenoclea zeylanica* and *Heliotropium* spp. When water remains in the lagoons and dambos, the aquatic water weed *Pistia stratiotes* is characteristic. Around the peripheries of lagoons and dambos as they dry out, typical herbaceous species are *Portulaca oleracea, Ludwigia stolonifera, Hibiscus articulatus, Alternanthera sessilis, Mimosa pigra* and *Sphaeranthus* spp.

F3. *Loudetia simplex-Hyparrhenia* dambo grassland

On the Muchinga Escarpment and hills of the NLNP (Chinshenda, Mvumvwe and Soma) the rivers and streams do not have a well-developed meander belt and, as a result, the herbaceous riverside vegetation is less well defined than in the valley. However, the numerous dambos and drainage channels associated with these watercourses do have a characteristic grass and herb component.

Dambo soils are poorly drained and compacted. They are typically leached illuvial soils, black, dark grey or dark brown in colour, and acid (pH 5–6).

Early in the rainy season, the dambos of the upper escarpment are characterised by the grasses *Loudetia simplex, Setaria sphacelata* and *S. pumila*. Later on, in April/May, *Hyparrhenia* species are ascendant: *H. diplandra, H. nyassae, H. rufa, H. schimperi, H. collina, H. variabilis* and *H. welwitschii* may all be found at this time. Other late season dominants are *Andropogon chinensis, Diheteropogon filifolius, Monocymbium ceresiiforme* and *Pennisetum unisetum*. Typical herbs associated with the dambos of the upper escarpment include *Gnidia chrysantha, Moraea bella, Satyrium carsonii, Cynorkis hanningtonii, Eulophia cucullata, Euphorbia cyparissioides, Gladiolus* spp. and *Thunbergia* spp. Common sedges are *Cyperus margaritaceus, C. cyperoides* and *Scleria* spp.

The dominant grasses and herbs found on the dambos and streams of the lower escarpment and hills are similar to those found in the upper escarpment. However, a number of water-associated grasses and herbs from the valley may also occur. Grasses include *Brachiaria brizantha, Digitaria milanjiana, Echinochloa colona, E. pyramidalis, Setaria pumila, S. sphacelata, Sporobolus pyramidalis, Themeda triandra* and *Urochloa mossambicensis*. Subshrubs and herbs include *Urena lobata, Senna occidentalis, Aeschynomene mimosifolia, Ageratum conyzoides, Acmella caulirhiza, Tragia lasiophylla, Alternanthera sessilis, Ludwigia stolonifera* and *Polygonum setulosum*.

Vegetation mosaics

The representation of vegetation as a series of discrete types, based on communities or associations is, to some extent, artificial in that observed vegetation associations are almost invariably part of a continuum or occur in mosaic with other communities (Craig 1983). This is a problem of scale. The larger the scale of the map to be produced, the smaller the area of association that can be represented. For practical purposes however, some vegetation communities will always be too small to map separately. This applies in areas of mosaic or in cases where vegetation communities occupy a microhabitat. The vegetation associated with termite mounds, for example, is distinctive (Fanshawe 1968) and may be important to the ecology of an area, yet as a type, it is often too dispersed to be mapped separately. In the present study, clear mosaics have been indicated on the map (Figure 1). Elsewhere, dominant associations, not necessarily pure associations, are depicted (see below).

CONCLUSIONS

Vegetation monitoring on any scale requires baseline data from which deviations, or trends, can be measured. Changes in woody cover over large areas, for example, can be discerned from aerial photographs and satellite images. In the case of the NLNP, mopane woodland for example, can be mapped from historic aerial photographs (1952, 1965 and 1983) and compared with the 1995 LANDSAT-derived digital data used in the present study (Figure 1).

Although aerial perspectives are useful records of large-scale trends, they provide little information about cause of change. Of much more use in this respect is ground study information about vegetation structure and species composition. In the present study, 353 relocatable plots were laid down and the precise data recorded in each of these plots provides the basis for monitoring vegetation changes in the future.

Finally, it is important to stress that this study presents a coarse stratification of the vegetation of the NLNP, useful for measuring changes in the park's vegetation at this scale. Although these vegetation units are fairly homogeneous, they still, in some cases, represent more than one plant community. A more detailed study of plant associations in the park is needed if we are to begin to comprehend the processes involved in maintaining plant communities. At the species level, it is the local combination of abiotic and biotic factors which make up a niche that is important. If we are to understand the autecology of species, or even the ecology of ecotypes, we need to understand the combinations of habitat components which make up the niche. The great potential of geographical information systems is that the detailed local picture can gradually be built up. Spatial information about geology, soil, topography, water relations, fire regimes, animal-plant interactions and numerous other factors can be collected over time and added to the picture. It is only through this process that we can understand enough about ecosystems to effectively manage them.

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REFERENCES

ANDERSON, G.D. & WALKER, B.H. 1974. Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Zimbabwe. *Journal of the South African Wildlife Management Association* 4: 1–14.

ASTLE, W.L. 1989. *South Luangwa National Park map—landscape and vegetation*. Department of Surveys, Lusaka.

ASTLE, W.L., WEBSTER, R. & LAWRANCE, C.J. 1969. Land classification for management planning in the Luangwa Valley of Zambia. *Journal of Applied Ecology* 6: 143–169.

BELL, R.H.V. 1984. Soil-plant-herbivore interactions. In R.H.V. Bell & E. Meshane-Caluzi, Conservation and wildlife management in Africa. *Proceedings of U.S. Peace Corps Workshop, Kasungu, Malawi*: 109–130.

BROWN, D. 1954. *Methods of surveying and measuring vegetation*. Bulletin No. 42, Commonwealth Bureau of Pastures and Field Crops, Hurley, Berks.

CAUGHLEY, G. 1976. The elephant problem—an alternative hypothesis. *East African Wildlife Journal* 14: 265–283.

COLE, M.M. 1963. Vegetation and geomorphology in Northern Rhodesia: an aspect of the distribution of the savanna of central Africa. *Geographical Journal* 129: 290–310.

COLE, M.M. 1982. The influence of soils, geomorphology and geology on the distribution of plant communities in savanna ecosystems. In B.J. Huntley & B.H. Walker, *Ecology of tropical savannas*: 145–174. Ecological Studies 42. Springer-Verlag, Berlin.

CONDIT, R., HUBBELL, S.P., LAFRANKIE, J.V., SUKUMAR, R., MANOKARAN, N., FOSTER, R.B. & ASHTON, P.S. 1996. Species-area and species-individual relationships for tropical trees: a comparison of three 50 ha plots. *Journal of Ecology* 84: 549–562.

COURTNEY, F.M. & TRUDGILL, S.T. 1988. *The soil—an introduction to soil study*, 2nd edn. Edward Arnold, London.

CRAIG, G.C. 1983. Vegetation survey of Sengwa. *Bothalia* 14: 759–763.

CURTIS, J.T. & MCINTOSH, R.P. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 52: 476–496.

DYE, P.J. & WALKER, B.H. 1980. Vegetation-environment relations on sodic soils of Zimbabwe Rhodesia. *Journal of Ecology* 68: 589–606.

EDMONDS, A.C.R. 1976. *Republic of Zambia: vegetation map*. Forest Department, Zambia.

FANSHAWE, D.B. 1968. The vegetation of Zambian termitaria. *Kirkia* 6: 169–179.

FANSHAWE, D.B. 1971. *The vegetation of Zambia*. Forest Research Bulletin No. 7. Government Printer, Lusaka.

GUY, P.R. 1981. Changes in the biomass and productivity of woodlands in the Sengwa Wildlife Research Area, Zimbabwe. *Journal of Applied Ecology* 18: 507–519.

KENT, M. & COKER, P. 1992. *Vegetation description and analysis—a practical approach*. CRC Press, Boca Raton, Florida.

LAWTON, R.M. 1978. A study of the dynamic ecology of Zambian vegetation. *Journal of Ecology* 66: 175–198.

LEADER-WILLIAMS, N., ALBON, S.D. & BERRY, P.S.M. 1990. Illegal exploitation of black rhinoceros and elephant populations: patterns of decline, law enforcement and patrol effort in Luangwa Valley, Zambia. *Journal of Applied Ecology* 27: 1055–1087.

LEBRUN, J.P. & STORK, A.L. 1991–1997 (4 volumes). *Enumération des plantes à fleurs d'Afrique Tropicale*. Conservatoire et Jardin Botaniques de la Ville de Genève, Genève.

LEWIS, D.M. 1991. Observations on tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *African Journal of Ecology* 29: 207–221.

NAYLOR, J.N., CAUGHLEY, G.J., ABEL, N.O.J. & LIBERG, O. 1973. *Luangwa Valley Conservation and Development Project, Zambia*. Game Management and Habitat Manipulation. FAO, Rome.

PHIRI, P.S.M. 1989. *The flora of the Luangwa valley and an analysis of its phytogeographical affinities*. Ph.D. thesis, University of Reading, UK.

PRAMER, D. & SCHMIDT, E.L. 1964. *Experimental soil microbiology*. Burgess Publishing, Minnesota, USA.

SMITH, P.P. 1998. A preliminary checklist of the vascular plants of the North Luangwa National Park, Zambia. *Kirkia* 16: 205–245.

STYLES, C.V. 1993. *Relationships between herbivores and* Colophospermum mopane *of the Northern Tuli Game Reserve, Botswana*. M.Sc. thesis, University of Pretoria.

TAYLOR, R.D. & WALKER, B.H. 1978. Comparisons of vegetation use and herbivore biomass on a Rhodesian game and cattle ranch. *Journal of Applied Ecology* 15: 565–581.

TIMBERLAKE, J.R., NOBANDA, N. & MAPAURE, I. 1993. Vegetation survey of the communal lands—north and west Zimbabwe. *Kirkia* 14: 171–272.

TRAPNELL, C.G. 1953. *The soils, vegetation and agriculture of North Eastern Rhodesia*, 2nd edn. Government Printer, Lusaka.

TRAPNELL, C.G., FRIEND, M.T., CHAMBERLAIN, G.T. & BIRCH, H.F. 1976. The effects of fire and termites on a Zambian woodland soil. *Journal of Ecology* 64: 577–590.

TRAPNELL, C.G., MARTIN, J.D. & ALLAN, W. 1950. *Vegetation-soil map of Northern Rhodesia*, 2nd edn. Government Printer, Lusaka, Zambia.

UTTING, J. 1976. *An introduction to the geological history of the South Luangwa National Park, Zambia*. Government Printer, Lusaka.

VESEY-FITZGERALD, D.F. 1963. Central African grasslands. *Journal of Ecology* 51: 243–273.

WALKER, B.H. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *South African Journal of Wildlife Research* 6: 1–32.

WHITE, F. 1983. *The vegetation of Africa*. Natural Resources Research No. 20. A descriptive memoir to accompany UNESCO/AETFAT/UNSO vegetation map of Africa. Unesco, Paris.

WILD, H. & BARBOSA, L.A.G. 1967. *Vegetation map of the Flora Zambesiaca area*. Supplement to Flora Zambesiaca. Collins, Salisbury, Rhodesia.