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Vegetation cover trends along the Botswana Kalahari transect

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Vegetative response aspects of climate change studies include the determination of vegetation cover changes across climatic gradients. Vegetation characteristics and soil moisture measurements were obtained from four locations with decreasing rainfall along the Botswana Kalahari transect. These are referred to as Pandamatenga, (698 mm year^{-1}), Maun (460 mm year^{-1}), Okwa (407 mm year^{-1}) and Tshane (365 mm year^{-1}). Trends in major vegetative cover and soil components included species types and richness assessments which reflected certain changes southward but also showed interesting degrees of variability. This occurred despite the apparent homogeneity of the Kalahari sands and predominantly semi-arid savanna shrub–woodland vegetation cover. Despite linear decreases, both in rainfall and soil moisture content, results indicated high soil moisture variability at the Okwa location which relates to unique climatic and geological factors. Also many species are unique to specific locations for instance Pandametanga is characterized by Zambesian species while the Maun location is characterized by *Colophospermum mopane*. This changes southwards as Acacias become more dominant and significantly co-occur with *Grewia flava*. While the average total numbers of plants decreased, total numbers of different species varied little from the wetter to the drier end of the moisture gradient. The association between rainfall and woody cover is negative implying that canopy cover extents (in terms of vegetation density) increase along the gradient due to increases in bush encroachment in drier areas. Therefore, while representing a continuum in terms of species numbers, in other respects (e.g. species types and ground cover components) vegetation zones in the Kalahari may be regarded as discontinuous units. Differences between mapped vegetation zones may be accounted for in terms of relatively unique ecosystem factors which function partly in response to geological conditions and partly in response to local (as opposed to regional) climatic factors. This appears to have led to ecosystem adaptive measures (in terms of species responses) rarely mirrored elsewhere along the gradient. Hence adaptability in terms of species migrations in response to relatively rapid climate changes may not readily take place over the Kalahari in Botswana.

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Introduction

Significant aspects of climate change studies include the determination of vegetation cover changes across climatic gradients so that responses in space can be substituted to some extent for responses in time (Steffen, 2000). This presupposes that field sites of a given size, chosen along the gradient and across known vegetation belts are representative of a gradual change in conditions and that underlying edaphic factors are constant (e.g. Scholes & Walker, 1993; Scholes & Parsons, 1997). However, this may be tenuous in such areas as the Kalahari as ecological adaptive factors may differ and contribute to the uniqueness of different ecosystems (e.g. Lewis *et al.*, 2000). For instance, the northern third of the Botswana Kalahari belongs to the Zambesian regional centre of endemism hence in terms of overall structure and function has greater affinity for areas further north (White, 1983). The southern two-thirds form part of the Kalahari–Highveld regional transition zone which extends through South Africa and Namibia (White, 1983). Varying degrees of disturbance and local climatic factors are also important (Ringrose *et al.*, 1996, 1999*c*; Chapinii *et al.*, 2000) with sometimes detrimental economic effects (Washington-Allen *et al.*, 1998). Degrees of landscape heterogeneity across vegetation zones may be also particularly significant with respect to the determination of sources and sinks of carbon critical to climate change impact analysis (Graves & Reavey, 1996; Potter, 2000).

Assessments of global change and their impacts are a major goal in the SAFARI2000 project which is presently underway in southern Africa (www.safari.gecp.virginia.edu). The SAFARI2000 project's ground-based activities were undertaken partly along the Botswana Kalahari transect (BKT). Climate change in Botswana has been predicted using a number of global change models (GCMs) of which a drying scenario under UKTRANS appears the most appropriate (Hulme, 1996). Vegetative responses, including the southward migration of the main vegetation belts have been predicted using the BIOME model (Leemans in Hulme, 1996; Chipanshi & Ringrose, 2001). Global change studies in Botswana have indicated that most measurable change in the south-central Kalahari occurs in the form of localized bush encroachment (Ringrose *et al.*, 1996, 1999*a*), most likely in response to human induced disturbances (cf. Campbell & Stafford Smith, 2000) although regional change is also apparent (Vanderpost *et al.*, 1998; Skarpe, 1990). If increased levels of CO_2 can be said to stimulate plant production even over the short term, then levels of heterogeneity may be increasing in Kalahari soils because of variable changes in soil carbon (Graves & Reavey, 1996; Ringrose *et al.*, 1998*a*). A major control in the degree of heterogeneity stems from land-use or land management changes (e.g. Trodd & Doughill, 1998). For instance increases in *Acacia* species or woody weed dominated areas as a result of cattle post establishment have already been recognized in south central Botswana particularly around settlements and cattle posts (Ringrose & Matheson, 1987; Ringrose *et al.*, 1996; Moleele, 1998; Moleele *et al.*, 2001).

The objectives of the research reported here from the four Botswana SAFARI2000 field locations are as follows:

- To provide a characterization of soils, species composition and vegetation cover types along the BKT.
- To assess the relative degree of spatial continuity across the main vegetation zones.
- To determine trends in species and vegetation cover types along the BKT for climate change studies.

Study area

The study area focuses on the 1000 km south-west to north-east transect across Botswana within which specific site data are drawn from four locations, referred to as Pandamatenga, Maun, Okwa Valley and Tshane (Fig. 1). The BKT in total extends from semi-arid-arid to semi-arid-subtropical vegetation zones along the main isohyets. Rainfall along the gradient varies from less than 200 mm in the south-west (CV = 45%) to over 650 mm in the north-east (CV = 35%) and occurs during the summer months (October–March). Much of the rainfall is localized in extent with frequent droughts (Bhalotra, 1987). Potential evapotranspiration rates vary from $>2000\,\mathrm{mm\,year^{-1}}$ in the south-west to between 1000–1500 $\mathrm{mm\,year^{-1}}$ in the north-east (Hulme, 1996).

Previously mapped vegetation communities along the line of the transect are characterized by arid shrub savanna in the south-west (Table 1). This zone is divided into more southerly arid shrub savanna, southern Kalahari bush savanna and more northerly central Kalahari bush savanna. Further north, tree savanna predominates and is referred to as the northern Kalahari tree and bush savanna. This extends northwards into the broadleaf mopane belt which merges northeastwards into the dry deciduous Chobe Forest area (Weare & Yalala, 1971; Soil Mapping and Advisory Services Project, 1991). Land uses vary from mixed wildlife with smallstock grazing in the south, to more intensive cattle grazing and browsing in the centre to mainly commercial farming and wildlife in the north. Fires are known to be widespread, especially in a dry season following heavy rains when the fuel load is high. Kalahari soils along the BKT comprise arenosols mapped by the Soil Survey and Advisory Services Project (1990) at 1:1,000,000 and 1:2,50,000. The arenosols are characterized by high fine sand percents (average 62%) in both surface and lower horizons. Organic carbon percentages vary (on average) from 0·20% in upper horizons to 0·08% in the subsoil (Joshua, 1981). The sandy soils have an average infiltration rate of $33\,\mathrm{cm\,hr^{-1}}$ (ranging from 54·3 to $18{\cdot}5\,\mathrm{cm\,h^{-1}}$) a porosity of around 40% and available moisture content of between 5% and 10% by volume. Much of the soil moisture is retained at a depth of 3–8 m which is beyond the immediate depth of loss by evaporation. The prevalence of this moisture horizon is believed to sustain moderately deep rooting trees and shrubs (Macvicar & Eloff, 1980) with only occasional deep rooting trees tapping ground-water levels (Ringrose *et al.*, 1998*b*; Moore & Attwell, 1999).

Methodology

Fieldwork took place in the wet season (March, 2000) based at four locations regarded as being representative of four typical vegetation zones (Table 1). Specific locations were based on access, perceived typicalness and being relatively undisturbed (e.g. Walker & Menaut, 1991). Twelve individual sites based on differences in topography, soils and known disturbance, were chosen based on random stratified techniques within a 30 km radius at each location to help determine local variability (*cf.* Huennecke *et al.*, 2001). Each site was located using a Garmin 75 Global Positioning System The same information (e.g. Ringrose *et al.*, 1996, 1998*b*) was collected from all sites and comprised:

- The identification of all species along $3 \times 90\,\mathrm{m}^2$ transects, ranged at 45 m apart.
- Visual estimation (tape measure and pacing) of canopy diameter along all $3 \times 90\,\mathrm{m}^2$ transects.

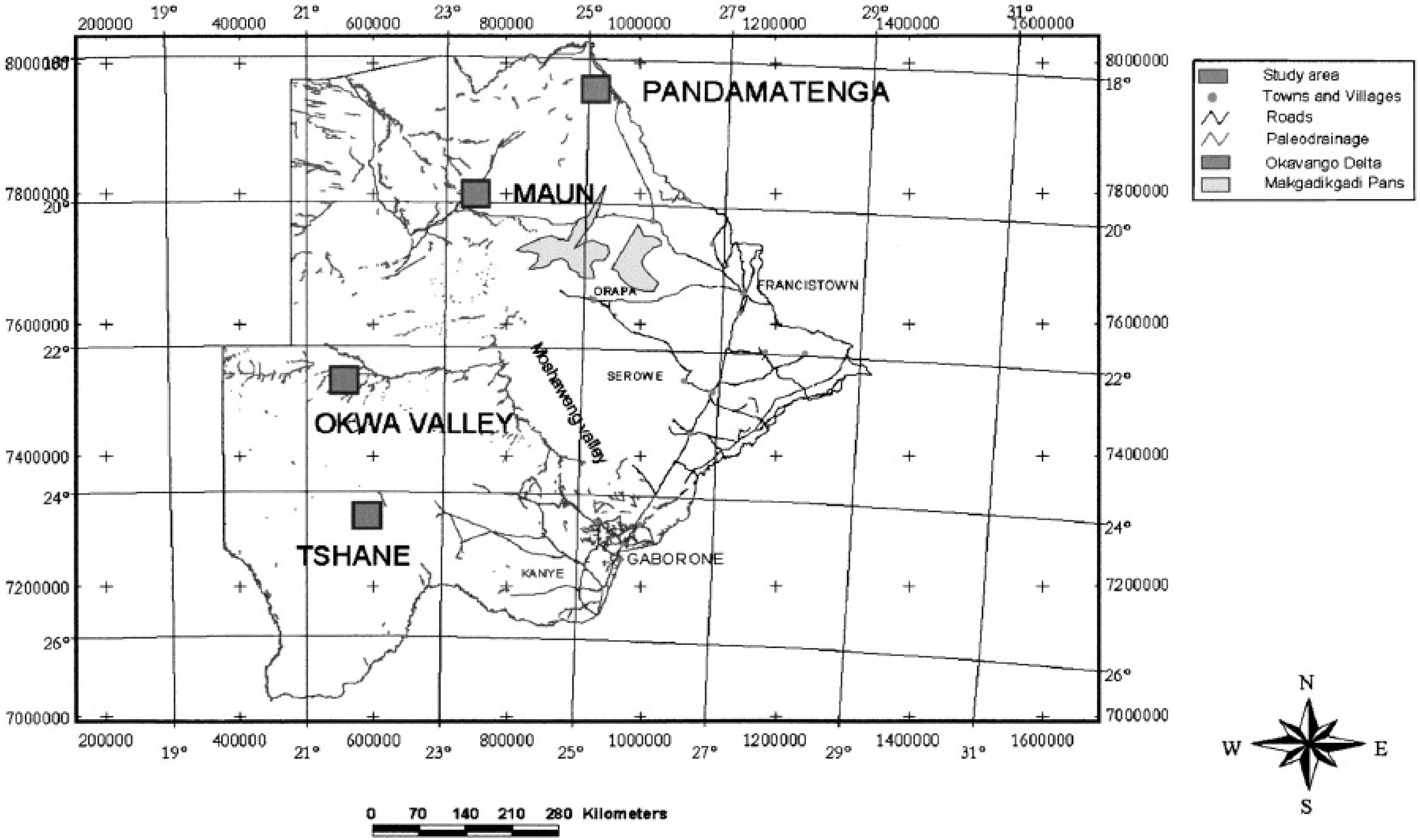


Figure 1. Approximate location of the Botswana Kalahari transect field locations in Botswana.

Table 1. *Main vegetation zones in Botswana and prevalent species (from field data Ringrose et al. 1998a; Weare & Yalala, 1971)*

Vegetation zone	Woody species	Herbaceous species
Pandmatenga Chobe dry deciduous forest	*Baikiaea plurijuga, Bauhinia spp., Schinzophton rautanenii, Pterocarpus angolensis, Burkea africana, Erythrophleum africanum, Lonchocarpus capassa, Terminalia sericea.*	*Schmidtia bulbosa, Aristidia uniplumis, A. meridionalis, Eragostis pallens, E. lehmanniana, Chloris virgata*
Maun Mopane woodlands	*Colophospermum mophane A. erubescens, Rhus tenuinervis, Ochna pulchra, Ximenia caffra, Commiphora spp.*	*Aristidia meridionalis, Eragostis pallens, Antephora pubescens,*
Okwa Central Kalahari bush savanna	*Acacia erioloba, A. mellifera, A. hebeclada, A. fleckii Terminalia sericea, Lonchocarpus nelsii, Boscia albitruna, Grewia flava, G. retinervis, Dichrostacys cinerea, Ziziphus mucronata*	*Aristidia uniplumis, Eragrostis latimanniana, Schmidtia bulbosa, Antephora pubescens, Aristida meridionalis*
Northern Kalahari tree and bush savanna	*Burkea africana, Pelphotorum africanum, Terminalia sericea, Croton spp., Lonchocarpus nelsii, Combretum spp. A. fleckii, A. luederitzii, A. mellifera, A. tortilis*	*Aristidia uniplumis, A. meridionalis, Eragostis pallens, E.superba, Antephora pubescens, Heteropogon contortus*
Tshane Southern Kalahari bush savanna	*Acacia erioloba, A. mellifera, A. hebeclada, Boscia albitruna, Grewia flava, G. retinervis, Dichrostacys cinerea, Ziziphus mucronata*	*Aristidia uniplumis, Eragrostis latimanniana, Schmidtia bulbosa, Antephora pubescens, Aristida meridionalis*

Table 2. *Field sites in terms of dominant landforms at the four BTK locations*

Location	Site number	Landform
Pandamatenga	1,3,6,7,8,9	Low dune slopes
	2,4,10,12	Low dune crests
	5,11	Swales adjacent to water
Maun	13,14,21,23	Centre of palaeo-islands
	19,20,24	Edgeof palaeo-islands
	16,17,18,22	Palaeo floodplains
Okwa	26,27,30	Valley slope
	28,31,32,34,36	Valley crest
	25,35	Valley floor
	29,33	Kalahari plateau
Tshane	39,40,41,42,43,44,45,46	Low dune crests
	37,47	Low dune slopes
	38,48	Pan margins

- Visual estimation of percent live and dead herbaceous cover, litter and bare soil using $3 \times 50\,\text{cm}^2$ quadrats spaced at 30 m intervals along each transect.

In addition to comprehensive species lists, vegetation components were calculated for each site comprising woody vegetation cover (WVC), green-alive herbaceous cover in terms of grass and forbs (AHC-grass/forbs), dead herbaceous cover (DHC), plant litter and bare soil. Species richness was calculated as the actual number of species per three transects ($270\,\text{m}^2$) at each site (Kent & Coker, 1996)

Augering of soil profiles to 1·5 m took place at four sites at each main location (Pandametanga, Maun, Okwa and Tshane). Soil moisture samples collected at 3, 50 and 120 cm in sealed cylindrical containers and bulk samples were also collected at 1·0 m for textural analysis. Bulk soil samples were subject to textural analysis using a nest of 12 sieves, shaken for 20 min and the contents weighed. The soil moisture samples were weighed, dried at 80° overnight and reweighed to obtain the volumetric moisture content. All statistical analyses were undertaken using Excel and SPSS, version 10.

Details of the topography were taken from browse IKONOS images made available to SAFARI2000 participants through NASA (Table 2). Vegetation data from 12 Pandametanga sites were obtained from a radius of 22 km from the main site (Fig. 2(a)). These sites comprised mainly *Baikiaea plurijuga* woodlands interspersed with mixed shrublands (Fig. 3(a)). A number of these sites occurred on washed dunes adjacent to former lacustrine plains (Thomas & Shaw, 1991). Topographically the Maun area, which lies to the south of the Okavango alluvial fan, is a former extension of the palaeo-fan which extended south-eastwards towards the Makgadigadi basin (Cooke & Verstappen, 1984; Ringrose *et al.*, 1999*b*). Much of this area comprises *Colophospermum mopane* woodlands and shrublands (Figs. 2(b) and 3(b)). The Okwa area lies along a dry valley which may owe its origin to higher rainfall during Tertiary times (e.g. Nash, 1997) with prevalent near surface calcrete (Ringrose *et al.*, 1999*c*). The area comprises dominantly shrubland interspersed with woodlands which become more prevalent southwards (Figs 2(c) and 3(c)). Topographically, the Tshane area is characterized by pan littoral zones and peripheral dune crests extending southwards to low aeolian dunes of the Kalahari plateau. In this area Acacia trees and shrubs are dominant (Figs 2(d) and 3(d)).

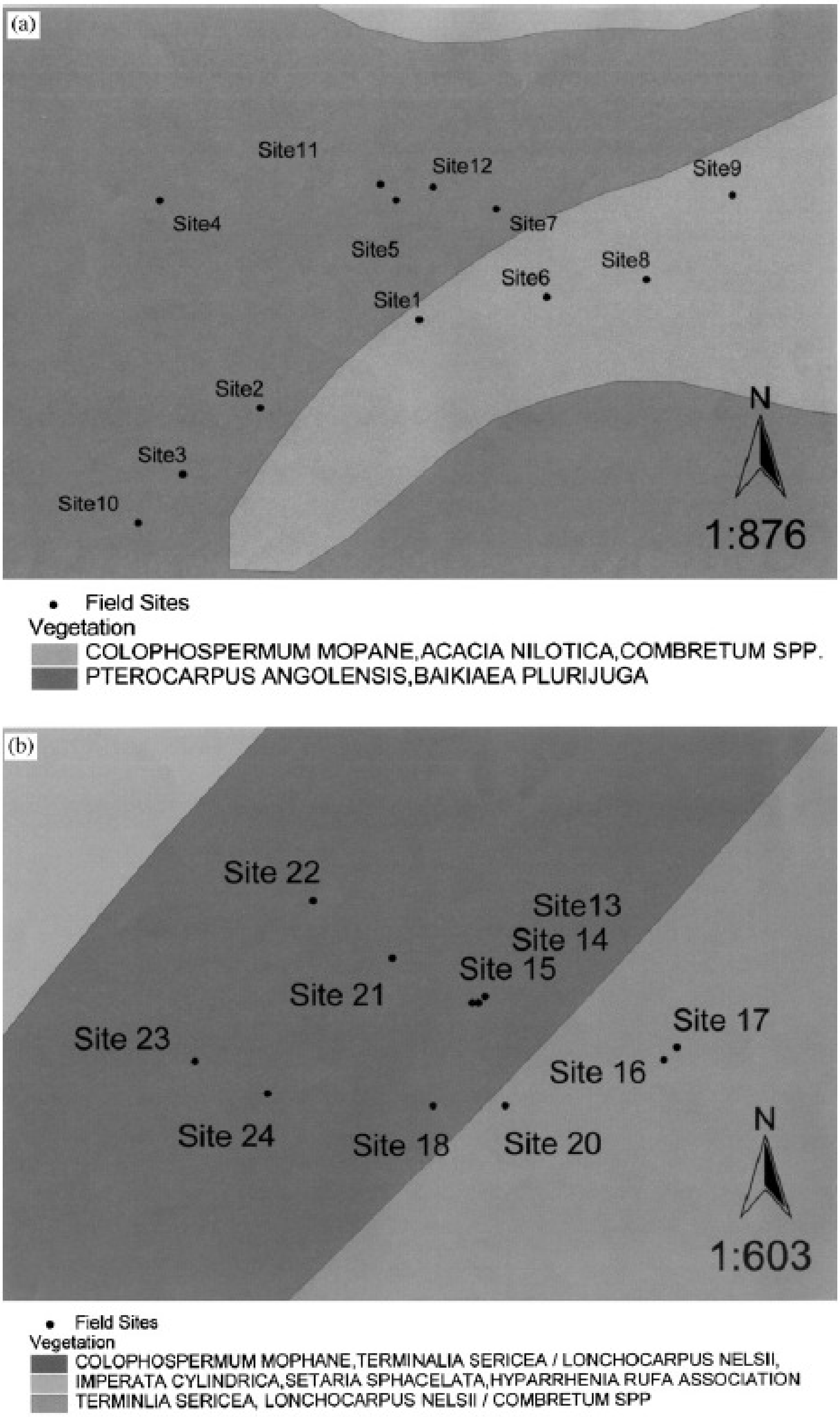
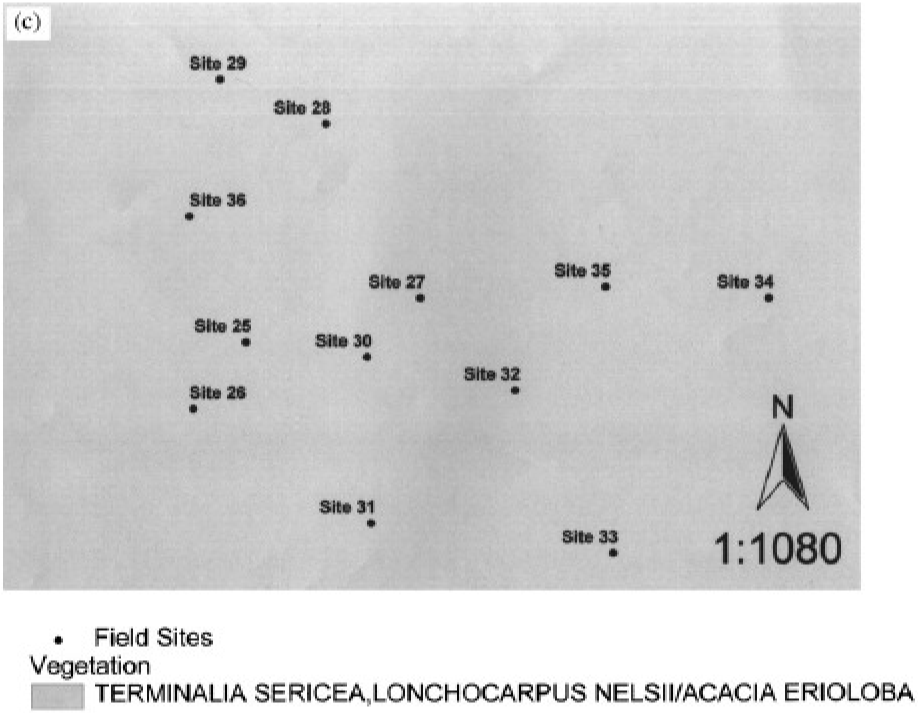


Figure 2. Detail of site locations along the Botswana Kalahari transect: (a) Pandametanga, (b) Maun, (c) Okwa and (d) Tshane (based on Soil Survey and Advisory Services map, 1991).



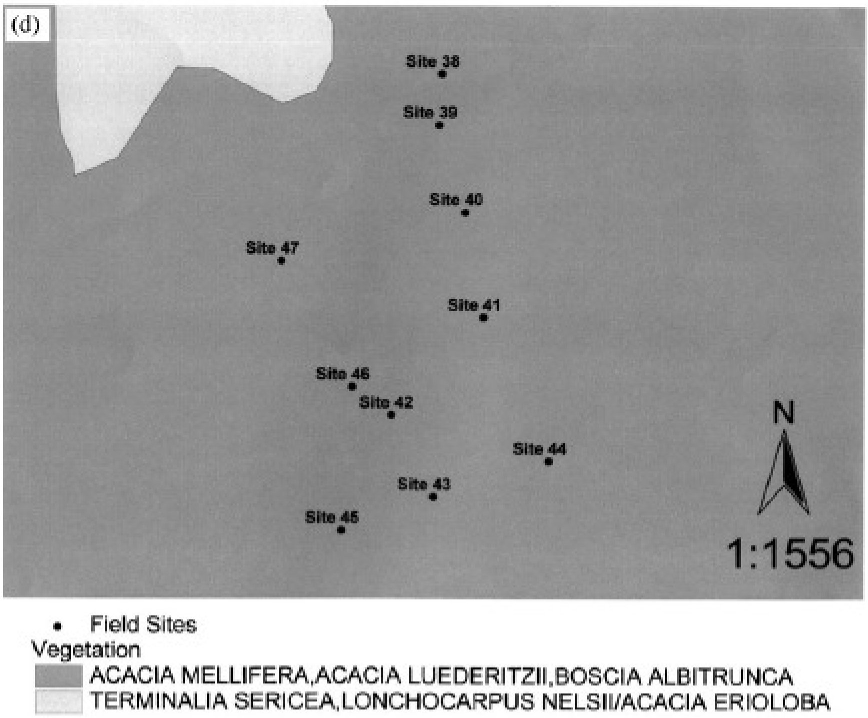


Figure 2—(*Continued*).

Results

Soil characteristics

The results of soil textural analysis revealed that samples taken from 1.0 m depth showed variable textural curves in the four locations. While all the samples are in the

Figure 3. Vegetation types at the four SAFARI2000 field locations: (a) Mixed Baikiea woodland at Pandametanga; (b) mopane woodland and shrubland at Maun; (c) open grassed shrubland at Okwa; (d) Acacia woodland and shrubland at Tshane.

sand size range, the Pandamatenga location comprised on average the coarsest sand with a modal value at 500 μm while sands from Maun, Okwa and Tshane have modal values at 180 μm (Table 3). The coarser nature of the Pandametanga sands may relate to the proximity of bedrock, while the remaining sands are deeper and more reworked

Figure 3—(*Continued*).

(*cf*. Ballieul, 1975; Thomas & Shaw, 1991; Moore & Atwell, 1999). While the results for Maun and Okwa are similar, the Okwa sands are slightly coarser. A measure of relative soil textural variability was taken as the standard deviation of the distribution or sorting (Folk, 1980). The results showed that most sorting was evident in the Pandametanga area and least in the Tshane area (Table 3). The results of soil moisture analysis also vary more along the moisture gradient. Total average vol% soil moisture

Table 3. *Locational data and summary soil statistics for BKT sites*

	Main site location	Average annual rainfall (mm year^{-1})	Soil texture-mode (μm)	Soil texture-standard deviation-(sorting)	Average soil moisture-wet season (vol%)	Soil moisture-standard deviation wet season
Pandamatenga	S 18.65956E025.49408	698	500	8·88	7·33	1·93
Maun	S 19.91311E 023.55992	460	180	6·83	4·21	2·54
Okwa	S 22.41323E 021.70887	407	180	7·98	5·00	3·12
Tshane	S 24.12690E 021.88083	365	180	6·38	1·89	0·83

from the Pandametanga sites was 7·33%, for Maun was 5·00%, for Okwa was 4·21% and for Tshane was 1·89%. Variability between the different main locations was calculated based on the standard deviation of all the soil moisture values. Results indicate most inherent soil moisture variability occurs in the Okwa area and least in the Tshane area (Table 3).

Vegetation species characteristics

Woody vegetation cover and forb species were recorded for all sites in addition to a listing of standing and recently fallen dead cover. In terms of canopy extent, the most extensive species in Pandametanga are *Schinziophyton rautanenii*, *Baikea plurijuga* and *Kirkia acuminata* trees. At Maun *Colophosphermum mopane* forms almost mono-specific stands along with less dominant Kalahari species, *Grewia flava* and *Terminalia* spp. This changes southwards at Okwa with *Grewia flava* and *Acacia mellifera* shrubs becoming most prevalent. At Tshane the *Acacia* species are most prevalent in tree and shrub species comprising mainly *Acacia mellifera* and *Acacia erioloba*. A listing of all species recorded and their frequencies is given as Table 4 for Pandametanga and Tshane and Table 5 for Okwa and Tshane. An assessment of the similarity or dissimilarity between species within the 12 sites at each of the four locations was

Table 4. *Species listings at the northern Pandametanga and Maun Kalahari transect locations*

Pandametanga species	Panda total	Maun species	Maun total
Baikiaea plurijuga	120	*Acacia arenaria*	1
Baphia spp.	564	*Acacia ataxacantha*	5
Bauhinia petersiana	320	*Acacia erioloba*	16
Brachystegia boehmii	61	*Acacia hebeclada*	1
Burkea africana	50	*Acacia fleckii*	20
Combretum molle	50	*Acacia luederitzii*	12
Commiphora africana	8	*Acacia mellifera*	2
Commiphora angolensis	1	*Acacia tortilis*	3
Commiphora mossambicensis	578	*Albizzia versicolor*	1
Croton gratissimus	15	*Asparagus sp.*	8
Diplorhynchus condylocarpon	291	*Bauhinia petersiana*	140
Erythrophleum africanum	31	*Boscia albitrunca*	11
Grewia monticola	114	*Catophractes alexandrii*	18
Kirkia acuminata	27	*Colophospermum mopane*	1018
Ochna pulchra	33	*Combretum albopunctatum*	19
Pseudolachnostylis maprouneifolia	4	*Combretum collinum*	40
Pterocarpus angolensis	1	*Combretum hereroense*	9
Rhus tenuinervis	8	*Commiphora africana*	45
Schinziophyton rautanenii	19	*Dichrostachys cineria*	78
Strynchos pungens	2	*Grewia bicolor*	21
Terminalia spp.	185	*Grewia flava*	152
		Grewia flavescens	2
		Lonchocarpus nelsii	41
		Rhus tenuinervis	12
		Solanum sp.	167
		Terminalia spp.	54
		Woody forb	92
		Ximenia americana	122

Table 5. *Species listings at the southern Okwa and Tshane Kalahari transect locations*

Okwa species	Okwa Total	Tshane species	Tshane total
Acacia erioloba	9	*Acacia erioloba*	51
Acacia fleckii	55	*Acacia hebeclada*	20
Acacia hebeclada	15	*Acacia luederitzii*	54
Acacia luederitzii	26	*Acacia mellifera*	193
Acacia mellifera	96	*Asparagus sp.*	5
Acacia nebrownii	154	*Boscia albitrunca*	47
Asparagus sp.	7	*Cadaba aphylla*	3
Bauhinia petersiana	114	*Dichrostachys cineria*	7
Boscia albitrunca	117	*Diospryos lyciodes*	6
Catophractes alexandrii	61	*Ehretia rigida*	6
Commiphora pyracanthoides	9	*Elephantorrhiza sp.*	359
Dichrostachys cineria	86	*Grewia flava*	261
Ehretia rigida	6	*Grewia retinervis*	1
Grewia flava	557	*Lycium cinerium*	35
Grewia retinervis	45	*Maytenus tenuispina*	9
Indigofera sp.	28	*Rhigozum brevispinosum*	58
Lonchocarpus nelsii	48	*Rhus tenuinervis*	39
Lycium sp.	2	*Terminalia spp.*	25
Rhigozum brevispinosum	225	*Solanum sp.*	256
Rhus tenuinervis	6	*Woody forb*	40
Solanum sp.	11		
Terminalia spp.	59		
Woody forb	29		
Ziziphus mucronata	1		

undertaken using Sorensen's functions (Kent & Coker, 1996). This resulted in low Ss values for all locations, specifically 15% for Pandametanga, 14% for Maun, 8% for Okwa and 17% for Tshane. This reflects the relatively high number of discrete species at all sites and infers low level of co-occurrence of species between the different sites.

An attempt was made to test the relationship between species at the main locations to determine whether there was any clear association between species (*cf*. Kent & Coker, 1996). The test was applied to those species which co-occurred at all the 12 sites at each location hence for the Pandametanga sites these were *Baphia massaiensis* and *Terminalia brachystemma*, for Maun these were *Colophospermum mopane* and *Grewia flava*, for Okwa these were *Grewia flava* and *Boscia albitrunca* and for Tshane these were *Acacia mellifera* and *Grewia flava*. Kendall's τ (tau) correlation coefficient was used to assess the strength of association between species with values of τ falling between –1 and 1, with 0 indicating no relationship. The result of this test suggested that no ecologically significant association was present at any of the locations. A further test was undertaken to determine whether one species was relatively dominant over another. Because of the small sample size (12) for testing the hypotheses, a test that was insensitive to character of distribution was chosen. Hence Wilcoxon signed rank test was used to test whether the abundance of plants of species A was equal to that of species B, i.e:

H0: mean count A = mean count B.

H1: mean count A > mean count B or mean count A < mean count B.

Table 6. *Results of Significance testing (Wilcoxon test) of co-occurring species at the four Kalahari transect sites in Botswana*

Location	Co-occurrent species	Mean count	No. of cases	*Z* statistic	Significance level	H0 (at 95% significance level)
Pandamatenga	*Baphia massaiensis*	47·0	12	−2·040	0·041	Reject
	Terminalia brachystemma	15·4				
Maun	*Colophospermum mopane*	84·8	12	−2·825	0·005	Reject
	Grewia flava	12·7				
Okwa	*Grewia flava*	46·4	12	−2·982	0·003	Reject
	Boscia albitrunca	9·7				
Tshane	*Acacia mellifera*	16·1	12	−1·805	0·071	Not reject
	Grewia flava	21·8				

The results indicate that at the Pandametanga, Maun and Okwa locations there is no relationship in terms of relative abundance between the co-dominant species (Table 6). However at Tshane the null hypothesis was not rejected suggesting that there may be some ecological significance between the co-association of *Acacia mellifera* and *Grewia flava* at the southern end of the transect.

The average total numbers of plants recorded in the BKT transect indicates a noticeable decrease along the transect gradient (Fig. 4). In absolute terms, this varies from a total of 2482 individuals counted in the 12 sites at Pandametanga, 2110 in the 12 Maun sites, 1766 in the 12 Okwa sites and 1475 in the 12 Tshane sites. In terms of total numbers of different species, this varied little from the wetter to the drier end of the BKT from 20 species identified at the Pandametanga sites, 29 species at the Maun sites, 24 species at the Okwa sites and 20 different species at the Tshane sites. Figure 5 shows the results of direct ordination of species along the environmental gradient (Kent & Coker, 1996). These results considered along with Tables 4 and 5 confirm the two main species groupings suggested by White (1983). The northern Pandametanga species belong mainly to the Zambesian centre of endemism and the remaining sites belong to the Karoo–Kalahari centre. The dominance of *Colosphermum mopane* around Maun is again relatively unique in terms of species gradations along the BKT. Other species for instance *Terminalia* spp. (mainly *T. sericea*) and *Bauhinia petersiana* are present at all locations but decrease with distance southward. South of Pandametanga, *Grewia flava* is most prevalent and increases southwards. Similarly the two most abundant Acacias (*Acacia mellifera* and *A. erioloba*) increase noticeably southwards reflecting the increasing aridity towards the southern end of the gradient.

The results of woody species counts and species richness analyses are depicted as a series of regression coefficients which were plotted in terms of rainfall along the Botswana gradient (Table 7). The results show significant correlations between rainfall and the average number of species and species richness at each location suggesting that numbers of species are directly related to long-term rainfall norms. Further analyses were undertaken to determine how the same parameters change with changes in soil moisture along the moisture gradient.

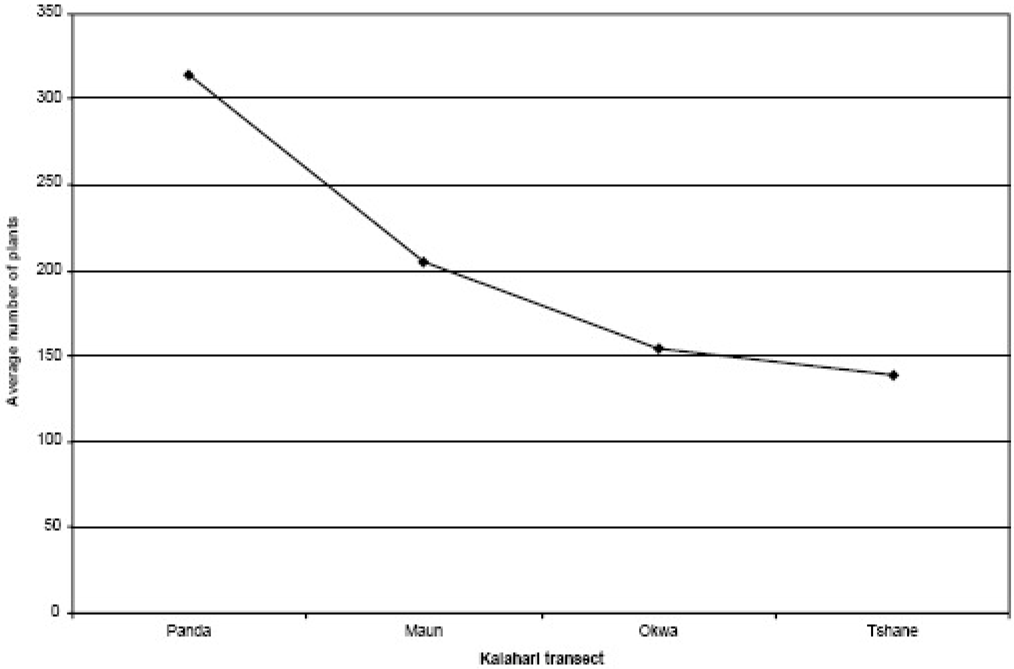


Figure 4. Decrease in the total number of plants along the Botswana Kalahari transect.

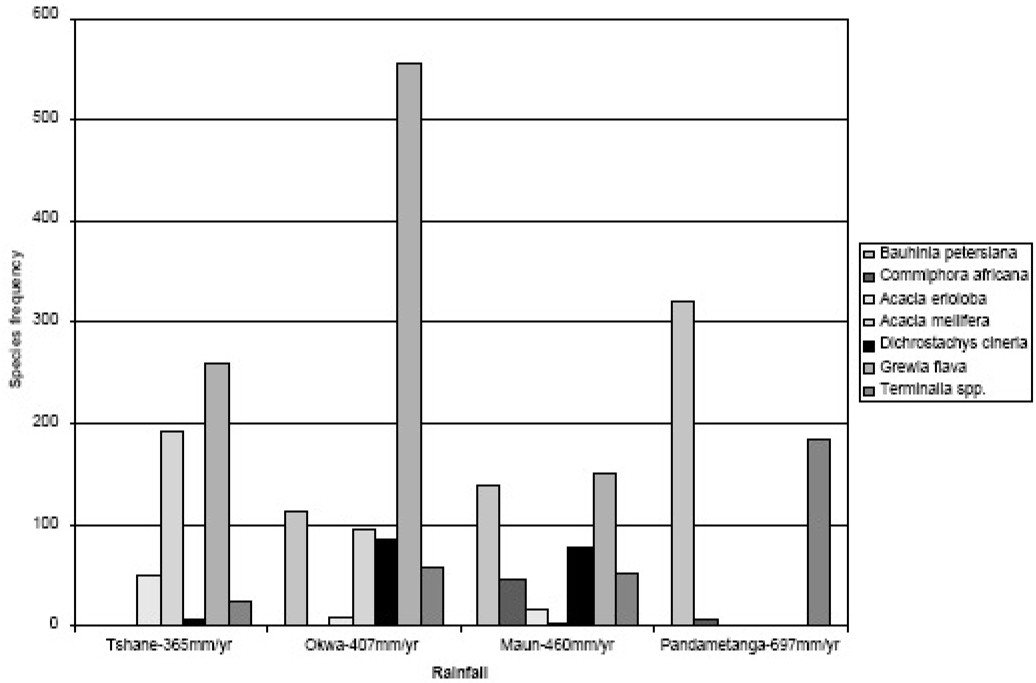


Figure 5. Distribution of species along the Botswana Kalahari transect.

Results show that both the average number of species and species richness are strongly correlated to soil moisture content (Table 8). This implies that increases or decreases in soil moisture due for instance to climate changes may have a considerable impact both on the number of individual plants present and on overall species survival.

Table 7. *Regression relationship of main vegetation components relative to long term average rainfall*

Vegetation components	Relationship	R^2	Significance (P)
Average number of plants	$y = 0.4276x$	0·95	<0·01
Species richness	$y = 0.0528x$	0·95	<0·01
Woody vegetation cover	$y = -0.0776x + 114.32$	0·88	<0·05
Dead herbaceous cover	$y = -0.0055x + 5.8893$	0·15	
Alive herbaceous cover (grass)	$y = 0.0319x - 4.1208$	0·78	<0·05
Alive herbaceous cover (forb)	$y = 0.0101x + 4.155$	0·23	
Litter	$y = 0.0115x + 1.8026$	0·04	
Bare soil	$y = -0.1256x + 106.6$	0·89	<0·01

Table 8. *Regression relationship of main vegetation components relative to soil moisture content*

Vegetative components	Relationship	R^2	Significance (p)
Average number of plants	$y = 32.965x + 50.949$	0·87	<0·01
Species richness	$y = 4.06x + 6.2876$	0·87	<0·01
Woody vegetation cover	$y = -4.888x + 99.386$	0·79	<0·05
Dead herbaceous cover	$y = -0.1925 + 4.1088x$	0·04	—
Alive herbaceous cover (grass)	$y = 1.7556x + 3.2007$	0·53	—
Alive herbaceous cover (forbs)	$y = 0.6154x + 6.1958$	0·20	—
Litter	$y = 1.3488x + 1.1223$	0·12	—
Bare soil	$y = -8.416x + 84.758$	0·91	<0·01

Vegetation cover component characteristics

The ground cover components considered in this work comprise green (alive) grass and forbs, herbaceous cover (AHC), dead herbaceous cover (DHC), plant litter and bare soil. A listing of the average vegetation components at each location as these varied along the moisture gradient is shown in Table 9. Correlation analysis, undertaken on the total data sets for the 12 sites at each location indicates a high degree of internal homogeneity with correlation coefficients ranging from 0·89 to 0·99 for the Pandametanga location. Similar results were obtained for the remaining three locations with correlation coefficients for Maun ranging from 0·99 to 0·79 for Okwa the between site correlations ranged from 0·99 to 0·85 and for Tshane these values ranged from 0·80 to 0·98. These data suggest that geographical variation at each location in terms of the different landforms (*cf*. Table 3) is not significant.

Results of vegetation component analysis show a series of regression coefficients which were plotted in terms of rainfall along the Botswana gradient (Table 7). The results show significant correlations between rainfall and woody vegetation cover, alive herbaceous cover (grass) and bare soil. There is no correlation between rainfall and alive herbaceous cover (forbs) nor between rainfall and litter. The association between rainfall and WVC is negative implying that canopy cover extents (in terms of vegetation density) increase along the gradient as rainfall decreases. While being counter intuitive, this may relate to increases in the amount of bush encroachment in drier areas (*cf*. Archer *et al.*, 2000; Moleele *et al.*, 2001). The amount of grass cover and conversely the amount of bare soil also increase slightly along the gradient

Table 9. *Statistical values of main vegetative components*

	Pandametanga average	Maun average	Okwa average	Tshane average
Number of individual plants	314·17	204·42	154·33	138·42
Species richness	0·039	25·22	19·05	17·09
WVC	61·27	72·60	87·30	86·27
AHC(grass)	19·04	6·79	10·60	8·74
AHC(forb)	11·78	5·41	11·46	7·48
DHC	2·11	1·85	6·42	2·51
Litter	7·00	19·56	0·53	2·26
Bare Soil	21·35	38·99	58·29	65·29
	Pandametanga S.D.	**Maun S.D.**	**Okwa S.D.**	**Tshane S.D.**
Total number of species	186·61	75·76	54·62	102·57
Species richness	0·023	9·31	6·74	12·66
WVC	17·01	12·93	3·31	3·99
AHC(grass)	8·63	10·65	6·79	8·34
AHC(forb)	12·04	3·74	5·24	3·07
DHC	2·23	2·25	4·54	2·68
Litter	5·16	14·69	0·57	2·61
Bare soil	14·19	8·63	10·17	6·56

suggesting that conditions for herbivores improves with distance southwards along with the extent of bare soil areas, which are foci for potential degradation (*cf*. Ringrose & Matheson, 1987).

Further analyses were undertaken to determine how the vegetation components changed with changes in soil moisture along the Botswana gradient (Table 7). Results show only two significant correlations between WVC and soil moisture content and bare soil and soil moisture. The relationship with WVC is negative suggesting a higher density of cover is related to areas of higher soil moisture. As with the similar relationship between WVC and rainfall, this may be due to increases in bush encroachment, especially in the Tshane area of the Kalahari. However a stronger negative relationship occurs between the extent of exposed soil and soil moisture content such that larger areas of exposed soil understandably have lower soil moisture contents and are therefore more susceptible to degradation for instance as a result of wind erosion (*cf*. Ringrose & Matheson, 1987).

Discussion and conclusions

Significant aspects of climate change studies include the determination of vegetation cover changes across climatic gradients so that responses in space can be substituted to some extent for responses in time (Steffen, 2000). This presupposes that field sites chosen along the gradient and across known vegetation belts should be representative of a gradual change in conditions and that underlying edaphic factors are constant (e.g. Scholes & Parsons, 1997). In general this work shows that trends in major vegetative cover components including species types and richness along the Kalahari transect reflect general decreases southward but also that overall trends are modified by degrees of variability. This occurs despite the apparent homogeneity of the Kalahari sands and predominantly semi-arid savanna shrub–woodland vegetation cover. Specific aspects include:

- Despite linear decreases both in rainfall and soil moisture content, results indicate that most inherent soil moisture variability occurs in the Okwa valley and least in the Tshane area.
- Many species are unique to specific locations for instance the Zambesian species at Pandametanga and *Colophosphermum mopane* at Maun both of which are geographically adapted. This changes southwards as the Acacias (*A. mellifera, A. erioloba, A. leuderitzii*) along with *Grewia flava* become more dominant. Hence despite some continuity south of Maun, there are three main groupings of species over the four locations (cf. White, 1983).
- There is little or no relationship between co-dominants except at the southern end of the BKT where *Grewia flava* and *Acacia mellifera* may form a species association.
- The average total numbers of plants decreases along the transect gradient at each location from a total of 2482 individuals at Pandametanga, to 1475 individuals within the Tshane sites. However in terms of total numbers of different species, this varied little from the wetter to the drier end of the moisture gradient ranging from 29 species at the Maun sites, to 20 different species at the Tshane sites.
- Results of plant numbers and species richness plotted against rainfall and soil moisture show significant correlations hence may be directly related both to long-term rainfall norms and soil moisture variabiltiy.
- The association between rainfall and WVC is negative implying that canopy cover extents (in terms of vegetation density) increases along the gradient — or increases as rainfall decreases. While being counter intuitive, this may relate to increases in the amount of bush encroachment in drier areas.

Therefore while representing a continuum in terms of plant numbers, in other respects (e.g. species types and ground cover components) vegetation zones in the Kalahari may be regarded as semi-discontinuous areas and maybe concepts of endemism play a more helpful role in understanding Kalahari species distributions than concepts of continuity. Differences within and between the mapped vegetation zones may be accounted for in terms of relatively unique ecosystem factors which function partly in response to geological conditions and partly in response to local (as opposed to regional) climatic factors (*cf*. Ringrose *et al.*, 1998, 1999*c*). For instance it appears that rooting habits of mopane woodland and shrubland takes place in response to unique soil moisture conditions (Timberlake, 1995). This leads to ecosystem adaptive measures (in terms of species responses) which are not mirrored elsewhere in the BKT system. Ecosystem adaptability in all the SAFARI2000 areas has likely taken place in response to local soil conditions which have evolved since Tertiary times, over some 5 million years (Scott, 1984, Moore & Atwell, 1999). This infers that adaptability in terms of the migration of species (BIOME model) in response to relatively rapid climate changes such as proposed by the drying UKTRANS scenario during the 21st century may not readily take place over the Kalahari (e.g. Hulme, 1996). Alternative scenarios should include the local dying off of species in northern areas which are currently adapted to relatively unique edaphic conditions and increased species uniformity in drier southern areas as a result of disturbances such a fires (e.g. Setshogo et al., 2000).

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