DOES A CHANGE IN LAND USE AFFECT WOODY VEGETATION IN SUB-HUMID SUDANIAN SAVANNA IN SENEGAL?*

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Little attention has been paid to response of sub-humid savannas to changes in management. The aim of the study was to test whether changes in management had any effect on richness, diversity, composition, and density of woody species in sub-humid West African savanna. In Fathala Forest (Senegal), we compared woody vegetation in communal land (FUC) with that on protected area fenced-off for 8 years either with (FFW) or without (FFE) wildlife. Species richness and diversity of woody plants were 5.6 and 0.5 per 0.02 ha plot on average and both were consistent throughout the study area. Density of all woody plants (saplings and full-grown trees together) was 4700 individuals per ha in FFW which was significantly higher than in FFE and FUC. No differences were found among densities of full-grown trees, while density of saplings in FFW (3429 individuals per ha) was higher, although this only differed significantly from FUC. Different management did not affect density of species used for construction, fodder or medicine probably due to low intensity of recent exploitation. We concluded that in sub-humid conditions, 8 years of fencing was not enough for manifestation of the change in management and human exploitation of lower intensity cannot be connected with degradation of sub-humid tropical woodlands.

woody plants density; diversity; management; recruitment; vegetation dynamics; West Africa

INTRODUCTION

It has been widely reported that human exploitation such as livestock grazing, timber logging, firewood collection, and harvesting of forest products, is responsible for the destruction of savanna forest vegetation (Shackleton, 1993). Livestock browsing greatly reduces seedling survival, suppresses growth of both the seedlings (Tsegaye et al., 2009) and the older/adult individuals (Tsegaye et al., 2010a), and decreases tree density (Noumi et al., 2010) and viability (Dhillion, Gustad, 2004). Overgrazing, in combination with fuelwood gathering and inappropriate cultivation practices, leads to desertification in arid areas (Mortimore, Turner, 2005). Moreover, when combined with unfavourable abiotic conditions, wildlife grazing or fires, the human exploitation may be detrimental to woody vegetation. Heavy browsing in combination with low rainfall leads to rapid tree loss (Prins, van der Jeugd, 1993; Birkett, Stevens-Wood, 2005). In addition, the interaction of burning and wildlife browsing (namely by elephants) limits the resprouting of woody plants and leads to woodland loss (Holdo et al., 2009). On the contrary, if properly managed, this interaction can help suppress bush encroachment (Schutz et al., 2011). In African savannas, heavy livestock grazing reduces the regeneration capacity of desired woody plants (Hejcmanová et al., 2010), opens grass sward, and thus decreases the frequency and intensity of fires (van Langevelde et al., 2003) and can also enable bush encroachment by unpalatable woody species (Roques et al., 2001).

According to state and transition models (Briske et al., 2005), in arid and semi-arid savanna ecosystems the exclusion of uncontrolled human exploitation may result in substantial changes in plant species composition and vegetation structure (Parsons et al., 1997; Oba et al., 2000; Weber, Jeltsch, 2000; Angassa et al., 2010; Tsegaye et al., 2010b; Mekuria, Veldkamp, 2012). More humid savannas, on the contrary, seem to be relatively stable ecosystems, where disturbances are counteracted by environmental mechanisms, for instance by rainfall (Shackleton, Scholes, 2011). Arid and semi-arid savanna ecosystems have been widely studied, whereas little attention has been paid to the response

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of sub-humid and humid savanna vegetation to changes in management (Leriche et al., 2003).

The aim of this study was, therefore, to test whether a change in management, applied for 8 years, had any effect on woody plant species community and woody plant densities in a sub-humid West African savanna. In particular, we asked whether: (1) there are any differences in woody plant species richness, diversity, composition, and density between areas with different management strategies; and (2) whether management has any effect on particular categories of woody plants, according to their preferred exploitation by local people.

MATERIAL AND METHODS

Study area

The study area is located in the Fathala Forest (Forêt de Fathala, FF), a savanna region of the Delta du Saloum National Park (DSNP) on the west coast of Senegal (13°39′N, 16°30′W) near the northern border of Gambia. The area is flat with dry plateaus, passing into shallow humid valleys. The region has a littoral sub-humid climate, with a pronounced dry season between November and May and a 5-month rainy season between June and October. The average annual precipitation is 1022 mm. Mean daytime temperatures are 31.2 °C in May and 26 °C in January (1951–2000, Banjul Yundum meteorological station). Soils are tropical ferric Luvisols and Nitosols on the plateaus and weakly-developed Gleysols in the lower valleys (FAO – UNESCO, 1977). The FF belongs to the transition zone between the phytochoria of the Sudanian region and the Guinea-Congolian/Sudanian transition zone (White, 1983). The principal vegetation aspects are wooded grassland, woodland and transitional woodland on the plateaus, with *Combretum nigricans-Prosopis africana* woodland, *Bombax costatum-Pterocarpus erinaceus* woodland, and *Piliostigma thonningii-Dichrostachys cinerea* thicket, giving way to *Erythrophleum suaveolens-Dialium guineense* gallery forests in the humid valleys (Lawesson, 1995; Nežerková-Hejcmanová et al., 2005).

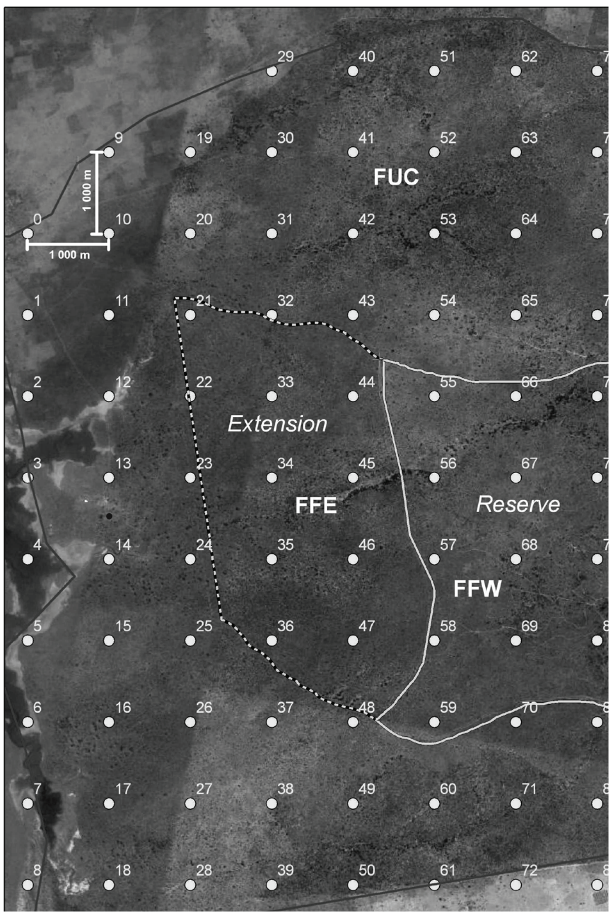

Fig. 1. Study area and location of sample plots (200 m^2) in the Fathala Forest. FUC represents the unfenced area with communal land use, FFW is the fenced area with large herbivores and FFE is the extended fenced area without animals and management interventions.

The FF area extends over more than 8500 ha and is surrounded by 11 villages, with one village situated directly within the FF. Until the year 2000, the FF was under a single common management, which kept the area under state control, limiting the rights of local people to exploit natural resources. For instance, while the harvesting of fruits and medicinal plants was allowed, crop cultivation and livestock grazing was restricted. In 2000, 2180 ha of the FF were fenced and the Fathala Reserve (FR) was established, partly as a wildlife enclosure with native and introduced herbivore species (Nežerková et al., 2004), and partly to protect the woody savanna ecosystem with its remnant fauna, which was exposed to ongoing uncontrolled human activities of relatively low intensity from the surrounding villages, including livestock grazing, the harvesting of wood, fruit, and bark, and illegal hunting of wildlife (Lykke, 1994). The FR was divided by managers into two controlled segments and, ultimately, three management systems were established within the original area of the FF: (1) 1070 ha of the fenced area within the FR, referred to as the FFW, is inhabited by wildlife, mostly grazers, such as African buffalo (*Syncerus caffer*), roan antelope (*Hippotragus equinus*), and defassa waterbuck (*Kobus ellipsiprymnus defassa)*; (2) 1110 ha of the fenced area within the FR, referred to as the FFE, is without animals or any other activities; and (3) 6390 ha of the unfenced area within the FF, referred to as the FUC, is under communal land use.

Data collection

Data were collected during the 2008 dry season (April–May). The first sampling plot was assigned randomly, on the north-western border of the FF, as

Table 1. List of the most abundant species with their families, codes used in the ordination diagrams and classification in exploitation categories according to Lykke (2000). Species with no exploitation category were not classified by Lykke as exploited plants.

Species	Family	Code	Exploitation category
Acacia ataxacantha DC.	Mimosaceae	AcaAta	
Acacia sp.	Mimosaceae	AcaSp	
Albizia chevalieri Harms	Mimosaceae	AlbChe	
Azadirachta indica A. Juss.	Meliaceae	AzaInd	
Bombax costatum Pellegr. et Vuillet	Bombaceae	BoxCos	Construction wood, livestock fodder
Combretum glutinosum Perr. ex DC.	Combretaceae	ComGlu	Medicine
Combretum micranthum G. Don	Combretaceae	ComMic	Medicine
Combretum nigricans Lepr. ex Guill. et Perr.	Combretaceae	ComNig	
Combretum paniculatum Vent.	Combretaceae	ComPan	Livestock fodder
Cordyla pinnata (Lepr. ex A. Rich.) Milne-Redhead	Caesalpiniaceae	CorPin	Construction wood, medicine
Daniellia oliveri (Rolfe) Hutch. et Dalz.	Caesalpiniaceae	DanOli	Construction wood, livestock fodder
Detarium microcarpum Guill. et Perr.	Caesalpiniaceae	DetMic	Medicine
Detarium senegalense Gmel.	Cesalpiniaceae	DetSn	
Diospyros mespiliformis Hochst. ex A. Rich.	Ebenaceae	DioMes	
Erythrophleum suaveolens (Guill. et Perr.)	Caesalpiniaceae	ErySua	
Ficus sp.	Moraceae	FicSp	Livestock fodder
Guiera senegalensis J.F. Gmel.	Combretaceae	GuiSn	Medicine, livestock fodder
Icacina senegalensis Adr. Juss.	Icacinaceae	IcaSn	
Lannea acida A. Rich.	Anacardiaceae	LanAc	
Lannea velutina A. Rich.	Anacardiaceae	LanVel	
Lonchocarpus laxiflorus Guill. et Perr.	Fabaceae	LonLa	
Maytenus senegalensis (Lam.) Exell	Celastraceae	MaySn	
Ozoroa insignis Del.	Anacardiaceae	OzoIn	
Parkia biglobosa (Jacq.) R. Br. ex G.Don	Mimosaceae	ParBig	
Piliostigma reticulatum (DC.) Hochst.	Caesalpiniaceae	PilRet	
Piliostigma thonningii (Schumach.) Milne-Redh.	Caesalpiniaceae	PilTho	
Prosopis africana (Guill. Et Perr.) Taub.	Mimosaceae	ProAfr	Construction wood
Pterocarpus erinaceus Poir.	Fabaceae	PteEri	Construction wood, livestock fodder
Saba senegalensis (A. DC.) Pichon	Apocynaceae	SabSn	
Sarcocephalus latifolius (Smith) Bruce	Rubiaceae	SarLa	Medicine
Sclerocarya birrea (A. Rich.) Hochst.	Anacardiaceae	SclBir	
Strychnos spinosa Lam.	Loganiaceae	StrSpi	
Terminalia avicennioides Guill. et Perr.	Combretaceae	TerAvi	
Terminalia macroptera Guill. et Perr.	Combretaceae	TerMa	Construction wood, medicine, livestock fodder

a starting point for setting up a regular geo-referenced grid (one point per 1 km) across the investigated area. GRILLE 2.0 software and ArcGIS 9.1 tools were used in order to avoid any bias caused by human factors during the selection of the sampling plots, although it led to unbalanced design. Square plots, 200 m^2 in area, were established at the intersections of the grid. A total of 71 plots were sampled (total area 1.42 ha, representing 0.017% from the total area of the FF): 12 (0.24 ha), 8 (0.16 ha), and 51 (1.02 ha) plots in the FFW, FFE, and FUC, respectively (Fig. 1).

In each plot we collected data on woody plant species composition and the number of individuals of each woody plant species. For the number of individuals, we distinguished woody plants < 1.5 m and > 1.5 m in height and classified them as saplings and full-grown woody plant individuals, respectively. To assess the alpha diversity of the area, species richness was determined as the number of plant species per plot, while the Simpson's index of diversity was used as a measure of the species diversity of a plot (Magurran, 2004). The plant species were identified *in situ*, the species nomenclature following Arbonnier (2002). Then we classified selected woody species into categories (Table 1), according to their preferred exploitation by local inhabitants:

construction wood, medicinal plants, livestock fodder, and a separate species, *Lonchocarpus laxiflorus*, which was referred as a plant species without any apparent use by local inhabitants. This categorization was defined in a study by L y k k e (2000), based on interviews with local inhabitants.

Data analyses

Linear regression was used to evaluate the relationship between sampling areas and the number of recorded species. Number of woody plant species per plot, in the FFE, FFW, FUC, and in the total sampled area were used to perform this analysis. Differences in species richness, species diversity, total density of all woody plants, density of saplings, density of full-grown individuals, and density of individuals within the species exploitation categories between the three management systems were evaluated by One-Way ANOVA. After obtaining significant results, *post-hoc* comparisons using Tukey's test were performed.

We performed two kinds of multivariate analyses: (1) with the total density of all woody plants as response variables; and (2) with categorization of the density of each species into saplings or full-grown individuals as response variables. Detrended correspondence analysis (DCA) was used to detect the length of the gradient and to detect similarities among individual research plots. To explore the pattern of woody plant density in relation to management, we used canonical correspondence analysis (CCA), followed by Monte Carlo with 999 permutations.

In the CCA, the management systems were used as three explanatory variables in the form of categorical (dummy) variables. The CCA was applied because the length of the gradient in the DCA was above 3.5 (L e p š , Š m i l a u e r , 2003). In order to avoid spatial autocorrelation among the plots within the grid, the effect of the distance to the sea, or any north-south gradient, we created a set of principal coordinates (B o r c a r d , L e g e n d r e , 2002) representing a matrix of geographical positions among sampling plots using the PrCord extension (t e r B r a a k , Š m i l a u e r , 2002). Using the CCA, we tested which principal coordinates had a significant effect on species density. These coordinates were used as covariates in subsequent multivariate analyses. All multivariate analyses were performed using Canoco (Version 4.5, 2002) for MS Windows and the results were visualized in the form of ordination diagrams using CanoDraw software.

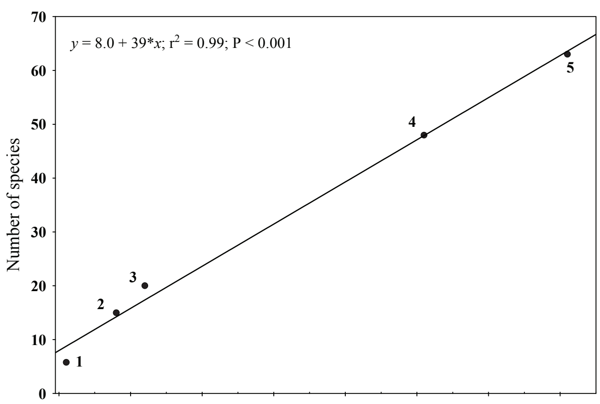

Fig. 2. Effect of sampling area size on the number of recorded woody species. Numbers 1 - 5 stand for the number of woody plant species per plot of 0.02 ha, the number of woody plant species recorded in the FFE, FFW, FUC, and the number of woody plant species recorded in the total sampled area, respectively.

RESULTS

Woody plant species richness and diversity

A total of 63 woody plant species were recorded in the total sampled area: 48 species (76.19% out of the total) in the FUC, 20 (31.75% out of the total) in the FFW, and 15 (23.81% out of the total) in the FFE. There was a linear increase in the number of species with sampling area, in the range of sampling areas from 0.02 to 1.42 ha (Fig. 2). Species richness per plot was 6.04 ± 0.43 S.E. in the FUC, 5.83 ± 0.98 S.E. in the FFW, and 4.87 ± 0.85 S.E. in the FFE, and did not differ significantly ($F_{2, 68} = 0.49$, $P = 0.615$). The Simpson's diversity index per plot was 0.49 ± 0.04 S.E. for the FUC, 0.50 ± 0.07 S.E. for the FFW, and 0.54 ± 0.12 S.E. for the FFE, and did not indicate significant differences between management systems ($F_{2, 68} = 0.11$, $P = 0.896$). The most abundant families were *Caesalpiniaceae* (16.3%), *Combretaceae* (16.3%), and *Mimosaceae* (12.2%).

Woody plant density

Using CCA, we revealed a significant effect of the three management types on the total density of all woody plants ($F = 1.62$, $P = 0.031$), with all constrained axes (combined) explaining 5.8% of the species (data) variability. (Fig. 3a). When the density of saplings and full-grown woody plant individuals was considered separately, the effect of management type was not significant ($F = 1.27$, $P = 0.140$), (and) the explained variability was 4.6% for all constrained axes (Fig. 3b).

Ficus sp., *Guiera senegalensis*, *Lonchocarpus laxiflorus*, *Prosopis Africana,* and *Ozoroa insignis* were the most frequent species in the protected FFE area. *Detarium senegalensis*, *Erythrophleum suaveolens*, *Saba senegalensis,* and *Sarcocephalus latifolius* were very frequent in the fenced FFW area. *Albizia chevalieri*, *Diospyros mespiliformis*, *Maytenus senegalensis,* and *Piliostigma thonningii* were the most abundant species in the FUC area under communal land use. However, the majority of the species catalogued were distributed across the whole area of the Fathala Forest, irrespective of the management systems.

DCA ordination showed limited effect of the management systems on the density of woody plants. No distinct groups of plots for particular management systems were apparent for either total density of all woody plants, or the separate densities of saplings and full-grown trees. In the analysis of total density, all unconstrained axes explained 25% of the species data variability. When the separate densities of saplings and full-grown woody plant were analyzed, all unconstrained axes explained 24.3% of the variability. The total density of all woody plants was the highest in the FFW (4700 individuals per ha) and differed significantly from densities in plots from the other management types ($F_{2, 68}$ = 4.52, P = 0.014). The density of saplings was the highest in the FFW (3429.167 individuals per ha), although this only differed significantly from the FUC area ($F_{2, 68}$ = 4.26, P = 0.018). No differences were found among densities of full-grown trees ($F_{2, 68}$ = 1.29, P = 0.282) (Fig. 4).

Woody plants exploitation categories

The type of management had no effect on the total density of all woody plants, saplings, or full-grown trees for all categories of exploitation (P >0.05 in all analyses, Fig. 5), with *Lonchocarpus laxiflorus* being the only exception. The total density ($F_{2, 68}$ = 4.63, P = 0.013) and sapling density ($F_{2, 39}$ = 5.88, P = 0.006) of *Lonchocarpus laxiflorus* were significantly higher in the FFE compared with the other management systems (Fig. 5a, b).

DISCUSSION

We recorded 63 out of the 89 woody species from the FF savanna vegetation reported by Lawesson (1995). The lower number of species (71%) recorded in our study was despite the fact we sampled an area 14 times larger than that investigated by Lawesson. This was probably a result of sampling strategy, as we used regular grid sampling, which generally reveals less species than selection of the most diverse plots. Our sampling represented 8 weeks of field work by two experienced researchers. The sampling design employed was, therefore, a compromise between the feasibility of the field work and the representativity of the collected data, since longer data collection was not possible due to phenological changes in the vegetation.

In addition, we collected the first density data ever published from the study area. The total number of woody species recorded in the FUC was more than

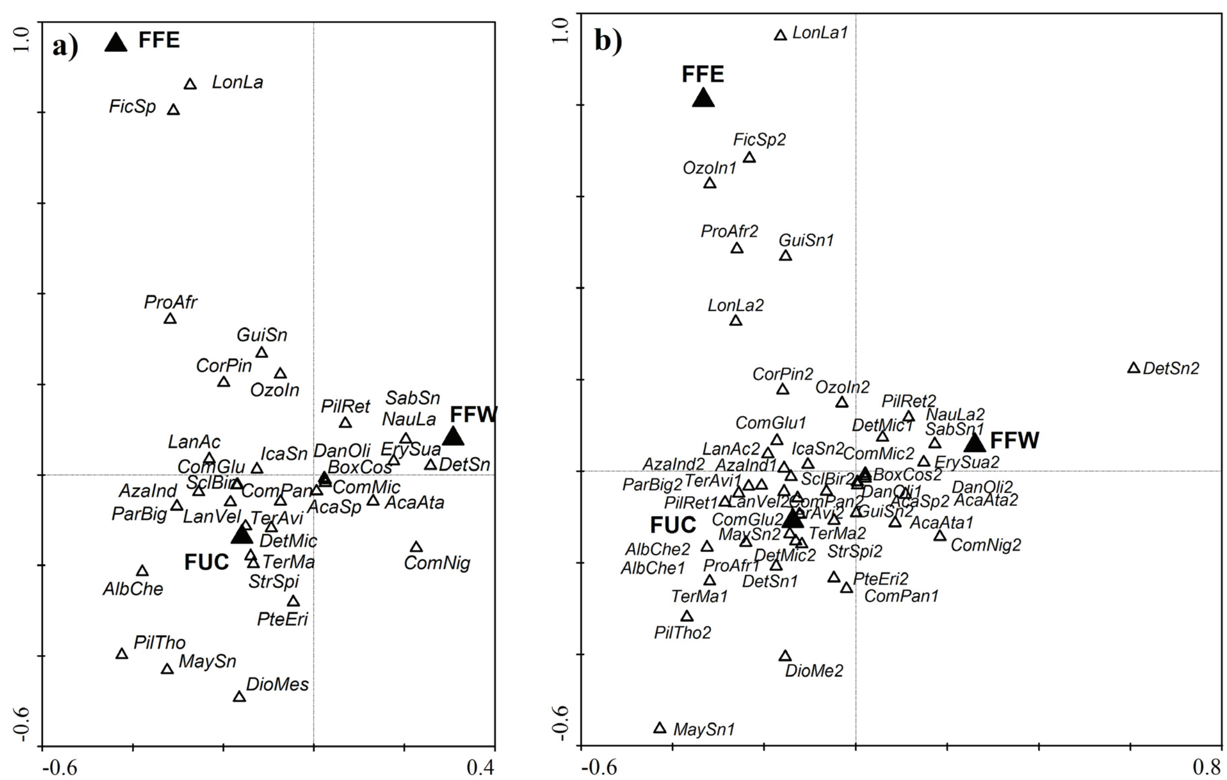

Fig. 3. Ordination diagrams showing results of the CCA analysis of: a) total density of all woody plant species in three areas with different management; b) density of woody plant species differentiating saplings and full-grown woody plant individuals in three areas with different management. FUC represents the area unfenced area with communal land use, FFW is the fenced area with large herbivores and FFE is the extended fenced area without animals and management interventions. For plant species codes see Table 1. Numbers at the end of species codes refer to saplings (1) and full-grown individuals (2).

twice that identified in either the FFW or FFE. This was attributed to the larger sampling area in the FUC, as the increase in species number per additional hectare was 3.9. A clear linear increase in the number of species within a sampling area was recorded for the range of sampling area sizes, from 0.02 ha to 1.42 ha. Further increase in sampling area size, above 1.42 ha, would almost certainly have resulted in a greater total number of recorded woody species, but probably at a lower rate of increase than in the studied range of sampling areas.

The lack of differences in species richness or species diversity of woody species per 0.02 ha plot among the three management systems agrees with the results of other studies of African savanna with similar climatic conditions, namely rainfall (Shackleton, 2000; Paré et al., 2010). In contrast to our study, lower species richness of woody species was recorded under communal grazing, compared to private reserves, in semi-arid areas (Higgins et al., 1999; Hejcmanová et al., 2010). In sub-humid areas where the intensity of exploitation is low, communal grazing does not appear to be detrimental to the species richness of woody plants.

The density of saplings of woody species seems to be more susceptible to management, in comparison to the species richness or density of full-grown individuals. Communal land use, as in the FUC area, frequently leads to a decrease in sapling density, cover or height, as also observed by other authors (Shackleton et al., 1994; Hejcmanová et al., 2010). In the FUC, saplings were exposed to relatively intensive browsing by livestock, removed during land clearing for crop cultivation on the periphery of the forest or harvested as fuelwood for local households. Consequently, recruitment of woody species was limited under communal land use and the density of saplings was low in this area. The highest density of saplings, recorded in the FFW, was probably due to the predominance of grazers, the low density of browsers, and the lack of human exploitation.

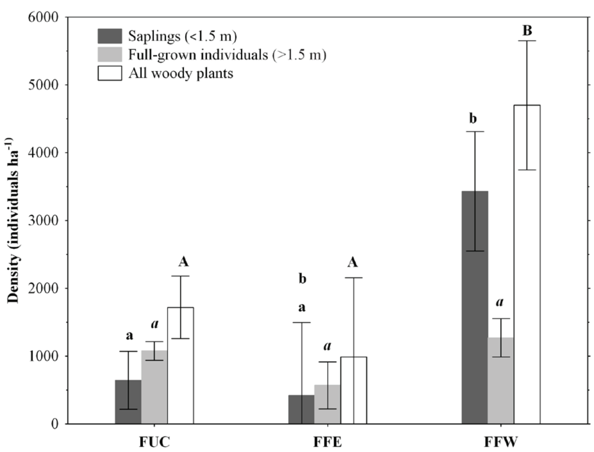

Fig. 4. The total density of all woody plants, density of saplings and density of full-grown individuals in three areas with different management (for abbreviations see Figure 1). Vertical bars indicate the standard error of the mean. The same letters above columns indicate non-significant results for the Tukey's HSD test for particular woody plant categories (saplings, full-grown individuals, all woody plants) compared among management systems.

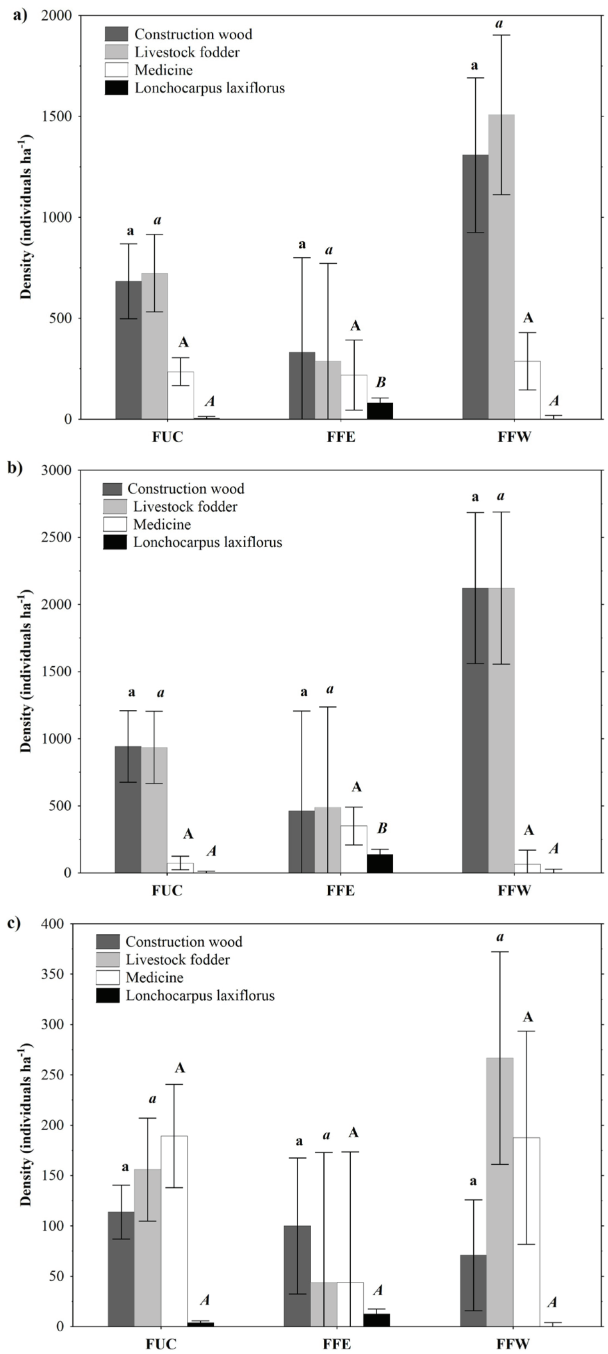

Fig. 5. The woody plant density in particular categories of preferred exploitation of plants in three areas with different management (for abbreviations see Fig. 1): a) total density of all woody plants; b) density of saplings; and c) density of full-grown individuals. Vertical bars indicate the standard error of the mean. The same letters above columns indicate non-significant results for the Tukey's HSD test for particular exploitation categories compared among management systems.

We expected that the fenced, and thereby undisturbed, FFE area would have a higher woody plant density than the unfenced FUC or the fenced FFW area inhabited by large herbivores, as was reported by Augustine, McNaughton (2004) or Pringle et al. (2007). However, our results showed the opposite to be the case. This can be explained by the seasonal inundation of part of the FFE area, which is dominated by grass *Schyzachirium sanguineum* or low forbs with bare areas (Nežerková-Hejcmanová et al., 2005). During the wet season, stagnant water creates anoxic conditions in this area, which limits the rooting and growth of woody plants and also the emergence of their seedlings.

The lack of the effect of management system on the density of woody species used for construction wood, fodder or medicinal purposes, can be explained by the low intensity of recent human exploitation. The higher density of *Lonchocarpus laxiflorus* saplings in the FFE area can be explained by browsing in the other management systems, as this species is considered to be palatable (Toutain, 1980).

CONCLUSION

The management of the Fathala Forest changed 8 years prior to our investigation. A change in land use may present an event that redirects ecosystem dynamics (Westoby et al., 1989; Fynn, O'Connor, 2000). We therefore expected the management system changes to initiate a more pronounced response in the woody vegetation, similar to that observed e.g. in the Bandia wildlife reserve in Senegal, where woody plant saplings were recruited within 5 years of the exclusion of human activities, and within 15 years woody savanna was fully re-established (Hejcmanová et al., 2010). However, since the Fathala Forest is a sub-humid savanna, a substantially slower response to a change in the management was recorded. Under the relatively humid conditions of the Fathala Forest, 8 years of fencing is not time long enough for a manifestation of the change in land use. Finally, we concluded that human land use of lower intensity cannot be connected with degradation of sub-humid tropical forests as climatic attributes, particularly precipitations, are driving force behind vegetation dynamics in these ecosystems (Ellis, Swift, 1988; Birkett, Stevens-Wood, 2005).

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