

Topo-edaphic, floristic and physiognomic gradients of woody plants in a semi-arid African savanna woodland

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Abstract

The variation in topo-edaphic conditions, woodland composition and physiognomic structure of a semi-arid savanna woodland, namely the 59 400 ha Klaserie Nature Reserve, was studied with multivariate techniques. Spatial variation in the texture and chemistry of both the A- and B- horizons was substantial. One gradient of the A-horizon was of increasing clay, silt, organic matter, pH and conductivity, while a second gradient was of increasing rockiness, slope and gravel content, associated in part with upper landscape positions. Physiognomic structure of the woodland also displayed substantial spatial variation. Variation in tree density had the greatest effect on total canopy volume, and the density of coppice and dead individuals were closely correlated. Topo-edaphic variation, after the effect of vegetation composition had been accounted for, had a direct effect on woodland structure, as clay content of soils or rockiness influenced shrub density, and catenal position together with silt- or gravel-content of soils influenced coppice density. Ordination analyses identified that the included topo-edaphic variables accounted for a significant amount of floristic variation, but also showed that important environmental variables were omitted. Floristic variation of woody elements was of the nature of a large number of relatively equivalent, independent gradients rather than of a few simple primary gradients. Ten woodland types were identified by TWINSpan which differed in their topo-edaphic and physiognomic character. Distinctive woodland assemblages were found on rocky outcrops or alluvial areas, on deep, sandy soils or on clay- or silt-rich soils. *Colophospermum mopane* formed the densest woodlands. Characteristics of the B-horizon were often dissimilar to those of the A-horizon, and seemed important for woodland composition.

Introduction

The savanna woodlands of Africa offer a browse resource of considerable importance to both domestic livestock and wildlife, but little study has been made of the patterns of utilization of, and consequent impact upon this resource, by an entire browser community at a landscape or ecosystem level. The amount of available browse for ungulates can be expected to vary among locations depending on woodland structure and composition because of differences among species in palatability and accessibility, and edaphic conditions because of its effect on the nutritive value of species (Bell 1982).

However, the pattern of browsing at this scale cannot be studied until there is a clear understanding of what factors determine the composition, abundance and dispersion of the browse resource. Topo-edaphic conditions, woodland composition and structure, and the amount of browse are not independent of one another. Topo-edaphic conditions are an important determinant of the composition and physiognomic structure of African savannas, and structure often corresponds with composition (Leistner & Werger 1973; Coetzee *et al.* 1976; Werger 1978; Van der Meulen 1979; Van Rooyen, Theron & Grobbelaar 1981a,b,c; Coetzee 1983; Van Rooyen 1983; Bredenkamp 1985; Bredenkamp & Theron 1985; Le Roux *et al.* 1988; O'Connor 1992). However, these previous studies

have not demonstrated a consistent finding about which topo-edaphic variables have the greatest influence on the vegetation properties of savanna woodlands.

The aim of this paper is to report a study on the vegetation-environment relationships of the savanna ecosystem under study. The following are the key questions addressed in this paper. (1) Does substantial variation in topo-edaphic properties exist in the study area? (2) If so, does this variation influence the composition and structure of the woody vegetation? (3) Can floristic woodland types be clearly identified (which would provide a higher level of description of system organization for the analysis of browsing patterns)? The implications of the factors investigated in this paper for patterns of browsing at an ecosystem scale will be dealt with in a second paper. Although this paper does not deal directly with any questions relating to browse, it should be recognized that the approach of the study was founded upon meeting this need.

Study area

The area chosen for the study was the Klaserie Private Nature Reserve (henceforth Klaserie), a 59 400 ha (30 km N-S, 27 km E-W) game-fenced reserve situated in the Transvaal lowveld of South Africa (22°22'-31' S, 31°2'-19' E). The Klaserie river drains approximately half the reserve and flows to the north-east into the Olifants river together with other seasonal drainage lines. Altitude ranges from 535 m in the south-west to 303 m in the north-east. The topography is undulating, being relatively flat in the southern and central parts, but becoming progressively more dissected towards the north, culminating in a series of relatively steep, rocky ridges adjacent to the Olifants river. The parent material is predominantly Archaean granites and gneisses. More details on the geomorphology (Venter & Bristow 1986), geology (Barton, Bristow & Venter 1986; Bristow & Venter 1986) and soils (Venter 1986) can be found elsewhere.

The climate is typical of southern African savannas, with a hot and relatively humid wet season from November to March, and a cooler drier period over the rest of the year. Temperatures are high (mean annual maximum of 29.5 °C and minimum of 12.5 °C at Skukuza, 70 km S) and frost is virtually absent. The mean annual rainfall at the centre of Klaserie was 435 mm for 1960–1981. The southern and western parts are wetter than the north-east on average by about 50 mm per annum. Pan evaporation at Phalabor-

wa (20 km N) was 2090 mm a⁻¹, greatly exceeding annual rainfall of 480 mm.

The vegetation is a densely wooded savanna occurring within the Sudano-Zambesian phytogeographical region (Werger & Coetsee 1978). Werger & Coetsee (1978) broadly divide the vegetation of this region into mopaneveld (dominated by *Colophospermum mopane*), broad orthophyllous plains bushveld (dominated by *Combretum apiculatum*) and microphyllous thorny plains bushveld (dominated by *Acacia* spp.). Nomenclature follows Arnold and de Wet (1993). Almost all species are deciduous.

Land uses of Klaserie were hunting, cattle ranching and very limited crop farming prior to its proclamation in 1972. Present land use is ecotourism, including animal viewing and limited hunting. Klaserie supports a diversity of large mammal species, including elephant, giraffe, kudu, impala, buffalo, zebra and wildebeest.

Methods

Vegetation sampling

Methods were selected which would allow a large number of woody plants and sites to be sampled in a relatively short period of time. Homogeneous areas were identified on aerial photographs, and sites were located in the centre of these areas. One hundred and sixty two sites were selected to sample the variation in vegetation and topography. From March to July 1980, a transect, 5 m wide and at least 50 m long, was sampled at each site. Transect length was governed by the density of the woody vegetation and the necessity to include at least 15 individuals of the most important species (Taylor & Walker 1978). All transects ran along contours to reduce topo-edaphic and vegetation variation. All woody plants (>0.5 m in height) rooted within the transect were identified to species and categorized as either trees (≥3 m in height, shrubs (<3 m), coppice (trees resprouting from the base after elephants have pushed them over), or dead. Trees with no available browse (no foliage below 5.5 m, the maximum browsing height of giraffe [Dayton 1978]) were also recorded. Trees and shrubs were respectively each assigned to one of four easily distinguishable size classes. For shrubs these were: <1 m²; 1–4 m²; 4–9 m²; and >9 m² in canopy area. For trees these were: 3–4 m; 4–6 m; 6–8 m; and >8 m in height. The midpoint of each height or canopy area size class was converted to a canopy volume by the use of regressions. These were

obtained from the woody plants in each of two 30 × 30 m randomly located quadrats in the mopaneveld, *Acacia* and *Combretum* vegetation types. The canopy height (H), lowest canopy height (h), maximum canopy diameter (C) and canopy diameter at right angles to the maximum (c) were measured on all woody plants and canopy volume calculated as follows:

$$\text{Canopy volume} = \pi(C.c)(H - h)/4.$$

The best fit of either a linear or power curve regression of canopy volume on height for trees and canopy volume on canopy area ($\pi(C.c)/4$) for shrubs was selected for each broad vegetation type (Dyer 1983; Witkowski 1983).

Environmental variables

The slope angle was measured using a clinometer and topographic position on the catena scored as follows: (1) bottom-land, (2) lower slope, (3) mid-slope, (4) upper slope/crest, and (5) rocky outcrop.

Composite (>4) soil samples (0–15 cm depth) were taken from between tree canopies along each transect (avoiding dung heaps and termite mounds), air-dried and passed through a 2 mm sieve. The Bouyoucos hydrometer method was used to determine sand, silt and clay fractions. Soil pH was determined on a 1:1 ratio of soil to 0.01 M CaCl₂ (w/v; Tomlinson *et al.* 1977), and organic matter by loss-on-ignition of a 10 g sample at 500 °C for 3 h. Electrical conductivity of the soil solution was determined on a 1:1 ratio of soil to de-ionized water (w/v) and measured with a conductivity bridge. Within each vegetation type delimited by TWINSpan classification (see section on *Vegetation classification*), typical representative sites (based on vegetation composition) were selected. Soil pits were excavated and samples taken from each horizon. In addition to the above analyses, exchangeable K, Ca, Mg and Na were extracted in 1 N ammonium acetate and concentrations determined by atomic absorption spectrophotometry. The percentage cover of rock and gravel were estimated visually on 25 1 m² quadrats placed at 5 m intervals along the length of the transect.

Data analysis

Vegetation-environment gradients

In order to address the question of variation in topographic properties within the study area, the main patterns of variation amongst the ten topographic variables (sand, silt, clay, gravel, rock, slope angle, landscape position, pH, conductance, organic matter) were summarized with a correlation-type principal component analysis (PCA) using procedures of SAS (1988). PCA also helps to identify redundancy (near linear dependencies) amongst variables.

A similar PCA was conducted for the six vegetation structure variables (canopy volume, tree density, shrub density, total [tree plus shrub] density, coppice density, density of dead individuals).

In all analyses involving environmental or vegetation structure variables the following transformations were used to normalize distributions, as tested with the Shapiro-Wilk statistic using procedures of SAS (1988): angular transformation of the percent sand and percent clay; log_e transformation of percent silt, percent organic matter, conductivity, slope (value + 0.1), percent gravel and percent rockiness (both value + 0.5), canopy volume, and density of trees, shrubs and all woody individuals; square root (+ 0.5) for the density of dead and of coppice individuals. The percentage of unavailable browse could not be normalized because of too many zero values, and was not included in the multivariate analyses.

The nature of the relationship between topographic variables and floristic composition of the woody elements was investigated with ordination techniques. The species (log_e-transformed values of canopy volume) by site data were ordinated by correspondence analysis (CA) and canonical correspondence analysis (CCA) using the CANOCO package (Ter Braak 1988). Ordination by CA is based on floristic data alone, and is subsequently passively related to environmental variables, whilst in CCA the ordination axes are constrained to be linear combinations of the included environmental variables. Thus, if there is a fundamental difference in the ordinations of CA and CCA, it is usually an indication that important environmental variables have been omitted. The significance of the overall CCA ordination and its first axis was tested with a Monte Carlo re-randomization procedure, which is a direct test of whether the included environmental variables have a significant effect on compositional variation. The environmental variables includ-

ed were the topo-edaphic variables described above, except that the percent sand was entered as a passive variable to eliminate collinearity with the percent silt or clay. An initial CA ordination identified three outlier samples, and these were subsequently entered as passive samples; eleven (of 78) species which occurred in only one or two samples were deleted; otherwise default options were used.

We wished to determine whether the physiognomic structure of a savanna woodland was simply a consequence of its composition, or whether topo-edaphic variation had an additional, independent influence on woodland structure. To this end, partial canonical correlation analysis (SAS 1988) was conducted on the six variables of woodland structure and ten variables of topo-edaphic variation described above. A partial canonical correlation analysis assesses the relationship between two sets of variables whilst holding a third variable constant. The influence of woodland composition was removed by using the site scores of the first eight axes of the correspondence analysis to partial out its effect.

Vegetation classification

The data for woody species canopy volume per transect were analyzed by two-way indicator species analysis (TWINSPAN; Hill, 1979), to obtain a classification of the vegetation types. Pseudospecies cut levels for the canopy volume data used were equivalent to 0, 300, 750, 1500 and 3000 m³ ha⁻¹, which are proportional to the default values. The output of TWINSPAN can be strongly influenced by the first step of ordinating the sites using correspondence analysis. Therefore a second classification technique, namely minimum dispersion, which is an agglomerative polythetic technique of cluster analysis, was employed. The results of the two techniques did not differ substantially (Witkowski, 1983), and therefore only those for TWINSPAN are reported.

Differences between vegetation types in each of the topo-edaphic and vegetation structure variables were tested with one-way analysis of variance, with means compared by Tukey's HSD test. Differences for the percent unavailable browse were tested with a Kruskal-Wallis analysis of variance, and means compared with pairwise Wilcoxon's tests at $p = 0.05/\text{number of pairwise comparisons}$. Canonical discriminant analysis (SAS 1988), using the first six components of the PCA of the ten topo-edaphic variables, was used to test if the topo-edaphic environment differed

among vegetation types. Similarly, canonical discriminant analysis, using the first four components of the above-described PCA of the six vegetation structure variables was used to test if vegetation types differed in their structure. Canonical discriminant analysis based on PCA scores rather than on the original observations is less likely to violate the assumptions of this statistical model (Williams 1983).

Results

Vegetation classification

The TWINSPAN classification identified ten vegetation types at various hierarchical levels from the data on canopy volume (Figure 1, Table 1). Vegetation types differed for eight of the ten topo-edaphic variables (Table 2), the exceptions being the percent silt and percent organic matter. However, differences for a number of the variables were due to only a few vegetation types. The canonical discriminant analyses of topo-edaphic variables provided a clear separation of most of the vegetation types (Figure 2a), which corresponded well with the TWINSPAN classification. The first canonical axis clearly separated the vegetation types in accordance with their topographic position. The topo-edaphic environment of the *Lonchocarpus capassa-Combretum hereroense* type (bottomland) was particularly different to that of any other vegetation type.

Vegetation types differed for six of the seven vegetation structure variables (Table 3), the exception being the density of dead individuals. The structure of the *Colophospermum mopane* woodland was distinct with the highest density of both shrubs and trees (Figure 2b). In contrast, the *Terminalia prunioides*, *Combretum imberbe*, *Pappea capensis*, *Grewia bicolor* and *Strychnos madagascariensis* woodlands were relatively open. The percentage of unavailable browse was low throughout (1–14%). The *Lonchocarpus capassa-Combretum hereroense* and *Spirostachys africana* woodlands had the highest fraction of unavailable browse, while the *Strychnos madagascariensis* and *Grewia bicolor* types had the highest densities of copice individuals.

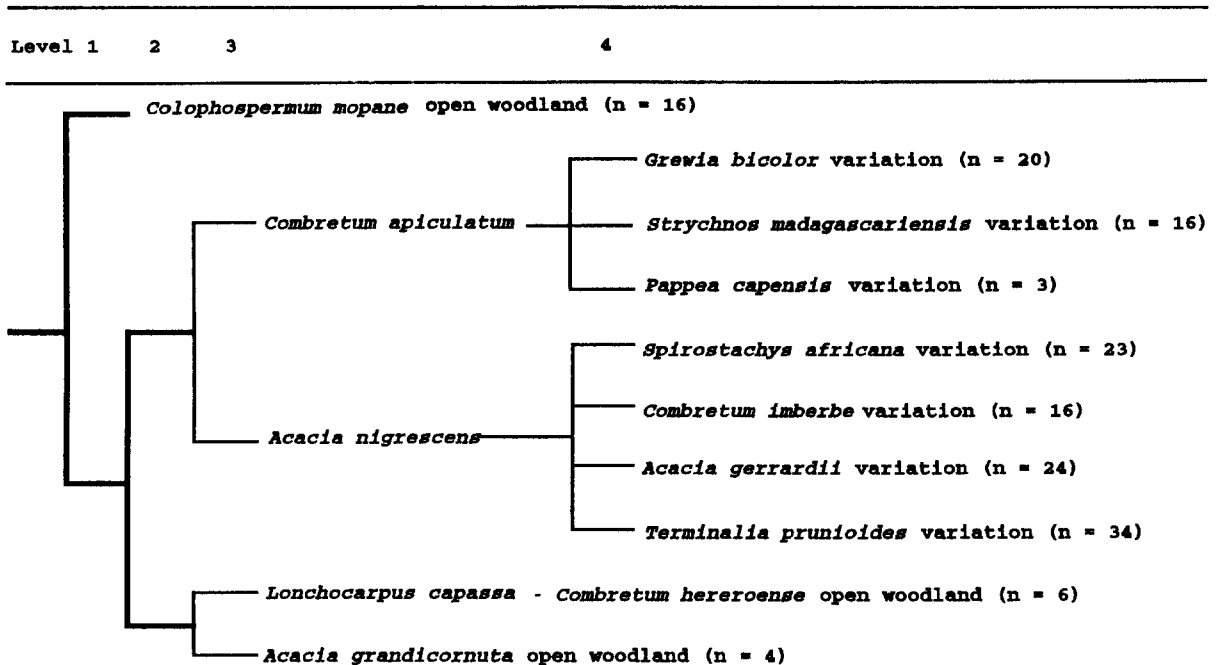


Figure 1. Dendrogram illustrating the divisions used in deriving the ten vegetation types from the TWINSpan classification. Numbers of transects in each vegetation type is indicated. See Results for descriptions of each vegetation type.

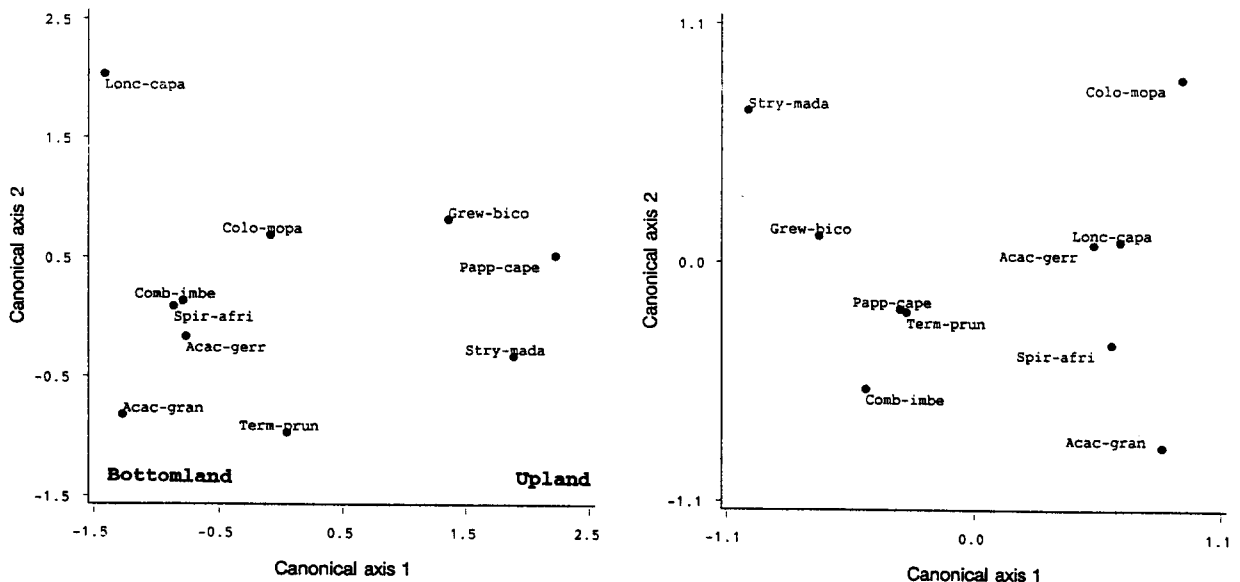


Figure 2. The class means for ten vegetation types ($n = 162$) of the first two axes of a canonical discriminant analysis of a) the first six components of a principal component analysis of ten topo-edaphic variables, and b) the first four components of a principal component analysis of six vegetation structure variables. See methods for further details. Key to vegetation types: Acac-gerr - *Acacia gerrardii* variation of *Acacia nigrescens* open woodland; Acac-gran - *Acacia grandicornuta* open woodland; Colo-mopa - *Colophospermum mopane* open woodland; Comb-imbe - *Combretum imberbe* variation of *Acacia nigrescens* open woodland; Grew-bico - *Grewia bicolor* variation of *Combretum apiculatum* open woodland; Lonc-capa - *Lonchocarpus capassa*-*Combretum hereroense* woodland; Papp-cape - *Pappea capensis* variation of *Combretum apiculatum* open woodland; Spir-afri - *Spirostachys africana* variation of *Acacia nigrescens* open woodland; Stry-mada - *Strychnos madagascariensis* variation of *Combretum apiculatum* open woodland.

Table 1. The mean canopy volume ($\text{m}^3 \text{ha}^{-1}$) of each woody plant species in each vegetation type. An entry of - denotes 0.

Species	Vegetation type												Total
	<i>Terminalia prunioides</i> variation	<i>Spirostachys africana</i> variation	<i>Combretum imberbe</i> variation	<i>Acacia gerrardii</i> variation	<i>Acacia nigrescens</i> woodland	<i>Grewia bicolor</i> variation	<i>Pappea capensis</i> variation	<i>Strychnos madagascariensis</i> variation	<i>Combretum apiculatum</i> woodland	<i>Colophospermum mopane</i> woodland	<i>Lonchocarpus capassa</i> woodland	<i>Acacia grandicornuta</i> woodland	
<i>Combretum apiculatum</i>	7025	6155	4347	5326	5918	8535	7988	11099	9596	4820	2509	6.2	6414
<i>Sclerocarya birrea</i>	2766	3395	1440	3005	2687	2665	3312	2237	2488	2227	1136	394	2509
<i>Acacia nigrescens</i>	1234	4820	2393	3746	2792	1517	1148	294	1011	96.3	4843	3092	2341
<i>Colophospermum mopane</i>	53.4	0.1	4.2	2.2	20.7	61.6	-	8.0	39.4	16346	-	-	830
<i>Grewia bicolor</i>	480	1148	1289	168	710	1495	763	216	965	439	981	1039	773
<i>Commiphora mollis</i>	257	589	133	68.7	259	2349	733	409	1546	271	11.8	-	532
<i>Albizia harveyi</i>	641	419	61.6	1462	667	53.3	35.5	116	79.2	72.7	324	336	475
<i>Grewia</i> sp.	396	479	517	544	472	611	343	294	480	232	290	115	443
<i>Combretum imberbe</i>	10.8	42.5	878	292	255	77.8	7.6	14.1	51.4	59.5	4337	282	383
<i>Terminalia prunioides</i>	408	421	169	149	303	343	270	1.2	201	97.6	943	1508	327
<i>Dichrostachys cinerea</i>	183	583	236	362	318	117	93.9	298	192	119	351	308	278
<i>Spirostachys africana</i>	33.4	1121	295	16.8	310	2.4	506	-	1.4	-	832	169	251
<i>Combretum hereroense</i>	19.3	649	240	102	214	73.5	17.7	1.2	43.6	25.5	1837	468	244
<i>Lonchocarpus capassa</i>	67.5	67.1	219	190	126	226	-	267	243	2.5	2287	-	239
<i>Acacia grandicornuta</i>	150	5.6	-	-	55.6	-	-	16.6	6.9	-	53.8	6411	185
<i>Peltophorum africanum</i>	136	178	124	241	166	79.4	402	114	93.7	79	591	-	165
<i>Cissus cornifolia</i>	239	169	180	112	183	123	72	210	159	125	70.8	11.8	164
<i>Dalbergia melanoxylon</i>	112	221	50.7	437	197	37.1	1.4	52.5	43.5	221	231	6.2	159
<i>Maytenus senegalensis</i>	27.6	169	121	71.4	85.9	29.5	-	12.1	22.3	27.6	1857	447	156
<i>Euclea divinorum</i>	9.8	335	55.5	35	92.8	1.2	58.4	1.2	1.2	151	157	1468	109
<i>Acacia erubescens</i>	30.5	82.6	130	4.3	55.3	340	782	139	257	-	-	-	105
<i>Acacia exualis</i>	103	43.3	170	254	138	30	86.2	77.9	49.8	25.9	3.4	17.4	104
<i>Commiphora pyracanthoides</i>	108	130	112	6.8	90.2	103	25.4	151	123	156	25.8	24.2	95.1
<i>Acacia nilotica</i>	127	139	223	50.1	129	16.7	30.3	47.2	29.3	2.5	19.4	40.4	92.4
<i>Schotia brachypetala</i>	-	332	95	-	88.4	-	258	-	-	-	543	235	91.5
<i>Ormocarpum trichocarpum</i>	87	83.4	76.8	211	113	8.4	-	3.3	6.3	6.1	58.2	227	82.4
<i>Grewia flavescens</i>	19.1	56.4	111	27.7	47.3	250	201	27.9	158	17.1	131	57.3	76.7
<i>Terminalia sericea</i>	235	3.9	8.9	32.2	95.1	16.6	-	127	62.3	-	2.8	-	75.3
<i>Bolusanthus speciosus</i>	46.7	202	86.6	106	101	15.9	6.3	-	9.3	5.4	156	-	74.6
<i>Grewia hexamita</i>	107	54.5	45.8	31.7	66.6	52.1	77.2	83	64.9	8.6	60.7	51.7	62.9
<i>Ziziphus mucronata</i>	39.4	45.5	24.7	86.7	48.6	26.2	259	8.8	19	-	153	92.9	48.9
<i>Maytenus heterophylla</i>	14.8	97.7	6.6	94	48.7	-	61.9	1.2	0.5	48.3	289	23	48.6
<i>Strychnos madagascariensis</i>	0.5	-	1.3	25.2	6.2	3.9	61.9	417	175	-	7.1	-	43.6
<i>Acacia tortilis</i>	4.9	68	205	4.3	57.9	23.9	-	-	14	-	-	23	41.1
<i>Diospyros mespiliformis</i>	-	2.9	39.7	2	9	-	-	-	-	-	711	-	38.1
<i>Pappea capensis</i>	8.3	74.2	65.9	25	37.4	14.2	339	2.7	9.5	5.2	-	247	37.8
<i>Securinega virosa</i>	16.3	55.9	25.9	48	33.8	6.3	74.2	10.9	8.2	41	77.7	86.5	32.4
<i>Euclea undulata</i>	-	8.7	5.6	2.8	3.6	19.9	-	-	11.7	-	569	-	30.7
<i>Acacia senegal</i>	83.5	26.7	3.9	-	36.6	3.5	-	-	2.1	25.1	11.5	207	30.6
<i>Ximenesia americana</i>	23.3	107	12.6	38.9	42.3	0.8	-	3.3	1.8	5.5	33.8	5.6	29.7
<i>Commiphora africana</i>	20.9	18.9	35	41.7	28.1	57.4	17.7	21	42.3	9.3	3.7	5.6	28.5
<i>Hippocratea longipetiolata</i>	-	102	1.3	-	21.5	51	244	-	29.9	-	53.8	-	27
<i>Grewia villosa</i>	18.2	28.9	38.4	17.6	24.3	41	2.7	10.2	28.3	10.3	25.8	40.4	24.6
<i>Grewia monticola</i>	7.7	27.1	6.5	67.2	25.1	25.9	59.5	14.2	21.1	-	53.8	-	24.3
<i>Cassine transvaalensis</i>	1.3	112	1.3	1.7	24.5	-	13.1	-	-	-	-	242	21.5

Description of the vegetation types

Each of the vegetation types is described in turn, with appropriate summaries given in Tables 1 (floristic composition), 2 (topo-edaphic features) and 3 (woodland structure).

The 'Acacia nigrescens open woodland', the most widespread vegetation type in Klaserie occurring throughout the relatively flat central and southern parts and adjacent to water courses, is characterized by microphyllous, usually thorny species. There is an emergent tree layer (10–12 m in height) dominated by *A. nigrescens* and *Sclerocarya birrea*, and a low tree and shrub layer dominated by *Combretum apiculatum*, *Grewia* spp., *Albizia harveyi* and *Dichrostachys cinerea*. The soils are relatively fine textured, deep and

calcium rich. The following four variations were recognized.

The 'Spirostachys africana variation', which occurs adjacent to seasonal watercourses both on relatively flat and on more dissected topography, is characterized by emergent *S. africana* trees, low *Combretum hereroense* trees, and shrubs of *Euclea divinorum*, *Commiphora mollis* and *Terminalia prunioides*. A-horizon soils have the highest clay content, organic matter, conductivity and cation concentrations within the B-horizon are also high (Table 2).

The 'Combretum imberbe variation' occurs on low-lying areas and mid-slopes on relatively flat topography. Characteristic emergent trees are *C. imberbe*, *Combretum hereroense*, *Acacia nilotica* and *Lonchocarpus capassa*. Soils have a relatively high silt

Table J. Continued.

Species	Vegetation type											Total	
	<i>Terminalia prunioides</i> variation	<i>Spirostachys africana</i> variation	<i>Combretum imberbe</i> variation	<i>Acacia gerrardii</i> variation	<i>Acacia nigrescens</i> woodland	<i>Grewia bicolor</i> variation	<i>Pappea capensis</i> variation	<i>Strychnos madagascariensis</i> variation	<i>Combretum apiculatum</i> woodland	<i>Colophospermum mopane</i> woodland	<i>Lonchocarpus capassa</i> woodland		<i>Acacia grandicornuta</i> woodland
<i>Boscia albitrunca</i>	-	-	0.3	-	0.1	134	123	3.3	79.7	25.5	5.6	-	21
<i>Mundulea sericea</i>	8.8	18.8	35.1	8.1	16	12.7	17.7	76.6	39.2	-	-	-	19.2
<i>Maerua parvifolia</i>	18.4	54.6	12.7	8.1	22.5	5.3	1.4	3.7	4.7	5.7	6.5	129	19.1
<i>Manilkara mochisia</i>	3.3	31.3	-	27	13.9	31.7	245	-	18.6	-	11.5	-	17.7
<i>Pavetta gardeniifolia</i>	-	-	-	2.4	0.5	94.3	252	-	55.3	-	-	-	16.6
<i>Balanites maughanii</i>	5	-	-	-	1.8	8.6	-	-	5	-	-	523	14.1
<i>Sterculia rogersii</i>	1.3	5.8	-	5.2	2.9	52	45.8	1.2	31	-	98.3	-	13.9
<i>Acacia gerrardii</i>	-	-	-	297	20.9	-	-	-	-	-	-	-	13.5
<i>Combretum mossambicense</i>	1.3	82.3	0.5	3.2	18.5	5.8	-	2.3	4.4	-	9.9	-	13.4
<i>Ximenia caffra</i>	2.2	16.3	10.1	29.8	13.1	4.7	13.1	-	2.8	-	61.7	-	12.1
<i>Hexalobus monopetalus</i>	-	-	-	-	-	48.8	103	23.7	38.4	28.2	7.9	-	11.9
<i>Cassia abbreviata</i>	-	1	40.9	0.3	8.5	1	-	65.6	27.7	-	-	-	11.5
<i>Ozoroa paniculosa</i>	19.2	2.9	0.7	6.3	9.1	11.9	17.7	19.8	15.2	33.5	-	-	11.2
<i>Strychnos spinosa</i>	-	-	-	-	-	-	-	-	-	-	235	-	10.7
<i>Bridelia mollis</i>	2.8	10.5	17.2	-	6.7	12.7	88.7	10	11.6	8.6	-	-	8.7
<i>Ehretia rigida</i>	7.1	23.8	2.9	13.3	11.2	0.7	-	4.6	2.3	0.4	-	-	7.8
<i>Ficus glumosa</i>	-	-	-	48.6	11.1	-	-	-	-	-	-	-	7.2
<i>Euclia natalensis</i>	-	-	1.4	3.4	1.1	1	104	6.5	3.3	-	41	-	5
<i>Gardenia volkensii</i>	1.7	12.3	6.5	4.1	5.4	-	-	-	-	-	2.8	-	3.6
<i>Rhus pentheri</i>	-	3.9	-	5.9	2.2	-	-	-	-	11.1	-	41	2.9
<i>Rhigozum zambesiacum</i>	-	-	-	-	-	-	-	-	-	-	5.6	111	2.8
<i>Dombeya rotundifolia</i>	4	-	6.5	0.2	2.8	1.7	6.3	3.3	2.4	-	-	-	2.4
<i>Rhus andulata</i>	0.1	-	-	0.7	0.2	-	-	-	-	-	-	-	1.4
<i>Cassine aethiopica</i>	-	-	-	-	-	-	-	-	-	-	-	-	63.5
<i>Bridelia micrantha</i>	-	-	0.1	-	0.02	-	-	-	-	25.5	-	-	1.3
<i>Capparis tomentosa</i>	-	-	-	-	-	-	-	-	-	-	14.3	-	0.6
<i>Adenium multiflorum</i>	-	-	-	-	-	-	20.2	-	-	-	-	-	0.3
<i>Vangueria infausta</i>	-	-	-	-	-	-	-	3.3	1.4	-	-	-	0.3
<i>Ochna pretoriensis</i>	-	-	-	-	-	1.7	-	-	1	-	-	-	0.2
<i>Carissa bispinosa</i>	0.4	-	-	-	0.2	-	-	-	-	-	-	0.6	0.1
<i>Pachypodium saundersii</i>	-	0.6	-	-	0.1	-	-	-	-	-	-	-	0.08
<i>Berchemia zeyheri</i>	-	-	0.1	-	0.02	-	-	-	-	-	-	-	0.01
<i>Bauhinia cf. galpinii</i>	-	0.1	-	-	0.02	-	-	-	-	-	-	-	0.01

content, while the B-horizons are deep and have high concentrations of Ca and K.

The 'Acacia gerrardii variation' is restricted to southern and south-western Klaserie, occurring on all topographic positions except hill-crests. The low tree layer is characterised by *A. gerrardii*, and the shrub layer by *Dalbergia melanoxylon* and *Acacia exuvialis*. Soil clay content and organic matter are relatively high.

The 'Terminalia prunioides variation' has a relative abundance of *Combretum apiculatum* and *Sclerocarya birrea*, while *Terminalia prunioides*, *Commiphora mollis* and *Cissus cornifolia* are characteristic species. The relatively deep soils are sandier, more acidic and less fertile than for the other three variations. This vegetation is ecotonal between *Acacia nigrescens* and *Combretum apiculatum* (see below) open woodlands.

The 'Combretum apiculatum open woodland', the second most widespread vegetation type, is found throughout the reserve predominantly on uplands and some mid-slopes but especially on the more dissected topography of the northern and western areas. Most trees are broad-leaved, non-spinescent and not tall. *Combretum apiculatum*, *Commiphora mollis* and *Acacia erubescens* form an open woodland of low trees with a few emergent *Sclerocarya birrea*. The shrub layer is dominated by *Grewia* spp. Soils are relatively sandy and acidic with low conductivities, organic matter and cation concentrations and vary from skeletal to deep. A description of the three variations follows.

The 'Strychnos madagascariensis variation' occurs mostly in the central and western parts of the reserve on usually deep sandy soil on mid- and upper-slopes and hill crests. The shrub layer is characterized by a high density of *Strychnos madagascariensis* and *Cissus cornifolia*. *Lonchocarpus capassa* is a characteristic tree. The A- and B-horizon soils were the sandiest, and conductivity and organic matter content the lowest, recorded in this study.

The 'Grewia bicolor variation predominates in the northern areas on shallow, gravelly soils with relatively high conductivities and pH, and high rock cover, on relatively steep middle and upper slopes and ridge tops. *Grewia bicolor* dominates the shrub layer, which is also characterized by *Boscia albitrunca* and *Pavetta gardeniifolia*.

The 'Pappea capensis variation' is similar to the *Grewia bicolor* variation but is characterised by

Table 2. Mean value of topo-edaphic variables for the A and B horizon for ten vegetation types in the Klaserie Nature Reserve. Means with the same subscript are not different ($p < 0.05$) by Tukey's HSD test on appropriately transformed data, although untransformed data are presented (sample sizes are indicated below names of vegetation types). The value for the B-horison and for cations of the A-horison is from a single soil pit dug at a nodal site for that vegetation type.

	<i>Terminalia prunioides</i>	<i>Spirostachys africana</i>	<i>Combretum imberbe</i>	<i>Acacia gerrardii</i>	<i>Acacia bicolor</i>	<i>Grewia bicolor</i>	<i>Strychnos madagascar-iensis</i>	<i>Pappea capensis</i>	<i>Colophospermum mopane</i>	<i>Acacia grandicornuta</i>	<i>Lonchocarpus capassa</i>	Overall ¹
	(34)	(23)	(16)	(24)	(20)	(16)	(3)	(16)	(4)	(6)	(162)	
Sand (%)	A 80 _{ab} B 72	77 _b 46	78 _b 69	78 _{ab} 62	80 _{ab} 73	83 _a 86	80 _{ab} -	77 _{ab} 67	82 _{ab} 65	79 _{ab} -	79 (7.5)	
Silt (%)	A 14 _a B 15	15 _a 17	16 _a 21	15 _a 12	15 _a 15	13 _a 6	14 _a 9	16 _a -	12 _a 7	16 _a -	15 (27)	
Clay (%)	A 6 _{ab} B 14	8 _{ac} 37	7 _{ab} 10	8 _a 25	5 _{bc} 12	4 _b 8	6 _{ab} -	7 _{ac} 24	7 _{ab} 28	5 _{ab} -	6 (47)	
pH	A 4.9 _c B 6.0	5.4 _{ac} 6.1	5.4 _{ac} 6.1	7.9 _{bc} 5.0	5.8 _{ab} 5.4	5.0 _c 5.3	4.8 _{ac} -	5.9 _a 7.5	4.7 _{bc} 5.1	6.1 _a -	5.3 (13.3) 116 (84)	
Conductivity ($\mu\text{mhos cm}^{-1}$)	A 74 _{ab} B 71	150 _a 2045	116 _{ab} 101	120 _a 67	134 _{ab} 30	64 _b 20	150 _{ab} -	157 _a 495	104 _{ab} 1255	159 _a -	-	
Calcium (mg g^{-1})	A 5.0 B 5.7	12.9 9.8	8.0 10.3	5.8 13.6	6.3 7.3	2.7 1.6	15.0 -	9.6 32.9	2.9 13.5	6.1 -	-	
Magnesium (mg g^{-1})	A 1.9 B 3.3	3.2 16.3	1.4 3.8	2.2 3.7	1.8 2.8	0.9 1.5	3.5 -	2.4 8.2	1.4 6.3	1.7 -	-	
Potassium (mg g^{-1})	A 1.9 B 0.4	4.7 2.0	1.6 2.3	1.8 0.4	2.1 0.7	1.5 0.7	2.3 -	2.3 7.3	1.3 1.1	2.0 -	-	
Sodium (mg g^{-1})	A 0.2 B 2.3	0.09 2.4	0.03 2.2	0.3 2.3	0.1 2.0	0.2 2.0	0.1 -	0.1 1.8	0.2 2.3	0.2 -	-	
Organic matter (%)	A 1.9 _a B 2.1	2.5 _a 3.3	2.2 _a 2.2	2.5 _a 2.4	2.4 _a 0.5	2.0 _a 0.9	3.9 _a -	3.3 _a 1.1	1.7 _a 2.5	2.2 _a -	2.3 (67)	
Rock (% cover)	0.3 _d	2.6 _{cd}	2.3 _{cd}	1.5 _{cd}	9.7 _{ab}	5.3 _{bc}	30.8 _a	3.5 _{cd}	0.1 _{cd}	3.0 _{bcd}	3.6 (221)	
Gravel (% cover)	3.3 _c	9.4 _{bc}	4.1 _c	4.6 _c	22.2 _a	17.5 _a	28.3 _{ab}	14.7 _{abc}	0.3 _c	3.7 _{bc}	9.7 (146)	
Slope (% cover)	1.1 _c	1.3 _{bc}	1.5 _{bc}	2.0 _{abc}	3.5 _{ab}	2.1 _{abc}	8.3 _a	2.5 _{abc}	1.3 _{bc}	3.4 _{ab}	2.0 (116)	
Position (mean rank)	3.7 _{abc}	2.3 _{de}	2.5 _{de}	2.8 _{cde}	4.0 _{ab}	4.4 _a	4.3 _{abcd}	3.2 _{abcd}	2.0 _{bcde}	1.2 _e	-	

¹ coefficient of variation given in parentheses

Table 3. Mean values of vegetation structure variables for ten vegetation types in the Klaserie Nature Reserve. Means with the same subscript are not different ($P < 0.05$) by Tukey's HSD test on appropriately transformed data, although untransformed data are presented². Sample sizes are given in Table 1.

	<i>Terminalia prunioides</i>	<i>Spirostachys africana</i>	<i>Combretum imberbe</i>	<i>Acacia gerrardii</i>	<i>Acacia bicolor</i>	<i>Grewia bicolor</i>	<i>Strychnos madagascar-iensis</i>	<i>Pappea capensis</i>	<i>Colophospermum mopane</i>	<i>Acacia grandicornuta</i>	<i>Lonchocarpus capassa</i>	Overall ¹
	(34)	(23)	(16)	(24)	(20)	(16)	(3)	(16)	(4)	(6)	(162)	
Shrub density (ha^{-1})	718 _{bd}	1100 _{ac}	802 _{bc}	1130 _{ac}	719 _{bd}	703 _{bd}	714 _{acd}	1609 _a	1118 _{ab}	1136 _{ab}	953 (63)	
Tree density (ha^{-1})	245 _{ab}	217 _{bcd}	144 _{bce}	254 _{ad}	280 _{ad}	261 _{ad}	258 _{ac}	431 _a	217 _{ade}	286 _{ab}	258 (62)	
Total density (ha^{-1})	981 _c	1319 _{abc}	976 _c	1406 _{ab}	1032 _{bc}	1006 _{bc}	992 _{abc}	2059 _a	1350 _{abc}	1448 _{abc}	1233 (54)	
Canopy volume ($\text{m}^3 \text{ha}^{-1}$)	16473 _b	23432 _{ab}	16177 _b	17908 _b	21791 _{ab}	17471 _{ab}	19615 _{ab}	31300 _a	23673 _{ab}	32143 _{ab}	20680 (54)	
Dead tree density (ha^{-1})	37 _a	47 _a	45 _a	31 _a	51 _a	32 _a	54 _a	34 _a	64 _a	44 _a	40 (71)	
Coppice density (ha^{-1})	14 _{bcd}	10 _{bc}	22 _{ab}	13 _{bc}	31 _{ad}	42 _a	16 _{ab}	19 _{bcd}	11 _{ac}	13 _{ac}	19 (113)	
Unavailable browse (%)	5 _{abc}	13 _{cd}	8 _{bc}	10 _{cd}	3 _{ab}	1 _a	3 _{abc}	1 _a	5 _{abc}	14 _{cd}	6 (134)	

¹ coefficient of variation given in parentheses

² types compared with pairwise comparisons using Wilcoxon's test ($\alpha = 0.0011$)

trees of *Pappea capensis*, *Manilkara mochisia*, *Hippocratea longepetiolata* and *Boscia albitrunca* and shrubs of *Euclea natalensis*, *Adenium multiflorum*, *Hexalobus monopetalus*, *Pavetta gardeniifolia* and *Sterculia rogersii* on rocky outcrops. Soil is confined to shallow gravelly pockets between rocks. Soil organ-

ic matter, conductivity and cation concentrations are relatively high.

The '*Colophospermum mopane* open woodland' occurs in the driest parts of the reserve in two main blocks; an eastern one on relatively deep, fine-textured soils and gently undulating topography, and a second

one in the north-east on dissected topography with shallow, gravelly soils. *Colophospermum mopane* is overwhelmingly dominant (mean of 63% of total canopy volume), and ranges in size from small shrubs to >10 m high emergent trees. *Combretum apiculatum* and *Sclerocarya birrea* are important in upland areas and *Dalbergia melanoxylon* and *Euclea divinorum* are prominent in lowlands. *Colophospermum mopane* is found in all topographic positions but in the south-east is found on bottomlands and lower slopes, forming a catena with *Combretum apiculatum* open woodland on the upper slopes. Soils are relatively fine textured and pH, conductivity and organic matter are relatively high. The B- horizons tend to have high cation concentrations and conductivity.

The 'Acacia grandicornuta open woodland' is found adjacent to a few large seasonal watercourses on the flattest topography in the centre of the reserve and is dominated by shrubs and trees (up to 10 m high) of *A. grandicornuta*. Other important trees are *Acacia nigrescens*, *Terminalia prunioides*, *Combretum hereroense* and *Balanites maughamii*. Important shrubs are *Euclea divinorum*, *Grewia bicolor*, *Maytenus senegalensis* and *Albizia harveyi*, while *Rhigozum zambesiaceum*, *Cassine* spp. and *Rhus* spp. are characteristic. Sandy acidic topsoils overlies finer textured and more base-rich soils below.

'*Lonchocarpus capassa*-*Combretum hereroense* woodland' occurring on base-rich, silty alluvial soils adjacent to the major watercourses, supports a characteristic woody vegetation with a high proportion of tall trees and a well-developed shrub layer (Table 2). Dominant trees are *Acacia nigrescens*, *Combretum imberbe*, *Lonchocarpus capassa*, *Combretum hereroense*, *Sclerocarya birrea*, *Diospyros mespiliformis*, *Peltophorum africanum* and *Schotia brachypetala*. *Maytenus senegalensis*, *Euclea undulata* and *Sterculia rogersii* are the dominant shrubs. Large trees of *Breonardia salicina*, *Ficus* spp. and *Xanthocercis zambesiaca* are found adjacent to the Olifants river.

Vegetation-environment gradients

There was substantial spatial variation in topo-edaphic conditions (Table 2). The first two principal components of the PCA of the ten topo-edaphic variables (accounting for 61% of the variance) identified an obvious primary textural gradient, with pH, conductivity and organic matter correlated with high silt and clay (Figure 3a). High rock and gravel cover on steep-

er slopes, to some extent correlated with landscape position, formed a secondary gradient.

Variation in vegetation structure across sites was likewise pronounced (Table 3). Three main gradients in vegetation structure are apparent (Figure 3b) on the basis of the first two axes of the PCA (accounting for 68% of the variance); (i) increasing density of shrub and of all individuals (which are highly correlated, $r = 0.94$, $p < 0.0001$), (ii) increasing canopy volume and density of trees ($r = 0.73$, $p < 0.0001$), and (iii) increasing density of mainly coppice but also dead individuals ($r = 0.17$, $p < 0.027$).

The CA and CCA ordinations were fundamentally different in their performance (Table 4). The first four axes of the CA accounted for 2.5 times the species variance accounted for by CCA, whilst the variance of the species-environment relation accounted for by CCA was not markedly greater than that accounted for by CA. These differences indicate that important environmental factors were not included in the analysis, and the CA results are therefore emphasized in preference to the CCA results. Despite this, the overall ordination and first axis of the CCA were significant ($P < 0.01$), confirming that the measured topo-edaphic variation explained a significant, if low, proportion of community variation.

The included environmental variables exercised a similar influence on the first axis of both the CA and CCA ordinations (Figure 4a, CCA not shown), but differed on the second and subsequent axes. An important feature of the ordinations were the small differences between axes in their eigenvalues (and hence variance of species data), an effect also apparent in axes 5–8 of the CA (Table 4). The pattern of floristic variation is therefore not a primary gradient with a few subsidiary gradients, but a composite of smaller, almost equivalent, independent gradients.

At least some of these gradients were in response to topo-edaphic variation, as indicated by the species-environment relation (Table 4). The first axis of CA corresponded with a gradient from low-lying, rock-free, relatively clay- and base-rich sites, through to higher-lying, sandy, gravelly, base-poor sites (Figure 4a). *Acacia grandicornuta*, *Cassine aethiopica*, *Cassine transvaalensis*, and *Rhus undulata* were associated with the former set of conditions, while *Terminalia sericea*, *Strychnos madagascariensis*, *Mundulea sericea*, *Dombeya rotundifolia* and *Ozoroa paniculosa* were characteristic of the latter. The second CA axis ranged from relatively clay- but not base-rich sites, characterised by *Colophospermum mopane*, through to

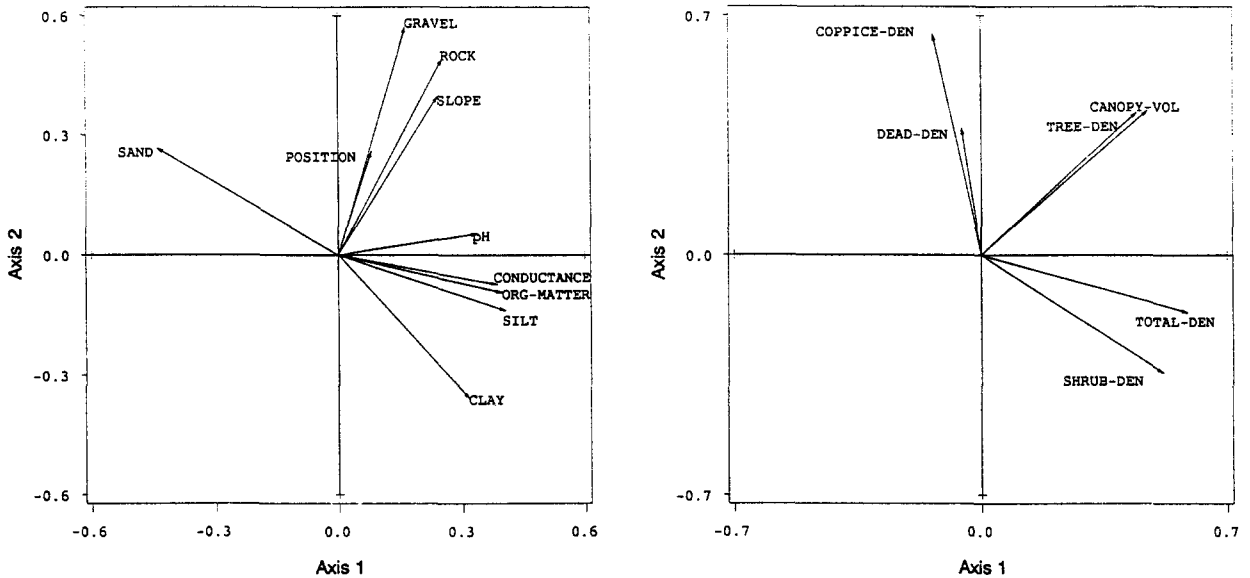


Figure 3. The eigenvector loadings on the first two axes of a correlation-type principal component analysis of a) ten topo-edaphic variables (eigenvalues: axis 1=3.96, axis 2=2.10; 61% of the variance), and b) six vegetation structure variables (eigenvalues: axis 1=2.67, axis 2=1.42; 68% of the variance). Variables are positively correlated if their arrows subtend a small angle, orthogonal if their arrows are at 90°, and negatively correlated if their arrows are in opposite directions.

relatively steep, rocky and gravelly sites, characterised by *Bridelia mollis*, *Hippocratea longepetiolata*, *Sterculia rogersii*, *Manilkara mochisia*, *Pappea capensis*, *Hexalobus monopetalus*, *Pavetta gardeniifolia* and *Boscia albitrunca*. An apparently repetitious pattern of the relation of environmental variables to floristic axes, specifically gradients in either soil chemical or physical properties, or jointly, in relation to gradients in landscape physiography appeared in the subsequent axes. At least some of these are interpreted as catenal sequences which differ because of unidentified causes, some of which are considered in the discussion section.

To facilitate interpretation of subsequent axes, two discrete clusters of samples ($n = 21$), dominated by *Colophospermum mopane* or *Acacia grandicornuta*, were deleted and the CA ordination satisfactorily redone (Table 4, detailed results not given). The first axis identified an association between alluvial sites with silt- and base-rich soils and species such as *Capparis tomentosa*, *Diospyros mespiliformis*, *Euclea undulata*, *Schotia brachypetala*, *Ximenia caffra*, *Spirostachys africana*, *Combretum imberbe* and *Combretum hereroense*, as well as an association between *Acacia gerrardii* and relatively clay-rich sites. It was noteworthy that in all the ordinations the most dominant species other than *Colophospermum mopane*, namely *Acacia nigrescens*, *Combretum*

apiculatum, *Dichrostachys cinerea*, *Sclerocarya birrea*, *Terminalia prunioides*, *Ziziphus mucronata* and *Grewia bicolor*, were not clearly related to environmental gradients, and are thus found toward the centre of the ordination diagrams (Figure 4a, b).

In summary, ordination analyses identified that important environmental variables had not been included, that topo-edaphic gradients significantly influenced floristic variation, and that floristic variation was of the nature of a large number of relatively equivalent, independent gradients.

The partial canonical correlation analysis indicated that topo-edaphic variation, independently of floristic variation, had a direct influence on the physiognomic structure of the Klaserie savanna woodlands. Only the first partial canonical correlation ($r = 0.51$, $p = 0.0063$) was effective in relating the soil and vegetation structure variables. This analysis identified that when sand, total density and tree density were taken into account (i.e. these were suppressor variables, SAS 1988), the main pattern of variation is a correlation between shrub density and clay-rich soils or rocky areas, and between coppice density and higher-lying areas with very silty or gravelly soils.

Table 4. Summary of the correspondence (CA) and canonical correspondence (CCA) analyses for the Klaserie Nature Reserve; a) CA-all samples included (3 passive), b) CA-all samples, axes 5–8, c) CA-21 samples deleted (see text in Results), and d) CCA-all samples included

		Axis order			
		1	2	3	4
a)	CA – all samples, axes 1–4				
	Eigenvalue	0.182	0.146	0.141	0.117
	Species-environment correlation	0.574	0.498	0.557	0.537
	Cumulative percentage variance of:				
	Species data	8.2	14.8	21.1	26.4
	Species-environment	21.0	33.6	48.9	60.8
b)	CA – all samples, axes 5–8				
	Eigenvalue	0.097	0.093	0.081	0.070
	Cumulative percentage variance of:				
	Species data	5.9	11.6	16.6	20.9
c)	CA-21 – samples deleted, axes 1–4				
	Eigenvalue	0.153	0.144	0.102	0.092
	Species-environment correlation	0.698	0.763	0.428	0.474
	Cumulative percentage variance of:				
	Species data	7.7	14.9	20.1	24.7
	Species-environment	25.4	54.0	60.4	67.4
d)	CCA – all samples, axes 1–4				
	Eigenvalue	0.099	0.063	0.040	0.026
	Species-environment correlation	0.803	0.687	0.663	0.552
	Cumulative percentage variance of:				
	Species data	4.5	7.3	9.1	10.3
	Species-environment	34.7	56.8	70.9	79.9

Discussion

Floristic variation

Floristic variation of southern African savanna woodlands shows a general correspondence to topo-edaphic variation (Joubert 1971; Leistner & Werger 1973; Coetzee *et al.* 1976; Van der Meulen 1979; Van Rooyen, Theron & Grobbelaar 1981a, b, c; Coetzee 1983; Whateley & Porter 1983; Van Rooyen 1983; Le Roux *et al.* 1988; O'Connor & Campbell 1986; O'Connor 1992), as was discerned in this study, yet the precise nature of this relationship remains elusive. The two broad divisions of *Acacia nigrescens* open woodland and *Combretum apiculatum* open woodland in Klaserie correspond to the microphyllous thorny and broad orthophyllous plains bushveld respectively of Werger and Coetzee (1978). *Colophospermum*

mopane woodlands are distinctive and widespread in southern Africa (Henning & White 1974; Werger & Coetzee 1978), but show significant floristic and physiognomic variation throughout their range (e.g.'s Louw 1970; Van Rooyen *et al.* 1981c; O'Connor 1992). Hygrophilous communities within these semi-arid savannas are invariably physiognomically and floristically distinct (e.g. Van Rooyen *et al.* 1981a), but insufficient of these have been described to allow comparison.

Woodland physiognomic structure

Woodland communities of southern African savannas invariably differ in their physiognomy (Werger 1978; Van Rooyen *et al.* 1981a, b, c; Coetzee 1983; Brendenkamp & Theron 1985; O'Connor 1992), as we have described for Klaserie. However, these previ-

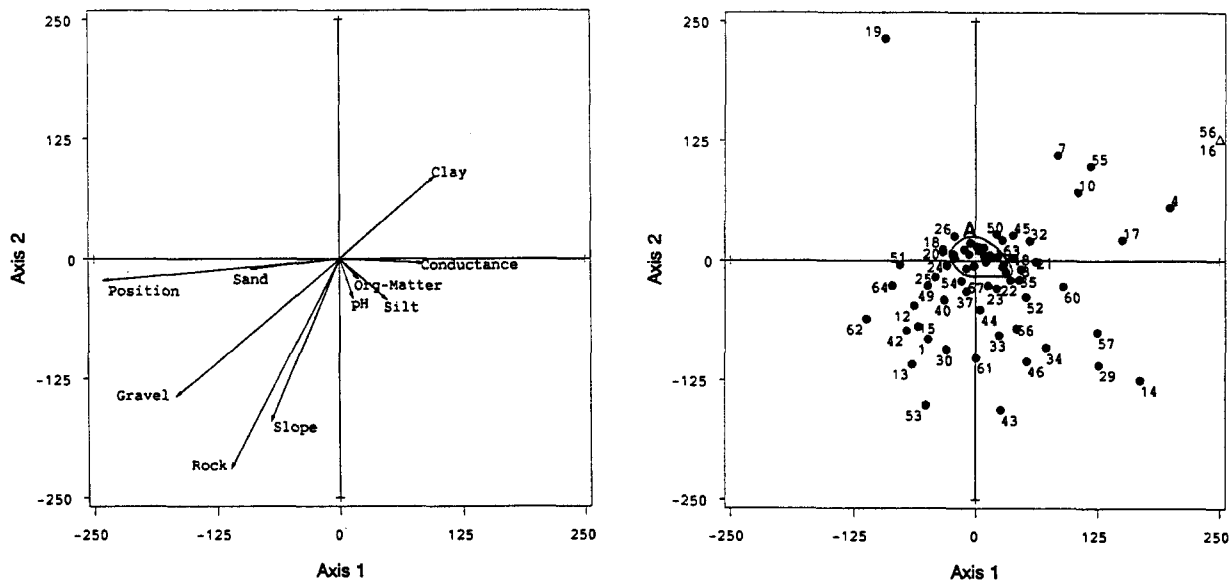


Figure 4. Plots of the first two axes of the correspondence analysis of all samples (3 passive): a) environmental variables, and b) species. Refer to Table 4 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle they are correlated; if they subtend an angle of 90° they are orthogonal; if they subtend an angle of $>90^\circ$ they are negatively correlated. The order of species along any environmental variable is obtained by dropping a perpendicular bisector from the species to the extended line of the arrow. Key to the species: 1 – *Acacia erubescens*; 2 – *Acacia exuvialis*; 3 – *Acacia gerrardii*; 4 – *Acacia grandicornuta*; 5 – *Acacia nigrescens*; 6 – *Acacia nilotica*; 7 – *Acacia senegal*; 8 – *Acacia tortilis*; 9 – *Albizia harveyi*; 10 – *Balanites maughamii*; 11 – *Bolusanthes speciosus*; 12 – *Boscia albitrunca*; 13 – *Bridelia mollis*; 14 – *Capparis tomentosa*; 15 – *Cassia abbreviata*; 16 – *Cassine aethiopica*; 17 – *Cassine transvaalensis*; 18 – *Cissus cornifolia*; 19 – *Colophospermum mopane*; 20 – *Combretum apiculatum*; 21 – *Combretum hereroense*; 22 – *Combretum imberbe*; 23 – *Combretum mossambicense*; 24 – *Commiphora africana*; 25 – *Commiphora mollis*; 26 – *Commiphora pyracanthoides*; 27 – *Dalbergia melanoxylon*; 28 – *Dichrostachys cinerea*; 29 – *Diospyros mespiliformis*; 30 – *Dombeya rotundifolia*; 31 – *Ehretia rigida*; 32 – *Euclea divinorum*; 33 – *Euclea natalensis*; 34 – *Euclea undulata*; 35 – *Gardenia spatulifolia*; 36 – *Grewia bicolor*; 37 – *Grewia flavescens*; 38 – *Grewia hexamita*; 39 – *Grewia hybrid*; 40 – *Grewia monticola*; 41 – *Grewia villosa*; 42 – *Hexalobus monopetalus*; 43 – *Hippocratea longepetiolata*; 44 – *Lonchocarpus capassa*; 45 – *Maerua parvifolia*; 46 – *Manilkara mochisia*; 47 – *Maytenus heterophylla*; 48 – *Maytenus senegalensis*; 49 – *Mundulea sericea*; 50 – *Ormocarpum trichocarpum*; 51 – *Ozoroa paniculosa*; 52 – *Pappea capensis*; 53 – *Pavetta gardenifolia*; 54 – *Peltophorum africanum*; 55 – *Rhus pentheri*; 56 – *Rhus undulata*; 57 – *Schotia brachypetala*; 58 – *Sclerocarrya birrea*; 59 – *Securinega virosa*; 60 – *Spirostachys africana*; 61 – *Sterculia rogersii*; 62 – *Strychnos madagascariensis*; 63 – *Terminalia prunioides*; 64 – *Terminalia sericea*; 65 – *Ximenia americana*; 66 – *Ximenia caffra*; 67 – *Ziziphus mucronata*. To avoid congestion, the following species groups are given in b), A=2, 3, 5, 6, 9, 11, 20, 21, 27, 28, 31, 36, 38, 39, 41, 47, 58, 59, 65. Triangles denote species whose co-ordinates were outside the plotted ordination space.

ous studies have not differentiated how much physiognomic variation of savanna woodlands is a direct result of environmental gradients rather than simply a reflection of compositional variation. The striking differences in the physiognomy of some savannas which are floristically very similar (Van der Meulen & Westfall 1980; O'Connor 1992) would suggest that factors, independent of compositional variation influence physiognomic variation. The results of the partial canonical correlation analysis of the structural and environmental variables, after accounting for the effect of composition, support this notion. The observed relationship between coppice density and higher-lying areas with silty or gravelly soils is most likely related to the elevated levels of elephant damage these areas experi-

ence (Witkowski 1983), that is, topo-edaphic conditions indirectly affect woodland physiognomy through a biotic agent rather than directly affecting it. Fire is unlikely to play a role because the whole area is on a three year burning cycle (interrupted by droughts) with minor differences in fuel loads among vegetation types. Grazing pressure is greatest in the central and riverine areas of Klaserie (Witkowski 1983) and may play a significant role by encouraging bush encroachment in those areas. There is no direct evidence of the cause for the relationship between shrub density and clay-rich soils or rocky areas, but it is suggested that the shrub growth form may be well-suited to the relatively drought prone conditions of heavier-textured soils in semi-arid environments.

Topo-edaphic variation

The primary textural gradient (silt and clay correlated with pH, conductivity and organic matter) of the soils of the Klaserie Nature Reserve is a not uncommon soil gradient of southern African savannas (Louw 1970; Leistner & Werger 1973; Dye & Walker 1980; Bredenkamp *et al.* 1983). There would seem to be two main reasons for this gradient in southern African savannas, both of which are considered to be relevant to Klaserie. In the first, different parent geologies (most notably granites and gneisses versus ultrabasic igneous formations - usually of dolerite, gabbro or basalt) give rise to sandy and finer textured soils respectively (Macvicar *et al.* 1977). However, Klaserie does not encompass the distinct geological contrasts of granite (gneiss) and basalt- or gabbro-derived landscapes which occur in adjacent savannas (e.g. Kruger National Park – Gertenbach 1978, 1983; Manyeleti - Bredenkamp *et al.* 1983). In the second, catenal differentiation of initially coarser granite- or gneiss-derived soils gives rise to sandy hill crests and illuviated clay complexes on the bottom slopes (e.g. Dye & Walker 1980). These two patterns occur at different spatial scales, and a clearer understanding of their relative influence on savanna woodlands would require different sampling approaches.

A gradient approach

The ordinations provided a meaningful description of floristic variation but did not fully identify the responsible environmental gradients. Other environmental variables which might have provided a more complete understanding of floristic variation are briefly considered. Rainfall invariably emerges as a predominant determinant of savanna woodland floristics when a sufficient rainfall gradient is sampled (e.g. Skarpe 1986; Palmer & van Staden 1992). However, although there was a gradient of decreasing rainfall from the southwest to the north-east of the reserve of about 50 mm per annum difference, it was not possible to obtain site-specific data for rainfall. The distribution of *Colophospermum mopane* (drier) and *Acacia gerrardii* (wetter) seems to correspond with this rainfall gradient, as the two species occurred on similar soil types (relatively clay- but not base-rich A-horizon), and possibly other species respond similarly. The obvious importance of soil moisture for the structure of a semi-arid ecosystem would suggest that profile depth (moisture storage capacity) might extract additional species variance for

soils of equivalent texture. The presence of a number of duplex soils meant that the properties of the A-horizon did not necessarily reflect those of the B-horizon, while the B-horizon seemed to exert a strong influence on the structure of the woody component of the *Acacia grandicornuta* and *Colophospermum mopane* vegetation types. The B-horizon similarly exercised a strong influence on plant species distribution in the wetter Manyeleti Game Reserve (Bredenkamp 1985). Future research in Klaserie would best concentrate on direct gradient analysis of catenal gradients on different parent material types studied along the rainfall gradient.

The savannas of southern Africa are most commonly found on extensive peneplains of considerable spatial extent (>20 000 km²), with generally only gradual gradients in climatic factors. Correspondingly, most savanna woodland species have extensive distributions (e.g. Coates Palgrave 1977). Almost all of the above-cited phytosociological studies conducted in southern Africa resemble this study in that a relatively small spatial area, usually a conservation unit smaller than the Klaserie Private Nature Reserve, was the object of study (e.g. of exceptions are Van der Meulen 1979; Skarpe 1986). The objectives of these studies have been to describe the vegetation of specific localities rather than the elucidation of the primary environmental gradients determining savanna structure. Consequently, only restricted climatic gradients and a small portion of the geographic range of most species have been sampled. We suggest a more realistic interpretation of the environmental gradients determining plant species and community variation will only be realised when studies are conducted over a sufficient range of the climatic (especially rainfall) variables, appropriately stratified for topo-edaphic conditions. While the overall effect of rainfall on savanna woodland composition over the sub-continent might appear obvious, its interaction with topo-edaphic conditions and more subtle climatic variables (e.g. temperature) is not, and requires an appropriately stratified sampling strategy to be revealed. This might be best realised through an amalgamation of the now quite prolific number of studies already completed.

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