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Biodiversity Islands in the Savanna – Analysis of the Phytodiversity on Termite Mounds in Northern Benin

Ivana Kirchmair, Marco Schmidt, Georg Zizka, Arne Erpenbach, Karen Hahn

Summary: Termite mounds represent abundant microhabitats of high biodiversity in tropical savanna ecosystems and are an important source of landscape heterogeneity in Sub–Saharan West Africa. Floristic composition as well as density, structure and zonation of plant cover on the mounds were investigated in northern Benin and compared to the adjacent savanna vegetation. A total of 57 abandoned and densely vegetated termite mounds of comparable size and similarly affected by erosion located in different types of savannas inside and outside of the W National Park and in cotton fields were studied. This study revealed that termitaria are special habitats differing in density, composition and structure from surrounding savannas. The plant cover of termite mounds showed a distinctive zonation. Succulents, geophytes, and lianas were much more abundant on mounds, the family Capparaceae was found exclusively on mounds. The floristic composition and vegetation on termitaria proved to be rather homogeneous; although those mounds located in cotton fields differed by higher abundance of Poaceae and lower species richness.

Key words: geophytes, succulents, termitaria, W National Park, zonation

Îles de la biodiversité dans la savane – Analyse de la phytodiversité sur les termitières dans le Nord Bénin

Résumé: Les termitières représentent de nombreux microhabitats riches en biodiversité dans les écosystèmes de savanes tropicales et sont une source importante d'hétérogénéité dans les paysages de l'Afrique de l'Ouest subsaharienne. La Flore des termitières a été étudiées dans le nord du Bénin, ainsi que la densité, la structure et la zonation de la couverture végétale. De plus ces données ont été comparées avec la végétation des savanes adjacentes. Au total 57 termitières abandonnées et densément végétalisées, de dimension et d'érosion similaire, ont été étudiées dans les savanes du Parc National de W ainsi que dans les savanes attenantes et dans des champs de coton. Nous démontrons que les termitières sont des habitats avec une zonation prononcée de la couverture végétale, différant de la savane environnante par leur densité, leur composition et leur structure. Les succulentes, les géophytes et les lianes sont plus abondants sur les termitières. De plus la famille des Capparaceae y est exclusivement restreinte. La flore et la végétation des termitières se révéle homogène bien que celles située en champs de coton différent par une plus grande abondance de graminées (Poaceae) et par une richesse spécifique plus basse.

Mots clés: géophytes, Parc National du W, succulentes, termitières, zonation

Biodiversitätsinseln in der Savanne – Analyse der Phytodiversität auf Termitenhügeln in Nord-Benin

Zusammenfassung: Termitenhügel sind häufig vorkommende Mikrohabitate hoher Biodiversität in tropischen Savannen-Ökosystemen und spielen eine wichtige Rolle für die Landschaftsheterogenität im subsaharischen Westafrika. In unserem Untersuchungsgebiet in Nordbenin wurden sowohl die floristische Zusammensetzung als auch Dichte, Struktur und Zonierung der Pflanzendecke untersucht und mit der angrenzenden Savannenvegetation verglichen. Insgesamt wurden 57 verlassene und dicht bewachsene Termitenhügel vergleichbarer Größe und gleichermaßen von Erosion betroffen, die sich in verschiedenen Savannentypen innerhalb und außerhalb des W-Nationalparks und in Baumwollfeldern befanden, untersucht. Unsere Untersuchungen zeigen, daß Termitenhügel spezielle Habitate darstellen, die sich in Vegetationsdichte, -zusammensetzung und –struktur deutlich von den sie umgebenden Savannen unterscheiden. Der Pflanzenbewuchs von Termitenhügeln zeigte eine ausgeprägte Zonierung. Sukkulente, Geophyten und Lianen wurden wesentlich häufiger, die Familie der Capparaceae ausschließlich auf Termitenhügeln gefunden. Die Flora und Vegetation auf Termitenhügeln stellte sich als ziemlich homogen heraus. Allerdings unterschieden sich die in Baumwollfeldern liegenden Hügel durch eine höhere Abundanz der Poaceae und eine geringere Artenvielfalt.

Schlagworte: Geophyten, Sukkulenten, Termitenhügel, W-Nationalpark, Zonierung

1 Introduction

The most dramatic changes for Sub-Saharan Africa in the last decades have been the increase in human population and consequentially an increase of land use, e.g., due to increasing cattle density and the extension of agricultural lands. These changes especially affected the Sudanian region and threaten the biodiversity of the Sudanian savannas and their sustainable use. In the study area, the agricultural area has considerably increased during the last 25 years (Brink & Eva 2009). In large part these areas are used for cotton cultivation, which generates 80% of the export receipts of Benin (UNEP 2008). The intensification of agriculture leads to pollution by pesticides and fertilizers and a reduced fertility of soil.

National parks and protected areas are a keystone to regional conservation strategies. The W National Park, named after a meander in the River Niger shaped like a "W", is the first transboundary biosphere reserve in Africa composed of protected areas in Benin, Burkina Faso and Niger and forms together with the Arly National Park in Burkina Faso, the Pendjari National Park in Benin and neighboring reserves and hunting zones the so-called WAP complex.

Several mound building termite species occur in W National Park. The largest mounds are constructed by two fungus–cultivating *Macrotermes* species, *M. subhyalinus* and *M. bellicosus*. Although we could not determine which *Macrotermes* species originally built the mounds, other genera of termites can be excluded as builders, since they show very different mound architectures.

Termite mounds of the genus *Macrotermes* provide specific habitats to plants and are a prominent feature in the savanna biome in West Africa. Nevertheless, detailed knowledge about their plant cover is lacking up to now. Their high abundance (up to 20.2 dead mounds per ha, Lepage 1984) can lead to a surface cover of up to 10 % (Wood 1988), even though in this study a single mound covers only a mean area of 69 m² (range from 16 to 149 m²). Termites have been identified to play an important role as ecosystem engineers modifying their environment and inducing changes in resource flow (Jones et al. 1994, Dangerfield et al. 1998). By changed chemical and physical soil properties due to bioturbation during the construction of mounds (Watson 1977, Bachelier 1978) they have a far–reaching effect on vegetation (Glover et al. 1964). The soil of termitaria is richer in minerals like nitrogen, calcium, magnesium, potassium and sodium (Watson 1977, Bachelier 1978, Joseph et al. 2012) and has higher clay and silt contents than the surrounding soil (Konaté et al. 1999). Through accumulation of bases the pH value of mound soil is higher than the pH value of the surrounding soil (Watson 1977). Termite mounds offer a better soil water availability for plants, especially in deeper soil horizons (Konaté et al.1999). These specific soil conditions and the modification of the habitat lead to a vegetation cover on the mounds that differs in density, composition and structure from the adjacent savanna (Smith & Yeaton 1998). Therefore, termite mounds are a source of landscape heterogeneity (Konaté et al. 1999), increasing biodiversity of an area. Furthermore, plants growing on termitaria provide additional ecosystem services to the human population, as they are used for medicinal and various other purposes (Nacoulma 1996, Arbonnier 2002, Krohmer 2004).

This study contributes to the knowledge of flora and vegetation on termite mounds, and differences in species composition compared to surrounding savannas in the study area in Northern Benin. We examined to what extent the termite mounds have an influence on the surrounding vegetation. Furthermore, the influence of human disturbance on termite mound vegetation in cotton fields was investigated, that is among others the influence of pesticides and fertilizers. Additionally, for the first time a zonation of plants on termitaria was investigated.

2 Materials and Methods

The study area was located in the North of the West African country Benin, close to the village Sampeto and the border of the W National Park (Fig. 1). The elevation is about 270 m a.s.l., annual precipitation (ca. 1000 mm) and mean temperature (27.3 °C) are within the characteristics of the Sudanian Zone. Climate is characterized by a dry season (October–April) and a short rainy season (May–September).

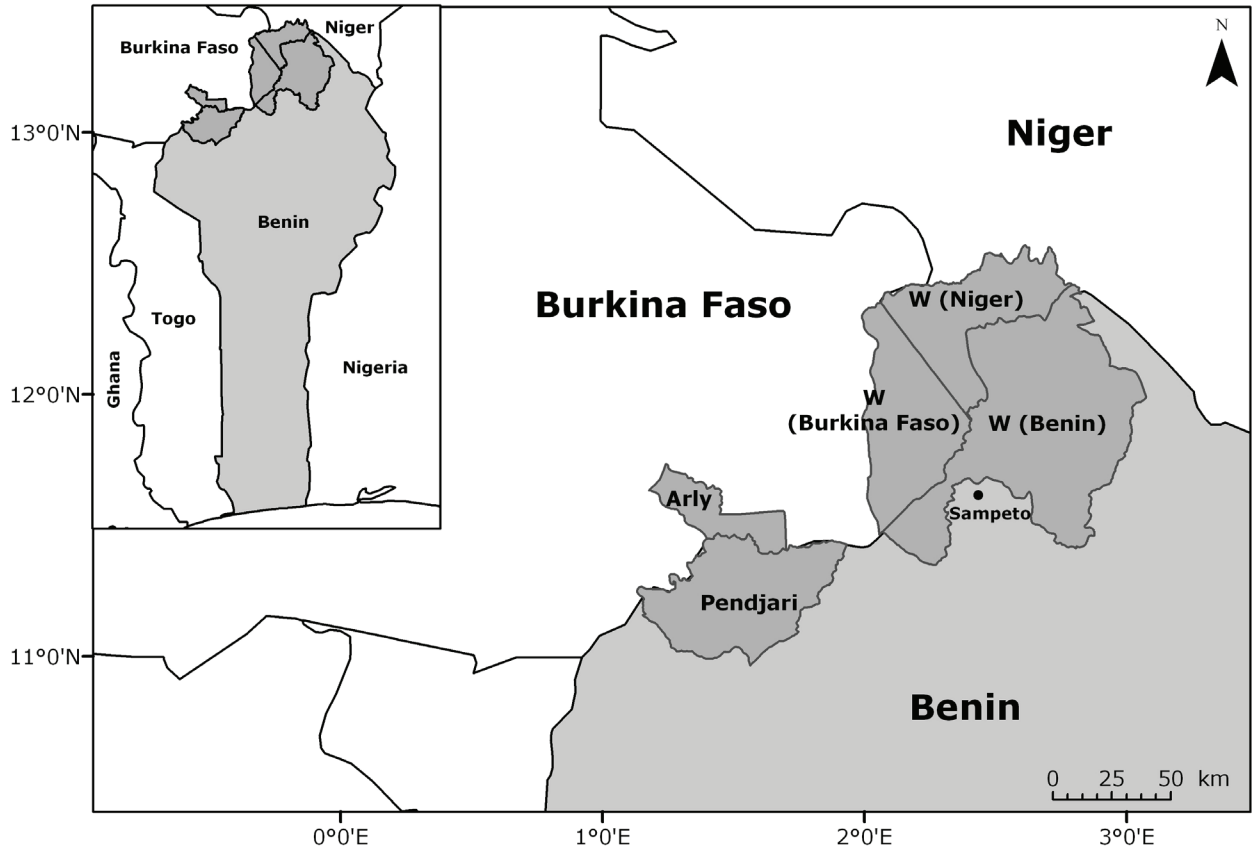

Fig. 1: Transboundary W National Park and neighboring national parks in the border region of Benin, Burkina Faso and Niger. / Parc national transfrontalier du W du Niger et parcs nationaux voisins dans la région frontalière du Bénin, Burkina Faso et Niger. / Grenzübergreifender W-Nationalpark und benachbarte Nationalparks in der Grenzregion von Benin, Burkina Faso und Niger.

We randomly chose 44 termite mounds in near-to-natural savanna vegetation (grass and shrub savannas), and 13 mounds in intensively fertilized cotton fields as a comparison under anthropogenic influence. Sampling was conducted from September to November 2007.

To ensure comparability, mounds of approximately similar size and stage of erosion were selected and their circumference was measured. Species inventory and abundance were documented by phytosociological relevés (these are available online from the West African Vegetation Database: Janssen et al. 2011, Schmidt et al. 2012). Species cover was estimated in percent of the total area for tree (> 5 m), shrub (1–5 m) and herb layer (< 1 m). We analyzed position of plants on the termitaria in three zones for herbaceous layers, and respectively five zones for woody layers from the central top to the peripheral bottom (see Fig. 2).

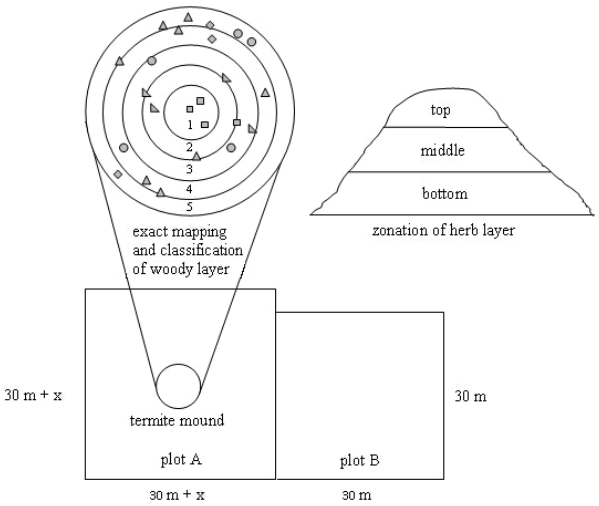

Fig. 2: Plot design and schema of exact mapping of individuals and classification of tree layer (class 1=center of termite mound up to class 5=periphery of termite mound) and herb layer zonation (top, middle, bottom). / Dessin et Schéma de la cartographie exacte des individus, de la classification des successions arborescentes (de la classe 1 (centre de la termitière) jusqu'à la classe 5 (périphérie de la termitière)) et de la zonation de la couche herbacée (haut, milieu, bas). / Schema der Aufnahmeflächen und der exakten Kartierung der Individuen, Zonierung der Baumschicht (Klasse 1=Zentrum bis Klasse 5=Peripherie) und Krautschicht (obere, mittlere, untere Zone).

To be able to compare the phytodiversity on mounds to that of the neighboring non–mound vegetation in the savanna, shrub and tree layer in two reference plots (A and B, see Fig. 2) were investigated to characterize the influence of termite mounds on the surrounding vegetation. Direct influence of the mound to adjacent vegetation was expected to be measurable in Plot A. Reference plot B was located at one side of plot A and selected to best represent the surrounding non–influenced vegetation. Both savanna plots were designed to have a total area of 900 m². Plot B had a side length of 30 m. Since plot A was placed around the termite mound itself, its side length was extended accordingly. No reference plots were studied for termitaria in cotton fields. The complete data collection was carried out by the same observer.

To reveal similarities or dissimilarities between termite mounds and the surrounding savanna regarding their phytodiversity, an ordination and a cluster analysis were performed with the program Community Analysis Package (Version 4.0) on species cover data. We used a starting configuration derived from a PCA to perform NMDS ordination based on Sørensen's Index of similarity. Two dimensions were chosen to be retained in the analysis. For the hierarchical agglomerative cluster analysis, we used Sørensen Index and Ward's linkage. To investigate diversities, Pielou's Evenness, Shannon's Index and Simpson's Index of Diversity were calculated in addition to species richness. We used Student's t-test to determine statistical significance of differences in diversity measures. For a comparison of the top, middle and bottom zone, respectively the classes 1–5, data were adjusted for area (individuals per area).

Collected specimens were determined using Arbonnier (2002), Hutchinson et al. (1954–1972), Akoègninou et al. (2006), Berhaut (1971–1988), Scholz & Scholz (1983) and Poilecot (1999). Furthermore, we used the West Africa Herbarium of the Research Institute Senckenberg (FR) and the online photo guide 'West African Plants' (Brunken et al. 2008). Life forms were assigned according to Aké Assi (2001–2002) and Guinko (1984). Nomenclature followed the online 'African Plants Database' (2011), based and maintained at the Geneva Botanical Garden.

3 Results

A total of 156 species of flowering plants from 49 families were recorded on termite mounds (see Appendix S1). Nearly 40 percent of the recorded species belong to four families. Most species–rich were Fabaceae s. l. with 27 species, followed by Malvaceae (18 spp.), Poaceae (17 spp.) and Vitaceae (8 spp.).

The woody plant layer comprised 54 species from 21 families. Fabaceae were most species rich with 14 species, followed by Combretaceae (6 spp.), Capparaceae (4 spp.) and Anacardiaceae (3 spp.). In our study, Capparaceae were found exclusively on termite mounds.

The woody species diversity found in the adjacent savanna habitats (plots A and B) comprised 63 species from 22 families. The Fabaceae were represented with 17 species, followed by Combretaceae (11), Rubiaceae (5) and Anacardiaceae (3).

Eleven woody species (which equals 20% of the termite mounds' ligneous flora) were either strictly limited to termitaria or at least four times more common on mounds than in surrounding savannas. The family Capparaceae, with the species *Boscia angustifolia*, *Boscia salicifolia*, *Capparis fascicularis* and *Maerua angolensis* and the species *Tamarindus indica* (Fabaceae/Caesalpinoideae) and *Rhus natalensis* (Anacardiaceae) were found exclusively on termite mounds. On the other hand, 17 species (nearly 30% of the recorded savanna ligneous flora) including *Terminalia avicennioides*, *Annona senegalensis*, *Piliostigma thonningii*, *Pteleopsis suberosa* were limited to the savanna reference plots and never occurred on termite mounds.

Regarding plant life forms, termite mounds display a high diversity of lianas (e.g., *Dioscorea dumetorum*, *Cucumis maderaspatanus*, *Cissus quadrangularis*), geophytes (e.g., *Chlorophytum macrophyllum*, *Chlorophytum pusillum*, *Tacca leontopetaloides*) and succulents (*Sansevieria liberica*,

Kalanchoe lanceolata, *Costus spectabilis*). The total flora of 156 species comprised 24 species of lianas, 16 species of geophytes, 5 species of succulents.

Termite mounds display a clear zonation with most of their species being unevenly distributed. Our field studies confirm a differentiation of 3 zones for the herb layer on the mounds. Species richness and coverage of the herb layer decreased from bottom to top of termite mounds. 87 species were found in the bottom zone, 56 species in the middle zone and 32 species in the top zone. This decrease in diversity went along with changes in abundance of life forms. Therophytes displayed higher abundance in the bottom zone, while succulents and geophytes occurred in highest abundance in the top zone (Fig. 3). Representatives of Poaceae, Malvaceae and Fabaceae were found principally in the bottom zone, while Anthericaceae, Vitaceae and Cucurbitaceae occurred principally in the middle zone and Araceae, Crassulaceae and Dracaenaceae on top of the mounds.

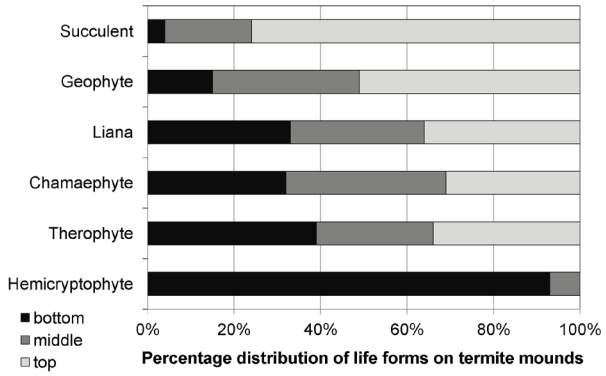

Fig. 3: Distribution of life forms (except phanerophytes) in top, middle and bottom zone of termite mounds (adjusted for area). Few species assigned to more than one life form. / Distribution des types biologiques (sauf les phanérophytes) dans les zones de la termitière (haut, milieu et bas) (Ajusté en fonction de la superficie). Un petit nombre d'espèces sont associées à plus d'un type biologique. / Verteilung der Lebensformen (ausgenommen Phanerophyten) in der oberen, mittleren und unteren Zone der Termitenhügel (flächenangepaßt). Einige Arten mehr als einer Lebensform zugeordnet.

Spatial preferences also became evident for woody plants. Species like *Tamarindus indica*, *Opilia amentacea*, *Capparis fascicularis*, *Combretum micranthum* and *Rhus natalensis* preferentially occurred in the central part of the mound, while others like *Combretum nigricans*, *Allophylus africanus* and *Anogeissus leiocarpa* were restricted to the periphery. Interestingly, species principally restricted to termite mounds like *Tamarindus indica* and *Rhus natalensis* were usually found growing in the central parts. Other species like *Combretum nigricans* and *Anogeissus leiocarpa* often found to occur also in the adjacent savanna vegetation (plots A and B) rather grew in the peripheral parts of the termite mounds (Fig. 4).

The detailed recording of woody species occurrence and abundance on the mounds and in the adjacent vegetation allowed an analysis of similarity of vegetation between the habitats. As described above, species diversity and abundance differed considerably between mounds and adjacent area, underlining the specific soil and microclimatic conditions these habitats offer. The analyses of species composition and abundance with a cluster analysis and an ordination (non–metric multidimensional scaling) displayed the termite mounds as a relatively homogeneous group which was clearly separated from the savanna plots A and B. The savanna plots A and B could not be separated by our analyses, although they were located in different (nevertheless fairly similar) savanna types found in the area. The cover of both the shrub and the tree layer was shown to be significantly higher ($p < 0.001$) on termite mounds than in the neighboring areas. Shannon's Index and Simpson's Index showed higher diversities on termitaria (see table 1).

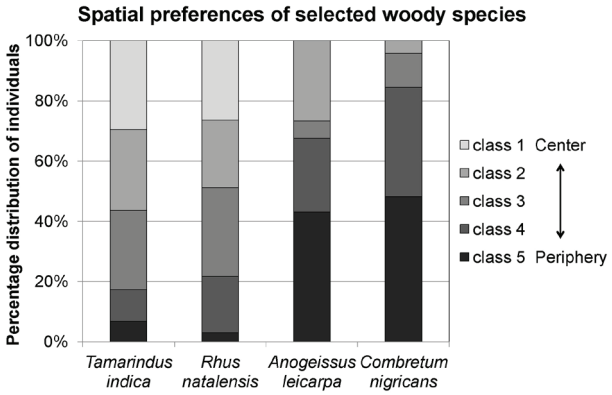

Fig. 4: Spatial preferences of *Tamarindus indica*, *Rhus natalensis*, *Anogeissus leiocarpa* and *Combretum nigricans* (Adjusted for area). / Préférences spatiales de *Tamarindus indica*, *Rhus natalensis*, *Anogeissus leiocarpa* et *Combretum nigricans* (Ajusté en fonction de la superficie). / Räumliche Präferenzen von *Tamarindus indica*, *Rhus natalensis*, *Anogeissus leiocarpa* und *Combretum nigricans* (flächenangepaßt).

The analyses documented no differences between termite mounds in different savanna types (grass and shrub savannas), but revealed differences between termite mounds in savanna environment and those located within cotton fields. The species richness of herb and shrub layer on the latter is significantly lower ($p < 0.001$) than on mounds in savannas. Especially the composition of the herb layer differs, with more Poaceae species found on the mounds in cotton fields and a significantly lower ($p < 0.01$) coverage of the shrub layer. The termite mounds in cotton fields were also characterized by the lowest diversity values of the Shannon and Simpson Index (see table 1).

4 Discussion

This study showed clearly that termite mounds represent diversity islands in the savanna biome, characterized by a spe-

Table 1: Means of Shannon Index, Simpson Index and Evenness (with standard deviation) for termite mounds in different surroundings and savanna plots. / Valeurs moyennes des Indices de Shannon, de Simpson et d'Équitabilité (avec écart-type) pour les termitières dans différentes régions et dans différents types de savanna. / Mittelwerte des Shannon-Index, Simpson-Index und Evenness (mit Standardabweichung) für Termitenhügel in verschiedenen Umgebungen und für Savannenflächen.

Location	Shannon Index	Simpson Index	Evenness
termite mounds	1,34±0,38	0,35±0,14	64,61±13,56
plots A	2,07±0,37	0,20±0,09	77,17±9,52
plots B	1,86±0,56	0,26±0,17	73,05±14,84
termite mound in savannas	2,16±0,26	0,19±0,05	62,56±6,57
termite mounds in cotton fields	1,85±0,20	0,26±0,06	61,68±5,11

cific, richer flora and usually denser vegetation than found in surrounding habitats. Similar results are reported by several other studies executed in different parts of Africa, for example in Uganda (Moe et al., 2009), Tanzania (Bloesch 2008) and Malawi (Bundschuh et al. 2010), describing a distinct floristic composition and dense thickets on termite mounds.

The differences in the species composition between termite mounds and savannas can be linked to favorable soil conditions due to an enrichment in clay, plant nutrients like carbon, nitrogen, calcium, potassium and magnesium (Watson 1977, Bachelier 1978, Bloesch 2008, Gudeta et al. 2010, Joseph et al. 2012) and a better water availability (Konaté et al. 1999) found on termitaria.

The systematic relationship of the species found on termite mounds is also noteworthy.

Studies on national park scale from the adjacent areas (Mbaygone et al. 2008, Ouedraogo et al. 2011) of the WAP-complex as well as on a country scale (Schmidt 2006) usually found Poaceae and Fabaceae to be the most diverse families. In the Pama Reserve and the whole of Burkina Faso, these two families have been followed in numbers by Cyperaceae, Rubiaceae, and Euphorbiaceae. The latter were less important on termite mounds, where Vitaceae and Poaceae followed Malvaceae and Fabaceae in species richness. The lower importance of Cyperaceae can easily be explained by their preference for humid or waterlogged localities which were not found on the mounds.

Considering their relatively small size of on average 69 m² in our study, especially woody plant diversity is strongly elevated on termite mounds. A very conspicuous feature of the unique woody plant cover on termite mounds is the family Capparaceae, which were found exclusively on termitaria in our study. A study of Dossou–Yovo (2009) from northern Benin also showed that Capparaceae are restricted to termite mounds. The study of Bundschuh et al. (2010) in Malawi found that 3 of 5 species restricted to termitaria belong to the family of Capparaceae.

A potential factor to explain the rather homogeneous species composition on termite mounds might be zoochorous seed dispersal. By far most of the species occurring principally on termitaria have diaspores for which zoochory can be assumed. Regarding the floristic composition of termite mound in our study, 61% of the species can be seen as being dispersed by animals (see Appendix S1).

While towards the top of the mounds the overall species diversity decreased, an increasing abundance of succulents (*Sansevieria liberica*, *Kalanchoe lanceolata*, *Cissus quadrangularis* and *Costus spectabilis*) could be observed. Succulent growth forms are commonly associated with high soil nutrient levels under arid conditions (Knight et al. 1989), and we expect a high surface water runoff at the top of the mound. Additionally, at the top of the termitaria, which offers a slight elevation above grass fires, succulents are well protected from fire as they are highly sensitive to it (Pérez–Garcia & Meave 2006). This might be less important for *Costus spectabilis* with leaves only appearing in the growing season.

While the plant cover of termite mounds located in different savanna types did not differ significantly, the vegetation of mounds surrounded by cotton fields proved to be less diverse and displayed a higher abundance of Poaceae. This may be due to the use of fertilizers, but nevertheless could also be caused by other factors like direct human impact to improve the conditions for crops.

Termite mounds are habitats of high socio-economic importance, 62% of the total termite mound flora is used medicinally (Nacoulma 1996, Arbonnier 2002, Krohmer 2004). Among these are *Tamarindus indica* (Fig. 5), *Stereospermum kunthianum*, *Diospyros mespiliformis*, *Combretum micranthum*, *Opilia amentacea*, and *Grewia bicolor*, which were shown to be restricted or to be much more abundant

Fig 5: Termite mound with *Tamarindus indica*. / Termitière avec *Tamarindus indica.* / Termitenhügel mit *Tamarindus indica*.

on termitaria (see Appendix S1). Several of these species have also been found to be restricted to termitaria in different phytogeographical districts of Benin by Fandohan et al. (2012).

We conclude that termite mounds represent abundant and specific sites with increased and specific diversity concerning species, life forms and vegetation structure. Thus, their preservation and conservation is of high importance for the biodiversity in this savanna region.

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Appendix S1

Plant taxa on 57 termitaria, surrounding and adjacent savanna plots in W National Park, North Benin. / Taxa des plantes sur 57 termitières des placeaux entourants et voisins en savane du Parc National du W, Nord-Bénin / Pflanzentaxa auf 57 Termitenhügeln der umgebenden und benachbarten Savannenflächen im W-Nationalpark, Nordbenin.

	location	life form	dispersal mode	medicinal use
Acanthaceae				
Asystasia gangetica (L.) T. Anderson	T	th	?	x
Blepharis maderaspatensis (L.) B. Heyne ex Roth	T	th	ep	
Justicia insularis T. Anderson	T	th	?	
Monechma ciliatum (Jacq.) Milne–Redh.	T	th	?	
Agavaceae				
Agave sisalana (Engelm.) Perrine	T	su	en	
Amaranthaceae				
Achyranthes aspera L.	T	th	ep	x
Pandiaka angustifolia (Vahl) Hepper	T	th	ep	x
Pupalia lappacea (L.) A.Juss.	T	he	ep	x
Amaryllidaceae				
Crinum ornatum (L. f. ex Aiton) Bury	T	ge	en	x
Scadoxus multiflorus (Martyn) Raf.	T	ge	en	
Anacardiaceae				
Lannea acida A. Rich.	T, A, B	ph	en	x
Lannea microcarpa Engl. & K. Krause	T, A, B	ph	en	x
Ozoroa obovata var. *obovata* (Oliv.) R. Fern. & A. Fern.	A	ph	en	x
Rhus natalensis Bernh. ex Krauss	T	ph	en	x
Annonaceae				
Annona senegalensis Pers.	A, B	ph	en	x
Hexalobus monopetalus (A. Rich.) Engl. & Diels	T, A, B	ph	en	x

	location	life form	dispersal mode	medicinal use
Anthericaceae				
Chlorophytum macrophyllum (A. Rich.) Asch.	T	ge	?	
Chlorophytum pusillum Schweinf. ex Baker	T	ge	?	
Apocynaceae				
Ceropegia racemosa N. E. Br.	T	ph, li	an	
Landolphia dulcis (Sabine) Pichon	T, A, B	ph, li	en	x
Araceae				
Amorphophallus dracontioides (Engl.) N. E. Br.	T	ge	en	
Stylochaeton lancifolius Kotschy & Peyr.	T	ge	en	
Asparagaceae				
Asparagus flagellaris (Kunth) Baker	T, A, B	ph, li	en	x
Asteraceae				
Aspilia africana (P. Beauv.) C. D. Adams	T	th	an	x
Aspilia bussei O. Hoffm. & Muschl.	T	th	an	
Aspilia helianthoides (Schumach. & Thonn.) Oliv. & Hiern	T	th	an	
Aspilia kotschyi (Sch. Bip.) Oliv.	T	th	an	x
Bidens bipinnata L.	T	th	ep	
Pseudoconyza viscosa (Mill.) D'Arcy	T	th	an	
Balanitaceae				
Balanites aegyptiaca (L.) Delile	T, A, B	ph	en	x
Bignoniaceae				
Stereospermum kunthianum Cham.	T, A, B	ph	en	x
Capparaceae				
Boscia angustifolia A. Rich.	T	ph	en	x
Boscia salicifolia Oliv.	T	ph	en	x
Capparis fascicularis DC.	T	ph	en	
Maerua angolensis DC.	T	ph	en	x
Celastraceae				
Gymnosporia senegalensis (Lam.) Loes.	T, A, B	ph	en	x
Cochlospermaceae				
Cochlospermum planchonii Hook. f.	T, A, B	ch	en	x
Colchicaceae				
Gloriosa superba L.	T	ge, li	en	
Combretaceae				
Anogeissus leiocarpa (DC.) Guill. & Perr.	T, A, B	ph	an	x
Combretum adenogonium Steud. ex A. Rich.	B	ph	an	x
Combretum collinum Fresen.	T, A, B	ph	an	x
Combretum glutinosum Perr. ex DC.	T, A, B	ph	an	x
Combretum micranthum G. Don	T, A	ph	an	x
Combretum molle R. Br. ex G. Don	T, A, B	ph	an	x
Combretum nigricans Lepr. ex Guill. & Perr.	T, A, B	ph	an	x
Pteleopsis suberosa Engl. & Diels	A, B	ph	an	x

	location	life form	dispersal mode	medicinal use
Terminalia avicennioides Guill. & Perr.	A, B	ph	an	x
Terminalia laxiflora Engl. & Diels	A, B	ph	an	x
Terminalia schimperiana Hochst.	A	ph	an	x
Commelinaceae				
Aneilema beniniense (P. Beauv.) Kunth	T	ch	an	
Commelina benghalensis L.	T	th	an	x
Commelina erecta L.	T	th	an	x
Cyanotis lanata Benth.	T	th	an	x
Convolvulaceae				
Ipomoea cairica (L.) Sweet	T, B	ph, li	an	
Ipomoea eriocarpa R. Br.	T	th, li	an	x
Crassulaceae				
Kalanchoe lanceolata (Forssk.) Pers.	T	th, su	an	
Cucurbitaceae				
Cucumis maderaspatanus L.	T, A	th, li	en	
Kedrostis foetidissima (Jacq.) Cogn.	T	th, li	en	
Cyperaceae				
Cyperus difformis L.	T	th	an	
Kyllinga debilis C. B. Clarke	T	th	an	
Dioscoreaceae				
Dioscorea dumetorum (Kunth) Pax	T, A, B	ge, li	an	x
Dioscorea quartiniana A. Rich.	T	ge, li	an	
Dioscorea togoensis R. Knuth	T, A, B	ge, li	an	
Dracaenaceae				
Sansevieria liberica Gérôme & Labroy	T	ge, su	en	x
Ebenaceae				
Diospyros mespiliformis Hochst. ex A.DC.	T, A, B	ph	en	
Euphorbiaceae				
Bridelia ferruginea Benth.	T, A, B	ph	en	x
Bridelia scleroneura Müll. Arg.	T, A	ph	en	x
Euphorbia baga A. Chev.	T	he	en	
Flueggea virosa (Roxb. ex Willd.) Voigt	T, A, B	ph	en	x
Jatropha gossypiifolia L.	T	ch	en	x
Tragia senegalensis Müll. Arg.	T	ph, li	en	
Fabaceae				
Acacia ataxacantha DC.	T, A	ph	en	x
Acacia erythrocalyx Brenan	T, A	ph	en	x
Acacia hockii De Wild.	T, A, B	ph	en	x
Acacia macrostachya Rchb. ex DC.	T, A, B	ph	en	x
Albizia chevalieri Harms	T	ph	en	x
Burkea africana Hook.	T, A, B	ph	en	x
Cassia mimosoides L.	T	ch	en	x
Cassia obtusifolia L.	T	ch	en	x

	location	life form	dispersal mode	medicinal use
Cassia sieberiana DC.	T, A, B	ph	en	x
Desmodium gangeticum (L.) DC.	T	ch	an	x
Desmodium tortuosum (Sw.) DC.	T	ch	an	
Desmodium velutinum (Willd.) DC.	T	ch	ep	x
Detarium microcarpum Guill. & Perr.	T, A, B	ph	en	x
Dichrostachys cinerea (L.) Wight & Arn.	T, A, B	ph	en	x
Entada africana Guill. & Perr.	A, B	ph	en	x
Indigofera dendroides Jacq.	T	th	en	x
Indigofera garckeana Vatke	A, B	ch	an	
Indigofera tinctoria L.	T	ch	an	x
Isoberlinia doka Craib & Stapf	T, A, B	ph	en	x
Parkia biglobosa (Jacq.) R. Br. ex G. Don	T, A, B	ph	en	x
Pericopsis laxiflora (Benth.) Meeuwen	A, B	ph	an	x
Philenoptera laxiflora (Guill. & Perr.) Roberty	A	ph	an	x
Piliostigma thonningii (Schumach.) Milne–Redh.	T, A, B	ph	en	
Prosopis africana (Guill. & Perr.) Taub.	A, B	ph	en	x
Pterocarpus erinaceus Poir.	T, A, B	ph	an	x
Rhynchosia buettneri Harms	T	th, li	en	
Rhynchosia minima (L.) DC.	T	th, li	en	
Tamarindus indica L.	T	ph	en	x
Tephrosia pedicellata Baker	T	th	an	
Uraria picta (Jacq.) DC.	T	ch	an	x
Vigna luteola (Jacq.) Benth.	T	th, li	an	
Vigna racemosa (G. Don) Hutch. & Dalziel	T	th, li	an	
Xeroderris stuhlmannii (Taub.) Mendonça & E.C.Sousa	B	ph	an	x
Lamiaceae				
Hoslundia opposita Vahl	T	ch	en	x
Hyptis suaveolens Poit.	T	th	?	x
Leucas martinicensis (Jacq.) R. Br.	T	th	ep	
Plectranthus gracillimus (T. C. E. Fr.) Hutch. & Dandy	T	th	an	
Solenostemon rotundifolius (Poir.) J. K. Morton	T	ch	an	x
Loganiaceae				
Strychnos innocua Delile	T, A, B	ph	en	x
Strychnos spinosa Lam.	T, A, B	ph	en	x
Loranthaceae				
Agelanthus dodoneifolius (DC.) Polhill & Wiens	T, A, B	pa	en	x
Malvaceae				
Abutilon ramosum (Cav.) Guill. & Perr.	T	ch	an	
Adansonia digitata L.	T	ph	en	x
Bombax costatum Pellegr. & Vuill.	T, A, B	ph	en	x
Gossypium hirsutum L.	T	ch	an	
Grewia barteri Burret	A	ph	en	
Grewia bicolor Juss.	T, A	ph	en	x
Grewia cissoides Hutch. & Dalziel	T	ch	en	x
Grewia flavescens Juss.	T, A, B	ph	en	x
Grewia lasiodiscus K. Schum.	A	ph	en	x
Grewia mollis Juss.	T, A	ph	en	x
Hibiscus cannabinus L.	T	th	an	x
Hibiscus sineaculeatus F. D. Wilson	A	ch	an	

	location	life form	dispersal mode	medicinal use
Sida alba L.	T	th	an	x
Sida rhombifolia L.	T	he	an	x
Sida urens L.	T	he	an	
Sterculia setigera Delile	T, A, B	ph	en	x
Triumfetta lepidota K. Schum.	B	ch	en	
Wissadula rostrata (Schumach.) Hook. f.	T	ch	an	x
Meliaceae				
Pseudocedrela kotschyi (Schweinf.) Harms	A	ph	an	x
Moraceae				
Ficus artocarpoides Warb.	A	ph	en	
Ficus exasperata Vahl	T	ph	en	
Ficus lutea Vahl	T	ph	en	
Olacaceae				
Ximenia americana L.	T, A, B	ph	en	x
Opiliaceae				
Opilia amentacea Roxb.	T, A, B	ph, li	en	x
Orchidaceae				
Eulophia guineensis Lindl.	T	ge	an	
Poaceae				
Andropogon gayanus Kunth	T	he	ep	x
Brachiaria villosa (Lam.) A. Camus	T	th	an	
Chasmopodium caudatum (Hack.) Stapf	T	th	an	
Digitaria ciliaris (Retz.) Koeler	T	th	an	
Digitaria horizontalis Willd.	T	th	an	
Hackelochloa granularis (L.) Kuntze	T	th	an	
Hyparrhenia involucrata Stapf	T	th	ep	
Loudetia togoensis (Pilg.) C. E. Hubb.	T	th	ep	
Microchloa indica (L. f.) P. Beauv.	T	th	an	
Pennisetum pedicellatum Trin.	T	th	ep	x
Pennisetum polystachion (L.) Schult.	T	th	ep	x
Rhytachne triaristata (Steud.) Stapf	T	th	ep	
Rottboellia cochinchinensis (Lour.) Clayton	T	th	an	x
Setaria barbata (Lam.) Kunth	T	th	an	x
Setaria pumila (Poir.) Roem. & Schult.	T	th	an	x
Sporobolus pyramidalis P. Beauv.	T	he	an	x
Zea mays L.	T	th	en	x
Polygalaceae				
Polygala multiflora Poir.	T	th	an	
Rhamnaceae				
Ziziphus abyssinica A. Rich.	T, A, B	ph	en	x
Ziziphus mucronata Willd.	T, A	ph	en	x
Rubiaceae				
Crossopteryx febrifuga (Afzel. ex G. Don) Benth.	T, A, B	ph	en	x
Feretia apodanthera Delile	T, A, B	ph	en	x

	location	life form	dispersal mode	medicinal use
Gardenia aqualla Stapf & Hutch.	A, B	ph	en	x
Gardenia ternifolia Schumach. & Thonn.	T, A, B	ph	en	x
Sarcocephalus latifolius (Sm.) E. A. Bruce	A, B	ph	en	x
Spermacoce radiata (DC.) Hiern	T	th	?	x
Spermacoce ruelliae DC.	T	th	?	x
Sapindaceae				
Allophylus africanus P. Beauv.	T, A	ph	en	x
Sapotaceae				
Vitellaria paradoxa C. F. Gaertn.	T, A, B	ph	en	x
Taccaceae				
Tacca leontopetaloides (L.) Kuntze	T	ge	en	x
Verbenaceae				
Vitex doniana Sweet	A, B	ph	en	x
Vitaceae				
Ampelocissus africana (Lour.) Merr. var. africana	T	ph, li	en	x
Ampelocissus leonensis (Hook. f.) Planch.	T, A	ph, li	en	
Cayratia gracilis (Guill. & Perr.) Suess.	T	ph, li	en	x
Cissus cornifolia (Baker) Planch.	T, B	ch	en	
Cissus populnea Guill. & Perr.	T, A, B	ph, li	en	x
Cissus quadrangularis L.	T	ph, li, su	en	x
Cyphostemma adenocaule (Steud. ex A. Rich.) Desc. ex Wild & R. B. Drumm. subsp. *adenocaule*	T	ph, li	en	
Cyphostemma cymosum (Schumach. & Thonn.) Desc. subsp. *cymosum*	T	ph, l	en	
Zingiberaceae				
Costus spectabilis (Fenzl) K. Schum.	T	ge, su	en	
Siphonochilus aethiopicus (Schweinf.) B. L. Burtt	T	ge	en	

Location: T= termite mound, A= plot A, B= plot B

Life form according to Aké Assi (2001–2002) and Guinko (1984): th=therophyte, ge=geophyte, he=hemicryptophyte, ph=phanerophyte, li=liana, ch=chamaephyte, su=succulent, pa=parasite

Dispersal mode according to Hovestadt et al. (1999) and own observations: an=anemochorous, ep=epizoochorous, en=endozoochorous, ?=unknown

Medicinal use according to Nacoulma (1996), Arbonnier (2002) and Krohmer (2004).

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

Alexandra Zwarg, Marco Schmidt, Thomas Janßen, Karen Hahn, Georg Zizka

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

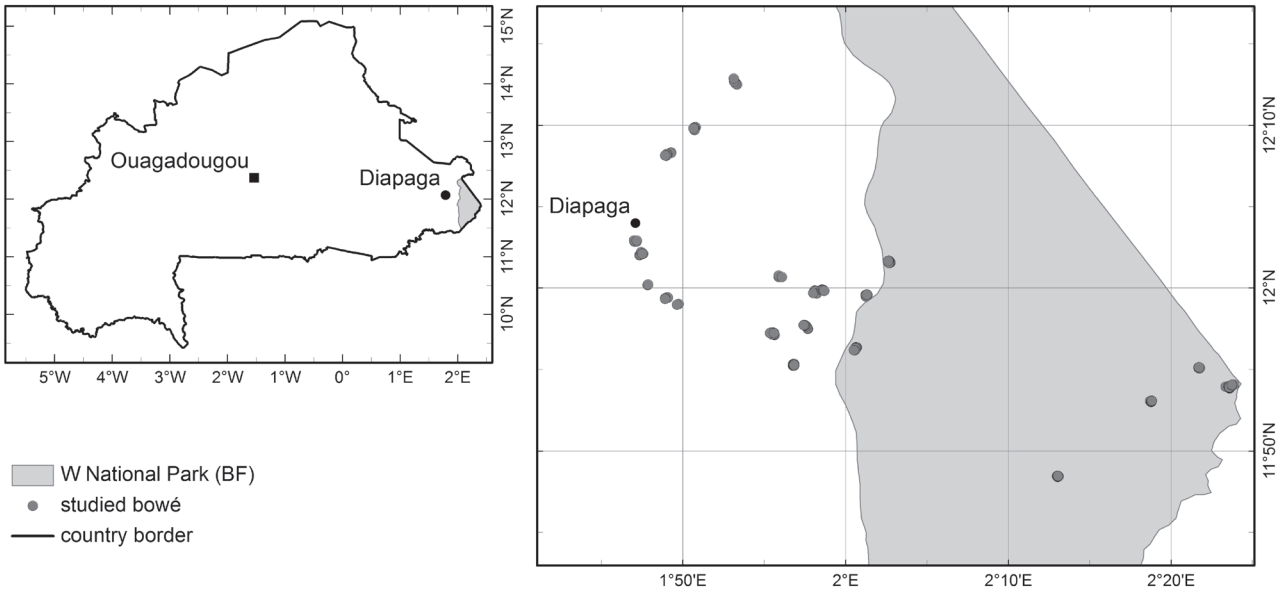

Fig. 2: Study area in the SE of Burkina Faso. Borders of W National Park are taken from IUCN & UNEP-WCMC (2010). / Aire de recherché dans le Sud-est du Burkina Faso. La frontière du Parc National est prise d'IUCN & UNEP-WCMC (2010). / Untersuchungsgebiet im Südosten Burkina Fasos. Grenzen des W-Nationalparks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

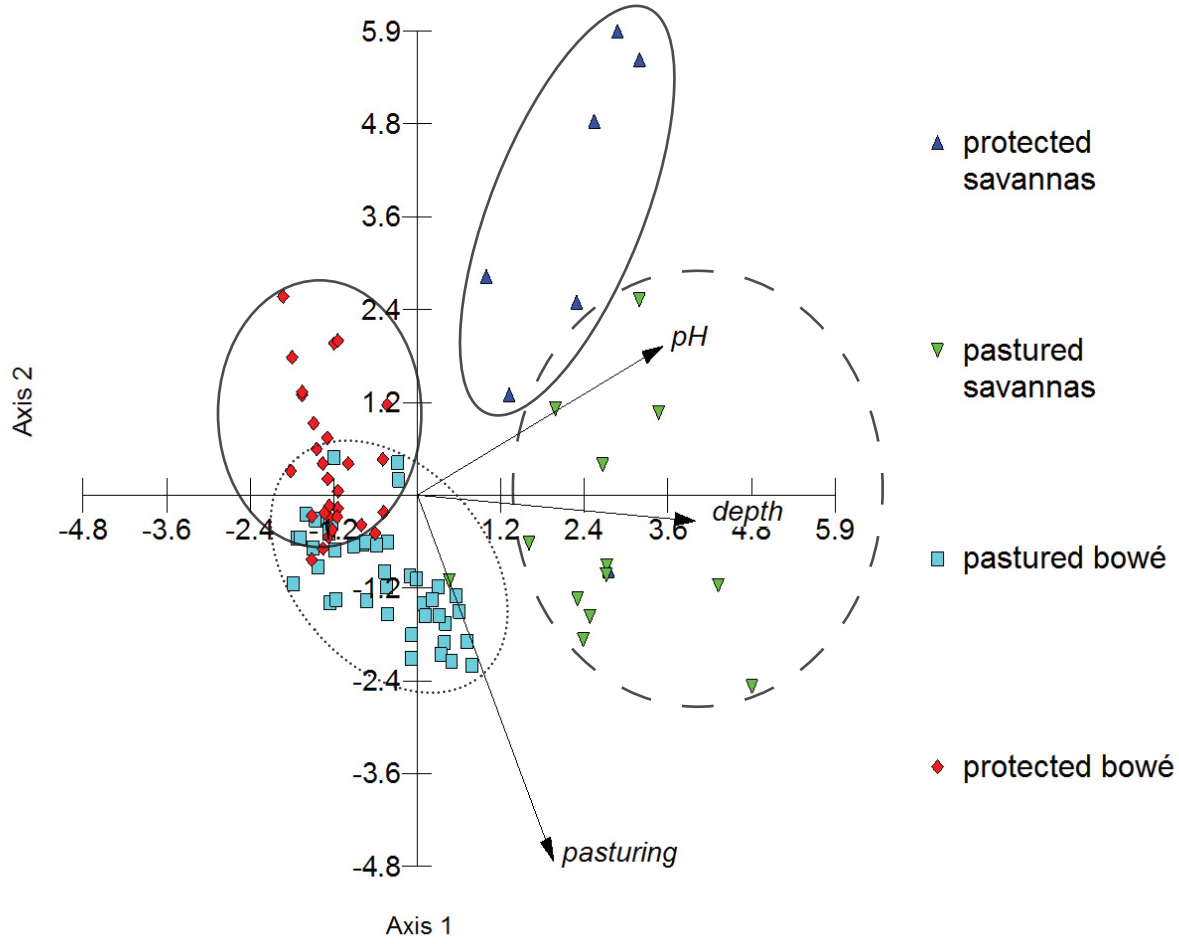

Fig. 3. Ordination diagram of the CCA. The symbols represent location of the plots within the bowé or in adjacent savannas and within or outside of the W National Park. / Diagramme d'ordination CCA. Les symboles représentent la location des sites sur bowé ou savanes et dans le parc ou dehors. / Ordinationsdiagramm 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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The Vegetation of Lateritic Crusts in Northwestern Benin (Atakora Region)

Robert Sieglstetter, Rüdiger Wittig, Karen Hahn

Summary: Most of the grass savannas on lateritic crusts found in the North-Western of Benin are free of trees and a shrub layer is only sparsely developed. The only constant member of the shrub layer, is *Terminalia laxiflora*. Intermediate constancy show *Entada africana* and *Annona senegalensis*. With regard to the herbaceous layer two types can be identified: On very shallow soils (<2 cm) *Loudetia togoensis* is highly constant and often dominating. The same is true for *Andropogon pseudapricus* on soils of a little bit more than 2 cm. In those types, *Lepidagathis anobrya* and *Spermacoce filifolia* show very high constancy (constancy class V) and *Cyanotis lanata* and *Melliniella micrantha* occur with high constancy (IV).

Key words: *Andropogon pseudapricus, Cyanotis lanata,* grass savanna, hardpan, *Lepidagathis anobrya*, *Loudetia togoensis*, *Spermacoce filifolia*, Sudanian zone, *Terminalia laxiflora,* West-Africa

La végétation des cuirasses latéritiques au Nord-Ouest du Bénin (région Atakora)

Résumé: Les savanes herbeuses des cuirasses latéritiques du Nord-Ouest Bénin ne contiennent presque pas d'arbres mais seulement une strate arbustive très clairsemée. Dans cette strate *Terminalia laxiflora* est la seule espèce régulière. *Entada africana* et *Annona senegalensis* possèdent une présence moyenne constante. Concernant la composition floristique de la strate herbacée, on peut distinguer deux types différents. Si la couche de sol au-dessus de la cuirasse latéritique est faible (moins de 2 cm), l'aspect du groupement est dominé par *Loudetia togoensis*. Si la couche de sol devient plus épaisse (plus de 2 cm), *Andropogon pseudapricus* devient l'espèce dominante. *Lepidagathis anobrya* et *Spermacoce filifolia* ont une présence constamment très élevée dans les deux types; *Cyanotis lanata* et *Melliniella micrantha* ont une présence constamment élevée.

Mots clés: Afrique de l'Ouest, *Andropogon pseudapricus,* cuirasses latéritiques, *Cyanotis lanata, Lepidagathis anobrya*, *Loudetia togoensis*, savane herbeuse, *Spermacoce filifolia*, *Terminalia laxiflora,* zone soudanienne

Die Vegetation auf Lateritkrusten im Nordwesten von Benin (Region Atakora)

Zusammenfassung: Die Grassavannen auf Lateritkrusten im Nordwesten von Benin besitzen nahezu keine Baum- und nur eine äußerst gering entwickelte Strauchschicht. In dieser ist *Terminalia laxiflora* die einzige hochstete Art. Mittlere Stetigkeiten weisen *Entada africana* und *Annona senegalensis* auf. Bezüglich der Zusammensetzung der Krautschicht sind zwei Typen zu unterscheiden: Ist über der Lateritkruste ein nur sehr geringmächtiger Boden vorhanden, so wird der Aspekt der Gesellschaft von *Loudetia togoensis* bestimmt, ist der Boden etwas mächtiger, so ist *Andropogon pseudapricus* die wichtigste Art. In beiden Typen gemeinsam treten *Lepidagathis anobrya* und *Spermacoce filifolia* mit sehr hoher Stetigkeit sowie *Cyanotis lanata* und *Melliniella micrantha* mit hoher Stetigkeit auf.

Schlagworte: *Andropogon pseudapricus, Cyanotis lanata,* Grassavannen, Lateritkrusten, *Lepidagathis anobrya*, *Loudetia togoensis*, *Spermacoce filifolia*, Sudanzone, *Terminalia laxiflora,* Westafrika

1 Introduction

Only a few relevés of the vegetation on lateritic crusts in West Africa have been taken to date. Moreover, these have been published in PhD theses and are not easily accessible (Nasi 1994, Hahn 1996, Küppers 1996, Sieglstetter 2002, Krohmer 2004). Therefore, this paper will present relevés taken on lateritic crusts in the region of Atakora (northwestern Benin).

2 Area of investigation

The study area is the territory of the Tipéti and Péperkou villages, situated in the Department of Atakora, in northwestern Benin. The climate of this area shows an annual alternation of dry and wet seasons. The wet season extends from the end of April through the end of October (or the first days of November), with 60% of the annual precipitation falling between July and September. The annual rainfall is approximately 1300 mm (Maurice 1986, Tente 2000). The highest temperatures (up to 38° Celsius average monthly maximum) occur in March and April. December and January are the coldest months.

Phytogeographically, the area belongs to the Sudanian zone (White 1983). Applying the criteria of Guinko (1984) for the division of this zone into a northern and a southern part, our area belongs to the South Sudanian zone.

3 Methods

The relevés were taken by the first author between September and the first days of December in the years 1999 to 2001 using the method of Braun-Blanquet (1964). In accordance with Hahn (1996), Küppers (1996), Krohmer, (2004) and Schumann et al. (2010), the woody layer and the herbaceous layer were surveyed separately. For the woody layer, we used a relevé area of 900 m^2; for the herbaceous layer, we used an area of 25 m^2. The woody layer was separated into the tree layer (higher than 5 m) and the shrub layer (below 5 m).

Nomenclature of species follows the "West African Plants Database" (http://www.westafricanplants.senckenberg.de) and the databse of the "Conservatoire et Jardin botaniques & South African National Biodiversity Institute" (http://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php?langue=an).

4 Results

A woody layer is only very slightly developed on lateritic crusts (Table 1). In most cases (15 of our 17 relevés), only a shrub layer exists. On average, the shrub layer covers 11% of the relevé area. The average number of woody species ranges between five and six. *Terminalia laxiflora* is the only species of the woody layer represented in nearly all relevés (constancy class V). Second in constancy are *Entada africana* and *Annona senegalensis* (III), followed by *Detarium microcarpum, Pteleopsis suberosa, Daniellia oliveri, Euphorbia unispina, Gardenia erubescens* and *Combretum fragans* (II). All other woody species only reach constancy class I at their maximum.

Table 1: Relevés of the tree and shrub layer / relevés des strates ligneuses / Aufnahmen der Baum- und Strauchschicht

Relevé No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Location	Pe	Pe	Pe	Pe	Ti	Pe	Pe	Ti	Ti	Pe	Pe	Pe	Pe	Ti	Ti	Pe	Pe
Day	22	26	16	27	10	19	19	18	15	27	26	21	11	29	8	23	21
Month	10	10	10	10	11	10	10	10	10	10	10	10	10	10	11	10	10
Year	01	99	00	99	99	01	01	01	00	99	99	00	00	00	99	00	00
Cover of the tree layer (%)	0	0	0	0	0	0	0	5	0	5	0	0	0	0	0	0	0
Height of the tree layer (m)	0	0	0	0	0	0	0	6	0	6	0	0	0	0	0	0	0
Species number (tree layer)	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0
Cover of the Shrub layer (%)	20	10	30	10	10	5	10	10	5	15	10	5	5	10	20	10	5
Height of the shrub layer (m)	3	4	5	2,5	2	2	3	2	3	3	3	1,5	1	2	2	2	2
Species number (shrub layer)	8	5	10	7	3	5	5	7	1	7	5	4	2	7	9	5	4
Tree layer																		C (%)	CC
Entada africana								2a										6	+
Lannea acida										1								6	+
Terminalia laxiflora										1								6	+
Shrub layer																			
Terminalia laxiflora	2a	1	1	1	1	1	1	1	1	1	1	1	+	+	+	+		94	V
Entada africana	1	1	1	+	+	+								+	+	+	+	59	III
Annona senegalensis	1	+		+		+	+							+	+		1	47	III
Detarium microcarpum			+	1				+		+	+							29	II
Pteleopsis suberosa			1			+		+						+	1			29	II
Euphorbia unispina	1										+	+	+					24	II
Daniellia oliveri			1							1				+	+			24	II
Gardenia erubescens					1			1							2b	1		24	II
Combretum fragans	+						+	1										18	I
Nauclea latifolia				+			+									+		18	I
Parinari curatellifolia								+							+		+	18	I
Pterocarpus erinaceus	+															+		12	I
Grewia mollis			+							1								12	I
Hymenocardia acida			2b								+							12	I
Vitellaria paradoxa						+	1											12	I
Stereospermun kunthianum								1						+				12	I
Crossopteryx febrifuga														+	2b			12	I
Combretum collinum	2a																	6	+
Lannea microcarpa		1																6	+
Dichrostachys cinerea			2a															6	+
Terminalia glaucescens																	2a	6	+

Additionally with + in relevé No. 1: *Gardenia aqualla;* No. 2: *Sterculia setigera*; No. 3: *Allophylus africanus* and *Lannea acida*; No. 4: *Erythrina senegalensis* and *Securinega virosa*; No. 10: *Combretum nigricans, Cussonia bateri* and *Tricalysia chevalieri*; No. 11: *Parkia biglobosa*; No. 12: *Hexalobus monopetalus* and *Strychnos spinosa*; No. 15: *Sphenostylis schweinfurthii*

Abbreviations: C (%) = relative constancy; CC = constancy class; Pi = Péperkou; Ti = Tipéti

Two communities can be identified in the herbaceous layer (Table 2). Where the soil is extremely shallow, *Loudetia togoensis* dominates the community, where it is developed a little more remarkably, *Andropogon pseudapricus* is dominant.

5 Discussion

A woody community, poor in species and more or less dominated by *Terminalia laxiflora*, also occurs in the Chaîne de Gobnangou in Burkina Faso (Küppers 1986). There, however, *Terminalia laxiflora* grows on sandstone soils. Consequently, the two *Terminalia laxiflora* communities are not similar throughout the species spectrum. According to Thies (1995), *Annona senegalensis*, on of the second most important species of in the community examined in the current study, is often found on sites that are regularly burned. In the Atakora region, lateritic crusts are the first to be burned because they become dry immediately at the end of the rainy season.

Table 2: Relevés of the herbaceaus layer / relevés des la srate herbacée / Aufnahmen der Krautschicht

Relevé No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**			**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	
Location	Ti	Ti	Ti	Ti	Pe	Pe	Pe			Pe	Pe	Ti	Pe	Pe	Ti	Ti	Pe	Ti	
Day	18	18	29	15	21	11	11			22	5	18	5	5	13	13	23	8	
Month	10	10	10	10	10	10	10			10	11	10	10	10	10	10	10	10	
Year	01	01	00	00	00	00	00			01	01	01	01	01	00	00	00	01	
Cover of the tree layer (%)	0	10	0	0	0	0	0			0	40	0	20	20	0	0	0	0	
Cover of the shrub layer (%)	10	20	10	0	5	5	5			20	30	15	20	20	0	0	10	0	
Cover of the herb layer (%)	70	70	60	60	40	30	30			80	70	70	70	70	30	30	40	20	
Height of the herb layer (m)	1,5	1,5	2	1	1	1,5	1			1,5	2	2	1,5	2	1	1	0,5	0,5	
Species number (herb layer)	14	26	15	14	16	15	12			26	26	27	11	21	18	12	19	27	
Differential species of the *Andropogon pseudapricus* community								C (%)	CC										C (%)	CC
Andropogon pseudapricus	2b	2a	2a	1	2a	+	+	100	V			1					+		22	II
Differential species of the *Loudetia togoensis* community																				
Loudetia togoensis										2a	2a	2a	2a	2a	2a	2a	1		89	V
Pandiaka heudelotii										+	+	+	+	+			+	+	78	IV
Polygala multiflora										+	+	+	+		+				56	III
Andropogon ascinodis										2b	2a	+			+	+			56	III
Aspilia rudis										+	+	1		+				+	56	III
Differential species of the vegetation on lateritic crusts																				
Lepidagathis anobrya	+	+	1	+	1	1	2a	100	V	1	+	+	+			1	2a	1	78	IV
Spermacoce filifolia	2a	2a	2a	1	1	+	+	100	V	1	+			1	1	1	2a	2a	78	IV
Cyanotis lanata		+	+		1	1	1	71	IV		+	+			+	+	1	+	67	IV
Melliniella micrantha		+	+		+	+		57	II	1		+		1		+	+	+	67	IV
Companions																				
Schizachyrium ruderale	2a			+	1	+	+	71	IV		+		1	2a		+	1		56	III
Loudetiopsis kerstingii		+	1				+	43	III	1	1		2a	2a	1			1	67	IV
Rhytachne gracilis		+	+	+	1			57	III			+			1	1	+	1	56	III
Cassia mimosoides	+	+	+					43	III		+	+		+		+	+		56	III
Ctenium villosum	1			1	+	1	+	71	IV								1	2a	22	II
Hyparrhenia subplumosa		3	2a					29	II	1		3	2a	2a				1	56	III
Tephrosia pedicellata	2b	2a				+		43	III		+	1			+		1		44	III
Andropogon fastigiatus						+	+	29	II	1				+	+		1		44	III
Abildgaardia abortiva	+	1			+			43	III	+		+						1	33	II
Hibiscus asper				1	+			29	II	+	+				+			+	44	III
Michrocloa indica					1	1	+	43	III				1		+			1	33	II
Cochlospermum tinctorium		1	+					29	II	1		+					+		33	II
Ctenium elegans		+				1	1	43	III			+					+		22	II
Desmodium hirtum					+			14	I	+				+		+		+	44	III

Relevé No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**			**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**		
Elionurus elegans					+	+	+	43	III								1	+	22	II
Andropogon gayanus		+						14	I		1	+		1					33	III
Indigofera geminata			+			+	+	43	III	+									11	I
Loudetia simplex		+		4				29	II			1					+		22	II
Scleria atrovirens	1	1						29	II			+						+	22	II
Urelytrum annum	1	+						29	II	1		+							22	II
Cochlospermum planchoni				+				14	I				+	+					22	II
Indigofera bracteolata	1							14	I	1								+	22	II
Macrotyloma biflorum		+						14	I	+		+							22	II
Monocymbium ceresiiforme	1	+						29	II			1							11	I
Basilicum polystachyon										+	+		+						33	II
Monechma ciliatum											+		+	+					33	II
Tephrosia flexuosa												+			+	+			33	II
Rhynchelytrum repens															+	+		+	33	II
Aeollanthus pubescens			+		+			29	II											
Chasmopodium caudatum													+	+					22	II
Bidens borianiana				+				14	I						+				11	I
Crotalaria leprieurii												+						+	22	II
Elymandra androphila											1			2b					22	II
Englerastrum gracillimum											+			+					22	II
Euclasta condylotricha			+					14	I		+								11	I
Euphorbia hyssopifolia		+						14	I			+							11	I
Hyparrhenia involucrata						+	+	29	II											
Micrageria filiformis		+						14	I						+				11	I
Neurotheca loeseloides		1						14	I									+	11	I
Orepethium spec.															+	+			22	II
Panicum brazzavillense										+								+	22	II
Tephrosia bracteolata					+			14	I								+		11	I
Polygala spec.	+							14	I			+							11	I
Andropogon schirensis	1							14	I											
Crotalaria microcarpa		2a						14	I											
Aspilia helianthoides										1									11	I
Rottboellia cochinchinensis										1									11	I
Pennisetum polystachion											2a								11	I
Indigofera dendroides														1					11	I
Genlisea africana																		1	11	I
Xyris straminea																		1	11	I

Additionally with + in relevé No. 1: *Tephrosia platycarpa*; No. 2: *Schizachyrium brevifolium*, *S. nodulosum* and *Scleria sphaerocarpa*; No. 3: *Eriosema linifolium*, *Hypoestes aristata* and *Polygala arenaria*; No. 4: *Annona senegalensis* juv., *Entada africana* juv., *Hackelochloa granularis*, *Parinari curatellifolia* and *Terminalia avicennioides* juv.; No. 5: *Indigofera pulchra* and *Vigna nigritia*; No. 6: *Crotalaria macrocalyx*; No. 8: *Ceratotheca sesamoides, Setaria pumila, Tridax procumbens, Triumfetta pentandra*; No. 9: *Spermacoce stachydea, Rourea coccinea, Dioscorea togoensis, Euphorbia kouandenensis, Mitracarpus hirtus, Panicum hochstetteri* and *Trachypogon spicatus*; No. 10: *Spermacoce spermacocina, Kohautia tenuis*; No. 12: *Biophytum umbraculum, Wahlenbergia hirsuta* and *Panicum pansum*; No. 13: *Heliotropium strigosum* and *Pandiaka involucrata*; No. 15: *Heteropogon contortus* and *Chlorophytum* spec.; No. 16: *Aeschynomene lateritia, Cassia nigricans, Drosera indica, Panicum* spec. and *Tripogon minimus*

Abbreviations: C (%) = relative constancy; CC = constancy class; Pi = Péperkou; Ti = Tipéti

Lepidagathis anobrya was also identified by Kéré (1998) as characteristic of flat soils on lateritic crusts in the area of Tenkodogo (Burkina Faso). Hahn-Hadjali (1998) describes a *Loudetia togoensis* community growing on lateritic crusts. Her relevés of this community, taken in the region of Fada n'Gourma and Pama (Burkina Faso), contain *Spermacoce filifolia* and *Melliniella micrantha*, both represented in our relevés with intermediate constancy. Küppers (1996) reports a *Loudetia togoensis* community from flat soils of the Chaîne de Gobnangou (Burkina Faso) that also shows certain congruences with our community because *Cyanotis lanata* and *Spermacoce filifolia* are represented with intermediate constancy. *Loudetia togoensis*, *Cyanotis lanata* and *Spermacoce filifolia* are mentioned by Zwarg et al. (2012) as important species on lateritic crusts in and around the Burkina Faso portion of the W National Park.

In Mali (Nasi 1994), *Lepidagathis anobrya*, *Loudetia togoensis* and *Spermacoce filifolia* are often found on lateritic crusts. Obviously, throughout the Sudanian zone of West Africa, lateritic crusts show a typical form of vegetation that deserves more attention.

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