**Published for**
**The African Wildlife Foundation's**
**FOUR CORNERS TBNRM PROJECT**
**by**
**THE ZAMBEZI SOCIETY and**
**THE BIODIVERSITY FOUNDATION FOR AFRICA**
**2004**

*PARTNERS*
*IN*
*BIODIVERSITY*
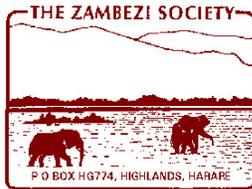
**The Zambezi Society**
**P O Box HG774**
**Highlands**
**Harare**
**Zimbabwe**
**Tel: +263 4 747002-5**
**E-mail: zambezi@mweb.co.zw**
**Website : www.zamsoc.org**

**The Biodiversity Foundation for Africa**
**P O Box FM730**
**Famona**
**Bulawayo**
**Zimbabwe**
**E-mail: bfa@gatorzw.com**
**Website: www.biodiversityfoundation.org**

The Zambezi Society and The Biodiversity Foundation for Africa are working as partners within the African Wildlife Foundation's Four Corners TBNRM project. The Biodiversity Foundation for Africa is responsible for acquiring technical information on the biodiversity of the project area. The Zambezi Society will be interpreting this information into user-friendly formats for stakeholders in the Four Corners area, and then disseminating it to these stakeholders.

**THE BIODIVERSITY FOUNDATION FOR AFRICA (BFA** is a non-profit making Trust, formed in Bulawayo in 1992 by a group of concerned scientists and environmentalists. Individual BFA members have expertise in biological groups including plants, vegetation, mammals, birds, reptiles, fish, insects, aquatic invertebrates and ecosystems. The major objective of the BFA is to undertake biological research into the biodiversity of sub-Saharan Africa, and to make the resulting information more accessible. Towards this end it provides technical, ecological and biosystematic expertise.

**THE ZAMBEZI SOCIETY** was established in 1982. Its goals include the conservation of biological diversity and wilderness in the Zambezi Basin through the application of sustainable, scientifically sound natural resource management strategies. Through its skills and experience in advocacy and information dissemination, it interprets biodiversity information collected by specialists like the Biodiversity Foundation for Africa and uses it to provide a technically sound basis for the implementation of conservation projects within the Zambezi Basin.

**THE PARTNERSHIP** between these two agencies was formed in 1996 as a result of mutual recognition of their complementarity. They have previously worked together on several major projects, including the biodiversity component of IUCN's Zambezi Basin Wetland project and the evaluation of biodiversity in Tete province described in detail in the first Four Corners TBNRM Biodiversity Information Package

# ACKNOWLEDGEMENTS

**CHAPTER 3. ECOLOGICAL PROCESSES WITHIN THE FOUR CORNERS AREA**

# CONTENTS

**TABLES**

**FIGURES**

# CHAPTER 3. ECOLOGICAL PROCESSES WITHIN THE FOUR CORNERS AREA

*Fay Robertson*

## CHAPTER 3. ECOLOGICAL PROCESSES WITHIN THE FOUR CORNERS AREA

*Fay Robertson*

### 3.1    INTRODUCTION

This chapter presents a detailed review of our current knowledge of the ecological processes, particularly moisture availability, nutrient flows, herbivory and fire, operating within or affecting the Four Corners area. It concentrates on terrestrial systems and floodplains as much of the information on aquatic biodiversity has already been reviewed under the Zambezi Basin Wetlands Biodiversity project (Timberlake 2000).

The area is not clearly delimited geographically and has no features that differentiate it from surrounding landscapes. However, there are some unifying features of climate, geology and topography. These include:

- a continental interior location, within an altitude range of ~ 900 to 1200 m;
- a savanna climate, with a wet season of 5 to 8 months;
- a rainfall gradient, along which mean annual rainfall ranges from about 900 mm in the north to about 400 mm in the south;
- evapotranspiration rates that increase from north to south, and exceed rainfall in all months of the year;
- occasional severe winter frosts, increasing in frequency and severity to the south; and
- a mineral-poor surface geology consisting of Kalahari sands or deeply weathered basement rocks, with occasional exposures of mineral-rich rocks.

This chapter describes and assesses the relative importance of the major ecological processes which, interacting with each other and with the biota within the limitations of climate, geology and topography, have produced the current patterns of biodiversity in the Four Corners area. It has proved particularly difficult to put figures to the rate at which any ecological process occurs as, with the exception of the Okavango swamps and Hwange National Park, no research has focused on hydrology or nutrient cycling, except for nutrient cycling by termites (Dangerfield, Chapter 11). There have been few studies on herbivory, with the exception of that by elephants (Conybeare, Chapter 15). Hundreds of reports on topics, including soil surveys, vegetation maps and large mammal counts, which give values (although seldom rates of change) for the biological features affected by ecological processes, were produced for governments or another commissioning agency, and are not generally available. Swedeplan (1988) lists such reports for northern Botswana.

What is known of each of the major ecological processes that act within the Four Corners area is reviewed in separate sections. Figures derived from similar vegetation types outside the Four Corners are used occasionally to give an idea of the order of magnitude that might reasonably be expected of a process rate. At the end of each section a summary of distinguishing features of the relevant process is given, followed by a consideration of the relative importance of ecological processes and their interactions on the structure and function of each major vegetation type. The chapter concludes with a description of areas and processes of conservation importance and suggestions for monitoring.

## 3.2    MOISTURE AVAILABILITY AND DRAINAGE

### 3.2.1 Rainfall and Evapotranspiration

Within the Four Corners area, 95% of the rain falls during a 5-8 month wet season (Table 3.1). Mean annual rainfall declines from north to south, ranging from approximately 900 mm in the north to approximately 400 mm in the south (Cumming 1999). The lower the mean annual rainfall, the more the annual rainfall varies between years. The coefficient of variation within that portion within Zambia and Zimbabwe increases from 15-20% near Kafue in northern Zambia to over 35% on the Gwayi River in Zimbabwe (Torrance 1972). Most rain falls during convective thunderstorms and the rainfall gradient is due to a decrease in the rate of storm arrivals rather than to a change in the mean storm depth, which at 10 mm per storm event is constant along the rainfall gradient (Porporato *et al.* 2003).

**Table 3.1.** Rainfall and evaporation characteristics of representative stations in the Four Corners Area.

| Weather station | Mean annual rainfall (mm) | Maximum annual rainfall (mm) | Minimum annual rainfall (mm) | Coefficient of variation [CV] (%) | Evaporation (mm) | No. months where rainfall > evaporation | No. months with > 25mm rainfall | Mean annual temperatures (°C) | Source & [years of record] |
|---|---|---|---|---|---|---|---|---|---|
| Kafue NP, Zambia | - | - | - | 15-20 | - | - | - | - | CV-Torrance 1972 |
| Shesheke, Zambia | 855.9 | - | - | 25-30 | - | - | - | 20.9 | Federal Met. Dept. 1963, CV-Torrance 1972 |
| Livingstone, Zambia | 779 | 1186 | 410 | 30-35 | 2303 | 2 | 8 | 21.8 | Torrance 1972 |
| Katima Mulilo, Namibia | 683 | - | - | | ± 2500 | 0 | 5 | | Mendelsohn & Roberts 1997, CV-Torrance 1972 |
| Hwange Main Camp, Zimbabwe | 647 | 1159 | 335 | 28.4 | 2088 | 0 | 5 | 20.3 | Dept. Met. Serv. 1978 & recent [1951-1971, 1918-2002 for rainfall] |
| Tjlolotjo, Zimbabwe | 560 | - | - | 35-40 | 2338 | 0 | 6 | 20.6 | Dept. Met. Serv. 1978 [1961-1976], CV-Torrance 1972 |
| Maun, Botswana | 490 | - | - | - | 2172 | 0 | - | - | McCarthy, Cooper, Tyson & Ellery 1993 [1925-1996] |
| Sehithwa (Lake Ngami) Botswana | 385 | - | - | - | - | - | - | - | Swedeplan 1988 [1959-1986] |

Evaporation exceeds rainfall in most, if not all, months of the year (Table 3.1). Potential evapotranspiration, based on the Penman formula, in the Four Corners parts of Zambia and Zimbabwe ranges from 1650 mm in northern Zambia, to >1800 mm in the hot, low-lying area around Victoria Falls (Torrance 1972). For all except the deepest rooted plants, water in excess of requirements is available for only a few months of the year.

Although mean annual temperatures have been rising steadily over the last few decades across southern Africa (Hulme 1996), there has been no systematic linear trend in rainfall during the twentieth century (Tyson *et al*. 2002). Within the summer rainfall areas there is a quasi-regular 18-year oscillation, in which about nine years wetter than average are followed by about nine years that are drier (Tyson 1986). While McCarthy *et al*. (2000) considered that this rainfall pattern extended from South Africa into southern Zambia, they noted that the rainfall record at Maun (1925-1996) did not show the clear 18-year oscillation obvious from rainfall records in areas to the east and south-east.

Extremely wet or dry years in the Four Corners are not unusual, but they are unpredictable. Hwange Main Camp is used as an example (Figure 3.1). During the 84 years of records, extremely wet years, during which annual rainfall exceeds the mean by more than 50%, occurred six times. Rainfall was never less than 50% of the mean, but drought years, in which the annual rainfall was < 400 mm, also occurred six times. Only once over this 84 years did two exceptionally wet years occur consecutively, and only once was a severe drought followed by an exceptionally wet year.
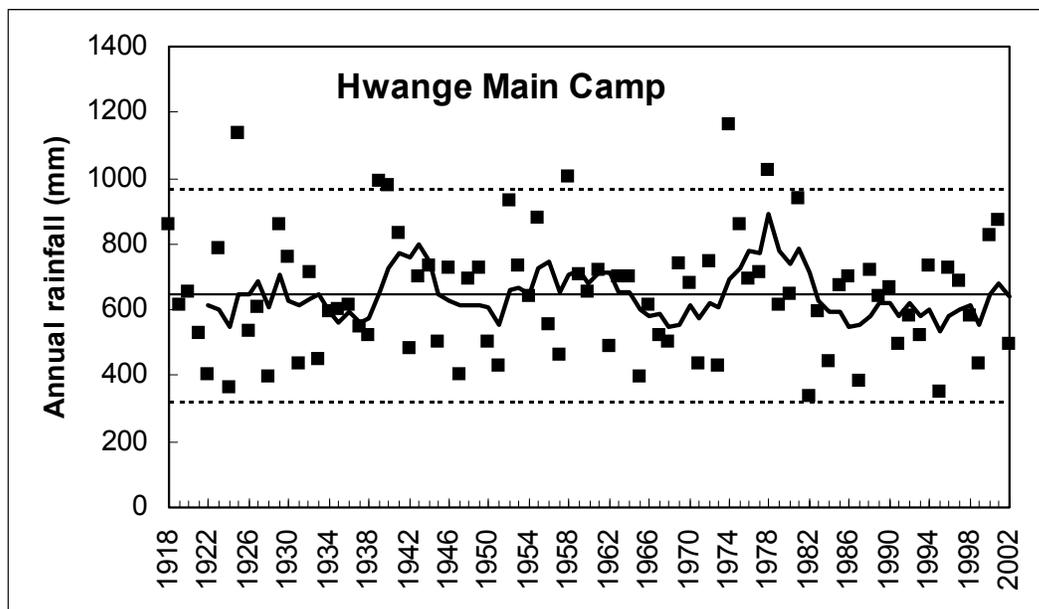


**Figure 3.1.** Annual rainfall at Hwange National Park Main Camp, Zimbabwe.
 The levels at which annual rainfall is equal to < 50% (thin line) or >150% (dashed lines) of the mean annual rainfall are marked. Bold line indicates five year running mean. Date is given as the year in which the rainfall season (July-June) ended. Data from the Dept. Meteorological Services, Harare.

Populations of perennial plants in the Four Corners are unlikely to experience steady rates of mortality or regeneration (Childes & Walker 1987). Episodic events, such as exceptionally wet or dry years, or a particular sequence of events such as a severe drought followed by two unusually wet years, determine the structure of plant populations by allowing mass regeneration or causing severe mortality (O'Connor 1999). Using ENSO data, the probabilities of an above-average or a below-average rainfall year can be estimated three or four months before the wet season begins, but there is no way of predicting the likelihood of a particular sequence of exceptionally dry or wet years.

Four major perennial rivers flow through the Four Corners. The Kavango, Cuito, Kwando and Zambezi Rivers all arise hundreds of kilometres to the north in the Angolan highlands or in northern Zambia, where annual rainfall is both greater (> 1000 mm) and less variable from year to year than it is in the Four Corners itself (McCarthy *et al.* 2000). The rivers have a complex history involving tectonic movements, ancient inland drainage basins and river capture (Moore, Chapter 2). Gradients are low and continuing tectonic movements retain the potential to disrupt and alter river flow.

On the basis of 89 years of data, McCarthy *et al.* (2000) suggest that there may be an 80-year climatic oscillation in the Zambezi River catchment that affects the river flows. These peaked in about 1960 and the periodicity of the oscillation suggested that flows would probably reach their lowest levels around 2000, before rising again to reach above-average flows during 2020. The historical record is consistent, suggesting there were high Zambezi floods between 1849 and 1900. Flow data collected since 1996 (Figure 3.2) does not support this theory as flow has been above-average during four of the last five years, but the record is still too short to be sure.
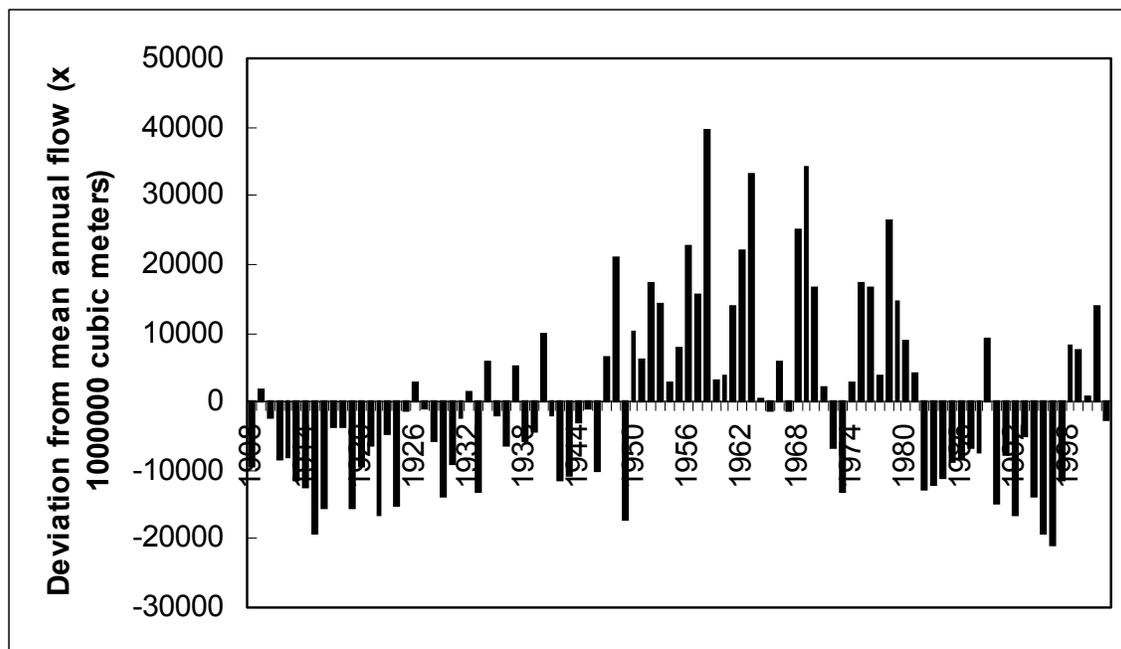


**Figure 3.2.** The Zambezi River flow record, based on data collected at Victoria Falls by the Zambezi River Authority.

### 3.2.2  Groundwater Supplies and Aquifers

Aquifers and groundwater levels in or under the Kalahari sands and their rates of recharge are a contentious issue. Kehinde & Loehnert (1989) suggest that the Kalahari sediments contain no aquifers in those areas where mean annual rainfall is less than 500 mm as the piezometric surface is located below the sands, within the underlying Karoo sandstone. However, infrequent heavy storms may recharge ancient ground water contained at depths of 40 m in Kalahari sediments surrounding the Okavango Delta (McCarthy, Bloem & Larkin 1998). Very intense rainfall events, preceded by conditions that increase soil moisture levels rather than average conditions, are required to replenish ground water (Ward 1975, Booth 1989).

Most boreholes in Hwange National Park yield 2-6 m$^3$ per hour at depths that usually exceed 40m (Jones 1989). Some yield water that is unpalatably salty. The recharge rate of the Kalahari sand aquifer near Main Camp, estimated from environmental tritium, was about 15 mm per annum (Anon. 1976).

The aquifers of the Zambian section of the Four Corners have not been explored. The gradient of increasing rainfall and reduced evapotranspiration to the north suggests that there are likely to be ground water reserves, that these are currently being recharged, and that there may be more productive aquifers in underlying permeable strata, especially where the Kalahari sands are shallow.

### 3.2.3  Soil Moisture

I am unaware of any figures for soil infiltration rates within the Four Corners. In general, sands such as those that cover most of the area have high infiltration rates, irrespective of litter cover (Young 1976).

As the clay content increases towards the lower-lying areas of the landscape, such as dambos and dune hollows, infiltration rates fall. Soils formed on Karoo mudstones, siltstones and shales have exceptionally low infiltration rates because they have a weakly developed and unstable microstructure and are prone to capping (Sweet 1971).

Kalahari sands are able to store water not because of any unusual ability to retain large quantities of water per unit volume of soil (Calvert 1986a), but because of their great depth, which exceeds 300 m in the centre of some of the Kalahari sub-basins such as that on the Botswana/Zimbabwe border (Moore & Larkin 2001, Moore, Chapter 2). In southern Barotseland the moisture-holding capacity of Kalahari sands was estimated at approximately 100 mm per 1-1.2 m of sand (Savory 1961 in Childes 1989). Rogers (1993) used FAO-Agritex figures suggesting that only 72 mm of rain is required to moisten Kalahari sands to a depth of 1 m and that the soil depths required for the storage of one year's rainfall in Hwange would be 7-9 m (assuming no evapotranspiration). In south-eastern Botswana, Timberlake (1980) concluded that the annual rainfall infiltrated 4-5 m into the Kalahari sand. Most of the water held in sands is held at tensions that make it readily available to plants (Landon 1991). By contrast, in a clay soil the field capacity is about 690 mm per metre of soil of which 400 mm is held at tensions below the permanent wilting point and the remaining 290 mm is available to plants (Landon 1991).

Horizons that are less permeable than the bulk of the soil profile, including layers of compacted sand, calcrete and other materials such as silica which restrict and direct subsurface drainage, are a recurrent theme in the Kalahari sands (Trapnell & Clothier 1937, Fanshawe & Savory 1964, Childes 1984, Childes & Walker 1987, Rogers 1993). These layers may be related to the sands' history as part aeolian and part lacustrine deposits, or to more recent leaching and deposition. In drier regions, especially in northern Botswana, cemented calcrete horizons within or on the

surface of the Kalahari sand restrict permeability, causing seasonal waterlogging in the dune hollows and allowing pans and old lake beds to fill with water during the wet season (Weir 1969, 1971, Rogers 1993).

Land use on the watersheds, through its effects on infiltration, transpiration, runoff and soil moisture storage, has a major influence on the water supply to dambos and wetlands. There have been no watershed clearance experiments on the Kalahari sands. The best way to maintain the seeps on the edges of dambos, where people cultivate rice in the Kalahari sands of western Zambia, may be to clear the watershed of woody plants, thus reducing transpiration and allowing more water to flow below the surface (McFarlane 1995).

### 3.2.4  Key Features of Hydrological and Soil Moisture Regimes
- For all except the deepest rooted plants, water in excess of requirements is available for only a very few months of the year.
- Temperature and rainfall have varied at timescales from decades to centuries for many thousands of years.
- Extremely wet or dry years in the Four Corners are not unusual, but they are unpredictable.
- Although the variance in rainfall between years is high, especially towards the south, there have been runs lasting for about nine years, during which the majority of years are wetter or drier than average.
- During the drier phases, substantial rainfall deficits may accumulate.
- High evapotranspiration rates, together with high infiltration rates, especially in the Kalahari sands, result in low rates of conversion of rainfall to surface runoff and a hydrological regime that is dominated by lateral subsurface flow.
- Shallow gradients and relatively impermeable soil layers, especially in low-lying ground, result in seasonally flooded grasslands, including swamps, floodplains, dambos and pans.
- With the exception of the Okavango swamps and the perennial rivers to the north, there is little surface water during the late dry season.
- The catchment areas of the perennial rivers that flow through the Four Corners lie in a higher rainfall zone and experience an 18-year oscillation that is out of phase with rainfall patterns in the south. This has a buffering effect on the water supply to the swamps and floodplains.
- Continuing tectonic movements retain the potential to disrupt and to alter river flow.
- The Kalahari aquifers and groundwater reserves in the southern section of the area are low-yielding and occasionally salty. Higher yielding sandstone aquifers are often buried beneath hundreds of metres of sand.

## 3.3    NUTRIENT FLOWS

### 3.3.1  Nutrient Distribution at the Landscape Scale
At a continental scale, ecologists divide the ecosystems of the seasonally dry tropics into wetter nutrient-poor (dystrophic) savannas growing on infertile soils and drier nutrient-rich (eutrophic) savannas growing on fertile soils (Bell 1982, Huntley 1982). Although there is probably a continuum rather than a sharp divide, the concept has been useful because many ecosystem features and processes are correlated with the relative availability of water and nutrients (Table 3.2), not only at the continental scale but also at landscape and catena scale.

**Table 3.2.** Characteristic features of nutrient-rich and nutrient-poor savannas (modified from Scholes 1990).

| Feature | Nutrient-poor | Nutrient-rich |
|---|---|---|
| **Soils**: % organic carbon | 0.2-1.0 | 1.0-3.0 |
| Mineralogy | Quartzitic or kaolinitic | Smectic (montmorillonitic) |
| Total exchangeable bases | < 5 milliequivalents/100g clay | >15 milliequivalents/100g clay |
| Parent material | Sands, sandstones, granite | Basalts, shales, mudstones |
| **Topography**: Slope position | Crest & upper slope | Lower slope, bottomlands, depositional basins |
| **Vegetation**: Tree taxonomy | Caesalpinioideae and Combretaceae dominate | Mimosoideae dominate |
| Leaf type | Simple or compound | Compound |
| Leaf length | >15 mm | 1-15 mm |
| Root:shoot ratio | High | Low |
| Grass taxonomy | Andropogoneae & Arundinelleae dominate | Chlorideae & Panicoideae dominate |
| Grass palatability | Low | High |
| Tree anti-herbivore strategy | Chemical (tannins, polyphenolics) | Structural (thorns) |
| Woody biomass | High, 15->50 t/ha | Low, 5-15 t/ha |
| Nodulated (potentially nitrogen fixing) | Understorey shrubs and herbs only | Canopy trees and understorey shrubs and herbs |
| Mycorrhizal types | Ectomycorrhizal and VA mycorrhizal | VA mycorrhizal |
| Litter layer | Conspicuous | Inconspicuous |

Under a high rainfall regime, more water flows through the soil taking nutrients with it, and rates of weathering and leaching are high. In more arid areas, rainfall is lower, evaporation rates are higher, less rain flows through the soil and more nutrients remain. The Kalahari sands are unusual in that they have already been leached, transported and sorted under previous wetter and drier cycles, so that few nutrients, or clays that are capable of retaining nutrients, remain. Excluding the Kalahari sands, the distribution of soil types across the Four Corners reflects a general increase in the availability of exchangeable bases from north to south (Table 3.3 and Fig. 2.6 in Cumming 1999). Nitrogen and phosphorus analyses are seldom undertaken in conventional soil surveys and there is no information on how levels of these key nutrients vary across the Four Corners.

The Four Corners area is predominantly nutrient-poor, especially in the north, but it is penetrated throughout by intermediate and nutrient-rich savannas. The pattern is repeated at four different scales:

- At a landscape scale (thousands of square kilometres) where the major river valleys of the Okavango, Kwando and the Zambezi, with their associated alluvial deposits, cut through savannas on less fertile soils
- At a geological scale (hundreds of square kilometres) due to a diverse sedimentary history, or to igneous intrusions
- At a catenary scale (tens of kilometres) in which soils of different texture and fertility occur in a characteristic pattern from the crest to the bottom of the slope
- At a local scale (tens of metres) where nutrients and fine particles have been concentrated in termite mounds (Dangerfield, Chapter 11).

**Table 3.3.** Distribution and descriptions of the major soil types within the Four Corners Area, simplified from the original FAO definitions (Landon 1991) (after map in Cumming 1999).

| FAO soil type | Simplified description, modified from FAO definitions | Chemical fertility of soil | Location in Four Corners |
|---|---|---|---|
| Ferralsols | Strongly weathered soils of the humid tropics with high iron & aluminium oxide contents | Low nutrient content, especially as the acidity of the soil binds nitrogen and phosphorus to the oxides | Kafue NP, African plateau surface |
| Arenosols | Sandy, generally weakly developed soils | Intrinsically low nutrient content | Kalahari sands, from N Zambia to Makgadikgadi |
| Podzols | Soils with an accumulation of organic matter and of free aluminium or iron sesquioxides, usually below a strongly bleached horizon | Low nutrient content in the topsoil. Nitrogen and phosphorus in the organic layer are generally unavailable because the soil is so acid | E of Sioma Ngwezi |
| Gleysols | Unconsolidated soils, poorly drained, with mottles and staining from reduced iron, even in the top 50cm | Moderate to high nutrient content associated with high levels of organic matter | Barotseland & along Zambezi |
| Vertisols | Dark montmorillonite-rich clays with characteristic shrinking and swelling properties | High nutrient content, may be deficient in potassium | N of Caprivi, Katimo Mulilo, Pandamatenga, S Zambia |
| Lithosols | Soils < 50cm deep or containing many stones and pebbles | Variable nutrient content depending on underlying rock | parts of Hwange & Matetsi |
| Cambisols | Weathered soils formed under arid conditions without significant additions or translocation of soil material | High exchangeable bases, may be low in nitrogen | Makgadikgadi |

The ecological pattern is the same, at all scales - from broadleaved woodlands, through intermediate broadleaved shrubland and open woodlands to vegetation with fine-leaved trees - along the gradients of reduced soil moisture availability and increased soil nutrient availability.

*Cryptosepalum, Baikiaea, Brachystegia* and *Burkea/Terminalia*-dominated vegetation of all structural types, from forest to disturbed grassland, share dystrophic features. At a geological scale, there is little eutrophic savanna in the Four Corners, except on the vertisols derived from basalts of Matetsi, Pandamatenga and Impalila Island, the *Combretum/Acacia* savanna in Zambia and vegetation types on fertile alluvial soils, especially in the Caprivi. Although maps often show northern Botswana as a eutrophic savanna (e.g. Huntley 1982), the soils are very infertile, the rainfall moderate and the area is dominated by broadleaved trees and shrubs (Scholes 1990). Mopane woodland is difficult to categorise, being dominated by a broadleaved tree growing on soils of variable nutrient status and supporting grass that may be a robust sward of low quality perennials, a sparse sward of high quality perennials such as *Sporobolus ioclados,* or annuals, depending on the soil type. The acacias that are characteristic of the fine-leaved eutrophic savannas of the arid Kalahari become more common towards the southern border of the Four Corners around Makgadikgadi. Grasslands on watershed plains dominated by *Loudetia* and on the plateau by *Hyparrhenia* are dystrophic, while those in depressions dominated by other non-Andropogoneae grass species, notably *Cenchrus, Cynodon* and *Panicum* in Makdgadikgadi and the Mababe depression, are eutrophic.

### 3.3.2  Nutrient Balance
There are four major pathways for nutrient inputs to a system (Scholes & du Toit 2002):

- atmospheric deposition
- mineral weathering

- nitrogen fixation
- anthropogenic inputs (e.g. chemical fertilizers).

Some of the nutrients made available to plants come not from nutrient inputs to the system, but through transformations of the nutrient from an unavailable to an available form.

The four major pathways for nutrient loss are:

- biomass removal
- wildfires
- erosion
- nutrient leaching beyond the rooting zone.

Nutrients immobilised in litter, peat or in the passive soil carbon pool are not lost, although they become unavailable to plants.

There are no nutrient budgets for any area within the Four Corners, except for nitrogen and phosphorus in the Okavango (Garstang *et al.* 1998).

### 3.3.3 Nutrient Gains to Ecosystems

Aerosol contributions to nutrient supplies may be important in the Four Corners area (Garstang *et al.* 1998, Tyson *et al.* 2002). During the dry season, much of southern and central Africa is blanketed in a dense haze. Under the anticyclonic conditions that occur during 40% of the year, several hazy layers of aerosols are held in place by subsiding air. The recirculating air contains aerosols consisting of fine mineral dust blown from the soil, smoke emissions from burning vegetation (especially abundant north of 20°S) and industrial sulphur (from the Copperbelt and the South African highveld). It also carries trace gases from biogenic, pyrogenic and industrial sources and other gases produced by living organisms, such as ammonia from the volatilisation of nitrogen. Much of this trapped air recirculates over Africa, often several times, before it leaves over the Indian or Atlantic Oceans. During recirculation, particulate nutrients in the air plumes are deposited over central and southern Africa, where they may contribute significantly to nutrient budgets, such as phosphorus in nutrient-poor systems (Garstang *et al.* 1998, Tyson *et al.* 2002).

Dew formation removes nitrogen oxides from the lower atmosphere during the night.

Various weatherable minerals provide a reserve of the cations Ca, Mg, and K to the soil. Apatite is the only mineral source of phosphorus. Few weatherable minerals remain in the Kalahari sands (Thompson & Purves 1978). A summary of soil properties from the Four Corners area is given in Table 3.4. There are no figures available on rates of weathering. The only rocks that are likely to contribute significantly to nutrient budgets are the relatively small areas of basalt exposed in north-west Matabeleland, the Pandamatenga area of Botswana, eastern Caprivi and southern Zambia, and some of the fine-grained sedimentary rocks, such as Madumabisa mudstone, that are exposed around the edges of the basins filled with Kalahari sand.

Few of the woody species in nutrient-poor savannas of the Four Corners are nodulated and therefore capable of nitrogen fixation (Hogberg 1986b). Nitrogen fixation by nodulating bacteria is probably unimportant in the miombo as the dominant tree genera, *Brachystegia* and *Julbernardia,* are non-nodulating. This may be due to: evolutionary history (Corby 1974, 1989); low phosphorus availability; low pH; aluminium toxicity; or any combination of these factors.

**Table 3.4.** Physical and analytical characteristics of soils from the Four Corners area (data from ([1]) Thompson & Purves 1978, ([2]) Sweet 1971).

| Locality | Parent rock | Depth (cm) | Sand (%) | | | Silt (%) | Clay (%) | pH (CaCl$_2$) | C (%) | N (%) | Exchangeable bases (milliequivalents/100g soil) | | | | | | Base saturation of clays (%) | Ext P as P$_2$O$_5$ (ppm) | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | coarse | med. | fine | | | | | | Ca | Mg | K | Na | CEC | TEB | | | |
| Kazangula, Zimbabwe | Kalahari sands | 0-30 | 10 | 58 | 28 | 2 | 2 | 4.9 | - | 0.030 | 0.78 | 0.28 | 0.02 | 0.01 | 1.2 | 1.09 | 90.8 | 3 (=1.32P) | 1 |
| | | 30-60 | 9 | 56 | 32 | 1 | 2 | 4.6 | - | 0.014 | 0.23 | 0.10 | 0.01 | 0.01 | 0.4 | 0.23 | 57.5 | 1 | |
| NW Hwange NP, Zimbabwe | Kalahari sands - dune | 25-35 | 20 | 44 | 32 | 1 | 3 | 5.5 | - | - | 0.7 | 0.2 | 0.06 | - | 1.5 | 0.9 | 60 | - | 2 |
| NW Hwange NP, Zimbabwe | Kalahari sands - dune trough | 20-30 | 12 | 46 | 29 | 2 | 11 | 5.1 | - | - | 5.4 | 1.9 | 0.08 | 0.05 | 7.8 | 7.4 | 95 | - | |
| | | 50-60 | 14 | 40 | 19 | 1 | 26 | 5.2 | - | - | 15.3 | 4.9 | 0.2 | 0.23 | 20.2 | 20.6 | 100 | - | 2 |
| NW Hwange NP, Zimbabwe | contact gneissic sands & basalt | 0-11 | 6 | 31 | 35 | 10 | 18 | 6.3 | - | - | 16.9 | 7.5 | 0.3 | 0.05 | 23.6 | 24.8 | 100 | - | 2 |
| NW Hwange NP, Zimbabwe | basalt | 40-50 | 1 (9% gravel) | 1 | 7 | 21 | 70 | 7.7 | - | - | 77.8 | 58.9 | 0.42 | 3.03 | 90.2 | 140.2 | 100 | - | 2 |
| NW Hwange NP, Zimbabwe | alluvial, highly sodic | 22-32 | 7 | 15 | 44 | 15 | 19 | 7.1 | - | - | 21.7 | 3.5 | 0.4 | 1..35 | 22.3 | 27 | 100 | | |
| | | 60-70 | 9 | 26 | 41 | 9 | 15 | 9.5 | - | - | 28.4 | 3.5 | 0.26 | 12.8 | 12.3 | 45 | 100 | - | 2 |
| NW Hwange NP, Zimbabwe | mudstone | 0-10 | 8 (2% gravel) | 4 | 18 | 30 | 40 | 7.6 | - | - | 18.5 | 4.8 | 0.99 | 0.2 | 22.8 | 24.6 | 100 | - | 2 |
| | | 50-60 | 3 (2% gravel) | 2 | 28 | 29 | 38 | 7.6 | - | - | 19.6 | 5.9 | 0.72 | 0.67 | 22.9 | 27.2 | 100 | - | 2 |

Note: CEC (cation exchange capacity) = the maximum amount of exchangeable cations (calcium, magnesium, potassium and sodium) that a soil can hold; TEB (total exchangeable bases) = the sum of exchangeable cations (Ca, Mg, K and Na) currently held by a soil. Base saturation = total exchangeable bases as a percentage of cation exchange capacity is an indicator of the degree of leaching that a soil has suffered, the lower the base saturation the higher the leaching.

The other dominant species in the area, *Baikiaea plurijuga, Guibourtia coleosperma, Burkea africana* and *Colophospermum mopane*, are non-nodulating. In the driest areas there is a decline in soil nitrogen and a relative increase in available phosphorus and many of the fine-leaved species characteristic of eutrophic savanna are capable of nodulating. The same pattern is repeated at a smaller (catenal) scale, with nodulating species on the valley bottoms and non-nodulating species on the crests.

Rates of nitrogen fixation in the ecosystems of the Four Corners are not known. Corby (1989) suggests that nitrogen fixation may be most important during the first year of a plant's life.

Anthropogenic inputs are low as most of the Four Corners area is under extensive cattle ranching or management as protected areas. Small-scale farmers manage much of the cultivated land, and few of them can afford mineral fertilizer.

### 3.3.4 Nutrient Losses from Ecosystems
*Timber*
There are no figures on past or current nutrient loss due to biomass removal from woodlands. If biomass is used locally, it is not a net loss to the system. The timber industry removed an average of 70,000 m$^3$ of high quality timber from the *Baikiaea* forests of western Zambia each year between 1930 and 1972 as railway sleepers, pitprops and parquet blocks (Huckabay 1986).

This was not sustainable and timber harvests had dropped to about 17,000 m$^3$ by 1983 (Huckabay 1986, Chingaipe & Jain 1986).

Estimates of the saw log timber that is currently harvestable in the teak woodlands of Zambia range from 1 to 5 m$^3$ per ha (Greenwood 1986) to 22 m$^3$ per ha (Musokotwane & Kufakwandi 1986), and from 1.5 to 7.6 m$^3$ in Tsholotsho, Zimbabwe (Mushove 1993). The rotations necessary to achieve this yield of exploitable timber are of the order of 40-100 years or more. *Baikiaea* wood has a specific density of about 930 kg per m$^3$. Given a wood nitrogen content of 0.8% and a phosphorus content of 0.01% (P. Frost, pers. comm.), and using the maximum yield of 22 m$^3$ per ha, the removal and export of all saw log timber from a harvestable *Baikiaea* woodland would entail a loss of about 164 kg N and 2.04 kg P per ha. Taken over 60 years, nitrogen loss would be 2.7 kg per ha per year and the loss of phosphorus 0.03 kg per ha per year. Because sawmills operate at about 30% efficiency, and the remainder is left as firewood and sawdust for local consumption (Musonda 1986), not all these nutrients would actually leave the region. Nutrient losses in timber might become significant regionally if exotic timber plantations replaced indigenous forests, as exotic species such as eucalypts are more productive and the rotations would be much shorter.

Charcoal supports a large industry that transfers nutrients from rural areas to urban centres in Zambia (Chidumayo 1993b). Charcoal production is not as widespread as it is in the Copperbelt as the Kalahari sands do not provide suitable clay for kilns. Hence there is no tradition of charcoal making (Musonda 1986) and there are few nearby urban centres, except Livingstone, to consume charcoal. Average charcoal consumption per household in rural Zambia was estimated at only 100 kg per year (Chidumayo 1993b).

*Wildfires*
When fire temperatures exceed 300°C, as they do in most wildfires, 3-69% of the phosphorus in plant material is volatilised (Newman 1995). About half of the nitrogen in biomass is volatilised when temperatures exceed 200°C, and all is volatilised at temperatures above 600°C (Scholes & Walker 1993). Only part of the volatilised phosphorus and nitrogen is transported long distances in fly ash, the remainder is deposited locally. Although experimental plots burned every year sometimes have lower levels of nitrogen in the soil, Scholes & Walker (1993) concluded there was no evidence that occasional fires had a deleterious effect on soil nutrient cycling in the long term. However, none of these fire plots was on Kalahari sand.

*Erosion*
The Kalahari sands are not particularly susceptible to erosion as the soils are very permeable and the landscape relatively flat, so long as vegetation cover is sufficient to protect against wind erosion (Jones 1989). Erosion rates are relatively low in the protected areas of Zimbabwe (Grohs & Elwell 1993, Whitlow & Campbell 1989), but even within Hwange National Park there are sodic soils and soils derived from fine-grained Karoo sediments that are subject to accelerated erosion (Sweet 1971, Jones 1989). In the Sinamatella region, high densities of impala may be maintaining high erosion rates in areas that were previously used by cattle (Tafangenyasha & Campbell 1990). Wind erosion rates are high on the fine sediments of seasonal pans such as the Makgadikgadi, especially when the vegetation has been removed by herbivores (Parris 1984, Swedeplan 1988).

Where crops are cultivated by small scale farmers, especially on shallow soils derived from Karoo sediments, erosion rates can be high (Table 3.5). Not all this soil is necessarily lost to the system as it may be deposited nearby in depressions or against barriers.

**Table 3.5.** Annual losses of soil, organic carbon, nitrogen and phosphorus due to sheetwash erosion from small-scale farmers' fields under current farming practices in three communal lands in Zimbabwean part of the Four Corners.
Soil loss rates taken from Grohs & Elwell (1993) and converted into carbon, nitrogen and phosphorus loss rates using Elwell & Stocking's (1988) formula for sandy soils for Tjolotjo and the formula for 'other' soils for Hwange and Maitengwe.

| Location | Dominant soil types | Soil loss (t/ha) | Nitrogen loss (kg/ha) | Phosphorus loss (kg/ha) | Organic carbon loss (kg/ha) |
|---|---|---|---|---|---|
| Hwange | Lithosols | >100 | >210 | >16 | >1540 |
| Tjolotjo | Kalahari sands | 5 | 5 | 1 | 54 |
| Maitengwe | Kalahari sands and vertisols | 5-20 | 26 | 2 | 193 |

*Leaching*
No nutrient leaching rates for soils in the Four Corners area are available. The dissolved mineral content of river water is an indicator of leaching (Whitlow 1983) and erosion rates in the catchment area (Bruijnzeel 1989). Conductivity and the dissolved nutrient levels of the Zambezi River water at Victoria Falls are low and have changed little during the past 50 years (Marshall 2000). There are few nutrients remaining in the Kalahari sands that cover much of the Upper Zambezi catchment and those that are lost to leaching are probably taken up by wetland systems before they reach Victoria Falls. Nutrient levels in the Kavango River are even lower than those in the Zambezi, especially for phosphate (Bethune 1991).

**3.3.5  A Matter of Scale: Nutrient Hotspots**
The previous section described nutrient gains and losses to whole systems. Local nutrient enrichment and depletion, often mediated and maintained by animals or by human activities (directly or indirectly), is equally important to ecosystem functioning.

*Waterpoints*
Cattle remove nutrients from the surrounding savanna and deposit them in their dung and urine at waterpoints. Soil near a waterpoint in eastern Botswana had three times the nitrogen levels of soils distant from boreholes, and phosphorus levels had increased 80-fold (Tolsma, Ernst & Verwey 1987). Phosphorus is strongly retained by soils and once it has been deposited it remains there, resulting in a permanent loss to the surrounding landscape. Phosphorus deficiency is widespread among domestic livestock in southern Africa including Botswana (APRU 1980), as the phosphorus content of grasses is too low for maintenance, especially during the wet season when phosphorus demands are high (van Niekerk 1997).

Intensively-used waterholes in the cattle areas of eastern Botswana create a nutrient drain on the landscape because domestic livestock does not eat the nutrient-enriched plants growing near the waterholes and so do not recycle nutrients (Tolsma, Ernst & Verwey 1987). Those resistant annual herbs that survive trampling are often toxic, while *Acacia* and *Dichrostachys cinerea* shrubs are resistant to browsing cattle, so shrub density increases around waterholes. Indigenous ungulates also remove nutrients from the surrounding landscape and deposit them near waterholes. Close to a pan supplied with borehole water in Hwange National Park, Weir (1971) found a pattern of nutrient enrichment similar to that from livestock.

It is only when herbivores regularly feed more often in one place and urinate and defaecate more frequently in another, as happens when they make daily movements to waterholes, are kraaled at night, or feed on land at night and return to the water during the day like hippos, that the nutrient levels in soils and vegetation are enriched or depleted by animal movements. Unlike with daily movements, seasonal movements by large mammals are not responsible for significant shifting of nutrients across the landscape of the Four Corners.

*Canopy Trees*

The soil beneath canopy trees often has higher nutrient levels than the soil under canopy gaps. The reasons for this effect are disputed and include: increased organic matter in the soil; aerosols captured by the canopy; reduced soil loss under the canopy as a result of reduced raindrop impact; reduced leaching; increased nitrogen supply through nitrogen fixation; increased activity of the soil fauna; and the attraction of birds and mammals whose excreta add nutrients (Campbell *et al*. 1993). Some have suggested that the effect is due to trees pumping up nutrients from the deeper layers of the soil that shallow-rooted plants are unable to reach (Nyamapfene 1991). Nutrient pumping is an unlikely cause where nutrient levels decline with depth (Kellman 1989) as they do in Kalahari sands (Table 3.4), although there may be ground water enriched with exchangeable bases at greater depth.

An animal-based explanation given for the concentration of phosphorus on deltaic islands in the Okavango (McCarthy, Ellery & Dangerfield 1998) is disputed by Garstang *et al*. (1998), who suggest that large trees growing on the islands may be trapping air-borne particulates in their canopies. Increased litter fall and the resultant improvement in the organic matter content of the soil are the most likely explanations. In which case nutrient enrichment beneath canopy trees would be particularly important in light-textured soils (such as the Kalahari sands) where most of the exchange capacity is in the soil organic matter (Campbell *et al.* 1993).

When canopy trees die, and assuming that nothing grows in the same place, the enriched soils gradually return to their pre-canopy tree state. Fire would distribute the nutrients more rapidly. There appears to be no work on the capacity of the Kalahari sands to adsorb, or the capacity of microbes, mycorrhizae and plant roots to take up, the sudden release of soluble nutrients that would occur when the first rains fell on the ash. This is an important information gap.

### 3.3.6 Carbon Cycle

*Plant Production*

Within the Kalahari sands of the Four Corners area, the basal area, height and cover of woody plants increase to the north along the rainfall gradient (Scholes *et al.* 2002). Basal area, which increases at a mean rate of 2.5 m$^2$ per ha per 100 mm of mean annual rainfall, is correlated with tree leaf area and biomass in the Kalahari, and so by inference with woody plant production.

Many vegetation types in the area, notably the wet grasslands with geoxylic suffrutices (underground trees) in western Zambia (White 1976), have considerably more than half their biomass below ground. Below-ground biomass averaged 35% of total biomass in dry Zambian miombo woodland (Chidumayo 1995). In *Combretum/Terminalia* shrubland in Hwange, more than 83% of woody biomass was belowground (Table 3.6). The root biomass of mopane shrub woodland is probably about equivalent to the aboveground biomass (Timberlake 1995).

In drier savannas, grass production in any year is strongly and linearly related to annual rainfall (Dye & Spear 1982), while in wetter savannas the relationship between annual rainfall and grass production is weak (Bell 1982, East 1984).

**Table 3.6.** Carbon stored in regularly burned and in unburned *Burkea/ Terminalia* shrubland plots in Hwange National Park.

| Location of carbon store | Unburned plot | | Burned plot | |
|---|---|---|---|---|
| | carbon content (kg/ha) | % of total carbon in system | carbon content (kg/ha) | % of total carbon in system |
| **Tree & shrub biomass** | | | | |
| Aboveground | 3,132 | 8.6 | 2,069 | 6.0 |
| Belowground (top 50 cm) | 16,814 | 46.1 | 15,182 | 44.1 |
| **Grass biomass** | | | | |
| Aboveground | 271 | 0.7 | 588 | 1.7 |
| Belowground (top 50 cm) | 282 | 0.8 | 612 | 1.8 |
| **Soil organic matter** | | | | |
| 0-10 cm | 11,424 | 31.3 | 11,424 | 33.2 |
| 11-40 cm | 4,553 | 12.5 | 4,553 | 13.2 |
| **Total** | **36,447** | | **34,427** | |

Note: Carbon content of organic matter calculated from dry mass (Rushworth 1978) assuming this is 50% carbon. Soil C content calculated from % C, bulk density and horizon depth in Kalahari sands at Nyamandhlovu (Nyamapfene 1991) using Young's (1976) calculations and assuming no difference in soil C between unburned and burned plots.

*Litter*

On the Kalahari sands litter mass also increases from south to north along the rainfall gradient (Scholes *et al.* 2002). The bulk of the potentially available forms of nitrogen and phosphorus are associated with organic matter, the mineralisation of which provides available forms of these nutrients for plants. The dominant trees of dystrophic woodlands produce low quality litter with high levels of structural carbohydrates (Tolsma *et al.* 1987, Scholes & Walker 1993). Within the broadleaved woodlands, decay rates in the absence of fire seem to depend more on the moisture regime than on nutrient limitations imposed on the decomposers by poor quality litter (Frost 1996). Litter in the eutrophic woodlands is more palatable and much reduced by herbivory, especially by domestic livestock during drought years.

Much of the litter in the vegetation types of the Four Corners is shed below ground. In the *Burkea/Terminalia* shrubland in Hwange, over 45% of organic carbon in the system was contained in root biomass and approx. 40% was in organic matter within the soil (Table 3.6).

### 3.3.7 Macronutrients
*Nitrogen*
The only nitrogen budget available for a terrestrial system similar to those in the Four Corners, *Burkea/Terminalia* savanna at Nylsvley in South Africa (Scholes & Walker 1993), suggests that the total input from wet and dry deposition (2.5 kg per ha) and biological fixation (8 kg per ha) exceeds the losses due to volatilisation in fires (5 kg per ha) and denitrification (4 kg per ha). This was under a regime of infrequent, early-morning fires during late winter, designed to minimise nutrient loss. Leaching losses were not considered significant in the undisturbed savanna at Nylsvley, although there was significant potential for leaching losses if the woody vegetation was removed (Scholes & Walker 1993).

In mixed *Acacia*-broadleaved woodland in eastern Botswana, nitrogen was translocated out of old leaves before they were shed (Tolsma *et al.* 1987). The difference in nutrient cycling patterns between fine-leaved and broadleaved savanna was reflected in higher nitrogen contents in the *Acacia* leaves, from which less nitrogen was translocated before leaf fall. As a consequence, leaf litter quality was relatively high. As there was little nitrogen in the soil, it seemed likely that the nitrogen was rapidly taken up by perennial grasses.

*Phosphorus*
Most of the phosphorus in savanna systems is bound into inorganic compounds that are relatively insoluble and unavailable to plants. The availability of phosphorus depends largely on soil pH (Hogberg 1986b); when soils are acid, most soil phosphorus is fixed as iron or aluminium phosphates. This is the situation in the northern, wetter Kalahari sands and in the miombo on basement rocks. In drier areas of the miombo woodland and in *Combretum/Acacia* woodlands, there is less free Fe and Al to bind the phosphorus and it is more available (Nyamapfene 1991). In very alkaline soils, such as around the Makgadikgadi pans and in some mopane woodlands, phosphorus is bound as calcium phosphate.

Aerosol deposition provides some available phosphorus, while that required for new growth comes from recycling within the plants' own tissues. Phosphorus is translocated out of the leaves of canopy trees before leaf shed in broadleaved woodland in Botswana (Tolsma *et al.* 1987) and from the leaves of canopy dominants in miombo woodland (Ernst 1975, Frost 1996). Its availability probably limits the production of flowers and fruit in many woody plants in Botswana, where 30-45% of the phosphorus contained in aboveground tissues was shed in flowers and fruit (Tolsma *et al.* 1987). Microbial oxidation releases mineral phosphorus from decaying litter and organic matter. Rates of mineralisation probably dominate the phosphorus cycle in most terrestrial systems in the Four Corners area. As mineralisation is a biological process, performed by soil microbes, it is controlled by soil moisture conditions and temperature and occurs during the wet season when microbial flora are most active.

*Sulphur*
There is no information on sulphur levels in the soils of the Four Corners, although sulphur is likely to be deficient in agricultural crops on sandy soils because of the low organic matter content of the soil (Grant 1981). Sulphur is volatilised by fire.

*Basic Cations*
The Kalahari sands, especially those in upland positions in the wetter areas, have very low levels of weatherable minerals (Thompson & Purves 1978). Their cation exchange capacity is low, largely occupied by $H^+$ and aluminium ions and seldom saturated with bases (Table 3.4). I am unaware of any work describing the pools or fluxes of exchangeable bases in systems on wetter Kalahari sands and am unable to say even whether, as seems likely, most of the exchangeable bases are contained in the biomass rather than the soil.

There is a major pedogenetic boundary at an annual rainfall of about 600 mm between soils in which there is a net loss of calcium over time and soils in which there is calcium accumulation (Young 1976). Above this rainfall level more soluble salts are leached out of the profile, and below this level calcium carbonate (and sometimes calcium sulphate and soluble salts) accumulate within the profile. The drier south of the area is unusual in that the Kalahari sands on higher ground have already been leached of bases under previous wetter climatic cycles, but levels of total exchangeable bases are high in depressions such as lake beds (Parris 1984) and dune hollows (Weir 1969, Rogers 1993) where excess calcium carbonate often precipitates out as a carbonate horizon.

### 3.3.8 Micronutrients

Agricultural experience suggests that there may be deficiencies in copper, zinc and boron in the Kalahari sands (Grant 1981), but levels in the soil limiting for crop plants do not necessarily limit the production of indigenous plants, especially if nutrients are efficiently recycled. Copper is complexed by acidic organic matter (Grubb 1989) and may be deficient in dambo and peaty soils, especially when the upper layer of soils dries out. Boron is known to be in short supply in the Okavango region and may interfere with internal translocation in papyrus (Worthington 1976).

### 3.3.9 Mycorrhizae

Mycorrhizae associated with plant roots improve the uptake of phosphorus and micronutrients such as zinc, copper, boron and molybdenum from the soil. These fungal symbionts are associated with the majority of terrestrial plants and the non-mycorrhizal state is the exception. They are thought to be particularly important to plants growing in nutrient-poor soils (Alexander 1989). Some of the early work on mycorrhizal associations in African systems was done within the Four Corners area, in western Zambia (Hogberg 1986). Although most of the vegetation types of the area grow on nutrient-poor Kalahari sands, the patterns of infection differ between them.

Because of the association between the Caesalpinoid genera *Isoberlinia, Brachystegia* and *Julbernardia* and ectomycorrhizae, the dominant trees in miombo are ectomycorrhizal, although the subcanopy trees and shrubs and the grasses are vescicular-arbuscular (VA) mycorrhizal (Hogberg 1986). In western Zambia, tree genera that were considered characteristic of Kalahari sand vegetation (*Baikiaea* and *Burkea/Terminalia* types) were all VA mycorrhizal (Hogberg & Piearce 1986). *Colophospermum mopane,* the dominant tree in mopane woodland, is also VA mycorrhizal (Hogberg & Piearce 1986), as are the dominant tree genera of *Combretum/Acacia* woodland. The absence of ectomycorrhizal infections among dominant trees in *Baikiaea* woodland which grow on very infertile Kalahari sands is an exception to a widely reported pattern (Hogberg 1986b) of ectomycorrhizal dominance among dystrophic woodlands and VA mycorrhizal dominance among intermediate and eutrophic vegetation types.

The type of mycorrhizal infection has implications for biodiversity. Miombo woodlands have probably the highest levels of macrofungal diversity in the world (C. Sharp, pers. comm.) because of the association between the roots of the dominant trees and many species of ectomycorrhizae. Other vegetation types in the Four Corners have relatively few non-mycorrhizal macrofungi supporting themselves on other substrates such as dead wood (Masuka & Ryvarden 1993) and termite mounds.

### 3.3.10        Nutrient Budget for the Okavango Delta

Tentative budgets for nitrogen and phosphorus, in the relatively simple system of the permanent swamps of the Okavango Delta, are the only budgets available for any ecosystem within the Four Corners (Garstang *et al.* 1998). The Okavango is an exceptionally nutrient-poor wetland as the Kalahari sands that underlie both the delta and most of the catchment area have a low nutrient status. Although peat in the permanent swamps contains very large reserves of nitrogen and phosphorus (173,000 kg per ha and 260 kg per ha to a depth of 50 cm for nitrogen and phosphorus, respectively), their rates of mineralisation are so low that they are largely unavailable to plants, except when they are remobilised by the occasional burning of peat (Ellery *et al.* 1989). The annual sediment load carried into the delta is 420,000 tonnes of dissolved material (mostly silica, calcium and magnesium bicarbonate) and 200,000 tonnes of particulate matter. Deposits from the atmosphere, spread over the delta's 12,000 km$^2$, are at least 250,000 tonnes per year. Aquatic inputs are 108 and 2.25 kg per ha per year of nitrogen and phosphorus

respectively, while aerosol inputs are 3.9 and 0.13 kg per ha per year. Nutrient uptake from the water is strongly patterned by plant use, while the aerosols are more evenly distributed.

The dense stands of very productive papyrus (*Cyperus papyrus*) that grow along the channel fringes obtain 90% of the nitrogen and 90% of the phosphorus that they require for growth directly from the water. Nutrients derived from aerosols are relatively unimportant in the channel fringes - 3.2% of nitrogen and 5.2 % of phosphorus requirements respectively. Water that flows through to the backswamps has therefore been effectively stripped of nitrogen and phosphorus. Here, and in the distal areas of the permanent swamps, aerosols contribute 30% of nitrogen and 52% of phosphorus requirements of papyrus; mineralisation of peat contributes the remainder (about 8.1 and 0.12 kg per ha per year, for nitrogen and phosphorus respectively). Most of the potassium in the system comes from river flow. The Okavango River terminates here and this system is unusual in that it is effectively a sink for nutrients, except for nitrogen which may be lost through burning and through biogenic emissions including volatilisation. Nutrients are occasionally remobilised by the burning of peat.

### 3.3.11        Key Features of Nutrient Supply and Cycling Within the Four Corners

- The Four Corners is predominantly nutrient-poor, especially in the north, because the surface geology is mostly Kalahari sands or weathered basement rocks, but the area is penetrated throughout by intermediate and nutrient-rich savannas at several spatial scales.
- The causes of this pattern are: geomorphology determined at spatial scales of thousands of $km^2$; geology, determined at spatial scales of hundreds of $km^2$; soil processes such as leaching and weathering; and nutrient hotspots created by animals or human activities at scales of tens of metres.
- Aerosols in the air plumes that recirculate over central and southern Africa may contribute significantly to nutrient budgets, such as phosphorus, in nutrient-poor systems.
- Mineral weathering and agricultural inputs contribute little to nutrient budgets.
- The ability to nodulate and so to fix nitrogen is more prevalent in the fine-leaved nutrient-rich vegetation types of the southern Four Corners area than in the north.
- Sales of timber and cattle could lead to significant losses of nutrients, especially of phosphorus.
- Frequent wildfires volatilise nitrogen and phosphorus, but these nutrients are often re-deposited locally.
- Kalahari sands are not particularly vulnerable to the loss of nutrients by erosion, but nutrient loss from cultivated fields can be significant on shallow soils derived from fine-grained sediments. Wind erosion is significant on seasonal pans in the south where the vegetation has been removed by herbivores.
- The capacity of soils and the remaining biomass to take up those nutrients that are suddenly released when woody plants are felled by foresters, cultivators or elephants, and burnt, and the magnitude of any losses, are unknown. These are important information gaps.
- Nutrient hotspots, where the levels of phosphorus and nitrogen are higher than in surrounding areas, develop around water points where animals congregate and deposit nutrients, in termite mounds and under canopy trees.
- Most of the phosphorus and nitrogen that is available for plant growth each year comes from the mineralisation of nitrogen and phosphorus contained in litter and in organic matter within the soil.
- 30-45% or more of the plant biomass is below-ground.

- Mycorrhizal symbionts improve the uptake of phosphorus and micronutrients, especially from nutrient-poor soils. The dominant trees in miombo woodland are ectomycorrhizal, while the dominants in the other vegetation types are VA mycorrhizal (endomycorrhizal).

## 3.4    HERBIVORY

### 3.4.1  Herbivory Estimates for Ecosystems

There are no estimates of the rates of herbivory for any complete ecosystem within the Four Corners area. The *Burkea-Terminalia* savanna on sandveld at Nylsvley in South Africa is the only model for herbivory in a dystrophic African savanna. These herbivores consumed in total about 10% of the annual production of grass and browse leaves, with ungulates consuming 5%, grasshoppers 3% and caterpillars 2% (Scholes & Walker 1993). The remainder, 90% of the annual production of grass and leaves, either decomposed or burned.

### 3.4.2  Large Mammals

*Wild Ungulates*

Large mammals consume a relatively small proportion of the plant production of nutrient-poor African savannas, where herbivory is controlled not by what is available (although much plant material is beyond the reach of most large mammals) but by what is acceptable to them (Scholes & Walker 1993). Secondary plant chemicals that inhibit browsers, rather than poor nutritional qualities, probably account for the generally low levels of browsing in the broadleaved savannas. Many tree and shrub leaves retain crude protein levels that are sufficiently high to maintain browsers even during the dry season, i.e. 10.6-22.4% in shrubland in Hwange (Rushworth 1978). Woody plants in miombo woodland, however, are defended by carbon-based polyphenols. These are costly to produce and not toxic to herbivores, but together with high levels of lignins and fibre, they reduce the digestibility of the leaves (Frost 1996). The geoxylic suffrutex *Dichapetalum cymosum*, whose fresh green leaves appear during the late dry season before most other plants have flushed, is so toxic that cattle are kept out of parts of *Baikiaea* woodland and *Burkea/Terminalia* savannas during winter and spring (Rattray 1957).

The fine-leaved trees in eutrophic savannas are defended by thorns rather than by secondary chemicals, probably because they are fast-growing and have high rates of nutrient-uptake. As fine-leaved trees can afford to lose some leaves to herbivores, defensive thorns which restrict rather than prevent herbivory are adequate, and they do not need to invest in more effective defensive chemicals. A key resource for large mammal browsers in both savanna types is palatable leaves within reach at the end of the dry season, after the deciduous trees have shed their leaves and before leaf flush (Scholes & Walker 1993).

For many, perhaps all, grazers, particularly in dystrophic savannas, the key resource is green grass during the dry season (Illius & O'Connor 1999). In the dystrophic savannas of western Zambia, only the green grass remaining in the sward, or the fresh grass regrowth that is produced after burning, have crude protein and phosphorus levels that are sufficient to maintain cattle during the dry season (Jeanes & Baars 1991a, Baars 1996). The crude protein content of standing grass as a percentage of dry matter is only 2.9%, while green grass leaves have a crude protein content of 5.1%. Fresh regrowth after burning contains 8.3% crude protein (Baars 1996). Corresponding phosphorus percentages are 0.08, 0.11 and 0.16. Cattle require an average of at least 7.5% crude protein content in their diet and 0.12% phosphorus (Jeanes & Baars 1991a) - if they are forced to eat grass of lower quality, they cannot maintain their gut flora and their appetites decline. Buffalo and cattle, being large-bodied and non-selective feeders, can digest the abundant low-quality grass of the dystrophic savannas, and elephant can also eat low-quality browse.

Translocation and loss of quality are not so pronounced in the shorter-lived and less robust grasses of eutrophic savannas, where grasses have a higher protein content that does not decline so rapidly during the dry season (Barnes 1982). But even in eutrophic savannas, grazing mammals lose weight during the dry season if they cannot feed selectively.

Grazers that are characteristic of the miombo and *Baikiaea* vegetation types (roan, sable antelope and Lichtenstein's hartebeest) are specialist feeders, preferring high-protein, growing grass (Frost 1996). They often feed at the edges of dambos or on the woodland/grassland ecotone (Huntley 1978) where there is sufficient moisture to produce a flush of green grass, even during the dry season, especially if the dambo has been burned. Such high-quality patches are small and scattered and these antelope occur at low densities. Grazing antelope associated with wetlands (southern reedbuck, defassa waterbuck, tsessebe, puku, lechwe and sitatunga) are able to select green grass all year around.

Most of the Four Corners area is covered by dystrophic woodlands such as *Baikiaea,* miombo and *Burkea/Terminalia*. Biomass densities of large herbivores predicted for nutrient-poor savannas (Fritz & Duncan 1994) range from 5627 kg per km$^2$ at 900 mm rainfall in the north to 1148 kg per km$^2$ at 400 mm in the south. Most figures available for large mammal biomass densities in the area are derived from aerial surveys designed to count elephant, and there is probably a significant, but so far unquantified, degree of undercounting for smaller animals (Table 3.7). Biomass densities in the Hwange/Matetsi complex were nearly twice that predicted from rainfall because of the high number of elephant. Road strip counts, conducted over many years, were used to quantify the differences in biomass densities between a wide range of nutrient-rich and nutrient-poor savannas at Matetsi, but results have not yet been published (V. Booth, pers. comm.).

**Table 3.7.** Biomass densities of large mammals in some protected areas and rangelands of the Four Corners area, converted from density estimates derived from aerial surveys using the average masses given by Coe, Cumming & Phillipson (1976), except for those extracted from East (1984), Mendelsohn & Roberts (1997) and Baars (1996) based on ground counts.

| Area surveyed | Mean annual rainfall (mm) | Year of survey | Biomass density (kg/km$^2$) | | | | Source |
| | | | elephant | wildlife excl. elephant | Domestic livestock | all large mammals | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Kafue NP, Zambia | 1000 | 1966 | 914 (50%) | 1086 (incl. hartebeest) | 0 | 2000 | East (1984) |
| Hwange NP & Matetsi complex, Zimbabwe | 647 | 2001 | 4282 (88%) | 582 | 0 | 4864 | Dunham (2002) |
| Forest Land, Zimbabwe | 550-650 | 2001 | 407 (51%) | 312 | 75 | 794 | Dunham (2002) |
| Protected Areas, N Botswana | 500-650 | 1993 & 1994 | ? | ? | ? | ? | ULG (1993, 1994a) |
| Protected Areas & Rangelands, Caprivi, Namibia | 500-700 | 1994 | 949 (38%) | 191 | 1327 | 2467 | ULG (1994b) |
| Protected areas & rangelands, Caprivi, Namibia | 500-700 | 1996 | not counted | not counted | 1221 [1] | - | Mendelsohn & Roberts (1997) |
| Western Province rangelands, Zambia | 700-1200 | 1990 | insignificant | insignificant | 1130 | 1130 | Baars (1996) |
| NW Matabeleland rangelands, Zimbabwe | 560 | 2001 | 36 (3%) | 21 | 1229 | 1286 | Dunham (2002) |
| Rangelands, N Botswana | 500-650 | 1993 & 1994 | ? | ? | ? | ? | ULG (1993, 1994a) |

Note: [1] ranging from <180 kg/km$^2$ to 10,800 kg/km$^2$, with most areas stocked at 900-4500 kg/km$^2$ (Mendelsohn & Roberts 1997).

*Domestic Livestock*

Most domestic livestock within the Four Corners area are kept by farmers for their own use. Owners do not give supplementary food, except from crop residues. Only basic veterinary services are provided by the national governments and there is little commercial cattle-rearing, except in parts of Botswana.

The biomass density of large mammals on the rangelands in Zambia and Zimbabwe (Table 3.7) is less than half of that predicted for nutrient-poor savannas under the rainfall regimes that they experience (Fritz & Duncan 1994). This is probably because browsing elephants that would make up most of the large mammal biomass in these landscapes have been eliminated. In western Zambia only the Shesheke area is considered to be overstocked with domestic livestock (Baars 1996, Jeanes & Baars 1991a). Here, the estimated carrying capacity for grazers is of 1850 kg per $km^2$, while the cattle biomass density during 1990 was 1930 kg per $km^2$. Lack of water during the dry season, tsetse fly, excessive burning and the poor quality of much of the grass were identified as major constraints to grazing and, although cattle populations were growing at 3% per annum, Baars (1996) considered that disease and husbandry problems would probably ensure that most of the province did not become overstocked.

Current stocking rates in the Zimbabwe communal lands of the Four Corners are around 1000 to 1600 kg per $km^2$ (Dunham 2002). As with the wildlife estimates, these numbers are derived from aerial surveys in which there is undercounting, but the impact of the frequent severe droughts during the 1980s and 1990s and the absence of boreholes to provide dry season water supplies, are probable causes for the low densities.

Stocking rates are a controversial issue, especially in arid savannas such as in Botswana. Behnke and Scoones (1993**)** suggest that there is no such thing as a fixed carrying capacity in an environment where interannual rainfall variability has an overriding control on vegetation dynamics. Accelerated erosion caused by heavy grazing can irreversibly reduce the productive capacity of ecosystems, unlike the changes in vegetation structure and composition (on which carrying capacity estimates are usually based) which are in theory reversible in the short to medium term.

*Large Mammal Community Structure*

Mammal communities dominated by large herbivores such as elephant and cattle may have a different ecological impact than communities in which biomass is more evenly distributed across a range of body sizes (Cumming & Cumming 2003). Biodiversity implications include the effects of fine-textured ruminant dung versus coarse-textured non-ruminant dung on the structure of dung beetle communities (Gardiner 1995).

### 3.4.3 Small Mammals

There are no estimates of rodent herbivory rates for the Four Corners Area. Because of their size (<100 gm), small rodents have a much higher basal metabolic rate than large mammals. In an undisturbed East African savanna when the biomass density of small rodents increased to 390 kg per $km^2$ they ate as much as a community of medium-sized ungulates living at a biomass density of 4800 kg per $km^2$ (Keesing 2000).

In *Hyparrhenia* grassland derived from *Baikiaea* woodland near Livingstone in Zambia, Chidumayo (1980) found that the density of the gerbil *Tatera leucogaster* declined steadily over three years from about 50 animals per ha to <1 per ha. In miombo grassland in central Zimbabwe, where the multimammate mouse *Mastomys natalensis* was abundant (41 animals per ha), the biomass density of small rodents of all species combined was about 375 kg per $km^2$

(C.M Swanepoel pers. comm.). Delany (1986) suggests that in most moist savannas, the total number of small rodents is about half that estimate, fluctuating around 10 to 30 animals per ha (average biomass density approximately 134 kg per km$^2$). At this density, rodents would eat about as much as medium-sized ungulates stocked at a density of 1680 kg per km$^2$.

In the semi-arid zones of Africa, small rodent density may reach 100 per ha during occasional outbreaks but then drops to only 5-10 per ha (Delany 1986). In the drier parts of the Four Corners area, *Mastomys natalensis,* the pygmy mouse *Mus minutoides*, the bushveld gerbil *Tatera leucogaster* and the highveld gerbil *Tatera brantsii* are all prone to episodic outbreaks, during which population densities may be so great that everything edible within the reach of rodents is eaten and the populations then crash (Smithers 1983, Wilson 1975). A population explosion of all four species occurred when copious rain fell in the Makgadikgadi area of Botswana following four years of drought (Smithers 1983).

The high proportion of fine to medium sand grains in the Kalahari sands prevents burrows from collapsing, favouring a large burrowing rodent, the spring hare *Pedetes capensis*, whose biomass densities may reach high levels in northern Botswana (Butynski 1973).

### 3.4.4 Invertebrates
*Above-ground Herbivory*
There is no information on above-ground invertebrate herbivory in the Four Corners area. Edible caterpillars belonging to six species are sufficiently numerous in good years to be an important source of food and income to people living in both miombo and mopane woodlands (A. Cunningham in Clarke *et al.* 1996, Styles & Skinner 1996). Because invertebrate populations decline during the long dry season, most invertebrate herbivory takes place during the rains (Frost 1996). Populations survive the bottleneck caused by the poor quality and/or absence of leaves during the late dry season by persisting as eggs or pupae. They are unaffected by thorns and may also be more tolerant than mammalian browsers of the secondary chemicals in the leaves of dystrophic woodlands.

Wet miombo (Malaisse 1978, Malaisse *et al.* 1972), dry miombo (Martin 1974, Reeler *et al.* 1991), and *Burkea/Terminalia* woodland (Scholes & Walker 1993) are all subject to episodic invertebrate population outbreaks, during which trees over large areas may be defoliated. Herbivorous insects are not noted as forest pests in *Baikiaea* woodland, although the bark-boring larvae of a moth may threaten seedlings (Chisempa & Shingo 1986).

Invertebrate outbreaks also occur in the eutrophic savannas of southern Africa, such as riverine woodlands (Dunham 1991). During outbreak years, "mopane worms", the edible caterpillars of the moth *Imbrasia belina*, may experience population peaks and consume more leaf material in six weeks than the elephants in that area could consume during a year (A. Gardiner pers. comm.).

*Below-ground Herbivory*
Figures on below-ground herbivory are hard to find for any African savanna or woodland. There are no estimates even for the biomass of the soil fauna in most of the vegetation types represented in the Four Corners (see Dangerfield, Chapter 11). Invertebrate herbivory may be more intense below ground than above because much of the plant biomass is below ground.

### 3.4.5 Regeneration

Herbivores probably affect plant populations most strongly through their effect on regeneration. Browsing ungulates may prevent seed production, for example keep *Acacia tortilis* within the reach of fire and other browsers (Dangerfield, Perkins & Kaunda 1996).

Rodents, notably *Tatera leucogaster,* can prevent *Baikiaea* seedling establishment in forestry plantations or when shrub and grass growth have been encouraged by the removal of the tree canopy (Chisempa & Shingo 1986, Wood 1986, Calvert 1986b). Duiker were initially blamed (Selander & Malaya 1986) for serious damage to both seeds and seedlings that is probably caused by springhares (Calvert 1992).

Bruchid, curculionid and cerambycid beetle larvae frequently infest the seeds of both the broadleaved Caesalpinoid legumes (Chidumayo 1993a) and the acacias, but as there is an understorey of suppressed seedlings in most broadleaved woodlands, and acacias produce abundant seed, these invertebrates, although conspicuous and frequently studied, are probably not particularly important as plant population regulators (Ernst, Decelle & Tolsma 1990).

### 3.4.6 Wetlands and Other Key Resource Areas

Wetlands are often likely to be key resource areas in the sense of Illius and O'Connor (1999) in that they provide green grass at a time when food quality is generally low. Grass species that grow in many wetlands are not necessarily known for their nutrient quality, except those such as *Setaria* that grow on fertile soils. But if the soil moisture is sufficient to allow the grasses to remain green, they have higher crude protein and phosphorus content than dry grass, and lower levels of indigestible fibre (Jeanes & Baars 1991a).

### 3.4.7 Key Features of Herbivory in the Four Corners Area

- Although protein levels in the leaves of woody plants and herbs in the nutrient-poor savannas may be adequate for animal nutrition, the leaves are defended by carbon-based herbivore deterrents and the densities of browsing mammals are therefore low.
- During the dry season, dry grass leaves have levels of nitrogen and phosphorus that are well below the maintenance requirements of large mammals, especially in the nutrient-poor savannas.
- Wetlands are a key resource for grazing antelopes. Grazers characteristic of the nutrient-poor savannas and woodlands of the Four Corners area (roan, sable and Lichtenstein's hartebeest) are specialist feeders, selecting high quality patches of green grass from locations such as dambos where the water table is close to the surface during the dry season. Antelope associated with grasslands (southern reedbuck, defassa waterbuck, tsessebe, puku, lechwe and sitatunga) select green grass from floodplains and swamps all year round.
- The biomass density of indigenous large herbivores is dominated by elephant (>50% of biomass in Zimbabwe) and buffalo, both of which are large-bodied non-selective feeders.
- The biomass densities of livestock (1100-1300 kg/km$^2$) in Zambia and Zimbabwe are below those predicted on the basis of mean annual rainfall, probably because of the absence of surface water during the dry season combined with the effects of recent droughts.
- Stocking rates are a controversial issue in the drier nutrient-rich savannas of the southern part of the area, where livestock numbers should perhaps be allowed to fluctuate in response to wet and dry periods, except in areas where the rates of soil loss due to erosion from unprotected soil are excessive.

- Large herbivores (excluding elephant) are unlikely to consume more than about 15% of the annual production of plants in nutrient-poor savannas.
- Rodents probably eat nearly as much of the annual plant production as the large herbivore community consumes. During rare outbreaks, especially in the semi-arid savannas, they can consume considerably more.
- Above-ground invertebrate herbivory probably exceeds large mammal herbivory in the Four Corners area, certainly during outbreak years.
- Below-ground invertebrate herbivory has never been quantified here, but as more than half the plant biomass is below ground, it may exceed above-ground herbivory.
- Herbivores probably exert an effect on plant populations most strongly through their effects on regeneration.

## 3.5    FIRE

### 3.5.1  Effects of Fire

The most recent account of fire as an ecological process within the Four Corners area is Frost's (1992) comprehensive review from the Western Province of Zambia. Extensive vegetation fires require: sufficient fuel to carry a fire without it dying out; a fire starter; and suitable climatic conditions for burning. All three conditions are met in most years in the majority of the vegetation types of the area. Standing grass provides most of the fuel together with shrub leaves and twigs and some leaf litter and fine woody material. Grass fires generally require a fuel load of at least 1000 kg per ha (McArthur 1977, Trollope & Potgieter 1983), although fires carry in teak woodlands with a herbaceous fuel load of <650 kg per ha if there is also abundant leaf litter (Calvert & Timberlake 1993). As available moisture largely determines grass production, the frequency and intensity of fires are broadly related to mean annual rainfall. At any one location, fuel loads vary from year to year and are heaviest in exceptionally wet years. Grass fuel may accumulate from one year to the next if an area is unburned, especially if rates of herbivory are low. Conversely, during exceptionally dry years, especially on soils with high clay content and no run-on water, there may be insufficient fuel to carry a fire. In arid woodlands, livestock, wildlife and termites often reduce the mass of grass below the minimum standing crop required to sustain a fire (Frost & Robertson 1987, Dangerfield, Chapter 11).

The standing crop of grass is also related to the density of the woody cover. Uplands in the Western Province of Zambia illustrate the importance of vegetation structure to the fuel load (Jeanes & Baars 1991a, Frost 1992). During the mid-dry season in a year when rainfall was 150-250 mm below the mean, the standing crop of grass ranged from 290 kg per ha under *Cryptosepalum* forests and thickets, to 330 kg per ha in *Baikiaea* forest. Grass cover was more substantial in woodland, ranging from 1050 to 1820 kg per ha in *Baikiaea*, Kalahari, miombo, *Acacia/Combretum* and mopane woodlands, while in the bushgroup woodland it rose to 2880 kg per ha. In woodlands and thickets, grass fuel is supplemented by twigs and leaf litter. On low-lying ground the standing grass crop is related to position in the landscape, being heaviest where water accumulates (Jeanes & Baars 1991a). Mean standing crop is 3000 kg per ha on dry watershed plains, on pans and in dambos, and may reach 10,000 kg per ha on floodplains and river plains (Frost 1992).

People start most fires, sometimes accidentally while clearing fields for cultivation, making charcoal, burning rubbish, or smoking bees to collect honey, but often deliberately to produce a green flush of grass regrowth to feed livestock, to clear paths so that people may walk safely, or to attract wildlife so that it may be hunted (Chidumayo & Frost 1996). Given the fuel loads and the long dry season, fires would occur eventually even without humans, as lightning is a natural ignition source. The average number of thunder days per year at Hwange Main Camp,

Zimbabwe, is 89 (Kreft 1972). Relating thunderdays to lightning strikes to the ground (Gaunt & Britten in Frost 1992) gives an average of 7 ground strikes per km[2] per year in Hwange. Most of these occur during the wet season when the grass is too wet to burn (Calvert 1986a), but ignition is possible during rare dry thunderstorms at the end of the dry season, at the start of the wet season, and when unusually prolonged periods without rain occur during the wet season. Accordingly, lightning fires are more probable in the late dry season and during the wet season, while people light fires throughout the dry season. Thus the timing as well as the frequency and intensity of fires in southern Africa changed when people rather than lightning became the major ignition source.

The four to seven month dry season provides ideal weather conditions for fires. These are most severe when the grass is dry, relative humidity is low, and air temperature and windspeed are high. Conditions at Hwange Main Camp (Figure 3.3) are used as an example for the Four Corners Area.
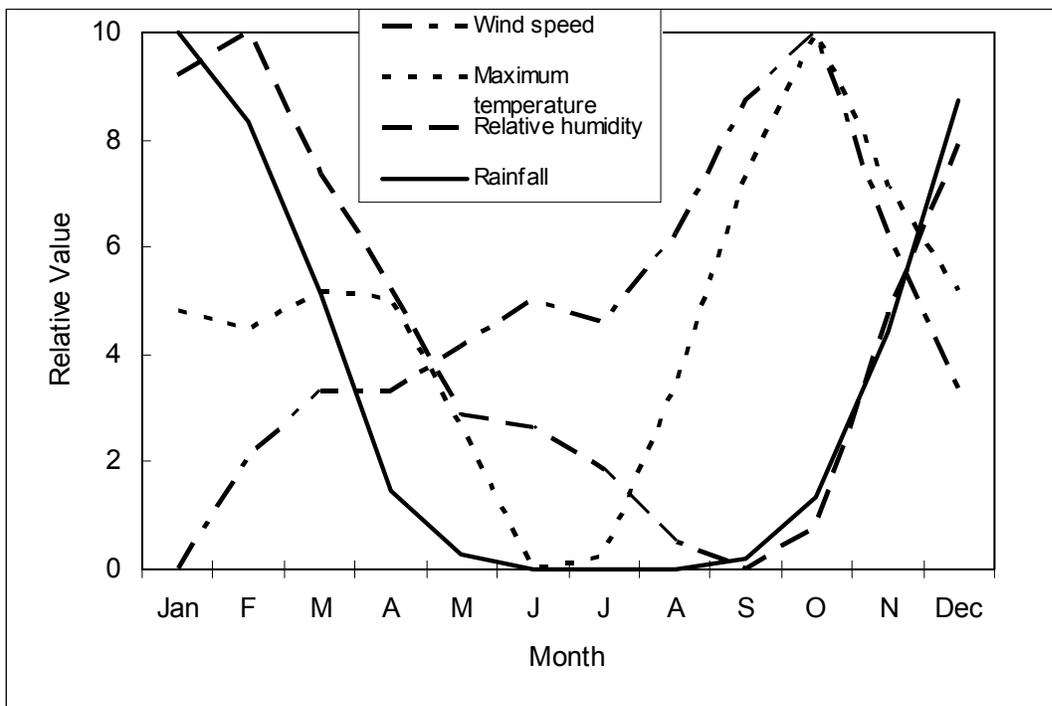


**Figure 3.3.** Fire intensity is at a maximum during September-October, when windspeed and air temperature are high and rainfall and humidity are low. Data for Hwange Main Camp from Dept. Meteorological Services (1978).

Fires are often described as 'early' or 'late' burns. Early burns occur at the start of the dry season, usually during April to June when there is still green grass in the sward and weather conditions are not conducive to severe fires. Late dry season burns occur during August to November, when the fuel load may have been reduced by grazing, but all the grass is dry and available as fuel and weather conditions favour intense burns. Late fires are much more intense and uniformly hotter than early ones (Robertson 1993).

Plants are most vulnerable to fire when they are actively growing. Because grasses and woody plants differ in their phenology, location of their growth points and resource allocation, the

timing of the burn affects these two life forms differently. Burning early in the dry season kills the stems of some woody plants, generally those less than 1-2 m tall, but reduces the fuel load and the probability of late dry season fires, favouring relatively fire-resistant woody plants. Late hot fires favour perennial grasses, largely by suppressing woody plants that would otherwise compete for water and nutrients. Most perennial grasses do not grow during the late dry season and their vulnerable growing points are below-ground. Although woody plants have their buds above ground, many of those in the Four Corners area also have substantial root stocks and can coppice by producing new buds just below ground level if the above-ground parts are removed by fire. Grasses are particularly vulnerable to burning during the wet season, as unlike woody plants they do not have reserves to compensate for material lost to burning. Complete protection from fire favours woody plants.

### 3.5.2  Current Fire Regimes

Frost (1992) estimated the recurrence interval of fire in each vegetation type in the Western Province of Zambia, assuming that the percentage of the area burned during July/August 1987 was broadly representative of all years. In the lowlands, 50-90% of the area of the various grassland types had burned, giving a recurrence time of one to two years in all except the *Loudetia* sandplains, where the fire interval was more than three years. On the uplands, vegetation types where trees were sparse or clumped had a recurrence interval of less than two years, while the woodlands burned once every two to three years. The area of *Cryptosepalum* forest and thicket that had burned was only 16%, giving a recurrence interval of six years, while the mopane woodland seldom or never burned. Most of the fires in western Zambia are lit by people and there are four different fire regimes, broadly related to four different grazing systems (Jeanes & Baars 1991a, Frost 1992, Baars 1996). In general, because most fires are lit by people early in the dry season to promote grass regrowth for grazing animals and because the fuel loads are low except in some low-lying areas, the fires burn patchily and are not particularly intense.

The Zimbabwe Department of National Parks has maintained records of the areas burned in Hwange National Park since 1967 (Rogers 1993, Rogers & Chidziya 1996) and since the 1970s in the Matetsi complex (S. Childes, V. Booth pers. comm.). A published map of the fire frequency categories in areas of Hwange during 1967-1991 shows a range of fire frequencies - from no fires during 24 years, to burning every second year on average (Rogers 1993). The fire regime is related to vegetation types: *Baikiaea* woodland and *Burkea/Terminalia* shrubland near the centre of the Park have burned once every six to twelve years, mopane woodland has burned once every four to twelve years, but on the western boundary, mopane bushland and bushland on basalt, both of which support substantial grass layers, have a fire recurrence interval of no more than two to four years.

The Forestry Commission maintains fire records for Forest Reserves in the Zimbabwe sector of the Four Corners area, based largely on observations from fire towers (Gondo 1993, Tacheba *et al.* 2002). Approximately 20% of the area of the Forest Reserves burned every year between 1928 and 1975, irrespective of fire management (Calvert 1992), suggesting a five year recurrence interval. Five to fifteen percent of the Forest Area burned each year during 1985-1989 (Gondo 1993). Although the majority of fires were lit by poachers, neighbours and travellers, 4% were caused by lightning. Most fires burned during the mid to late dry season, with 60% during August to October. There are no fire records in the communally owned rangelands that surround protected areas.

### 3.5.3  Fire Effects on Herbivores

Perennial grasses that regrow after a fire have higher levels of phosphorus and protein in their foliage than unburned plants (Frost & Robertson 1987, Jeanes & Baars 1991a), probably because the regrowth is younger and more leafy. Improving the quality of grazing for domestic livestock is one of the commonest reasons that people give for lighting fires in western Zambia (Baars 1996).

There is no published work on the effect of fire on herbivores in the Four Corners, other than for elephant (see Conybeare, Chapter 15). Work in other African savannas suggests that the density of insects and small mammals is lower in savannas that are frequently burned (Gillon 1983).

### 3.5.4  Key Features of Fire in the Four Corners

- For the majority of vegetation types there is sufficient standing grass to fuel an extensive fire in most years, and suitable climatic conditions for burning are present.
- The frequency and intensity of fires are broadly related to mean annual rainfall. At any one location, fuel loads vary from year to year and are heaviest in exceptionally wet years.
- The time of greatest fire hazard is midday during the months of September and October when all weather factors combine to maximise fire intensity.
- The timing of a fire affects grasses and woody plants differently. Burning late in the dry season favours perennial grasses, while complete protection from fire favours woody plants.
- Although people start most of them, fires would occur eventually anyway given the fuel load and the long dry season, as lightning is a natural ignition source.
- Most areas burn at intervals ranging from once a year to once every six to twelve years, depending on the vegetation type and the sources of ignition. A few areas with inadequate fuel loads never burn.

## 3.6    FROST

Seasonal variation in air temperature is least nearest the equator, and increases towards the south where winters are progressively colder (Scholes *et al.* 2002). Frosts occur during two to four months of the dry season over much of the Four Corners area, except the Okavango Swamps and in the Caprivi. The effects of frost are patchy, being most severe in hollows, where a distinct thermal inversion layer develops at 3-5 m, and less severe on uplands such as dune crests (Childes & Walker 1987). Canopy trees add to the patchiness, by protecting underlying shrubs (Rushworth 1978). Low humidity during winter, the absence of cloud cover and the high reflectivity and low thermal conductivity of Kalahari sand accentuate the effects of the cold, dry, south-westerly air that blows off the Atlantic two or three times a year (Huckabay 1986a, Childes & Walker 1987). Occasionally the air is so dry that dew cannot form, no latent heat is released and continued radiation into the clear night skies causes air temperatures to drop at a rate of more than about 1°C per hour overnight (Rushworth 1975, Dudley 1999). When temperatures drop to -6.7°C or lower, sap freezes in plants, killing stems and leaves and leaving them with a scorched and blackish appearance, hence the name "black frost". No conventional "white" frost is formed unless temperatures actually drop below the frostpoint, which may be very low because the air is so dry (Hattle 1972). In Hwange National Park black frosts occur once every 3-5 years on average, but at irregular and unpredictable intervals (Childes & Walker 1987, Rogers 1993).

The greatest increases in temperature associated with global warming are likely to be in winter minima, leading to a reduced incidence of frost in southern Africa (Tyson *et al.* 2002). There has been a warming trend in mean monthly maximum temperatures of 1.5°C over the period 1951-1995 at Hwange Main Camp (Dudley 1999), and a reduction in the frequency of severe frost events, from eight winters with killing frosts during the 23 years prior to 1973 (a recurrence interval of 3 years) to four winters with killing frosts during 1974 to 1997 (a recurrence interval of 6 years) (Dudley 1999). Although frosts have been less frequent, they have not been less severe: the absolute minimum of –14.4°C recorded during the winter of 1990 was a record low.

## 3.7 ECOLOGICAL PROCESSES AND INTERACTIONS AS DETERMINANTS OF VEGETATION STRUCTURE

There have been changes in the structure of most vegetation types in the Four Corners area as a direct or indirect result of human activities during the 20th Century. Especially in the north, some areas that were once forest or woodland are now shrublands or wooded grasslands, as a result of clearing (for timber, fuel or cropland) and severe fires. While in the south, shrubs have increased at the expense of trees and grasses as a result of browsing by elephant, severe grazing by domestic livestock, drought, falling water tables in wetlands and fire suppression. These trends suggest that across the Four Corners area there is homogenisation in vegetation structure in the direction of shrubland, especially in those resilient vegetation types which respond to disturbance by resprouting from their reserves of underground biomass.

### 3.7.1 *Cryptosepalum* Forest, Woodland and Thicket
Under the current rainfall regime, this dry forest type is probably confined to sites located on perched water tables in deep sand. Evergreen forests and thickets contain tree and shrub species that are thin-barked and sensitive to fire. Repeated fires transform the species composition of *Cryptosepalum* forest, reducing species richness of the woody plants that are characteristic of mature forest by more than 75% (Cottrell & Loveridge 1966).

### 3.7.2 *Baikiaea* Forest and Woodland
*Baikiaea* forest and woodland are currently restricted to sites on deep Kalahari sands under an annual rainfall regime of slightly less than 600 mm to more than 1000 mm (Huckabay 1986a). In freely draining Kalahari sands, evapotranspiration dries out the upper 45-60 cm of soil soon after the rains have ended, and these layers stay dry until the first rains (Calvert 1986a, Hogberg 1986a, Huckabay 1986). *Baikiaea plurijuga* roots to a depth of 6-9 m with few fine roots close to the soil surface and an extensive, but not abundant, network of roots at depth (Hogberg 1986a). Childes & Walker (1987) established that depth of sand and soil moisture regime were the predominant factors determining the structure of undisturbed vegetation on the Kalahari sands of Hwange National Park.

*Baikiaea* is at the dry end of its range in the Four Corners. If seedlings can germinate and establish only during exceptionally wet years (J. Gambiza in Mosugelo *et al.* 2002), and these coincide with rodent population peaks, repeated re-establishment of the *Baikiaea* canopy may be difficult in the long-term.

The slow-growing, timber-producing trees dominating the canopy in *Baikiaea* forest and woodland are vulnerable to fire. In Gwayi Forest Reserve, even 34 years of annual or biennial late dry season fires did not remove the woody plants (Calvert & Timberlake 1993). Frequent fire drove the woody plants underground, where a resilient reserve of underground rootstocks survived the burning and continued to produce multi-stemmed coppice, year after year. A reserve of about 1500 rootstocks per ha of timber species remained, many more than the 20-30

rootstocks per ha that would be required to replace the canopy trees. Once the canopy trees had been removed, only complete protection from fire for 50-100 years, during the vulnerable sapling stage, would permit development towards dense woodland dominated by *Baikiaea* or *Guibourtia*. In Zimbabwe woodlands, *Baikiaea* plants do not become immune even to low-intensity fires until they have grown a stem that is at least 10 cm in diameter at breast height. This does not occur until they are 50 to 95 years old (Calvert & Timberlake 1993).

*Baikiaea* is particularly sensitive to the interaction between fire and frost. Once the canopy trees have been removed, for instance by selective timber-felling, frequent frost and fire can prevent regrowth of the disturbed forest canopy and transform *Baikiaea* forest into thicket and eventually into grassland, whereas disturbed *Baikiaea* woodlands are maintained as shrubland by repeated burning, unless the rootstocks are deliberately removed. Although there are changes in the relative abundance and above-ground biomass of woody species in *Baikiaea* woodland, there are no major changes in species composition, unlike in *Cryptosepalum* and *Baikiaea* forest.

*Baikiaea* and *Guibourtia* do not appear to be attractive to elephant and the loss of canopy woodland to elephant browsing is not yet a major feature of this vegetation type (Conybeare, Chapter 15).

### 3.7.3 *Burkea/Terminalia* Woodland and Scrub

Although the woody species that dominate this vegetation type are more resistant to fire and frost than the canopy species of *Baikiaea* woodland, its structure is maintained by these two processes, assisted in some protected areas by elephant herbivory (see Conybeare, Chapter 15). Species differ strongly in their frost-hardiness. Stems of vulnerable species do not escape the risk of death by severe frost until they have reached heights of 2-3 m. There are few tall trees to protect the shrubs from the effects of frost, and this, combined with a relatively high grass biomass, leads to frequent fires (Childes & Walker 1987). As the standing crop of grass is doubled in frequently burned areas compared to unburned areas, there is a positive feedback between fire and fuel load (Rushworth 1975, 1978). Although frost and fires may kill the main stem, woody plants coppice profusely from rootstocks and this vegetation type is very resilient.

### 3.7.4 Brachystegia/Julbernardia Woodland (Miombo)

Miombo woodland trees suppress grass growth, probably through competition for water, and grass standing crop declines exponentially as woody plants increase, until it levels off when the tree canopy cover is nearly complete (Robertson 1990, Desanker *et al.* 1997).

There has been no experimental work on fire in miombo growing on Kalahari sands. Woody species differ in their sensitivity to fire, the dominant *Brachystegia* and *Julbernardia* species being relatively intolerant of hot fires, while some species such as *Pterocarpus angolensis* are tolerant (even of late dry season fires), and others are intermediate in their response (Trapnell 1959, Lawton 1978, Cauldwell & Zieger 2000). Work in the Copperbelt of Zambia (Trapnell 1959, White 1983) and at Marondera on the Zimbabwe highveld (Strang 1974, Frost 1992) is broadly applicable to wetter and drier miombo, respectively.

After clearing, and so long as the rootstocks are not destroyed, both wetter and drier miombo woodland will grow back more or less unchanged if they are protected from fire (Boultwood & Rodel 1981, Chidumayo 1988). Fire during regrowth will kill fire-intolerant species and reduce stem density, as does severe browsing by livestock (Chidumayo & Frost 1996, Grundy 1996). The likelihood that miombo coppice will regrow into miombo woodland is greater the longer the interval between fires (Frost 1996).

Interactions between fire and frost are not a feature of this vegetation type. Miombo woodland does not occur where mean minimum temperatures are less than 4°C (Werger & Coetzee 1978). Elephants move into *Brachystegia* woodland during the dry season when browse predominates in their diet and tree-felling and the stripping of bark are common (Conybeare, Chapter 15). Even when they are living at relatively low densities (<0.5 per km$^2$), elephants in combination with fire can reduce *Brachystegia* woodland to shrubland within a few years.

### 3.7.5 *Colophospermum mopane* Woodland (Mopane) and Shrubland

Mopane is often mono-dominant because of its superior ability to survive in soils that are unusually dry due to low infiltration rates, low water potentials (high tensions) and impermeable sodic or other soil horizons (Timberlake, Nobanda & Mapaure 1993). While *C. mopane* is generally shallow-rooted, its occurrence in two growth forms, as a shrub and as a tall canopy tree, is probably related to differences in soil moisture availability due to differences in effective rooting depth (Timberlake 1995).

There appears to be strong competition between large mopane trees in northern Botswana, judging by the uniform distribution patterns of large individuals (Caylor *et al.* 2003). Often there is a large population of suppressed suffrutices and mopane coppices readily. An even-size structure is common, but it is not known whether this reflects an even-age structure (Timberlake 1995).

There is no experimental work on the effects of fire on mopane within the Four Corners area. Fire generally has little effect on mature mopane woodland because the grass cover is poor (Guy 1981) and there is little other fuel at ground level. However, grass cover is very variable in other mopane types, depending on soil moisture, the biomass of woody plants and grazing intensity (Frost 1992). Mopane leaves make a significant contribution to the fuel load and increase the fire intensity, especially in shrubland, because they contain resin which raises the temperature of ignition and allows shoots to burn even while green (Trollope & Potgieter 1983). The resin can volatilise, causing spectacular, fast-moving crown fires under hot, dry weather conditions, which can damage even mature trees. The fuel load may be considerably increased by an early frost that kills the branches and prevents leaf fall, but may be reduced, especially in drought years, by browsers eating the leaves.

Mopane is sensitive to low temperatures, the limit to its distribution apparently being controlled by the 5°C mean daily isotherm for July, although it does occur in frost-prone areas (Timberlake 1995). The interaction between fire and frost is likely to be important. It is also a principal food for elephant (Ben-Shahar 1996), and woodland within some protected areas has been transformed into shrubland by elephant and fire (Conybeare, Chapter 15).

### 3.7.6 *Acacia/Combretum* Woodland (Munga)

This woodland is a floristically-rich vegetation type which lacks clearly defined dominant species. Although it has sometimes been regarded as secondary vegetation invading other woodlands when they have been severely disturbed (Fanshawe 1969, White 1983), it grows on different, drier and more fertile situations than surrounding vegetation and is a eutrophic rather than a dystrophic savanna. Within the Four Corners area it occurs on fertile soils on the plateau in the Game Management Areas south of Kafue National Park, on the north bank of the Zambezi in the Machili area, and on lower slopes elsewhere as part of the catenary sequence. The *Acacia, Combretum* and *Terminalia* species and various members of the Papilionoideae that grow scattered or clumped through the tall grass layer are very fire and frost-resistant (Fanshawe 1969, Frost 1992). The standing crop of grass is high (Robertson 1984) and fires are intense.

### 3.7.7 Bushgroup and Savanna

Termite mounds with their distinctive, sometimes evergreen, flora and their generally low grass load are less prone to severe burning than many other vegetation types. Mounds often occur in a matrix of tall grassland in a distinctive bushgroup savanna that covers large areas of south-west Zambia and on the lower parts of many catenas elsewhere. Frequent fire sharpens the boundary between wooded mounds and the burned grassland.

### 3.7.8 Kalahari *Acacia* Transition Woodland

Although Moore and Attwell (1999) attribute the overall distribution of broadleaved and fine-leaved savannas to the decrease in mean annual rainfall towards the south of the Four Corners area, they also suggest a correlation with sand grain size and heavy mineral content at a geological scale. Broadleaved trees and shrubs, including *Terminalia sericea*, which have well-developed lateral root systems that are adapted to exploit near-surface water, dominate on the deep sands, but where the Kalahari sand thins towards the edge of a basin, deeper rooting *Acacia* species which are able to exploit aquifers in the bedrock, increase (Moore, Chapter 2). Vegetation structure is also correlated with soil texture, with extremely fine-grained soils favouring shrub savanna while coarser-grained soils are associated with tree savanna.

An increase in the size and density of woody shrubs (bush encroachment) is common in *Acacia* savanna communities where the perennial grasses have been weakened by drought and/or heavy grazing by livestock or wild ungulates (van Vegten 1983, Tolsma *et al.* 1987, Skarpe 1986, 1990a, b). A shallow-rooting habit is correlated in the acacias with the ability to invade disturbed communities (Tolsma *et al.* 1987). There are two possible explanations for this pattern. Those *Acacia* that are shallow-rooted have a higher nitrogen content in their leaves than the deeper-rooted species, and Tolsma *et al.* (1987) suggest that better opportunities for infection with nitrogen-fixing bacteria enable them to grow faster and make them better able to compete with deeper-rooted species. Alternatively, shallow-rooted shrubs such as *Acacia mellifera* may have better access to water in the upper layers of soil compared to those species with deep root systems, especially when the perennial grasses have been weakened by overgrazing (Skarpe 1990b). Shallow-rooted shrubs are also able to use the rainfall from small showers, flushing earlier when the grass layer has been reduced.

Insect herbivory may exert an indirect effect on mammalian herbivores in *Acacia* woodland. After *Faidherbia albida* trees had lost their leaves to caterpillars they flushed again, but the fruit crop was reduced (Dunham 1991). *Faidherbia* pods are an important, perhaps key, dry season food resource for large mammals in riverine woodland. *Acacia erioloba* pods are similarly important in the sandveld of northern Botswana and western Zimbabwe.

### 3.7.9 Riverine Woodlands

Little is known of ecological processes in riverine woodlands in the Four Corners area, despite their importance as dry season concentration areas for mammals. Riverine woodland might be incapable of regeneration under the current soil moisture regime, when combined with high levels of herbivory.

Riverine woodlands do burn, but are usually grazed so severely that there is little grass to carry a fire. During 1998, fire was no longer a dominant factor close to the Chobe River, as there was insufficient fuel, although in excess of 50% of trees growing more than 7 km from the river did have fire scars (Mosugelo *et al.* 2002).

### 3.7.10    Secondary Grasslands

Grasslands derived from the severe disturbance of other vegetation types, usually involving the

removal of woody rootstocks, are maintained as such by fires which prevent the establishment of woody plants (White 1983, Wood 1986).

### 3.7.11    Dambos and Pans
Dambos reflect the substrate (Whitlow 1991). Within the Four Corners there are three types:

- peaty dambos on Kalahari sand under higher rainfall regimes, best developed in western Zambia,
- acid hydromorphic dambos with pale grey to whitish sandy clay soils, often mottled at depth, occurring particularly on Basement complex rocks on flatter terrain in Zambia, e.g. Kafue National Park,
- calcic hydromorphic dambos with dark grey to black clayey topsoils that crack upon drying. These develop on fine-textured rocks in low-rainfall areas and are best developed on basalt soils in relatively flat terrain, e.g. Matetsi Safari Area in Zimbabwe.

The origins and hydrological relations of dambos are not well understood. As the only piece of work on dambos in the Four Corners area is unpublished (McFarlane 1995), the account given here is conjectural and subject to correction.

On the Kalahari sands, especially in the wetter parts of northern Zambia, where the terrain is flat and there is insufficient runoff for an above-ground drainage system to develop, drainage is predominantly subsurface. Linear dambos and circular pans rather than streams have developed in the upper catchments. Leaching is important in dambo development, as it is in most soil processes in the Kalahari sands. When the watertable is low, subsurface leaching removes silica in solution and the dambo or pan surface collapses (McFarlane 1995). Where the watertable is high, fine material is deposited in the pans and dambos forming a seal that allows them to hold water, even for some months into the dry season when the ground water table has dropped. Ground water emerges in seeps at the edge of these dambos and under anaerobic conditions the vegetation growing here is transformed into peat. The nature of the fine material, and why it should be an extremely effective seal, as it must be to prevent drainage into the Kalahari sands beneath, is not clear. Fanshawe and Savory (1964) suggested that silica gel underlies some pans in the Kalahari sands.

Dambos are not sponges that allow the slow release of water to rivers, maintain baseflow and increase dry season flows as scientists, legislators and extension workers have presumed (Whitlow 1991). If anything, dambos reduce dry season stream flow, because some of the sub-surface water moving downslope from the upland interfluve evaporates or is transpired when it emerges at the dambo margin (Bullock 1994). There has been no work on basalt dambos in the Four Corners area.

Recently, peat fires have burned on the Barotse floodplains where water levels have dropped and rice-cultivators burn off crop residues (Bingham 2000). Peat fires also occur in the Liambezi-Linyanti floodplain grasslands (Mendelsohn & Roberts 1997) and in vleis in the Hwange area, in Dete, Jijima and part of Sikumi (P. Frost pers. comm.). The ash adds nutrients to the soil and the post-burn vegetation is more nutrient-rich and more attractive to herbivores.

### 3.7.12    Watershed Plains
In the grassy watershed plains of western Zambia the watertables are so high that tree seedlings are unable to establish. During the dry season the plains support no green grass as there is little moisture near the soil surface (Jeanes & Baars 1991a), but these soils are moist at depths of greater than one metre (Trapnell & Clothier 1937).

### 3.7.13        Floodplains

Floodplains cover extensive areas of southern Zambia, the Caprivi and parts of northern Botswana. Their hydrological relations are complicated by past earth-movements and by a terrain that is so level that watercourses may flow in different directions depending on their flood levels relative to neighbouring watercourses (Schlettwein *et al.* 1991). River gradients are very low and the flood waters of the Kwando River used to take six months to percolate through the dense papyrus swamps of the Linyanti to reach Lake Liambezi. Much of the former bed of Lake Liambezi is now cultivated. The diversity of the soil moisture regimes on the floodplains of the Caprivi is reflected in the diversity of the soils and the vegetation types and in the ways in which they are used for agriculture (Mendelsohn & Roberts 1997).

Floodplain, dambo and watershed grasslands have a high fuel load and are burned deliberately in most years. There is no experimental work on the effects of fire on these grasslands. Frequent burning probably prevents the establishment of woody plants where the water table has dropped due to a change in the water regime, thus maintaining them as grasslands. Perennial grasses are generally tolerant of fire and may require burning to remain productive if herbivory rates are low and moribund grass accumulates in the sward, shading the new shoots (Frost 1992).

### 3.8        AREAS AND PROCESSES OF CONSERVATION IMPORTANCE

### 3.8.1  Climate, Soil Moisture Balance and Drainage

Tyson *et al.* (2002) review the probable effects of climate change on the hydrological systems of southern Africa, including the area covered by the Four Corners. Under the business-as-usual scenario, globally-averaged surface air temperatures will rise by 1.0-1.7°C over the next 50 years (IPCC 2001). Within the continental interior of Africa, the predicted temperature increase of >2°C will be greatest (Hulme 1996). Temperature increases during the cool dry season are already evident in the reduced frequency of frost in Hwange.

The majority of climate-change models predict decreases in rainfall, runoff and soil moisture levels in Africa south of about 10°S. The frequency of exceptionally wet or dry years is expected to increase. Magadza (2000) discusses the probable effects of climate change and changes in land use on wetlands of the Four Corners area. Most of the riverflow here is not currently devoted to human use, but there is the potential for the commercial use of irrigation water on the more fertile alluvial soils of the Caprivi and in the Gomare-Nokaneng area of Botswana. There is also an increasing demand for water for urban use, especially in Maun and Orapa.

Because the soil moisture balance has such a profound influence on vegetation structure, changes in rainfall and evapotranspiration would be expected to change the distribution of plant communities. On the relatively uniform substrate of the Kalahari sands, such changes might be predicted from current distributions, combined with climate data. Lake Liambezi and the swamps in the Mamili National Park, Caprivi, and many of the Caprivi wetlands, are unstable, shifting between different vegetation states as a result of changes in rainfall in the catchment areas of rivers hundreds of kilometres away. There is not much that can be done about this, but plans should be made for species such as lechwe that are dependent on permanent swamps, so that populations can return either through corridors or through re-introduction when the next wet phase materialises. A transfrontier approach to these species would be crucial.

There is likely to be an increase in dambo cultivation as the demand for land increases. Changes in land use on the interfluves, especially the clearing of woody vegetation and the resulting reduction in evapotranspiration, will alter the hydrology of dambos more profoundly and may lead to breaching of the thin but impermeable clay layer that lines dambos on basement rocks,

due to a rise in the subsurface water table (McFarlane 1994). The effects of irrigation or tree clearing on the Kalahari dambos are not well understood.

### 3.8.2 Nutrient Flows
*Low Input/Low Output Farming*
Although relatively prosperous people in Caprivi (el Obeid & Mendelsohn 2001), and perhaps elsewhere, earn money in other ways and then invest in livestock and commercial farming, most rural people in the Four Corners will probably rely on low-input low-output farming for the foreseeable future due to a lack of opportunities for alternative income. The often complex traditional farming systems described by Trapnell & Clothier (1937) depend on a period of fallow to improve the soil structure, increase the organic matter content and replace the nutrients lost to cultivation. Shifting cultivation is an effective response to farming on low-nutrient soils, where the burning of woody material on the plots raises the soil pH, releases exchangeable bases and makes phosphorus and nitrogen available to plants (Stromgaard 1984, Chidumayo 1993b, 1995, 1999). When population density is such that people are no longer free to move and fallow periods are reduced, the nutrient losses in erosion and crop harvest cannot be compensated for by natural and human inputs (Drechsel *et al*. 2001). The consequences are sustained nutrient loss, decreased food security and the clearing of land that is less suitable for cultivation (Cumming, Guveya & Matose 2002). Nutrient loss rates may decline with years of cultivation, but so do crop yields (Grant 1981).

*Waterholes*
Artificial water supplies are responsible for locally high biomass densities of large mammals in rangeland and protected areas. The absence of naturally-occurring surface water supplies during the late dry season, with the exception of the major rivers whose perennial sources lie outside the Four Corners, is a defining feature of the undisturbed Kalahari sands. As most aquifers in the area lie in formations underlying the Kalahari sands they are often too deep to be accessible, but ground water can be extracted from the sands at low rates. South-west Zambia and eastern Angola are probably the only areas where the current biomass densities of large mammals are not maintained by artificial water supplies. The spacing and density of waterholes determines the distribution of grazing intensity and of the nutrients cycled through urine and faeces, and should be re-assessed in all protected areas and most rangelands.

*Nutrient Loss and Elephants*
We do not know the consequences for nutrient cycling of the conversion of woodland to shrubland by elephants (Conybeare, Chapter 15). This is a major information gap.

### 3.8.3 Fire
*Carbon Sinks*
The Four Corners area has the potential to absorb more carbon, especially as much of the biomass is below ground and so inaccessible to fire. Scholes (1996) suggests that reducing the fire frequency from once every year or two to once a decade, could increase carbon storage over the next 20-50 years until woodlands reached a new equilibrium carbon density.

*Fire Regimes*
The blanket application of one fire regime, such as early-burning in the Forest Reserves, is no longer appropriate. Greater consideration should be given to a variety of fire regimes that differ in frequency and seasonality, especially in protected areas, some designed to maintain a particular woodland structure, some to exclude elephant from sensitive areas during the dry season, some perhaps to replicate a lightning-fire regime, and others to encourage rare plant or animal communities.

### 3.8.4 Herbivory

Elephants are likely to have major effects on the numbers of other animals, not only through changes in habitat structure, but also through the quantity of food that they eat, especially in Hwange National Park where they are now 88% of the large mammal biomass.

The availability of key resources, which for ungulates are green grass throughout the dry season or browse leaf at the end of the dry season, are likely to decline as the rainy season becomes shorter. The greater likelihood of food shortages at critical times of year will increase the probability of local extinctions.

### 3.8.5 Invasive Plants

Changes in the structure and functioning of vegetation types in the Four Corners area, whether caused by land-use change, atmospheric composition change or climate change, will provide further opportunities for alien plants and animals and weedy indigenous species to invade. *Mimosa pigra*, a thorny alien shrub, is a potential problem on floodplains, especially when these become drier as a result of prolonged droughts in the catchment.

*Cenchrus biflorus*, an annual grass that produces fruits with robust spikes, was probably introduced near Lake Ngami during the late 1940s (Setshogo 2002). Although *C. biflorus* is palatable when young, its ripe fruits cling to the coats of livestock and wildlife, sometimes causing injuries and even blindness. It is now widespread in the Kalahari sands of northern Botswana, especially around boreholes and other places where the soil has been disturbed by severe grazing and erosion.

### 3.9    MONITORING

Cumming, Guveya and Matose (2002) proposed a number of performance criteria for biophysical and ecological indicators within the Miombo Ecoregion and used these in an assessment of the conservation status of three transboundary areas, including the Four Corners. They were unable to score many criteria because information was not readily available. The suggestions for monitoring below are based on their framework.

Considering the remote and rural nature of most of the Four Corners area, there are more baseline data on ecological processes than might be expected. The problem is that the data are not readily available in a useable form. Records over many decades are held by the government departments that collect the data and have seldom been analysed, let alone published. Mendelsohn & Roberts (1997) however provide an example of the quality of the information that can be extracted from such records, supplemented by the analysis of more recent satellite imagery and some ground-truthing. It is a model for assessment.

### 3.9.1 Aerial Photograph Record

The aerial photographic record is extensive in both space and time. Hwange National Park has blanket black and white aerial photographs approximately every six years since 1959 until the mid-1980s (Jones 1989), since when coverage has been less frequent. In Caprivi aerial photographs were taken during 1943, 1972 and 1996 (Mendelsohn & Roberts 1997). The whole of western Zambia was photographed between 1973 and 1982 (Jeanes & Baars 1991b). Aerial photographs covering northern Chobe National Park were taken in 1962, 1985 and 1998 (Mosugelo *et al.* 2002). However, few aerial photographs have been taken recently.

### 3.9.2 Soil Moisture, Drainage and Hydrology

*Climate*

There is a network of weather stations across the area, many of which have maintained records for more than 40 years (Hutchinson 1974, Torrance 1981, Muchinda 1985, Bhalotra 1987, Agritex 1989). These should be supported, particularly in view of the likely impact of climate change on the region. In both Zambia and Zimbabwe, the government departments that are responsible for weather monitoring are short of funding and have started to charge for some services. Information from satellite data, such as the Tropical Rainfall Measuring Mission products available from the Goddard Space Flight Center, cover the entire area of the Four Corners. Weather stations are complementary, providing a greater range of accurate weather information so long as they are properly maintained by trained people, supplied with spares, and records are kept.

*Water*

The Zimbabwe River Authority (ZRA) is a model for cross-border co-operation and the exchange of information to manage a common resource. Recently ZRA has been relying more heavily on satellite imagery, particularly for the inaccessible parts of Angola, and this greater coverage has considerably increased the accuracy of its flow predictions (I.W. Robertson, pers. comm.).

Dam capacity as a percentage of total water supply is a measure of the ability of the river systems to absorb change and of the water remaining for use by indigenous plants and animals. The Four Corners Area has relatively few small dams (Marshall 2000).

Borehole levels provide a record of groundwater depth and quality and historical data are available for some sites (Swedeplan 1988, Jones 1989, Mendelsohn & Roberts 1997). Monitoring the number and location of artificial water supplies is particularly important in protected areas and in rangelands because of the effects of local concentrations of herbivores on vegetation structure and nutrient cycling.

There is baseline information on the quality of the water in the Okavango (Bethune 1991, Garstang *et al*. 1998) and the Zambezi rivers (Marshall 2000), both of which currently have low sediment loads and organic matter contents and very low nutrient concentrations. Changes in water quality will be an index of changes in nutrient flows in the catchments, the floodplains and the riverine vegetation. Without more baseline sampling stations, however, it may be hard to determine the causes of any change.

*Wetland Areas*

The percentage of the wetland area intact, flooded or drained, and the dambos that have dried or gullied, might be monitored by a combination of recent satellite imagery and historical aerial photographs. For dambos this will require accurate ground-checking as changes in the structure of grassland are hard to distinguish on photographs or images, and it is not always possible to distinguish fields from undisturbed grassland.

### 3.9.3 Nutrients

If population growth in southern Africa is coupled with a lack of alternatives to subsistence agriculture as a means of earning a living (Tyson *et al*. 2000), the loss of nutrients from arable lands and rangeland, and the progressive impoverishment of the soil and the people dependent on it (Drechsel *et al*. 2001, Cumming *et al*. 2002), may become major issues.

Large-scale erosion mapping, such as that carried out by Whitlow and Campbell (1989) using aerial photographs, identifies problem areas on the country-wide scale, but is very time-consuming. Much of the Four Corners are on Kalahari sand is not particularly vulnerable to erosion. Areas that are likely to suffer most severely from accelerated erosion include sites on shallow soils, on fine-grained Karoo sediments, on basalt and on pan sediments. Monitoring might concentrate on these areas, especially if they are subject to land use change. Aerial photographs have been used successfully to monitor the history of some eroded sites (Jones 1989).

### 3.9.4 Changes in Vegetation Structure

Changes in vegetation structure, which can involve either a loss of woody biomass, such as the death of canopy trees as a result of elephant browsing, or a gain in woody biomass such as the transformation of wooded grassland to shrubland by bush encroachment, are the most visible consequences of changes in the rates of some ecosystem processes, especially fire and herbivory.

Aerial photographs have been used to monitor change in vegetation structure although there have been problems in their interpretation (e.g. Rogers & Chidziya 1996), probably because the usual technique does not distinguish between shrub and tree canopies. Ideally, a new monitoring technique, using a stereo-viewer with 10x binoculars to distinguish between the different canopy layers should be developed. The new high resolution SPOT vegetation imagery should be tested to see if it could be used to monitor changes in vegetation structure, but it will only be really useful if it is possible to identify different height categories.

Existing plots for the long-term monitoring of changes in vegetation structure should be maintained. Long-term monitoring plots in dambo grasslands are conspicuously lacking in southern Africa, which is unfortunate considering their importance as key resource areas for herbivores.

### 3.9.5 Fire

The Southern African Fire Network (SAFNet), based at the University of Botswana, facilitates the transboundary exchange of information, specifically on fire. The current focus is the validation of MODIS fire products by comparison with burned area maps derived from Landsat ETM time-series data, in partnership with the University of Maryland and NASA. The MODerate resolution Imaging Spectroradiometer (MODIS) was launched during December 1999 on NASA's TERRA satellite and has provided daily observations over southern Africa since the late dry season of 2000. Real time maps of active fires in the area of the Four Corners are available on a website (ftp://maps.geog.umd.edu/S_Africa/). Unfortunately, these maps lack a cloud mask, so they cannot reliably tell you where there are no fires.

The most useful satellite-derived tool for fire monitoring will be the MODIS burned area product at resolutions of 250 and 500 m. Within the next few years, this should be made available at low cost through a regional data centre when the algorithm to determine burned areas accurately has been validated for southern African conditions (D. Roy, pers. comm.).

There are historical data on the frequency, extent and timing of fires in Hwange National Park (Rogers 1993) and Matetsi Safari Area (V. Booth, pers. comm.) at the Department of National Parks and at the Zimbabwe Forestry Commission which have not been fully analysed or published. These might be used for comparative purposes.

### 3.9.6 Herbivory

Domestic livestock stocking rates have often been assessed by government agencies that keep dip tank records, but they are not always current and the records are likely to be suspended when economic circumstances are harsh.

Government agencies and NGOs, sometimes working together, have estimated population numbers of some large mammal species in protected areas and in surrounding communal-wildlife areas at intervals of several years, using aerial survey techniques. Unfortunately, survey methods have often differed and the size and location of the areas covered have changed from year to year, with the result that when these data are used to look for trends in populations, such as of buffalo, tsessebe, sable and roan, they are often not particularly useful (Martin 2002, 2003). The surveys are usually designed to count elephant (Booth 1996) and might be improved with minor modifications for other species, such as using higher intensity sampling in selected areas. A cross-border approach would be important here as large mammals are known to move across frontiers. The EU-funded ELESMAP Project undertook simultaneous elephant surveys in northern Botswana and north-west Zimbabwe during 1995-1997, thus avoiding the possibility of double counts.

Road strip counts conducted by the Zimbabwe Department of National Parks in Matetsi Safari Area and Hwange National Park provide information on herbivore densities over many years at a much finer scale than the aerial surveys (V. Booth pers. comm., Jones 1989) These data have been analysed every year until the early 1990s to provide animal population estimates from which to set hunting quotas, but they have not been analysed for trends nor published.

### 3.9.7 Extreme Events

The biological consequences of extreme events, such as cyclone effects, severe drought and black frost, have seldom been monitored in southern Africa, despite their known influence on mortality and regeneration in plant and animal populations. There is anecdotal evidence of the severe effects of the 1991/1992 drought on perennial plants in southern Africa (e.g. Tiffen & Mulele 1994), but only one published paper on its effects on perennial grass populations in Zimbabwe (Moyo, Sikosana & Gambiza 1995). It is difficult to disentangle the causes and patterns of mortality and regeneration long after the event (O'Connor 1999).

### 3.10   REFERENCES

Agritex (1989). Agro-climatological summaries and analysis (rainfall and potential evapotranspiration), Volume 1. Early Warning/Food Security Unit, AGRITEX, Ministry of Agriculture, Harare.

Alexander, I. (1989). Mycorrhizas in tropical forests. In: *Mineral Nutrients in Tropical Forest and Savanna Ecosystems* (edited by J. Proctor), pp.169-188. Special Publication No. 9, British Ecological Society. Blackwell Scientific, Oxford.

Anon. (1976). Groundwater investigations in the environs of Main Camp, Wankie National Park. Ministry of Water Development, Harare.

APRU (1980). *Ten Years of Animal Production and Range Research in Botswana*. Animal Production Research Unit, Ministry of Agriculture of Botswana, Gaborone.
Baars, R.M.T. (1996). *Condition and Management of the Rangelands in the Western Province of Zambia*. Doctoral thesis, Wageningen Agricultural University, Wageningen, Netherlands.

Barnes, D.L. (1982). Management strategies for the utilization of southern African savanna. In: *Ecology of Tropical Savannas* (edited by B.J. Huntley & B.H. Walker), pp. 626-656. Springer, New York.

Behnke, R.H. & Scoones, I. (1993). Rethinking Rangeland Ecology: Implications for Rangeland Management in Africa. In: *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas* (edited by R.H. Behnke, I. Scoones & C. Kerven), pp. 1-30. Overseas Development Institute, London.

Bell, R.H.V. (1982). The effect of soil nutrient availability on community structure in African ecosystems. In: *Ecology of Tropical Savannas* (edited by B.J. Huntley & B.H. Walker), pp. 193-216. Springer, New York.

Ben-Shahar, R. (1996). Woodland dynamics under the influence of elephants and fire in northern Botswana. *Vegetatio* **123**: 153-163.

Bethune, S. (1991). Kavango river wetlands. *Madoqua* **17**(2): 77-112.

Bhalotra, Y.P.R. (1987). *Climate of Botswana*. Part II, Elements of Climate: Rainfall. Dept. of Meteorological Services, Gaborone.

Bingham, M. (2000). Land use changes on the floodplains of the Upper Zambezi in Western Zambia. In: *Biodiversity of the Zambezi Basin Wetlands* (edited by J. Timberlake), Vol. 3, pp. 1-18. BFA, Bulawayo & Zambezi Society, Harare.

Booth, V.R. (1989). Indications of desiccation in the Matetsi/Deka catchment of north-western Zimbabwe. *S. Afr. J. Sci.* **85**: 528-532.

Booth, V.R. (1996). *Elephant census in Zimbabwe: 1980-1995. An analysis and review*. Consultancy report for Ministry of Environment & Tourism, Zimbabwe. Price Waterhouse, Harare.

Boultwood, J.N. & Rodel, M.G.W. (1981). Effects of stocking rate and burning frequency on *Brachystegia/Julbernardia* veld in Zimbabwe. *Proc. Grassl. Soc. S. Africa* **16**: 111-115.

Bruijnzeel, L.A. (1989) Nutrient cycling in moist tropical forests: the hydrological framework. In: *Mineral Nutrients in Tropical Forest and Savanna Ecosystems* (edited by J. Proctor), pp. 383-415. Special Publication No. 9, British Ecological Society. Blackwell Scientific, Oxford.

Bullock, A. (1994). Hydrological studies for policy formulation in Zimbabwe's communal lands. In: *Wetlands Ecology and Priorities for Conservation in Zimbabwe: Proceedings of a seminar on wetlands in Zimbabwe* (edited by T. Matiza & S.A.Crafter), pp. 69-81. IUCN Wetlands Programme no.14. IUCN, Gland.

Burger, W.K. (1993). Enumeration and management of the indigenous woodlands of northern Botswana. In: *The Ecology and Management of Indigenous Forests in Southern Africa* (edited by G.D. Piearce & D.J. Gumbo), pp. 16-24. Forestry Commission, Harare.

Butynski, T.M. (1973). Life history and economic value of the springhare (*Pedetes capensis* Forster) in Botswana. *Botswana Notes & Records* **5**: 200-213.

Calvert, G.M. (1986)a. The ecology and management of the Kalahari Sand forest vegetation of south-western Zimbabwe. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 132-157. Forest Department, Ndola, Zambia.

Calvert, G.M. (1986b). *Baikiaea* regeneration and damaging agencies in Barotseland. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 465-469. Forest Department, Ndola, Zambia.

Calvert, G.M. (1992). Indigenous forest management and research in Matabeleland – a personal view. In: *Forestry Research in Zimbabwe* (edited by G.D. Piearce & P. Shaw), pp 193-213. Forestry Commission, Zimbabwe.

Calvert, G.M. & Timberlake, J.R. (1993). Burning trials in *Baikiaea* Woodland, Gwayi Forest, Zimbabwe. In: *The Ecology and Management of Indigenous Forests in Southern Africa* (edited by G.D. Piearce & D.J. Gumbo), pp. 347-365. Forestry Commission, Harare.

Campbell, B.M., Frost, P., King, J. Mwanza, M. & Mhlanga, L. (1993). The influence of trees on soil fertility and microbial activity, Matobo, Zimbabwe. In: *The Ecology and Management of Indigenous Forests in Southern Africa* (edited by G.D. Piearce & D.J. Gumbo), pp. 197-208. Forestry Commission, Harare.

Cauldwell, A.E. & Zieger, U. (2000). A reassessment of the fire-tolerance of some woody species in the Central Province, Zambia. *Afr. J. Ecol.* **38**: 138-146.

Caylor, K.K., Shugart, H.H., Dowty, P.R. & Smith, T.M. (2003). Tree spacing along the Kalahari transect in southern Africa. *J. Arid Environ.* **54**: 281-296.

Chidumayo, E.N. (1980). Population ecology of *Tatera leucogaster* (Rodentia) in southern Zambia. *J. Zool. (London)* **190**: 325-336.

Chidumayo, E.N. (1988). A re-assessment of the effects of fire on miombo regeneration in the Zambian Copperbelt. *J. Trop. Ecol.* **4**: 361-372.

Chidumayo, E.N. (1993a). *Responses of Miombo to Harvesting: Ecology and Management.* Stockholm Environment Institute, Stockholm.

Chidumayo, E.N. (1993b). *Inventory of wood used in charcoal production in Zambia.* BSP Publication No. 169. Biodiversity Support Program, Washington DC.

Chidumayo, E.N. (1995). *Handbook of Miombo Ecology and Management.* Stockholm Environment Institute, Stockholm.

Chidumayo, E.N. (1996). Ash-fertilisation for agriculture. In: *The Miombo in Transition: Woodlands and Welfare in Africa* (edited by B. Campbell), p. 45. CIFOR, Bogor, Indonesia.

Chidumayo, E.N. (1999). *Using natural fertilizers in miombo woodlands.* BSP Support Program Publication No. 26. Biodiversity Support Program, Washington DC.

Chidumayo, E.N. & Frost, P.G.H. (1996). Population biology of miombo trees. In: *The Miombo in Transition: Woodlands and Welfare in Africa* (edited by B. Campbell), pp. 59-71. CIFOR, Bogor, Indonesia.

Childes, S.L. (1984). *The population dynamics of some woody species in the Kalahari sand vegetation of Hwange National Park*. MSc thesis, University of the Witwatersrand, Johannesburg.

Childes, S.L. (1989). Phenology of nine common woody species in semi-arid deciduous Kalahari sand vegetation. *Vegetatio* **79**: 151-163.

Childes, S.L. & Walker, B.H. (1987). Ecology and dynamics of woody vegetation on the Kalahari sands in Hwange National Park, Zimbabwe. *Vegetatio* **72**: 111-128.

Chingaipe, T.M. & Jain, M.K. (1986). Propagation, management and protection of Zambezi Teak in Zambia. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 178-184. Forest Department, Ndola, Zambia.

Chisempa, T.T. & Shingo, J. (1986). Research and management problems in the artificial regeneration of Zambezi teak. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 384-389. Forest Department, Ndola, Zambia.

Clarke, J., Cavendish, W. & Coote, C. (1996). Rural households and miombo woodlands: use, value and management. In: *The Miombo in Transition: Woodlands and Welfare in Africa* (edited by B. Campbell), pp. 101-135. CIFOR, Bogor, Indonesia.

Coe, M.J., Cumming, D.H. & Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* **22**: 341-354.

Corby, H.D.L. (1974). Systematic implications of nodulation among Rhodesian legumes. *Kirkia* **9**(2): 301-330.

Corby, H.D.L. (1989). Types of rhizobial nodules and their distribution among the Leguminosae. *Kirkia* **13**(1): 53-124.

Cottrell, C.B. & Loveridge, J.P. (1966). Observations on the *Cryptosepalum* forest of the Mwinilunga district of Zambia. *Proc.& Trans. Rhod. Sci. Assoc.* **51**: 79-120.

Cumming, D.H.M. (1999). *Study on the Development of Transboundary Natural Resource Management Areas in Southern Africa - Environmental Context, Natural Resources, Land Use and Conservation*. Biodiversity Support Program, Washington, DC.

Cumming, D.H.M. & Cumming, G.S. (2003). Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia* **134**: 560-568.

Cumming, D.H.M., Guveya, E. & Matose F. (2002). *A framework for examining social-ecological linkages in the conservation of the Miombo Ecoregion*. Consultants report for WWF Miombo Ecoregion Project. WWF SARPO, Harare.

Dangerfield, J.M., Perkins, J.S. & Kaunda, S.K. (1996). Shoot characteristics of *Acacia tortilis* (Forsk.) in wildlife and rangeland habitats of Botswana. *Afr. J. Ecol.* **34**: 167-176.

Delany, M.J. (1986). Ecology of small rodents in Africa. *Mammal Review* **16**(1): 1-41.
Department of Meteorological Services (1978). Climatological Summaries: Rhodesia. Climate Handbook Supplement No. 5. Dept. Meteorological Services, Harare.

Desanker, P.V., Frost, P.G.H., Justice, C.O. & Scholes, R.J. [editors] (1997). *The Miombo Network: framework for a terrestrial transect study of land-use and land-cover change in the Miombo ecosystems of central Africa.* IGBP Report 41. IGBP, Stockholm, Sweden.

Drechsel, P., Giyele L., Kunze, D. & Cofie, O. (2001). Population density, soil nutrient depletion, and economic growth in sub-Saharan Africa. *Ecol. Econ.* **38**: 251-258.

Dudley, J.P. (1999). Elephant-frost-fire interactions among woodland and scrubland habitats in Hwange National Park, Zimbabwe. In: *Foraging Ecology and Conservation Biology of African Elephants*, pp. 67-93. PhD dissertation, University of Alaska, Fairbanks.

Dunham, K. M. (1991). Phenology of *Acacia albida* trees in Zambezi riverine woodlands. *Afr. J. Ecol.* **29**: 118-129.

Dunham, K.M. (2002). Aerial census of elephants and other large herbivores in North West Matabeleland, Zimbabwe: 2001. WWF-SARPO Occasional Paper No. 6. WWF SARPO, Harare.

Dye, P.J & Spear, P.T. (1982). The effect of bush clearing and rainfall on grass yield and composition in south west Zimbabwe. *Zimb. J. Agric. Res.* **20**: 103-108.

East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. *Afr. J. Ecol.* **22**(4): 245-270.

el Obeid, S. & Mendelsohn, J. (2001). *A Preliminary Profile of the Kavango Region in Namibia.* Nambia Nature Foundation, Windhoek.

Ellery, W.N., Ellery, K., MacCarthy, T.S., Cairncross, B. & Oelofse R. (1989). A peat fire in the Okavango Delta, Botswana, and its importance as an ecosystem process. *Afr. J. Ecol.* **27**: 7-21.

Elwell, H.A. & Stocking, M.A. (1988). Loss of soil nutrients by soil erosion is a major hidden farming cost. *Zimbabwe Sci. News* **22**(7/8): 79-85.

Ernst, W.H.O. (1975). Variation in the mineral content of leaves of trees in miombo woodlands in south central Africa. *J. Ecol.* **63**: 801-808.

Ernst, W.H.O., Decelle, J.E. & Tolsma, D.J. (1990). Predispersal seed predation in native leguminous shrubs and trees in savannas of southern Botswana. *Afr. J. Ecol.* **28**: 45-54.

Fanshawe, D.B. (1969). *The Vegetation of Zambia*. Forestry Research Bulletin No. 7. Kitwe, Zambia.

Fanshawe, D.B. & Savory, B.M. (1964) *Baikiaea plurijuga* dwarf-shell forests. *Kirkia* **4**: 185-190.

Federal Meteorological Department (1963). *Climatological summaries, Southern Rhodesia, Northern Rhodesia, Nyasaland*. Federal Meteorological Department, Salisbury.

Fritz, H. & Duncan, P. (1994). On the carrying capacity for large ungulates of African savanna ecosystems. *Proc. R. Soc. Lond. B.* **256**: 77-82.

Frost, P.G.H. (1992). *A policy framework for fire management in the Western Province of Zambia*. Consultants report. RDP Livestock Services, Mongu, Zambia.

Frost, P.G.H. (1996). The ecology of miombo woodlands. In: *The Miombo in Transition: Woodlands and Welfare in Africa* (edited by B. Campbell), pp. 11-57. CIFOR, Bogor, Indonesia.

Frost, P.G.H. & Robertson, F. (1987). The ecological effects of fire in savannas. In: *Determinants of Tropical Savannas* (edited by B.H. Walker), pp 93-104. IRL Press, Oxford.

Gardiner, A.J. (1995). *The Effect of Large Mammalian Herbivore Community Structure on the Composition and Ecological Function of the Coprophagous Scarab Beetle Fauna (Coleoptera: Scarabaeidae)*. DPhil. thesis, University of Zimbabwe, Harare.

Garstang, M., Ellery, W.N., McCarthy, T.S., Scholes, M.C., Scholes, R.J. & Tyson, P.D. (1998). The contribution of aerosol and water-borne nutrients to the functioning of the Okavango Delta ecosystem, Botswana. *S. Afr. J. Sci.* **94**: 223-229.

Geldenhuys, C.J. (1993). The use of diameter distributions in sustained-use management of forests: examples from Southern Africa. In: *The Ecology and Management of Indigenous Forests in Southern Africa* (edited by G.D. Piearce & D.J. Gumbo), pp. 154-167. Forestry Commission, Harare.

Gillon, D. (1983). The fire problem in tropical savannas. In: *Tropical Savannas* (edited by F. Bourliere). Ecosystems of the World No. 13. Elsevier, Amsterdam.

Gondo, P.C. (1993). Fire management in the demarcated indigenous forests of Zimbabwe. In: *The Ecology and Management of Indigenous Forests in Southern Africa* (edited by G.D. Piearce & D.J. Gumbo), pp. 366-374. Forestry Commission, Harare.

Grant, P.M. (1981). The fertility of sandy soil in peasant agriculture. *Zimbabwe Agric. J.* **78**: 169-176.

Greenwood, D.E.(1986). Zambezi teak in Zambia. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 470-473. Forest Department, Ndola, Zambia.

Grohs, F. & Elwell, H.A. (1993). Estimating sheetwash erosion from cropland in the communal areas of Zimbabwe. *Trans. Zimb. Sci. Assoc.* **67**: 6-12.

Grubb, P.J. (1989) The role of mineral nutrients in the tropics. In: *Mineral Nutrients in Tropical Forest and Savanna Ecosystems* (edited by J. Proctor), pp. 417-439. Special Publication No. 9, British Ecological Society. Blackwell Scientific, Oxford.

Grundy, I. (1996). Regeneration and management of *Brachystegia spiciformis* Benth. and *Julbernardia globiflora* (Benth.) Troupin in miombo woodland, Zimbabwe: Towards a sustainable management strategy. In: *Sustainable Management of Indigenous Forest in the Dry Tropics* (edited by P.T. Mushove, E.M. Shumba & F. Matose),  Forestry Commission & SAREC-SIDA, Harare.

Guy, P.R. (1981). Changes in the biomass and productivity of woodlands in the Sengwa Wildlife Research Area, Zimbabwe. *J. Appl. Ecol.* **18**: 507-519.

Hattle, J. (1972). *Wayward Winds*. Bundu Series, Longman, Rhodesia.
Hogberg, P. (1986a). Rooting habits and mycorrhizas of *Baikiaea plurijuga*. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 92-100. Forest Department, Ndola, Zambia.

Hogberg, P. (1986b). Soil nutrient availability, root symbioses and tree species composition in tropical Africa: a review. *J. Trop. Ecol.* **2**: 359-372.

Hogberg, P. & Piearce, G.D. (1986). Mycorrhizas in Zambian trees in relation to host taxonomy, vegetation type and successional pattern. *J. Ecol.* **74**: 775-785.

Huckabay, J.D. (1986). The exploitation of Zambezi Teak in Zambia. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 329-341. Forest Department, Ndola, Zambia.

Hulme, M. [editor] (1996). *Climate change and Southern Africa: an exploration of some potential impacts and implications in the SADC region*. Climate Research Unit, University of East Anglia, Norwich/WWF International, Gland.

Hungwe, A. (1998). Land Use Studies. In: *Batoka Gorge Hydro Electric Scheme Feasibility Report*. Volume 4a , Further Environmental Assessment, pp.289-328. Civil Consult & Soils Incorporated, Harare.

Huntley, B.J. (1978). Ecosystem conservation in southern Africa. In: *Biogeography and Ecology of Southern Africa* (edited by M.J.A. Werger & A.C. van Bruggen), pp. 1333- 1384. W. Junk, The Hague.

Huntley, B.J. (1982). Southern African Savannas. In: *Ecology of Tropical Savannas* (edited by B.J. Huntley & B.H. Walker). Ecological Studies; Springer, New York pp. 101-119.

Hutchinson,P.J. (1974). *The Climate of Zambia*. Occasional Studies No. 7. Zambia Geographical Association, Lusaka.

Illius, A.W. & O'Connor, T.G. (1999). On the relevance of non-equilibrium concepts to semi-arid grazing systems. *Ecol. Applic.* **9**: 798-813.

IPCC (2001). Summary for policymakers - climate change 2001: The Scientific Basis. Intergovernmental Panel on Climate Change, Working group I. Third Assessment Report, IPCC. Available at http://www.ipcc.ch/ pub/tar/index.htm.

Jeanes, K.W. & Baars, R.M.T. (1991a). *The vegetation, ecology and rangeland resources, Western Province, Zambia*. Volume 1: Main Report. RDP Livestock Services, Mongu, Zambia.

Jeanes, K.W. & Baars, R.M.T. (1991b). *The vegetation ecology and rangeland resources, Western Province, Zambia*. Volume 2: Appendices. RDP Livestock Services, Mongu, Zambia.

Jones, M.A. (1989). *Hwange National Park Management Plan*. Dept. National Parks & Wild Life Management, Zimbabwe.

Keesing, F. (2000). Cryptic consumers and the ecology of an African savanna. *BioScience* **50**(3): 205-215.

Kehinde, M.O. & Loehnert, E.P. (1989). Review of African goundwater resources. *J. Afr. Earth Sci.* **9**(1): 179-185.

Kellman, M. (1989). Mineral nutrient dynamics during savanna-forest transformation in Central America. In: *Mineral Nutrients in Tropical Forest and Savanna Ecosystems* (edited by J. Proctor), pp. 137-151. Special Publication No. 9, British Ecological Society. Blackwell Scientific, Oxford.

Kreft, J. (1972). The distribution of thunderstorm days over Rhodesia. Climate Information Sheet No. 44. Dept. Meteorological Services, Harare.

Landon, J.R. [editor] (1991). *Booker Tropical Soil Manual: A Handbook for Soil Survey and Agricultural Land Evaluation in the Tropics and Subtropics*. Longman, London.

Lawton, R.M. (1978). A study of the dynamic ecology of Zambian vegetation. *J. Ecol.* **66**: 175-198.

Magadza, C. (2000). Human impacts on wetlands and biodiversity in the Zambezi Basin. In: *Biodiversity of the Zambezi Basin Wetlands* (edited by J. Timberlake ), Vol. 3, pp.107-122. Biodiversity Foundation for Africa, Bulawayo & Zambezi Society, Harare.

Malaisse, F. (1978). The Miombo Ecosystem. In: *Tropical Forest Ecosystems: A State of Knowledge Report*, pp. 589-606. UNESCO, Paris.

Malaisse, F., Alexandre, J., Freson, R., Goffinet, G. & Malaisse-Mousset, M. (1972). The miombo ecosystem: a preliminary study. In: *Tropical Ecology with an Emphasis on Organic Production* (edited by P.M. Golley & F.B. Golley), pp. 363-405. University of Georgia, Athens, USA.

Marshall, B. (2000). Freshwater fishes of the Zambezi Basin. In: *Biodiversity of the Zambezi Basin Wetlands* (edited by J. Timberlake), Vol. 3, pp. 393-459. Biodiversity Foundation for Africa, Bulawayo & Zambezi Society, Harare.

Martin, R.B. (1974). *Structure, Biomass and Utilization of Vegetation in the Mopane and Miombo Woodlands of the Sengwa Wildlife Research Area*. Certificate in Field Ecology thesis, University of Rhodesia, Salisbury.

Martin, R.B. (2002). *Species report for southern savanna buffalo*. Study for Transboundary Mammal Project of Ministry of Environment & Tourism, Namibia. Namibia Nature Foundation & WWF LIFE Programme, Windhoek.

Martin, R.B. (2003). *Species report for roan, sable and tsessebe.* Study for Transboundary Mammal Project of Ministry of Environment & Tourism, Namibia. Namibia Nature Foundation & WWF LIFE Programme, Windhoek.

Masuka, A.J. & Ryvarden, L. (1993). Parasitic macrofungi on indigenous trees in Zimbabwe. In: *The Ecology and Management of Indigenous Forests in Southern Africa* (edited by G.D. Piearce & D.J. Gumbo), pp. 375-382. Forestry Commission, Harare.

McArthur, A.G. (1977). *Grassland Fire Danger Meter: Mark V.* County Fire Authority, Victoria, Australia.

McCarthy, T.S. & Bloem, A. & Larkin, P.A. (1998). Observations on the hydrology and geohydrology of the Okavango Delta. *S. Afr. J. Geol.* **101**: 111-117.

McCarthy, T.S., Cooper, G.R.J., Tyson, P.D. & Ellery, W.N. (2000). Seasonal flooding in the Okavango Delta, Botswana – recent history and future prospects. *S. Afr. J. Sci.* **96**: 25-33.

McCarthy, T.S., Ellery, W.N. & Dangerfield, J.M. (1998). The role of the biota in the initiation and growth of islands on the floodplain of the Okavango alluvial fan, Botswana. *Earth Surface Processes & Landforms* **23**: 291-316.

McFarlane, M.J. (1994). Dambo gullying in parts of Zimbabwe and Malawi: A reassessment of the causes. In: *Wetlands Ecology and Priorities for Conservation in Zimbabwe* (edited by T. Matiza & S.A. Crafter), pp. 105-116. IUCN Wetlands Programme No.14. IUCN, Gland.

McFarlane, M.J. (1995). *Pan and dambos of Western Province, Zambia. A preliminary consideration of their geomorphology/hydrology.* Unpublished report. Land & Water Management Project, Department of Agriculture, Mongu, Zambia.

Mendelsohn, J. & Roberts, C. (1997). *An Environmental Profile and Atlas of Caprivi.* Directorate of Environmental Affairs, Namibia.

Moore, A.E. & Attwell, C.A.M. (1999). Geological controls in the distribution of woody vegetation in the central Kalahari, Botswana. *S. Afr. J. Geol.* **102**(4): 350-362.

Moore, A.E. & Larkin, P.A. (2001). Drainage evolution in south-central Africa since the breakup of Gondwana. *S. Afr. J. Geol.* **104**: 47-68.

Mosugelo, D.K., Moe, S.R., Ringrose, S. & Nelleman, C. (2002). Vegetation changes during a 36-year period in Chobe National Park, Botswana. *Afr. J. Ecol.* **40**(3): 232-240.

Moyo, C.S., Sikosana, J.L.N. & Gambiza, J. (1995). Recovery of eutrophic rangeland after a severe drought. *Proc. 5th Int. Rangeland Cong.*, pp. 385-386.

Muchinda, M.R. (1985). *The Agricultural Climates of Zambia.* Agrometeorological Report No. 9. Meteorological Dept., Lusaka.

Mushove, P.T. (1993). Fifty-five years of timber commercialisation in Tsholotsho communal land. In: *The Ecology and Management of Indigenous Forests in Southern Africa* (edited by G.D. Piearce & D.J. Gumbo), pp. 320-329. Forestry Commission, Harare.

Musokatwane, I.E.O. & Kufakwandi, S.F. (1986). The importance of the teak forests in the Zambian economy. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 375-381. Forest Department, Ndola, Zambia.

Musonda, W.M. (1986). Fuelwood Problems in the Teak Forests. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 462-464. Forest Department, Ndola, Zambia.

Newman E.I. (1995). Phosphorus inputs to terrestrial ecosystems. *J. Ecol.* **83**: 713-726.

Nyamapfene, K. (1991). *Soils of Zimbabwe*. Nehanda Publishers, Harare.

O'Connor, T.G. (1999). Impact of a sustained drought on a semi-arid *Colophospermum* savanna. *Afr. J. Range & Forage Sci.* **15**(3): 83-91.

Parris, R. (1984). Pans, rivers and artificial waterholes in the protected areas of the south-western Kalahari. Supplement to *Koedoe*: 63-82.

Porporato, A., Laio, F., Ridolifi, L., Caylor, K., & Rodriguez-Iturbe, I. (2003). Soil moisture and plant stress dynamics along the Kalahari precipitation gradient. *J. Geophysic. Res.* **108** (D3), 4127.

Rattray, J.M. (1957). The grasses and grass associations of Southern Rhodesia. *Rhod. Agric. J.* **54**: 197-234.

Reeler, B., Campbell, B. & Price, L. (1991). Defoliation of *Brachystegia spiciformis* by a species-specific insect *Melasoma quadrilineata*, over two growing seasons. *Afr. J. Ecol.* **29**: 271-274.

Robertson, E.F. (1984). *Regrowth of Two African Woodland Types after Shifting Cultivation.* PhD thesis, University of Aberdeen, Aberdeen

Robertson, E.F. (1993). Early-burning in the *Brachystegia* woodland of the Parks and Wildlife Estate. *Zimb. Sci. News* **27**(7/9): 68-71.

Robertson, E.F. (1990). The management of elephants and fire in *Brachystegia* woodland. In: *Management of Hwange Ecosystem*, Proceedings of a USAID workshop, Hwange July 1990. Unpublished paper.

Rogers, C.M.L. (1993). *A woody vegetation survey of Hwange National Park*. Department of National Parks & Wild Life Management, Zimbabwe.

Rogers, C.M.L. & Chidziya, E. (1996). The change in the tree canopy cover in Hwange National Park between 1959 and 1994 (preliminary results). In: *Elephant Management in Zimbabwe* (editors R.B. Martin, G.C. Craig & V.R. Booth), pp. 97-106. Dept. National Parks & Wild Life Management, Harare.

Rushworth, J.E. (1975). *The Floristic, Physiognomic and Biomass Structure of Kalahari Sand Shrub Vegetation in Relation to Fire and Frost in Wankie National Park, Rhodesia*. MSc thesis, University of Rhodesia, Harare.

Rushworth, J.E. (1978). Kalahari sand scrub – something of value. *Rhod. Sci. News* **12**(8): 193-195.

Schlettwein, C.G.H., Simmons, R.E., MacDonald A. & Grobler, H.J.W. (1991). Flora, fauna and conservation of East Caprivi wetlands. *Madoqua* **17**(2): 67-76.

Scholes, M.C. & du Toit, B. (2002). Nutritional sustainability of Eucalyptus plantations: A case study at Karkloof, South Africa. *S. Afr. Forestry J.* **195**: 63-72.

Scholes, R.J. (1990) The influence of soil fertility on the ecology of southern African dry savannas. *J. Biogeog.* **17**: 415-419.

Scholes, R.J. (1996). Miombo woodlands and carbon sequestration. In: *The Miombo in Transition: Woodlands and Welfare in Africa* (edited by B. Campbell), p. 28. CIFOR, Bogor, Indonesia.

Scholes, R.J., Dowty, P.R., Caylor, K., Parsons, D.A.B., Frost, P.G.H. & Shugart, H.H. (2002). Trends in savanna structure and composition along an aridity gradient in the Kalahari. *J. Veget. Sci.* **13**: 419-428.

Scholes, R.J. & Walker, B.H. (1993). *An African Savanna: Synthesis of the Nylsvley Study.* Cambridge University Press, Cambridge.

Selander, J. & Malaya, F.M. (1986). Protection of young Zambezi Teak plantations against weeds and game damage. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 271-283. Forest Department, Ndola, Zambia.

Setshogo, M.P. (2002). *Cenchrus biflorus*: an alien invasive grass in the Botswana flora. *SABONET News* **7**(3): 181-182.

Skarpe, C. (1986). Plant community structure in relation to grazing and environmental changes along a north-south transect in the western Kalahari. *Vegetatio* **68**: 3-18.

Skarpe, C. (1990a). Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *J. Appl. Ecol.* **27**: 873-885.

Skarpe, C. (1990b). Structure of the woody vegetation in disturbed and undisturbed arid savanna, Botswana. *Vegetatio* **87**: 11-18.

Smithers, R.H.N. (1983). *The Mammals of the Southern African Subregion* (first edition). University of Pretoria, Pretoria.

Strang, R.M. (1974). Some man-made changes in successional trends on the Rhodesian highveld. *J. Appl. Ecol.* **11**: 249-263.

Stromgaard, P. (1984). The immediate effects of burning and ash fertilization. *Plant & Soil*. **80**(3): 307-320.

Styles, C.V. & Skinner, J.D. (1996). Possible factors contributing to the exclusion of saturniid caterpillars (mopane worms) from a protected area in Botswana. *Afr. J. Ecol.* **34**: 276-283.

Swedeplan (1988). *Programme for the Planning of Resource Utilisation in the Okavango Delta Region.* Volume 1. Natural Resource & Utilisation Inventory. Ministry of Local Government & Lands, Gaborone.

Sweet, C.P. (1971). Report on the soils of the north west section of Wankie National Park. Departmental Report CS/3/2/32. Branch of Chemistry & Soil Science. DR & SS, Harare.

Tacheba, B., Dube, O.P., Roy, D., Justice, C.O., Muhwandagara, K., Mukungwa, S., Frost, P., Gumbo, K., Leroux, J., Mushove, P. & Landmann, T. (2002). Southern African Fire Network (SAFNet) of the Global Observation of Forestry Cover (GOFC): Developing Capacity for Operational Fire Monitoring and Management Systems in Southern Africa. Third Meeting: University of Botswana, 29 July -1 August 2002.

Tafangenyasha, C. & Campbell, B.M. (1990). Past human activities in the Sinamatella area of Hwange National Park, Zimbabe. *J. Appl. Sci. Sth. Africa* **1**: 63-71.

Thompson, J.G. & Purves, W.D. (1978). *A guide to the soils of Rhodesia*. Chemistry & Soil Research Institute, DR & SS, Harare.

Tiffen, M. & Mulele, M.R. (1994). The environmental impact of the 1991-92 drought on Zambia. IUCN, Gland.

Timberlake, J.R. (1980). *Vegetation map of south eastern Botswana.* Ministry of Agriculture, Gaborone.

Timberlake, J.R. (1995). *Colophospermum mopane*: annotated bibliography and review. Zimbabwe Bulletin of Forestry Research No. 11. Forestry Commission, Harare.

Timberlake, J.R. [editor] (2000). *Biodiversity of the Zambezi Basin Wetlands*. Occasional Papers in Biodiversity No. 8. Biodiversity Foundation for Africa, Bulawayo & Zambezi Society, Harare.

Timberlake, J.R., Nobanda, N. & Mapaure, I. (1993). Vegetation survey of the communal lands - north and west Zimbabwe. *Kirkia* **14**(2): 171-270.

Tolsma, D.J., Ernst, W.H.O. & Verwey, R.A. (1987). Nutrients in soil and vegetation around two artificial waterpoints in eastern Botswana. *J. Appl. Ecol.* **24**: 991-1000.

Tolsma, D.J., Ernst, W.H.O., Verweij, R.A. & Vooijs, R. (1987). Seasonal variation in nutrient concentrations in a semi-arid savanna ecosystem in Botswana. *J. Ecol.* **75**: 775-779.

Torrance, J.D. (1972). Malawi, Rhodesia and Zambia. In: *Climates of Africa* (edited by J.F. Griffiths), pp. 409-460. World Survey of Climatology, Volume 10. Elsevier, Amsterdam.

Torrance, J.D. (1981). *Climate handbook of Zimbabwe*. Government Printer, Harare.

Trapnell, G.C. (1959). Ecological results of woodland burning experiments in Northern Rhodesia. *J. Ecol.* **47**:129-168.

Trapnell, G.C. & Clothier, J.N. (1937). *The soils, vegetation and agricultural systems of North-Western Rhodesia*. Government Printer, Lusaka.

Trollope, W.S.W. & Potgieter, A.L.F. (1983). Characteristics of fire behaviour in the Kruger National Park. Unpublished report, University of Fort Hare & Division of Nature Conservation, Kruger National Park, South Africa.

Tyson, P.D. (1986). *Climatic Change and Variability over Southern Africa*. Oxford University Press, Cape Town.

Tyson, P., Odada, E., Schulze, R., Vogel, C., Arntzen, J., Chanda, R., Gatebe, C., Hoffman, T., Lutjeharms, J., Marufu, L., Midgley, G., Monteiro, P., Obura, D., Otter, L., Partridge, T., Perks, L., Ringrose, S., Scholes, M.C., Scholes, R.J. (2002). Regional-global change linkages: Southern Africa. In: *Global-Regional Linkages in the Earth System* (edited by P. Tyson, R. Fuchs, C. Fu, L. Lebel, A.P. Mitra, E. Odada, J. Perry, W. Steffen & H.Virji), pp 3-73. IGBP Series, Springer, Berlin.

ULG (1993). *Aerial census of Animals in Northern Botswana, September 1993*. ULG Consultants & Dept. Wildlife & National Parks, Gaborone.

ULG (1994a). *Aerial census of Animals in Northern Botswana, Dry Season 1994*. ULG Consultants & Dept. Wildlife & National Parks, Gaborone.

ULG (1994b). *Aerial Census of Animals in the Caprivi Strip, Namibia, Dry Season 1994*. ULG Consultants & Dept. Wildlife & National Parks, Gaborone.

van Niekerk, B.D.H. (1997). Are grazing ruminants being over-mineralized? *Proceedings 35th South African Society of Animal Scientists Congress*, July 1997, pp. 63-67.

van Vegten, J.A. (1983). Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio* **56**: 3-7.

Ward, R.C. (1975). *Principles of Hydrology*, second edition. McGraw-Hill, Maidenhead.

Weir, J.S. (1969). Chemical properties and occurrence on Kalahari sand of salt licks created by elephants. *J. Zool. Soc. Lond.* **158**: 293-310.

Weir, J.S. (1971). The effect of creating additional water supplies in a Central African Park. In: *The Scientific Management of Animal and Plant Communities for Conservation* (edited by E. Duffey & A.S. Watt), pp 367-385. Blackwell, Oxford.

Werger, M.J.A. & Coetzee, B.J. (1978). The Sudano-Zambezian region. In: *Biogeography and Ecology of Southern Africa* (edited by M.J.A. Werger), pp 301-462. Junk, The Hague.

White, F. (1976). The underground forests of Africa: a preliminary review. *Gardens' Bull. (Singapore)* **29**: 55-71.

White, F. (1983). *The Vegetation of Africa: a descriptive memoir*. UNESCO, Paris.

Whitlow, J.R. (1983). Hydrological implications of land use in Africa, with particular reference to Zimbabwe. *Zimb. Agric. J.* **80**(5): 193-212.

Whitlow, R.C. (1991). Wetland use and abuse in Zimbabwe. *Trans. Zimb. Sci. Assoc.* **65**: 24-33.

Whitlow, J.R. & Campbell, B. (1989). Factors influencing soil erosion in Zimbabwe: a statistical analysis. *J. Environ. Mgmnt.* **29**: 17-29.

Wilson, V.J. (1975). *Mammals of the Wankie National Park, Rhodesia.* Museum Memoir No. 5. National Museums & Monuments, Bulawayo.

Wood, A.P. (1986). Man's impact upon the mukusi forests of Zambia, with special reference to Shesheke District. In: *The Zambezi Teak Forests. Proceedings of the First International Conference on the Teak Forests of Southern Africa* (edited by G.D. Piearce), pp. 24-42. Forest Department, Ndola, Zambia.

Worthington, E.B. (1976). The Conservation of Wetlands in Africa. In: *Proceedings of the Symposium of the Okavango Delta and its Future Utilisation* (edited by Botswana Society), pp. 61-79. Botswana Society, Gaborone.

Young, A. (1976). *Tropical Soils and Soil Survey*. Cambridge University Press, Cambridge.