Effects of termite mounds on composition, functional types and traits of plant communities in Pendjari Biosphere Reserve (Benin, West Africa)

Alain K. Gbeffe[1]*, Thierry D. Houehanou[1,2], Muhashy Habiyaremye[3], Emeline S. P. Assede[1,2], Alain S. Yaoitcha[1], Luc Janssens de Bisthoven[3], Etotépé A. Sogbohossou[1], Marcel Houinato[1] and Brice A. Sinsin[1]

[1]Laboratory of Applied Ecology, School of Environment Management, Faculty of Agronomics Sciences, University of Abomey – Calavi (LEA/FSA/UAC), 03 PO Box 2819, Cotonou, Benin, [2]Faculty of Agronomy, University of Parakou (FA/UP), PO Box 123, Parakou, Benin and [3]Royal Belgian Institute of Natural Sciences (RBINS), Vautier Street 29, B-1000, Brussels, Belgium

Abstract

Understanding the role of termite mounds in biodiversity and ecosystem functioning is a priority for the management of tropical terrestrial protected areas dominated by savannahs. This study aimed to assess the effects of termite mounds on the diversity of plant functional types (PFTs) and herbaceous' net aboveground primary productivity (NAPP) in plant communities (PCs) of the Pendjari Biosphere Reserve. PCs were identified through canonical correspondence analysis performed on 96 phytosociological 'relevés' realized in plots of 900 m^2. PFTs' diversity was compared between savannahs and mounds' plots using generalized linear models. In each plot, 7 m^2 subplots were harvested and NAPP was determined. Linear mixed models were performed to assess change in herbaceous NAPP regarding species richness, graminoids' richness, specific leaf area and termite mounds. There is no specific plant community related to mounds. However, the occurrence of termite mounds induced an increase of woody and forbs diversity while the diversity of legumes and graminoids decreased. These diversity patterns led to decreasing of PCs' NAPP. This study confirms that termite-induced resource heterogeneity supports niche differentiation theory and increased savannah encroachment by woody species.

Key words: net aboveground primary productivity, Pendjari Biosphere Reserve, plant functional diversity, Savannah ecosystems, termite mounds

Résumé

Il est primordial de bien comprendre le rôle des termitières dans la biodiversité et le fonctionnement d'un écosystème pour la gestion des aires protégées (AP) terrestres tropicales dominées par la savane. Cette étude devait évaluer les effets des termitières sur la diversité des traits fonctionnels des plantes (TFP) et la productivité primaire nette aérienne (PPNA) dans les communautés végétales (CV) de la Réserve de la Biosphère de la Pendjari. Les CV ont été identifiées par une analyse canonique des correspondances réalisée sur 96 relevés faits dans des placeaux de 900m². La diversité des TFP a été comparée entre les placeaux de savanes et de termitières à l'aide des modèles linéaires généralisés. Dans chaque placeaux, des sous-placeaux de 7m² ont été récoltées, et la PPNA a été déterminée. Des modèles linéaires mixtes ont été réalisés pour évaluer les changements de PPNA herbacée en ce qui concerne la richesse en espèces, en graminoïdes, la surface foliaire spécifique et la présence des termitières. Il n'y a pas de communauté spécifique de plantes liée aux termitières ; cependant, la présence de termitières induisait une augmentation de la diversité d'arbustes et de buissons alors que les légumineuses et les graminoïdes diminuaient. Ces structures de diversité entraînaient une diminution de la PPNA des CV. Cette étude confirme que l'hétérogénéité des ressources induite par les termites supporte la théorie de la différenciation de niche et augmente l'envahissement des savanes par les ligneux.

Introduction

Savannahs constitute one of the largest biomes of the world, covering about 20% of the land surface. Most of

Correspondence: E-mail: agbeffe@gmail.com

the world's savannahs occur in Africa, with smaller part in South America, India and Australia (Van Wilgen, 2009). In Africa, savannahs have existed for at least 30 million years, and their distribution and structure are largely determined by water and nutrient availability, herbivory, fire (Van Wilgen, 2009) and termites. Furthermore, a majority of protected areas (PAs) in Africa are established in savannah–woodlands biome (Burgess *et al.*, 2004). In such biome, termites are one of the key ecosystem engineers (Jones, Lawton & Shachak, 1994; Davies, Parr & Van Rensburg, 2010). Indeed, they build mounds which reduce fire intensity, increase soil nutrient content (chemical engineer) and water availability (Sileshi *et al.*, 2010; Van der Plas *et al.*, 2013). Thus, the relation termite ecosystem leads to resource heterogeneity and consequently changes vegetation patterns in savannahs (Sileshi *et al.*, 2010). The ability of termites to induce spatial heterogeneity in resources has both theoretical and practical involvements (Sileshi *et al.*, 2010). Resources or shelter heterogeneity created by termites may lead to an increase in niche segregation and competition, which will ultimately result in an increase of species richness (Tielbörger & Kadmon, 2000; Soliveres *et al.*, 2011). Resource heterogeneity hypothesis states that increasing habitat complexity for a given area increases the number of species that can coexist, resulting in higher species diversity (Tilman, 1982; Mittelbach *et al.*, 2001). These changes in spatial heterogeneity caused by termites imply changes in habitat diversity, and influence the diversity of plants and consumers, including insects to birds and mammals (Palmer, 2003; Brody *et al.*, 2010). Thus, this variation in the components of biodiversity affects ecosystem service delivery (Díaz *et al.*, 2006; Cardinale *et al.*, 2012) and key determinants of a variety of ecosystem services such as fodder and wood provision, carbon sequestration, soil nutrient retention, pollination, biotic control by insects or vertebrates (Díaz *et al.*, 2006; De Bello *et al.*, 2010) and net primary productivity of plant communities. Despite the increasingly recognized role played by termite mounds in conserving biodiversity of savannah ecosystems, few studies so far have addressed plant communities related to termite mounds and were focused either on the tree (Støen *et al.*, 2013) or herb (Moe, Mobæk & Narmo, 2009; Okullo & Moe, 2012a,b; Davies *et al.*, 2014) plant communities.

The Pendjari Biosphere Reserve is a PA located in the Sudanian zone, which is the most managed PA in Benin (Delvingt, Heymans & Sinsin, 1989; Houehanou *et al.*, 2013), maintaining natural ecological processes and native species (Hansen & Defries, 2007). Management strategies, such as the regular early bush fire, patrols against poaching and others, applied in this PA aim at conserving large and visible wild animals as these latter provide almost all financial resources obtained from the reserve valorization through tourism (Houehanou *et al.*, 2013). In this PA dominated by savannah landscapes, the density of termite mounds is steadily increasing and needs to be integrated in the management strategies for savannahs, as they represent crucial habitats for both plant and animal species and provide essential contributions to spatial structure and complexity (Erpenbach, Wittig & Hahn, 2014). In addition to these effects, termite-driven alteration of soils and herbaceous vegetation benefits multiple savannah taxa, even mitigating climate change effects (Bonachela *et al.*, 2015). Thus, termites and termite mounds are a priority for the management of tropical PAs dominated by savannah landscapes. Although termite mounds can be used as proxies for ecosystem change and are important contributors to savannah heterogeneity, they are potentially vulnerable to change (Davies, Baldeck & Asner, 2016). If ecosystem conditions change, due to climate or land use change, termites and their mounds might be adversely affected. Savannah ecosystems may become more homogenous and vulnerable to ecosystem collapse, with impacts on ecosystem components such as soils, biogeochemistry, vegetation and animal distributions. Obviously, termites play a key supporting function as ecosystem service provider. This ecosystem support probably gains importance as community complexity increases (McIntire & Fajardo, 2014). However, the precise ways in which termite mounds influence the spatial pattern of plant functional groups within natural savannah vegetation and the extent of these effects on ecosystem services such as net primary productivity over the landscape remain poorly understood. In this context, it remains important to study termite-induced changes related to savannahs functioning to really integrate termite-induced heterogeneity in terrestrial PAs management strategies.

This study aimed to (i) analyze the ecological pattern of plant communities around termite mounds, (ii) analyze how termite mounds have impacted the diversity of plant species functional groups within plant communities and (iii) assess the influence of both herbaceous species features and termite mounds on grassland's net aboveground

primary productivity (NAPP) in natural savannah ecosystems. We hypothesized that (i) termite mounds enhance the functional diversity of plant communities in natural savannah ecosystems through enrichment of forbs and woody species and (ii) increasing functional diversity created by termite-induced resources heterogeneity leads to the increase of herbaceous' net primary biomass of plant communities. Therefore, the presence of termite mounds, the richness of graminoids, the specific leaf area (SLA) of dominant species and the whole-plant communities' richness are analyzed. Testing those hypotheses in PAs will allow bridging the gap of information about the ecological role of termite mounds in conserving the functional diversity of plant communities within PAs dominated by savannah ecosystems. It will also help to understand and predict how communities and ecosystem properties might be affected by environmental change induced by termite mounds.

Study area

The study was undertaken in the UNESCO Man and Biosphere Reserve of Pendjari located within Atacora district (10°30′–11°30′N, 0°50′–2°00′E) (Fig. 1) in North Benin, a West African country. It is one of the most important and better managed West African fauna reserves in term of plants and animals diversity conservation (Delvingt, Heymans & Sinsin, 1989; Houehanou *et al.*, 2013). It covers an area of 4661 km^2 and is composed of the National Park of Pendjari (2660 km^2), the hunting zone of Pendjari (1750 km^2) and the hunting zone of Konkombri (251 km^2). Pendjari Biosphere Reserve is located in the Sudanian zone with a climate characterized by one rainy season (April/May–October) and one dry season (November–March). The mean annual rainfall is 1000 mm with 60% falling between July and September. The mean annual daily temperature is 27°C. The
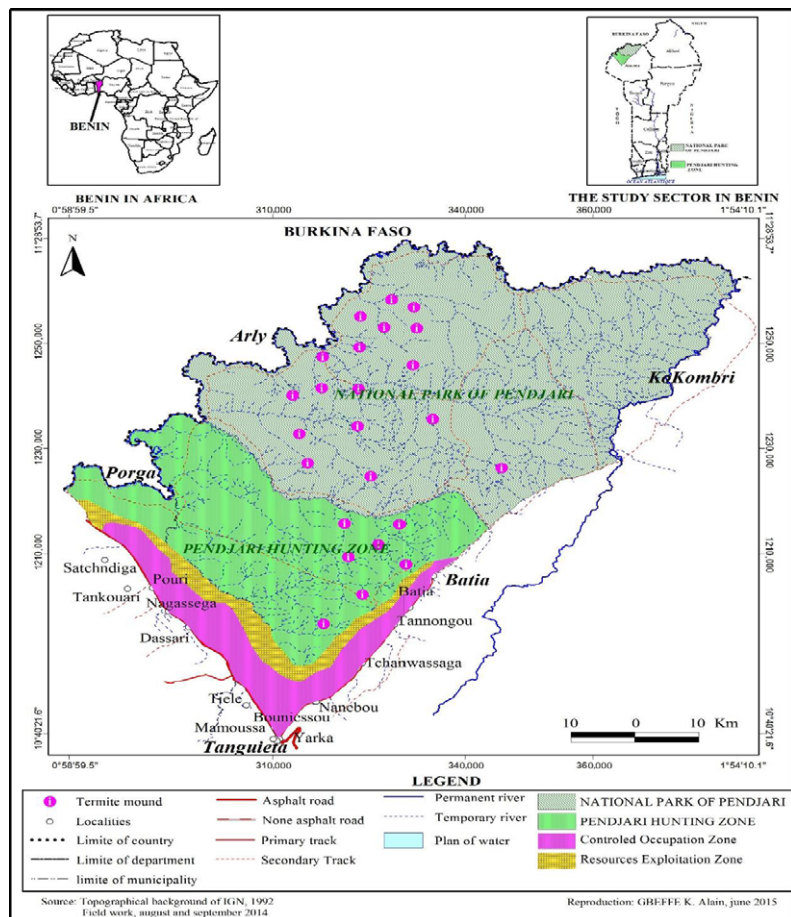
Fig 1 Maps showing the location of the study country Benin in West Africa as well as the study area Biosphere Reserve of Pendjari in Northern Benin

vegetation is a mosaic of shrubs and trees savannahs, woodland, gallery forest and grassland (Assede, 2013) regularly burned every year to provide fresh pasture to herbivores that dominate the reserve. The reserve also contains some large ponds which are managed for retaining water for wildlife and increase visibility for touristic and hunting activities. Rocky outcrops, ferruginous and silty soils support savannahs while gallery forest soil is clayey (Azihou, Kakaï & Sinsin, 2013).

Material and methods

The biological material used in this study was characterized by the vegetation on and around termite mounds with a given size in the Biosphere Reserve of Pendjari in northern Benin.

Sampling design and data collection

Twenty-four termite mounds characterized by a basal area ranging from 1.8 m to 3.6 m and holding at least one tree were randomly selected and considered as the centre of the sampling design. Thus, three plots were established at 150 m around termite mounds' plots following three transects. An angle of 120° was taken between consecutive transects (Fig. 2).

The termite mound plot is located at the junction of these three transects. The sizes of the plots were of 30 m × 30 m for the woody layer (Adomou, 2005) and 10 m × 10 m for the herbaceous layer. In both

□ : Plots of 10 m x 10 m established within savannah

● : The termite mounds

▯ : Plots of 10 m x 10 m established surrounding the termite

Fig 2 The Sampling design used for data collection

herbaceous and woody plots, 'phytosociological relevés' were performed using Braun-Blanquet's abundance–dominance scale (Braun-Blanquet, 1932): + (0–1%), 1 (1–5%), 2 (5–25%), 3 (25–50%), 4 (50–75%) and 5 (75–100%). Living aboveground biomass was cut in $7 \times 1 \ m^2$ subplots randomly set in each plot and was weighted. One hundred grams of fresh biomass was sampled and dried in the incubator at 65°C for 72 h to assess the NAPP of plant communities. The species richness, the graminoids' richness, the SLA of dominant herbaceous species and the presence of termite mounds in the communities were used as the predictor of plant communities' NAPP. As LI-3000C portable leaf area metre was not available, SLA was determined from length (Li) and width (Wi) of standardized leaves (sampling leaves through a regular 'rectangle' form) and its dry matter content (Kindomihoun, 2005). The standardized leaves sampled were dried to determine the dry matter content (DMC) of a dominant herbaceous species leaves per plot (Pérez-Harguindeguy et al., 2013). The areas of standardized leaves (Sf) were calculated as the product of standardized leaves' length (Li) and width (Wi). Both Sf and DMC were used to calculate the specific leave area (SLA) as follows:

$$SLA = \frac{Sf}{DMC},$$

where Sf is the area of the standardized leave, which is calculated as: $Sf = Li \times Wi$ (Kindomihoun, 2005).

Data processing and analyses

Ordination of 96 'phytosociological relevés' and 160 plant species was performed, using canonical correspondence analysis (CCA) with the package 'Vegan' version 2.2-1 (Oksanen et al., 2015) of the software R version 3.1.2 (R Development Core Team, 2014) to represent a bidimensional geometric structure based on the observed dissimilarity or similarity between termite mounds and savannah plots. This analysis is a weighted method of environmental data (vegetation type, tree cover, species richness, soil types, herb cover and the presence of mound in plots) performed at each permutation step using permutated weights (Assede, 2013). The purpose of CCA was to display the groups explained by the environmental factors. The characterization of the plant communities was based on the 'characteristic species' (Assede, 2013), which were
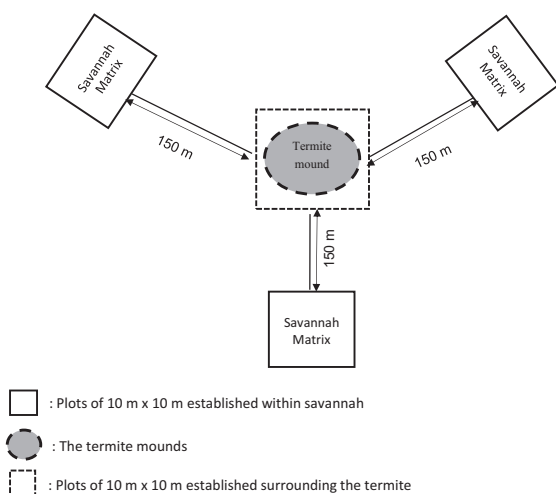
determined using IndVal index with the package Indicspecies 1.6.7 (De Caceres & Legendre, 2009). In each plant community, the indicator value of each species was calculated based on their relative abundance and relative frequency (fidelity), using Indicspecies programme. The significance of indicator values was tested, through Monte Carlo with 999 permutations between indicator values of each species in all plant communities (Dufrêne & Legendre, 1997). The two species with the highest indicator values in each plant community were used (one in the herbaceous layer and the other one in the woody layer) to characterize the plant communities.

Plant communities were compared on the one hand and termite mounds and savannah matrix plots of each plant community on the other hand regarding their plant functional types (PFTs) diversity and species diversity using a generalized linear model through the package 'Stats' (R Development Core Team, 2014) with the common Poisson distribution. The Student–Neumann–Keuls test was applied when significant differences appear between the plant communities, using the package 'Agricolae' (De Mendiburu, 2015). The variation of the NAPP of herbaceous layer was assessed in relation to the termite mounds, the SLA of the dominant herbaceous species, the species richness of plant communities and the graminoids' richness. Thus, the plant communities were considered as a random factor because they represented a random sample from all possible plant communities (Bates, 2010), and were obtained according to some phytosociological classification criterion. Series of linear mixed effect models' regressions (LMM) were performed with the 'lmer' function related to the package 'lme4' (Bates *et al.*, 2014) and its dependencies according to the continuous nature of the dependent variable. The significance of the individual coefficients based on the confident intervals was calculated using Wald statistics (Quinn & Keough, 2002) related to the package 'arm' (Gelman *et al.*, 2014). The goodness of fit of the overall regression model was examined by comparing the log-likelihood of the full models to that of the reduced model (null model) and their explanatory power $R^2_{LMM(c)}$ (Nakagawa & Schielzeth, 2013). All of the analyses were performed using R software (R Development Core Team, 2014).

Results

Ecological pattern of plant communities

The ordination (Fig. 3) of 96 'phytosociological relevés' and 160 plant species showed five plant communities: the plant communities of (i) *Loudetia togoensis* (Pilg.) C.E.Hubb. and *Crossopterix febrifuga* (G. Don) Benth, (ii) *Andropogon gayanus* Kunth and *Combretum collinum* Fresen, (iii) *Hyparrhenia glabriuscula* (A.Rich.) Stapf and *Mitragyna*
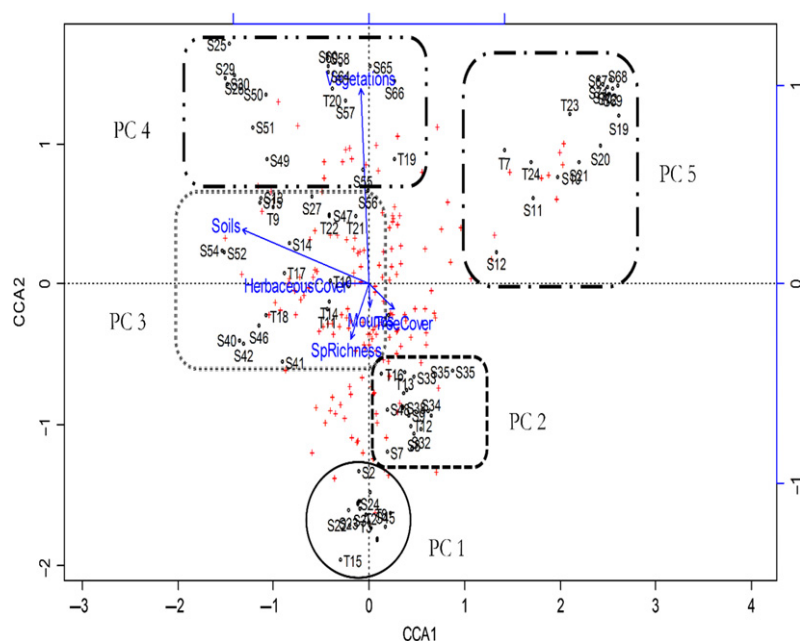
Fig 3 Ordination pattern of plant communities. Si: indicates plots established in savannah; Ti: indicates plots which contain termite mound; (PC1): *Loudetia togoensis* and *Crossopterix febrifuga*'s plant community, (PC2): *Andropogon gayanus* and *Combretum collinum*'s plant community, (PC3): *Hyparrhenia glabriuscula* and *Mitragyna inermis*' plant community, (PC4): *Hyparrhenia involucrata* and *Afzelia africana*'s plant community, (PC5): the plant community of *Hyparrhenia rufa* and *Burkea africana*

Table 1 Correlation of environment variables with axes of CCA. Only values greater than 0.5 contribute substantially to the axes

Variables	CCA 1	CCA 2
Soil types	**−0.936**	0.274
Vegetation types	0.060	**0.980**
Species richness	−0.137	−0.276
Tree cover	0.184	−0.129
Herbaceous cover	−0.177	0.003
Termite mound	0.010	−0.115

The bold values are correlation coefficient values of variables with ordination axes, greater than 0.5 which contribute substantially to the axes. Those variables were interpreted on those axes.

inermis (Willd.) Kuntze, (iv) *Hyparrhenia involucrata* Stapf and *Afzelia africana* Smith and (v) *Hyparrhenia rufa* (Nees) Stapf and *Burkea africana* Hook.

The first axis (CCA 1) shows the plant communities according to the soil-type gradient while the second axis (CCA 2) expresses the vegetation gradient (Table 1). The projection of the plant communities on the axis 1 showed that *H. glabriuscula* and *M. inermis*, *H. involucrata* and *Af. africana* plant communities are characteristic for slimy-clayed soils. The *H. rufa* and *B. africana* plant community expanded on rocky soils while the *L. togoensis* and *C. febrifuga*, as well as the *A. gayanus* and *C. collinum* plant communities developed on soils without or with fine gravels. The second axis 2 presents plant communities of scrub savannah (*L. togoensis* and *C. febrifuga*, and *A. gayanus* and *C. collinum* plant communities) and those of tree savannahs and woodland (*H. glabriuscula* and

M. inermis, *H. involucrata* and *Af. africana*, *H. rufa* and *B. africana* plant communities). Differences appear among plant communities with Ij < 50%. The plant community of *L. togoensis* and *C. febrifuga* is more distinctive (Ij = 41.67%) to the one of *H. glabriuscula* and *M. inermis*. The most similar groups were the plant communities of *H. rufa* and *B. africana*, and of *H. involucrata* and *Af. africana* (Ij = 65.99%).

Effects of termite mounds on plant functional group species richness

As the number of termite mound plot in the plant community of *A. gayanus* and *C. collinum* was not sufficient to guarantee statistical precision, it was not considered in the comparison. PFTs' species richness varied significantly across plant communities ($P < 0.05$, Table 2), and generally there were significantly more species within PFTs and higher species richness when termite mounds were present in plant communities, except for the graminoids' PFT. The interactions between plant communities and termite mounds were not significant regarding only the richness of forbs and graminoids functional groups ($P > 0.05$, Table 2). The effect of termite's presence on forbs and graminoids' richness did not vary across plant communities whereas the effect on species richness and legumes and woody's richness depended on plant communities. In the *L. togoensis* and *C. febrifuga* plant community, the average forbs' richness ($P < 0.001$) in mound plots is higher than in savannah

Table 2 Two ways of comparisons of functional groups species richness

Levels of comparison		Species functional types' richness				Plant communities' species richness
		Forbs	Graminoids	Legumes	Woody	
Plant communities	PC1	7.45	2.95	3.10	6.45	19.95
	PC3	3.80	3.00	2.26	8.00	17.06
	PC4	5.04	4.33	3.33	6.79	19.50
	PC5	3.78	3.10	2.05	9.42	18.36
Significance *P*-value		**	*	**	***	ns
Termite mounds	Presence	9.31	3.54	1.59	8.77	23.22
	Absence	3.46	3.37	3.21	7.10	17.16
Significance *P*-value		***	ns	***	*	***
Interactions		ns	ns	**	*	**

(PC1): *Loudetia togoensis* and *Crossopterix febrifuga*'s plant community, (PC3): *Hyparrhenia glabriuscula* and *Mitragyna inermis*' plant community, (PC4): *Hyparrhenia involucrata* and *Afzelia africana*'s plant community and the plant community of *Hyparrhenia rufa* and *Burkea africana* (PC5). (ns) Not significant $P > 0.05$; * Significant difference $P < 0.05$; **High significant difference $P < 0.01$ and ***Very high significant difference $P < 0.001$.

matrix plots. Conversely, the average richness of graminoid ($P = 0.038$) and legumes ($P < 0.001$) are higher in savannah matrix plots than in the mound one.

In the *H. glabriuscula* and *M. inermis* plant community, there is no difference between mounds and savannah plots regarding the average richness of graminoids ($P = 0.713$), the legumes ($P = 0.362$) and the woody plants ($P = 0.265$). However, the forbs' richness ($P = 0.00014$) and the species richness (0.0018) in mound's plots are higher than those in savannah matrix ones. In *H. involucrata* and *Af. africana* plant community, the mean richness of forbs ($P = 0.000$), legumes ($P = 0.032$), woody plants ($P = 0.000$) and species richness ($P = 0.000$) of termite mounds and savannah matrix were significantly different. However, as far as the richness of graminoids' functional group ($P = 0.229$) is concerned, there is no significance. In the plant community of *H. rufa* and *B. africana*, forbs' richness ($P = 0.002$) and species richness ($P = 0.03$) were significantly higher in termite mounds' plots whereas the plots of savannah hold meanly the significant higher richness of legumes ($P = 0.004$). However, no significant difference was found between savannah and mounds' plots for graminoids ($P = 0.469$) and woody ($P = 0.124$) functional group richness.

Influences of graminoids functional group feature and termite mounds on the plant communities' net primary productivity

Table 3 presents eight candidates models of the productivity estimation of identified plant communities using their biotic features. The main biotic features are species richness, graminoids' richness, SLA of the dominant species and the termite mound (presence or absence) in the plant communities. In all of the proposed models, the variations of the independent variables explain more than 50% of the variations of net aboveground biomass productivity. The models 1, 2, 3 and 6 are significant. The models 4, 5, 7 and 8 were not significant, hence leading to their disqualification as eligible models in explaining the productivity of net aboveground biomass of the herbaceous layer. Therefore, the best selected models based on the Akaike information criterions (AIC) and the explanatory power $R^2_{LMM(c)}$ in the remaining models were model 1, model 3 and model 6. The proportions of information explained by the fixed and random factors in those three selected models (model 1, model 3 and model 6) are, respectively, 54.61%, 54.83% and 54.32%. The AIC are, respectively, 1536.8; 1534.9 and 1538 with the

model 3 as the best one. Therefore, species richness of the plant community (S), the graminoid functional group's richness (graminoid richness) and the herbaceous dominant species SLA can explain the variability of the net aboveground biomass productivity of the plant communities' herb layer. The variability of the plant community biomass productivity explained by the selected model is 54.83%, meaning that the most part of this variability is between plant communities that are considered here as a random factor. The variability of the fixed factors in the best model explained 15.46% of the biomass productivity in the identified plant communities.

Discussion

Ecological patterns of plant communities in relation to termite mounds

In this study, the plant communities form a mosaic of savannah with some patches of termite mounds. Indeed, all the discriminated plant communities are composed of termite mounds' plots and savannah ones. Such pattern of termite mounds and savannah plots contrasts with others studies (Erpenbach *et al.*, 2013; Erpenbach, Wittig & Hahn, 2014) which have shown a discrimination of termite mounds' plots from savannah matrix ones. Indeed, these last authors considered the herbaceous species or the regeneration or woody species separately in their studies. Our study handled both herbaceous and woody layers. Phytodiversity was found to be higher on termite mounds, and such trend was already reported in several studies of the same phytogeographical zone (Traoré *et al.*, 2008a; Kirchmair *et al.*, 2012; Erpenbach *et al.*, 2013; Erpenbach, Wittig & Hahn, 2014). The high species richness recorded in termite mound plots for the five plant communities is due to the habitat heterogeneity that termite mounds create within the ecosystems through resource heterogeneity. Globally, the main mound indicator plant families were Ebenaceae (16%) and Capparaceae (12%), while Fabaceae (42%) and Rubiaceae (25%) families dominated the adjacent savannah areas. Termite mounds have often been recognized as refuges for woody plants within seasonally burned savannahs (Traoré *et al.*, 2008b; Joseph *et al.*, 2011). Specifically, plants with evergreen leaves like the Capparaceae are sensitive to burning (Erpenbach *et al.*, 2013) and are regularly found on termite mounds. Vegetation on termite mounds is commonly associated with higher woody densities than adjacent savannah areas (Moe, Mobæk & Narmo,

Table 3 Models of plant community net aboveground primary productivity estimation from some biotic features of graminoids functional groups and termite mounds

Model name / Fixed effects	Null model b [95% CI]	Model 1 b [95% CI]	Model 2 b [95% CI]	Model 3 b [95% CI]	Model 4 b [95% CI]	Model 5 b [95% CI]	Model 6 b [95% CI]	Model 7 b [95% CI]	Model 8 b [95% CI]
Intercept	2834 [1876, 3792]	2834 [1876, 3792]	2714.44 [1717, 3711]	2801.5 [1888, 3714]	3447.96 [2608, 4287]	2835.67 [1874, 3796]	3407.53 [2615, 4199]	2311.30 [1456, 3166]	3287.95 [2425, 4150]
SLA	—	10.69 [1.14, 20.24]	9.86 [−0.06, 19.8]	10.72 [1.21, 20.23]	—	9.61 [−0.3, 19.53]	—	10.43 [0.63, 20.23]	—
Species richness	—	−42.76 [−85.12, −0.39]	−2.67 [−36.36, 31.01]	−39.63 [−72.54, −6.71]	−42.47 [−85.49, 0.5]	−10.63 [−38.8, 17.54]	−38.41 [−71.84, −4.97]	—	−4.22 [−38, 29]
Graminoids' richness	—	159.42 [51.01, 267.6]	—	154.63 [54.36, 254.9]	151.55 [41.7, 261.43]	—	145.55 [43, 247]	85.72 [1.5, 169.9]	—
Termite mound	—	45.98 [−344, 436]	−163.81 [−540, 213]	—	59.68 [−336, 455]	—	—	—	−141.45 [−521, 238]

Random effect	Null model CV	Model 1 CV	Model 2 CV	Model 3 CV	Model 4 CV	Model 5 CV	Model 6 CV	Model 7 CV	Model 8 CV
Plant communities	526,845	357,329	396,942	355,952	460,608	407,114	458,001	410,132	500,898
Residuals	448,684	412,805	445,088	408,450	425,574	443,260	421,322	426,823	454,082
Fixed factors	—	139,331.2	80,271.52	139,834.8	43,792.9	70,808.46	43,124.54	101,511	5630.33
$R^2_{LMM(m)}$	—	15.32%	8.70%	15.46%	4.7%	7.68%	4.67%	10.81%	0.58%
$R^2_{LMM(c)}$	—	54.61%	51.74%	54.83%	54.23%	51.88%	54.32%	54.51%	52.72%
AIC	1542.4	**1536.8**	1543.2	**1534.9**	1539.9	1542	**1538**	1538.6	1545.2
BIC	1550.1	15,584.8	1558.6	1550.3	1555.3	1554.8	1550.8	1551.4	1558.1
Model significativity	—	0.024	0.045	0.0000	1.0000	0.069	0.0000	1.0000	1.000

CI, confidence interval; SLA, specific leaf area; AIC, Akaike information criterion; BIC, Bayesian information criterion; ML, maximum likelihood; REML, restricted maximum likelihood; CV, component of variance. 95% CI was estimated by assuming an infinitely large degree of freedom (i.e. *t* = 1.96). AIC and BIC values were calculated using ML, but other parameters were from REML estimations.

2009). The main reason is the supporting role of termite mound in savannah ecosystems which facilitates the establishment and the development of some gallery forest tree species (*Anogeissus leiocarpa*, *Cassia sieberiana*, *Daniellia oliveri*, *Khaya senegalensis*, and *Tamarindus indica*) in savannah despite frequent fires (Bloesch, 2008; Azihou *et al.*, 2013). Termite mounds offer a more favourable environment for plants by providing higher nutrient and moisture availability in an otherwise deficient ecosystem (Jouquet *et al.*, 2006; Sileshi *et al.*, 2010). In addition, positive effect (protection from fire and flooding disturbance) of termite mounds is directly caused by a slight elevation of land surrounding the mound (Bloesch, 2008; Joseph *et al.*, 2013). It can also be an indirect effect of insufficient dry biomass to sustain burning in mounds' plots.

Effects of termite mounds on plant functional group species richness

First, whatever the plant community, the presence of termite mound promotes the abundance of forbs and woody functional group by creating appropriate conditions for their development. Moreover, our findings showed that species richness of woody and forb functional groups were higher in savannah matrix plots than those in termite mounds, except for the case of the *H. involucrata* and *Af. africana* plant community where the woody functional group richness was higher in termite mounds' plots than in the savannah matrix ones. These findings support resource heterogeneity hypothesis, which states that increasing habitat complexity for a given area increases the number of species that can coexist, resulting in higher species diversity (Tilman, 1982; Mittelbach *et al.*, 2001). At small scale, heterogeneity in soil and microclimatic conditions on mounds promote the coexistence of plant species with different habitat requirements (Moe, Mobæk & Narmo, 2009; Sileshi & Arshad, 2012; Moeslund *et al.*, 2013; Stein, Gerstner & Kreft, 2014). Most studies show that large mounds built by fungus-growing termites support more different vegetation in the surrounding landscape than on the mound sites with some exclusive species on the mound sites (Traoré *et al.*, 2008b; Sileshi *et al.*, 2010). Consequently, such situation generates diversity and affects the overall productivity of the plant community (Jouquet *et al.*, 2011).

Among the multiple factors that limit tree success in savannah, fire appears to be the most widespread and universal (Bond & Keeley, 2005; Staver, Archibald &

Levin, 2011). In the absence of fire, the increase in tree density is a gradual process involving recruitment of new trees as well as growth of existing stems. Other studies showed that fire interrupts this process by reducing the size of existing trees through top kill (i.e. loss of aboveground biomass), combined with a small whole-plant mortality (Holdo & McDowell, 2005; Higgins *et al.*, 2007). In other words, fires limit the recruitment of woody species by exposing their seedlings and saplings. This effect is mitigated by the termite mounds in the savannah matrix because termite mounds offer some degree of shelter and protection from fire disturbance (Joseph *et al.*, 2013). The role of fire in tree dynamics of savannah ecosystems is fundamentally different from that in many other flammable ecosystems, due primarily to the presence of a continuous grass layer (graminoid functional groups) that regains its flammability very quickly after burning (Hoffmann *et al.*, 2012).

Influences of graminoids functional groups' features and termite mounds on the plant communities' net primary productivity

Our findings show that species richness of the plant community, graminoids' richness and the herbaceous dominant species SLA affect the productivity of plant communities. The loss of species will have negative effects on ecosystem functions such as productivity and carbon storage (Hooper *et al.*, 2005). For the Pendjari Biosphere Reserve core, the mass ratio hypothesis predicts that graminoids which make up more than 60% of the aboveground biomass should have a greater effect on ecosystem properties than either forbs (38%) or legumes (12%). The influence of a species or group of species on ecosystem functioning is proportional to their input in primary productivity. It is very important at this level to know that the plant community identity plays a key role in determining the productivity of its net aboveground primary biomass. This confirms the high value of the variance component obtained. The explanation power (1546%) of the fixed factors in proposed models was weak due to the fact that aboveground net primary productivity was influenced by many abiotic factors such as nutrients and water availability, climatic parameters (temperature, humidity and rainfall). Any of those abiotic factors were not associated with the present study. Among the existing biotic factors that have significant influence on ecosystem services, only the richness of different kinds of taxonomic groups and SLA of dominant species were used in this

study. Aboveground net primary productivity was strongly linked to functional diversity defined as the value, range and relative abundance of plant functional traits in a given ecosystem (Diaz & Cabido, 2001).

Conclusion and implications for management

In this study, there is no typical plant community associated with termite mounds. The termite mounds in savannah ecosystems enhance the richness of woody and forbs species. The consistency of the results related to the occurrence of forest species on termite mounds within savannahs landscape is confirmed by its function as drivers for strengthening forest and savannah species coexistence in savannahs landscapes. Finally, the species richness, graminoids' richness and the dominant herbaceous species SLA are determinant in the net primary biomass productivity of the herbaceous layer within savannahs ecosystems. The species richness, graminoids' richness and the SLA of dominant herbaceous species are potential monitoring indicators of the state of habitat and rangeland shaped by the occurrence of termite mounds in West African natural savannahs. Further research is required to highlight the diversity of termites and the influence of specific termites on the conservation of plant communities. The drivers of the dynamics of termite mounds and their contribution to the carbon pool within Pendjari Biosphere Reserve ecosystems could also be envisaged.

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