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Ecological and structural differentiation of the Sudanian woodlands in the Biosphere Reserve of Pendjari, Benin

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Abstract

Aims: This study aims to: i) differentiate the plant associations in the Biosphere Reserve of Pendjari (BRP), ii) determine the ecological characteristics of their habitats and iii) present distribution maps on different soil types. **Study area**: The BRP, located in the Sudanian Zone of Benin. **Methods:** 202 phytosociological relevés were sampled according to the Braun-Blanquet method within the BRP. Ordination was performed using Detrended Correspondence Analysis to evaluate vegetation patterns. Soil parameters were used to characterize the vegetation types. **Results:** The numerical analysis of 202 plots and 249 plant species showed two major floristic groups that correlated with a moisture gradient: drylands versus wetlands. The dryland group was a mixture of woodland and shrub savanna, the dominant ecosystems of the study area. The wetland group encompassed species primarily from riparian forest, tree savanna and grass savanna on floodplains. Syntaxonomical analysis of the dryland group showed rocky and gravelly soil associations (*Burkeo africanae-Detarietum microcarpi*) and soils associated with or without fine gravels (*Andropogono gayani-Terminalietum avicennioidis*, *Andropogono gayani-Senegalietum dudgeonii* and *Terminalietum leiocarpae*). Syntaxonomical analysis of the wetland group showed riparian forest associations on sandy-clay soil (*Coletum laurifoliae*, *Borassetum aethiopi* and *Hyparrhenio glabriusculae-Mitragynetum inermis*) and floodplain associations on silt-clay soil (*Terminalio macropterae-Mitragynetum inermis*, *Brachiario jubatae-Terminalietum macropterae*, *Sorghastro bipennati-Vachellietum hockii*). **Conclusions:** Eleven new associations were identified in this study. If the distribution of plant associations was determined by different soil properties, the soil humidity would be one of the main ecological factors determining the establishment of plant species and thus plant association development.

Taxonomic reference: Akoègninou et al. (2006), Angiosperm Phylogeny Group classification for the orders and families of flowering plants (APG IV, 2016).

Abbreviations: BRP = Biosphere Reserve of Pendjari; CBD = Convention on Biological Diversity; CCA = Constrained Correspondence Analysis; DCA = Detrended Correspondence Analysis; GPS UTM = Global Positioning System Universal Transverse Mercator.

Keywords

association, ecology, vegetation pattern, Pendjari reserve, woodland, Sudanian zone, Benin

Introduction

Vegetation formations such as woodlands (from open to closed), and grasslands, are some of the most diverse natural ecosystems that provide goods and services for sustenance of human populations worldwide (Amenaglo et al. 2018). In the tropical region, these ecosystems are continuously exposed to threats such as intensive grazing, clearing for agriculture and illegal logging of tree species (Assèdé et al. 2023). The Convention on Biological Diversity (CBD), in the current context of strong and widespread environmental degradation, recommends a strategy such as creation of protected areas for biodiversity conservation (Gnoumou et al. 2021). In Benin, tropical forests represent 25% of the land area whose management plans have been developed and implemented for a sustainable conservation of biodiversity (Toko et al. 2018). However, these are not always managed with consideration for ecological, social, economic, or policy factors (Gnoumou et al. 2021). The basis for developing site-specific and sustainable management strategies of ecosystems is a clear understanding of the flora, plant groups (vegetation pattern) and their ecology (Gnoumou et al. 2021).

Floristic and phytosociological knowledge (plant groups and plant associations) allows for the conservation and development of safeguarding programs for natural resources (Rebbas et al. 2012; Gnoumou et al. 2021). Phytosociologists very early-on wondered about the structure of the basic units of different vegetation types for sustainable conservation planning. This led to the concept of "ecological groups". Duvigneaud (1946) firstly designed and defined the ecological group as "a group of species having between them a more or less large sociological affinity, marked by a tendency to gather in a given biotope".

Understanding the phyto (plant) diversity, the synecological link between co-existing plant communities and the dependency relationships with their environment is a baseline for successful vegetation management (Gnoumou et al. 2021) in a conservation area like the Biosphere Reserve of Pendjari (BRP).

Previous studies on the vegetation of the BRP focused on the description of the general physiognomy (Delvingt et al. 1989) or related to specific ecological concepts (Houéhanou et al. 2011; Azihou et al. 2013a, 2013b; Houéhanou et al. 2013; Azihou et al. 2014; Salako et al. 2017). As a result, the previous systems of analyses of the BRP vegetation do not reach the detailed level necessary to identify plant associations and the total diversity of plant communities. In conservation planning, the classification of the flora into plant associations and their characterization by habitats is important for sustainable and efficient management planning (Pinder and Rosso 1998). The objectives of this study are to: i) differentiate the plant associations in the BRP, ii) determine the ecological characteristic of their habitat and iii) present their distribution on different soil types of the BRP.

Study area

The study was conducted in the Biosphere Reserve of Pendjari (BRP) located in the Atacora district of Benin with two distinct components: Pendjari National Park and Pendjari Hunting zone (Figure 1). The BRP extends from 10°30'N and 11°30'N latitudes to 0°50'E and 2°00'E longitudes in the Sudanian region of Benin (White 1983; Adomou 2007; Assèdé et al. 2018). The area has two clearly different seasons: a rainy season (April-May to October) and a dry season (November to March) (Assèdé et al. 2018). The mean

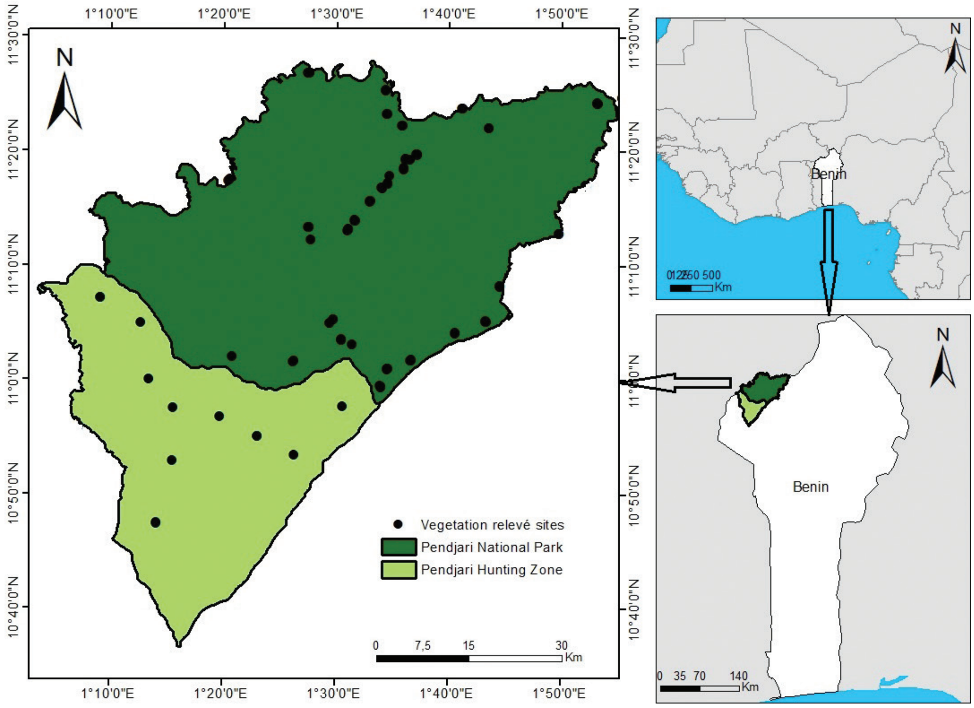

Figure 1. Location of the study area: Top right is Map of Benin (white), Bottom right (Map of Benin showing Biosphere Reserve of Pendjari) and left is study area with relevé sites.

annual rainfall varies from 1000 to 1100 mm with 60% falling between July and September. Temperature varies from 21°C during the night up to 40°C during the day (Assédé et al. 2015). The mean temperature varies from 25° to 28°C during the cooler period of the dry season and 30° to 33°C during the hot period of the dry season with a mean of 27°C (Assédé et al. 2015). The vegetation consists of a mosaic of wooded grassland, shrublands, grassy woodland, grassland and gallery forest intermingled with some patches of closed deciduous woodland and dry forest (Sokpon et al. 2001). The BRP is located on a peneplain with a flat relief and altitudes ranging from 105 m to 200 m. The peneplain is flooded or waterlogged during the rainy season, forming extensive wetland areas. In the reserve, the soil is mainly ferruginous (Willaine and Volkof 1967).

Methods

Vegetation study

Existing vegetation and soil maps of the BRP (Willaine and Volkoff 1967; König 2005) were used as a basis for the selection of study sites. Phytosociological relevé sampling was conducted in 2013 using Braun-Blanquet's (1932) method, as used by previous studies in the study area for vegetation analysis (Adomou et al. 2007; Houessou et al. 2019). Sites supporting the major plant communities (semi-deciduous forest, gallery forest, woodland, and savanna) of the BRP were investigated. At each site, uniform physiognomy stands were selected for sampling, following the variation in dominant plant species. Rectangular plots of 30 m × 30 m were used (as minimum area) for woodland sampling within the study area (Houessou et al. 2019). In the gallery forests, plots of 20 m × 25 m were used as the minimum area to sample plots (Natta et al. 2003). Smaller plots (10 m × 10 m) placed at the center of the larger plots (30 m × 30 m and 20 m × 25 m) were used as the minimum area for sampling the herbaceous layer (Figure 2) (Houessou et al. 2019).

The site coordinates and altitude were noted using a GPS (Garmin 64). The main environmental factors such as topography (valley, slope, and plateau) and soil conditions (texture, flooding, etc.) were noted. The vegetation structure (number of layers, their cover) was described. Observations were made in measurement plots considered sufficiently homogeneous. The adopted species cover-abundance categories of Braun-Blanquet (1932) scale were transformed to a percentage scale of mean cover (MR) as follow:

5: species covering 75–100% of the survey area and at 87.5% MR;
4: species covering 50–75% of the survey area and MR 62.5%;
3: species covering 25–50% of the survey area and MR 37.5%;
2: species covering 5 to 25% of the survey area and MR of 15%;
1: species covering 1 to 5% of the survey area and MR of 3%;
+: species covering less than 1% of the ground area and at MR of 0.5%;

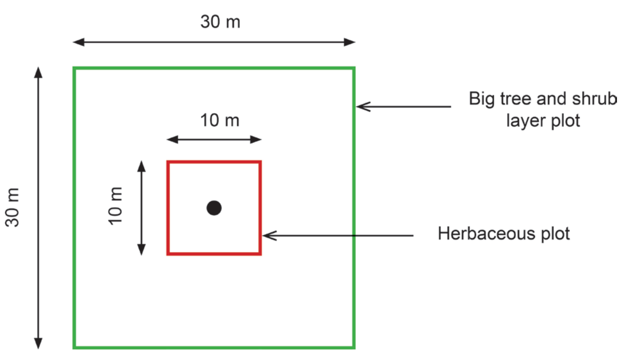

Figure 2. A schematic illustration of sampling plots for phytosociological relevé in the Biosphere Reserve of Pendjari.

In total 202 plots were sampled in this study (Table 1). Plant species were identified in the field using Hutchinson and Dalziel (1954–1972), Akoègninou et al. (2006) and Lisowski (2009) and confirmed at the National Herbarium of Benin. Voucher specimens were provided for most plant species.

Table 1. Number of plots sampled in the different ecosystem types.

Ecosystem	Gallery forest	Woodland on floodplains	Woodland on dryland	Savanna on dryland	Total
Protected area	23	50	44	85	202

Soil sampling

Soil samples at 20 cm depth were collected at five locations (from the four corners and center of each plot) within each representative relevé of plant communities (Assèdé et al. 2015). Analyses were conducted by the Laboratory of Soil Sciences at the University of Abomey-Calavi. The soil pH (pH_{water} and pH_{KCl}) and particle size (silt, clay and sand) were determined by potentiometric methods and Robinson's Pipette, respectively (Peech 1965). All chemical analyses were performed on air-dried soil samples (<2 mm grain size). The concentration of exchangeable cations such as K^+, Ca^{2+}, Na^+ and Mg^{2+} was determined by neutral ammonium acetate extract (Mattila and Rajala 2022). Organic carbon content (C) was determined using the dry combustion method, while Organic matter (OM) was determined by the gravimetric method (Soon and Abdoud 1991; Tiessen and Moir 1993). Total nitrogen concentration (N) was determined by the Kjeldahl method (Bremner 1960). The available phosphate (P) and phosphorus pentoxide (P_2O_5) were measured by titration with ammonium fluoride (NH_4F) (Kumawat et al. 2017).

Data analysis

Floristic data

Data analysis of the 202 relevés was undertaken using Vegan, an R (version 2.12.2) computer package (R Core Team 2022). A bidimensional geometric structure was built based on the observed dissimilarity or similarity between plots. A set of multivariate analyses of the data matrices was used to explore the plant community structure of the major floristic units of the BRP. Ordination was performed using Detrended Correspondence Analysis (DCA) for a global analysis. The DCA aims to provide a numerical score for each relevé of vegetation, indicating its position along the axis of the main trend of variation in the floristic data. Each major floristic unit was partially analysed to generate smaller floristic units or plant communities. The geographical interpretation of ordination clusters was based on the spatial distribution of vegetation relevé groupings. The classification of plant communities followed Schmitz (1988), Sokpon et al. (2001), Natta et al. (2003) and Wala (2004). The nomenclature of vegetation types follows Aubreville (1957).

The naming of each plant community was derived from the characteristic species, i.e. species restricted to one or a few habitat types. The characteristic species were determined using the indicator value (IndVal) index (Dufrêne and Legendre 1997) with the Indicspecies 1.6.7 package of the software R 2.15.1 (R Core Team 2022). The Indicspecies program calculates for each plant species, the relative abundance, frequency (or fidelity) and indicator value. In each plant community, the indicator value represented by the product of the mean abundance in a plant community with the relative frequency of occurrence of a species (Dufrêne and Legendre 1997) was determined for each and two combined plant species. The statistical significance test of Monte Carlo was conducted for 999 permutations under the equality assumption between indicator values of each species in all plant communities. The indicator value ranged from 0% (no indication) to 100% (perfect indication). Perfect indication means the exclusive presence of a species to a plant community. Conversely, low indication means the species was common and abundant in several plant communities. The two plant species with the highest indicator values of a plant community were used to name the plant community (Dufrêne and Legendre 1997).

Plant communities were then classified into syntaxonomic groups (Theurillat et al. 2021) based on large phytosociological units or taxa (alliances, orders and classes) defined for tropical plant communities by Schmitz (1988), Lebrun (1947), Lebrun and Gilbert (1954), Mullenders (1954), Duvigneaud (1950), Sinsin (1994), Oumorou (2003), Mahamane (2005) and, Ouédraogo (2009). Based on ecological properties and floristic differentiations (characteristic species), each plant community was raised to association rank. Associations were arranged within alliances, alliances into orders and orders into classes. The nomenclature of syntaxa followed Weber et al. (2000) and Theurillat et al. (2021).

Species with a frequency greater than 50% were defined as constant species (Seiler et al. 2021). Diagnostic species were identified using the phi coefficient as a measure of fidelity (Chytrỳ et al. 2002). The phi-coefficient ranges from -1 (maximum negative fidelity) to +1 (maximum positive fidelity). Therefore, a species with phi coefficient higher than 0.25 was considered diagnostic for a particular plant association. To exclude the species having a non-significant fidelity, we used the Indicspecies package of the R software to perform the simultaneous calculation of the Fisher exact test (Cáceres and Legendre 2009).

The species richness (S) was determined in each plant community. The mean species richness (Sn) per relevé was determined in each plant community using the formula (Steffen et al. 2013):

$$S_n = \frac{\Sigma_i^n S_i}{n}$$

S_n: mean species richness.
S_i: number of species in relevés *i*.
n: number of relevés in the plant community.

The similarity between plant communities was tested using Jaccard index (*Ij*):

$$I_j = \frac{C}{(A + B - C)}$$

$I_j \geq 50\%$: similarity.
$I_i < 50\%$: absence of similarity.
A: number of species belonging to the plant community I.
B: number of species belonging to the plant community II.
C: number of species common to both communities I and II.

The geographic coordinates of representative relevés of each plant community were projected on the soil map to identify its soil groups.

Soil properties

The mean value of each soil parameter (including organic carbon, organic matter, total nitrogen and soil pH) was calculated for each plant community. Representative relevés (Table 4) of plant associations and soil groups were used to establish the distribution map of plant associations on different soil types of the BRP.

Results

Partition of sampling plots based on vegetation and indirect environmental gradients

The DCA analysis of 202 relevés and 249 plant species (Figure 3A) showed that a major floristic component was correlated with soil moisture status (Axis 1) (drylands versus wetlands with *Ij* = 0. 07). Two groups were discriminated:

The group G1 included 73 relevés and 177 plant species from riparian forest, woodland, shrub savanna and grass savanna on floodplains and well drained sites with slightly raised elevation that were rarely inundated. The common plant species in the tree layers included *Cola laurifolia*, *Diospyros mespiliformis*, *Borassus aethiopum* and *Terminalia leiocarpa*. The shrub layer essentially included *Mitragyna inermis*, *Terminalia macroptera*, *Acacia dudgeonii*, *Combretum micranthum*, *C. nigricans*, *C. molle* and *C. glutinosum*. The herbaceous layer was dominated by *Andropogon tectorum*, *Merremia aegyptia*, *Hyparrhenia rufa*

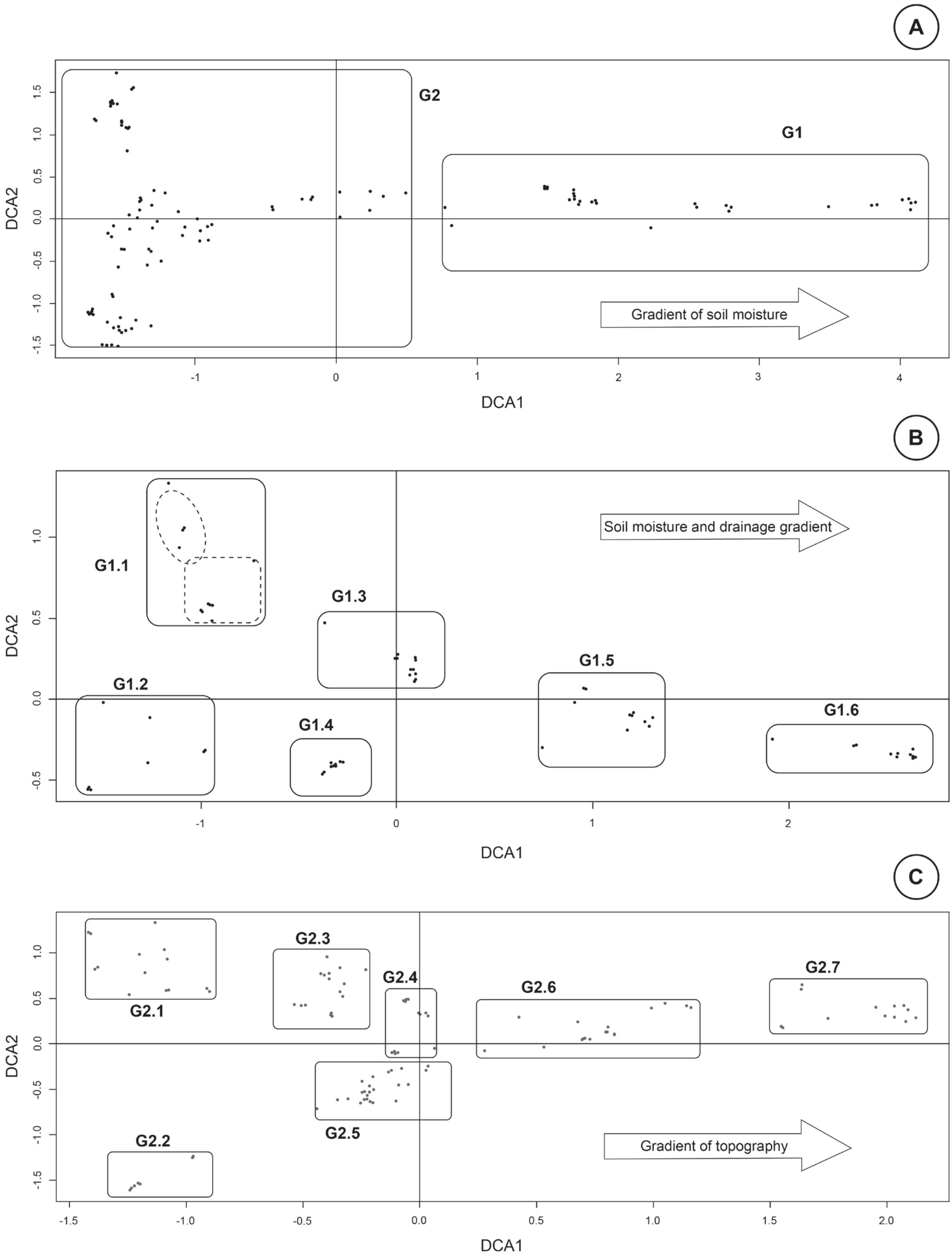

Figure 3. DCA ordination: **A)** 202 relevés and 249 plant species recorded in natural vegetation of the BRP, showing two clusters along axis 1: G1: Wetland group of vegetation; G2: Dryland group of vegetation; **B)** partial ordination of G1 (73 relevés and 177 plant species recorded in riparian forests and floodplains in the BRP), showing six plant associations: G1.1: *Hyparrhenio glabriusculae-Mitragynetum inermis*; G1.2: *Terminalio macropterae-Mitragynetum inermis*; G1.3: *Sorghastro bipennati-Vachellietum hockii*; G1.4: *Brachiario jubatae-Terminalietum macropterae*; G1.5: *Borassetum aethiopi*; G1.6: *Coletum laurifoliae*. **C)** Partial ordination of G2 (129 relevés and 206 plant species recorded in tree and shrub savannas in the BRP), showing five associations and two plant communities. G2.1: *Terminalietum leiocarpae*; G2.2: *Andropogono gayani-Combretetum glutinosi*; G2.3: Plant community of *Crossopteryx febrifuga*; G2.4: *Andropogono gayani-Terminalietum avicennioidis*; G2.5: Plant community of *Vitellaria paradoxa* and *Andropogon gayanus*; G2.6: *Burkeo africanae-Detarietum microcarpi*; G2.7: *Andropogono gayani-Senegalietum dudgeonii*.

and *Chrysopogon nigritanus*. The vegetation corresponded to formations that only established on moist to wet soils with temporary flooding. The moisture status of the soil was related to the extent of the rainy periods.

The group G2 included 129 relevés and 206 plant species from a mixed stand of savannas and woodland on dry soils (plateau), the dominant ecosystems of the BRP. The common plant species of shrub and tree layers included *Crossopteryx febrifuga*, *Terminalia leiocarpa*, *Combretum glutinosum*, *Burkea africana*, *Vitellaria paradoxa*, *Terminalia avicennioides*, *Combretum collinum* and *Detarium microcarpum*. The herbaceous layer was dominated by *Andropogon gayanus* and *Indigofera pulchra*.

A partial ordination of 73 relevés and 177 plant species of the group G1 (Figure 3B) showed a major floristic factor correlated with soil moisture and drainage status (Axis 1) (plant communities on well drained and temporary inundated soil versus plant communities on poorly drained floodplains and temporary inundated), and plant recovery (Axis 2) (woodland versus shrub and grass savanna). These vegetation types were distributed along the Pendjari River in the northern part of the BRP. The species composition changed along the moisture gradient from riparian forest (dominated by *Cola laurifolia*) to a landscape with tree savanna. Six plant associations were discriminated: *Hyparrhenio glabriusculae-Mitragynetum inermis* (G1.1), *Terminalio macropterae-Mitragynetum inermis* (G1.2), *Sorghastro bipennati-Vachellietum hockii* (G1.3), *Brachiario jubatae-Terminalietum macropterae* (G1.4), *Borassetum aethiopi* (G1.5) and *Coletum laurifoliae* (G1.6).

The DCA analysis of 129 relevés and 206 plant species of the sub-group G2 (Figure 3C) showed major floristic grouping associated with vegetation cover (Axis 1) (savanna versus woodland) and relief (Axis 2) (savanna on hill with rocky soil versus savanna on plateau without gravel). Five plant associations and two plant communities were discriminated: *Terminalietum leiocarpae* (G2.1), *Andropogono gayani-Combretetum glutinosi* (G2.2), plant community of *Crossopteryx febrifuga* (G2.3), *Andropogono gayani-Terminalietum avicennioidis* (G2.4), plant community of *Vitellaria paradoxa* and *Andropogon gayanus* (G2.5), *Burkeo africanae-Detarietum microcarpi* (G2.6) and *Andropogono gayani-Senegalietum dudgeonii* (G2.7).

Similarity between plant communities

Clear differences appeared among wetland plant communities with Jaccard index $I_j < 50\%$ (Table 2). The closest groups were the plant communities *Cola laurifolia* and p *Borassus aethiopum* ($I_j = 0.46$). However, there were similarities between some dryland groups (Table 2). The most similar groups ($I_j = 0.66$) were the plant communities *Crossopteryx febrifuga*, and *Vitellaria paradoxa* and *Andropogon gayanus* Kunth. Both groups were similar to the plant community of *Terminalia avicennioides* and *Andropogon gayanus*.

From these results, we retained six associations on wetland and five associations on dryland for the study area.

Table 2. Floristic similarity (I_j) between wetland and dryland plant communities.

	Wetland					
Plant communities	**G1.6**	**G1.5**	**G1.2**	**G1.4**	**G1.1**	
G1.6						
G1.5	0.46					
G1.2	0.09	0.08				
G1.4	0.12	0.13	0.31			
G1.1	0.12	0.16	0.38	0.37		
G1.3	0.09	0.13	0.27	0.30	0.31	
	Dryland					
Plant communities	**G2.1**	**G2.2**	**G2.4**	**G2.3**	**G2.6**	**G2.7**
G2.1						
G2.2	0.41					
G2.4	0.43	0.39				
G2.3	0.57	0.48	0.41			
G2.6	0.42	0.44	0.42	0.49		
G2.5	0.5	0.43	0.42	0.66	0.48	
G2.7	0.19	0.26	0.19	0.18	0.18	0.18

G1.1: *Hyparrhenio glabriusculae-Mitragynetum inermis*; G1.2: *Terminalio macropterae-Mitragynetum inermis*; G1.3: *Sorghastro bipennati-Vachellietum hockii*; G1.4: *Brachiario jubatae-Terminalietum macropterae*; G1.5: *Borassetum aethiopi*; G1.6: *Coletum laurifoliae*.
G2.1: *Terminalietum leiocarpae*; G2.2: *Andropogono gayani-Combretetum glutinosi*; G2.3: Plant community of *Crossopteryx febrifuga*; G2.4: *Andropogono gayani-Terminalietum avicennioidis*; G2.5: Plant community of *Vitellaria paradoxa* and *Andropogon gayanus*; G2.6: *Burkeo africanae-Detarietum microcarpi*; G2.7: *Andropogono gayani-Senegalietum dudgeonii*.

Characterisation of associations

The synoptic table and characteristic plant species of each association are presented in Table 3. The type relevés of the associations are provided in Table 4. The full phytosociological table is provided in Suppl. material 1. The photos, the life forms and chorology spectra of each association are presented in Appendix 1.

Association of wetlands

***Hyparrhenio glabriusculae-Mitragynetum inermis* Assèdé ass. nova**
Holotypus: Table 4, relevé A4

This association (Table 3, G1.1) described with 11 relevés was a riparian forest association observed in tree savannas on floodplain as a continuum of riparian forest of *Cola laurifolia*. *Hyparrhenio glabriusculae-Mitragynetum inermis* occurred in floodplains where the topography favored a prolonged flooding period. In these alluvial plains, the soils were deep with a slimy-clay texture without gravel. The association was a pure stand of *Mitragyna inermis*. The soil moisture status was temporarily wet and more related to stream proximity. The flooding period was around 5 months (from July to November) and the wet period can extend up to 6 months (from June to November).

Two layers were identified. The tree layer was essentially composed of *Mitragyna inermis* with 20% to 65% cover and a height between 5 m and 7 m. The well-developed herbaceous layer was dominated by *Hyparrhenia glabriuscula* with a cover of 85%–90% and a height between 1.5 m and 2 m. The di-

Table 3. Shortened synoptic table of the eleven plant associations. See Suppl. material 2 for the full version of this table. Constancies are given as percentages; diagnostic (> 0.25) phi values are marked in light grey, highly diagnostic (> 0.5) values in dark grey. Significant values p<0.01 are marked with "**", highly significant values p<0.001 with "***". Name of plant associations: G1.1: *Hyparrhenio glabriusculae-Mitragynetum inermis*; G1.2: *Terminalio macropterae-Mitragynetum inermis*; G1.3: *Sorghastro bipennati-Vachellietum hockii*; G1.4: *Brachiario jubatae-Terminalietum macropterae*; G1.5: *Borassetum aethiopi*; G1.6: *Coletum laurifoliae*; G2.1: *Terminalietum leiocarpae*; G2.2: *Andropogono gayani-Combretetum glutinosi*; G2.4: *Andropogono gayani-Terminalietum avicennioidis*; G2.6: *Burkeo africanae-Detarietum microcarpi*; G2.7: *Andropogono gayani-Senegalietum dudgeonii*; C: Constancy.

Plant associations	G1.1		G1.2		G1.3		G1.4		G1.5		G1.6		G2.1		G2.2		G2.4		G2.6		G2.7	
Number of relevés	11		12		13		14		11		12		14		20		12		20		15	
Species richness (S)	121		54		53		64		43		39		136		81		65		94		33	
Mean S ± Std Dev	38 ± 10.9		33.3 ± 5.3		25.3 ± 2.7		29.8±4.1		23.7 ± 2.4		24.3±2.4		41 ± 11.2		37.9 ± 6.7		38.3 ± 5.6		39.4 ± 7.8		24 ± 2.1	
	C	Phi	C	Phi	C	Phi	C	Phi	C	Phi	C	Phi	C	Phi	C	Phi	C	Phi	C	Phi	C	Phi
Hyparrhenio glabriusculae-Mitragynetum inermis																						
Hyparrhenia glabriuscula	100	1***																				
Merremia aegyptia	81	0.73***															33	0.26				
Setaria pumilla	45	0.66***																				
Crotalaria leprieurii	27	0.51**																				
Hygrophila pobeguinii	27	0.51**																				
Mukia maderaspatensis	27	0.51**																				
Sida linifolia	27	0.51**																				
Mitragyna inermis	100	0.45**	100	0.47							100	0.47										
Terminalio macropterae-Mitragynetum inermis																						
Capparis sepiaria			100	1***																		
Terminalia macroptera			100	0.45***																		
Tinnea barteri			50	0.35**																		
Sorghastro bipennati-Vachellietum hockii																						
Combretum glutinosum					53	0.72***																
Trichilia emetica					46	0.66***																
Sorghastrum bipennatum					38	0.60**																
Vachellia hockii					53	0.36**																
Brachiario jubatae-Terminalietum macropterae																						
Paspalum scrobiculatum							100	0.84***														
Brachiaria jubata							71	0.83***														
Ludwigia octovalvis							57	0.74***														
Ipomoea argentaurata							57	0.61***														
Hibiscus articulatus							57	0.26**							75	0.48			60	0.34		
Borassetum aethiopi																						
Hypoestes aristata									91	0.95***												
Morelia senegalensis									81	0.90***												
Borassus aethiopum									91	0.82***												
Pterocarpus santalinoides									100	0.76**	58	0.42										
Strophanthus sarmentosus									45	0.66***												
Rourea coccinea									72	0.64**	41	0.35										
Ipomoea blepharophylla									45	0.59***												
Cryptolepis nigrescens									36	0.59**												
Neocarya macrophylla									36	0.59***												
Coletum laurifoliae																						
Vitex chrysocarpa											75	0.86***										

Plant associations	G1.1		G1.2		G1.3		G1.4		G1.5		G1.6		G2.1		G2.2		G2.4		G2.6		G2.7	
Number of relevés	**11**		**12**		**13**		**14**		**11**		**12**		**14**		**20**		**12**		**20**		**15**	
Species richness (S)	**121**		**54**		**53**		**64**		**43**		**39**		**136**		**81**		**65**		**94**		**33**	
Mean S ± Std Dev	**38 ± 10.9**		**33.3 ± 5.3**		**25.3 ± 2.7**		**29.8±4.1**		**23.7 ± 2.4**		**24.3±2.4**		**41 ± 11.2**		**37.9 ± 6.7**		**38.3 ± 5.6**		**39.4 ± 7.8**		**24 ± 2.1**	
	C	**Phi**	**C**	**Phi**	**C**	**Phi**	**C**	**Phi**	**C**	**Phi**	**C**	**Phi**	**C**	**Phi**	**C**	**Phi**	**C**	**Phi**	**C**	**Phi**	**C**	**Phi**
Cola laurifolia									**45**	0.30	**100**	0.83**										
Paullinia pinnata									**100**	0.66	**100**	0.69**										
Terminalietum leiocarpae																						
Combretum micranthum													**35**	0.54**								
Terminalia leiocarpa													**100**	0.66**								
Andropogono gayani-Combretetum glutinosi																						
Commelina benghalensis															**40**	0.61***						
Ziziphus mucronata															**40**	0.61***						
Combretum collinum															**95**	0.52**					**66**	0.25
Combretum glutinosum															**100**	0.48**	**100**	0.36	**100**	0.48		
Andropogono-gayani-Terminalietum avicennioidis																						
Aspilia bussei																	**66**	0.81***				
Dioscorea abyssinica					**30**	0.28											**58**	0.58***				
Terminalia avicennioides															**85**	0.38	**100**	0.38**				
Burkeo africanae-Detarietum microcarpi																						
Burkea africana																			**100**	1***		
Detarium microcarpum															**95**	0.56			**90**	0.52***		
Andropogono gayani-Senegalietum dudgeonii																						
Afrocayratia ibuensis																					**100**	1***
Cyperus hortensis																					**100**	1***
Echinochloa stagnina																					**100**	1***
Senegalia dudgeonii																	**100**	0.40			**100**	0.45**
Spermacoce Octodon			**100**	0.56																	**100**	0.63**
Other species																						
Cyperus cyperinus	**54**	0.42																	**30**	0.26		
Hibiscus cannabinus															**95**	0.57			**90**	0.53		
Siphonochilus aethiopicus	**63**	0.37													**40**	0.26						
Chlorophytum blepharophyllum			**66**	0.41											**55**	0.42						
Cissus cornifolia			**50**	0.38													**66**	0.54				
Combretum molle															**60**	0.36			**55**	0.32		
Combretum nigricans															**90**	0.47			**70**	0.30		
Crateva adansonii			**66**	0.64																		
Crossopteryx febrifuga			**100**	0.68																		
Gardenia ternifolia															**70**	0.42	**100**	0.52				
Lonchocarpus laxiflora			**50**	0.28											**70**	0.58						
Oldenlandia herbacea			**66**	0.30																	**100**	0.61
Aspilia ciliata					**30**	0.35									**20**	0.26						
Corchorus trilocularis					**23**	0.45																
Cyphostemma sokodense																						
Eragrostis tenella					**61**	0.41									**70**	0.62						
Grewia barteri																	**66**	0.35	**50**	0.30		
Microstachys chamaelea					**23.08**	0.46																
Ampelocissus africana													**14.29**	0.38								
Ampelocissus bombycina															**20**	0.32						

Table 4. Type relevés of plant associations. L: Layer; H: Herb; A: Tree. G1.1: *Hyparrhenio glabriusculae-Mitragynetum inermis*; G1.2: *Terminalio macropterae-Mitragynetum inermis*; G1.3: *Sorghastro bipennati-Vachellietum hockii*; G1.4: *Brachiario jubatae-Terminalietum macropterae*; G1.5: *Borassetum aethiopi*; G1.6: *Coletum laurifoliae*; G2.1: *Terminalietum leiocarpae*; G2.2: *Andropogono gayani-Combretetum glutinosi*; G2.4: *Andropogono gayani-Terminalietum avicennioidis*; G2.6: *Burkeo africanae-Detarietum microcarpi*; G2.7: *Andropogono gayani-Senegalietum dudgeonii*. The geographical coordinates are in the WGS 84 datum and the UTM zone 31 N projection system.

Plant associations		**G1.1**	**G1.2**	**G1.3**	**G1.4**	**G1.5**	**G1.6**	**G2.1**	**G2.2**	**G2.4**	**G2.6**	**G2.7**
Plot ID	**L**	**A4**	**B10**	**C9**	**D8**	**E2**	**F10**	**G4**	**H5**	**I10**	**J3**	**K8**
Soil texture		**slimy-clay**	**silty-clay**	**clayey-silt**	**clay-silt**	**clayey-sand**	**clayey-sand**	**clay**	**gravelly sandy**	**sandy-clay**	**clay**	**clayey-silty-sand**
Tree cover (%)		**20**	**50**	**10**	**40**	**90**	**95**	**90**	**45**	**50**	**70**	**70**
Herb cover (%)		**85**	**60**	**40**	**80**	**30**	**5**	**20**	**55**	**40**	**60**	**60**
Latitude		**1248794**	**1257012**	**1257311**	**1218922**	**1253160**	**1240105**	**1221167**	**1257039**	**1210750**	**1217472**	**1223930**
Longitude		**318930**	**361057**	**347099**	**341072**	**379056**	**372162**	**333932**	**360984**	**345640**	**342618**	**340064**
Number of species		**37**	**31**	**19**	**23**	**18**	**24**	**28**	**35**	**45**	**46**	**25**
Diagnostic species of *Hyparrhenio glabriusculae-Mitragynetum inermis*												
Crotalaria leprieurii	H											
Cyperus cyperinus	H											
Hibiscus cannabinus	H	+							+		+	
Hygrophila pobeguinii	H											
Hyparrhenia glabriuscula	H	+								+		
Merremia aegyptia	H	1								+		
Mitragyna inermis	A	4	3			+	+					
Mukia maderaspatensis	H											
Scoparia dulcis	H	+		+							+	
Setaria pumilla	H											
Sida linifolia	H											
Siphonochilus aethiopicus	H	+							+	+		
Diagnostic species of *Terminalio macropterae-Mitragynetum inermis*												
Capparis sepiaria	H		+									
Chlorophytum blepharophyllum	H		+									
Cissus cornifolia	H		+									
Combretum molle	A		+						3	+	+	
Combretum nigricans	A		+	0.5					+	+	+	+
Crateva adansonii	H		+									
Crossopteryx febrifuga	A		+									+
Gardenia ternifolia	A		+						+	+		
Lonchocarpus laxiflora	A		+							+		
Oldenlandia herbacea	H		+						+			+
Terminalia macroptera	A		2	+	2							
Tinnea barteri	H		+						+			
Diagnostic species of *Sorghastro bipennati-Vachellietum hockii*												
Aspilia ciliata	H											
Combretum glutinosum	A			+								
Corchorus trilocularis	H	+		+								
Cyphostemma sokodense	H								+		+	
Dioscorea abyssinica	H											
Eragrostis tenella	H								+			
Grewia barteri	A										+	
Microstachys chamaelea	H			+								
Sorghastrum bipennatum	H			2								
Trichilia emetica	A											
Vachellia hockii	A			2				+				
Vachellia sieberiana	A				+							
Diagnostic species of Brachiario jubatae-Terminalietum macropterae												
Brachiaria jubata	H				+							
Hibiscus articulatus	H				+						+	
Ipomoea argentaurata	H				+							
Ludwigia octovalvis	H				+							
Paspalum scrobiculatum	H				+		+					
Diagnostic species of Borassetum aethiopi												
Borassus aethiopum	A					2	+					
Cryptolepis nigrescens	H					+						
Hypoestes aristata	H					+						
Ipomoea blepharophylla	H					+						
Morelia senegalensis	A					+						
Neocarya macrophylla	H											
Pterocarpus santalinoides	A					+	+					
Rourea coccinea	H						+					
Strophanthus sarmentosus	H					+						

Plant associations		**G1.1**	**G1.2**	**G1.3**	**G1.4**	**G1.5**	**G1.6**	**G2.1**	**G2.2**	**G2.4**	**G2.6**	**G2.7**
Plot ID	**L**	**A4**	**B10**	**C9**	**D8**	**E2**	**F10**	**G4**	**H5**	**I10**	**J3**	**K8**
Soil texture		slimy-clay	silty-clay	clayey-silt	clay-silt	clayey-sand	clayey-sand	clay	gravelly sandy	sandy-clay	clay	clayey-silty-sand
Tree cover (%)		**20**	**50**	**10**	**40**	**90**	**95**	**90**	**45**	**50**	**70**	**70**
Herb cover (%)		**85**	**60**	**40**	**80**	**30**	**5**	**20**	**55**	**40**	**60**	**60**
Latitude		**1248794**	**1257012**	**1257311**	**1218922**	**1253160**	**1240105**	**1221167**	**1257039**	**1210750**	**1217472**	**1223930**
Longitude		**318930**	**361057**	**347099**	**341072**	**379056**	**372162**	**333932**	**360984**	**345640**	**342618**	**340064**
Number of species		**37**	**31**	**19**	**23**	**18**	**24**	**28**	**35**	**45**	**46**	**25**
Diagnostic species of Coletum laurifoliae												
Cola laurifolia	A					+	4					
Paullinia pinnata	A					+	+					
Vitex chrysocarpa	A											
Diagnostic species of Terminalietum leiocarpae												
Ampelocissus africana	H											
Ampelocissus bombycina	H											
Combretum micranthum	A							+				
Terminalia leiocarpa	A							4		+		
Diagnostic species of Andropogono gayani-Combretetum glutinosi												
Combretum collinum	A								1	+	+	+
Combretum glutinosum	A								3	+	+	
Commelina benghalensis	H								+			
Ziziphus mucronata	A								+			
Diagnostic species of Andropogono gayani-Terminalietum avicennioidis												
Aspilia bussei	H									+		
Terminalia avicennioides	A		+					+	+	3		
Diagnostic species of Burkeo africanae-Detarietum microcarpi												
Burkea africana	A										3	
Detarium microcarpum	A								+	+	2	
Diagnostic species of *Andropogono gayani-Senegalietum dudgeonii*												
Afrocayratia ibuensis	H											+
Cyperus hortensis	H											3
Echinochloa stagnina	H											+
Senegalia dudgeonii	A		+							+		+
Spermacoce Octodon	H		+		+							+
Other species												
Afzelia africana	A		+									
Allophylus africanus	A					+	+					
Amorphophallus abyssinicus	H									+		
Amorphophallus dracontioides	H							+		+		
Ampelocissus Multistriata	H				+				+			+
Andropogon gayanus	H							1	2	3	2	3
Andropogon schirensis	H	+		+	+							
Andropogon tectorum	H	3				2	1					
Annona senegalensis	A							+	+	1	+	
Asparagus africanus	H	+										
Asparagus africanus	H										+	
Aspilia kotschyi	H	+							+			
Aspilia rudis	H	+	+		+				+		+	+
Balanites aegyptiaca	A	+	+					+	+			
Bombax costatum	A							+		+	+	
Brachiaria deflexa	H				+							
Bridelia ferruginea	A									+		
Chamaecrista mimosoides	H		+	+	+				+			
Chlorophytum stenopetalum	H		+	+	+						+	
Cienfuegosia heteroclada	H				+							
Cissus rufescens	H	+	+								+	+
Cochlospermum planchoni	H									+	+	
Combretum paniculatum	A	+					+					
Commelina benghalensis	H		+									
Commelina erecta	H	+		+								
Corchorus aestuans	H	+										
Corchorus tridens	H				+							
Crinum zeylanicum	H									+		
Crossopteryx febrifuga	A								+	+	+	
Crotalaria macrocalyx	H											
Crotalaria microcarpa	H								+			
Cyperus brevifolius							+					
Cyperus rotundus	H			+	+	+						
Dichrostachys cinerea	A	+	+				+					
Dioscorea dumetorum	H										+	

Plant associations		G1.1	G1.2	G1.3	G1.4	G1.5	G1.6	G2.1	G2.2	G2.4	G2.6	G2.7
Plot ID	**L**	**A4**	**B10**	**C9**	**D8**	**E2**	**F10**	**G4**	**H5**	**I10**	**J3**	**K8**
Soil texture		slimy-clay	silty-clay	clayey-silt	clay-silt	clayey-sand	clayey-sand	clay	gravelly sandy	sandy-clay	clay	clayey-silty-sand
Tree cover (%)		20	50	10	40	90	95	90	45	50	70	70
Herb cover (%)		85	60	40	80	30	5	20	55	40	60	60
Latitude		1248794	1257012	1257311	1218922	1253160	1240105	1221167	1257039	1210750	1217472	1223930
Longitude		318930	361057	347099	341072	379056	372162	333932	360984	345640	342618	340064
Number of species		37	31	19	23	18	24	28	35	45	46	25
Diospyros mespiliformis	A	+					2			+		
Dombeya quinqueseta	A									+	+	
Drimia altissima	H	+								1		
Ekebergia capensis	A										+	
Entada africana	A									+		
Excoecaria grahamii	H	+									+	
Feretia apodanthera	A	+										
Ficus capreifolia	A						+					
Flueggea virosa	H	+						+	+	+		+
Gardenia aqualla	A	+		+				+		+	+	
Gardenia erubescens	A	+						+		+		
Grewia flavescens	A	+						+				+
Grewia lasiodiscus	A							+				
Grewia mollis	A							+				
Gymnosporia senegalensis	H								+	+	+	
Hexalobus monopetalus	A										+	
Hymenocardia acida	H									+	+	
Hyparrhenia involucrata	H				+	+	+					
Hyparrhenia rufa	H	+									+	
Hypoestes cancellata						+	+					
Indigofera paniculata	H			+					+		+	
Indigofera pulchra	H								+		+	
Khaya senegalensis	A						+	+				
Kigelia africana	A						+					
Lannea acida	A							+			0.5	
Mimosa pigra	A						+					
Monechma ciliatum	H	+										
Oncoba spinosa	A						+					
Ozoroa insignis	A				+						+	
Parinari curatellifolia	A	+										
Pericopsis laxiflora	A										+	
Piliostigma thonningii	A	+	+	+		+		+		+	+	+
Pleurolobus gangeticus	H										+	
Prosopis africana	A									+		
Pseudocedrela kotschyi	A											+
Pterocarpus erinaceus	A	+	+					+	+	2	+	+
Raphionacme excisa	H									+		
Rhus natalensis	H							+				
Rottboellia cochinchinensis	H					+						
Securidaca longipedunculata	A									+	+	
Senegalia ataxacantha	A											
Senegalia gourmaensis	A			+				+				+
Sida acuta	H	+								+		
Spermacoce filifolia	H				+				+			
Sporobolus pyramidalis	H				+						+	+
Sterculia setigera	A							+	+		+	
Stereospermum kunthianum	A		+					+	+	+	+	+
Strychnos nigratana	A						+	+	+	+	+	
Stylochaeton hypogaeum	H	+	+									
Stylochaeton lancifolium	H			+	+	+	+			+		+
Syzygium guineense	A											
Tacca leontopetaloides	H	+							+	+	+	
Tamarindus indica	A		+					+				+
Tephrosia bracteolata	H	+	+	+	+				+		+	+
Tephrosia nana	H	+										
Terminalia engleri	H							+		+	2	
Vachellia seyal	A									+		
Vangueria agrestis	H	+								+	+	
Vitellaria paradoxa	A						+					
Vitex doniana	A							+				
Ximenia americana	A						+					+
Ziziphus abyssinica	A		+					+				

agnostic plant species include *Mitragyna inermis*, *Hyparrhenia glabriuscula*, *Merremia aegyptia*, *Hygrophila pobeguinii*, *Mukia maderaspatana*, *Setaria pumila*, and *Sida linifolia*. The species richness was 121 plant species with 86.8% in the herbaceous layer and 13.2% in the tree layer. The average number of plant species per relevé was 38 ± 10.9 species (Table 3).

There was a clear predominance of phanerophytes (40% of abundance and 53% in dominance), hemicryptophytes (31% in abundance) and Sudanian species (24.6% of abundance and 80% in dominance) (Appendix 1).

***Terminalio macropterae-Mitragynetum inermis* Assèdé ass. nova**
Holotypus: Table 4, relevé B10

This association (Table 3, G1.2) of 12 relevés was observed in the northern part of the BRP. The vegetation was tree savanna located on floodplains with temporary inundation. The association was a mixed stand of *Mitragyna inermis* and *Terminalia macroptera*. The soil was a deep silty-clay without gravel. The high soil moisture status was a combined effect of the rainy period and the presence of streams. The flooding period was 3 or 4 months, and the wet period could be extended up to 5 months.

Two layers were identified. The tree layer dominated by *Mitragyna inermis* and *Terminalia macroptera* presented a cover of 25% to 75% and a canopy up to 5 m. The well-developed herbaceous layer was dominated by *Chrysopogon fulvibarbis* with a cover of 50%–85% and a height of 2 m. The diagnostic plant species are *Capparis sepiaria*, *Terminalia macroptera*, and *Tinnea barteri*. In total, 54 plant species were recorded with 83.3% in the herbaceous layer and 17.7% in the tree layer. The average plant species richness per relevé was 33.3±5.3 species (Table 3).

There was a clear predominance of phanerophytes (63% of abundance and 82.5% in dominance). Chorological spectra were dominated by Sudanian plant species (28% of abundance and 87% in dominance) (Appendix 1).

***Sorghastro bipennati-Vachellietum hockii* Assèdé ass. nova**
Holotypus: Table 4, relevé C9

Described from 13 relevés, this association (Table 3, G1.3) was a tree savanna on temporary floodplains. The flooding period does not exceed 2 months (from August to September) and the wet period covers 3 months (from July to October). The soil is a deep clayey-silt.

Two layers were identified. The tree layer dominated by *Vachellia hockii* with an average of 20% to 30% cover presents a canopy up to 5 m height. The herbaceous layer is well-developed with 50%–70% cover and dominated by *Sorghastrum bipennatum* and *Hyparrhenia glabriuscula*. The height of the herbaceous layer is up to 3 m. The diagnostic plant species include *Vachellia hockii*, *Combretum glutinosum*, and *Sorghastrum bipennatum*. The species richness was 53 plant species with 58.5% in the herbaceous layer and 41.5% in the tree layer. The average species richness was 25.3 ± 2.7 species per relevé (Table 3).

There was an abundance of phanerophytes (43%) but a clear dominance of hemicryptophytes (73.7%) and Sudanian plant species (78%) (Appendix 1).

***Brachiario jubatae-Terminalietum macropterae* Assèdé ass. nova**
Holotypus: Table 4, relevé D8

Described from 14 relevés, this association (Table 3, G1.4) was observed in both the northern and southern parts of the BRP. The deep soils have a clay-silt texture without gravel. In the northern part it was observed as a continuum of *Hyparrhenio glabriusculae-Mitragynetum inermis* on drained sites of temporal inundation. In this case the wet period did not exceed 3 months (from July to October). However, in the southern part, *Brachiario jubatae-Terminalietum macropterae* was observed on the floodplain directly associated with a stream. The soil moisture status in this case was more related to the proximity of the stream with the flooding period extending to 5 months (from July to November). Along a moisture gradient, *Brachiario jubatae-Terminalietum macropterae* represented the transition from the floodplain to dryland plant communities.

The association was a tree savanna on wetlands. Physiognomically, this association covers 30%–50% on average with 5 m–7 m height. The tree layer was composed of *Terminalia macroptera*. The herbaceous layer was dominated by *Hyparrhenia glabriuscula* and *Brachiaria jubata* with 60%–90% cover. The height of the herbaceous layer was around 2 m. The diagnostic plant species include *Brachiaria jubata*, *Paspalum scrobiculatum*, and *Ludwigia octovalvis*. The species richness was 64 with 10.6% of species in the tree layer and 89.4% in the herbaceous layer. An average of 29.8±4.1 species were recorded per relevé (Table 3).

Even if phanerophytes were the most represented in the association (51% of abundance), hemicryptophytes (60% in dominance) and Sudanian species (83.5% in dominance) were the most important (Appendix 1).

***Borassetum aethiopi* Assèdé ass. nova**
Holotypus: Table 4, relevé E2

This association (Table 3, G1.5) was described from 11 relevés. It represented one of the most important ecosystems in the northern part of the BRP. It is located along the Pendjari River and in the temporary inundated floodplain (drained sites). The soil is a clayey-sand without gravel.

The association was a woodland of less than 15 m height. The canopy cover was closed with a 70–90% tree cover on average dominated by *Borassus aethiopum*, *Kigelia africana* and *Combretum paniculatum*. A well-developed understory layer with cover of up to 60% or more in some places is dominated by *Borassus aethiopum* regeneration. The diagnostic plant species include *Hypoestes aristata*, *Morelia senegalensis*, *Borassus aethiopum*, *Pterocarpus santalinoides*, *Strophanthus sarmentosus*, *Ipomoea blepharophylla*, and *Neocarya macrophylla*. In total, 43 plant species were recorded with the most present in the herbaceous layer (56%). Trees and lianas contributed 44%

and 9% of total richness respectively. The average species richness was 23.7 ± 2.4 plant species per relevé (Table 3).

Phanerophytes (56% of abundance and 45% in dominance) and hemicryptophytes (47% in dominance) were the predominant life forms. Sudanian species were the dominant plant species (46.6%), while Sudano-Guinean species were the abundant plant species (24.4%) (Appendix 1).

***Coletum laurifoliae* Mahamane ex Assèdé ass. nova**
Holotypus: Table 4, relevé F10

Synonym: *Coletum laurifoliae* Mahamane 2005 nom. inval. (Art. 1)

Coletum laurifoliae (Table 3, G1.6) corresponded to a riparian forest of *Cola laurifolia* represented by 12 relevés along the Pendjari River in the northern part of the BRP. Geomorphologically, this association occurs mainly along the Pendjari River, at the riverine end of the riparian forest with frequent inundation. The flooding period exceeds 6 months (from July to December). The soil is a deep clayey-sand without gravel.

Coletum laurifoliae was a continuous stand of trees at least 10 m tall, with crowns of adjacent trees touching each other. Three layers were distinguished. The tree layer with cover 80–90% on average was dominated by *Cola laurifolia*, *Diospyros mespiliformis*, *Kigelia africana* and *Khaya senegalensis*. The shrub layer with 10% cover was dominated by *Mitragyna inermis*, *Paullinia pinnata*, *Oncoba spinosa*. The herbaceous layer was sparse (with 5% of total cover and sometimes absent) and represented by *Syzygium guineense*, *Cissus rufescens* and *Paspalum scrobiculatum*. The diagnostic plant species are *Cola laurifolia*, *Vitex chrysocarpa*, and *Paullini pinnata*. The appearance of the association was mainly shaped by trees and liana species. Trees and lianas contributed 36% and 15.4% of total richness respectively. In total, 39 plant species were recorded with an average of 24.3±2.4 species per relevé (Table 3).

There was a clear predominance of phanerophytes (64.1% of abundance and 88.1% in dominance). Sudano-Guinean plant species were the most dominant plant species in this vegetation type (58%) (Appendix 1).

Association of drylands

***Terminalietum leiocarpae* Mahamane ex Assèdé ass. nova**
Holotypus: Table 4, relevé G4

Synonym: *Anogeissetum leiocarpae* Mahamane 2005 nom. inval. (Art. 1)

The description of *Terminalietum leiocarpae* (Table 3, G2.1) is based on 14 woodland relevés from the Pendjari National Park (the core zone) and the Pendjari hunting zone of the BRP (Figure 1). The most important stand was observed in the core zone of the BRP and located on a plateau. The soil was deep clay without gravel. There is an important deposit of organic matter on the topsoil.

The tree layer entirely dominated by *Terminalia leiocarpa* was characterised by a 75%–85% cover on average and 12 m to 17 m height. The physiognomy of the understory layer was heterogeneous but dominated by liana species, sometimes with a cover of less than 40%. However, a shrub layer dominated by *Combretum micranthum* can be identified with 10% cover. The very sparse herbaceous layer was represented by *Wissadula rostrata* and *Ampelocissus africana*. The diagnostic plant species are *Terminalia leiocarpa* and *Combretum micranthum*. In total, 136 plant species were recorded with 47.7% tree species. The average species richness was 41 ± 11.2 species per relevé (Table 3).

There was a clear predominance of phanerophytes (55.4% of abundance and 79.8 in dominance) and Sudanian species (33.7% of abundance and 89.1% in dominance) (Appendix 1).

***Andropogono gayani-Combretetum glutinosi* Mahamane ex Assèdé ass. nova**
Holotypus: Table 4, relevé H5

Synonym: *Andropogono-Combretum glutinosae* Mahamane 2005 nom. inval. (Art. 1)

Andropogono gayani-Combretetum glutinosi (Table 3, G2.2) was described from 20 relevés. In the BRP, this association colonized shrub or grass savanna. The association was observed on trays battleships with gravelly sandy soils and low soil drainage.

Physionomically, *Andropogono gayani-Combretetum glutinosi* presented two clearly different forms: a scrub savanna with an average tree cover of 10% and a tree savanna with 20%–40% tree cover on average. Sometimes, the tree savanna cover could reach 75%. In any case, the tree layer is above 2.5 m height, dominated by *Combretum collinum*, *C. glutinosum*, *C. nigricans* and *Terminalia avicennioides*. The structure of the herbaceous layer remains homogeneous for the two tree cover types with 40%–65% cover and 2 m to 2.5 m height. The herbaceous layer was dominated by *Andropogon gayanus*. The diagnostic plant species include *Combretum glutinosum*, *C. collinum*, and *Commelina benghalensis*. In total, 81 plant species were recorded with an average of 37.9 ± 6.7 per relevé (Table 3). The association was predominated by phanerophytes (59.2% of abundance and 76% in dominance) and hemicryptophytes (16.2% in dominance). The chorological types were dominated by Sudanian species (36% of abundance and 65% in dominance) (Appendix 1).

***Andropogono-gayani-Terminalietum avicennioidis* Ouédraogo ex Assèdé ass. nova**
Holotypus: Table 4, relevé I10

Synonym: *Andropogono-Terminalietum avicennioidis* Ouédraogo 2009 nom. inval. (Art. 1)

Andropogono gayani-Terminalietum avicennioidis (Table 3, G2.4), described from 12 tree savanna relevés, defined the physiognomy of the Pendjari hunting zone (Figure 1). It is the most common vegetation unit in the hunting zone of the BRP but was also observed in the northern part of the reserve. It occurs on the plateau and soil is deep sandy-clay.

Two layers were clearly identified. The tree layer was dominated by *Terminalia avicennioides* and *Pterocarpus erinaceus* with a 40–50% cover on average. The canopy is up to 5 m height. The well-developed herbaceous layer was dominated by *Andropogon gayanus* and *Hyparrhenia involucrata* with a cover of up to 100% or more. A shrub layer with less than 5% cover can be identified with *Combretum glutinosum*, *Gardenia erubescens*, and *Gardenia ternifolia* as dominant plant species. The diagnostic plant species are *Terminalia avicennioides*, *Aspilia bussei* and *Dioscorea abyssinica*. In total, 65 species were recorded with 12.5% in the tree layer and 87.5 in the understory layer. The average species richness was 38.3 ± 5.6 species per relevé (Table 3). The association was characterised by the predominance of phanerophytes (68.2% of abundance and 58% in dominance) and hemicryptophytes (68.2% of abundance and 58% in dominance). The chorological types were dominated by Sudanian species (34% of abundance and 78.2% in dominance) (Appendix 1).

***Burkeo africanae-Detarietum microcarpi* Mahamane ex Assèdé ass. nova**
Holotypus: Table 4, relevé J3

Synonym: *Burkeo-Detarietum microcarpae* Mahamane 2005 nom. inval. (Art. 1)

Burkeo africanae-Detarietum microcarpi (Table 3, G2.6) was described from 20 tree savanna relevés from the Pendjari National Park and Pendjari hunting zone of the BRP (Figure 1). It was distributed on the hill slopes with quartzitic sandstone boulders and stones of variable size, on saxicolous, flagstone or rocky ferruginous soils. The presence of crevices promotes the creation of microhabitats with the accumulation of plant debris important for species establishment. This substrate type is characterised by a strong surface flow during the rainy season. In the dry season, it is part of the first fire prone vegetation.

This association has two dominant layers and a canopy of 5 m to 10 m height. The tree layer with a 40–50% cover on average is dominated by *Detarium microcarpum*, *Burkea africana*, *Vitellaria paradoxa*, *Pteleopsis suberosa*, *Sterculia setigera* and *Combretum glutinosum*. The herbaceous layer is dominated by *Andropogon gayanus*, *Hyparrhenia rufa*, *Hyparrhenia involucrata* and *Indigofera pulchra* with 45% to 85% cover. The diagnostic plant species are *Burkea africana* and *Detarium microcarpum*. A total of 94 plant species were recorded. The average species richness was 39.4 ± 7.8 plant species per relevé (Table 3). The association was dominated by phanerophytes (54.1% of abundance and 68.7% in dominance), Sudanian species (31.2% of abundance and 40% in dominance) and Sudano-Zambesian species (31.2% of abundance and 51.1% in dominance) (Appendix 1).

***Andropogono gayani-Senegalietum dudgeonii* Assèdé ass. nova**
Holotypus: Table 4, relevé K8

Andropogono gayani-Senegalietum dudgeonii (Table 3, G2.7), described from 15 relevés of scrub savanna, marked a transition between the floodplain and the dryland group of plant communities in terms of change in soil moisture and texture. The soil is clayey-silty-sand with little or without gravel.

The canopy of 2 m to 4 m height was preferentially dominated by a shrub layer of small trees of *Senegalia dudgeonii*, *Pseudocedrela kotschyi* and *Senegalia gourmaensis*. The tree cover varies between 40% and 50% on average. The herbaceous layer of up to 70% and more covers 2 m to 2.5 m height dominated by *Aspilia rudis*, *Tephrosia bracteolata* and *Ampelocissus multistriata*. The diagnostic plant species include *Cyperus hortensis*, *Senegalia dudgeonii*, *Spermacoce octodon*, *Echinochloa obtusiflora* and *Afrocayratia ibuensis*. In total, 33 plant species were recorded with 18.2% in the tree layer and 81.8% in the herbaceous layer. The average species richness was 24 ± 2.1 species per relevé (Table 3).

The association was characterised by the predominance of phanerophytes (63.6% of abundance and 49.4% in dominance) and hemicryptophytes (46.3% in dominance). The chorological types were dominated by Sudanian species (36.4% of abundance and 90.2% in dominance) (Appendix 1).

Soil groups and soil parameters of associations
Table 5 shows the distribution of the eleven (11) defined plant associations over eight of the ten soil groups of the BRP (Figure 4). Soil group B, typically associated with the Pendjari River, is poorly developed with hydromorphic intake on river sand. It supports the associations of riparian forests (G1.5 and G1.6) with low clay (3%) and high sand (47%) content. The floodplain associations (G1.1, G1.2, G1.3 and G1.4), with neutral pH_{water}, important organic matter (OM) and organic carbon (OC) contents (4.3% and 2.5% respectively), were associated with soil groups I and C, characterised by their hydromorphy. Plant associations on rocky soil (G2.6) were located on raw mineral soils of lithic erosion on armor (soil group G) and rocky outcrops or sub-outcrops (soil group H) with a low clay and silt content. Ferruginous (soil groups A, F and E) and ferralitic soils (soil group D) shared the plant association of the plateau (G2.1, G2.4, and G2.7). They have a high sand content (up to 70%) with very low OM and enough clay contents (1.1% ≤ OM ≤ 1.6%; 15.25 ≤ clay ≤ 21.50).

Discussion

Vegetation

The vegetation of the Sudanian zone was in general a mosaic of woodland, savanna and riparian forest with a predominance of savanna ecosystems (White 1983). The Biosphere Reserve of Pendjari (BRP) was a typical example with a clear predominance of savanna ecosystems (CENAGREF 2016). The flora of wetland associations was very different from that of dryland associations. Many plant species colonising the dryland had great ecological amplitude. The transition zone between plant communities was large enough to allow the coexistence of similar plant communities even when the geomorphological conditions were quite distinct. Soil mois-

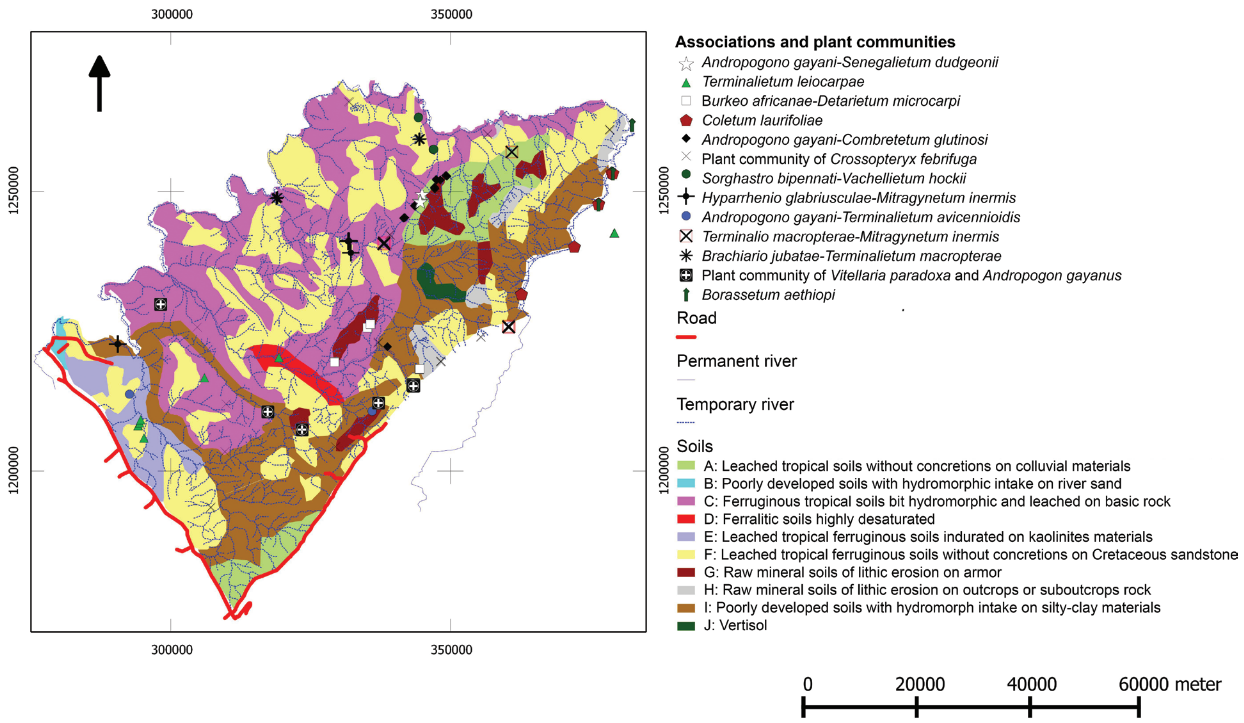

Figure 4. Map of the plant associations distribution in relation to soil types in the Biosphere Reserve of Pendjari.

Table 5. Site characteristics of the identified plant associations in terms of soil groups and physico-chemical parameters of the soils. G1.1: *Hyparrhenio glabriusculae-Mitragynetum inermis*; G1.2: *Terminalio macropterae-Mitragynetum inermis*; G1.3: *Sorghastro bipennati-Vachellietum hockii*; G1.4: *Brachiario jubatae-Terminalietum macropterae*; G1.5: *Borassetum aethiopi*; G1.6: *Coletum laurifoliae* ; G2.1: *Terminalietum leiocarpae*; G2.2: *Andropogono gayani-Combretetum glutinosi*; G2.3: Plant community of *Crossopteryx febrifuga*; G2.4: *Andropogono gayani-Terminalietum avicennioidis*; G2.5: Plant community of *Vitellaria paradoxa* and *Andropogon gayanus*; G2.6: *Burkeo africanae-Detarietum microcarpi*; G2.7: *Andropogono gayani-Senegalietum dudgeonii*.

Associations	Soil groups	pH_{water}	pH_{KCl}	Particle size % Coarse silt	% Silt	% Clay	% sand	% Coarse sand	% OM	% OC	% N total	C/N
G1.5	B	6.75	6.48	18.25	12.25	22.50	27.00	20.00	2.88	1.67	0.087	19.21
G1.6	B	6.75	6.48	18.25	10.5	33.50	25.00	23.00	2.00	1.5	0.077	19.5
G1.2	IC	7.00	6.78	11.50	14.50	27.50	16.10	31.40	4.25	2.50	0.102	24.51
G1.4	I	7.00	6.70	11.50	16.50	25.50	17.10	29.40	4.15	2.51	0.100	25.10
G1.3	C	7.00	6.75	11.50	15.50	26.50	17.10	30.70	4.35	2.49	0.101	24.65
G1.1	C	7.00	6.78	11.50	14.50	28.50	17.10	30.40	4.55	2.52	0.102	24.71
G2.7	A	6.70	6.50	3.75	3.25	15.75	29.00	48.25	1.60	0.93	0.056	16.54
G2.4	GE	7.04	6.78	18.50	9.25	15.25	44.75	12.25	1.1	0.66	0.049	13.54
G2.6	GH	6.98	6.73	10.25	12.75	18.25	34.25	24.50	2.65	1.54	0.074	20.75
G2.1	D	6.68	6.40	11.75	1.00	21.50	50.25	15.50	1.40	0.81	0.067	12.12
G2.2	C	6.82	6.58	17.25	5.50	21.50	39.30	16.45	1.82	1.06	0.07	15.10

ture seems to be one of the main ecological parameters which determines the distribution of plant associations in the BRP. Various associations derived from this study showed a specialisation of wetland species compared to dryland species. Different studies carried out in the protected areas close to the BRP, in particular the W National Park of Niger (Mahamane 2005), the National Park of Arly (Ouédraogo 2009) and the W National Park of Burkina Faso (Nacoulma 2012), came to the same conclusions. The similarity between the National Park of Arly and the BRP was of note. In addition to sharing 54% of their floristic richness, 79% of the BRP families and 61% of the BRP genera were recorded in Arly National Park (Assédé et al. 2012). This study emphasized the fidelity of the species for an ecosystem type. The relevance of this assertion was demonstrated through four associations (*Coletum laurifoliae*, *Burkeo africanae-Detarietum microcarpi*, *Terminalietum leiocarpae*, *Andropogono gayani-Terminalietum avicennioidis*) described in the three reserves of WAP complex (the W National Park, the National Park of Arly and the Biosphere Reserve of Pendjari). The same comparison could be possible with the W National Park of Niger and the W National Park of Burkina Faso. Despite the lack of a comparison of the smaller basic units of the vegetation, a global analysis of the different components of these two protected areas with the BRP (Thiombiano 1996; Hahn-Hadjali 1998; Wittig et al. 2000; Inoussa et al. 2011; Assédé et al. 2012) showed the similarity between plant association distributions along the topographical and hydrological gradients within the same phytogeographical zone. *Hyparrhenio glabriusculae-Mitragynetum inermis* would present a sub-association or variant. However, this study did not provide sufficient information or data to confirm this observation.

One of the shortcomings of this study was the absence of defined pond associations given the presence of a well-developed pond ecosystem network in the study area. The floristic patterns of the dry season were also not investigated in this study, which would have allowed for a better comparison of plant patterns between the dry and wet seasons. Further studies are therefore necessary to address these shortcomings.

Soil

Soil properties are factors determining the distribution of plant associations. If at the regional scale the climate appeared as the key factor in the plant association distribution, the distribution of plant associations on a local scale would be more related to soil conditions. However, soil conditions were directly related to topography, which is one of the main environmental factors structuring floristic diversity (Asefa et al. 2020). The topography is a result of the underlying geology and the geomorphology of the landscape. The consequences of that are soil nutrient status is related to the geology, and drainage patterns are related to the geomorphology, geology and climatic variables (including amount and seasonality of rainfall, temperature regime, wind patterns around topographic barriers driving fires, drying out of the system). From the perspective of Daws et al. (2002) and Seibert et al. (2007), the topography represented the major factor explaining the hydrological and edaphical processes. According to Wilson et al. (2004), topography explains between 26% and 64% of the variation of soil moisture. In the BRP, the landscape physiography (which includes topography, slope aspect) and substrate conditions are important because they determine the drainage patterns (Okou et al. 2014), and define the distribution and structuring of the plant communities (Assédé et al. 2015; Diwediga et al. 2015). Thus, soil moisture regimes could be the main factors discriminating the plant associations. For example, the distribution of the sample plots within the *Burkeo africanae-Detarietum microcarpi* could be explained by topographic differences. *Burkea africana* was observed in two soil types. On saxicolous rocky soils, the species was associated with *Detarium microcarpum*, but the latter species was absent when *B. africana* was established on a plain with clay soils without gravel. In the BRP, subtle differences in drainage patterns associated with micro-topography that are not always obvious or clear with general observation would exist.

However, topography was not the main determinant for all defined associations and plant communities identified in this study. A good example is the plant community of *Crossopteryx febrifuga*. The central position of the broad groupings in Figure 3C could explain their aptitude to colonise either saxicolous or plain soils. Soil moisture status was determinant for the establishment of some plant species (Assédé et al. 2015; Stocker et al. 2018). For example, *Coletum laurifoliae*, *Borassetum aethiopi* and *Hyparrhenio glabriusculae-Mitragynetum inermis* colonised only the riparian forests and the floodplains. On a finer scale, in addition to the micro-topography, the physicochemical properties of the soil may influence this distribution of plant associations (Ouédraogo 2009; Nacoulma 2012). Even if statistical analysis were performed to highlight the relation between physicochemical properties of the soil and plant associations, their distribution in relation to soil groups of the BRP was in some way a demonstration of this relationship.

From another perspective of analysis and understanding, the development of the plant associations, their actual composition and distribution was very much determined by disturbance factors and regimes, which was not easy to evaluate in the context of the BRP. The two mains disturbance factors are fire regime and elephant impact on plant communities. In the context of the BRP, fire regime appeared to be a very critical factor and may even override the soil moisture factor. It is therefore necessary to establish the relationship between the fire regime and the distribution of plant associations in the BRP.

Syntaxonomic relationships of the associations

The syntaxonomic classification of the identified association was presented under the hierarchical structure (class, orders and alliance) of edaphic forest and savanna formations occurring in West and Central Africa. Thus far, in the BRP such a general system of plant communities' classification was not available.

Mitragynetea

All tropical African riparian forests belong to the *Mitragynetea* Schmitz 1963, (Schmitz 1971, 1988). As for gallery forests of the Congo basin (Lebrun and Gilbert 1954), riparian forest of Benin has either a Guinean or Sudanian-Zambesian tendency (Natta et al. 2003). In Benin the most frequent plants of the *Mitragynetea* are *Pterocarpus santalinoides*, *Cola laurifolia*, *Syzygium guineense*, *Dialium guineense*, *Morelia senegalensis*, *Parinari congensis*, *Manilkara multinervis*, *Phaulopsis barteri*, *Taccazea apiculata*, *Achyranthes aspera*, *Afzelia africana*, *Xylopia parviflora*, and *Antidesma venosum*. Within this class Mahamane (2005) described *Coletalia laurifoliae* and *Colion laurifoliae*.

Mahamane (2005) described the association of *Cola laurifolia* as characteristic of *Colion laurifoliae* along the banks of the Mékrou river in the National Park of W of Niger, with *Cola laurifolia*, *Paullinia pinnata*, *Vitex chrysocarpa*, *Taccazea apiculata*, *Morelia senegalensis*, *Sesbania sesban*, *Pterocarpus santalinoides* as characteristic species.

Mahamane (2005) defined in W National Park of Niger an association of *Celtis toka* and *Borassus aethiopum* along Niger river. This association, dominated by *Borassus aethiopum*, occurs in the same habitat type (riparian forest) with *Borassetum aethiopi* defined in the BRP. However, the Mahamane (2005) did not list the characteristic species of the association.

Based on field data, similarities of ecological conditions and floristic composition, the riparian forest associations (*Coletum laurifoliae* and *Borassetum aethiopi*) are classified into *Coletalia laurifoliae* and *Colion laurifoliae*.

Mahamad (2005) defined in W National Park of Niger *Mitragynetalia inermis* in flooded areas relatively far from the rivers. *Mitragyna inermis* forms a hydrophilic forest. It is developed along the marshy shores and wet soils. The topographic level of the habitat is low, allowing the formation of wide forest with *Mitragyna inermis* as the dominant tree species. The characteristic species are *Mitragyna inermis*, *Kigelia africana*, *Pseudocedrela kotschyi* and *Crateva adansonii* (Mahamane 2005). The *Mitragynion inermis* is a characteristic alliance. The characteristic species of the alliance are the same as those of the order.

Mitragynion inermis Mahamane 2005 includes riparian forests from 50 to 150 m wide and 5 m height. *Mitragynetum inermis* is characteristic of *Mitragynion inermis*.

Hyparrhenio glabriusculae-Mitragynetum inermis described on flooded plains in this study is grouped into *Mitragynetalia inermis* and *Mitragynion inermis*.

***Hyparrhenietea* Schmitz 1963**

This class includes the non-steppe savannas, mainly of the Sudano-Zambezian zone, both grassy shrubby and wooded (Schmitz 1988). This class is recognized by many authors in Ghana (Jenik and Hall 1976), in tropical secondary vegetation (Hoff and Brisse 1983) and in most of the tree savannas of *Isoberlinia doka* (Houinato 2001) in Sudanian woodland. In the herb layer, the most common species are *Andropogon gayanus*, *A. schirensis* and *A. chinensis*. In the BRP, the herb layer is dominated by *Andropogon gayanus* var. *bisquamulatus*, *Hyparrhenia rufa*, *H. glabriuscula* and *H. involucrata*. Within this class *Andropogonetalia gayani* var. *bisquamulati* Sinsin 1994 was described as shrubby, tree savannas and savanna woodlands on alluvial deposit in depression or dry land.

The characteristic species are *Andropogon gayanus* var. *bisquamulatus*, *Ischaemum amethystinum*, *Euclasta condylotricha*, *Brachystelma togoensis*, *Panicum nervatum*, *Sapium grahamii* and *Brachiaria falcifera*.

Several alliances are included in this order (Sinsin 1994). *Hyparrhenio-Andropogonion tectorum* Sinsin 1994 is presented on hydromorphic or filter soils. The characteristic species include *Hyparrhenia rufa*, *Andropogon tectorum*, *Sorghastrum bipennatum*, *Sapium grahamii*, *Aneilema paludosum*, *Amorphophallus abyssinicus* and *Indigofera nigritana*.

Acacietum dudgeoni Mbayngone 2008 is described in the Partial Fauna Reserve of Pama in Burkina Faso with *Acacia dudgeonii* as dominant and the characteristic species. The association is established on silt-sandy, clay-sandy or sand-silty and gravelly soils. Based on floristic component and soil type, *Acacietum dudgeoni* and *Andropogono gayani-Senegalietum dudgeonii* are similar. The main difference is the dominant species of the herbaceous layer. *Andropogon pseudapricus*, dominant in *Acacietum dudgeoni*, is replaced by *Andropogon gayanus* Kunth. in *Andropogono gayani-Senegalietum dudgeonii*. Thus, *Andropogono gayani-Senegalietum dudgeonii* is positioned in *Andropogonetalia gayani* var. *bisquamulati*. However, it is not part of *Hyparrhenio-Andropogonion tectorum* (because soils are dry), nor *Schizachyrio-Loxoderion ledermanii* (because none of the characteristic species of this alliance are part of the floristic component of *Andropogono gayani-Senegalietum dudgeonii*). *Andropogono gayani-Senegalietum dudgeonii* could be included in *Andropogono-Crossopterygion* Duvigneaud (1949) Schmitz 1988 of savannas on heavy, compact or gravelly soils like *Acacietum dudgeonii*.

Andropogono gayani-Terminalietum avicennioidis was firstly described in the National Park of Arly (Burkina Faso). Established on sandy and deep soil with roughly neutral pHeau, *Terminalia avicennioides* is the main characteristic species. The association is positioned in *Andropogonetalia gayani* var *bisquamulati* and *Hyparrhenio-Andropogonion tectorum*.

The plant community of *Terminalia macroptera* and *Vachellia sieberiana* is described in the BRP by Delvingt et al. (1989) on floodplains with *Terminalia macroptera* and *Vachellia sieberiana* as dominant and characteristic species. *Brachiario jubatae-Terminalietum macropterae* defined in this study, and the plant community of *Terminalia macroptera* and *Vachellia sieberiana*, are observed in the same habitat with *Terminalia macroptera* as dominant tree species. They colonised the depressions with hydromorphic clay soils. Even if *Vachellia sieberiana* is present in *Brachiario jubatae-Terminalietum macropterae*, it is not a characteristic species. The floristic composition and the diagnostic species of *Brachiario jubatae-Terminalietum macropterae* make it possible to differentiate this association.

Similar associations to *Terminalio macropterae-Mitragynetum inermis* are observed in the same habitat types in West Africa. In the BRP, Delvinght et al. (1989) defined the association of *Vachellia sieberiana* and *Mitragyna inermis* on floodplains. In Burkina Faso, Guinko (1984) described *Mitragyna inermis* and *Crateva adansonii* plant community in the Sudanian woodland as a continuation of the *Cola laurifolia* and *Morelia senegalensis* association along riparian zones. *Crateva adansonii* and *Mitragyna inermis* are the remarkable elements of this continuum. *Terminalio macropterae-Mitragynetum inermis* can be a variant of the plant community of *Mitragyna inermis and Crateva adansonii*. The two plant communities are observed as a continuum of *Cola laurifolia* along riparian forest. They are also dominated by *Mitragyna inermis* in their tree layer. However, the abundance of *Terminalia macroptera* within *Terminalio macropterae-Mitragynetum inermis* could justify the difference.

Brachiario jubatae-Terminalietum macropterae and *Terminalio macropterae-Mitragynetum inermis* are included in *Andropogonetalia gayani* var *bisquamulati* and *Terminalio-Schizachyrion sanguinei*.

The *Schyzachirio-Burkion africanae* Nasi 1994 alliance belongs to rocky soil. A variant is described by Nasi (1994) on the Manding plateau and the Sudanian region. The affected stations are burned annually. The plant community of *Burkea africana* and *Detarium microcarpum* was first described by Sokpon et al. (2001) on skeletal soil in the hunting zone of the BRP. *Burkeo africanae-Detarietum microcarpi* was firstly isolated in W National Park of Niger (Mahamane 2005). The same association was then described in the same habitat types in Arly National Park (Ouédraogo 2009) and W National Park of Burkina Faso (Nacoulma 2012) with three common characteristic species: *Burkea africana*, *De-*

tarium microcarpum and *Combretum glutinosum*. *Burkeo africanae-Detarietum microcarpi* belong to *Andropogonetalia gayani* var *bisquamulati* and *Schyzachirio-Burkion africanae*.

Acacietalia seyal Mahamane 2005 is an order of the Sudanian zone, but typical of the Sahelian transition zone defined by White (1983). In the Sudanian zone, *Acacietalia seyal* is characteristic of waterlogged depressions. The soil is clay (generally greater than 50% content), with significant cracks in the dry season (Dos Santos 1981; Djitèye 1988). *Acacion seyal* Mahamane 2005 is characteristic of *Acacietalia seyal*.

Acacion seyal is defined to group the vegetation on low soil at the end of the slope. The characteristic species are *Acacia seyal*, *Cadaba arinose*, *Pterocarpus erinaceus* Poir, *Cordia cinensis*, *Acacia amythethophylla*, *Vachellia hockii* and *Gymnospora senegalensis*. *Acacietum* seyal is characteristic of *Acacion seyal*. *Acacio-Sorghastretum bipennatae*, described in this study, is positioned in *Acacietalia seyal* and *Acacion seyal*.

Combretetalia micranthi Mahamane 2005 is defined to group the vegetation on plains. The soils are battleships and their slopes correspond to the primary savannas. The characteristic species are *Combretum nigricans*, *Combretum micranthum*, *Guiera senegalensis*, *Boscia senegalensis* and *Boscia angustifolia*. *Combretion micranthi* Mahamane 2005 is characteristic of *Combretetalia micranthi*. *Combretion micranthi* is created to bring together plant communities on the plains and slopes of the Sudano-Sahelian transition zone. The characteristic species are *Combretum micranthum*, *Cassia sieberiana*, *Grewia flavescens*, *Grewia fabreguesii*, *Senegalia ataxacantha*, *Acacia macrostachya* and *Acacia erythrocalyx*. *Andropogono gayani-Combretetum glutinosi* was first described in the National Park of W (Mahamane 2005) in typical gravelly sandy soil with the same characteristic species. *Andropogono gayani-Combretetum glutinosi* is grouped in the *Combretion micranthi* alliance, *Combretetalia micranthi* order and *Hyparrhenietea* class.

Erythropleetea africani

Erythropleetea africani Schmitz 1963 groups woodlands of the Sudano-Zambezian zone. It is composed of *Julbernardio-Brachystegietalia spiciformis* Schmitz 1988 (for woodland of the Zambezian zone) and *Lophiretalia lanceolatea* Lebrun and Gilbert 1954 (for woodland of the Sudanian zone). Houinato (2001) defined *Anogeission leiocarpae* as an alliance of *Lophiretalia lanceolatae* in Monts Kouffé (Benin). The characteristic species include *Isoberlinia doka*, *Isoberlinia tomentosa*, *Uapaca togoensis*, *Detarium senegalense*, *Lophira lanceolata*, *Monotes kerstingii*, *Parkia biglobosa*, *Vitellaria paradoxa* and *Parinari kerstingii*. *Anogeission leiocarpae* Houinato 2001 includes dry deciduous forest of the Sudanian zone. These forests are found in the area of tropical woodland of *Isoberlinia doka*, with occasional Guinean plant species of primary and secondary forests of *Erythropleetea africani*. The characteristic species are *Terminalia leiocarpa*, *Aframomum alboviolaceum*, *Allophylus africanus*, *Holarrhena floribunda*, *Terminalia laxiflora*, *Paullinia pinnata*, *Pouteria alnifolia*, *Anchomanes difformis*, *Diospyros mespiliformis*, *Cola gigantea*, *Albizia ferruginea*, *Crateva adansonii*, *Ceiba pentandra*, *Manilkara obovata* and *Smilax anceps*.

Terminalietum leiocarpae is positioned in *Lophiretalia lanceolatea* Lebrun and Gilbert 1954 and *Anogeission leiocarpae* Houinato 2001.

Conclusion

Vegetation in the BRP was common to the Sudanian zone within two groups: the wetland vegetation and the dryland vegetation. The two groups belong to eleven (11) newly described plant associations with a clear predominance of savanna ecosystems. If the topography was one of the determinant parameters of the distribution of the plant associations, soil moisture would be one of the main ecological parameters which determine the establishment of plant species and through them, the plant associations.

Data availability statement

The data is not available online, but they are available from the corresponding author of the manuscript on request.

Author contributions

E.S.P.A., S.S.H.B. and B.S. formulation of the research ideas and coordination of data collection and manuscript writing. H.O., M.O., J.C.G. and P.W.C. assisted in data analysis and proof editing.

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Appendix 1

Unweighted and weighted spectra of life forms and chorological types of syntaxa defined in Sudanian woodland of Benin.

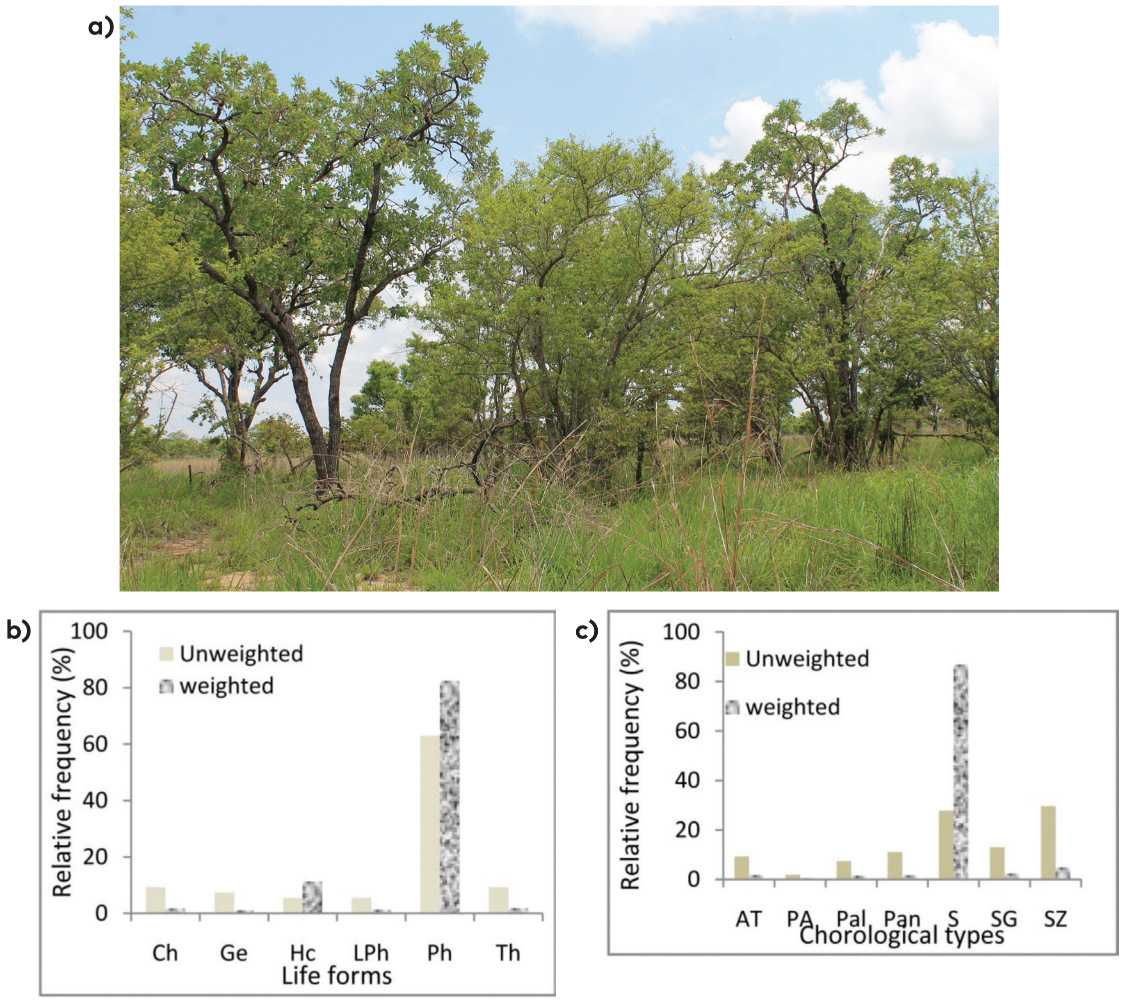

Figure A1. *Terminalio macropterae-Mitragynetum inermis*. **a)** Photo of tree savanna of *Terminalio macropterae-Mitragynetum inermis* located on floodplain with temporary humidity; **b)** Life form spectra; **c)** Chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

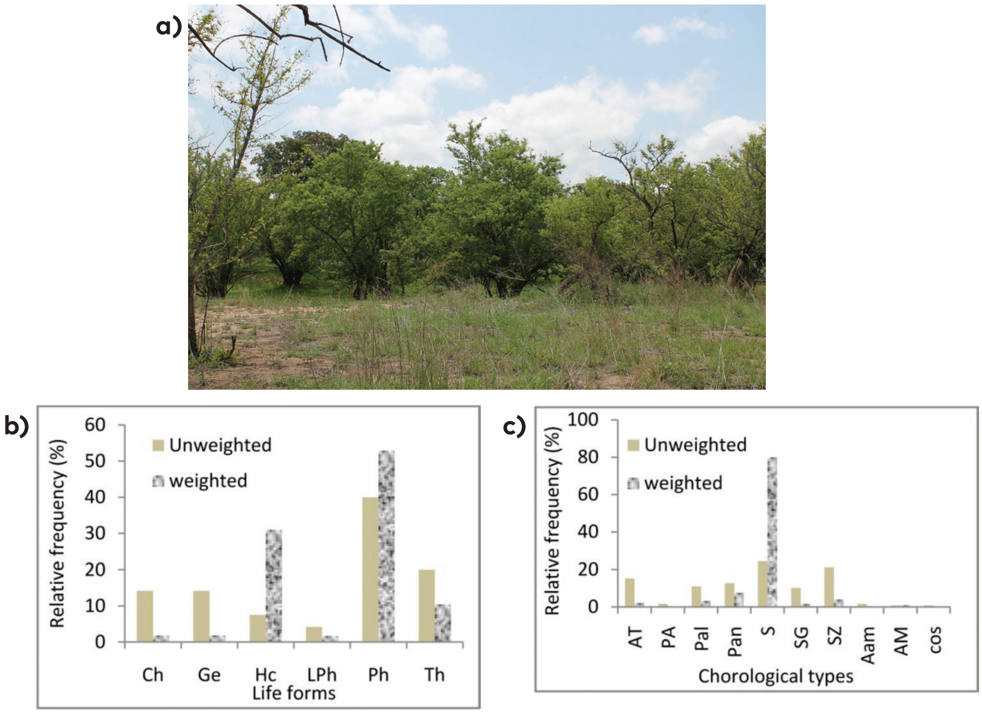

Figure A2. *Hyparrhenio glabriusculae-Mitragynetum inermis*. **a)** Photo of tree savanna of *Hyparrhenio glabriusculae-Mitragynetum inermis* located on floodplain with temporary humidity; **b)** Life form spectra; **c)** Chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

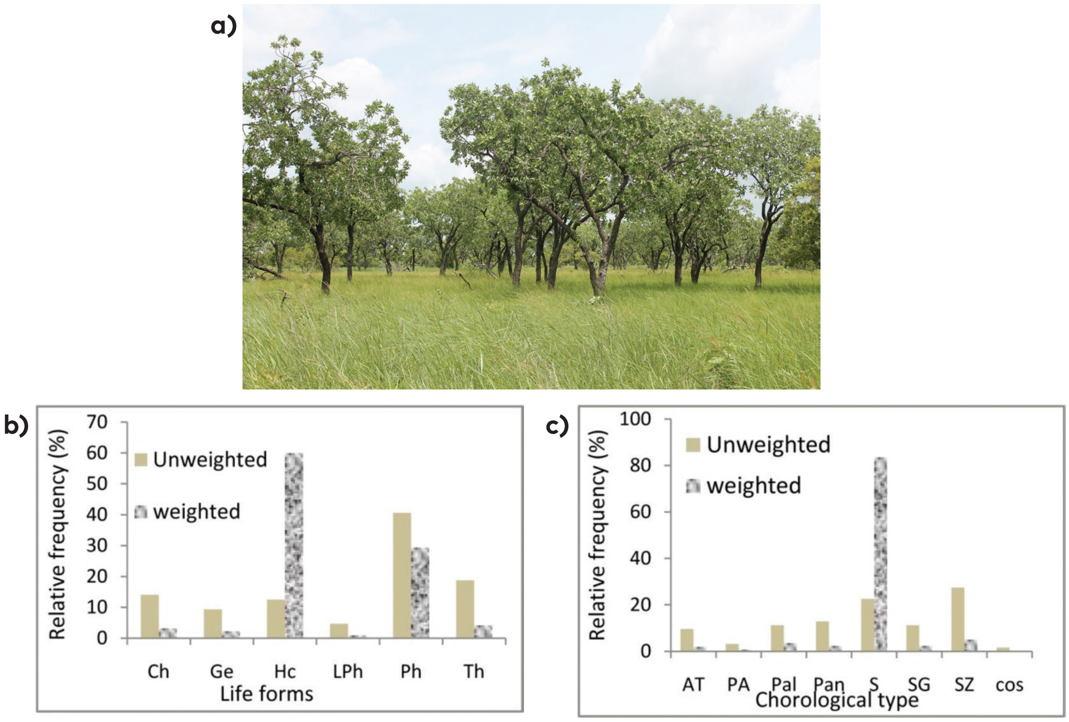

Figure A3. *Brachiario jubatae-Terminalietum macropterae*. **a)** Photo of tree savanna of *Brachiario jubatae-Terminalietum macropterae* located on floodplain with temporary humidity; **b)** Life form spectra; **c)** Chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

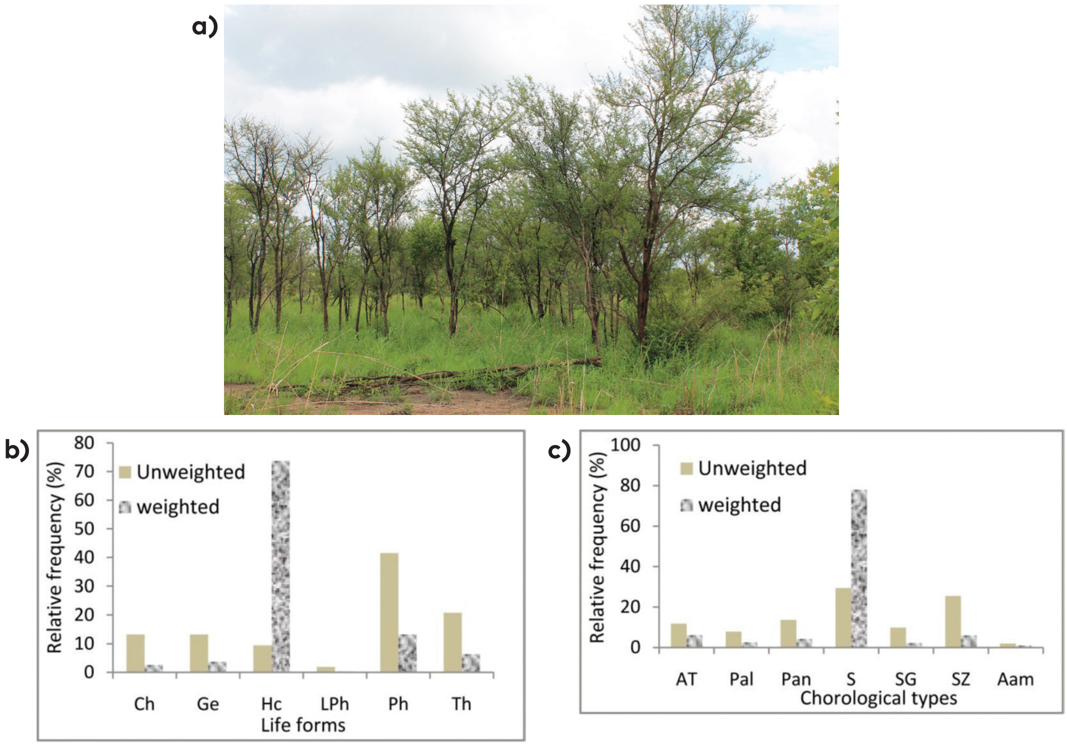

Figure A4. *Sorghastro bipennati-Vachellietum hockii*. **a)** Photo of tree savanna of *Sorghastro bipennati-Vachellietum hockii* located on floodplain; **b)** Life form spectra; **c)** Chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

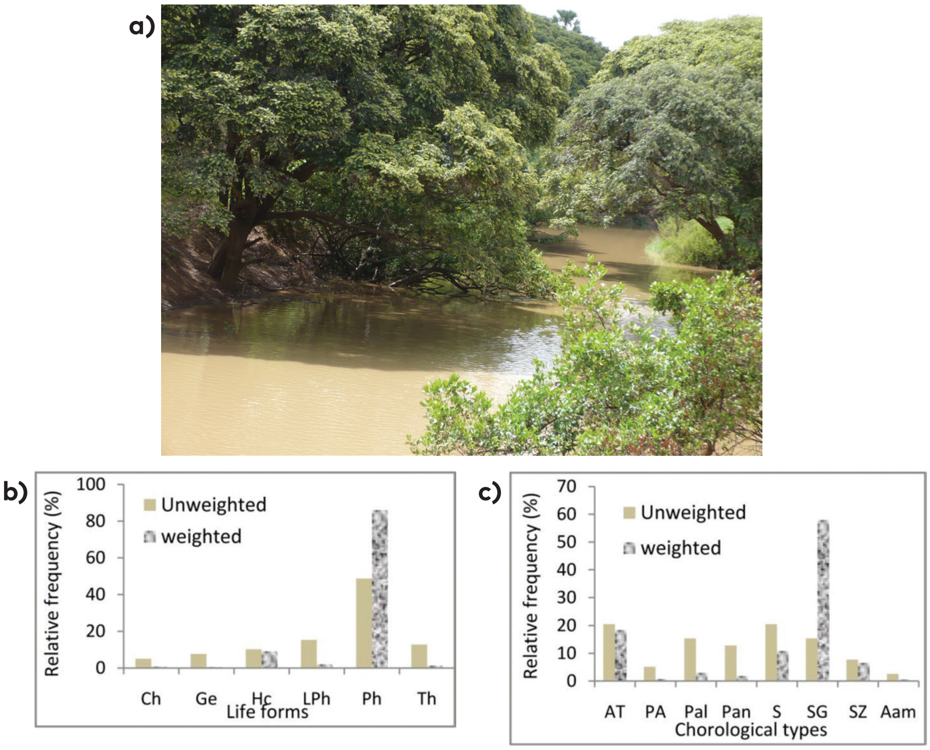

Figure A5. *Coletum laurifoliae* **a)** Photo of riparian forest of *Coletum laurifoliae* located along Pendjari river. **b)** Life form spectra; **c)** Chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

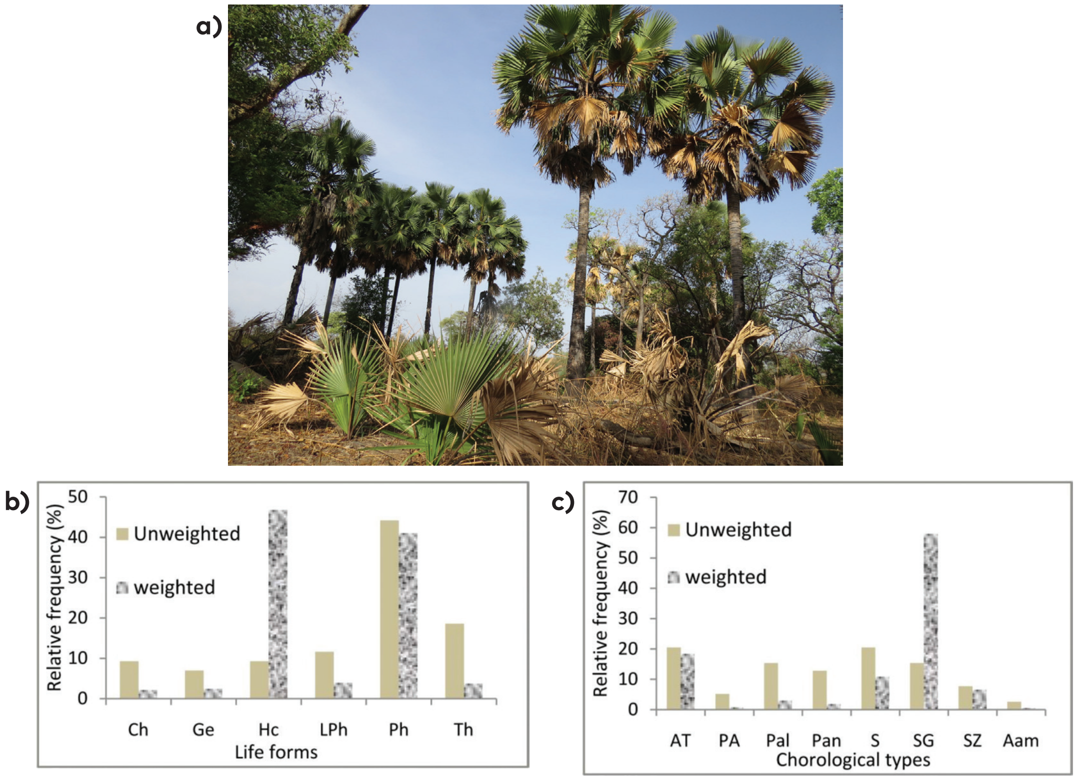

Figure A6. *Borassetum aethiopi*. **a)** Photo of riparian forest of *Borassetum aethiopi* along Pendjari river; **b)** Life form spectra; **c)** Chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

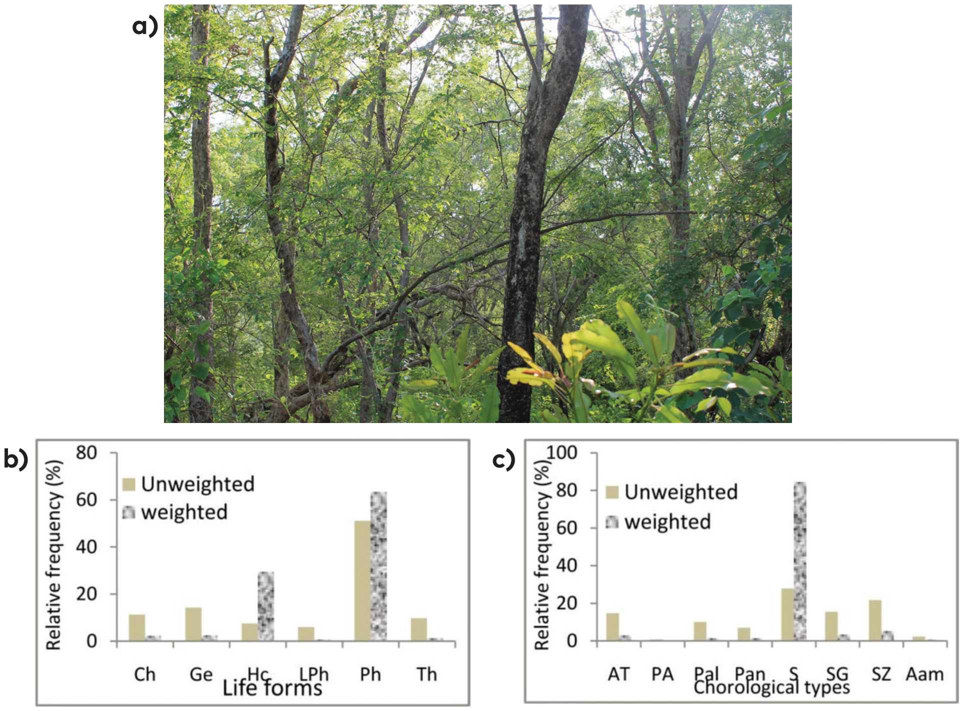

Figure A7. *Terminalietum leiocarpae*. **a)** Photo of woodland of *Terminalietum leiocarpae* located on clay soil; **b)** Life form spectra; **c)** Chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

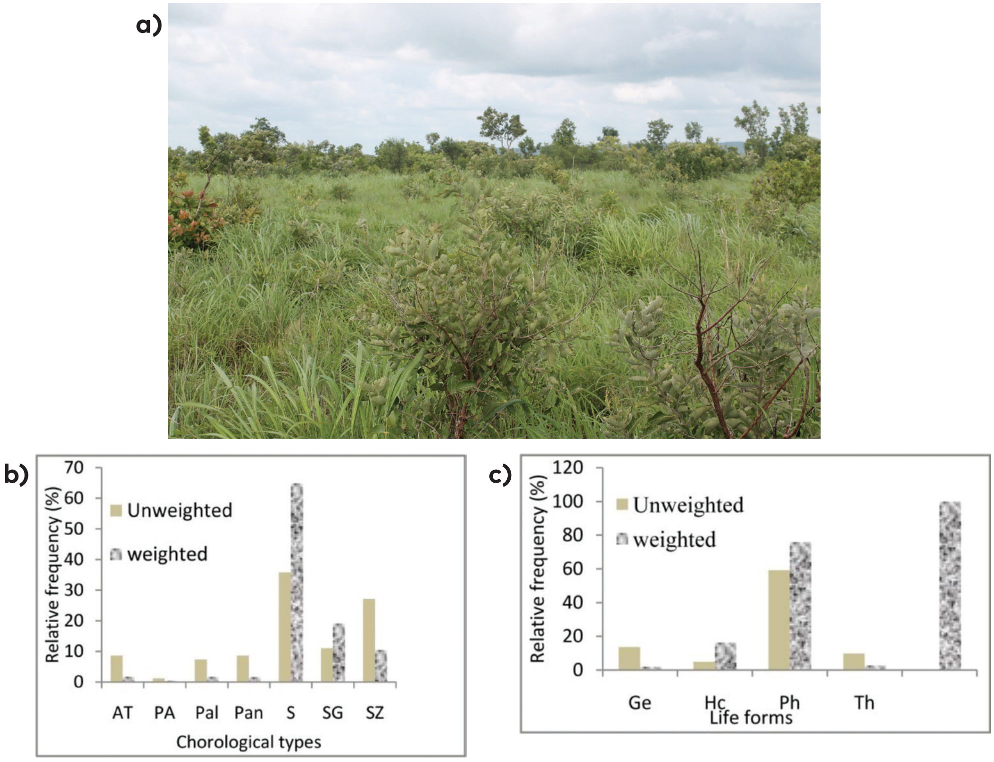

Figure A8. *Andropogono gayani-Combretetum glutinosi*. **a)** Photo of shrub savanna of *Andropogono gayani-Combretetum glutinosi* on gravelly soil; **b)** Life form spectra; **c)** Chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

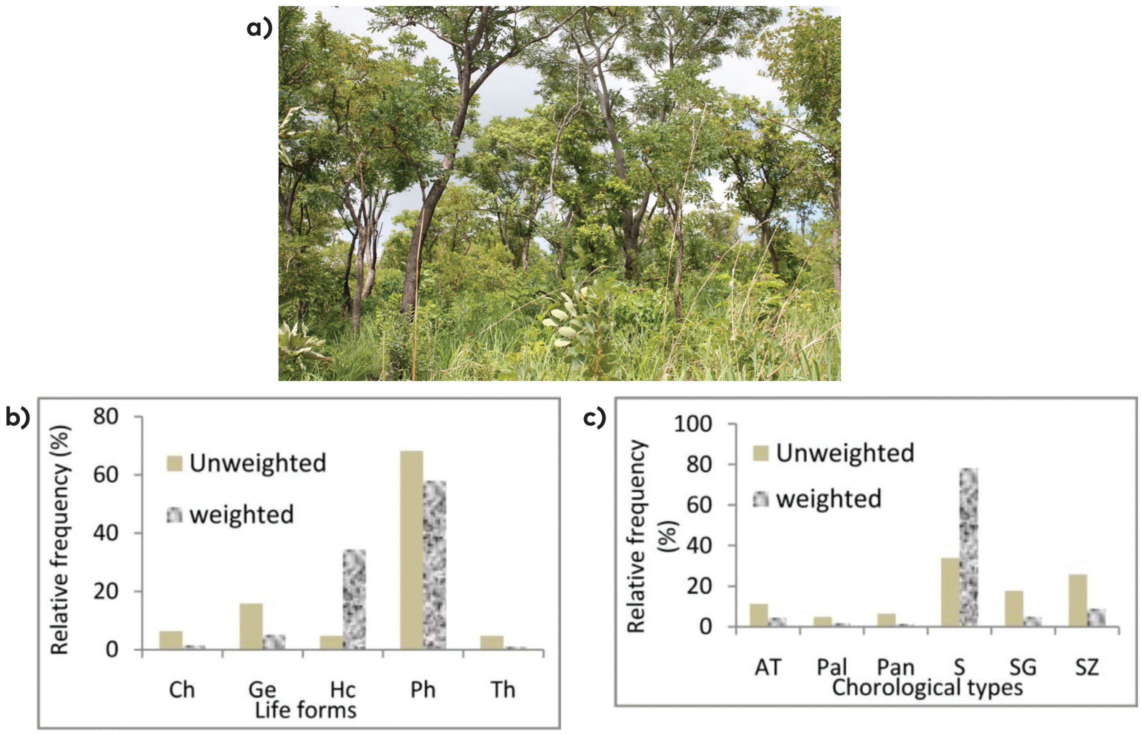

Figure A9. *Andropogono gayani-Terminalietum avicennioidis*. **a)** Photo of tree savanna of *Andropogono gayani-Terminalietum avicennioidis*; **b)** Life form spectra; **c)** Chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

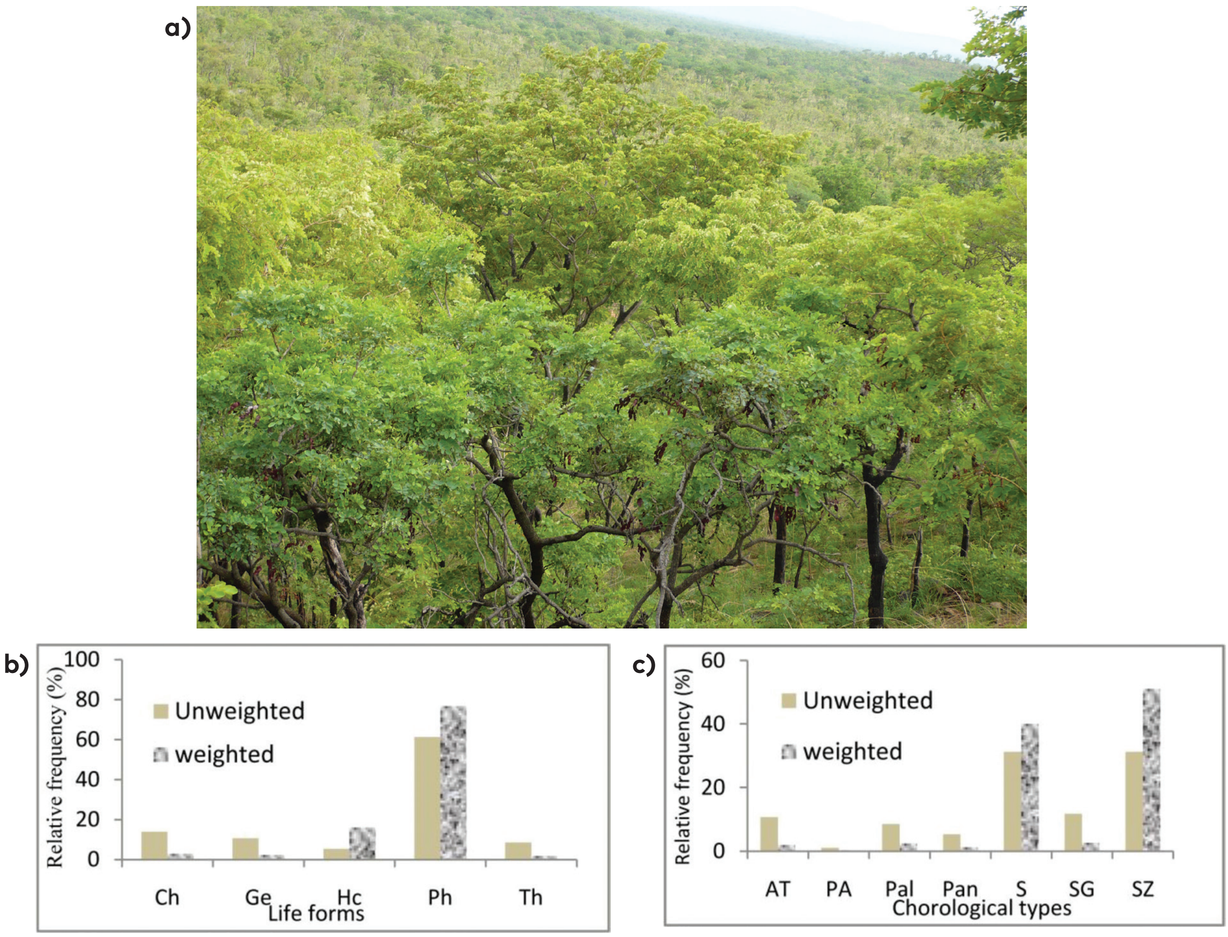

Figure A10. *Burkeo africanae-Detarietum microcarpi*. **a)** Photo of tree savanna of *Burkeo africanae-Detarietum microcarpi* on hills sides; **b)** Life form spectra; **c)** Chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

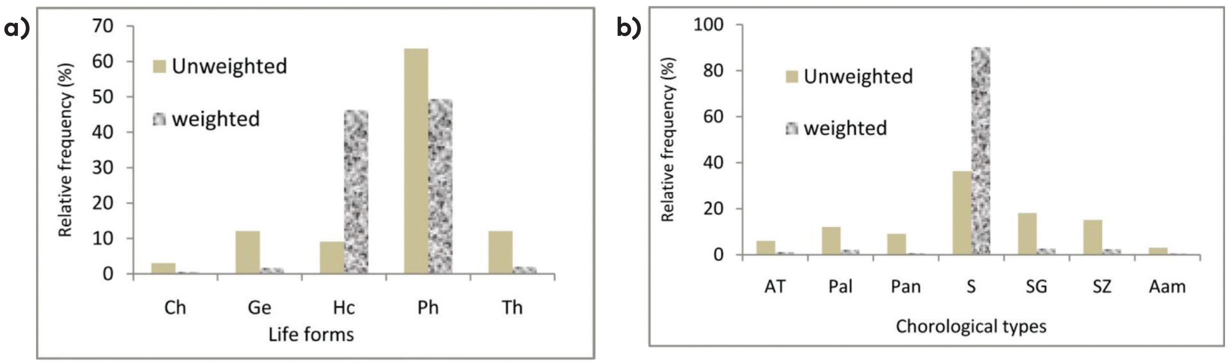

Figure A11. *Andropogono gayani-Senegalietum dudgeonii* **a)** Life form spectra; **b)** chorological spectra. Therophytes (Th), Hemicryptophytes (Hec), Geophytes (Ge), Chameophytes (Ch), Phanerophytes (Ph), Liana phanerophytes (LPh), Cosmopolitan (Cos), Pantropical (Pan), Paleotropical (Pal), Afro-American (Aam), Sudano-Zambesian (SZ), Sudano-Guinean (SG), Afrotropical (AT), Pluri-regional African species (PA), Guineo-Congolian species (GC), Sudanian species (S).

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Supplementary material

Supplementary material 1
Phytosociological tables of the plant associations showing the typus relevé of each association. *.xlsx (Excel spreadsheet)
Link: https://doi.org/10.3897/VCS.91126.suppl1

Supplementary material 2
Full synoptic table with percentage frequency and fidelity values. *.xlsx (Excel spreadsheet)
Link: https://doi.org/10.3897/VCS.91126.suppl2

Supplementary material 3
Header data of the relevés of the plant associations. *.xlsx (Excel spreadsheet)
Link: https://doi.org/10.3897/VCS.91126.suppl3