

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 étudiée 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 révèle homogène bien que celles situées en champs de coton diffèrent 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 verlassen und dicht bewachsene Termitenhügel vergleichbarer Größe und gleichermaßen von Erosion betroffen, die sich in verschiedenen Savanntypen 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, Sukkulente, 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 Be-

nin (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).

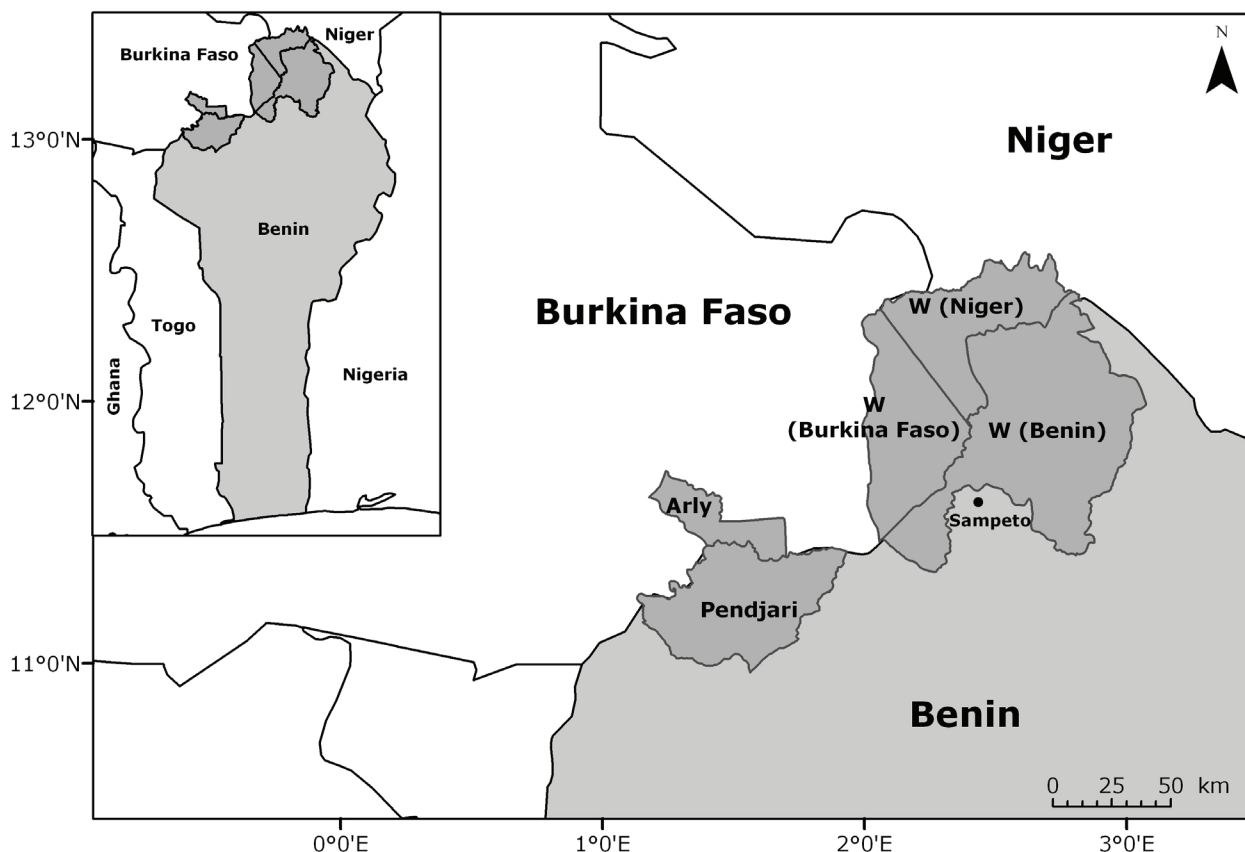


Fig. 1: Transboundary W National Park and neighboring national parks in the border region of Benin, Burkina Faso and Niger. / Parc national transfrontalier du W du Niger et parcs nationaux voisins dans la région frontalière du Bénin, Burkina Faso et Niger. / Grenzübergreifender W-Nationalpark und benachbarte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

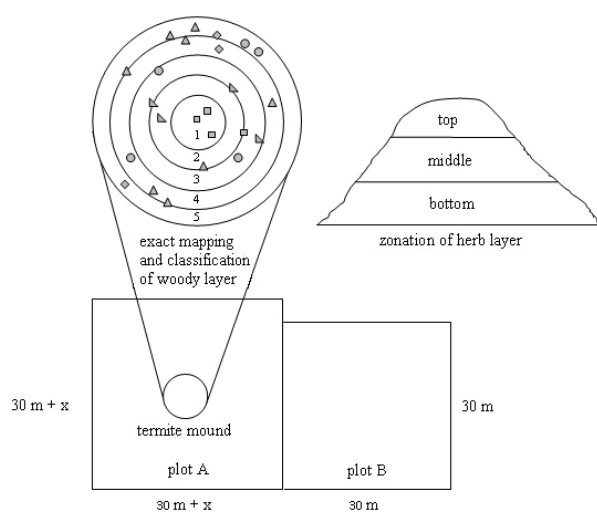


Fig. 2: Plot design and schema of exact mapping of individuals and classification of tree layer (class 1=center of termite mound up to class 5=periphery of termite mound) and herb layer zonation (top, middle, bottom). / Dessin et Schéma de la cartographie exacte des individus, de la classification des 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 (Ver-

sion 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), AKOËGNINOU 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.

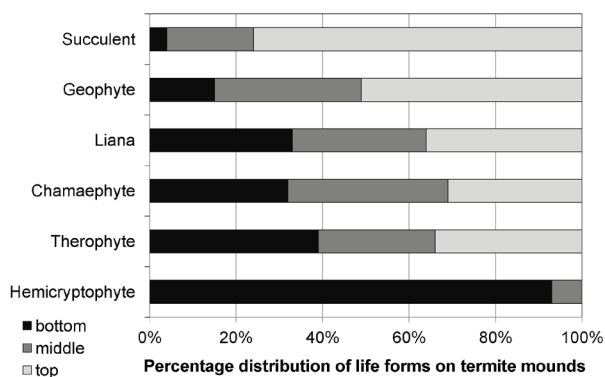


Fig. 3: Distribution of life forms (except phanerophytes) in top, middle and bottom zone of termite mounds (adjusted for area). Few species assigned to more than one life form. / Distribution des types biologiques (sauf les phanérophytes) dans les zones de la termitière (haut, milieu et bas) (Ajusté 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 termi-

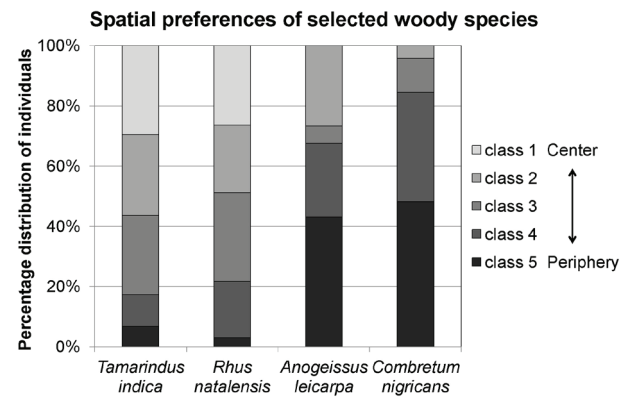


Fig. 4: Spatial preferences of *Tamarindus indica*, *Rhus natalensis*, *Anogeissus leiocarpa* and *Combretum nigricans* (Adjusted for area). / Préférences spatiales de *Tamarindus indica*, *Rhus natalensis*, *Anogeissus leiocarpa* et *Combretum nigricans* (Ajusté en fonction de la superficie). / Räumliche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

te 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).

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 FANDOCHAN 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.

Acknowledgments

We thank BIOTA West for funding the fieldwork (funding code 01LC0617D1) and the LOEWE research centre “Biodiversity and Climate” (BiK-F) as well as the UNDESERT project (EU FP7, grant 243906) for financial support (MS, KH) during the compilation of the manuscript.

We are grateful to Prof. Dr. Brice Sinsin, Université d’Abomey-Calavi, and his group for the good cooperation and support.

References

AFRICAN PLANTS DATABASE VERSION 3.3.4 (2011): Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria. Available at <http://www.ville-ge.ch/musinfo/bd/cjb/africa/> (accessed August 2011).

AKÉ ASSI L, (2001–2002): Flore de la Côte d’Ivoire: catalogue systématique, biogéographie et écologie. Vol. I–II. Boissiera 57–58. Conservatoire et Jardin botaniques de Genève.

AKOËGNINOU A, VAN DER BURG WJ & VAN DER MAESEN LJG (2006): Flore analytique du Bénin. Backhuys Publishers, Wageningen. 1034 p.

ARBONNIER M (2002): Arbres, arbustes et lianes des zones sèches d’Afrique de l’Ouest (2nd ed.). CIRAD / MNHN, Montpellier / Paris. 574 p.

BACHELIER G (1978): La faune des sols, son écologie et son action. Documentations techniques 38. ORSTOM, Paris. 391 p.

BERHAUT J (1971–1988): Flore Illustrée du Senegal. Vol. I–VI. Ministère du Développement Rural et l’Hydraulique / Direction des Eaux et Forêts, Dakar.

BLOESCH U (2008): Thicket clumps: A characteristic feature of the Kagera savanna landscape, East Africa. J. Veg. Sci. 19: 31–44.

BRINK AB & EVA HD (2009): Monitoring 25 years of land cover change dynamics in Africa: A sample based remote sensing approach. Appl. Geogr. 29: 501–512.

BRUNKEN U, SCHMIDT M, DRESSLER S, JANSSEN T, THIOMBIANO A. & ZIZKA G (2008): West African plants – a photo guide. www.westafricanplants.senckenberg.de. Forschungsinstitut Senckenberg, Frankfurt/Main, Germany

BUNDSCHUH TV, WITTIG R & HAHN K (2010): Effects of human impact on miombo woodland in northern Malawi. Flora et Vegetatio Sudano-Sambesica 13: 22–34.

DANGERFIELD JM, MCCARTHY TS & ELLERY WN (1998): The mound-building termite *Macrotermes michaelsoni* as an ecosystem engineer. J. Trop. Ecol. 14: 507–520.

DOSSOU-YOVO CHO (2007): Diversité des plantes en relation avec les termitières dans le Parc National de la Pendjari et dans les terroirs riverains. Agricultural engineer thesis. University of Abomey-Calavi, Benin.

FANDOCHAN B, ASSAGBADJO AE, SALAKO VK, VAN DAMME P & SINSIN B (2012): Which one comes first, the tamarind or the *Macrotermes termitarium*? Acta Botanica Gallica 159: 345–355.

GLOVER PE, TRUMP EC & WATERIDGE LED (1964): Termitaria and vegetation patterns on the Loita Plains of Kenya. J. Ecol. 52: 367–377.

GUDETA WS, ARSHAD MA, KONATÉ S & NKUNIKA POY (2010): Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns. J. Veg. Sci. 21: 923–937.

GUINKO S (1984): Végétation de la Haute-Volta. PhD thesis. Université de Bordeaux III. 394 p.

HOVESTADT T, YAO P & LINSSENMAIR KE (1999): Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). Plant Ecol. 144: 1–25.

HUTCHINSON J, DALZIEL JM, KEAY RJW & HEPPER FN (1954–1972): Flora of West Tropical Africa. Vol. I–III. The Whitefriars Press Ltd., London, Tonbridge.

JANSSEN T, SCHMIDT M, DRESSLER S, HAHN K, HIEN M, KONATÉ S, LYKKE AM, MAHAMANE A, SAMBOU B, SINSIN B, THIOMBIANO A, WITTIG R & ZIZKA G (2011): Addressing data property rights concerns and providing incentives for collaborative data pooling: the West African Vegetation Database approach. J. Veg. Sci. 22: 614–620.

JONES CG, LAWTON JH & SHACHAK M (1994): Organisms as ecosystem engineers. Oikos 69: 673–386.

JOSEPH GS, SEYMOUR CL, CUMMING GS, CUMMING DHM & MAHLANGU Z (2012): Termite mounds as islands: woody plant assemblages relative to termitarium size and soil properties. J. Veg. Sci. Doi: 10.1111/j.1654-1103.2012.01489.x.

KNIGHT RS, REBELO AG & SIEGFRIED WR (1989): Plant assemblages on Mima-like earth mounds in the Clanwille district, South Africa. S. Afr. J. Bot. 55: 465–472.

KONATÉ S, LE ROUX X, TESSIER D & LEPAGE M (1999): Influence of large termitaria on soil characteristics, soil water regime, and tree leaf shedding pattern in a West African savanna. Plant and Soil 206: 47–60.

KROHMER J (2004): Umweltwahrnehmung und –klassifikation bei Fulbegruppen in verschiedenen Naturräumen Burkina Faso und Benins. PhD thesis. Johann-Wolfgang-Göthe-Universität, Frankfurt am Main. 302 p.

LEPAGE M (1984): Distribution, density and evolution of *Macrotermes bellicosus* nests (Isoptera: Macrotermitinae) in the North-East of Ivory Coast. J. Anim. Ecol. 53: 107–117.

MBAYNGONE E, SCHMIDT M, HAHN-HADJALI K, THIOMBIANO A & GUINKO S (2008): Magnoliophyta of the partial faunal reserve of Pama, Burkina Faso. Check List 4: 251–266.

MOE RS, MOBAEK R & NARMO AK (2009): Mound building termites contribute to savanna vegetation heterogeneity. Plant Ecol. 202: 31–40.

NACOUUMA O (1996): Plantes médicinales et pratiques médicales traditionnelles au Burkina-Faso: cas du plateau central. PhD thesis. Université de Ouagadougou. 261 p.

OUÉDRAOGO O, SCHMIDT M, THIOMBIANO A, HAHN K, GUINKO S & ZIZKA G (2011): Magnoliophyta, Arly National Park, Tapoa, Burkina Faso. Check List 7: 85-100.

PÉREZ-GARCIA EA & MEAVE JA (2006): Coexistence and divergence of savanna and tropical dry forest in southern Mexico. J. Biogeogr. 33: 438-477.

POILECOT P (1999): Les Poaceae du Niger. Boissiera 56. Conservatoire et Jardin botaniques de Genève / IUCN / CIRAD, Geneva. 766 p.

SCHMIDT M (2006): Pflanzenvielfalt in Burkina Faso - Analyse, Modellierung und Dokumentation. PhD thesis. Johann-Wolfgang-Goethe-Universität, Frankfurt am Main. 188 p.

SCHMIDT M, JANSSEN T, DRESSLER S, HAHN K, HIEN M, KONATÉ S, LYKKE AM, MAHAMANE A, SAMBOU B, SINSIN B, THIOMBIANO A, WITTIG R & ZIZKA G (2012): The West African Vegetation Database. Biodiversity & Ecology 4: 105-110.

SCHOLZ H & SCHOLZ U (1983): Graminées et Cyperacées du Togo. J. Cramer, Vaduz. 360 p.

SMITH FR & YEATON RI (1998): Disturbance by the mound-building termite, *Trinervitermes trinervoides*, and vegetation patch dynamics in a semi-arid, southern African grassland. Plant Ecol. 137: 41-53.

UNEP (2008): Africa: Atlas of Our Changing Environment. UNEP, Nairobi.

WATSON JP (1977): The use of mounds of the termite *Macrotermes falciger* (Gerstäcker) as soil amendment. J. Soil Sci. 28: 664-672.

WOOD TG (1988): Termites and the soil environment. Biol. Fertil. Soils 6: 228-236.

ADDRESSES OF THE AUTHORS

Ivana Kirchmair^{1,2,3}, **Marco Schmidt**^{1,2,3,*}, **Georg Zizka**^{1,2,3}, **Arne Erpenbach**³ & **Karen Hahn**^{2,3}

⁽¹⁾ Senckenberg Research Institute, Departement of Botany and molecular Evolution, Senckenberganlage 25, 60325 Frankfurt, Germany

⁽²⁾ Biodiversity and Climate Research Center (BiK-F), Senckenberganlage 25, 60325 Frankfurt, Germany

⁽³⁾ Johann Wolfgang Goethe University, Institute for Ecology, Evolution and Diversity, Max-von-Laue-Str. 9, 60438 Frankfurt, Germany

* Corresponding author. E-mail address: marco.schmidt@senckenberg.de

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

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

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

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

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

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