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South African Journal of Botany 72 (2006) 256 – 262
SOUTH AFRICAN JOURNAL OF BOTANY
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A canonical correspondence analysis (CCA) of the vegetation–environment relationships in Sudanese savannah, Senegal

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Received 7 January 2005; accepted 7 September 2005

Abstract

The effect of environmental variables on the structure of woody vegetation within one geomorphological unit (500 ha) in Niokolo Koba National Park in Senegal was investigated. A total of 59 woody species from 25 families were recorded in 43 relevés. Canonical Correspondence Analysis (CCA) was used to evaluate the effect of soil type, topography and termitaria presence on the vegetation structure. The effects of soil type and topographical position were significant and respectively explained 15.9% and 5.2% of the species data variability. Termitaria presence was non-significant and had just a marginal influence on the vegetation structure and explained only 1.7% of the data variability. One-way ANOVA was used to evaluate the effect of soil type on total cover of particular layers. Significant differences were revealed for low shrub (0–2 m) and tree layers (6–20 m). The low shrub layer was the best developed on the plinthitic hardpan, the best-developed tree layer occurred on granite outcrops. High shrub layer (2–6 m) did not show any dependence on the soil type. In conclusion, we found that soil type and topography were the main factors affecting woody vegetation of the locality.

Keywords: Niokolo Koba National Park; Soil type; Ordination; Vegetation structure; West Africa

1. Introduction

Niokolo Koba National Park (NKNP) in southeastern Senegal covers 913 000 ha and is Senegal's largest and oldest national park. Its importance as a well-preserved ecosystem of Sudanese and Sudano-Guinean savannah with extraordinary rich biodiversity concerns the entire region of West Africa. NKNP has always attracted the attention of zoologists due to its high number of vertebrate species (Dekeyser, 1956; Dupuy, 1971; Verschuren, 1982; McBeath and McGrew, 1982, Harisson, 1983; Galat, 1992; Nežerková and Hájek, 2000), but also botanists for its high vascular plant diversity (Bâ et al., 1997). To date, botanical studies there were focused on floristic explorations (Chevalier, 1900a,b, 1920; Adam, 1963, 1968, 1971; Berhaut, 1967) or vegetation classification (e.g. Trochain, 1940; Adam, 1966; Roure, 1956; Schneider and Sambou, 1982).

Trochain (1940) showed that the most important factors determining the vegetation in Senegal are climatic conditions at the primary and edaphic conditions at the secondary level. According to Madsen and Sambou (1998), vegetation types of different floristic composition or vegetation cover density in NKNP are predetermined by geomorphology, soil conditions, and water regime. Recent ecological studies of woody savannah are based on a number of 1 ha physiognomically homogeneous plots in different, well distinguished geomorphological units (Madsen et al., 1996; Lykke and Sambou, 1998; Madsen and Sambou, 1998; Goudiaby et al., 2001). The most popular method for data evaluation is the use of the importance value index (IVI) and size-class structure of the woody stratum according to Mueller-Dombois and Ellenberg (1974).

Sudanese savannah is in general considered very heterogeneous and is characterised by many transition zones between vegetation units determined by environmental gradients (Lawesson, 1995). Even on a large scale, within one geomorphological unit, different soil types and topographical characteristics can be found. Although the variability of Sudanese woody savannah is relatively high also on the small scale, causes of this small-scale heterogeneity have not been investigated yet. Thus the aim of our study was to reveal environmental variables most affecting the structure of woody

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doi:10.1016/j.sajb.2005.09.002

vegetation on a small scale (500 ha) in NKNP. The use of a direct ordination approach enabled us to determine the variability of vegetation data explained by observed environmental variables.

2. Material and methods

2.1. Study site

The study site (500 ha) is located in the central part of NKNP between the sites Patte d'Oie and Lingué Kountou, north of the Niokolo River (13°02′35″N, 13°05′51″W, Fig. 1). The area was selected to create a protective breeding enclosure for the critically endangered western subspecies of the giant eland (*Taurotragus derbianus derbianus*) (Nežerková et al., 2004). The climate is characterised by a pronounced rainy season from July to October with an annual rainfall ranging from 800 to 1100 mm. The average monthly temperature is 25 °C from November to January and 33 °C from April to May (Tambacounda and Kédougou meteorological stations). A non-perennial stream, Béré Boulo To River, runs through the site during the rainy season. The study area comprises flat terrain that is underlain by metamorphic rock of birrmien plinth and by sediments of the Continental Terminal Formation, consisting of sandstone, shale, marl, sand and clay. Scattered granite outcrops also occur in the study area. Soils are predominantly ferric luvisols, lithosols on hardpans, regosols, alluvial and hydromorphic.

The area belongs to the transition zone between the phytochoria of the Sudanian Regional Centre of Endemism and the Guinea-Congolia/Sudania transition zone (White, 1983). The generalised vegetation–landscape type is Sudano-

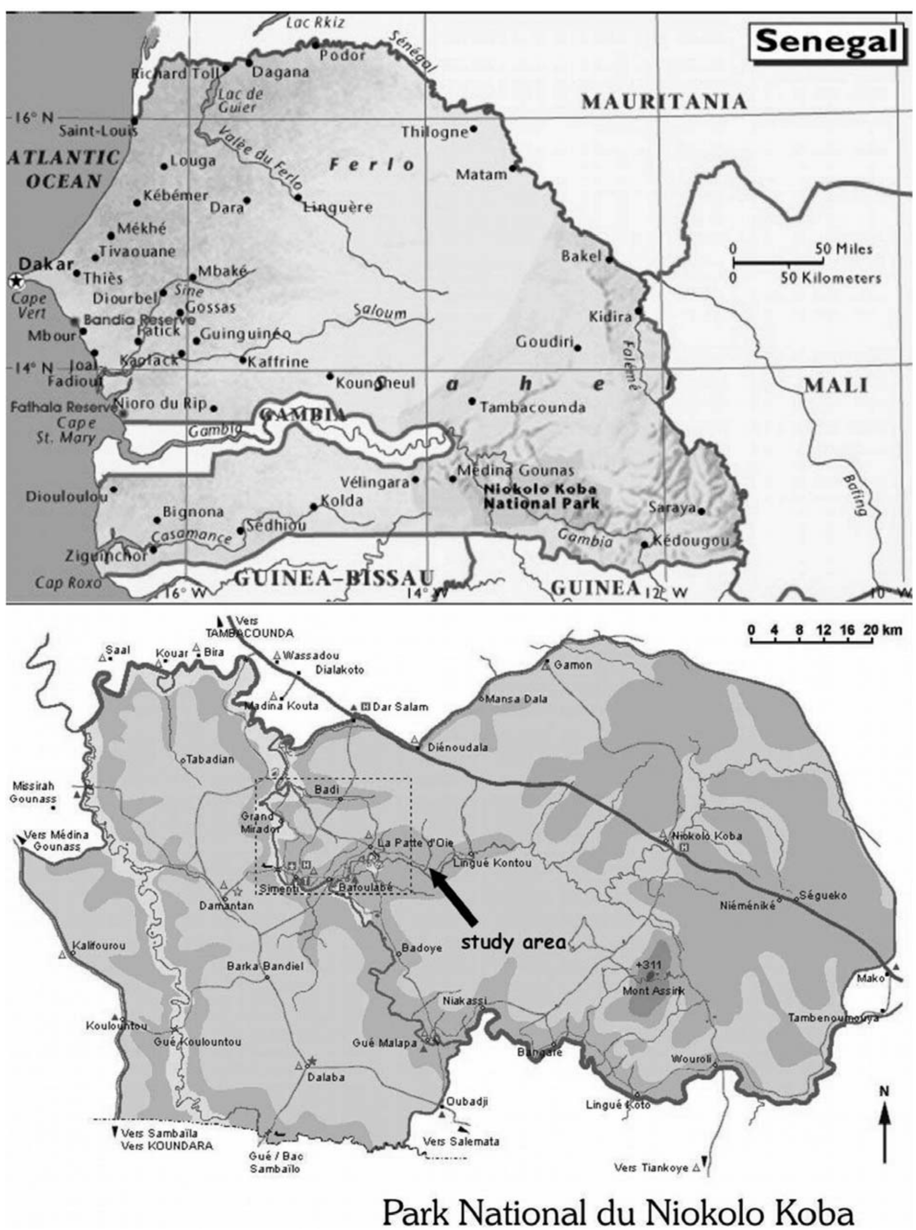

Fig. 1. Map of Senegal and Niokolo Koba National Park with the location of the study area.

Guinean woodland–grassland mosaic (Frederiksen and Lawesson, 1992). The principal vegetation type of the study area is *Combretum glutinosum–Annona senegalensis* woodland and a mosaic of grass and woody savannah characterised by *Combretum nigricans*, *Guiera senegalensis*, *Lannea microcarpa*, *Terminalia avicennoides*, and *Crossopteryx febrifuga*. *Andropogon gayanus*, *Cymbopogon giganteus*, *Ctenium newtonii*, *Schizachyrium sanguineum* and *Diheteropogon amplectens* are the most frequently occurring grasses (Lawesson, 1995).

2.2. Vegetation data

The present study was carried out in May and June 2001, at the end of the dry season and the beginning of the rainy season. A strategy of random sampling was used where the vegetation appeared to be homogeneous in structure and floristic composition. A total of 43 phytosociological relevés of 20 × 20 m (400 m^2) was collected over the area. Woody plants' composition and percentage cover of individual species were recorded in each plot. For the evaluation of particular vegetation layers, height classes were determined as follows: E1—low shrub layer (0–2 m), E2—high shrub layer (2–6 m), E3—tree layer (6–20 m). Nomenclature is according to Arbonnier (2000), Geerling (1982) and Berhaut (1967).

2.3. Environmental data

Environmental data such as soil type, topography and termitaria presence were recorded in each relevé. As the topsoil layer is probably the most important source of nutrients for plants and the easiest to sample, attention was given to the topsoil layer during this study. Five categories of soil types were recognised according to Vieillefon (1971) (Table 1). We recognised two topographical categories (To): depressions and plains. Particular nutrient-rich conditions were found around termite mounds, thus creating particular associated vegetation patterns, which was the main reason to record the presence of termitaria (T). All environmental data were categorical, coded in the form of dummy variables.

Table 1
Description of soil types in the study area

Designation	Soil type	Description (according to Vieillefon, 1971)
SL	Sandy loam	Little developed sandy deposits in alluvial zones and on bounds of plateaus
LG	Lateritic soil with gravel	Type of regosol with fine gravel, associated with fragments of ferric soils
FM	Ferralitic soil with medium stones	Complex of lithosols associated with gravel, hydromorphic and ferric soils with fairy stones
GO	Granite outcrops	Granite massive orientated southeast–northwest, outcrops constituted by big granite boulders on hills
PH	Plinthitic hardpan	Type of lithosol with ferrolateritic concretions

Table 2
Recorded species and their mean cover (%) in the study area

Family	Species	E1	E2	E3
Anacardiaceae	*Lannea acida*	0.29	3.13	10.33
	Lannea microcarpa	1	1	8.73
	Lannea velutina	0.49	4.1	1.75
Annonaceae	*Annona senegalensis*	1.54	0	0
	Hexalobus monopetalus	1	4.53	2.5
Apocynaceae	*Saba senegalensis*	0	44.25	0
Arecaceae	*Borassus aethiopum*	1	0	19.25
Bignoniaceae	*Stereospermum kunthianum*	0.2	0	0
Bombacaceae	*Bombax costatum*	0.1	0.64	1.2
	Ceiba pentandra	0	0	1
Caesalpiniaceae	*Burkea africana*	1.87	2	9.33
	Cassia sieberiana	0	0.1	0
	Cordyla pinnata	0.58	0	10.85
	Daniellia oliveri	0.36	3.39	1
	Detarium microcarpum	0.1	0	0
	Piliostigma reticulatum	0.2	1	0
	Piliostigma thonningii	1	0	15
	Tamarindus indica	0.4	0	1
Capparaceae	*Capparis tomentosa*	0.1	0	0
Celastraceae	*Maytenus senegalensis*	0.1	0	0
Cochlospermaceae	*Cochlospermum tinctorium*	4.61	0	0
Combretacea	*Anogeissus leiocarpus*	0.1	0	3.39
	Combretum collinum	23.75	0	0
	Combretum fragrans	0	1.5	0
	Combretum glutinosum	13.14	10.5	0
	Combretum micranthum	0	1	0
	Combretum molle	0.1	0	0
	Combretum nigricans	0.6	4.68	1.75
	Combretum tomentosum	1	0	0
	Guiera senegalensis	10.49	0	0
	Terminalia avicennoides	6.53	7.86	0
	Terminalia laxiflora	0.1	0	0
	Terminalia macroptera	1.47	0	8.75
Ebenaceae	*Diospyros mespiliformis*	0	8	1
Euphorbiaceae	*Euphorbia poissonii*	1	0	0
Fabaceae	*Indigofera* sp.	4.275	0	0
	Pterocarpus erinaceus	0.4	1.12	3.86
	Pterocarpus lucens	0	21.7	0
Hymenocardiaceae	*Hymenocardia acida*	0	0.44	0
Icacinaceae	*Icacina senegalensis*	0.4	0	0
Lamiaceae	*Hyptis suaveolens*	0.3	0	0
Loganiaceae	*Strychnos spinosa*	0.1	2.26	0
Mimosaceae	*Acacia ataxacantha*	0	1.83	0
	Acacia sp.	0	9.9	0
	Dichrostachys cinerea	0.14	1.5	0
Mimosaceae	*Entada africana*	0.96	3.8	0
Olacaceae	*Ximenia americana*	0	0.55	0
Poaceae	Grasses	14.29	0	0
Rhamnaceae	*Ziziphus mauritiana*	0	0.55	0
	Ziziphus mucronat	0	0.1	0
Rubiaceae	*Crossopteryx febrifuga*	0.58	2.08	0
	Feretia apodanthera	0.26	0	0
	Gardenia ternifolia	0.25	0	0
	Mitragyna inermis	0	1	19.25
	Nauclea latifolia	0	1	0
Sterculiaceae	*Sterculiasetigera*	0.1	0.1	0
Tiliaceae	*Grewia barteri*	0.1	0	0
	Grewia bicolor	0	0.36	0
	Grewia cissoides	0.1	0	0
	Grewia flavescens	0	0.73	0
Verbenaceae	*Vitex madiensis*	1.09	0	0
Vitaceae	*Cissus populnea*	0.33	0	0

E1—low shrub layer (0–2 m), E2—high shrub layer (2–6 m), E3—tree layer (6–20 m).

Table 3
Results of CCA analyses of cover estimates of low shrub, high shrub and tree layers

Tested hypotheses	Explanatory variables	Covariables	% explained variability (all)	*F*-ratio (all)	*P*-value (all)
A1	SL, LG, FM, GO, PH	T, To	6.1 (15.9)	2.33 (1.70)	0.004 (0.002)
A2	T	SL, LG, FM, GO, PH, To	3.0	1.13	0.30
A3	SL, LG, FM, GO, PH, T	To	5.9 (16.2)	2.27 (1.57)	0.006 (0.002)
A4	To	SL, LG, FM, GO, PH, T	5.2	1.92	0.01
A5	SL, LG, FM, GO, PH, To	T	5.8 (17.2)	2.23 (1.72)	0.014 (0.002)
A6	SL, LG, FM, GO, PH, To, T		5.8 (17.8)	2.23 (1.74)	0.014 (0.002)

% explained variability—species variability explained by canonical axis 1 (all axes), *F*-ratio—*F* statistics for the test of particular analysis axis 1 (all), *P*-value—corresponding probability value obtained by the Monte Carlo permutation test for axis 1 (all). Abbreviations: GO, FM, LG, PH, SL—soil types according to Table 1. To—topographical position, T—termite hill.

A1—Is the species composition specific for the particular substratum? Yes.

A2—Is the species composition influenced by the presence of a termite hill? No.

A3–A6—Is the species composition related to the tested variables? Yes.

2.4. Data analysis

Classification (e.g. Siebert et al., 2002) or ordination (e.g. Pavlů et al., 2003) are two possible means to obtain results from multivariate data analysis. We preferred a direct ordination method to enable us to test environmental variables collected for each relevé. All ordinations were performed in the Canoco program (Version 4.5) (ter Braak and Šmilauer, 2002).

Detrended Correspondence Analysis (DCA) was used to detect the length of the environmental gradient. After DCA, Canonical Correspondence Analysis (CCA) was applied because the data set was relatively heterogeneous and therefore the length of ordination axes in DCA was relatively long (Lepš and Šmilauer, 2003). The Monte Carlo permutation test was used to reveal the effect of the obtained explanatory variables (environmental in Canoco terminology) on the plant species composition. Variability of vegetation data explained by the tested environmental variables (e.g. soil type, topography, termitaria presence) was used as explanatory power measure for each environmental variable. Therefore we are able to reveal the relative variability of vegetation data explained by environmental factors. We used unrestricted permutations because relevés were collected by random sampling without obvious spatial arrangement. A total of 499 permutations were performed and results of the analyses were visualised in the form of ordination diagrams in the Canodraw for Windows program (ter Braak and Šmilauer, 2002). One-way ANOVA, followed by a post-hoc comparison Tuckey test, in the STATISTICA program (Version 6) was used for evaluation of univariate data.

3. Results and discussion

We recorded 59 woody species from 25 families in the study area. The most abundant families were *Combretaceae* (18.6%), *Caesalpiniaceae* (13.5%), *Rubiaceae* (8.5%), *Mimosaceae* (6.8%), and *Tiliaceae* (6.8%). *Combretum collinum*, *C. glutinosum* and *G. senegalensis* followed by *T. avicennoides*, *Indigofera* sp., and *Cochlospermum tinctorium* were the most abundant woody species in the low shrub layer, *Saba senegalensis*, *Pterocarpus lucens*, *C. glutinosum*, and *Acacia* sp. in the high shrub layer, and *Mitragyna inermis*, *Borassus aethiopum*, *Piliostigma thonningii*, *Cordyla pinnata*, *Lannea acida* and *Burkea africana* in the tree layer (Table 2).

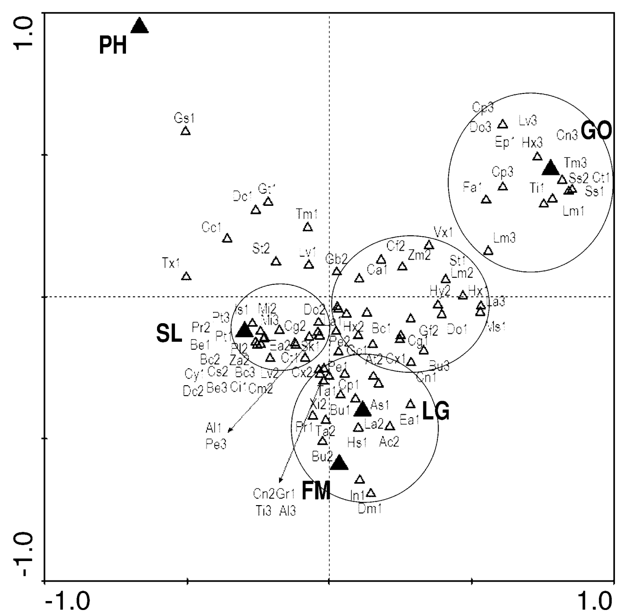

Fig. 2. Ordination diagram showing the result of CCA analysis (A1 in Table 3). Abbreviations: SL—sandy loam, LG—lateritic soil with gravel, FM—ferralitic soil with medium stones, GO—granite outcrops, PH—plinthitic hardpan; 1—low shrub layer (0–2 m), 2—high shrub layer (2–6 m), 3—tree layer (>6 m), At—*Acacia ataxacantha*, Ac—*Acacia* sp., As—*Annona senegalensis*, Al—*Anogeissus leiocarpus*, Bc—*Bombax costatum*, Be—*Borassus aethiopum*, Bu—*Burkea africana*, Ca—*Capparis tomentosa*, Cs—*Cassia sieberiana*, Cp—*Ceiba pentandra*, Ci—*Cissus populnea*, Ct—*Cochlospermum tinctorium*, Cc—*Combretum collinum*, Cf—*C. fragrans*, Cg—*C. glutinosum*, Cm—*C. micranthum*, Cl—*C. molle*, Cn—*C. nigricans*, Ct—*C. tomentosum*, Cp—*Cordyla pinnata*, Cx—*Crossopteryx febrifuga*, Cy—Cyperaceae, Do—*Daniellia oliveri*, Dm—*Detarium microcarpum*, Dc—*Dichrostachys cinerea*, Ds—*Diospyros mespiliformis*, Ea—*Entada africana*, Ep—*Euphorbia poissonii*, Fa—*Feretia apodanthera*, Gt—*Gardenia ternifolia*, Gr—*Grewia barteri*, Gb—*G. bicolor*, Gc—*G. cissoides*, Gf—*G. flavescens*, Gs—*Guiera senegalensis*, Hx—*Hexalobus monopetalus*, Hy—*Hymenocardia acida*, Hs—*Hyptis suaveolens*, Is—*Icacina senegalensis*, In—*Indigofera* sp., La—*Lannea acida*, Lm—*L. microcarpa*, Lv—*Lannea velutina*, Ms—*Maytenus senegalensis*, Mi—*Mitragyna inermis*, Pr—*Piliostigma reticulatum*, Pt—*P. thonningii*, Pe—*Pterocarpus erinaceus*, Pl—*P. lucens*, Ss—*Sterculia setigera*, Sk—*Stereospermum kunthianum*, St—*Strychnos spinosa*, Ti—*Tamarindus indica*, Ta—*Terminalia avicennoides*, Tx—*T. laxiflora*, Tm—*T. macroptera*, Vx—*Vitex madiensis*, Xi—*Ximenia americana*, Za—*Ziziphus mucronata*, Zm—*Z. mauritiana*.

The effect of soil type was significant and explained 15.9% of the species data variability (Table 3, Analysis A1 results for all axes). Results of this analysis were visualised in the form of an ordination diagram (Fig. 2). The tree layer was best developed on the granite outcrops (GO) and was represented by full-grown individuals of *C. nigricans*, *C. pinnata*, *Daniellia oliveri*, *Hexalobus monopetalus*, *L. microcarpa*, *Lannea velutina*, *Sterculia setigera* and *Terminalia macroptera*. Granite outcrops were the only locality for *Euphorbia poissonii*. Sporadic woody vegetation represented only by *G. senegalensis* in the herb and shrub layers was recorded on plinthitic hardpan (PH). All vegetation layers were well developed on sandy loam soil. *Anogeissus leiocarpus*, *B. aethiopum*, *Cissus populnea*, *C. tinctorium*, *Icacina senegalensis* and *Stereospermum kunthianum* occurred in the low shrub layer; *Bombax costatum*, *Cassia sieberiana*, *C. glutinosum*, *C. micranthum*, *Dichrostachys cinerea*, *Entada africana*, *L. velutina*, *M. inermis*, *Piliostigma reticulatum*, *P. lucens* and *Ziziphus mucronata* in the high shrub layer; *B. costatum*, *M. inermis*, *P. thonningii* and *Pterocarpus erinaceus* in the tree layer.

Lateritic soil with gravel (LG) and ferralitic soil with medium stones (FM) are very similar soil types and do not show considerable difference in species composition. Common species such as *A. senegalensis*, *B. africana*, *C. glutinosum*, *C. nigricans*, *C. pinnata*, *C. febrifuga*, *E. africana*, *Grewia barteri*, *Hyptis suaveolens*, *Indigofera* sp., *P. reticulatum*, *P. erinaceus* (many seedlings) and *T. avicennoides* were recorded in the low shrub layer; *Acacia ataxacantha*, *B. africana*, *C. nigricans*, *L. acida*, *T. avicennoides* and *Ximenia americana* were predominant species in the high shrub layer; full-grown *A. leiocarpus*, *B. africana* and *Tamarindus indica* in the tree layer. A group of species that occurred in the middle of the ordination diagram (Fig. 2) is ubiquitous and does not show any particular relation to soil type.

Table 4
Effect of soil type on the total cover of particular layers

Layer	*df*	MS	*F*-ratio	*P*-value
E1	4	3099	4.33	0.006*
E2	4	892	1.49	0.223
E3	4	1849	3.18	0.024*

df—degree of freedom, MS—mean of squares, *F*-ratio—*F* test value, *P*-value—probability value, *—significant result, E1—low shrub layer (0–2 m), E2—high shrub layer (2–6 m), E3—tree layer (6–20 m).

The second most significant factor was the topographical position (To) of relevés, especially in relation to moist depressions which explained 5.2% of the variability (Table 3, Analysis A4). *C. populnea*, *C. tinctorium*, *C. glutinosum*, *P. erinaceus*, *T. macroptera* and *Vitex madiensis* were woody species more abundant in depressions in the low shrub layer; *C. glutinosum*, *C. nigricans*, *Diospyros mespiliformis*, *E. africana*, *H. monopetalus*, *L. acida* and *S. senegalensis* in the high shrub layer; *B. aethiopum*, *M. inermis*, *P. thonningii* and *P. erinaceus* in the tree layer. The effect of termitaria presence (T) was not significant and explained only 1.7% of the vegetation data variability (Table 3, Analysis A2). Nevertheless, *Feretia apodanthera* was a species with obvious presence on termite mounds. Soil types, termitaria presence and occurrence of depressions explained together 17.8% of the species data variability (Table 3, Analysis A6).

The effect of soil type on total cover of particular layers was significant only for low shrub and tree layers (Fig. 3, Table 4). The low shrub layer was best developed on the

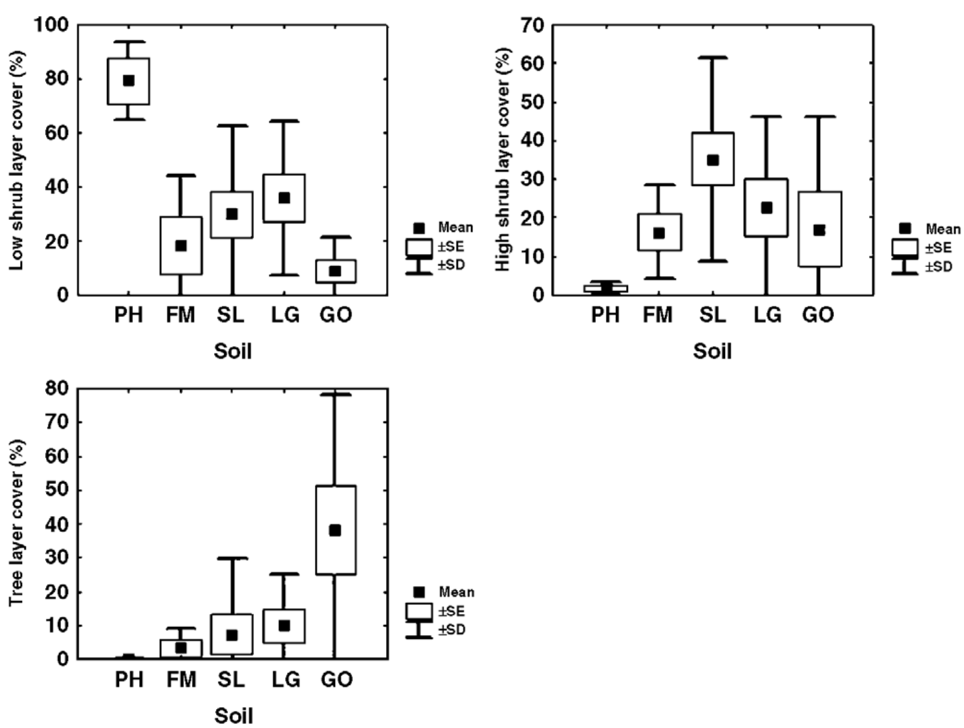

Fig. 3. Cover of low shrub, high shrub and tree layers in relation to soil types. For abbreviations see Table 1.

plinthitic hardpan. Significant differences of cover in the layer were recorded for the following couples: PH-GO, PH-FM, and PH-SL. A significantly different cover was revealed between the soil types PH and SL. Mean values of cover in the low shrub layer were 79%, 18%, 30%, 36% and 9% on the soil types PH, FM, SL, LG and GO, respectively. Mean values of cover in the high shrub layer were 2%, 16%, 35%, 22% and 17% on the soil types PH, FM, SL, LG and GO, respectively. Mean values of coverage in the tree layer were 0, 3%, 7%, 10% and 38% on the soil types PH, FM, SL, LG and GO, respectively.

4. Conclusion

Niokolo Koba National Park (NKNP) has a particularly high floristic and physiognomic diversity with an estimated number of plant species exceeding 1000 (Madsen et al., 1996). A recent study of woody vegetation identified about 100 species of phanerophytes in NKNP (Lawesson, 1995). Traoré (1997) recorded 106 woody species on an area of 228 km^2. Although we investigated only an area of 5 km^2, we recorded 59 species of trees and shrubs. Therefore the study site included approximately 56% of woody species typical of the park. *Combretaceae*, *Caesalpiniaceae*, *Rubiaceae* and *Mimosaceae* were the most important families in our study area. This is in accordance with floristic studies covering the whole area of the national park (Roure, 1956; Adam, 1968; Traoré, 1997; Sonko, 2000; Kane, 2001).

In accordance with Traoré (1997), we recognised soil type and topography as the main factors influencing vegetation pattern in the study area. This is not in compliance with Lawesson's (1997) study of woody vegetation in Senegal that ascribes vegetation patterns to climatic factors. Results of similar studies are evidently scale dependent because a climate gradient can hardly exist in the relatively small study area. According to Cox and Gakahu (1985), termite mounds create more favourable nutrient conditions with specific associated vegetation. Despite of this, the effect of termitaria presence was not significant, probably due to the scale of data collection. To investigate vegetation–termitaria relations, it seems to be more appropriate obtaining data on a smaller scale.

A relation between cover of particular layers and soil type was apparent, especially on the plinthitic hardpan. A shallow soil layer on the hardpan enables growth of annual grasses only and is weakly covered with woody vegetation. The same phenomenon was described by Madsen et al. (1996). Another conspicuous characteristic in layer cover occurred on granite outcrops where the tree layer constituted a closed canopy, while the low shrub layer remained poor.

We investigated the floristic composition, vegetation structure and its relationships to selected environmental factors at the site proposed as an enclosure for the giant eland conservation in Niokolo Koba National Park. Soil type and topography were the main factors affecting the diversity and distribution of woody vegetation.

Acknowledgements

The study was supported by grant no. IAA6093404. We are indebted to the Ministry of Foreign Affairs of the Czech Republic and the Directorate of National Parks in Senegal, namely to Issa Thiam, Mbay Diop, Cheikh Diagne and Christophe Sadio. We thank Bienvenu Sambou and Abdoul Aziz Camara for their help with species identification, and Petr H. Verner, Vaclav Zeleny and two reviewers for their useful comments.

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