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Plant diversity, functional traits and soil conditions of grass savannas on lateritic crusts (bowé) in south eastern Burkina Faso

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Summary: Grass savannas on lateritic crusts are characteristic landscape elements of the Sudanian savannas. In the W National Park and its surroundings in SE-Burkina Faso, plant diversity of savannas on and adjacent to bowé was assessed by a survey of 19 bowal areas with relevés along transects in each of these. The vegetation structure and species composition of the herb and shrub strata, soil depth, particle size and the concentration of Na^+, K^+, Mg^{2+}, Ca^{2+}, H^+, C and N were recorded on each bowal and its surroundings. Our results show that soils on lateritic crusts are rather shallow and acidic compared to the surrounding savanna woodlands. Nutrient availability is hence comparatively low. The observed flora comprises 130 species mainly belonging to the families Combretaceae, Cyperaceae, Leguminosae and Poaceae with a predominance of therophytes and a comparatively high share of C4 species. In the pastures surrounding the National Park a higher species richness was found than inside the Park due to the occurrence of pioneers, ruderal and unpalatable plants. Savannas on lateritic crusts exhibit due to their extreme edaphic and hydrological conditions a specific flora distinct from their surroundings.

Key words: grass savanna, hardpan, phytodiversity, plant functional types, savanna woodland, Sudanian zone, West Africa

Phytodiversité, traits fonctionnels et conditions du sol des savanes herbeuses sur cuirasse latéritique (bowé) au sud-est du Burkina Faso

Résumé: Les savanes herbeuses sur cuirasse lateritique sont des elements de paysage typiques de la savane soudanienne. Dans le Parc national de la W et ses environs au Sud-est du Burkina Faso, la phytodiversité des savanes sur bowé et à côté d'eux étais saisi sur 19 sites de bowal avec des relevés suivant des transects. La structure de la végétation et la composition spécifique des strates herbacée et ligneuse, la profondeur du sol, la taille du grain et la concentration de Na^+, K^+, Mg^{2+}, Ca^{2+}, H^+, C et N étaient notés pour chaque bowal et ses environs. Nos résultants montrent que les sols sur cuirasse latéritique sont peu profonds et acidiques par rapport aux savanes voisines. La disponibilité de nutriments et relativement basse. Les 130 espèces observées pour la plupart font parti des familles Combretaceae, Cyperaceae, Leguminosae and Poaceae avec une prédominance des thérophytes et une proportion élevée des espèces C4. Dans les aires pâturées autour du parc national, une richesse spécifique plus élevée qu'à l'intérieur était trouvé par l'occurrence des espèces pionnières et des plantes rudéraux et non comestibles. Les savanes sur cuirasse latéritique montrent une flore distincte de ses environs à cause des extrêmes édaphiques et hydrologiques.

Mots clés: Afrique de l'Ouest, cuirasse latéritique, phytodiversité, savane boisée, savane herbeuse, types fonctionnels de plantes, zone soudanienne

Phytodiversität, Lebensformen, Photosynthesewege und Bodenverhältnisse von Savannen auf Lateritkrusten (bowé) im Südosten von Burkina Faso

Zusammenfassung: Grassavannen auf Lateritkrusten sind charakteristische Landschaftselemente der sudanischen Savannen. Im zu Burkina Faso gehörenden Teil des W-Nationalparks und seiner Umgebung wurde die pflanzliche Diversität der Savannen auf und in der Umgebung von 19 Bowé-Flächen entlang von Transekten untersucht. Vegetationsstruktur und Artenzusammensetzung der Kraut- und Gehölzschicht, Bodentiefe, Körnung und die Gehalte an Na^+, K^+, Mg^{2+}, Ca^{2+}, H^+, C und N wurden auf jeder Fläche und in deren Umgebung ermittelt. Unsere Ergebnisse zeigen, dass die Böden auf den Lateritkrusten im Vergleich zu denen der umgebenden gehölzreichen Savannen ziemlich flach und sauer sind. Die Nährstoffverfügbarkeit ist daher vergleichsweise niedrig. Die Flora umfasst 130 Arten, insbesondere aus den Familien Combretaceae, Cyperaceae, Leguminosae und Poaceae, wobei Therophyten dominieren. Bemerkenswert ist auch ein verhältnismäßig hoher Anteil an C4 Arten. Auf den Nationalpark umgebenden beweideten Flächen wurde eine höhere Artenzahl gefunden als innerhalb des Parkes, was auf die höhere Zahl von Pionieren, ruderalen und ungenießbaren Arten zurückzuführen ist. Aufgrund ihrer extremen edaphischen und hydrologischen Bedingungen besitzen die Savannen auf den Lateritkrusten eine deutlich von den angrenzenden Flächen unterschiedene spezifische Vegetation.

Schlagworte: Bodenverhältnisse, Grassavannen, Lateritkrusten, Lebensform, Photosyntheseweg, Phytodiversität, Gehölzsavannen, Sudanzone, Westafrika

1 Introduction

Increasing land use and climate change are major drivers of the loss of biodiversity in tropical regions. Especially in West Africa due to population growth and resulting land use pressure, the natural flora and fauna is more and more restricted to wildlife reserves or non-arable habitats like e.g. mountain ridges, inselbergs and lateritic crusts (König et al. 2007). These habitats exhibit a rather uniform vegetation that differs from their surroundings (Fig.1) and often contain rare plant species, e.g. carnivores of the Lentibulariaceae and Droseraceae (Müller 2007; Porembski & Watve 2005).

In contrast to inselbergs and mountain ridges, only little information is available about habitat conditions and the vegetation cover of lateritic crusts as well as their importance for the savanna ecosystem of the Sudanian Zone. These

Fig. 1: A typical bowal in W National Park between Kabougou and Point Triple. The bowal is free of woody plants. / Un bowal typique dans le Parc National de la W entre Kabougou et Point Triple. Le bowal est dénué des plantes ligneuses. / Ein typischer Bowal im W-Nationalpark zwischen Kabougou und Point Triple. Der Bowal ist frei von Gehölzen.

landscape elements are typical for tropical semiarid areas where physical and chemical weathering is promoted and are hence widespread in West Africa. Their development takes place during humid periods when iron is leached from the top soils and transferred into deeper soil layers. Later, during dry periods, this material is hardened and becomes resistant to erosion (Brown et al. 1994).

In West Africa, lateritic crusts form broad plains known there as bowé (sing.: bowal, pl.: bowé; derived from the Fula word stem woow-/boow- : monotony, uniformity; to get accustomed to something; pers. comm. Dr. Abdourahmane Diallo). The impermeable crusts are only covered by a thin soil layer. During the rainy season, they are often waterlogged and afterwards extremely dry. These harsh conditions restrain the development of a woody layer and lead to the formation of grass savannas, only occasionally interspersed by trees.

Bowé are usually not cultivated and pasturing intensity is comparatively low due to the low fodder quality of the dominating herbs. Mostly, they are visited by game during the rainy season (Krohmer 2004). Only a few general surveys on savanna vegetation in Burkina Faso, Mali and Benin (Nasi 1994, Hahn 1996, Küppers 1996, Sieglstetter 2002, Krohmer 2004) include descriptions of the species composition on lateritic crusts. Besides, a few studies on vegetation in temporarily wet habitats on lateritic crusts exist (Müller 2007). A complete and detailed survey of the phytodiversity and soil conditions of lateritic crusts as well as the role of human impact on these features does not exist.

2 Study area

The Study area is located in the Sudanian Zone of SE - Burkina Faso between 11°48' and 12°12' N and 1°47' and 2°24' E within and adjacent to the W National Park (Fig. 2). This transnational reserve in Niger, Benin and Burkina Faso was founded in 1954 and belongs together with the Pendjari National Park, the Arly National Park and adjacent reserves and hunting zones to the so-called "WAP – complex". Since 1996, the park is listed as a UNESCO world heritage site. The semiarid climate in this region has a rainy season lasting from June to November and an average rainfall of 800 mm/a. The mean annual temperature is about 28° C (ASCENA 1993). The landscape is more or less flat except for solitary hills and the sandstone mountains of Gobnangou. On watersheds and lower slopes, albi-petric plinthosols, on upper and middle slopes, endosceleti-albic acrisols, and on lateritic crusts, shallow leptosols with low water-holding capacities can be found (FAO-ISRIC-ISSS 1998). The vegetation consists mainly of shrub and tree savannas with most species from the families of Combretaceae, Leguminosae and Poaceae. The fauna of the WAP-complex includes numerous large mammals, e.g. elephants, antelopes and buffalos, also endangered species such as leopards, cheetahs as well as many threatened birds (Thiollay 2006, Lamarque 2004, Rabeil 2003). The Southeast of Burkina Faso is mainly populated by the ethnic group of the Gulimanceba traditionally living on sorghum and maize farming; important minorities include the Djerma, Mossi and Fulani. A lot of wild plants are used by the local population. Characteristic for this area are the so-called park savannas that are formed by important useful trees like baobab (*Adansonia digitata*), shea butter tree (*Vitellaria paradoxa*) and African locust bean (*Parkia biglobosa*) left in the fields and fallows (Boffa 1999). But also grazing and the regular setting of bushfires have their effects on vegetation and are key factors responsible for the genesis and maintenance of savannas (Sankaran et al. 2008, Guinko 1984).

3 Methods

3.1 Site selection

The selection of sites was based on ASTER-Satellite images from October 2006. In these images, the bowé can be easily distinguished from their surroundings by their sparse woody vegetation, resulting in a distinct reflection signal. Another

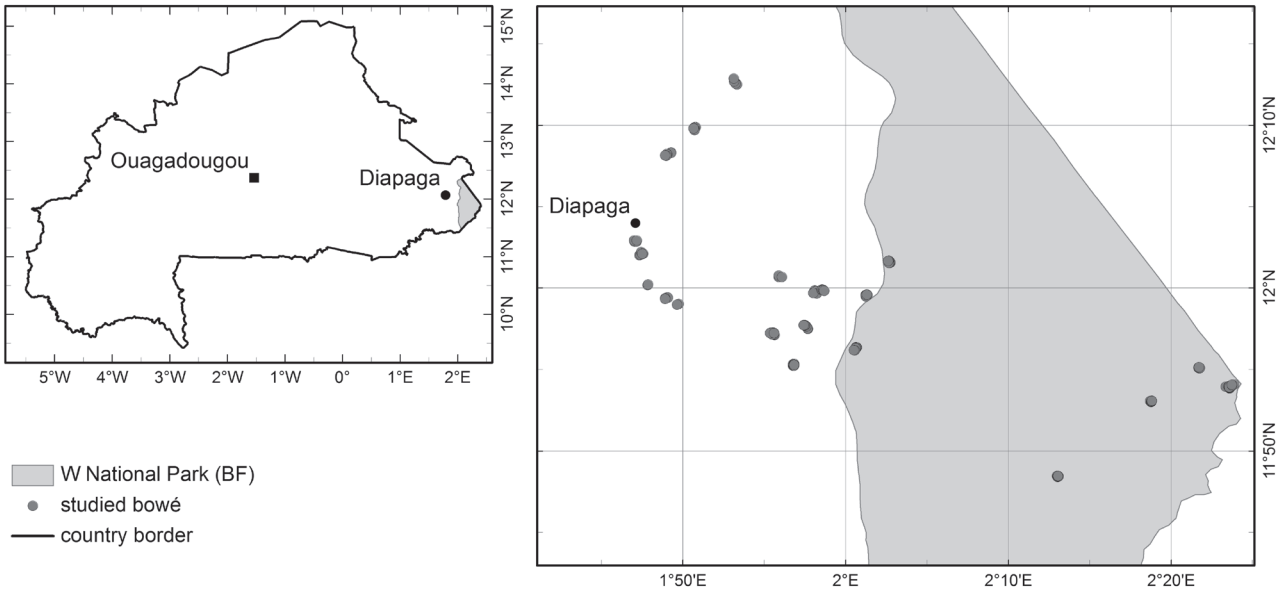

Fig. 2: Study area in the SE of Burkina Faso. Borders of W National Park are taken from IUCN & UNEP-WCMC (2010). / Aire de recherché dans le Sud-est du Burkina Faso. La frontière du Parc National est prise d'IUCN & UNEP-WCMC (2010). / Untersuchungsgebiet im Südosten Burkina Fasos. Grenzen des W-Nationalparks sind aus IUCN & UNEP WCMC (2010).

criterion of choice was the accessibility of the sites, especially within the National Park where access was limited to the vicinity of roads. Surveys were conducted at the end of the rainy season from September to November in 2007 when many plants, e.g. most grasses were flowering and before the setting of fire started. On four sites in the protected area of W National Park as well as on 15 sites in several adjacent pastures soils, vegetation structure and floristic composition were analysed.

3.2 Relevé plot design

On each site relevé plots along three parallel transects were constructed. For the herb layer, a plot size of 10 x 10 m², and for the woody layer, a plot size of 30 x 30 m² were chosen. Soil samples were taken in each corner in 1 m distance from the edge and in the centre of the plot.

3.3 Sampling of soil data

In each plot soil depth was measured and five samples were taken from the topsoil and merged to a mixed sample. Sand fractions were separated by grading, silt and clay fractions by the pipette method (Köhn 1928). The pH-Value was measured by a replicate set of pH readings in 0.1 N KCl according to Dewis & Freitas (1970). For determination of cations (Mg^{2+}, Ca^{2+}, K^{+}, Na^{+}), the method of Mehlich (1948) was used. Carbon and nitrogen were determined through dry combustion in oxygen by CN-Analysers (LECO).

3.4 Sampling of vegetation data

Total coverage and mean height of vegetation as well as abundance of species of the herbaceous and ligneous stratum were recorded separately on each relevé plot. Species of the woody layer were separated at a height of 5 m in shrubs and trees. Cover was recorded in percentages. The complete relevé data are stored in the West African Vegetation Database (Janssen et al. 2011, Schmidt et al. 2012).

Each species has been documented by herbarium specimens stored in the Herbarium Senckenbergianum (FR) of the Research Institute Senckenberg. The respective records are available via the Senckenberg collection database (http://sesam.senckenberg.de/).

3.5 Plant functional traits

Information on life form and photosynthetic pathways was taken from the species list of the partial faunal reserve of Pama (Mbayngone et al. 2008) and the vegetation database VegDa (Schmidt 2006).

3.6 Statistical Analysis

Patterns of floristic compositional differences were detected by an ordination analysis in CANOCO (Ter Braak 1988). Data were at first subjected to a detrended correspondence analysis (DCA) for obtaining the length of the floristic gradient. This was followed by a canonical correspondence analysis (CCA), conducted to test whether soil conditions or grazing account for the variance in species composition. A Monte Carlo permutation test was used to prove if the results of the ordination are significant (Ter Braak 1988).

4 Results

4.1 Soil

Soils on the examined lateritic crusts are significantly less profound than in the surrounding savannas but show a great variety in depth because of cleavages in the crust or its uneven surface. Base saturations, pH values, Ca and Mg contents are considerably lower and the clay fraction is slightly higher on lateritic crusts than on the surroundings.

Surprisingly humus and nitrogen show constantly high and C/N-ratio low values (Table 1).

4.2 Species richness

Within the 145 plots, 130 plant species were found. In the woody layer, 44 species are represented, 20 of them occurring on the bowé and 42 in the adjacent savannas. Of the 106 herb species, 84 occurred on lateritic crusts and 76 in the surrounding savanna. As compared to the sites within W National Park, more species were found in the surrounding pasture areas due to the occurrence of pioneers, ruderal and unpalatable plants. In general, the bowé are poor in species, on average only 12 (+/-3) different species were found per plot which is, compared to other common vegetation types in this region, a very small number.

4.3 Families

In the woody layer, species from 19 families and in the herb layer from 26 families were found. Most of them belong to the Leguminosae and Combretaceae. In the herb layer the Poaceae are strongly represented. All grass species occurring in our plots are C4 plants (Table 2), known to have a high water and nitrogen use efficiency (e.g. Simioni et al. 2004). Another family, which is common in Burkina Faso, but in this study was only found on the bowé are the Cyperaceae. Other families that occur exclusively on the bowé plots (but are represented only by one or two species) are the Caryophyllaceae, Convallariaceae, Ophioglossaceae, Moraceae and Portulacaceae.

Table 1: Chemical and physical properties of the topsoils on lateritic crusts and their surrounding savannas. / Propriétés chimiques et physiques des horizons A sur cuirasses latéritiques et savanes avoisinants. / Chemische und physikalische Eigenschaften des Oberbodens auf Lateritkrusten und benachbarten Savannen.

Soil parameters													
Vegetation type	Depth *	pH **	Base sat.	CEC	Na	K	Mg**	Ca**	H-ions	Texture	C	N	C/N-ratio
	cm		%	mmol / (z*100g Boden)						clay:silt:sand	%	%	
Bowé savanna	**10**	**5,4**	**51,4**	**13,3**	**0,17**	**0,25**	**1,36**	**5,12**	**6,37**	**16:51:33**	**1,99**	**0,17**	**11,5**
SD	(5,8)	(0,4)	(14,1)	(3,8)	(0,26)	(0,33)	(0,7)	(2,3)	(2,45)		(0,71)	(0,05)	(1,5)
surrounding savanna	**20**	**5,9**	**68,5**	**15,1**	**0,09**	**0,33**	**2,08**	**8,44**	**4,18**	**11:52:37**	**2,15**	**0,18**	**11,8**
SD	(9)	(0,5)	(15,5)	(7,8)	(0,17)	(0,31)	(1,18)	(6,16)	(2,01)		(1,04)	(0,09)	(1,6)
Students t-test, * $p < 0.001$; ** $p < 0.01$ are significant differences for the vegetation types.													

4.4 Plant functional traits

Differences were also found regarding the life form spectrum as well as photosynthetic pathways. On the bowé, the number of therophytes and C4 plants is higher than in the surrounding savanna which, in turn, contains considerably more phanerophytes and C3 plants. This can be ascribed to the adaptation of plants to the extremely short vegetation periods combined with shortage of water and nitrogen on lateritic crusts.

4.5 Species composition

The few woody species occurring on bowé are resistant against drought and have high regeneration potentials like e.g. *Acacia macrostachya*, *Combretum glutinosum*, *Combretum nigricans*, *Detarium microcarpum* and *Lannea microcarpa* (Table 2). The herb layer is strongly dominated by the grasses *Loudetia togoensis* or *Loudetiopsis kerstingii*. Other common but not highly abundant species are *Abildgaardia abortiva*, *Indigofera geminata* and *Polygala arenaria*. Many of these species are mentioned by several authors (Ataholo 2001; Lebrun et al. 1991; Poilecot 1995) as typical plants of bowé or other dry habitats with shallow soils. Some species occur that are known to be adapted to seasonal waterlogging, as e.g. the only fern *Ophioglossum reticulatum*, the rare Asparagaceae *Eriospermum flagelliforme*, *Cyanotis lanata* and *Spermacoce filifolia*.

In the surrounding savannas where water and soil conditions are more favourable, many more woody species occur, including *Anogeissus leiocarpa*, *Combretum molle, Grewia lasiodiscus* and *Vitellaria paradoxa*.

The herb layer is dominated by the grass *Andropogon fastigiatus* that is often accompanied by *Andropogon gayanus* and *Tephrosia bracteolata*. Another remarkable fact is, that some species do not occur on examined sites outside the reserve and vice versa. A species only found in the reserve is e.g. *Ctenium elegans*. Species found exclusively on the grazed plots are e.g. *Waltheria indica*, *Hackelochloa granularis* and *Eragrostis turgida*.

Table 2: List of species found on bowé (B) and adjacent savannas (S), alphabetically ordered by families with life forms (LF: C = chamaephyte, T = therophyte, P = phanerophyte, HP = hemiparasite, H = hemicryptophyte), types of photosynthesis (PS), occurrence in herb (H) - and woody layer (W). / Liste d'espèces trouvées sur bowé (B) et savanes avoisinants (S), en ordre alphabétique de familles avec types biologiques (LF: C = chaméphyte, T = thérophyte, P = phanérophyte, HP = hémiparasite, H = hémikryptophyte), types de photosynthèse (PS), présence dans la strate herbacée (H) ou ligneuse (W). / Liste der auf Bowé (B) und angrenzenden Savannen (S) gefundenen Arten, alphabetisch nach Familien geordnet, mit Lebensform (LF: C = Chamaephyt, T = Therophyt, P = Phanerophyt, HP = Hemiparasit, H = Hemikryptophyt), Photosynthesetyp (PS) und Vorkommen in Kraut- (H) oder Gehölzschicht (W).

Species	LF	PS	H	W	B	S
Acanthaceae						
Blepharis maderaspatensis Heyne ex Roth	T	C3	x			x
Justicia insularis T. Anderson	P	C3	x		x	x

Species	LF	PS	H	W	B	S
Lepidagathis anobrya Nees	P	C3	x		x	x
Monechma ciliatum (Jacq.) Milne-Redh.	T	C3	x		x	x
Amaranthaceae						
Achyranthes aspera L.	T	C3	x		x	x
Pandiaka angustifolia (Vahl) Hepper	T	C3	x		x	x
Anacardiaceae						
Lannea acida A. Rich.	P	C3		x	x	x
Lannea microcarpa Engl. & K. Krause	P	C3		x	x	x
Annonaceae						
Annona senegalensis Pers.	P	C3	x	x	x	x
Asparagaceae						
Chlorophytum laxum R. Br.	G	C3	x			x
Eriospermum flagelliforme Baker	G	C3	x		x	
Asteraceae						
Aspilia bussei O. Hoffm. & Muschl.	T	C3	x		x	x
Aspilia paludosa Berhaut	T	C3	x			x
Bignoniaceae						
Stereospermum kunthianum Cham.	P	C3	x			x
Bixaceae						
Cochlospermum planchonii Hook. f.	C	C3	x			x
Caryophyllaceae						
Polycarpaea corymbosa (L.) Lam.	T	C4	x		x	
Celastraceae						
Gymnosporia senegalensis (Lam.) Loes.	P	C3		x		x
Combretaceae						
Anogeissus leiocarpa (DC.) Guill. & Perr.	P	C3		x		x
Combretum collinum Fresen.	P	C3	x	x	x	x
Combretum glutinosum Perr. ex DC.	P	C3	x	x	x	x
Combretum micranthum G. Don	P	C3		x		x
Combretum molle R. Br. ex G. Don	P	C3	x	x		x
Combretum nigricans Lepr. ex Guill. & Perr.	P	C3	x	x	x	x
Guiera senegalensis J.F. Gmel.	P	C3	x	x		x
Pteleopsis suberosa Engl. & Diels	P	C3	x	x	x	x
Terminalia macroptera Guill. & Perr.	P	C3		x		x
Commelinaceae						
Commelina nigritana var. *gambiae* Benth.	C	C3	x		x	
Cyanotis lanata Benth.	T	C3	x		x	x
Convolvulaceae						
Ipomoea coscinosperma Hochst. ex Choisy	T	C3	x		x	x
Ipomoea eriocarpa R. Br.	T	C3	x		x	x
Cyperaceae						
Abildgaardia abortiva (Steud.) Lye	T	C3	x		x	
Cyperus reduncus Hochst. ex Boeck.	T	C3	x		x	
Kyllinga erecta Schumach.	G	C4	x		x	
Mariscus squarrosus (L.) C.B. Cl.	T	C4	x		x	
Pycreus pumilus (L.) Domin.	T	C4	x		x	
Lipocarpha kernii Raymond	T	C4	x		x	
Scleria sphaerocarpa (E.A.Rob.) Napper	T	C3	x		x	
Euphorbiaceae						
Euphorbia convolvuloides Hochst. ex Benth.	T	C3	x		x	
Fabaceae, subfam. **Caesalpinoideae**						
Burkea africana Hook.	P	C3	x	x		x
Cassia absus L.	C	C3	x		x	
Cassia mimosoides L.	T	C3	x		x	x
Cassia sieberiana DC.	P	C3	x	x	x	x
Detarium microcarpum Guill. & Perr.	P	C3	x	x	x	x
Isoberlinia doka Craib & Stapf	P	C3		x		x
Piliostigma thonningii (Schumach.) Milne-Redh.	P	C3		x		x
Tamarindus indica L.	P	C3		x		x

Species	LF	PS	H	W	B	S
Fabaceae, subfam. **Mimosoideae**						
Acacia dudgeonii Craib	P	C3		x		x
Acacia hockii De Wild.	P	C3		x		x
Acacia macrostachya Reichb. ex G. Don	P	C3	x	x	x	x
Albizia chevalieri Harms	P	C3		x	x	
Dichrostachys cinerea (L.) Wright & Arn.	P	C3	x	x		x
Entada africana Guill. & Perr.	P	C3	x	x		x
Prosopis africana (Guill. & Perr.) Taub.	P	C3		x	x	x
Fabaceae, subfam. **Papilionoideae**						
Alysicarpus ovalifolius (Schum. & Thonn.) J. Léonard	T	C3	x		x	
Crotalaria goreensis Guill. & Perr.	P	C3	x			x
Crotalaria leprieurii Guill. & Perr.	T	C3	x		x	x
Desmodium adscendens (Sw.) DC.	C	C3	x		x	
Desmodium velutinum (Willd.) DC.	C	C3	x			x
Indigofera bracteolata DC.	C	C3	x		x	x
Indigofera congolensis De Wild. & T. Durand	T	C3	x		x	
Indigofera dendroides Jacq.	T	C3	x		x	x
Indigofera geminata Baker	T	C3	x		x	
Indigofera senegalensis Lam.	T	C3	x		x	
Indigofera stenophylla Guill. & Perr.	T	C3	x		x	
Melliniella micrantha Harms	T	C3	x		x	x
Pterocarpus erinaceus Poir.	P	C3	x	x	x	x
Stylosanthes erecta P. Beauv.	C	C3	x			x
Tephrosia bracteolata Guill. & Perr.	T	C3	x		x	x
Tephrosia pedicellata Baker	T	C3	x		x	x
Tephrosia platycarpa Guill. & Perr.	T	C3	x		x	x
Xeroderris stuhlmannii (Taub.) Mendonca & E.P. Sousa	P	C3		x		x
Zornia glochidiata Reichb. ex DC.	T	C3	x		x	
Lamiaceae						
Hyptis spicigera Lam.	T	C3	x		x	x
Platostoma africanum P. Beauv.	T	C3	x			x
Tinnea barteri Gürke	C	C3	x			x
Vitex simplicifolia Oliv.	P	C3		x		x
Loganiaceae						
Strychnos spinosa Lam.	P	C3		x	x	x
Malvaceae						
Bombax costatum Pellegr. & Vuillet	P	C3	x	x		x
Corchorus tridens L.	T	C3	x		x	
Grewia cissoides Hutch. & Dalziel	C	C3	x			x
Grewia lasiodiscus K. Schum.	P	C3	x	x	x	x
Hibiscus cannabinus L.	T	C3	x		x	x
Sida alba L.	T	C3	x		x	x
Sterculia setigera Delile	P	C3	x	x		x
Triumfetta rhomboidea Jacq.	C	C3	x		x	x
Waltheria indica L.	C	C3	x		x	x
Wissadula rostrata (Schumach.) Hook.f.	T	C3	x		x	x
Meliaceae						
Khaya senegalensis (Desr.) A. Juss.	P	C3		x		x
Moraceae						
Ficus glumosa Delile	P	C3		x	x	
Olacaceae						
Ximenia americana L.	P	C3		x		x
Ophioglossaceae						
Ophioglossum reticulatum L.	G	C3	x		x	
Orobanchaceae						
Buchnera hispida Buch.-Ham. ex D. Don	HP	C3	x		x	x
Striga asiatica Kuntze	HP	C3	x		x	
Striga aspera (Willd.) Benth.	HP	C3	x		x	x
Phyllanthaceae						
Bridelia scleroneura Muell.Arg.	P	C3	x	x	x	x

Species	LF	PS	H	W	B	S
Flueggea virosa (Roxb. ex Willd.) Voigt	P	C3	x	x		x
Phyllanthus amarus Schum. & Thonn.	P	C3	x		x	
Poaceae						
Andropogon fastigiatus Sw.	T	C4	x		x	x
Andropogon gayanus Kunth	H	C4	x			x
Aristida kerstingii Pilg.	T	C4	x		x	
Brachiaria villosa (Lam.) A. Camus	T	C4	x		x	x
Ctenium elegans Kunth	T	C4	x		x	
Digitaria gayana (Kunth) Stapf ex A. Chev.	T	C4	x		x	x
Eragrostis tremula Hochst. ex Steud.	T	C4	x			x
Eragrostis turgida (Schumach.) De Wild.	T	C4	x		x	
Hackelochloa granularis (L.) Kuntze	T	C4	x		x	x
Loudetia flavida (Stapf) C.E. Hubb.	H	C4	x		x	x
Loudetia togoensis (Pilg.) C.E. Hubb.	T	C4	x		x	x
Loudetiopsis kerstingii (Pilg.) Conert	T	C4	x		x	x
Microchloa indica (L. f.) P. Beauv.	T	C4	x		x	x
Panicum pansum Rendle	T	C4	x		x	x
Pennisetum pedicellatum Trin.	T	C4	x		x	x
Pennisetum polystachion (L.) Schult.	T	C4	x		x	x
Schoenefeldia gracilis Kunth	T	C4	x			x
Setaria pumila (Poir.) Roem. & Schult.	T	C4	x		x	x
Sporobolus festivus Hochst. ex A. Rich.	H	C4	x		x	x
Tripogon minimus (A. Rich.) Hochst. ex Steud.	H	C4	x		x	x
Polygalaceae						
Polygala arenaria Willd.	T	C3	x		x	
Polygala multiflora Poir.	T	C3	x		x	x
Securidaca longipedunculata Fresen.	P	C3		x		x
Portulacaceae						
Portulaca foliosa Ker Gawl.	C	C3	x		x	
Rhamnaceae						
Ziziphus abyssinica Hochst. ex A. Rich.	P	C3		x		x
Rubiaceae						
Crossopteryx febrifuga (Afzel. ex G. Don) Benth.	P	C3	x	x	x	x
Feretia apodanthera Delile	P	C3		x		x
Kohautia tenuis (Bowdich) Mabb.	T	C3	x		x	
Mitracarpus hirtus (L.) DC.	T	C3	x		x	
Spermacoce filifolia (Schumach. & Thonn.) J.P.Lebrun & Stork	T	C3	x		x	x
Spermacoce stachydea DC.	T	C3	x		x	x
Sapotaceae						
Vitellaria paradoxa C.F. Gaertn.	P	C3		x	x	x
Zygophyllaceae						
Balanites aegyptiaca Delile	P	C3		x	x	x

4.6 Ordination

The DCA axis 1 showed a gradient length of 4.1 which means that species are unimodally distributed.

In the CCA, the significant effect of soil conditions on compositional change was the variable most strongly correlated with axis 1 (Fig. 3; $P < 0{,}01$). The impact of grazing was significant on axis 2, being the most strongly correlated variable with this axis (Fig. 3; $P < 0{,}01$).

5 Discussion

5.1 Soil

Nutrient availability of soils on bowé is relatively low compared to other vegetation types in this region. In comparison to other surveys, on bowé contents of nitrogen, humus and cations as well as cation exchange capacity are slightly increased. Although contents on humus and nitrogen are comparatively high, the effective nutrient availability for plants is still strongly limited because of drought and low pH-values. Significant differences of bowé inside and outside the national park were not found. Hence, there is no indication of human impact on soil conditions across our study sites.

5.2 Flora

Grass savannas with dominance of *Loudetia togoensis* and most of the species encountered in this study are also described by several authors on bowé in Côte d'Ivoire (Poilecot 1995), Mali (Nasi 1994), Benin (Sieglstetter 2002) and several regions of Burkina Faso (Schmidt 2006; Müller 2007; Krohmer 2004; Hahn-Hadjali 1998). The species composition on bowé in different climatic regions of West Africa seems to be very similar due to the extreme soil and water conditions but differs very much from the surroun-

	Axis 1	Axis 2
Eigenvalues	0,144	0,086
Percentage	8,191	4,874
Cum. Percentage	8,191	13,065
Cum.Constr.Percentage	49,261	78,574
Spec.-env. correlations	0,690	0,627

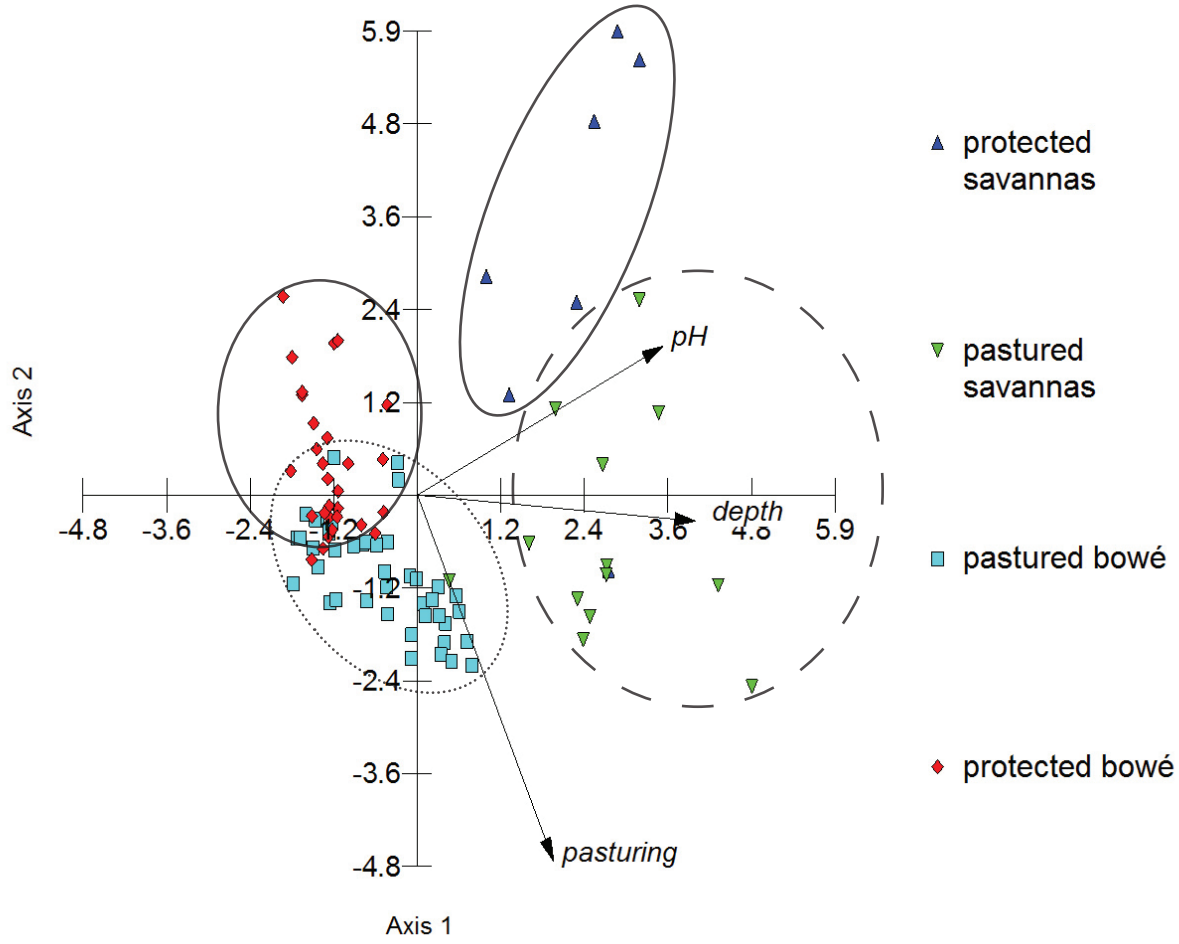

Fig. 3. Ordination diagram of the CCA. The symbols represent location of the plots within the bowé or in adjacent savannas and within or outside of the W National Park. / Diagramme d'ordination CCA. Les symboles représentent la location des sites sur bowé ou savanes et dans le parc ou dehors. / Ordinationsdiagramm der CCA. Die Symbole stehen für die Lage der Aufnahmeflächen in Bowé oder angrenzenden Savannen und innerhalb oder außerhalb des W-Nationalparks.

dings. The bowé form natural grass savanna islands in savanna woodlands, which are typical for the Sudanian zone of West Africa.

Regarding species richness, the bowé are relatively poor in species compared to other vegetation types in this region (Krohmer 2004; Hahn 1996), but, due to their extreme edaphic and hydrological conditions they contain a specific flora distinct from their surroundings. This includes the dominant family Poaceae, with dominance of *Loudetia togoensis* or *Loudetiopsis kerstingii* as opposed to the typical Sudanian savannas where Andropogoneae dominate the herb layer (Schmidt et al. 2011). Many of the bowal species do only rarely occur in other habitats. Some of them were also found on plateaus of the sandstone mountains of Gobnangou in SE Burkina Faso (Küppers 1996) and inselbergs in West Africa (Porembski & Watve 2005) that exhibit similarly harsh edaphic conditions.

5.3 Human impact

In agreement with the studies of Hahn-Hadjali et al. (2006), more species were found in the pastured areas due to the occurrence of pioneers, ruderal and unpalatable plants. The increase of plants resistant to grazing as well as the decline of species sensitive to grazing outside the National Park could also be ascertained with the CCA where a significant change of floristic composition became obvious along the second axis.

6 Conclusions

For the first time an inventory of the flora on bowé within the W National Park and its adjacent areas has been accomplished. The examined lateritic crusts exhibit shallow acidic soils combined with impermeable compact crusts beneath. Plants are exposed to nitrogen shortage, seasonal water log-

ging and long dry periods and exhibit functional traits in adaptation to these conditions. Most of them are therophytes and either pursue C4-photosynthesis (Poaceae, Cyperaceae, Caryophyllales) or establish symbiosis with rhizobia (Leguminosae). Therefore, the flora of lateritic crusts contains a distinct set of species that is differing from the surrounding savanna woodlands.

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