

Trends in savanna structure and composition along an aridity gradient in the Kalahari

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Abstract. The Kalahari sand sheet occupies 2.5 million ha in southern Africa. It is an area with relatively similar deep aeolian soils, and a strong south to north gradient in rainfall, from 200 to 1000 mm mean annual precipitation (MAP) in the region studied. This provides an excellent basis for gradient studies at the subcontinental scale. This paper briefly reviews the literature on the vegetation of the Kalahari and describes the vegetation structure and composition at 11 new sites. There is a clear gradient in woody plant biomass (as indexed by basal area) from south to north. Above the minimum level of 200 mm MAP, the woody basal area increases at a rate of ca. 2.5 m².ha⁻¹ per 100 mm MAP. Mean maximum tree height also increases along the gradient, reaching 20 m at ca. 800 mm MAP. The number of species to contribute > 95% of the woody basal area increases from one at 200 mm to 16 at 1000 mm MAP. Members of the *Mimosaceae* (mainly *Acacia*) dominate the tree layer up to 400 mm MAP. They are replaced by either the *Combretaceae* (*Combretum* or *Terminalia*) or *Colophospermum mopane* of the *Caesalpinaceae* between 400 and 600 mm MAP, and by other representatives of the *Caesalpinaceae* above 600 mm MAP. The vegetation is largely deciduous up to 1000 mm MAP, except for species that apparently have access to groundwater, which may be locally dominant above about 600 mm MAP.

Keywords: Biomass; Rainfall; Species number; Shrubland; Southern Africa; Tree height; Woodland.

Abbreviation: MAP = Mean annual precipitation.

Introduction

The sand-covered area of interior southern Africa occupies 2.5 million km², stretching from 29° S to the equator and 14° E to 28° E, forming one of the largest sand seas in the world (Fig. 1; McKee 1979; Baillieu 1975). The sands reach a depth of 100-200 m in the centre of the basin. The latitudinal spread and the location of the sand sheet in relation to the main features of

the regional circulation (Tyson & Crimp 1998) combine to establish a south to north gradient of increasing mean annual precipitation (MAP), from ca. 150 mm.yr⁻¹ to over 1200 mm.yr⁻¹. The area south of about 20° S, which receives less than 600 mm.yr⁻¹ and has no permanent surface water due to the generally freely-draining sands, is known as the 'Kalahari desert', although neither the climate nor the vegetation is consistent with a true desert.

The relative vertical and horizontal homogeneity of the sandy substrate, the flat topography and the untransformed nature of much of the land surface make the Kalahari an ideal environment for studying large-scale trends in vegetation structure and function. The International Geosphere-Biosphere Programme has promoted the 'Kalahari Transect' as one of its global set of 'megatransects', designed to explore continental-scale links between climate, biogeochemistry and ecosystem structure and function (Koch et al. 1995; Scholes & Parsons 1997). The rainfall gradient across the Botswana has independently been used as an organising concept in several studies (Skarpe 1986; Chanda et al. 1998; Ringrose et al. 1999b).

There is an extensive literature on the Kalahari and its flora, starting with Passarge (1904). Published reports of the vegetation of the Kalahari provide lists of species, general descriptions of structure, maps and occasional photographs, but not the detailed quantification of composition, cover and height needed for the purposes of satellite image interpretation and global vegetation modelling. This paper has two purposes: to provide a synthesis of vegetation floristic and structural trends in the area covered by Kalahari sands, between 10° S and 29° S, herein referred to as the 'Kalahari'; and to quantify the structural characteristics of a range of sites within that area. Some of the data presented here were collected during 'Kalahari Transect' projects since 1995, and the rest during the Safari campaign in February 2000.

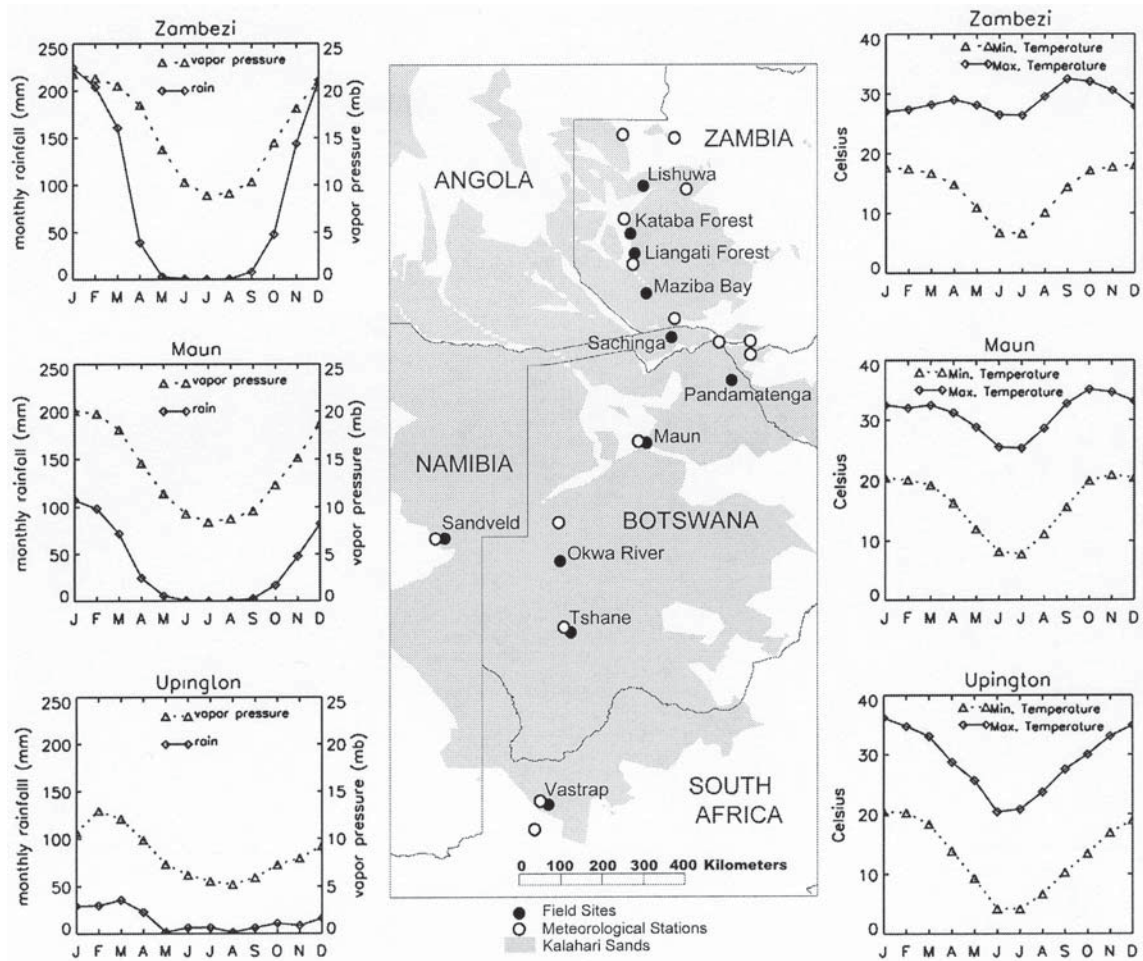


Fig. 1. Locations of field sites and nearby meteorological stations. Seasonal climate patterns are indicated for Zambezi, Maun and Upington. The extent of soils dominated by Kalahari sands as indicated by Anon. (1995). This does not include soil units where Kalahari sands are present but not dominant.

Synopsis of the vegetation of the Kalahari

A generalized synthesis of the arid and mesic Kalahari, coupled with a rationalisation of the nomenclature used to describe the vegetation types, is proposed in Table 1.

Vegetation types on deep, well-drained sand occupy more than three-quarters of the Kalahari landscape, and are the exclusive focus of the main part of this paper. These form a relatively orderly progression of increasing woody plant cover and height from south to north. The fine-leaved savannas (also referred to as arid, eutrophic or nutrient-rich savannas by some authorities) typically indicate systems with relatively palatable grass and therefore high ungulate biomass and relatively few fires (Scholes 1990; Scholes & Walker 1993). They give way to broad-leaved woodlands (also called moist/dystrophic/nutrient-poor savannas) along

a line extending NW-SE through Botswana. Broad-leaved woodlands are less palatable, have fewer ungulates and more frequent fire. The dividing line corresponds to White's division between the Highveld-Kalahari Transition Zone and Zambezian Domain. In areas more arid than about 500 mm.yr⁻¹, a distinction is made between the vegetation on the red sands, which are typically dune fields, and the whitish calcareous sands (van Rooyen & van Rooyen 1998). The red dunes are usually the older sands. White and grey sands are usually the younger redistributed sands that have not yet been coated with iron oxide or, in drainage lines or river beds, where the iron oxide coating has been removed. The sands in the wetter areas of the Kalahari are also light-coloured, possibly due to leaching, but are not calcareous.

Rocky exposures of the underlying geology are rare within the main body of the sand sheet: the hills at

Tsodilo, Savuti and Aha are exceptional. Calcrete ridges are sometimes exposed in the south. These 'hard' geologies typically support more woody vegetation than their more sandy surrounds. The pans and dry river valleys (fossil drainage from Pleistocene times: Shaw & Thomas 1996; Deacon & Lancaster 1988), particularly prominent in the south and centre of the Kalahari, have more clayey soils. The drainage lines are typically grassy, with tree clumps. The pans show concentric bands of vegetation associated with different flooding and soil environments (van Rooyen & van Rooyen 1998). Saline areas such as the vast Makgadigadi pan support halophytic shrubs and grasses or are bare. Non-saline pans, for example at Nxai pan, support sedge- and grasslands, sometimes with tree clumps on slightly more elevated ground. The banks of the perennial rivers (the Okavango, Kwando, Linyanti/Chobe, and Zambezi) and seasonal rivers (e.g. Botlelele) have fringing forest belts a few metres wide. Permanent swamps, such as the Okavango 'delta', support *Papyrus* in the shallower water, and floating macrophyte communities in the deeper water (Ellery et al. 1993). Seasonally-waterlogged, broad drainage lines (known locally as *dambo*, *omaramba* or *vlei*) are common in the north, and support grass- and sedgeland. The transition between the woodlands of the interfluves and the *dambo* grasslands is marked by regularly spaced tree clumps, each occupying a termitarium.

Patterns of vegetation structure within the Kalahari sand sheet

The key determinants of structure and composition of savanna vegetation include patterns of rainfall, nutrient availability, fire and herbivory (Huntley & Walker 1982; Scholes & Walker 1993). Vegetation patterns in relation to these determinants have been studied, mainly at the local scale (e.g. Ben-Shahar 1998; Frost et al. 1985; Parker & Witkowski 1999; Ringrose & Matheson 1991; Skarpe 1991; Tothill & Mott 1985; Verlinden 1998 and references in Huntley & Walker 1982; Walker 1985; White 2000). Remote sensing techniques are commonly used for regional studies (Palmer & van Rooyen 1998; Ringrose et al. 1999a, 2000).

Although the sands are deep, and to the eye relatively homogeneous, Moore & Attwell (1999) provide evidence from the central Kalahari that the particle size distribution in the sand fraction (which makes up in excess of 96% of the soil mass) shows subtle regional variation. The variation may be related to the depth to the underlying hard geology, and is reflected in patterns of woody plant composition at the local scale.

O'Brien (1993) determined pattern of woody plant diversity over southern Africa, including the central and southern Kalahari region. She found a strong positive relationship between moisture (mean annual rainfall) and diversity in the region as a whole with a weaker but

Table 1. Broad floristic and structural vegetation types occurring on deep sands in the Kalahari, based on published descriptions. Shrublands are defined as having a tree cover (> 2.5 m tall) less than 5% but a cover by woody plants shorter than 2.5 m occupying more than 10% of the area; savannas as having a cover by trees greater than 10% but less than 33%, and woodlands by having a tree cover greater than 33% but less than 66%. 'Broad-leaved' refers to the leaves or leaflets of the dominant woody species being larger than about 20 mm (major axis); fine-leaved is smaller than 20 mm, and usually less than 2 mm. Deciduous means that > 90% of all tree and shrub leaves are lost for at least three months, evergreen means that > 80% of tree leaf is retained year round, and semi-deciduous is in between. T = tree; S = shrub; G = grass.

Structural type	Floristic subtype	Characteristic species
Grassy shrubland	<i>Rhigozum</i>	T: <i>Boscia albitrunca</i> , <i>Acacia erioloba</i> S: <i>Rhigozum trichotomum</i> , <i>Acacia haematoxylon</i> G: <i>Stipagrostis uniplumis</i> , <i>S. ciliaris</i> ,
Fine-leaved savanna	<i>Acacia</i>	T: <i>Acacia mellifera</i> , <i>A. luedertzii</i> , <i>A. erioloba</i> , <i>Terminalia sericea</i> S: <i>Grewia flava</i> , <i>G. flavescens</i> G: <i>Schmidtia kalahariensis</i> , <i>Eragrostis lehmaniana</i>
Mixed fine-and broad-leaved savanna	<i>Acacia</i> / <i>Combretum</i>	T: <i>Acacia mellifera</i> , <i>A. luedertzii</i> , <i>A. erioloba</i> , <i>Combretum collinum</i> <i>C. hereroense</i> , <i>C. imberbe</i>
Broad-leaved deciduous woodland	Mopane Kalahari	T: <i>Colophospermum mopane</i> T: <i>Pterocarpus angolensis</i> , <i>Schinziophyton rautanenii</i> , <i>Guibourtia coleosperma</i> , <i>Burkea africana</i>
Broad-leaved semi-deciduous woodland	Miombo	T: <i>Brachyegia spiciformis</i>
Broad-leaved evergreen woodland	Baikiaea	T: <i>Baikiaea plurijuga</i>
Broad-leaved evergreen woodland	<i>Cryptosepalum</i>	T: <i>Cryptosepalum exfoliatum</i> (= <i>pseudotaxus</i>)
Disturbed lands	'Piospheres' Fields Old fields	Thickets of <i>Dichrostachys cinerea</i> , <i>Acacia mellifera</i> , or bare Millet, sorghum < 600 mm MAP; maize, cassava > 600 mm MAP <i>Terminalia sericea</i> and/or <i>Dicrostachys cinerea</i>

still positive relationship in the Kalahari region. Sekhwela et al. (2000) reported structural attributes (stem density, heights and biomass) of woody vegetation at two contrasting sites in Botswana. Ringrose et al. (1998) presented data from 57 sites spanning the Botswana portion of the Kalahari, including estimates of woody, live and dead herbaceous and litter cover as well as soil organic carbon. These variables show a weak positive relationship with MAP.

Only a small part of the Kalahari has been transformed by humans through crop agriculture or settlement; nonetheless human action has been an important determinant of vegetation structure (Skarpe 1990). People are the main igniters of fires, and probably have been for millennia. Most of the valuable timber species in the northern woodlands have been heavily logged. There is increasing grazing pressure in the centre and south as cattle replace migratory wildlife, following the introduction of fences and boreholes.

Methods

Sites

The sites were selected to be on deep sand (with the exception of Okwa River, which was sand underlain at some metres depth by calcrete, and possibly Maun, which may have a finer-textured impervious layer at ca. 2 m depth). They were chosen, using high-resolution satellite images, to be representative of a large surrounding area. They showed varying degrees of disturbance due to tree cutting and grazing, but none was very highly transformed, since they were all several kilometres from the nearest significant human settlement or major road. The sites were distributed as evenly as possible across a rainfall gradient from 200 to 1000 mm.yr⁻¹, taking into account the difficulty of access to much of the area (Table 2).

Survey methods

Six sites were visited in 1995 and 1997 (Vastrap, Sandveld, Sechinga, Maziba, Liangati, Lishuwa). One representative plot several ha in size was sampled at each site except at Vastrap, where three plots were used to capture variation in the landscape: a dune, a freely draining 'red' interdune and a 'white' interdune with a subsurface calcrete layer. Litter mass was sampled at the 1995-1997 sites using a 0.25-m² quadrat with a minimum of 40 samples at each site. At these sites the sub-canopy shrub layer was sampled only if it was a substantial component of the vegetation.

'Shrubs', defined as long-lived (> 2 yr) woody plants

less than 2.5 m tall and typically multi-stemmed at the base, include many small individuals of the species forming the tree layer. The shrub category is included because basal area is an inefficient way of measuring multi-stemmed plants. There are typically thousands of stems per ha, but each is less than 2 cm in diameter; therefore the total contribution to the basal area is less than 1 m².ha⁻¹. The shrub contribution to canopy cover, on the other hand, can be up to 25%. Sampling techniques for the shrub layer were selected on a site-by-site basis. Generally, all plants excluding forbs and grasses within a specific height range were included in this sampling (including tree seedlings or saplings). To estimate shrub basal area and density, the T-square technique (Besag & Gleaves 1973; Diggle 1977) was used at 100 sample points at Lishuwa (0.5-1.5 m layer), Liangati (0-1.5 m), Maziba (0.5-1.5 m), and Sachinga (0-0.5 m). Conditioned distance sampling (Cox 1976) was used at the white interdune sample plot at Vastrap (0-1.5 m).

The other five sites (Kataba, Pandamatenga, Maun, Okwa & Tsane) were visited in February 2000. On these sites, tree basal area and height were measured in 42 circular quadrats (whose radius varied from 4 to 8 m, depending on the density of the vegetation), distributed in a 6 × 7 grid over an area of 250 m × 300 m. These are referred to as the landscape-scale sites. Tree height was estimated using a clinometer. Tree cover in the same area was estimated by summing the length of line segments with crown overhead on a line transect 1200 m long, and shrub cover using 300 m of line intercept. Herbaceous species composition was determined using the dry-weight-rank technique. Simultaneous measurements of leaf area index, leaf photosynthesis and spectral properties are reported elsewhere (J.L. Privette et al. pers. comm.; R.J. Scholes et al. pers. comm.).

At every site except Okwa River, detailed stem maps were constructed of the woody vegetation within a smaller intensive sample plot nested within the larger landscape-scale sample site.

Climate

The general climate patterns over the Kalahari region are well documented (Tyson 1986; Tyson & Crimp 1998). Meteorological stations are far apart in this region and it is often not possible to obtain detailed data for a particular site. The meteorological stations used in this study are shown in Fig. 1. Of the 11 sites in this study, only three are within 20 km of a rainfall recording station and four are more than 60 km to the nearest station. An inverse-distance weighted average was used to estimate mean annual rainfall at some of the stations (indicated in Table 2).

The seasonal patterns of rainfall, vapour pressure

Table 2. The location of field sites described in detail in this paper and the meteorological stations used to represent the climate at each site. For some sites without a nearby site, an inverse distance weighted average was used to estimate mean annual rainfall.

Site	Latitude	Longitude	Vegetation type (Dominant genera)	MAP (mm)	Meteo stations used	Data record used	Distance to site (km)	MAP (mm)
Lishuwa Communal Forest Lukulu, Zambia	14.42 S	23.52 E	Evergreen woodland (<i>Cryptosepalum</i>)	970	Mongu	1951-95	93	936
					Kaoma	1953-95	103	917
					Zambezi	1955-94	131	1048
					Kabompo	1961-92	138	1007
Kataba Forest Reserve Mongu, Zambia	15.44 S	23.25 E	<i>Miombo</i> woodland (<i>Brachystegia</i>)	879	Mongu	1951-95	36	936
Liangati Forest Reserve Senanga, Zambia	15.86 S	23.34 E	<i>Miombo</i> woodland (<i>Brachystegia</i>)	811	Senanga	1953-95	28	764
					Mongu	1951-95	74	936
Maziba Bay Forest Sioma, Zambia	16.75 S	23.61 E	<i>Miombo</i> woodland (<i>Brachystegia</i>)	737	Senanga	1953-95	78	764
					Sesheke	1950-94	85	707
Sachinga Agricultural Station Katima Mulilo, Namibia	17.70 S	24.08 E	Woodland (<i>Combretum</i>)	707	Sesheke	1950-94	48	707
Pandamatenga Agricultural Station Pandamatenga, Botswana	18.66 S	25.50 E	Woodland (<i>Schinziophyton</i> , <i>Baikiaea</i>)	698	Kasane	1922-87	100	667
					Victoria Falls	1904-89	72	693
					Livingstone	1904-88	99	735
Harry Oppenheimer Okavango Research Centre, Maun, Botswana	19.93 S	23.59 E	Woodland (<i>Colophospermum</i>)	460	Maun	1922-87	20	460
Sandveld Research Station Gobabis, Namibia	22.02 S	19.17 E	Wooded grassland (<i>Terminalia</i>)	409	Sandveld Res Stn	1970-96	1	409
Okwa River Crossing Trans-Kgalagadi Hwy (post 460) TshaneTshane, Botswana	22.41 S	21.71 E	Shrubland (<i>Acacia</i>)	407	Ghanzi	1922-87	79	426
					Tshane	1959-80	180	365
Vastrap Weapons Range Upington, South Africa	27.75 S	21.42 E	Shrubland (<i>Acacia</i>)	216	Altimet Farm	1973-95	5	232
					Upington	1978-95	60	151

and minimum and maximum temperatures are shown in Fig. 1 for three stations spanning the north-south range of the field sites. The dry season between May and September is associated with depressed vapour pressure and cooler temperatures. The southernmost field site, Vastrap, records some winter rainfall in association with mid-latitude disturbances. The seasonal variation in temperature is strongest in the south, weakening towards the equator.

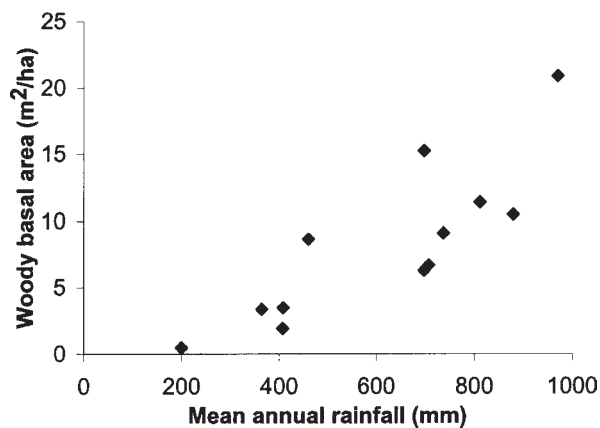


Fig. 2. The relationship between mean annual rainfall and woody plant basal area.

Results

The rainfall information for each of the sites is given in Table 2. The trend of increased aridity with increasing latitude is clear. There is a parallel trend of decreasing mean annual temperature, due to progressively colder winters, but the mean temperature during the summer (moist, growing season) varies much less, and is in fact higher in the south than the north.

The basal area of live woody plants per site is given in Table 3, and its relationship to MAP is illustrated in Fig. 2. Basal area correlates well with tree leaf area and biomass in the Kalahari (R.J. Scholes et al. pers. comm.), and by inference, with woody productivity. ‘Woody plants’ in this case are taken to include all lignified, long-lived species, regardless of height. At the moist end of the gradient, they are almost entirely ‘trees’ (i.e. > 2.5 m tall), but at the arid end, the category includes many individuals that never reach this height, even when mature. The overall trend is for the woody biomass, basal area, cover and height to increase with increasing availability of water to the plants. The relationship between rainfall and the mean height of the tallest 10% of trees is shown in Fig. 3. There is a trend in towards greater woody plant species richness and equitability with increasing rainfall, in agreement with O’Brien (1993). Fig. 4 shows the increase in the number of

Table 3. Woody plant basal area, canopy cover, and mean grass and litter mass for the study sites. The uncertainty range is one standard error. At some sites, open and under canopy areas were stratified and sampled separately. These were combined into a mean site value in proportion to canopy cover. In the sites without a basal area standard error value the basal area was only determined from a total count within a stem-mapped plot, the size of which is given in the table. In the other sites the basal area was determined by the circular pot technique as well; the basal area within the nested mapped stem plot is given in parentheses. Canopy cover results based on line intercept except at Vastrap, where cover was estimated from the stem map canopy spread data. Grass biomass was only collected at the 1995-1997 sites, which were samples at the end of an average rainy season. The February 2000 sites were visited during a mid-season drought.

Site	Basal area (m ² ha ⁻¹)	Stem map canopy plot size (ha)	Cover mean biomass (%)	Grass (g.m ⁻²)	Mean litter mass (g.m ⁻²)
Lishuwa	20.9	0.25	84.4 ± 2.6	54 ± 8	1412 ± 93
Kataba	8.5 (10.5) ± 1.1	0.25	64.8 ± 4.7	-	-
Liangati	11.4	0.5	53.7 ± 3.5	122 ± 8	685 ± 48
Maziba Bay	9.1	1.0	61.0 ± 3.0	90 ± 8	327 ± 35
Sachinga	6.7	1.0	29.9 ± 3.0	235 ± 24	117 ± 23
Pandamatenga ¹	6.3	0.5	32.3 ± 2.3	-	-
Maun	8.7 (10.1) ± 1.2	0.25	36.1 ± 5.4	-	-
Sandveld	3.5	1.0	19.1 ± 5.5	151 ± 17	86 ± 20
Okwa River	1.93 ± 0.4	n/a	32.1	-	-
Tshane	5.3 (3.4) ± 1.1	1.0	13.8 ± 3.7	-	-
Vastrap – red interdune	0.6	1.0	5.8 ±	80 ± 4	-
Vastrap – white interdune	0.0	-	-	420 ± 37	-
Vastrap – dune	0.13	1.5	2.2 ±	89 ± 5	-

¹Pandamatenga site is a mosaic of woodland and closed-canopy groves of *Schinziophyton rautanenii*. The total 'landscape' level basal area is 15.2 m²ha⁻¹. The value in the table is for the woodland parts only.

woody species making up 95% of the woody basal area at a site with increase in rainfall; the species are tabulated in App. 1. The total woody species richness is typically two to three times the number of species that make up 95% of the site basal area.

On sandy substrates between 200 and 400 mm.yr⁻¹ the woody cover and basal area is more than 95% dominated by the *Mimosaceae*; particularly *Acacia*, but also *Dichrostachys*, *Albizia* and other genera (Fig. 5). Above 600 mm, the family *Caesalpinaceae* (and particularly one tribe, the *Dialeumae*) constitute around 80% of the basal area. Between 400 and 600 mm.yr⁻¹ two separate patterns appear. On soils that are free-

draining or rocky, the *Combretaceae* (*Terminalia* and *Combretum*) make up about half of the basal area. Soils with an impeded layer (often sodic or calcareous) within the rooting zone are 90% dominated by *Colophospermum mopane*, an ecologically and morphologically atypical member of the *Caesalpinaceae*. The *Colophospermum mopane* woodlands woodlands in northern Botswana mostly occupy the floor of a former inland lake, of which the Makgadigadi saline depression is the last remnant. Elsewhere, they occupy clayey, alkaline soils derived either from Triassic shales and mudstones, in the valleys of the Zambezi, Limpopo and Cunene rivers and their major tributaries, or from Jurassic basalts.

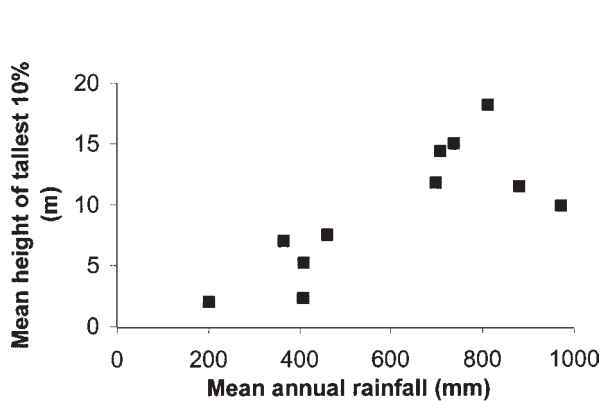


Fig. 3. The relationship between the mean height of the tallest 10% of trees and mean annual precipitation.

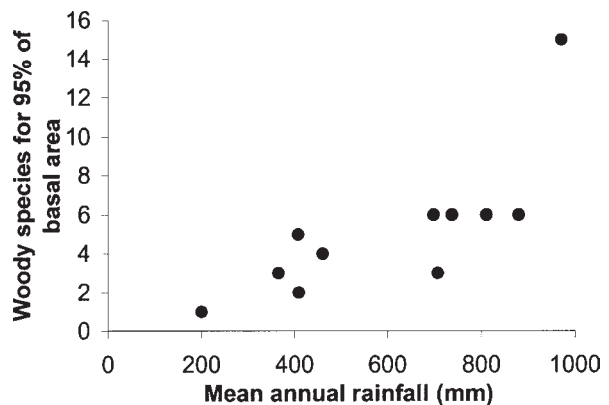


Fig. 4. The number of woody species which contribute 95% of the site basal area, as a function of mean annual rainfall.

The increase in woody cover is associated with a decrease in the relative importance of grasses as contributors to the site biomass (and presumably to the site productivity). The absolute grass biomass (Table 3) increases with increasing rainfall up to ca. 600 mm, and then decreases under the increased competition from woody plants at higher rainfall levels. The species and genera contributing to this biomass are listed in App. 2. Identification to species level was impossible at some sites due to the time of year at which sampling occurred.

Discussion

The fraction of the woody vegetation of these well-drained sands that is evergreen is broadly associated with increasing rainfall. Even in the wetter north there is a distinct dry season lasting several months. It has been suggested that the semi-deciduous (*Baikaea plurijuga*) and evergreen species (*Cryptosepalum pseudotaxus*) must have access to sub-surface water. The water table in the southern and central parts of the Kalahari is generally 100 m or more below the surface, which is thought to be out of reach of all species, even the exceptionally deep-rooted Kalahari trees (Jennings 1974). We believe that an accessible water table (possibly 'perched' i.e. held above the 'true' water table by a lens of less-permeable material) at a depth of less than 20-m controls the very distinct distribution of evergreen woodlands in more northern parts of the Kalahari.

In the northerly sites – Lishuwa, Kataba and Liangati – circular pans (seasonally flooded depressions) are often found situated on the interfluves. Many of these retain water for extended periods during the dry season. Likewise, perennial seep zones are found alongside drainage lines bisecting these woodlands. The drainage lines and seeps are seldom more than 50 m lower in elevation than the interfluve crests. This suggests that not all the water is draining down to the regional water table. If the trees have access to groundwater for much of the dry season, as appears to be the case in these northern sites, and in the absence of any marked temperature constraint (also a feature of the northern sites), then they would have an effective growing season longer than that indicated by the length of the wet season and annual rainfall alone, and thus should sustain a higher biomass, other things being equal. This hypothesis is supported by the curvilinear relationship between basal area ($\text{m}^2 \cdot \text{ha}^{-1}$) and rainfall (mm):

$$\text{BA} = 2 \times 10^7 \text{MAP}^{2.711}; \quad r = 0.890 \quad (1)$$

The curvilinear relationship accounts for a marginally greater percent of total variance (79.2%) than does a

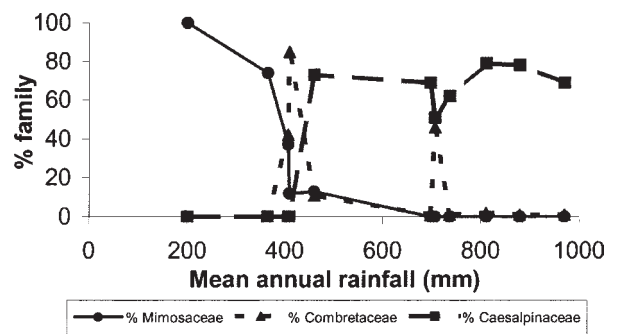


Fig. 5. The percentage of the site basal area occupied by members of three diagnostic plant families in African savannas.

linear relationship (71.3%).

The pattern of dominance of the woody plants by selected families supports the broad pattern which has been proposed for southern African savannas – for instance, in Scholes (1999), building on earlier work e.g. Bell (1982). This pattern has many functional and environmental correlates, including plant defence strategy (thorns in the arid areas, tannins in the moist infertile areas), leaf nitrogen (higher in drier areas), and leaf size (smaller in drier areas) (Scholes 1999). The increasing richness of the tree biota with increasing moisture is confounded with a number of other effects. The northern sites are closer to the equator, where tree richness is generally higher. They are also located on, or adjacent to, extremely old land forms (the Africa Surface), which have accumulated species over hundreds of millions of years. The *Caesalpinaceae* (and especially the tribe *Dialeumae*) are characteristic of this land form and would appear to be the more ancient of the legumes, not having the capacity to fix nitrogen. The *Mimosaceae*, which at least potentially can fix nitrogen, evolved more recently into the hotter, drier environments which developed after the break-up of Gondwanaland, ca. 150 Myr ago. The predominance of tiny, bipinnately compound leaves in the *Mimosaceae* is assumed to be related to the aridity and high temperatures of their core habitat.

The general floristic pattern among the grass genera supports the trends outlined in Tohill & Mott (1985) for tropical grasslands worldwide. The *Aristididae* (*Aristida* and *Stipagrostis*) dominate in the arid south, the *Panicoidae* in the semi-arid centre (*Panicum*, *Digitaria*, *Bracharia*) and the *Andropogonae* (*Hypharrhenia*, *Heteropogon*) in the moist north. This pattern has many functional correlates: in the south the grasses tend to produce large numbers of very small seeds, distributed by wind or animals, while in the north smaller numbers of larger seeds, often bird-distributed, are produced (Ellery 1992). There are also correlates with the photo-

synthetic enzyme system. The NAD-me form of C₄ photosynthesis dominates at the arid end while the NADP-me pathway dominates in more mesic areas (Ellis et al. 1980), and with leaf nitrogen dynamics (although the latter was not measured in this study). In southern African rangeland terms, the arid regions would be 'sweetveld' (i.e. having sufficient leaf protein to be digestible throughout the year), while the moist areas would be 'sourveld', dropping below the digestion threshold for most of the dry season (Ellery et al. 1995). Sourveld supports a much lower biomass of large mammalian grazers than does sweetveld; as a result the predominant zone of savanna fires in southern Africa is located there. The grass is not eaten by grazers, so it burns, assisted by pastoralists desiring to stimulate the regrowth of more digestible green shoots.

The transition between the fine-leaved, *Mimosaceae*-dominated savannas of the arid areas and the broad-leaved, *Cesalpiniaceae*-dominated woodlands in wetter areas has analogues in West Africa and northern Australia, and perhaps in the savannas of North and South America. In West Africa the transition between the *Acacia*-dominated Sahelian zone and the *Isobertinia* and *Guibourtia* dominated Sudanian zone occurs above 500 mm MAP (White 1983). In northern Australia, the transition is from *Acacia* domination to *Myrtaceae* (*Eucalyptus*), and occurs around 500 mm MAP as well (Egan & Williams 1996; Williams et al. 1996). In this case, the *Acacia* has generally replaced its fine, bipinnate leaf form with cladodes, at least in mature individuals. The abruptness of the transition in southern Africa, despite the gradual climate gradient, led Scholes (1990) to speculate that a feedback mechanism must be operating. Current thinking is that the feedback involves phosphorus, nitrogen and fire (Scholes 1999): the ancient surfaces have insufficient phosphorus to support biological nitrogen fixation, hence they cannot be intensively grazed due to indigestibility in the dry season, and therefore they burn more frequently, thus perpetuating the nitrogen deficiency. In the Kalahari, with its homogeneous substrate, the primary phosphorus supply is probably quite similar from north to south, but relative to plant needs, it is higher in the south. This hypothesis remains to be rigorously tested.

Shrub cover and relative importance in the Kalahari are apparently controlled by two inversely correlated factors: aridity and fire. With increasing aridity, the stature of woody plants decreases, to the point where below ca. 300 mm most are shorter than the arbitrary 2.5 m threshold used here to distinguish trees from shrubs. Many of the shrubs encountered in the moister areas are the coppice forms of woody plants that could reach tree height, but are prevented from doing so by fire and cutting. Since fire and cutting are more frequent at the

moister end of the gradient, and drought-stunting dominates at the dry end, the absolute cover by shrubs shows no overall trend in relation to rainfall.

There are thus two opposing trends: grass production increases with increasing rainfall, but so does tree canopy cover and height, which suppresses grass production. Since fire intensity increases with the dry season standing crop of grass, and damage to woody plants is a positive function of fire intensity, fire damage increases with increasing grass production. The impact of fire is expected to be greatest in the intermediate area of the rainfall gradient (ca. 550-750 mm). The exception is where people have removed the trees from more mesic woodlands, but not converted them to agricultural land. Shrub dynamics become important in this case (known as *chipya*). If shrubs establish in sufficient density when the trees are removed, they will still be able to suppress grass production, though they themselves also form a distinct component of the fuel load, and suppress the emergence of a tree canopy.

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