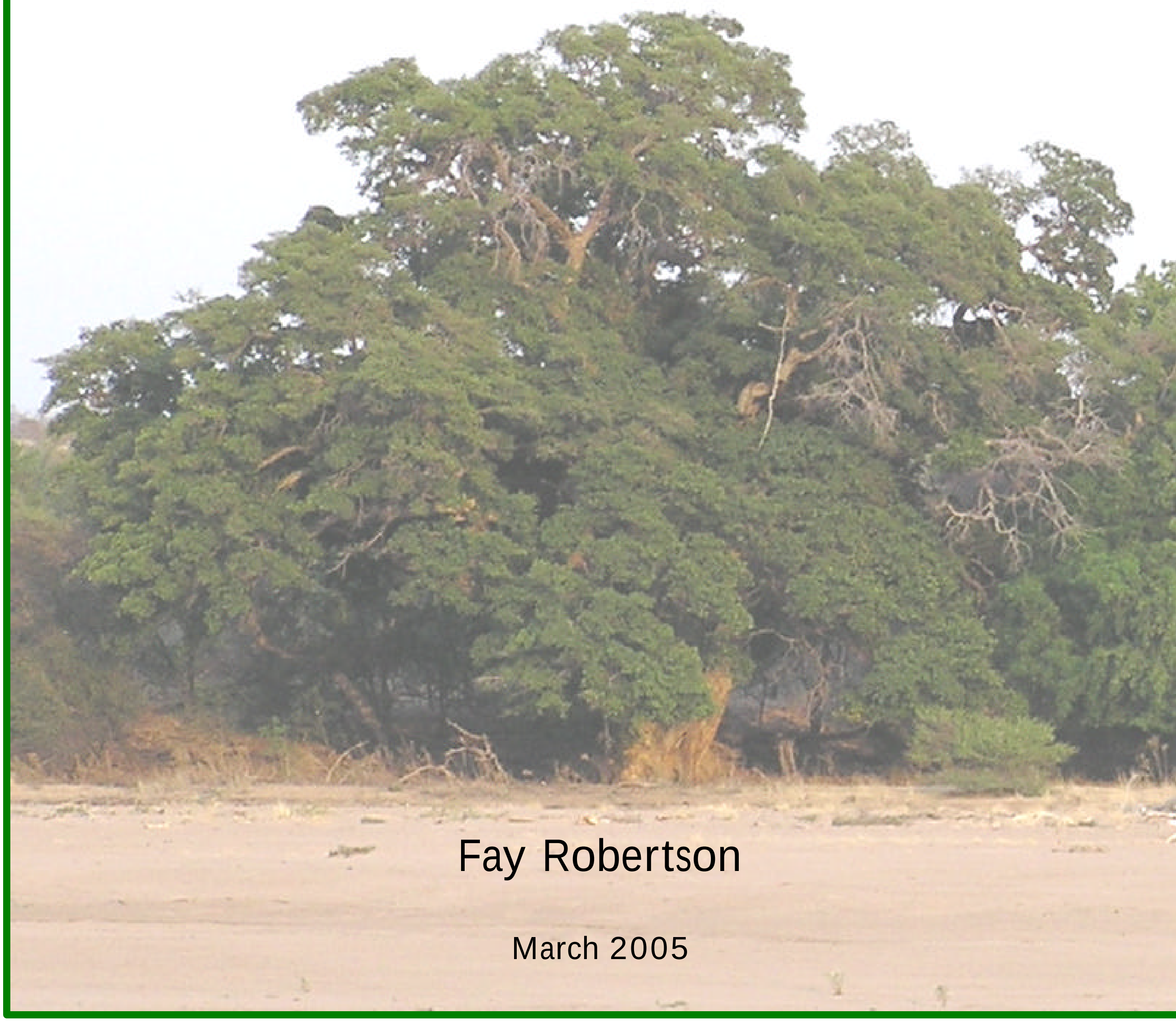
ECOLOGICAL PROCESSES
within the
FOUR CORNERS AREA



Fay Robertson

March 2005

Occasional Publications in Biodiversity No. 16

ECOLOGICAL PROCESSES WITHIN THE FOUR CORNERS AREA

Fay Robertson

March 2005

Note: An edited version of this paper was originally published as Chapter 3 in Timberlake, J.R. & Childes, S.L. (204). *Biodiversity of the Four Corners Area: Technical Reviews*. Volume 1. Occasional Publications in Biodiversity No. 15. BFA, Bulawayo / Zambezi Society, Harare. This was a study commissioned by the African Wildlife Foundation with USAID funding.

Occasional Publications in Biodiversity No. 16

Biodiversity Foundation for Africa
P.O. Box FM 730,Famona, Bulawayo, Zimbabwe

LIST OF CONTENTS

Tables and Figures

1. INTRODUCTION

This paper provides 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 Transfrontier Area in south-central Africa. Centred on Victoria Falls, this area crosses the boundaries of five African nations and incorporates northern Botswana (including the Okavango Delta, Lake Ngami and the Makgadikgadi Pans), the Caprivi in Namibia, NW Zimbabwe to the west of the Gwayi River, SE Angola, SW Zambia north to Senanga, and the Kafue National Park (but not the Kafue Flats). The total extent is about 290,000 km^2. As much of the aquatic biological information for the area has already been reviewed under the Zambezi Basin Wetlands Conservation project (Timberlake 2000), this paper concentrates on terrestrial systems and floodplains.

It was prepared under the auspices of a sub-grant given to the Biodiversity Foundation for Africa and the Zambezi Society by USAID, through the African Wildlife Foundation, as part of the latter's Four Corners Transboundary Natural Resources Management project. A shortened version is given in the BFA/Zambezi Society Four Corners Technical reviews (Robertson 2004).

Although the Four Corners area is an artificial concept and has no features that differentiate it from surrounding landscapes, 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 growing season of 5-8 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.

The paper 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 2004) and there have been few studies on herbivory, with the exception of that by elephants (Conybeare 2004). 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 is reviewed in separate sections. Figures derived from similar vegetation types outside the Four Corners area are used occasionally to give the order of magnitude for a process rate that might reasonably be expected. 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 review concludes with a description of areas and processes of conservation importance and suggestions for monitoring.

2. MOISTURE AVAILABILITY AND DRAINAGE

2.1 Rainfall and Evapotranspiration

Within the Four Corners area, 95% of the rain falls during a 5-8 month wet season (Table 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 over that portion in Zambia and Zimbabwe increases from 15-20% near Kafue in N 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).

Evaporation exceeds rainfall in most, if not all, months of the year (Table 1). Potential evapotranspiration, based on the Penman formula, in the Four Corners portion of Zambia and Zimbabwe ranges from 1650 mm in N 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.

Long Term Climate Change
Tyson *et al*. (2002) review climate change in southern Africa from the late Quaternary to the present. During the last 6000 years there has been a high degree of variability in temperature and rainfall at timescales ranging from decades to centuries.

Recent Rainfall Trends
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). McCarthy *et al.* (2000) describe the factors which are known to control rainfall in the catchment areas of the Okavango, and those trends in rainfall that are identifiable from records and historical accounts. Within the summer rainfall areas of southern Africa there is a quasi-regular 18-year oscillation, in which about nine years that are 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 seen in rainfall records in areas to the east and south-east. This may be due to the modulating effect of the Okavango swamps (McCarthy *et al.* 2000), or perhaps because rainfall in the Kalahari falls mainly in convective storms. This produces a large variability in the inter-annual rainfall amounts recorded at any one station that obscures any oscillation (Caylor *et al.* 2003).

Table 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 exceeds evaporation	No. months with > 25mm rainfall	Mean annual temperature (°C)	Source [years of record]
Kafue National Park, Zambia	-	-	-	15-20	-	-	-	-	CV from Torrance 1972
Shesheke, Zambia	855.9	-	-	25-30	-	-	-	20.9	Federal Met. Dept 1963; CV from 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 from Torrance 1972
Hwange Main Camp, Zimbabwe	647	1159	335	28.4	2088	0	5	20.3	Dept. Met. Serv. 1978 & recent comm.unications [1951-1971] [1918-2002 for rainfall]
Tsholotsho, Zimbabwe	560	-	-	35-40	2338	0	6	20.6	Dept. Met. Serv. 1978 [1961-1976] CV from Torrance 1972
Maun, Botswana	490	-	-	-	2172	0	-	-	McCarthy *et al.* 2000 [1925-1996]
Sehithwa (Lake Ngami) Botswana	385	-	-	-	-	-	-	-	Swedeplan 1988 [1959-1986]

During the 20th century in the Caprivi, there have been runs of years lasting for approximately a decade, during which the majority of years are wetter or drier than average (Mendelsohn & Roberts 1997, Martin 2003). Rainfall data from Hwange National Park (Figure 1) also suggests an oscillation, but the dry period beginning during the early 1980s has not yet ended, as might have been expected if a strong 18-year oscillation was still maintained here. During the period of rainfall records in Hwange, the 1980s and 1990s have been unusual in that there have been no exceptionally wet years and instead many years with average and below-average annual rainfall, including three of the driest years on record.

During the recent dry decades, substantial rainfall deficits have accumulated in the Caprivi (Martin 2003).

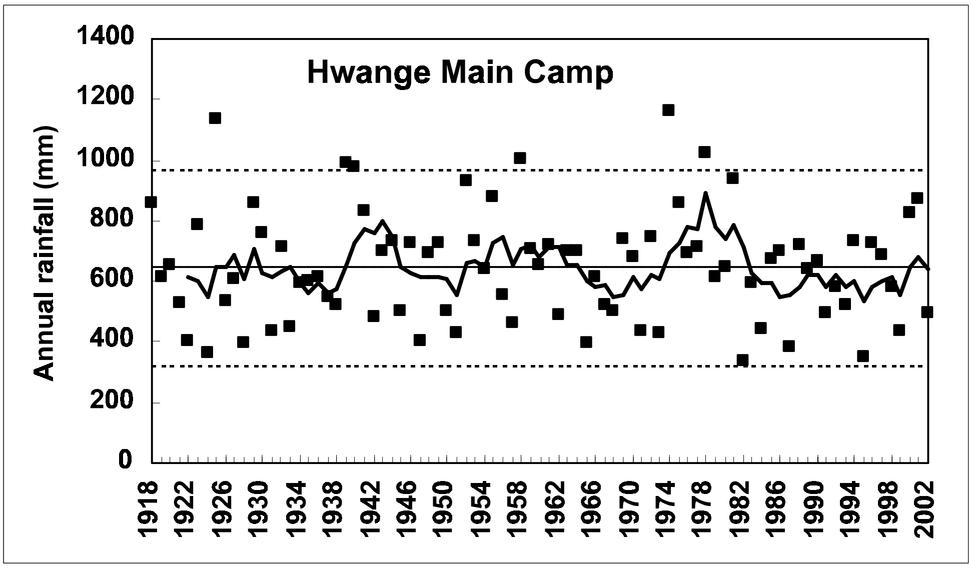


Figure 1. Annual rainfall at Hwange National Park Main Camp, Zimbabwe. Dashed lines indicate levels at which annual rainfall is equal to < 50 or >150% of mean annual rainfall. Bold line indicates 5-year running mean. Year refers to the year in which the rainfall season ended. Data from Dept. of Meteorological Services, Harare.

Extreme Rainfall Years

Extremely wet or dry years in the Four Corners area are not unusual, but they are unpredictable, as seen from Hwange Main Camp (Figure 1). During the 84 years of records, extremely wet years, during which annual rainfall exceeds the mean by more than 50%, occurred 6 times (1925, 1939, 1940, 1954, 1974, 1978). Rainfall was never less than 50% of the mean, but drought years, in which the annual rainfall was <400 mm, also occurred six times (1924, 1928, 1965, 1982, 1985, 1987). Only once in 84 years, during 1939 and 1940, did two exceptionally wet years occur consecutively, and only once, in the years 1924 and 1925, was a severe drought followed by an exceptionally wet year.

Populations of perennial plants in the Four Corners area 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 (http://www.cdc.noaa.gov/enso/), but there is no way of predicting the likelihood of a particular sequence of exceptionally dry or wet years.

2.2 Rivers

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 N Zambia, where annual rainfall is both greater (>1000 mm) and less variable from year to year than it is in the Four Corners area itself (McCarthy *et al.* 2000). The rivers have a complex history involving tectonic movements, ancient inland drainage basins and river capture (Moore 2004). 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) suggested that there may be an 80-year climatic oscillation in the Zambezi River catchment that affects 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 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.

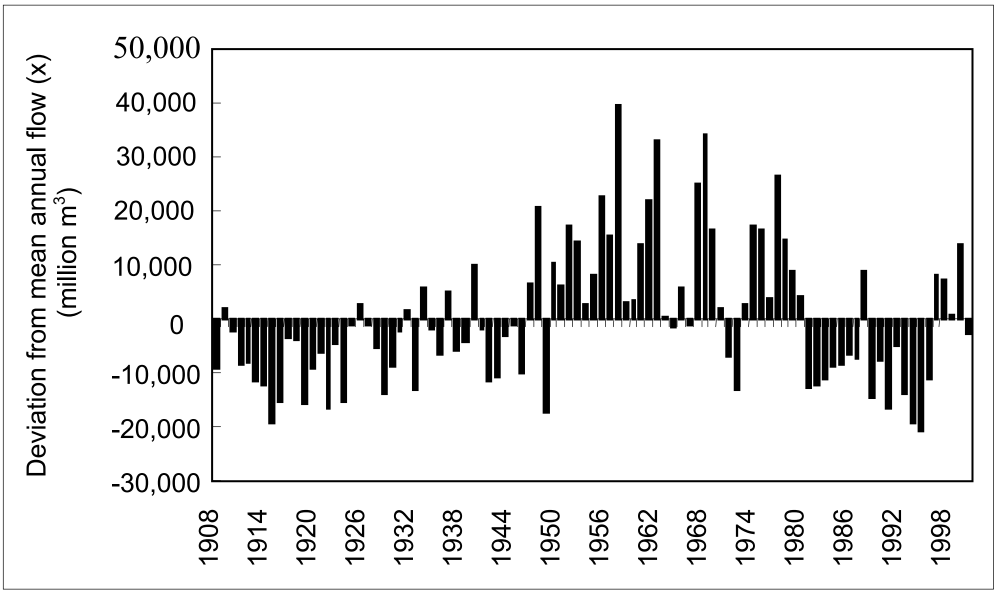


Figure 2. Zambezi River flow record, based on data collected at Victoria Falls by Zambezi River Authority, Oct 1907-Sept 2002.

2.3 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).

In the western Caprivi, a shallow (<20 m) Kalahari sand aquifer is thought to be recharged by water seeping in a north-easterly direction from higher ground to the south (el Obeid & Mendelsohn 2001). Most boreholes in this area produce in excess of 1-5 m^3 per hour. In eastern Caprivi, the watertable is generally 10-40 m below the surface, but borehole yields are similarly low and the water is sometimes unpalatable, especially in the areas around the Linyanti swamps (Mendelsohn & Roberts 1997).

Most boreholes in Hwange National Park currently yield 2-6 m^3 per hour at depths that usually exceed 40 m (Jones 1989). Some yield water that is unpalatably salty. In a test borehole near Main Camp, the Cretaceous 'pipe' sandstones that underlie the Kalahari sands yielded most of the flow (Anon. 1976). The sandstone was probably a better aquifer than the Kalahari sands, because of the sandstone's greater permeability. 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 area 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 in the Kalahari sands, that these are currently being recharged, and that there may be more productive aquifers in underlying permeable strata, especially where the sands are shallow.

2.4 Soil Moisture

Infiltration rates
I am not aware 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). Infiltration rates into the soils under miombo woodland are generally high because clay particles form microaggregates under the influence of organic carbon in the soil, giving these soils the permeability of more sandy soils (Frost 1996).

As the clay content increases towards the lower-lying areas of the landscape, such as dambos and dune hollows, infiltration rates fall. Clays, such as those formed on basalt soils, have low infiltration rates, but these may be increased by litter cover, perennial grass cover and flow along the stems and roots of woody plants. Deep cracks in vertisols promote infiltration (Young 1976). 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). The high levels of sodium in sodic soils disperse the clay fraction and block the soil pores, thus reducing infiltration rates, and the compacted B-horizon reduces permeability (Purves & Blyth 1969, Nyamapfene 1991).

Water Holding Capacity
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 2004). Even towards the edge of the Kalahari deposits, the sands are generally more than 10 m deep. Field capacities are said to vary considerably, depending on the particle size of the sand, but there do not appear to be any figures giving the field capacity of a soil profile within the Four Corners area. Trapnell & Clothier (1937) suggested that the transitional Kalahari sands of western Zambia could hold more water than the undifferentiated Kalahari sands, because the former have a higher proportion of fine sand. In southern Barotseland the moisture-holding capacity of Kalahari sands was estimated at approximately 100 mm per 1-1.2 m of sand (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 SE Botswana, Timberlake (1980) said that the annual rainfall infiltrated 4-5 m into the Kalahari sand. Most of the water held in sand 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).

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

2.5 Deforestation, Runoff and Flow Regimes

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. Small watersheds on the headwaters of the Kafue River (mean annual rainfall 1314 mm) were cleared of all trees except for a strip of miombo woodland around the dambos and converted to small fields and pasture under traditional agricultural use (Mumeka 1986). As a result of these changes mean annual streamflow increased by 56-74%. Flood peaks were higher and were attained sooner after rain had fallen than the flood peaks in undisturbed watersheds. Both wet and dry season stream flows were greater in the cleared watersheds.

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 W Zambia, may be to clear the watershed of woody plants, thus reducing transpiration and allowing more water to flow below the surface (McFarlane 1995).

2.6 Key Features of the Hydrological and Soil Moisture Regimes of the Four Corners

- For all except the deepest rooted plants, water in excess of requirements is available for only a 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 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 south of the area are low-yielding and occasionally salty. Higher yielding sandstone aquifers are often buried beneath hundreds of metres of sand.

3 NUTRIENT FLOWS

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 2), not only at the continental scale but also at landscape and catenal scales.

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 capable of retaining nutrients, remain. Nutrient levels in Kalahari sands are not high even in the drier savannas, except where finer soils have accumulated on floodplains and in depositional basins. Excluding the Kalahari sands, the distribution of soil types across the Four Corners area reflects a general increase in the availability of exchangeable bases from north to south (Cumming 1999, Table 3, Figure 2.3). 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 area.

Table 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/100 gm clay	>15 milliequivalents/100 gm clay
Parent material	Sands, sandstones, granite	Basalts, shales, mudstones
Topography		
Slope position	Crest & upper slope	Lower slope, bottomlands, depositional basins
Vegetation		
Tree taxonomy	Caesalpinioideae & 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

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 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 2004).

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. The landscape-scale pattern on the Zimbabwe/Botswana border south of Pandamatenga as mapped by Wild and Barbosa (1967) compares with catenary diagrams illustrating vegetation types in relation to the topography of fossil dune and redistributed sand (Rogers 1993). Moving southeastwards, the mapped vegetation changes from *Baikiaea* woodland through *Baikiaea-Colophospermum* tree savanna to *Terminalia sericea* savanna and eventually, 500 km from the start, to *Acacia luederitzii-Acacia erioloba* tree savanna. Within one fossil dune, the vegetation changes from *Baikiaea-Combretum* woodland and thicket on the dune crests to *Terminalia sericea-Baikiaea* bushland on the dune slope and various bushed grasslands with *Acacia-Combretum-Commiphora* species in the dune hollow.

Table 3. Distribution (after map in Cumming 1999) and descriptions simplified from the original FAO definitions (Landon 1991) of major soil types within the Four Corners area.

FAO soil type	Simplified description	Chemical fertility	Location
Ferralsols	Strongly weathered soils of humid tropics with high iron and aluminium oxide contents.	Low nutrient content, especially as acidity binds nitrogen and phosphorus to 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 accumulation of organic matter and free aluminium or iron sesquioxides, usually below a strongly bleached horizon	Low nutrient content in topsoil. Nitrogen and phosphorus in the organic layer are generally unavailable because soil is so acid	E of Sioma Ngwezi
Gleysols	Unconsolidated soils, poorly drained, with mottles and staining from reduced iron, even in top 50 cm	Moderate to high nutrient content associated with high levels of organic matter	Barotseland and along Zambezi River
Vertisols	Dark montmorillonite-rich clays with characteristic shrinking and swelling properties	High nutrient content, may be deficient in potassium	N of Caprivi, Katimo Mulilo, Panda-matenga, S Zambia
Lithosols	Soils <50 cm deep or containing many stones and pebbles	Variable nutrient content depending on underlying rock	Parts of Hwange and 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

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 area, except on the vertisols derived from basalts of Matetsi, Pandamatenga and Impalila Island, the *Combretum-Acacia* savannas 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 Makgadikgadi and the Mababe depression, are eutrophic.

3.2 The Nutrient Balance

There are four major pathways for nutrient inputs to a system (Scholes & du Toit 2002): atmospheric deposition; mineral weathering; nitrogen fixation; and anthropogenic inputs (e.g. chemical fertilizers).

Lateral fluxes such as drainage and movement of fauna may be important in some systems.

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 and 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).

Nutrient Gains to Ecosystems: Atmospheric Deposition
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 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). As the nutrients are derived from African savannas, some systems must also be suffering losses. Whether these are significant or not depends on the balance between inputs and outputs in the system from which the nutrients have come.

Dew formation removes nitrogen oxides from the lower atmosphere during the night. The clear skies and cold nights that occur during winter over much of the Four Corners area, especially those covered by Kalahari sands, may encourage this process (P.G.H. Frost, pers. comm.).

Nutrient Gains to Ecosystems: Mineral Weathering

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 4. There are no figures available on rates of weathering, but nutrients derived from this source are likely to be few. The only estimates for probable rates of weathering in basement rocks, such as those on the Zambian plateau, are low and come from Zimbabwean granite (Owens & Watson 1979).

The only rocks that are likely to contribute significantly to nutrient budgets are the relatively small areas of basalt exposed in NW 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.

Nutrient Gains to Ecosystems: Nitrogen Fixation

Few of the woody species in nutrient-poor savannas are nodulated and therefore capable of nitrogen fixation (Högberg 1986b). Only 31% of the Caesalpinioideae form root nodules and these are generally herbaceous species (Corby 1989). 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. Among the *Baikiaea* and *Burkea-Terminalia* vegetation types 20-50% of the woody basal area is made up of potentially nodulating species which are especially common among the understorey shrub layer, but the dominant species *Baikiaea plurijuga, Guibourtia coleosperma* and *Burkea africana* are non-nodulating. The dominant tree in mopane woodland, *Colophospermum mopane,* does not nodulate.

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 – 90% of the Mimosoideae and 98% of the Papilionoideae form nodules (Högberg 1986b, Corby 1989, 1990). 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 when active nodules supply nitrogen to enable the plant to establish.

Nutrient Gains to Ecosystems: Anthropogenic Inputs

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. Crop yields are accordingly low: maize 338 kg/ha, sorghum 365 kg/ha, millet 197 kg/ha, groundnuts 484 kg/ha for Hwange Communal Land during a season (1995/1996) of above-average rainfall (Hungwe 1998). In Caprivi anthropogenic inputs

Table 4. Physical and analytical characteristics of soils from the Four Corners area. Results from (1) Thompson & Purves 1978, (2) Sweet 1971.

Locality	Parent rock	Depth (cm)	Sand (%)			Silt (%)	Clay (%)	pH ($CaCl_2$)	C (%)	N (%)	Exchangeable bases (milliequivalents/100gm soil)						Base saturation of clays (%)	Ext P as P_2O_5 (ppm)	Source
			coarse	medium	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 between sands on gneiss & 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; an indicator of the degree of leaching that a soil has suffered, the lower the base saturation the higher the leaching.

and yields are similarly low: 30-700 kg/ha of maize and 70-445 kg/ha of sorghum and mhunga (Mendelsohn & Roberts 1997).

Nutrient Losses from Ecosystems: Biomass Removal

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 1986b). This was not sustainable and timber harvests had dropped to about 17,000 m^3 by 1983 (Huckabay 1986b, 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/ha (Greenwood 1986) to 22 m^3/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/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/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/ha. Taken over 60 years, nitrogen loss would be 2.7 kg/ha/year and phosphorus loss 0.03 kg/ha/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, but would leave the logging site. Nutrient losses in timber might become significant regionally if exotic timber plantations replaced indigenous forests as species such as eucalypts are more productive and 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 to consume charcoal, except Livingstone. Average charcoal consumption per household in rural Zambia was estimated at only 100 kg/year (Chidumayo 1993b).

Rural populations in the area use wood for fuel and construction (Tietema 1993, Chidumayo 1993b, Mendelsohn & Roberts 1997). As the twigs and branches of woody plants contain more nutrients than the boles, their removal for fuelwood and for fencing (approximately 1000 kg/person/year for both uses) was thought likely to affect nutrient cycling adversely in savannas in Botswana (Ernst & Tolsma 1989).

Nutrient losses from ecosystems can occur if crops are exported to urban areas. Phosphorus and nitrogen in particular are removed in harvested grain crops (Newman 1995, 1997). Maize grains contain approximately 1.5 mg P/gm and millet contains approximately 2.7 mg P/gm (Newman 1997). Harvesting an average crop of 300 kg/ha would remove between 0.45-0.8 kg P/ha from the field, depending on the type of grain. However, there is no evidence of the large-scale export of crops from the area, except from Caprivi where 20 % of the 1995/1996 maize crop was sold (Mendelsohn & Roberts 1997). Most crops are consumed locally.

When cattle are sent to abattoirs rather than consumed locally, the losses to the system of phosphorus and manganese exported in the carcasses may be sufficient to make it necessary to supply additional bone meal to sustain cattle productivity (APRU 1980). Only 2-3% of cattle were sent to abattoirs in Caprivi during 1996, and few would have been exported from NW Zimbabwe.

Nutrient Losses from Ecosystems: 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, as some is deposited locally. Although experimental plots burned every year sometimes have lower levels of soil nitrogen, Scholes & Walker (1993) concluded there was no evidence that occasional fires had a long term deleterious effect on soil nutrient cycling. However, none of these fire plots were on Kalahari sands.

Nutrient Losses from Ecosystems: 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, judging by the lack of evidence of severe erosion as seen from aerial photographs (Grohs & Elwell 1993, Whitlow & Campbell 1989), although 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 1998). 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 5). Not all this soil is necessarily lost to the system as it may be deposited in depressions or against barriers. In the Maitengwe Communal Land in Zimbabwe, over 16% of basalt-derived soils had experienced soil erosion that was sufficiently severe to be visible in aerial photographs (Whitlow & Campbell 1989).

Table 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 the Zimbabwean part of the Four Corners area.

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
Tsholotsho	Kalahari sands	5	5	1	54
Maitengwe	Kalahari sands and vertisols	5-20	26	2	193

Note: 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 Tsholotsho and the formula for 'other' soils for Hwange and Maitengwe.

Nutrient Losses from Ecosystems: Leaching

No nutrient leaching rates for soils are available from the Four Corners area. 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). Few nutrients remain 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 phosphate (Bethune 1991).

Nutrient levels in Kafue water, although not especially high, are higher than those in Zambezi water (Marshall 2000). Most of the Kafue catchment lies on basement rock rather than Kalahari sand, and the higher nutrient content may be due to higher nutrient levels in the soil and decaying rock, or to more disturbance and higher rates of leaching and erosion in the catchment area below the major dams.

3.3 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.

Water Points

Cattle remove nutrients from the surrounding savanna and deposit them in their dung and urine at water points. Soil near a water point in eastern Botswana had three times the nitrogen levels of soils distant from boreholes, and phosphorus levels had increased 80-fold (Tolsma, Ernst & Verwey 1987a). Some nitrogen is permanently lost from the soils by leaching and denitrification (Högberg 1989), but as the majority is probably volatilised and redistributed in rainfall, nitrogen lost from the areas distant from water points may be replaced by aerosol deposition (Augustine 2003). Phosphorus is strongly retained by soils and once it has been deposited around waterholes it remains there, resulting in a permanent loss to the surrounding landscape. In eastern Botswana the area within foraging distance of a 30 year-old borehole (3 km) was calculated to have lost 17% of its soil P, all of which was deposited within 20 m of the waterhole (Tolsma, Ernst & Verwey 1987a). 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 do not eat the nutrient-enriched plants growing near the waterholes and so do not recycle nutrients (Tolsma, Ernst & Verwey 1987a). 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 seen from livestock. Phosphate levels were over 20 ppm in soil near the pan compared to 7.5 ppm in the soils under neighbouring grassland and woodland. During the wet season, the standing crop of grass within one square metre contained 0.1 gm of phosphate when the grass was harvested close to the pan. Phosphate levels in the grass fell sharply with distance from the pan to only 0.05 gm/m^2 at 4 km away. Differences in nutrient concentration around the pan may have been intensified by fires which did not affect the grassland nearest to the pan, but burned through the neighbouring vegetation, ashing the dung and presumably volatilising some of the phosphorus (Conybeare 2004, Dangerfield 2004).

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 such 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 soil under canopy gaps. 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 4), although there may be ground water enriched with exchangeable bases at greater depth.

Levels of nitrogen, potassium and phosphorus in the topsoil under the canopies of *Acacia erioloba* trees in the Kalahari are 2-2.5 times greater than levels in the topsoil of the surrounding grassy shrubland (Dean, Milton & Jeltsch 1999). This was thought to be due to nutrient input from the excreta and carcasses of animals that were attracted to the shade and food resources of large isolated trees. 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 there 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 Kalahari sand), 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, as the inputs (whether they are derived from animals, root extraction, aerosol capture or litter) slowly cease (Dean, Milton & Jeltsch 1999, Belsky & Canham 1994). New hotspots develop under other trees. Fire would redistribute the nutrients more rapidly. At two sites where large trees growing in the Kalahari sands of Hwange National Park had burned, the pH levels of the ash-containing soils were 7.9-8.2 compared to 5.0-5.7 in soils nearby (Weir 1972). The levels of total exchangeable bases in the ash-enriched soils were 17.5-18.9 m.e. % compared to 1.5-2.3 m.e. % elsewhere. Phosphate levels were 112-124 ppm compared to 5-22 ppm in soils from other similar woodlands nearby. Total exchangeable bases exceeded the exchange capacity fivefold. 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.

3.4 Carbon Cycle

Plant Production

Within the Kalahari sands, 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/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 below ground (Table 6). The root biomass of mopane shrub woodland is probably about equivalent to the above ground biomass (Timberlake 1995).

Table 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)	% total carbon in system	carbon content (kg/ha)	% total carbon in system
Tree & shrub biomass				
aboveground	3,132	8.6	2,069	6
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 to be 50% carbon (Nye & Greenland 1960). C content of soil calculated from % C, bulk density and depth of horizon in Kalahari sands at Nyamandhlovu (Nyamapfene 1991), using Young's (1976) calculations and assuming no difference in soils between unburned and burned plots.

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). Most of the rain that falls on the drier savannas in the Four Corners is taken up from the surface soil by grass or shallow-rooted shrubs, especially in fine-textured soils (Moore & Attwell 1999), while much of the rain that falls in the wetter savannas reaches deeper layers in the soil. In SW Zambia, Jeanes and Baars (1991a) noted that grass production was strongly and negatively related to the biomass of woody vegetation and to the position of a site in the landscape.

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. Rates of litter decomposition determine the rates at which these minerals become available (Dangerfield 2004). The dominant trees of dystrophic woodlands produce low quality litter with high levels of structural carbohydrates (Tolsma *et al.* 1987b, 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). In wet miombo 77-90% of aboveground litter disappeared in the first year, in dry miombo 60% disappeared within a year, while only 12% disappeared in *Burkea/Terminalia* savanna. 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 area is shed below ground. In *Burkea-Terminalia* shrubland in Hwange, over 45% of organic carbon in the system was contained in root biomass and approximately 40% was in organic matter within the soil (Table 6).

3.5 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/ha) and biological fixation (8 kg/ha) exceeds the losses due to volatilisation in fires (5 kg/ha) and denitrification (4 kg/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). Most of the nitrogen required for plant growth in *Burkea-Terminalia* savanna at Nylsvley is not derived from net inputs to the system, but from the mineralisation of nitrogen contained in litter and in organic matter within the soil. This process, which is controlled by the microbial flora, supplies about 40 kg/ha of nitrogen. The soil flora takes up nitrogen as well as releasing it, and N immobilisation by microbes is important early in the season because it minimises losses to leaching.

In mixed *Acacia*/broadleaved woodland in eastern Botswana, nitrogen was translocated out of old leaves before they were shed (Tolsma *et al.* 1987b). 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 (Högberg 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 iron and aluminium 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.* 1987b) 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 above-ground tissues was shed in flowers and fruit (Tolsma *et al.* 1987b). 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 microbes 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 1962). Very acid (pH 4.2), leached Kalahari sands in high rainfall (~800 mm) areas of Zimbabwe are so deficient in sulphur that liming alone, which ordinarily makes more sulphur available to plants, was insufficient to produce normal growth in pot trials (Grant 1962). 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 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) accumulates within the profile. The drier south of the area is unusual in that 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.

3.6 Micronutrients

Agricultural experience suggests that there may be deficiencies in copper, zinc and boron in the Kalahari sands (Grant 1962), but levels 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).

3.7 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; 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 (Högberg 1986b). Although most of the vegetation types in the area grow on nutrient-poor Kalahari sand, the patterns of infection differ between them.

Ectomycorrhizal associations have so far been identified in only four plant families, within the Caesalpinioideae, in the tribe Amherstieae (*Brachystegia, Isoberlinia, Julbernardia* spp.) and with some species in the tribe Deteriaeae (*Afzelia quanzensis*), with a few members of the Papilionoideae (*Swartzia* spp. and *Pericopsis angolensis*), with all the Dipterocarpaceae (*Marquesia, Monotes* spp.), and with some members of the Euphorbiaceae (*Uapaca* spp.) (Högberg 1986b, Alexander 1989, Högberg 1989). Vescicular arbuscular (VA) mycorrhizal (endomycorrhizal) infection is much more widespread than ectomycorrhizal infection, occurring among many plant families, including the grasses.

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

The ecological reasons for the differing associations are not well understood. Ectomycorrhizae produce phosphatase enzymes that would allow them to use the phosphate in organic matter and they may also be able to use organic nitrogen, while VA mycorrhizas promote the uptake of inorganic forms of phosphorus and nitrogen (Allen 1991). The substantial ectomycorrhizal sheath that forms around infected roots is able to store minerals and water during the wet season and make them available to plants through the long dry season. But as the fungal sheath is around 50% of the combined root/fungal mass, and the total mass of fungal tissue in root/VA mycorrhizal associations is only 17% (Högberg 1989), ectomycorrhizae are probably more costly to the plant in terms of the carbon that is required to maintain the fungus. In miombo woodlands, sclerophylly, high levels of secondary compounds and the withdrawal of nutrients before leaf shed combine to produce a low quality litter. Such features are thought to favour ectomycorrhizae (Alexander 1989), but are also present in the non-ectomycorrhizal *Baikiaea* woodlands.

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 area have relatively few non-mycorrhizal macrofungi supporting themselves on other substrates such as dead wood (Masuka & Ryvarden 1993) and termite mounds.

3.8 A Nutrient Budget for a Wetland in the Four Corners Area: 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 nutrient budgets available for any ecosystem within the Four Corners area (Garstang *et al.* 1998). The Okavango Delta 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 the peat in the permanent swamps contains very large reserves of nitrogen and phosphorus (17,300 kg/ha and 260 kg/ha to a depth of 50 cm for nitrogen and phosphorus respectively), the rates of mineralisation of these nutrients 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 12,000 km^2 of the delta, are at least 250,000 tonnes per year. Aquatic inputs are 108 and 2.25 kg/ha/year of nitrogen and phosphorus respectively, while aerosol inputs are 3.9 and 0.13 kg/ha/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 the phosphorus requirements of the papyrus; mineralisation of peat contributes the remainder (about 8.1 and 0.12 kg/ha/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.

3.9 Nutrient Restoration After Disturbance

The organic matter in the vegetation and the nutrients that it recycles through the decomposition of litter and root material are crucial to maintaining production in soils such as the Kalahari sands, where nutrient reserves in the soil are low, there is low nutrient retention capacity and the soils are permeable and vulnerable to leaching.

The shifting cultivation practices that people use when human population densities are low are good indicators of the fertility of the system and its ability to recover after severe disturbance. There were a number of different cultivation systems in western Zambia, but most involved 5-10 years of cultivation, followed by 20-30 years of rest that allowed the woody plants to regenerate before the land was cultivated again (Trapnell & Clothier 1937). Only on some heavy dambo soils derived from basement rocks was it possible to cultivate continuously for 15 or more years.

3.10 Key Features of Nutrient Supply and Nutrient Cycling within the Four Corners

- The area is predominantly nutrient-poor, especially in the north, because the surface geology is mostly Kalahari sands or weathered basement rocks, but it 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 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 hence 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 is 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 other vegetation types are VA mycorrhizal (endomycorrhizal).

4 HERBIVORY

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 in a dystrophic African savanna. There 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, either decomposed or burned. The biomass density of large mammals in Nylsvley was about 2869 kg/km^2 (see Table 7 for comparable biomass densities in the Four Corners). Had the indigenous large mammals been allowed to reach their pre-colonial biomass density, estimated as about 3768 kg/km^2, all the herbivores combined would still have eaten only about 15% of the annual production of the plants (12% of grass production and 3.4% of woody plant leaf production). Small mammal herbivory was not included in these calculations.

Herbivory rates in nutrient-enriched patches of fine-leaved savannas at Nylsvley have not been quantified, but were estimated at close to 50-80% of annual production (Scholes & Walker 1993). In another eutrophic savanna, the Zambezi riverine woodland, large mammals consumed 53-99% of the annual production of the annual grasses (Dunham 1990). Termites ate 3-18% of grass production and, although there were no fires, very little litter was available for decomposers.

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 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 leaf digestibility (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).

Table 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)				Authority
			Elephant	Wildlife excluding elephant	Domestic livestock	All large mammals	
Kafue NP, Zambia	1000	1966	914 (50%)	1086 (incl. hartebeeste)	0	2000	East (1984)
Hwange NP & Matetsi complex, Zimbabwe	647	2001	4282 (88%)	582	0	4864	Dunham (2002)
Forest Land, Zimbabwe	?	2001	407 (51%)	312	75	794	Dunham (2002)
Protected areas, N Botswana	500-650	1993 & 1994	?	?	?	?	ULG (1995)
Protected areas & rangeland, Caprivi	500-700	1994	949 (38%)	191	1327	2467	ULG (1994)
Protected areas & rangelands, Caprivi	500-700	1996	not counted	not counted	1221[a]	not applicable	Mendelsohn & Roberts (1997)
Western Province rangelands, Zambia	700-1200	1990	insignifican t	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 (1995).

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

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 green grass remaining in the sward or the fresh grass regrowth that is produced after burning have crude protein and phosphorus levels 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.

Translocation and loss of quality are not so pronounced in the shorter-lived and less robust grasses of eutrophic savannas, which 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. On the Kalahari sands of western Botswana, in a savanna that is drier than any in the Four Corners (mean annual rainfall 300-350 mm), the crude protein and phosphorus levels of perennial grasses were so low that they seldom met the maintenance requirements of cattle (Skarpe & Bergström 1986). Woody species had higher nutrient levels and cattle probably maintained themselves by grazing selectively and supplementing their diet with browse.

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. In protected areas within the Four Corners, elephant alone form 38-80% of the large mammal biomass (Table 7), and are capable of altering the structure of woodlands by their tree-felling and browsing activities (Conybeare 2004).

Characteristic grazers 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/km^2 at 900 mm rainfall in the north to 1148 kg/km^2 at 400 mm rainfall in the south. However, 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 7). Biomass densities in the Hwange/Matetsi complex were nearly twice that predicted from rainfall because of the high number of elephant (Dunham 2002).

Local biomass densities of large mammals, especially in riverine woodlands and around seasonal pans such as the Makgadikgadi (Kgathi & Kalikawe 1993), may be much higher (Conybeare 2004, Cumming 2004). I am unaware of any published work that compares mammal biomass densities between the different vegetation types within the Four Corners area. 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 in Matetsi Safari Area, but results have not yet been published (V. Booth, pers.comm.).

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 7) is less than half of that predicted for nutrient-poor savannas (Fritz & Duncan 1994). In western Zambia only the Sesheke area is considered to be overstocked (Baars 1996, Jeanes & Baars 1991a), with an estimated carrying capacity of 1850 kg/km^2, while cattle biomass density in 1990 was 1950 kg/km^2. Estimated grazing capacities ranged from 0-750 kg/km^2 for forest and thicket, through 750-1750 kg/km^2 for woodland, to 2500-2750 kg/km^2 for dambos, and up to 2750-53,250 kg/km^2 for the floodplains. Although lowlands such as dambos, pans, floodplains and riverine woodlands cover only 30% of Western Province, they have the potential to support 70% of its cattle. East of the Zambezi River, cattle could be supported at nearly four times the biomass density at which they were stocked during 1990. 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.

Suggested stocking rates for the Caprivi range from 900 kg/km^2 (mass of the average beast assumed to be 180 kg) on poor pastures, such as *Baikiaea* shrubland, to 1800 kg/km^2 on moderate pastures such as mopane-*Aristida* woodland, and 2700 kg/km^2 on good pastures such as the Okavango-Kwando floodplain grassland and riverine woodland (Mendelsohn & Roberts 1997). Cattle numbers more than doubled during the eleven years from 1985 to 1997. There is overstocking in some habitats on the eastern floodplains, especially along the main roads and in riverine woodlands where the biomass density of cattle may reach 7200-10,800 kg/km^2. Goats are also common.

Current stocking rates in Zimbabwean communal lands within the Four Corners areaa are around 1000 kg/km^2 in mopane and mopane/miombo woodlands of Tsholotsho East and Maitengwe, rising to 1600 kg/km^2 in the Kalahari sand woodlands of Tsholotsho North (Dunham 2002). As with wildlife estimates, 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 such 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. In savannas where the coefficient of variation in annual rainfall is greater than 33%, drought-induced mortality intervenes before animal numbers build up sufficiently to cause irreversible changes in the vegetation (Ellis & Swift 1988). Others suggest that, even in arid savannas, high stocking rates can affect vegetation dynamics in the long term, especially during and following drought on upland sites vulnerable to erosion (Fynn & O'Connor 2000). As Abel (1993) suggests for communal grazing systems in Botswana, what is required is to identify sites that are at particular risk of erosion. Elsewhere, drastically reducing livestock densities may make little difference to the rates of soil loss. Accelerated erosion 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.

There appears to be a gradient in the processes controlling livestock densities from within-year to between-year constraints. In the wetter areas of western Zambia, rainfall is relatively reliable, but livestock densities are low because of constraints that operate every year, such as the poor quality of grass during the dry season. In drier savannas such as the communal lands of Zimbabwe and northern Botswana, livestock densities are reduced by periodic severe droughts.

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). The estimated area of soil trampled is greater in communities dominated by larger animals, which has implications for rates of soil erosion on vulnerable soils in cattle-dominated rangelands and in those protected areas that are elephant-dominated. Other possible ecological consequences of differences in community body-size structure, such as herbivory rates, dung quality and dung deposition rates, are unknown (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).

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, the metabolic consumption of small rodents living at a biomass density of 240 kg/km^2 was 68% of the consumption of the large mammal community. When the ungulates were excluded by fences, the biomass density of small rodents increased to 390 kg/km^2, at which point they ate as much as a community of medium-sized ungulates living at a biomass density of 4800 kg/km^2 would have eaten (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/ha to <1 animal/ha, possibly as a result of a decline in grass standing crop in response to decreasing rainfall. In miombo grassland in central Zimbabwe, where the multimammate mouse *Mastomys natalensis* was abundant (41 animals/ha), the biomass density of small rodents of all species combined was about 375 kg/km^2 (C.M Swanepoel, pers. comm.), similar to that estimated for the East African savanna after the ungulates had been removed (Keesing 2000). Delany (1986) suggests that in moist savannas the total number of small rodents is about half that estimate, fluctuating around 10 to 30 animals/ha (average biomass density approximately 134 kg/km^2). At this density, rodents would eat about as much as medium-sized ungulates stocked at a density of 1680 kg/km^2 would.

In the semi-arid zones of Africa, small rodent densities may reach 100/ha during occasional outbreaks, but then drop to only 5-10/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 their reach 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). Even in non-outbreak years, *Mastomys* are omnivorous and opportunistic, tending to increase when vegetation recovers after a disturbance. On the Chobe floodplain, *Mastomys* was abundant in the early dry season (Sheppe & Haas 1981).

The high proportion of fine to medium sand grains in the Kalahari sands prevents burrows from collapsing, favouring the spring hare *Pedetes capensis*, a large burrowing rodent whose biomass densities may reach high levels in northern Botswana (Butynski 1973). Scrub hares *Lepus saxatilis* are widespread in woodland and scrub and in and around cultivated lands, wherever there are shrubs and some grass cover, but they are seldom found in open grassland (Smithers 1983). Within the Four Corners, Cape hares *Lepus capensis* occur only on the grasslands of the Makgadikgadi pans. Both species are grazers, preferring short, green shoots, and are most common around villages where domestic livestock keeps the grass short. Hares are solitary and their populations are not prone to outbreaks, hence their contribution to herbivory is probably insignificant. Initially at least, their numbers are likely to increase under increased grazing pressure from large herbivores or domestic livestock as they prefer short grassland.

This largely indirect evidence suggests that in moist savannas of the Four Corners area, rodents probably eat nearly as much of the annual plant production as the large herbivore community would consume. During rare outbreaks, especially in the semi-arid savannas, they can consume considerably more.

4.4 Invertebrates

Above-ground Invertebrate 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 (Cunningham 1996, Styles & Skinner 1996). Because invertebrate populations decline during the long dry season, most invertebrate herbivory takes place during the wet season (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 of the secondary chemicals in the leaves of dystrophic woodlands than mammalian browsers.

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 (Styles 1996).

Below-ground Invertebrate 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 soil fauna in most of the vegetation types represented in the Four Corners (Dangerfield 2004). Invertebrate herbivory may be more intense below ground than above because much of the plant biomass is below ground, especially in vegetation types on Kalahari sands.

4.5 Regeneration

Herbivores probably affect plant populations most strongly through their effect on regeneration. Herbivory also stimulates regeneration. Browsing ungulates may prevent seed production, for example, and keep *Acacia tortilis* within the reach of fire and other browsers (Dangerfield, Perkins & Kaunda 1996). *Acacia erubescens* shrubs growing in a browser-free environment near Gaborone displayed compensatory growth in response to an episode of simulated browsing (Dangerfield & Modukanele 1996). Such a response would minimise the time that a shrub was within reach of the majority of mammalian browsers and also vulnerable to fire, allowing it to reach reproductive size more rapidly. Elephant disperse the seeds of *Acacia erioloba* 20-50 km (Dudley 1999b).

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 (Calvert 1986c, Chisempa & Shingo 1986, Wood 1986). Duiker were initially blamed for serious damage to both seeds and seedlings (Selander & Malaya 1986) that was probably caused by springhares (Calvert 1992).

Bruchid, curculionid and cerambycid beetle larvae frequently infest the seeds of both broadleaved Caesalpinioid legumes (Chidumayo 1993a) and the fine-leaved 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).

4.6 Wetlands and Other Key Resource Areas

Wetlands are 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, thus regulating the density of the animals that are dependent on it. Wetland grass species are not known for their nutrient quality, except those such as *Setaria* that grow on fertile soils. But if soil moisture is sufficient to allow grasses to remain green, they have higher crude protein and phosphorus content than dry grass and lower levels of indigestible fibre (Jeanes & Baars 1991a).

4.7 Key Features of Herbivory in the Four Corners Area

- Although protein levels in leaves of woody plants and herbs in 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 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.
- 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 in the south 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 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 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.

5 FIRE

5.1 Fire Behaviour

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. He describes fire behaviour in southern Africa, summarises the ecological effects of fire in each vegetation type using examples drawn from similar vegetation elsewhere, characterises the fire regimes in the area and outlines the use of fire in management.

Extensive 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 most years in most vegetation types in the area. Standing grass provides much 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/ha (McArthur 1977, Trollope & Potgieter 1983), although fire carries in teak woodlands with a herbaceous fuel load of <650 kg/ha if there is also abundant leaf litter (Calvert & Timberlake 1993). As grass production is largely determined by available moisture, 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 if an area is not burned, 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 2004).

The standing crop of grass is also related to the density of 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/ha under *Cryptosepalum* forests and thickets, to 330 kg/ha in *Baikiaea* forest. Grass cover was more substantial in woodland, ranging from 1050 to 1820 kg/ha in *Baikiaea*, Kalahari, miombo, *Acacia-Combretum* and mopane woodlands, while in bushgroup woodland it rose to 2880 kg/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/ha on dry watershed plains, pans and in dambos, and may reach 10,000 kg/ha on floodplains (Frost 1992).

Most fires are started by people, 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 thunderdays per year at Hwange Main Camp is 89 (Kreft 1972). Relating thunderdays to lightning strikes to the ground (Gaunt & Britten 1990) gives an average of 7 ground strikes/km^2/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 five 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) are used as an example. The time of greatest fire hazard is midday during the months of September and October when all weather factors combine to maximise fire intensity. About 91% of rain falls from November to March. In most years, grass will be dry by early June. Mean relative humidity drops steadily as the dry season progresses and is lowest from August to October. The hottest months are September to April (mean daily maximum temperature 28.7-33.2°C) while the coolest months are May to July.

Maximum temperatures may reach 39.2°C in October. Mean windspeeds increase from 4 knots in April to a maximum of 5.6 knots in November.

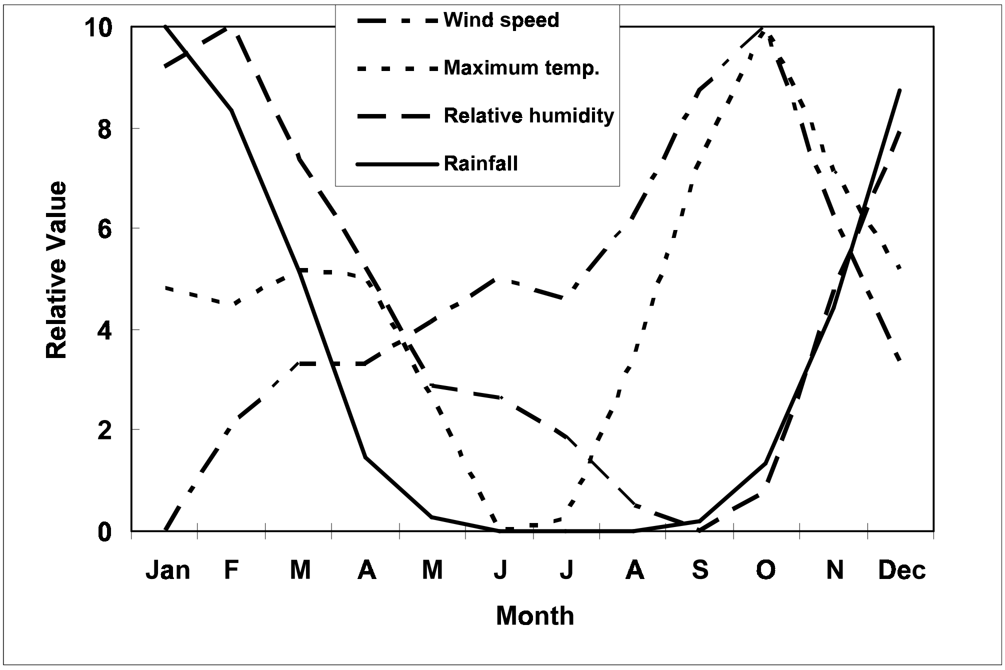


Figure 3. Meteorological conditions at Hwange Main Camp, Zimbabwe. Fire intensity is at a maximum during September-October, when windspeed and air temperature are high, and rainfall and humidity are low. Data from Dept. Meteorological Services (1978).

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). Fires may also be lit during the wet season, usually in November/December after the first spring rain or occasionally in February/March. Because the fuel is moist, fires at this time tend to be less intense.

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 also have substantial rootstocks and can coppice by producing new buds just below ground level if the above-ground parts are destroyed 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.

5.2 Ancient Fire Regimes

Although hominids using a cave in southern Africa manipulated fire for their own purposes a million years ago (Brain 1994), the incidence of fire in sub-Saharan Africa was low until about 400,000 years BP (Bird & Cali 1998). Since then, episodes of intense vegetation fires have occurred during periods when the climate was changing from a glacial to an inter-glacial phase. People have altered fire regimes in Africa for the last 10,000-40,000 years (Bird & Cali 1998, van Zinderen Bakker & Clark 1962). In Hwange National Park there are charcoal and ash in rockshelters where people camped about 2500 years ago, and sand-dunes have lenses of charcoal at about 1-2 m below the surface, dated to about 1900-2000 years BP (G. Haynes, pers. comm.). The frequency of fire probably increased with the arrival of the Iron Age, as selected trees were felled to provide fuel for iron-smelting furnaces, and cultivators used fire to clear fields and to fertilise them with the ash from burning vegetation. Sites on dambos in the Victoria Falls region, dated to the 9th century AD, consist of settled villages with domestic animals, cultivation of cereals, iron smelting and iron tool manufacture (Vogel 1975, Ndoro & Chikumi 1998). Further alterations in fire regimes have occurred during the last 100 years. Human and livestock population densities have increased in settled areas, changing the fuel load and adding new sources of ignition, while attempts at fire exclusion have been made in protected areas.

5.3 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 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.

In Caprivi, the human population density is high, firebreaks are no longer maintained and there are few barriers to fire in the forest areas, although high cattle densities and the spread of human settlement have probably reduced fuel loads in rangeland. Sixty percent of the Caprivi burned in 1996, mostly during the late dry season, after a wet season when rainfall was about 100 mm below average (Mendelsohn & Roberts 1997). The only vegetation type that remained largely unburned was the mopane-*Aristida* woodland where grass cover is low. The pattern of burning was similar during 1994 (ULG 1994).

The Department of National Parks and Wild Life Management in Zimbabwe 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 fire frequency categories in areas of Hwange during 1967-1991 shows a range from no fires during 24 years to burning every second year on average (Rogers 1993). The most frequently burned areas lie close to heavily settled localities along the Botswana border and along the railway line, where sparks from steam trains, largely discontinued since 1991 (G. Pattison, pers.comm.), ignited the grass. The fire regime is related to vegetation types: *Baikiaea* woodland and *Burkea/Terminalia* shrubland near the centre of the Park have burned once every 6 to 12 years, mopane woodland has burned once every 4 to 12 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 2 to 4 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 burned every year between 1928 and 1975, irrespective of fire management (Calvert 1992), suggesting a five year recurrence interval. Five to 15 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.

Fire records are collected in Botswana, but are patchy and have not been analysed. During 2001, extensive areas of the Ngamiland and Central districts burned between July and September and, according to anecdotal evidence, there has been a recent increase in the frequency and extent of fires in the Okavango Delta (Tacheba *et al.* 2002). All four of the sites in northern Botswana that had suffered high fire damage were in *Baikiaea* woodland, or in mixed *Baikiaea* woodland with *Terminalia, Burkea* and mopane (Ben-Shahar 1993).

5.4 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). Burning can however lead to food shortages in areas where the soil moisture is insufficient to sustain grass growth until the rains. I am unaware of any work on the effects on medium-sized browsers of a probable reduction in the key resource, the green leaves of trees and shrubs, as a result of burning during the dry season.

There is no published work on the effect of fire on herbivores in the Four Corners area, other than for elephant (Conybeare 2004). Elephants tend to avoid areas of miombo and mopane woodland that have been early-burned. In the Luangwa Valley they prefer to browse in unburned areas of mopane woodland during the dry season, probably because the grass roots that they eat in addition to mopane leaves are difficult to dig up once the above-ground parts of the grasses have been burned (Lewis 1987). In Malawi, elephants avoid the scorched browse foliage in burned areas of miombo woodland (Bell & Jachmann 1984).

Work in other African savannas suggests that the density of insects and small mammals is lower in savannas that are frequently burned (Gillon 1983). Changes in vegetation structure appear to affect the populations of smaller herbivores at least as much as changes in food quality, perhaps because of the necessity for protection from predators. Although small rodent population densities were not immediately affected by a fire, 6 to 15 weeks after a burn the mortality rate of those animals that had remained in the burned area was higher than the mortality rate in the unburned area (Swanepoel 1981). Lowered root production or a less favourable microclimate reduced the emergence of beetle larvae from the soil two months after a fire (Gandar 1982). Early-burning in miombo woodland appears to improve the food value for Saturniid moth caterpillars of some woody species that are otherwise less preferred (Mughogho 1995).

5.5 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.
- Humans have altered fire regimes in Africa for the last 10,000-40,000 years. The frequency of fire probably increased with the arrival of the Iron Age. Further alterations in fire regimes within the Four Corners have occurred during the last 100 years.
- 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 6 to 12 years, depending on the vegetation type and the sources of ignition. A few areas with inadequate fuel loads never burn.
- Changes in vegetation structure as a result of burning appear to affect populations of smaller herbivores at least as much as changes in food quality, perhaps because of the necessity for protection from predators.

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, although they are less common in the Okavango swamps and the Caprivi. The effects of frost are patchy, being most severe in hollows where a distinct thermal inversion layer develops at 3 to 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 1999a). 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 minimum temperatures, 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 1999a), and there has also been 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 1999a). 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.

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 of vegetation structure in the direction of shrubland, especially in those resilient vegetation types that respond to disturbance by resprouting from their underground rootstocks.

Cryptosepalum Forest, Woodland & 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. All that now remains are small islands of forest in the sea of grassland that has been created, and is now maintained, by cultivation and burning (White 1983, Jeanes & Baars 1991a). Although undisturbed forest has a low fuel load because low light intensities exclude grass, the forest edges are vulnerable to fire (Cottrell & Loveridge 1966). Any gap in the canopy, such as a fire hole where honey collectors have left a tree to smoulder or an abandoned field, may be expanded by repeated burning. 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). If the forest canopy is removed and the site is protected from burning, the thicket rapidly re-establishes from rootstocks and eventually the forest species will recreate the canopy (Trapnell 1959). Under repeated burning, either tall grassland with fire-resistant trees or woodland dominated by miombo species will replace the *Cryptosepalum* forest, depending on the soil moisture regime (Frost 1992).

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, Högberg 1986a, Huckabay 1986a). *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 (Högberg 1986a). Childes & Walker (1987) established that depth of sand and soil moisture regime were the predominant factors determining the structure of undisturbed vegetation on Kalahari sands in Hwange National Park. Tall *Baikiaea* trees grow only where there are no compacted sand layers to restrict drainage and a deep (>10m) soil profile is available for this deep-rooted species. The shrubby thicket species that grow in the understorey of *Baikiaea* forest and woodland, such as *Baphia massaiensis* and *Pterocarpus lucens* (a species that may develop into a tree or take thicket form), are shallow-rooted with a dense network of fine roots near the surface (Huckabay 1986a, Timberlake & Calvert 1993). The upper layers of the soil are so thoroughly exploited that comparatively little grass grows under the thicket.

The curious dwarf shell *Baikiaea* forests of SW Zambia seem to be stunted by an overabundance of water draining from upslope and they respond to seasonal waterlogging by producing many short-lived shoots from a much-branched root system (Fanshawe & Savory 1964).

Baikiaea is at the dry end of its range in the Four Corners area. If seedlings can germinate and establish only during exceptionally wet years (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. Competition for moisture with shallow-rooted shrub species makes it virtually impossible for *Baikiaea* seedlings to establish in those areas of northern Zambia where the thicket is dense (Chisumpa 1986, Calvert 1986c). There are currently more than enough suppressed rootstocks to replace the canopy trees in Zimbabwean woodlands (Calvert & Timberlake 1993). It is not the smallest stems, but stems in the intermediate size-class measuring 5-25 cm in diameter at breast height, that are missing in many *Baikiaea* woodlands in Zambia (De Meo 1986), Zimbabwe (Calvert & Timberlake 1993) and northern Botswana (Burger 1993, Geldenhuys 1993), probably because of the combined effects of frost and fire.

The slow-growing, timber-producing trees dominating the canopy in *Baikiaea* forest and woodland are vulnerable to fire. In the Gwayi Forest Reserve, where experimental burning plots and their unburned controls were maintained from 1956 to 1990, 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. The effects of fire were least severe during the mid-dry season during May to July. Even the larger stems were destroyed by August-September fires. A reserve of about 1500 rootstocks/ha of timber species remained, many more than the 20-30 rootstocks/ha that would be required to replace the canopy trees. There was a shift in species composition away from *Guibourtia* and *Baikiaea* and a 15% reduction in species diversity under the annual burning regimes. Among the non-timber species, five were intolerant of fire, five were intermediate and four were tolerant. 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.* Even then, regrowth to mature woodland would require 250-300 years (Calvert & Timberlake 1993).

Baikiaea is particularly sensitive to the interaction between fire and frost. In Zambian *Baikiaea* forest and woodlands, where there is dense thicket undergrowth a severe frost early in the season before the leaves have fallen can reduce the understorey to a tinder-dry network of twigs and leaves (Huckabay 1986a). Dry season fires burning through these abundant, well-aerated fuelbeds are so severe that they can kill canopy trees and reduce forest to thicket (Fanshawe 1969, Wood 1986, Zimba 1986). Although they resprout initially, even the thicket species are killed by repeated burning and secondary grassland replaces the forest. *Baikiaea* woodlands in Zimbabwe do not have such a dense understorey, but once the canopy trees have been removed, for instance by selective timber-felling, frequent frost and fire can trap this vegetation in a scrub phase. Once the frost-sensitive canopy regrowth reaches a height of 4-5 m, it is relatively safe from fire and frost, but this requires many years of uninterrupted growth (Calvert 1986b, Childes & Walker 1987, Calvert & Timberlake 1993). The differing reports from Zambia and Zimbabwe suggest a fundamental difference between the regrowth behaviour of *Baikiaea* forests and *Baikiaea* woodland after the canopy trees have been removed by a severe disturbance. Repeated burning can prevent regrowth of the disturbed forest canopy and transform 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.

Ben-Shahar (1996) concluded that there would be a net loss of trees from *Baikiaea* woodlands in northern Botswana, even in the absence of elephant, if more than 50% of the *Baikiaea* woodland area was burned each year (a recurrence interval of less than two years). This conclusion is correct, but his model underestimates the long-term threat to *Baikiaea* woodland of less severe fire regimes than biennial burns. It is flawed by the assumption that, in the absence of fire and herbivory, the seedlings of *Baikiaea plurijuga* would grow at rates that allowed them to reach a height of 3 m by the time they were 15 years old, at which height (and age) they would no longer be vulnerable to fire. Ben-Shahar's figures were derived from a model that used the observed growth rates of *Acacia tortilis* seedlings in East Africa (Dublin, Sinclair & McGlade 1990). *Baikiaea plurijuga* is a slow-growing hardwood, increasing in diameter at rates of 1.0 to 2.6 mm per year (Calvert 1986a,b; Mushove, Gondo & Gumbie 1993). In Zimbabwean 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 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 2004).

Burkea-Terminalia Woodland and Scrub (Kalahari Sand Woodland)

In Hwange National Park, scrub with small *Terminalia* and *Burkea* trees grows where there is a hard layer of sand at a depth of 2.0-2.5 m and the site receives sub-surface water draining laterally down the slope (Childes & Walker 1987). During the rains, the hard layer impedes drainage and creates waterlogged conditions so that only shallow-rooted species such as *Terminalia sericea* or *Erythrophleum africanum* are able to survive. Compacted sand horizons are difficult to detect as they differ from the overlying sand only in the ease with which they can be penetrated with an auger (S. Childes, pers. comm.) and in a higher content of free iron oxides. Childes and Walker (1987) suggested that these hard layers might have been created when well-sorted pluvial Kalahari sands were laid down over the old dune ridges.

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 (Conybeare 2004). 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. In Namibia, woody regrowth in plots protected from fire was double the volume of regrowth under annual early dry season, mid dry season or late dry season burning regimes (Geldenhuys 1977). Of the four fire regimes, late wet season burning (March/April) was the least damaging to woody regrowth.

Brachystegia/Julbernardia Woodland (Miombo)
In miombo woodlands on basement rocks, moisture tensions in the upper 30 cm of the soil are below wilting point for three months of the year, but at depths beyond 90 cm, the soil remains moist throughout the dry season (Strang 1969). *Brachystegia spiciformis* has a large, well-developed root system and extensive surface laterals, which may account for the sparse understorey in miombo woodland and its ability to invade *Baikiaea* woodland if the canopy trees are removed (Calvert 1986a). 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).

The canopy trees of *Brachystegia* woodland have explosive dehiscent pods, containing large seeds that are all dispersed within about 50 m of the parent plant (Chidumayo & Frost 1996). There is no dormancy mechanism and all viable seed germinates when the rains begin, leaving no seed bank in the soil (Strang 1966, Robertson 1984, Ernst 1988). Many seedlings die if the first rain is followed by a dry period; others are eaten by insects. After establishment, the mortality rate is low and suffrutices may persist for many years as dwarf plants, accumulating reserves in their roots and awaiting an opportunity, such as the death of a tree, to grow into the canopy. Many woody plants survive fire, browsing or felling (Strang 1974). Even when no above-ground parts survive, new shoots sprout from adventitious buds which develop below ground.

There has been no experimental work on fire in miombo growing on Kalahari sands. Woody species of 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. Forty years of annual late burning have reduced the wetter miombo woodland in Zambia to tall grassland with isolated fire-hardy trees. Although all canopy trees of the former dominant genera, *Julbernardia* and *Brachystegia,* have been killed, they and many other woody species survive as suffrutices whose underground rootstocks coppice every year. Under an annual early-burning regime, the original woodland has changed relatively little in species composition or in structure. Wetter miombo, protected from fire for 40 years, has been invaded by trees and shrubs and is reverting to dry evergreen forest, but only on the deeper soils. Edaphic factors seem to be involved as woodland on shallower soils nearby has not developed into forest, despite fire-protection (White 1983). The drier miombo woodland at Marondera on the Zimbabwe highveld has not developed into forest, nor has its species composition changed under protection from fire. Even under an annual burning regime the dominant *Brachystegia* and *Julbernardia* species have not been eliminated.

After clearing, and so long as the rootstocks are not destroyed, both the wetter and drier miombo woodlands 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). Once the dominant *Brachystegia* and *Julbernardia* have reached a height of 2-3 metres they are less vulnerable to burning and begin to suppress grass growth, creating a positive feedback between lower fuel loads, more rapid regrowth by trees and shrubs and more effective competition with grass (Robertson 1984, Robertson 1990). If fires are frequent the regrowth may remain trapped in a shrub phase, where *Brachystegia* and *Julbernardia* are still present as suffrutices, but *Combretum* and other shrubby species dominate (Starfield *et al.* 1993). This and site differences are probably the basis for Stromgaard's (1986) erroneous observation that *Combretum*-dominated woodland develops on abandoned fields that were miombo woodland prior to clearing.

Interactions between fire and frost are not a feature of this vegetation type. The dominant trees are not frost-tolerant (Ernst 1971) and miombo woodland does not occur where mean minimum temperatures are less than about 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 2004). Even when they are living at relatively low densities ($<0.5/km^2$), elephants in combination with fire can reduce *Brachystegia* woodland to shrubland within a few years. There is *Brachystegia* in Matetsi Safari Area, in some of the Zimbabwean Forest Reserves, in Zambian Game Management Areas and in Kafue National Park.

Colophospermum mopane (Mopane) Woodland and Shrubland

Mopane is often monodominant 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 *Colophospermum 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). Intense inter-tree competition was a precondition for the die-back of patches of *Colophospermum mopane* on soils that had been degraded by a loss of grass cover and accelerated erosion during 50 years of livestock ranching in South Africa (MacGregor & O'Connor 2002). Vulnerable patches of soil had changed from sinks for water to sources of runoff water and could no longer meet the water requirements of all the mopane trees within the patch during drought years.

Colophospermum mopane reproduces by means of large wind-dispersed seeds that lack dormancy (Timberlake 1995). There is usually 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.

There is no experimental work on the effects of fire on mopane within the Four Corners area (Timberlake 1995). 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 allow 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 in drought years by browsers eating the mopane leaves.

Burning at any time during the dry season reduced the canopy volume and height of mopane shrubs in shrub mopane in Kruger National Park (Gertenbach & Potgieter 1979) and in the SE lowveld of Zimbabwe (Walters 2000), but increased the number of coppice stems. As mopane coppices vigorously from underground rootstocks, repeated dry-season burning may produce dense mopane shrubland, especially if the burning is followed by a period of protection from fire. Anthropogenic fires, lit predominantly during the dry season, may produce a different structure to that produced by lightning fires which burn at the start of the wet season. In Kruger National Park, burning mopane shrubveld during the early wet season produced a savanna with fewer coppice stems and in which leaf material was higher off the ground than in mopane shrubveld that was burned during the dry season (Kennedy & Potgieter 2003).

Mopane is sensitive to low temperatures, the limit to its distribution apparently being controlled by the 5^{o}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.

Mopane 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 2004).

Acacia-Combretum (Munga) Woodland

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 the 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. *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.

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 SW Zambia and on the lower parts of many catenas elsewhere. Frequent fire sharpens the boundary between wooded mounds and the burned grassland.

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 2004). 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*. 1987b, Skarpe 1986, 1990a,b). Some *Acacia* species such as *Acacia erioloba, A. karroo, A. robusta* and *A. nilotica* are very deep-rooted, while others including *A. erubescens, A. fleckii, A. mellifera* and *A. tortilis* are shallow-rooted (Tolsma *et al*. 1987b, Moore & Attwell 1999). A shallow-rooting habit is correlated in the acacias with the ability to invade disturbed communities (Tolsma *et al*. 1987b). There are two possible explanations for this pattern. Those *Acacia* species that are shallow-rooted have a higher nitrogen content in their leaves than the deeper-rooted species, and Tolsma *et al*. (1987b) 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.

Although most acacias have hard-coated seeds that are impermeable to water (Timberlake, Fagg & Barnes 1999) there is no reliable information on whether or not most African *Acacia* species have a long-lived seed bank in the soil (Midgley & Bond 2001). Many acacias can resprout from underground rootstocks if the stems are removed. Ben-Shahar (1996) considered that under contemporary rates of elephant browsing and fire damage, sufficient trees were recruited to replace the canopy trees in *Acacia erioloba* woodland. Although ungulates, which were more numerous in *Acacia erioloba* woodland than in other vegetation types, reversed seedlings to smaller size classes their impact was insufficient to prevent recruitment. Conybeare (2004) found the optimistic preditions derived from Ben-Shahar's model surprising, given the reported decline in the density of this species in Chobe National Park.

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 N Botswana and W Zimbabwe.

Riverine Woodlands
Little is known of ecological processes in riverine woodlands, despite their importance as dry season concentration areas for mammals. Herremans (1995) suggests that *Acacia* woodlands growing along the rivers in N Botswana may have germinated during the 19th Century under a more humid climate, with low densities of wildlife and livestock as a result of the rinderpest outbreak and low numbers of elephant as a result of hunting. 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).

Secondary Grasslands
Grasslands derived from the severe disturbance of other vegetation types, usually involving the removal of woody rootstocks, are maintained by fires which prevent the establishment of woody plants (White 1983, Wood 1986). However, Jeanes & Baars (1991a) considered that most of the grassland in western Zambia that had been derived from woodland, and then left fallow following the abandonment of cultivation was reverting to shrubland and would ultimately become woodland or thicket again. Abandoned fields in the Caprivi are covered in pioneer shrubs and weeds (Mendelsohn & Roberts 1997).

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. Management has been based on how they were thought to function, rather than on facts (Whitlow 1991). Recent ideas have overturned former models of dambo functioning (McFarlane 1994, Bullock 1994) and 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 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.

Groundwater is not stored in dambos but in the deep sands on the interfluves, from where it flows laterally into the dambos. The water relations and the fertility of the Kalahari dambos are so complex that there are seven distinctive methods of cultivating gardens within dambos, based on position in the landscape and differences in local drainage caused by features such as termite mounds (Trapnell & Clothier 1937: 42).

McFarlane (1994) suggests that dambos formed on igneous rocks are also the result of subsurface weathering. Deep and permeable soils on the interfluves, and the layer of weathered rock that underlies them, store any water that seeps into the dambos during the dry season (Bullock 1994). 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 streamflow, because some of the subsurface water moving downslope from the upland interfluve evaporates or is transpired when it emerges at the dambo margin (Bullock 1994).

Basalt dambos are also characteristic of flat or undulating terrain where there are few streams and subsurface drainage predominates (Booth 1989, Clegg 1999). There has been no work on basalt dambos in the Four Corners area. On such dambos in the south-east lowveld of Zimbabwe, the wettest sites occurred in depressions where water accumulated. Water was not distributed throughout the profile, but stored in the upper layers of the soil, where it provided sufficient soil moisture during the dry season to allow green grass to grow, so providing a key resource for animals during the dry season (Clegg 1999).

Recently, peat fires have burned on the Barotse floodplains where water levels have dropped and rice-cultivators burn the 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.G.H. Frost, pers.comm.). The ash adds nutrients to the soil and the post-burn vegetation is more nutrient-rich and more attractive to herbivores.

Watershed Plains

In the grassy watershed plains of western Zambia (Frost 1992) the wet season watertables are so high that tree seedlings are unable to establish. They may be underlain by an impermeable subsurface layer creating a perched water table (Trapnell & Clothier 1937), or the high watertable may result from slow subsurface lateral flow because there is little surface drainage on these flat plains. 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).

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 and *Cyperus* swamps of the Linyanti to reach Lake Liambezi. The lake has been dry due to low rainfall in the Angolan catchment since the 1980s, but partially filled recently (R.B. Martin, pers.comm.). A portion of the Linyanti swamp in Mamili National Park also dried up and dense shrubby vegetation dominated by *Diospyros* shrubs replaced the grassland that had been heavily used by wildlife. Much of the former bed of Lake Liambezi is now cultivated. The diversity of soil moisture regimes on the floodplains of the Caprivi is reflected in the diversity of 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).

8 AREAS AND PROCESSES OF CONSERVATION IMPORTANCE

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 Four Corners area. 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 in the Four Corners area. Tyson *et al.* (2002) concluded that despite the uncertainties associated with modelling, changes in the variability of stream flow between years were likely to be considerable. 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. Bethune's (1991) comment that abstracting water at a rate of 3 m^3/second from the Okavango River that was <10% of mean annual flow would remove 20% of flow in dry years and 47% of flow in extreme drought years is pertinent to all the other major rivers in the Four Corners.

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. Bioclimatic modelling of the distribution envelopes of key plant species has been used to predict the probable future distributions of plants and animals in South Africa (Tyson *et al*. 2002). Modelling of this kind would be useful in designing effective corridors for the dispersal of plant and animal species between protected areas and in locating additional protected areas. A transfrontier approach to these species will be crucial.

Lake Liambezi, the swamps in the Mamili National Park 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.

Dambos
There is likely to be an increase in dambo cultivation as the demand for land increases. Current thinking suggests that the cultivation of dambos is unlikely to increase evapotranspiration if the fields are not irrigated (Anon. 1994). On basement rocks, even irrigation will not affect downstream water supplies significantly, as long as the extent of irrigated cultivation does not exceed 10% of the catchment area or 30% of the dambo area, whichever is the smaller (Bullock 1994). This level of irrigation would increase evapotranspiration by 60% and deplete the groundwater under the interfluve by only 17%, insufficient to disrupt the soil moisture regime.

Changes in land use on the interfluves, especially the clearing of woody vegetation and the resulting reduction in evapotranspiration, will alter the hydrology of the dambos 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.

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 area 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 and 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). Chemical fertilizer cannot necessarily solve the problem of nutrient depletion. In northern Zambia the application of subsidised fertilizer without lime, lowered the pH of the soil sufficiently to reduce crop yields further (Chidumayo 1999).

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 area, 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. Southwest 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 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 2004). Nutrients will continue to cycle, but a proportion are likely to be permanently lost from the riverine, miombo and mopane woodlands in particular and the rates of nutrient cycling may alter. This is a major information gap.

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. But even if a reduced burning frequency was achievable, it will probably be offset by the high rate of clearing of land for cultivation. In the Caprivi, the total area cleared for new fields has increased at an average rate of 4.1% each year since 1943 (Mendelsohn & Roberts 1997).

Fire Regimes
The blanket application of one fire regime, such as early-burning in 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. This may require the consideration of species' requirements, which will differ slightly, but can probably be divided into broad categories by their fire-sensitivity. The requirements for successful recruitment of dominant species such as *Baikiaea plurijuga,* which contain most of the biomass in *Baikiaea* woodland and largely determine its structure, would often have priority, especially in Forest Reserves.

Orchids and bryophytes increase markedly, especially in the wetter dambos of northwestern Zambia if these are protected from fire (White 1983). But fire exclusion may suppress the semi-woody suffrutices that flower and leaf immediately after burning and before the perennial grass grows. The solution in protected areas may be a mosaic of different fire regimes, 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.

8.4 Herbivory

Elephants
Elephants are likely to have a major effect 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. A CIRAD-funded project that will analyse the Wildlife Society of Zimbabwe's long-term record of water hole counts of all large mammals in Hwange and attempt to separate the effects of the growing elephant population from the effects of other ecological processes, such as the prolonged drought of the 1980s and 1990s, is currently underway (Valeix 2002a,b).

Key Resources
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.

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. The aquatic weeds *Salvinia molesta* and *Pistia stratiotes* have already invaded the Caprivi wetlands and the NE Botswana wetlands. The *Salvinia* infestation which had the potential seriously to disrupt flooding regimes here and in the Okavango is currently under biological control (Schlettwein *et al.* 1991, Mendelsohn & Roberts 1997). *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 competes with arable crop plants and the seeds make cultivation by hand or using work animals difficult. 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. Seeds carried on livestock appear to be the major cause of spread.

9.0 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, modified or extended where thought appropriate in view of the conservation concerns outlined in the previous section.

9.1 Opportunities

Considering the remote and rural nature of most of the Four Corners area, there is more baseline data on ecological processes than might be expected. These include climate records, borehole depth and water quality records, river flow records, counts of cattle at dip tanks, wildlife counts, fire records and, in some areas, blanket aerial photography. 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 and 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. Monitoring would require repeating the analyses that underlie the many maps and diagrams portrayed in the atlas, using current data.

9.2 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.

9.3 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, large and often inaccessible 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 duplicate records are kept.

An analysis of the width of tree rings in *Canthium burtii* growing in Hwange National Park suggests that there was an extended drought in the Hwange area during the 1880s to 1890s (Stahle *et al.* 1996). The analysis of tree rings in *Canthium* and perhaps other species shows potential for investigating the palaeoclimate of this area.

River Flows
The Zimbabwe River Authority (ZRA) is a model of 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. Robertson, pers.comm.).

Water Abstraction and Dam Capacity
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, compared to the rest of southern Africa (Marshall 2000). The only large dams are two on the Kafue River, the Itezhitezi and the Kafue Gorge dams, one at each end of the Kafue Flats.

Aquifers
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.

Water Quality
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 that is 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.

9.4 Nutrients

Nutrient Depletion in Crops and Animal Products
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, but they will not be easy to monitor. There are many uncertainties, such as the intensity of the negative impact of HIV/Aids on social and economic growth (Barnett & Whiteside 2003) and the possibility that the wider use of fertilizers and cattle feed supplements, the control of disease and the improvement of infrastructure may lead to changes in land use towards commercial rather than subsistence agriculture (Desanker *et al.* 1997).

Erosion
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 area 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 (Tafangenyasha & Campbell 1998).

9.5 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 successfully to monitor change in vegetation structure, although there have been problems in their interpretation of changes in woody structure in southern Africa, for example in Hwange National Park (Rogers & Chidziya 1996). This is probably because the usual technique, overlaying a calibrated grid of pin points or cross hairs on the photograph, noting the intercepts as 'canopy' or 'not canopy' and calculating percentage woody cover from the percentage of hits on canopy, does not distinguish between shrub and tree canopies. Thus an entire canopy tree layer could disappear without any apparent change in woody cover, so long as subcanopy trees and shrubs remained. Monitoring changes in the area covered by different structural types, the technique adopted in Chobe (Mosugelo *et al.* 2002) is another approach, which gives more information about structural changes. 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.

9.6 Vegetation Monitoring: Existing Data Sets

Existing plots for the long-term monitoring of changes in vegetation structure include those set up by Richard Bell as a baseline for monitoring changes in the vegetation of northern Botswana, and plots set up by Conybeare (1991) in Hwange National Park. Long-term vegetation monitoring plots in dambo grasslands are conspicuously lacking in southern Africa, which is unfortunate considering their importance as key resource areas for herbivores.

9.7 Fires

Frequency, Extent and Timing of Fires
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 (currently at: http://maps.geog.umd.edu/activefire,asp). Unfortunately, these maps lack a cloud mask, hence cannot reliably indicate 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 m and 500 m (Roy, Lewis & Justice 2002). 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 & S. Childes, 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.

9.8 Herbivory

Domestic Livestock
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.

Large Mammals
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 NW 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.

9.9 Extreme Events

The biological consequences of extreme events, such as cyclone events, 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 (but see Plowes 2002). 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).

10 REFERENCES

Abel, N.O.J. (1993). Reducing cattle numbers on southern African communal range: Is it worth it? 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. 173-195. Overseas Development Institute, London.

Agritex (1989). Agro-climatological summaries and analysis (rainfall and potential evapotranspiration), Volume 1. Early Warning/Food Security Unit, Department of Agriculture, Technical and Extension Services, Zimbabwe.

Alexander, I. (1989). Mycorrhizas in tropical forests. In: *Mineral Nutrients in Tropical Forest and Savanna Ecosystems* (edited by J. Proctor), pp. 169-188. Blackwell Scientific, Oxford.

Allen, M.F. (1991). *The Ecology of Mycorrhizae*. Cambridge University Press, Cambridge.

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

Anon. (1994). Observations and research highlights. 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. 177-181. IUCN Wetlands Programme No.14. IUCN, Gland, Switzerland.

APRU (1980). *Ten Years of Animal Production and Range Research in Botswana*. Animal Production Research Unit, Ministry of Agriculture, Gaborone.

Augustine, D.J. (2003). Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *Journal of Applied Ecology* **40**: 137-149.

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-Verlag, Berlin.

Barnett, T. & Whiteside, A. (2003). *AIDS in the 21st Century: Disease and Globalisation*. Palgrave.

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.

Bell, R.H.V. & Jachmann, H. (1984). Influence of fire on the use of *Brachystegia* woodland by elephants. *African Journal of Ecology* **22**: 157-163.

Belsky, A.J. & Canham, C.D. (1994). Forest gaps and isolated savanna trees. *BioScience* **44**: 77-84.

Ben-Shahar, R. (1993). Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation* **65**: 249-256.

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**: 77-112.

Bhalotra, Y.P.R. (1987). Climate of Botswana. Part II, Elements of climate: 1 Rainfall. Dept. 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.

Bird, M.I. & Cali, J.A. (1998). A million year record of fire in sub-Saharan Africa. *Nature* **394**: 767-769.

Booth, V.R. (1989). Indications of desiccation in the Matetsi/Deka catchment of north-western Zimbabwe. *South African Journal of Science* **85**: 528-532.

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

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

Brain, C.K. [editor] (1994). *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum Monograph No. 8. Transvaal Museum, Pretoria.

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. 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, Zimbabwe.

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. (1986a). The ecology and management of the Kalahari sand forest vegetation of south-western Zimbabwe. In: *The Zambezi Teak Forests* (edited by G.D. Piearce), pp. 132-157. Forest Department, Ndola, Zambia.

Calvert, G.M. (1986b). Fire effects in *Baikiaea* woodland, Gwai Forest Reserve. In: *The Zambezi Teak Forests* (edited by G.D. Piearce), pp. 319-325. Forest Department, Ndola, Zambia.

Calvert, G.M. (1986c). *Baikiaea* regeneration and damaging agencies in Barotseland. In: *The Zambezi Teak Forests* (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, Harare.

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. *African Journal of Ecology* **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. *Journal of Arid Environments* **54**: 281-296.

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

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

Chidumayo, E.N. (1993a). *Responses of miombo to harvesting: ecology and managemen*t. Stockholm Environment Institute, Stockholm.

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

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

Chidumayo, E.N. (1999). *Using Natural Fertilizers in Miombo Woodlands*. BSP Publication No. 26. Biodiversity Support Program, WWF, Washington DC.

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

Childes, S.L. (1984). *The population dynamics of some woody species in the Kalahari sand vegetation of Hwange National Park*. Unpublished MSc thesis, University of 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* (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* (edited by G.D. Piearce), pp. 384-389. Forest Department, Ndola, Zambia.

Chisumpa, S.M. (1986). Mukusi ecological associations and environmental effects. In: *The Zambezi Teak Forests* (edited by G.D. Piearce), pp. 102-108. Forest Department, Ndola, Zambia.

Clegg, B. (1999). *Plant ecology and degradation of basalt-derived dambos in semi-arid south eastern Zimbabwe*. Unpublished MSc in Agriculture, University of Natal, Pietermaritzburg.

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.

Conybeare, A.M. (1991). *Elephant occupancy and vegetation change in relation to artificial water points in a Kalahari sand area of Hwange National Park*. Unpublished DPhil thesis. University of Zimbabwe, Harare.

Conybeare, A.M. (2004). Elephant impacts on vegetation and other biodiversity in the broadleaved woodlands of South-Central Africa. In: *Biodiversity of the Four Corners Area* (edited by J.R. Timberlake & S.L. Childes), pp. 477-508. Occasional Publications in Biodiversity No. 15. BFA, Bulawayo/Zambezi Society, Harare.

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

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

Corby, H.D.L. (1990). The incidence of rhizobial nodulation among legumes dominant in the Flora Zambesiaca area of Africa. *Kirkia* **13**: 365-375.

Cottrell, C.B. & Loveridge, J.P. (1966). Observations on the *Cryptosepalum* forest of the Mwinilunga district of Zambia. *Proceedings and Transactions of Rhodesian Scientific Association* **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, WWF, Washington DC.

Cumming, D.H.M. (2004). Movements and migrations of large mammals in the Four Corners area. In: *Biodiversity of the Four Corners Area* (edited by J.R. Timberlake & S.L. Childes), pp. 449-460. Occasional Publications in Biodiversity No. 15. BFA, Bulawayo/Zambezi Society, Harare.

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 Miombo Ecoregion Project. WWF Southern Africa Regional Programme Office, Harare.

Cunningham, A.B. (1996). Saturniid subsidy: cash and protein from edible caterpillars of Zambesian woodlands. In: *The Miombo in Transition: Woodlands and Welfare in Africa* (edited by B. Campbell), pp. 107-108. CIFOR, Indonesia.

Dangerfield, J.M. (2004). Soil fauna of the Four Corners area. In: *Biodiversity of the Four Corners Area* (edited by J.R. Timberlake & S.L. Childes), pp. 409-426. Occasional Publications in Biodiversity No. 15. BFA, Bulawayo/Zambezi Society, Harare.

Dangerfield, J.M. & Modukanele, B. (1996). Overcompensation by *Acacia erubescens* in response to simulated browsing. *African Journal of Ecology* **12**: 905-908.

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

Dean, W.R.J., Milton, S.J. & Jeltsch, F. (1999) Large trees, fertile islands and birds in arid savanna. *Journal of Arid Environments* **41**: 61-78.

Delany, M.J. (1986). Ecology of small rodents in Africa. *Mammal Review* **16(1)**: 1-41.

DeMeo, T. (1986). The case for a natural regeneration system in managing the Zambezi Teak forests. In: *The Zambezi Teak Forests* (edited by G.D. Piearce), pp. 392-398. Forest Department, Ndola, Zambia.

Department of Meteorological Services (1978). Climatological Summaries: Rhodesia. *Climate Handbook Supplement No. 5.* Department of 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. International Geosphere-Biosphere Programme, Stockholm.

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

Dublin, H.T., Sinclair, A.R.E. & McGlade J. (1990). Elephants and fire as causes of mulitiple stable states in the Serenegeti-Mara woodland. *Journal of Animal Ecology* **59**: 1147-1164.

Dudley, J.P. (1999a). 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. Unpublished PhD thesis, University of Alaska, Fairbanks.

Dudley, J.P. (1999b). Seed dispersal of *Acacia erioloba* by African bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology* **37**: 375-385.

Dunham, K.M. (1990). Biomass dynamics of herbaceous vegetation in Zambezi riverine woodlands. *African Journal of Ecology* **28**: 200-212.

Dunham, K.M. (1991). Phenology of *Acacia albida* trees in Zambezi riverine woodlands. *African Journal of Ecology* **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, Harare.

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

East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology* **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., McCarthy, T.S., Cairncross, B. & Oelofse R. (1989). A peat fire in the Okavango Delta, Botswana, and its importance as an ecosystem process. *African Journal of Ecology* **27**: 7-21.

Ellis, J.E. & Swift, M.J. (1988). Stability of African pastoral ecosystems: Alternate paradigms and implications for development. *Journal of Range Management* **41**: 450-459.

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

Ernst, W. (1971). Zur Ökologie der Miombo-Wälder. *Flora* **160**: 317-331.

Ernst, W.H.O. (1975). Variation in the mineral content of leaves of trees in miombo woodlands in South Central Africa. *Journal of Ecology* **63**: 801-808.

Ernst, W.H.O. (1988). Seed and seedling ecology of *Brachystegia spiciformis*, a predominant tree component in miombo woodlands in south central Africa. *Forest Ecology and Management* **25**: 195-210.

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. *African Journal of Ecology* **28**: 45-54.

Ernst, W.H.O. & Tolsma, D.J. (1989). Mineral nutrients in some Botswana savanna types. In: *Mineral Nutrients in Tropical Forest and Savanna Ecosystems* (edited by J. Proctor), pp. 97-120. Blackwell Scientific, Oxford.

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. *Proceedings of Royal Society London, B*. **256**: 77-82.

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

Fynn, R.W.S. & O'Connor, T.G. (2000). Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology* **37**: 491-507.

Gandar, M.V. (1982). Description of a fire and its effects on in the Nylsvley Nature Reserve: a synthesis report. *South African National Scientific Programmes Report* **63**: CSIR, Pretoria.

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)*. Unpublished 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. *South African Journal of Science* **94**: 223-229.

Gaunt, C.T. & Britten, A.C. (1990). Insulation co-ordination for overhead distribution lines in high lightning areas. In: First All-Africa International Symposium on Lightning, Harare, April-May 1990.

Geldenhuys, C.J. (1977). The effect of different regimes of annual burning on two woodland communities in Kavango. *South African Forestry Journal* **103**: 32-42.

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.

Gertenbach W.P.D. & Potgieter A.L.F. (1979). Veldbrandnavorsing in die struikmopanieveld van die Nasionale Krugerwildtuin. *Koedoe* **22**: 1-28.

Gillon, D. (1983). The fire problem in tropical savannas. In: *Tropical Savannas* (edited by F. Bourliere), pp. 617-641. 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. (1962). Trace element deficiencies in Kalahari sands. *Rhodesia Agricultural Journal* **59**(6): 310-311.

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

Greenwood, D.E.(1986). Zambezi teak in Zambia. In: *The Zambezi Teak Forests* (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. *Transactions of Zimbabwe Scientific Association* **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. 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), pp. 174-188. Forestry Commission & SAREC-SIDA, Harare.

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

Hattle, J. (1972). *Wayward Winds*. Bundu Series. Longman, Harare.

Herremans, M. (1995). Effects of woodland modification by the African elephant *Loxodonta africana* on bird diversity in northern Botswana. *Ecography* **18**: 440-454.

Högberg, P. (1986a). Rooting habits and mycorrhizas of *Baikiaea plurijuga*. In: *The Zambezi Teak Forests* (edited by G.D. Piearce), pp. 92-100. Forest Department, Ndola, Zambia.

Högberg, P. (1986b). Soil nutrient availability, root symbioses and tree species composition in tropical Africa: a review. *Journal of Tropical Ecology* **2**: 359-372.

Högberg, P. (1989). Root symbioses of trees in savannas. In: *Mineral Nutrients in Tropical Forest and Savanna Ecosystems* (edited by J. Proctor), pp. 121-136. Blackwell Scientific, Oxford.

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

Huckabay, J.D. (1986a). The geography of Zambezi Teak. In: *The Zambezi Teak Forests* (edited by G.D. Piearce), pp. 5-23. Forest Department, Ndola, Zambia.

Huckabay, J.D. (1986b). The exploitation of Zambezi Teak in Zambia. In: *The Zambezi Teak Forests* (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*. Vol. 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), 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), pp. 101-119. Springer, New York.

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 nonequilibrium concepts to semi-arid grazing systems. *Ecological Applications* **9**: 798-813.

IPCC (2001) Summary for policymakers. Climate change 2001: the scientific basis. Intergovernmental Panel on Climate Change, Third Assessment Report. Available at http://www.ipcc.ch/pub/tar/index.htm. IPCC, Switzerland.

Jeanes, K.W. & Baars, R.M.T. (1991a). *The vegetation, ecology and rangeland resources, Western Province, Zambia.* Volume 1. RDP Livestock Services/Dept. Veterinary & Tsetse Control Services, Mongu.

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

Jones, M.A. (1989). *Hwange National Park Management Plan*. Dept. National Parks & Wildlife Management, Harare.

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

Kehinde, M.O. & Loehnert, E.P. (1989). Review of African groundwater resources. *Journal of African Earth Sciences* **9**: 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. Blackwell Scientific Publications, Oxford.

Kennedy, A.D. & Potgieter, A.L.F. (2003). Fire season affects size and architecture of *Colophospermum mopane* in southern African savannas. *Plant Ecology* **167**: 179-192.

Kgathi, D.K. & Kalikawe, M.C. (1993). Seasonal distribution of zebra and wildebeeste in Makgadikgadi Pans Game Reserve, Botswana. *African Journal of Ecology* **31**: 210-219.

Kreft, J. (1972). The distribution of thunderstorm days over Rhodesia. Climate information sheet No. 44. Dept. of 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. *Journal of Ecology* **66**: 175-198.

Lewis, D.M. (1987). Elephant response to early burning in mopane woodland, Zambia. *South African Journal of Wildlife Research* **17**: 33-40.

MacGregor, S.D. & O'Connor, T.G. (2002). Patch dieback of *Colophospermum mopane* in a dysfunctional semi-arid African savanna. *Austral Ecology* **27**: 385-395.

Magadza, C.H.D. (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. Natural Resources Research 14. 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.

Marshall, B.E. (2000). Freshwater fishes of the Zambezi Basin. In: *Biodiversity of the Zambezi Basin Wetlands* (edited by J. Timberlake), 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*. Unpublished Certificate in Field Ecology thesis, University of Rhodesia, Salisbury.

Martin, R.B. (2002). Species report for southern savanna buffalo. Study for Transboundary Mammal Project, Ministry of Environment & Tourism. Namibia Nature Foundation & World Wildlife Fund, Windhoek.

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

Masuka, A.J. & Ryvarden L. (1993). Parasitic macrofungi on indigenous trees in Zimbabwe. pp.375-382. 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. *South African Journal of Geology* **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. *South African Journal of Science* **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 and 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: Proceedings of a seminar on wetlands in Zimbabwe* (edited by T. Matiza & S.A.Crafter), pp. 105-116. IUCN Wetlands Programme No.14. IUCN, Gland, Switzerland.

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

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

Midgley, J.J. & Bond, W.J. (2001). A synthesis of the demography of the African acacias. *Journal of Tropical Ecology* 17(6): 871-886.

Moore, A.E. (2004). The geomorphology of the Four Corners area. In: *Biodiversity of the Four Corners Area* (edited by J.R. Timberlake & S.L. Childes), pp. 27-66. Occasional Publications in Biodiversity No. 15. BFA, Bulawayo/Zambezi Society, Harare.

Moore, A.E. & Attwell, C.A.M. (1999). Geological controls in the distribution of woody vegetation in the central Kalahari, Botswana. *South African Journal of Geology* **102**: 350-362.

Moore, A.E. & Larkin, P.A. (2001). Drainage evolution in south-central Africa since the breakup of Gondwana. *South African Journal of Geology* **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. *African Journal of Ecology* **40**: 232-240

Moyo, C.S., Sikosana, J.L.N. & Gambiza, J. (1995). Recovery of eutrophic rangeland after a severe drought. *Proceedings of the Fifth International Rangeland Congress*. pp. 385-386.

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

Mughogho, D.E.C. & Munthali, S.M. (1995). Ecological interaction between *Gonimbrasia belina* (L.) and *Gynanisa maia* (L.), and the impact of fire on forage preference in a savanna ecosystem. *African Journal of Ecology* **33**: 84-87.

Mumeka, A. (1986). Effect of deforestation and subsistence agriculture on runoff of the Kafue river headwaters, Zambia. *Hydrological Sciences Journal* **31**: 543-554.

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.

Mushove, P.T., Gondo, P.C. & Gumbie, C. (1993). The effect of silvicultural cleaning on diameter increment in *Baikiaea plurijuga*. In: *The Ecology and Management of Indigenous Forests in Southern Africa* (edited by G.D. Piearce & D.J. Gumbo), pp. 182-190. 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* (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* (edited by G.D. Piearce), pp. 462-464. Forest Department, Ndola, Zambia.

Ndoro, W. & Chikumi, D. (1998). Archeology and paleontology studies. In: *Batoka Gorge Hydro Electric Scheme Feasibility Report*. Volume 4a, pp. 178-232 of Further Environmental Impact Assessment Studies. Civil Consult & Soils Incorporated, Harare.

Newman E.I. (1995). Phosphorus inputs to terrestrial ecosystems. *Journal of Ecology* **83**: 713-726.

Newman, E.I. (1997). Phosphorus balance of contrasting farming systems, past and present. Can food production be sustainable? *Journal of Applied Ecology* **34**: 1334-1347.

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

Nye P.H. & Greenland D.J. (1960). The soil under shifting cultivation. Commonwealth Bureau of Soils Technical Communication No. 51.

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

Owens, L.B. & Watson, J.P. (1979). Rates of weathering and soil formation on granite in Rhodesia. *Soil Science Society of America Journal* **43**: 160-166.

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

Plowes, R.M. (2002). Tree damage by Cyclone Eline in the Bunga Forest, Zimbabwe. *Kirkia* **18**: 63-71.

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

Purves, W.D. & Blyth, W.B. (1969). A study of associated hydromorphic and sodic soils on redistributed Karoo sediments. *Rhodesian Journal of Agricultural Research* **7**: 99-109.

Rattray, J.M. (1957). The grasses and grass associations of Southern Rhodesia. *Rhodesia Agricultural Journal* **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. *African Journal of Ecology* **29**: 271-274.

Robertson. E.F. (1984). *Regrowth of two African woodland types after shifting cultivation.* Unpublished PhD thesis, University of Aberdeen, Aberdeen.

Robertson, E.F. (1990). The management of elephants and fire in *Brachystegia* woodland. Presentation given at a workshop on Management of the Hwange Ecosystem. Proceedings of a USAID workshop, Hwange Safari Lodge, 9-13 July 1990.

Robertson, E.F. (1993). Early-burning in the *Brachystegia* woodland of the Parks and Wildlife Estate. *Zimbabwe Science News* **27**: 68-71.

Robertson, E.F. (2004). Ecological processes within the Four Corners area. In: *Biodiversity of the Four Corners Area* (edited by J.R. Timberlake & S.L. Childes), pp. 69-118. Occasional Publications in Biodiversity No. 15. BFA, Bulawayo/Zambezi Society, Harare.

Rogers, C.M.L. (1993). *A woody vegetation survey of Hwange National Park*. Dept. of National Parks and Wildlife 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), Appendix 12, pp. 97-106. Dept. of National Parks & Wildlife Management, Harare.

Roy, D., Lewis, P. & Justice, C. (2002). Burned area mapping using multi-temporal moderate spatial resolution data - a bidirectional reflectance model-based expectation approach. *Remote Sensing of Environment* **83**: 263-286.

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*. Unpublished MSc thesis, University of Rhodesia.

Rushworth, J.E. (1978). Kalahari sand scrub – something of value. *Rhodesia Science News* **12**: 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**: 67-76.
Scholes, M.C. & du Toit, B. (2002). Nutritional sustainability of *Eucalyptus* plantations: a case study at Karkloof, South Africa. *Southern African Forestry Journal* **195**: 63-72.
Scholes, R.J. (1990) The influence of soil fertility on the ecology of southern African dry savannas. *Journal of Biogeography* **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.M. 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. *Journal of Vegetation Science* **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* (edited by G.D. Piearce), pp. 271-283. Forest Department, Ndola.
Setshogo, M.P. (2002). *Cenchrus biflorus*: an alien invasive grass in the Botswana flora. *SABONET News* **7**: 181-182.
Sheppe, W.F. & Haas, P. (1981). The annual cycle of small mammal populations along the Chobe River, Botswana. *Mammalia* **45**: 157-176.
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. *Journal of Applied Ecology* **27**: 873-885.
Skarpe, C. (1990b). Structure of the woody vegetation in disturbed and undisturbed arid savanna, Botswana. *Vegetatio* **87**: 11-18.
Skarpe, C. & Bergström, R. (1986). Nutrient content and digestibility of forage plants in relation to plant phenology and rainfall in the Kalahari, Botswana. *Journal of Arid Environments* **11**: 147-164.
Smithers, R.H.N. (1983). *The Mammals of the Southern African Subregion*. University of Pretoria, Pretoria.
Stahle, D.W., Cleaveland, M.K., Haynes, G.A., Klimowicz, J., Ngwenya, P. & Mushove, P. (1996). Preliminary tree-ring investigations of indigenous trees in Zimbabwe. In: *Sustainable Management of Indigenous Forests in the Dry Tropics* (edited by P.T. Mushove, E.M. Shumba & F. Matose), pp. 57-61. Zimbabwe Forestry Commission & SAREC-SIDA, Harare.
Starfield, A.M., Cumming, D.H.M., Taylor, R.D. & Quadling, M.S. (1993). A frame-based paradigm for dynamic ecosystem models. *AI Applications* **7**(2&3): 1-13.
Strang, R.M. (1966). The spread and establishment of *Brachystegia spiciformis* Benth. and *Julbernardia globiflora* (Benth.) Troupin in the Rhodesian highveld. *Commonwealth Forestry Review* **45**: 253-256.
Strang, R.M. (1969). Soil moisture relations under grassland and under woodland in the Rhodesian highveld. *Commonwealth Forestry Review* **48**: 26-40.
Strang, R.M. (1974). Some man-made changes in successional trends on the Rhodesian highveld. *Journal of Applied Ecology* **11**: 249-263.

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

Stromgaard, P. (1986). Early secondary succession on abandoned shifting cultivator's plots in the miombo of South Central Africa. *Biotropica* **18**: 97-106.

Styles, C.V. (1996). The biological ecology of *Imbrasia belina* (Saturniinae, Saturniidae) with reference to its behaviour, physiology, distribution, population dynamics, impact within mopane veld and utilization within South Africa. In: *Phane*, Proceedings of the First Multidisciplinary Symposium on Phane, June 1996 (edited by B.A. Gashe, K. Leggett & S.F. Mpuchane), pp. 9-13. Dept. Biological Sciences/Kalahari Conservation Society, Gaborone.

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

Swanepoel, C.M. (1981). The effect of fire on a small mammal community. *South African Journal of Zoology* **16**: 232-236.

Swedeplan (1988). *Programme for the Planning of Resource Utilisation in the Okavango Delta Region.* Consultancy report for 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. Department of Research & Specialist Services, 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 Sytems in Southern Africa.* Third meeting, University of Botswana, 29 July-1 August 2002.

Tafangenyasha, C. & Campbell, B.M. (1998). Initiation and maintenance of degraded landscape in the Sinamatella area of Hwange National Park, Zimbabwe. *Journal of Environmental Management* **52**: 69-78.

Thompson, J.G. & Purves, W.D. (1978). *A Guide to the Soils of Rhodesia*. Department of Research & Specialist Services, Harare.

Tietema, T. (1993). Possibilities for the management of indigenous woodlands in southern Africa: a case study from Botswana. In: *The Ecology and Management of Indigenous Forests in Southern Africa* (edited by G.D. Piearce & D.J. Gumbo), pp. 134-142. Zimbabwe Forestry Commission, 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*. Division of Land Utilization, Ministry of Agriculture, Botswana.

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

Timberlake, J.R. [editor] (2000). *Biodiversity of the Zambezi Basin Wetlands*. Report for IUCN ROSA, 4 vols. BFA, Bulawayo/Zambezi Society, Harare.

Timberlake, J.R. & Calvert, G.M. (1993). Preliminary root atlas for Zimbabwe and Zambia. Zimbabwe Bulletin of Forestry Research No. 10. Zimbabwe Forestry Commission, Harare.

Timberlake, J.R., Fagg, C. & Barnes R.D. (1999). *Field Guide to the Acacias of Zimbabwe*. CBC Publishing, Harare.

Timberlake, J., Nobanda, N. & Mapaure, I. (1993). Vegetation survey of the communal lands - north and west Zimbabwe. *Kirkia* **14**: 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. *Journal of Applied Ecology* **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. *Journal of Ecology* **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.

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

Trapnell, G.C. (1959). Ecological results of woodland burning experiments in Northern Rhodesia. *Journal of Ecology* **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.

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, MC., Scholes, RJ. (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 (1994). Aerial census of animals in the Caprivi Strip, Namibia, dry season 1994. Technical Assistance on Wildlife Conservation in Northern Botswana. Report to the Dept. of Wildlife & National Parks, Botswana. ULG Consultants, Warwick, UK.

ULG (1995). Final report: Aerial surveys. Technical Assistance on Wildlife Conservation in Northern Botswana. Report to the Dept. of Wildlife & National Parks, Botswana. ULG Consultants, Warwick, UK.

Valeix, M. (2002a). Wildlife counts at waterholes in Hwange National Park. BFA seminar series No. 22. BFA, Bulawayo.

Valeix, M. (2002b). *Structure of ungulate communities: a test for the role of megaherbivores in inter-specific competition*. Unpublished MSc thesis, University of Pierre et Marie Curie VI, Paris.

van Niekerk, B.D.H. (1997). Are grazing ruminants being over-mineralized? *Proceedings of the 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.

van Zinderen Bakker, E.M. & Clark, J.D. (1962). Pleistocene climates and cultures in north-eastern Angola. *Nature (London)* **196**: 639-642.

Vogel, J.C. (1975). The Iron Age archeology of the Victoria Falls region. In: *The Later Prehistory of Eastern and Southern Africa* (edited by D.W. Phillipson), pp. XX-XX. Heinemann, London.

Walters, M.J. (2000). *Effects of season and type of fire on* Colophospermum mopane *woodland in the south-eastern lowveld of Zimbabwe*. Unpublished MSc thesis, Department of Agriculture, University of Natal, Pietermaritzberg.

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

Weir, J.S. (1969). Chemical properties and occurrence on Kalahari sand of salt licks created by elephants. *Journal of the Zoological Society of London* **158**: 293-310.
Weir, J.S. (1971). The effect of creating additional water supplies in a Central African Park. In: *The Scientific Managment of Animal and Plant Communities for Conservation* (edited by E. Duffey & A.S. Watt), pp. 367-385. Blackwell Scientific, Oxford.
Weir, J.S. (1972). The spatial distribution of elephants in an African National Park in relation to environmental sodium. *Oikos* **23**: 1-13.
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' Bulletin (Singapore)* **29**: 55-71.
White, F. (1983). *The Vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map*. UNESCO, Paris.
Whitlow, J.R. (1983). Hydrological implications of land use in Africa, with particular reference to Zimbabwe. *Zimbabwe Agricultural Journal* **80**: 193-212.
Whitlow, R.C. (1991). Wetland use and abuse in Zimbabwe. *Transactions of the Zimbabwe Scientific Association* **65**: 24-33.
Whitlow, J.R. & Campbell, B. (1989). Factors influencing soil erosion in Zimbabwe: a statistical analysis. *Journal of Environmental Management* **29**: 17-29.
Wild, H. & Barbosa, L.A.G. (1967). *Vegetation map of the Flora Zambesiaca region*. M.O. Collins, Salisbury.
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* (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*, pp. 61-79. Botswana Society, Gaborone.
Young, A. (1976). *Tropical Soils and Soil Survey*. Cambridge University Press, Cambridge.
Zimba, S.C. (1986). Fire protection and related management problems in the Zambian Teak forests. In: *The Zambezi Teak Forests* (edited by G.D. Piearce), pp. 302-312. Forest Department, Ndola, Zambia.