

Floristic diversity of *Piliostigma* associations in relation to latitudinal gradient, soil and climate variables in Burkina Faso, West Africa

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Abstract: We examined the floristic composition and its relationship with environmental factors across 80 floristic relevés of *Piliostigma* stands distributed along a north-south gradient in Burkina Faso. Various diversity indices were computed. Detrended Correspondence Analysis and Canonical Correspondence Analysis (CCA) were used to explore the relationship between species occurring in *Piliostigma* stands and environmental variables. The results showed that *Piliostigma* communities show only limited variation in species composition among sites. The first two axes of the DCA together explained 16.5 % of the floristic variation. The CCA showed that climatic variables explain 42 % of the species variance. The *Piliostigma reticulatum* association is adapted to reduced rainfall and sandy soil, whereas the *P. thonningii* association occurs preferentially on clay soil.

Resumen: Examinamos la composición florística y su relación con factores ambientales en 80 levantamientos florísticos en rodales de *Piliostigma* distribuidos a lo largo de un gradiente norte-sur en Burkina Faso. Se calcularon varios índices de diversidad. Se usó un Análisis de Correspondencia sin Tendencias (DCA) y un Análisis Canónico de Correspondencia (CCA) para explorar la relación entre las especies presentes en los rodales de *Piliostigma* y las variables ambientales. Los resultados revelaron que las comunidades de *Piliostigma* sólo muestran una variación limitada en composición de especies entre sitios. Los dos primeros ejes del DCA explicaron en conjunto 16.5 % de la variación florística. El CCA mostró que las variables climáticas explican 42 % de la varianza de las especies. La asociación de *Piliostigma reticulatum* está adaptada a una precipitación reducida y suelo arenoso, mientras que la asociación de *P. thonningii* se presenta preferentemente en suelo arcilloso.

Resumo: Examinamos a composição florística e a sua relação com os fatores ambientais e os levantamentos florísticos de *Piliostigma* em 80 parcelas distribuídas ao longo de um gradiente norte-sul, em Burkina Faso. Vários índices de diversidade foram calculados. Análise de correspondência retificada e análise de correspondência canônica (CCA) foram utilizados para explorar a relação entre as espécies que ocorrem em parcelas de *Piliostigma* e as variáveis

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ambientais. Os resultados mostraram que as comunidades de *Piliostigma* evidenciaram apenas limitada variação na composição de espécies entre os locais. Os dois primeiros eixos da DCA juntos explicaram 16,5 % da variação florística. A CCA mostrou que as variáveis climáticas explicam 42 % da variação das espécies. A associação de *Piliostigma reticulatum* está adaptada a uma precipitação reduzida e ao solo arenoso, enquanto a associação de *P. thonningii* ocorre preferencialmente em solo argiloso.

Key words: Disturbance, environmental factors, habitat specialization, ordination, species distribution.

Introduction

Africa's forested landscapes are seriously threatened (FAO 2010), mainly as a result of the increased pressure exerted by the rapidly growing human population (Adekunle *et al.* 2013; Lambin *et al.* 2003). Fragmentation of the landscape is one of the greatest threats to biodiversity (Darkoh 2003) and compromises the supply of various commodities such as firewood, food, construction materials and medicine to local people. Currently, species richness and distribution are seriously affected by partial heterogeneity, stochastic events, especially the dominant influence of fluctuating annual precipitation, and the resilience of the ecosystems (Marks *et al.* 2009; Vincke *et al.* 2010).

Generally, the distribution range and colonization capability of a species are determined by a suitability gradient found in habitats along a latitudinal gradient (Willig *et al.* 2003). The latitudinal gradient ultimately reflects geographic, biotic and abiotic factors, together with stochastic forces (Schemske 2002). Plant diversity is found to mirror the primary variables associated with the latitudinal gradient, such as temperature, rainfall, solar input and seasonality, which are likely to vary continuously from lower to higher latitudes (Gaston 2007). In the tropics, plants occurring at higher latitude are likely to face particularly harsh environmental stress, mainly water stress (Slot & Poorter 2007). Understanding species recruitment along the latitudinal gradient may thus provide valuable information on the plasticity of response of a plant species and its evolutionary potential to cope with environmental conditions, and insight into the role of local adaptation. Habitat quality or habitat type is important in determining species richness (Harrison & Bruna 1999). Local factors

affecting the occurrence and abundance of plant species within a habitat patch include resource supply (soil nutrients, and physical characteristics such as water and light) and biotic interactions among plants and between trophic levels (e.g. competition, facilitation, herbivory) (Kumar & Mathur 2014; Lortie *et al.* 2004). For example, a plant canopy may provide different microhabitats which can be exploited by species with specialized competitive abilities (Oliveira-Filho *et al.* 1998).

In phytosociology, patterns of floristic differentiation of species richness and vegetation-environment relationships are often investigated to compare different vegetation units in contrasting environment and to study species responses along an environmental gradient. This helps to reveal species fidelity, the degree to which a species is concentrated in a given vegetation unit and diagnostic species - species that show a preference for a given biotic community, and, therefore, are useful in field surveys for the identification of community types (Chytrý *et al.* 2002; Dufrêne & Legendre 1997). In Burkina Faso, the vegetation physiognomy is marked by the occurrence of *Piliostigma* species (often called "fallow species" (Devineau 2001; Somé *et al.* 2000; Yaméogo *et al.* 2005; Yélémou *et al.* 2007). The abundance of these species, and the floristic diversity in their stands, constitute an indicator of the fertility of fallow soils recognized by the local farmers. Indeed, for many authors, the woody species reflect best the local environmental factors (Higgins *et al.* 1999). *Piliostigma reticulatum* and *P. thonningii* are subject to various types of exploitation all year round. In recent years, with the increase of anthropogenic pressure, depletion of *Piliostigma* species has been observed in some places (Yélémou *et al.* 2007). Like many other woody species exploited for domestic uses, the

distribution of *Piliostigma* remains far from comprehensively known. The two species of the genus appear more and more in the agroforestry parklands for soil conservation (Yélémou *et al.* 2007). According to Lehman *et al.* (2002) and Nyadoi *et al.* (2014) in the agro-ecosystems, good management of forests and of species requires information on their distribution and potential growth with respect to the environmental variables. However, the sahelian countries in particular are places where the biological diversity at all levels has still remained less researched (Ouédraogo 2006; Traoré 2008). Very few studies exist on the influence of environmental factors including latitudinal variation on the actual and potential distribution of tree species in Burkina Faso (Bognounou *et al.* 2009; Bognounou *et al.* 2010). It is, therefore, necessary to identify the different environmental factors explaining the distribution of plant species through the different phyto-geographical zones. It is important to design a good management plan for *Piliostigma* species considering their socio-economic importance in the agro-ecosystems (Bosma *et al.* 2004; Yélémou *et al.* 2007). Besides, knowledge of the role of *Piliostigma* in the maintenance of plant diversity could help towards a better integration of *Piliostigma* species in the restoration of degraded areas and reforestation programs. Thus, the present study was undertaken with the following objectives: (a) to assess the species diversity (richness and evenness) of *Piliostigma* plant communities; and (b) to determine the influence of soil characteristics and rainfall on species richness, species composition, and abundance.

Material and methods

Study area

The research area stretches from latitude 10° 80' N to 14° 30' N, and from longitude 1° 30' W to 2° 97' W (Fig. 1). At all sites, the vegetation is strongly seasonal; virtually all woody species are deciduous, and most herbs are either annual or die back each dry season. The altitude of most sites was about 300 m a.s.l. Phytogeographically, the study area is located, from north to south, in the following sectors defined by Fontes & Guinko (1995):

A. The South Sahelian sector comprising Yatenga

and Passoré provinces, with a mean annual rainfall ranging between 600 and 700 mm, and between 40 and 50 rainy days per annum (Fig. 2). The most frequently soils encountered are lithosols on hardpan occupying 33% of the region and tropical ferruginous poorly evolved erosional soils overlying gravelly material covering 40%. The vegetation is characterized by *brousse tigrée* ("tiger bush"), a patterned vegetation community consisting of alternating bands of trees or shrubs, separated by bare ground or low herb cover and typical of the sahelian climate. Patchy shrub savanna is encountered over a large part of this sector, in which species of the families Combretaceae and Mimosaceae dominate the woody vegetation; the herbaceous vegetation is dominated by Poaceae. Common woody species are *Acacia* spp., *Combretum* spp. and *Piliostigma reticulatum*. In respect of land use, fallow lands are interspersed with mainly traditional agroforestry parklands with annual food crops, in which the common woody species are, *Combretum* spp., *Diospyros mespiliformis*, *Lannea microcarpa*, *Parkia biglobosa* and *Vitellaria paradoxa*.

B. The North-Sudanien sector (Boulkiemdé province, with the provincial city Koudougou) has a mean annual rainfall ranging between 600 and 900 mm, the number of rainy days per annum being between 50 and 70.

C. The South-Sudanien sector (Sissili and Ziro provinces with capital cities Leo and Sapouy) receives a mean annual rainfall ranging between 800 and 900 mm distributed over 60 - 80 days.

In the North-Sudanien and South-Sudanien sectors more than 90 % of the soils encountered are tropical ferruginous soils. The vegetation is of the Sudanien savanna type characterized by the coexistence of trees and grasses. The natural vegetation consists mostly of dry forest, and a mixture of shrublands and tree savanna community types not growing above 7 m height. There is also a tree savanna typical for the South-Sudanien climate and essentially constituted of trees of 7 to 12 m. A high proportion of the two Sudanien sectors is used in the form of parklands where useful trees are spared from cutting, while sorghum, maize, millet or other crops are culti-

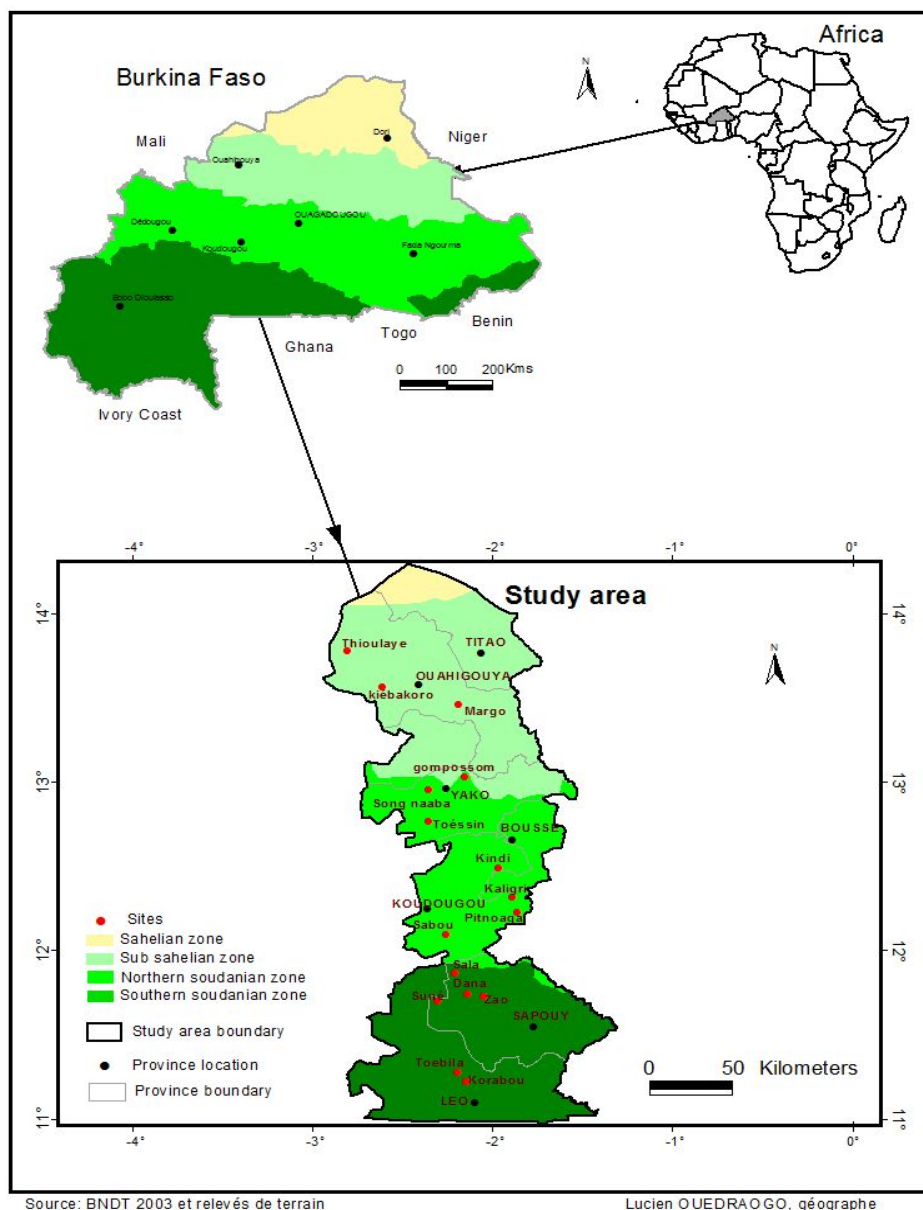


Fig. 1. Phytogeographical map of Burkina Faso with isohyets and location of the study sites.

vated beneath. Dominant tree species often belong to the families Caesalpiniaceae and Combretaceae; some *Acacia* species are also encountered. The most common species are: *Adansonia digitata*, *Anogeissus leiocarpa*, *Burkea africana*, *Combretum micranthum*, *Crossopteryx febrifuga*, *Detarium microcarpum*. *Isoberrlinia doka*, *Lannea microcarpa*, *Parkia biglobosa*, *Piliostigma thonningii*, *Pterocarpus erinaceus* and *Vitellaria paradoxa*. The dominant grass species are usually Andropogoneae, especially the genera *Andropogon* and *Hyparrhenia*; on shallow soils the genera *Aristida* and *Loudetia* are found.

Site selection and data collection

The existence of a *Piliostigma* population was a prerequisite to selecting a site. A population of *Piliostigma* was defined by the relative dominance (canopy cover > 5%) of *Piliostigma* species over at least 1 ha. The sites were chosen for homogeneity, and to represent the widest possible range of stand conditions, mainly reflected by stand quality and density of the species (number of individuals per unit area). All the sites were located in protected areas (forests reserves) or on old fallows (more than 20 years old) from former agricultural lands.

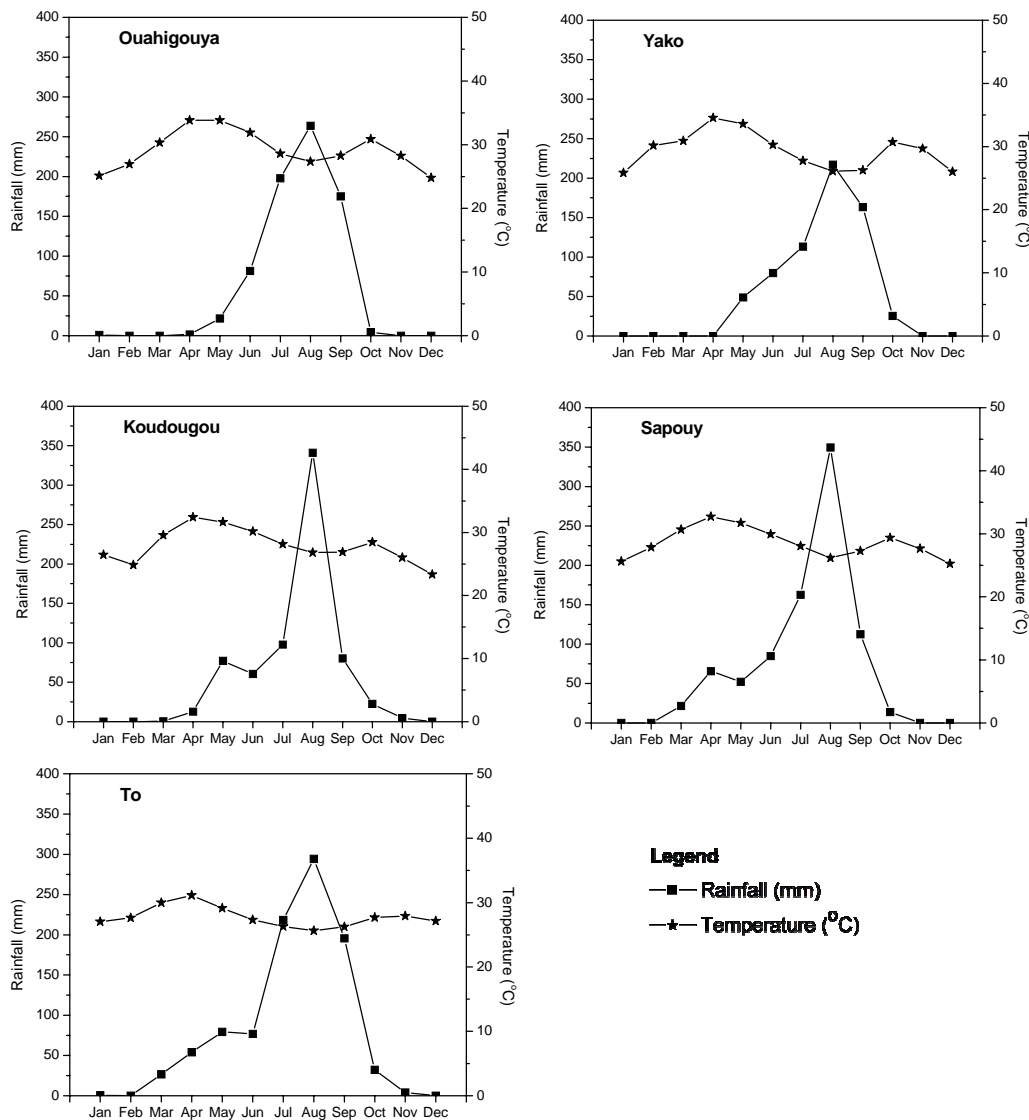


Fig. 2. Ombrothermic charts, of the period 1977-2007 in 5 meteorological stations close to the study sites.

In total, 16 sites were selected with populations of *P. reticulatum*, or of *P. thonningii* in the south and north sudanian sectors (Fig. 1); they ranged in size from 3 to 50 ha. Prior to plot sampling, the site identification was recorded; the geographic coordinates and the altitude of the site centre were measured by a GPS receiver (Garmin eTrex) and the slope was estimated by eye.

Environmental data

Along with vegetation variables, at each site a range of quantitative and qualitative environmental variables which were expected to have an effect on species composition were recorded. The fallow age of each site was estimated following

informal interviews with local farmers. In each case, farmers who had the prime responsibility for the land were asked to estimate the time since the vegetation was cleared, following the procedure described by Dalle & de Blois (2006). All possible disturbances (fire, cutting, lopping and grazing) at each site were also discussed.

The climatic variable, annual rainfall for the period 1977 - 2007, was based on data collected by the Department of Meteorology; information for each site was gathered from the nearest weather station which was situated 10 to 30 km away. The soil physical and chemical characteristics for the sites were determined. At the time of conducting the vegetation sampling, four composite soil samples, 0 - 20 cm depth, were taken from four

random locations (north, south, west and east) within a radius of 15 m from each site centre. Each sample was divided into two and bagged; one half was sent to the National Soil Laboratory (BUNASOLS) for the determination of physical parameters, and the second half to the Soils Water and Plants Laboratory of the Institute of Environment and Agricultural Research (INERA) for the chemical characteristics. Soil texture was determined based on three granulometric fractions (clay, sand and silt) according to the procedure described by Day (1965). For the chemical characteristics, total nitrogen was determined following the Kjeldahl method; total organic carbon was measured following the Walkley & Black (1934) method, total phosphorus using an automatic colorimetric technique by the phosphomolybdenum blue complex after acid mineralization (Houba *et al.* 1988). The pH_{water} was determined directly using an electronic pH meter in a 1:2.5 (soil : water) suspension.

Botanical data

At each site a stratified systematic sampling procedure was used based on the communities of the two species studied. The sampling unit (relevé) was a 30 m square. A similar sampling unit has been adopted by many authors working in the savanna-woodland of Burkina Faso (Hahn-Hadjali 1998; Ouédraogo 2006; Traoré 2008). In total, 80 relevés were sampled, from two to eight at each site (see Appendix Table 1). Floristic data were collected according to the method of Braun-Blanquet, using the modified cover-abundance scale (Wilmanns 1989) (Table 1). Woody species were recorded according to a vertical stratification distinguishing the adult individuals from the regeneration (diameter at the base < 1 cm). Identification of species and families of plants followed Hutchinson *et al.* (1954).

Table 1. Braun-Blanquet cover-abundance scale for the vegetation analysis.

Code*	Cover class	Significance
1	+	Cover less than 1%
2	1	Cover of less than 5%
3	2a	Cover between 5 and 15%
4	2b	Cover between 15 and 25%
5	3	Cover between 25 and 50%
6	4	Cover between 50 and 75%
7	5	Cover more than 75%

*This is a personal annotation used in data analysis.

Data analysis

Specific diversity parameters of the vegetation units

For a better understanding of plant community composition, richness and diversity indices were computed. Species richness (S) is expressed by the number of species encountered in a relevé. The Shannon-Wiener diversity index (H') was calculated using the equation:

$$H' = -\sum p_i \ln p_i$$

where, p_i is the proportion of individuals belonging to the i th species in the dataset of interest (Magurran 2004). In these data, the value of H' ranges from 0.5 (weak specific diversity) to 4.5 (strong specific diversity).

The equitability index was calculated as

$$E = H'/H_{\max}$$

where, $H_{\max} = \ln S$. This is an expression of the balance in the distribution of individuals among the species. Its value approaches 0 when one species is highly dominant, and approaches 1 when all species have similar densities.

Diagnostic species determination

Species fidelity can be measured using various statistical methods. In vegetation science the most widely used index of fidelity strength is the *Phi* (ϕ) coefficient of association (Sokal & Rohlf 1995). In the present case, this coefficient was based on presence/absence data, following the procedure described by Chytrý *et al.* (2002). Fidelity here expresses the concentration of species in relevés of a particular vegetation type compared to relevés of other vegetation types (Tichý & Chytrý 2006); it is a numeric expression of the diagnostic value of a species within a given zonal complex. The equation (Eq. 1) used by Bruelheide (2000), Chytrý *et al.* (2002), and Tichý & Chytrý (2006) was employed in the computation:

$$Phi = \frac{N.n_p - n.N_p}{\sqrt{n.N_p.(N - n).(N - N_p)}} \quad (\text{Eq. 1})$$

where, N is the total number of relevés, N_p the number of relevés belonging to association p , n the number of species recorded in the whole data set, and n_p the number of species recorded in association p .

The *Phi* coefficient depends on N_p . To suppress this dependence on the size of vegetation units it may be adjusted by

$$N_p' = sN_p$$

where, s is a value between $1/N$ and $(N-1)/N$ indicating the relative proportion of the association considered (Tichy & Chytrý 2006). The *Phi* coefficient takes values ranging from -1 (maximum negative fidelity) to +1 (maximum positive fidelity) and is equal to the Pearson correlation coefficient computed between two binary descriptors. It is equal or close to zero when the species occurrence in the data set does not show any preference or avoidance of the target association. Species with positive *Phi* coefficients are more or less closely linked with an association. Higher values indicate that occurrences of that species are concentrated in the association in question, and lower values indicate that the species is under-represented in that association. A value of 1 indicates that the species occurs in all sites of the association and nowhere else; a value of -1 indicates the reverse pattern. The statistical significance of species faithfulness was determined using Fisher's exact test for the right-tailed hypothesis, which is a suitable measure of statistical fidelity of species to associations (Chytrý *et al.* 2002). Using the software Juice 7.0 (Tichy 2002), Table 3 has been prepared showing the species recorded for each association, with their *Phi* coefficients and their frequency.

Revealing patterns in the data

Ordination techniques help to explain community variation (Gauch 1979), and they can be used to evaluate trends through time as well as space (Ter Braak & Smilauer 2002). The data collected were first subjected to Detrended Correspondence Analysis (DCA) in order to assess the overall variation patterns in species composition. This is a method of indirect gradient analysis which best expresses the dissimilarity in floristic composition of vegetation samples in an ordination diagram (Hill & Gauch 1980; Ter Braak & Smilauer 2002). Detrended Correspondence Analysis is well suited to estimate the latent environmental variables (gradient lengths) because its axes are scaled in standard deviation units of the species turnover (Jongman *et al.* 1995). This method measures the similarity of the relevés based on their floristic composition and permits the communities to be categorized (Traoré 2008). Subsequently we examined vegetation-environment relationships, based on species density using community matrices and environmental matrices. The effect of the environmental variables on the floristic composition was quantified using Canonical Correspondence Analysis model (CCA).

The CCA shows environmental variables as predictors of species presence or abundance-dominance. Since a test of significance of the relationship between species composition and a set of explanatory variables was needed, the weights given to rare species are relevant; we, therefore, used the Hellinger transformation, which is an appropriate method allowing low weight to rare species (Legendre & Gallagher 2001). The statistical significance of the relationship was evaluated using Monte Carlo permutation tests ($P < 0.05$ after 499 permutations). Each environmental variable was tested separately for marginal effects -- how well each individual environmental variable alone explained the variance in the species matrix. The environmental variables that produced a significant CCA axis were ranked by eigenvalue and tested for conditional effects by forward selection (Ter Braak & Verdonschot 1995). The statistical analyses were performed using the software package CANOCO 4.5 and the ordination diagrams were drawn in CANODRAW (Ter Braak & Smilauer 2002).

Results

Floristic diversity of Piliostigma associations

Overall, 79 tree species were encountered in the sample plots. These taxa included 28 families and 57 genera. The most common families were Mimosaceae (16 species) followed by Combretaceae (12) and Caesalpiniaceae (8). About 40% of the families encountered were represented by only one species. In the two *Piliostigma* associations, the mean number of species in a relevé was 14 and 21 (Table 2). The Shannon-Wiener diversity index, which combines species richness and evenness into a single value, was in all cases above 1, with a maximum of 3.05. It also indicated that the *P. thonningii* association was more diverse (1.94) than the *P. reticulatum* association. The equitability indices were similar - 0.63 for the *P. reticulatum* association, and 0.61 for the *P. thonningii* association.

Table 2. Diversity indices of *Piliostigma* associations in the central part of Burkina Faso (values are given as Mean \pm SD).

Associations	No. of species	Shannon-Wiener index	Maximal index	Equitability index
<i>P. reticulatum</i>	14 \pm 6	1.56 \pm 0.55	2.64 \pm 1.85	0.61 \pm 0.15
<i>P. thonningii</i>	21 \pm 4	1.92 \pm 0.35	3.05 \pm 1.26	0.63 \pm 0.11

Diagnostic species of Piliostigma associations

The synoptic tables (Table 3) of the two *Piliostigma* associations display the diagnostic taxa identified according to the *Phi* coefficient of fidelity. Diagnostic taxa are listed for each vegetation unit and ordered from the highest to the lowest phi coefficient. The two associations were distinguished by their diagnostic species, showing a clear set of diagnostic taxa in each association. Diagnostic species were fewer in the *P. reticulatum* association (10). Three of these species were from the family Combretaceae and three from the Caesalpiniaceae; all the other species represented one family each. Highly diagnostic species were *Anogeissus leiocarpa*, *Combretum micranthum* and *Guiera senegalensis*, all belonging to the family Combretaceae. The *P. thonningii* association had a larger number of diagnostic species (27). Each of the families Caesalpiniaceae, Combretaceae, Mimosaceae and Rubiaceae was represented by four diagnostic taxa. Two of the remaining species belong to the Anacardiaceae, the nine others were each sole representatives of their family. Species fidelity to the *P. thonningii* community was greater, with high values of the *Phi* coefficient.

Gradients in species composition of Piliostigma populations

The abundance-based Detrended Correspondence Analysis (DCA) revealed two gradients in species composition along the first two axes. The lengths of the gradient were 3.29 and 2.55 SD units, respectively for axis 1 and 2. The total inertia was 4.57 (Table 4). The length of the gradient on the first axis was less than 4 SD (standard deviations) and since the detrending as performed by segments and Hill-scaling, it, therefore, estimates the beta diversity in the data set. The first axis was also correlated with the rainfall gradient ($r = 0.94$); the correlation for the other axes is quite low, but suggests a gradient of edaphic characteristics. In the study zone most species reach an optimum following a unimodal response pattern with the different gradients. The first and second axes explained together 16.9 % of the floristic variation; the corresponding eigenvalues were 0.496 and 0.276. The axes 3 and 4 only explained 7.70 % of the variation in the species composition. The ordination diagram for the first two axes allows a discrimination of two distinct vegetation units (associations) showing the degree of floristic dissimilarity of the *Piliostigma* associations (Fig. 3). Relevés of the *Piliostigma*

reticulatum association were scattered along the axis 1 and did not show clear dissimilarity in their floristic composition. In contrast, the *P. thonningii* association included two clear sets of relevés, divided at the value of 3.0 on Axis 1 (and relevé Su). Axis 2 seems to separate three groups within the *P. reticulatum* association - groups which are not statistically distinct - but does not distinguish the two associations, and so fails to provide a clear expression of the differences among the relevés.

Ordination of vegetation in relation to climatic variable

The ordination of the floristic relevés by the CCA taking into account only the climatic factor shows that this parameter is determinant in the distribution and diversity pattern of *Piliostigma* associations. The climatic variable explains 42 % of the species variance (sum of all canonical eigenvalues) (Table 5). The species - environment correlations indicate how much of the variation in species composition is explained by this environmental variable. The large value of 0.94 indicates that most of the variation in species composition can be attributed to the rainfall variability. Of the four canonical axes, only the axis 1 showed a relatively high correlation with the environmental variables ($r \geq 0.27$). The eigenvalue measures the importance of each of the axes and was highest for the first axis; together, the eigenvalues of the four canonical axes were less than 50 %, and explained only 37 % of species variance. The species-environmental correlation measures the strength of the relationship between species and environment data. After the first canonical axis, the changes in species-environment relationship remained relatively low (63.7 to 5.4 %).

Ordination of species in relation to pedoclimatic variables

The ordination of floristic relevés by the CCA taking into account pedoclimatic variables shows

Table 3a. Number of species in the two *Piliostigma* associations.

Vegetation unit	<i>P. reticulatum</i> Association	<i>P. thonningii</i> Association
Number of relevés	49	31
Number of species	69	63
Number of diagnostic species	10	30

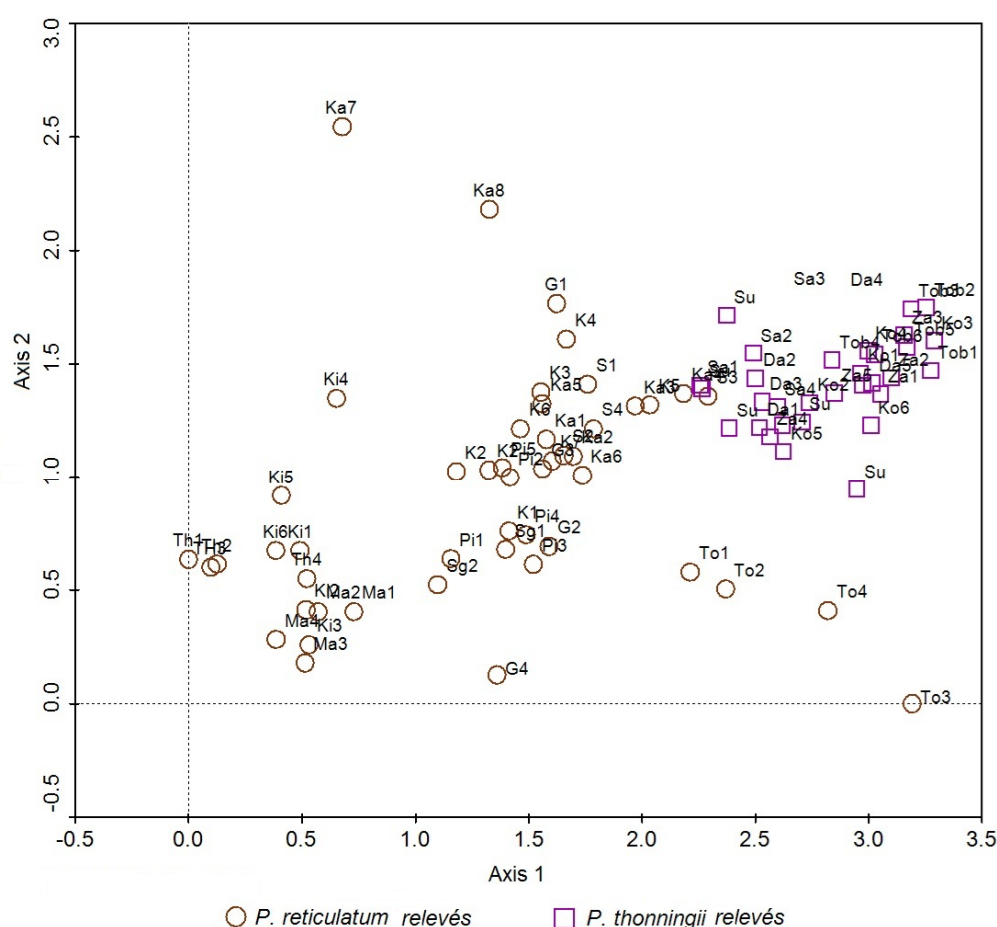
Table 3b. Synoptic table of the relevés of *Piliostigma* Associations. Diagnostic species were subjectively selected as those with $\Phi \geq 0.18$. Species are ordered according to descending fidelity.

	Phi Coefficient ¹ $\times 100$		Frequency (%)	
	In <i>P.reticulatum</i> Association	In <i>P.thonningii</i> Association	In <i>P.reticulatum</i> Association	In <i>P.thonningii</i> Association
Diagnostic species of <i>P. reticulatum</i> Association	..	-		
<i>Piliostigma reticulatum</i>				
<i>Combretum micranthum</i>	58.37	0	58	0
<i>Guiera senegalensis</i>	47.47	0	58	13
<i>Anogeissus leiocarpa</i>	36.93	0	52	7
<i>Gardenia erubescens</i>	35.04	41.43	27	60
<i>Cassia singueana</i>	28.08	0	23	3
<i>Cassia sieberiana</i>	20.53	12.59	27	10
<i>Balanites aegyptiaca</i>	18.49	0	23	10
<i>Acacia macrostachya</i>	18.25	16.74	8	50
<i>Grewia flavescens</i>	18.25	0	6	0
Diagnostic species of <i>P. thonningii</i> Association				
<i>Piliostigma thonningii</i>	-	95.98	40	100
<i>Annona senegalensis</i>	-	67.30	19	87
<i>Strichnos spinosa</i>	-	62.86	0	53
<i>Securinea virosa</i>	-	61.44	35	97
<i>Dichrostachys cinerea</i>	-	58.00	35	93
<i>Pteleopsis suberosa</i>	-	54.81	6	53
<i>Bridelia ferruginea</i>	-	50.03	4	13
<i>Terminalia macroptera</i>	-	49.31	6	50
<i>Crossopteryx febrifuga</i>	-	48.89	15	60
<i>Detarium microcarpum</i>	-	47.33	21	67
<i>Feretia apodanthera</i>	11.86	45.04	21	67
<i>Gardenia erubescens</i>	35.04	41.43	27	60
<i>Maytenus senegalensis</i>	-	40.90	8	57
<i>Terminalia avicennioides</i>	-	40.61	25	70
<i>Vitellaria paradoxa</i>	-	38.76	52	90
<i>Pterocarpus erinaceus</i>	-	34.51	6	33
<i>Lannea acida</i>	-	34.29	31	70
<i>Combretum molle</i>	-	32.46	0	17
<i>Burkea africana</i>	-	32.46	0	17
<i>Afromosia laxiflora</i>	-	32.46	0	17
<i>Azelia africana</i>	-	29.85	2	20
<i>Bridelia ferruginea</i>	-	28.84	4	47
<i>Prosopis africana</i>	-	28.84	0	13
<i>Securidaca longepedunculata</i>	-	28.84	0	13
<i>Entada africana</i>	-	28.52	4	23
<i>Sterculia setigera</i>	-	24.82	0	10
<i>Lannea velutina</i>	-	24.24	6	23
<i>Gardenia ternifolia</i>	-	20.13	13	23

¹ Dashes indicate negative fidelity.

Table 4. Summary of the four first axes of Detrended Correspondence Analysis (DCA) and amount of the variance of the species data explained.

Axes	1	2	3	4	Total Inertia
Eigenvalues	0.50	0.28	0.20	0.15	4.57
Lengths of gradients	3.29	2.55	2.49	1.87	
Cumulative percentage variance of species data	10.9	16.9	21.3	24.6	
Sum of all eigenvalues					4.57

**Fig. 3.** Ordination diagram for first two axes of Detrended Correspondence Analysis on species data of 16 study sites.**Table 5.** Summary of the CCA (Canonical Correspondence Analysis) when only climatic factors are considered.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.27	0.05	0.03	0.02	1.00
Species-environment correlation	0.94	0.88	0.70	0.69	
Cumulative percentage variance of species data	26.5	31.4	34.4	36.7	
Cumulative percentage variance of species-environment relation	63.7	75.4	82.7	88.1	
Sum of all eigenvalues					1.00
Sum of all canonical eigenvalues					0.42

Table 6. Summary of the CCA (Canonical Correspondence Analysis) when pedoclimatic factors are considered.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.43	0.21	0.13	0.10	4.57
Species-environment relationship	0.95	0.91	0.61	0.77	
Cumulative percentage variance of species data	9.5	14.0	16.9	19.1	
Cumulative percentage variance of species-environment relation	37.0	54.7	65.7	74.4	
Sum of all eigenvalues					4.57
Sum of all canonical eigenvalues					1.17

that they largely governed the distribution of *Piliostigma* associations. Pedoclimatic variables explain 26 % of species variation (Table 6). The four canonical axes only express 19.1 % of species variation. Furthermore, the species-environment relationship of the four canonical axes is very weak ($r \geq 0.10$), ranging from 37 to 8.7 %. The axis 1 is the dominant gradient that determines the typology of *Piliostigma* formations.

All conditional effects on the variance of species variables are significant although their marginal effects were relatively weak (Table 7). The automatic forward selection of environmental variables by CANOCO showed that rainfall explained most of the variance (0.30), pH_{water} and total nitrogen explaining only 0.10 and 0.13 respectively. The matrix of species-canonical axes relationship and pedoclimatic variables shows negligible relationships between the axes (Table 8). The rainfall variable gives the strongest relationship (negative) with the axis 1 ($r = -0.73$) while the total phosphorus presents the strongest

positive relationship with the axis 1 ($r = 0.55$). The silt content shows the strongest relationship with the axis 2 ($r = 0.77$).

Most of the pedoclimatic variables were negatively related. The most important relationship was found between sand and clay ($r = -0.82$), and between silt and sand ($r = -0.75$). Total phosphorus presents a strong relationship with clay ($r = 0.53$) and total nitrogen ($r = 0.75$). Organic carbon and pH_{water} had the weakest relationships with other variables.

The CCA analysis of vegetation indicated that axis 1 is significantly correlated with the climatic gradient ($r = -0.73$) and the axis 2 with the silt ($r = -0.77$). The CCA-biplot of species and environmental variables (Fig. 4) shows the relationship between the species distribution and environmental variables governing the distribution and pattern of *Piliostigma* associations. The *P. reticulatum* association is characterized by adaptation to low rainfall, and to soil with sandy texture and

Table 7. Marginal effects (independent of the variables) and conditional effects on the variance of pedoclimatic variables obtained from forward selection in CANOCO and arranged by decreasing order of lambda value (when $P < 0.05$, the conditional effects are significant).

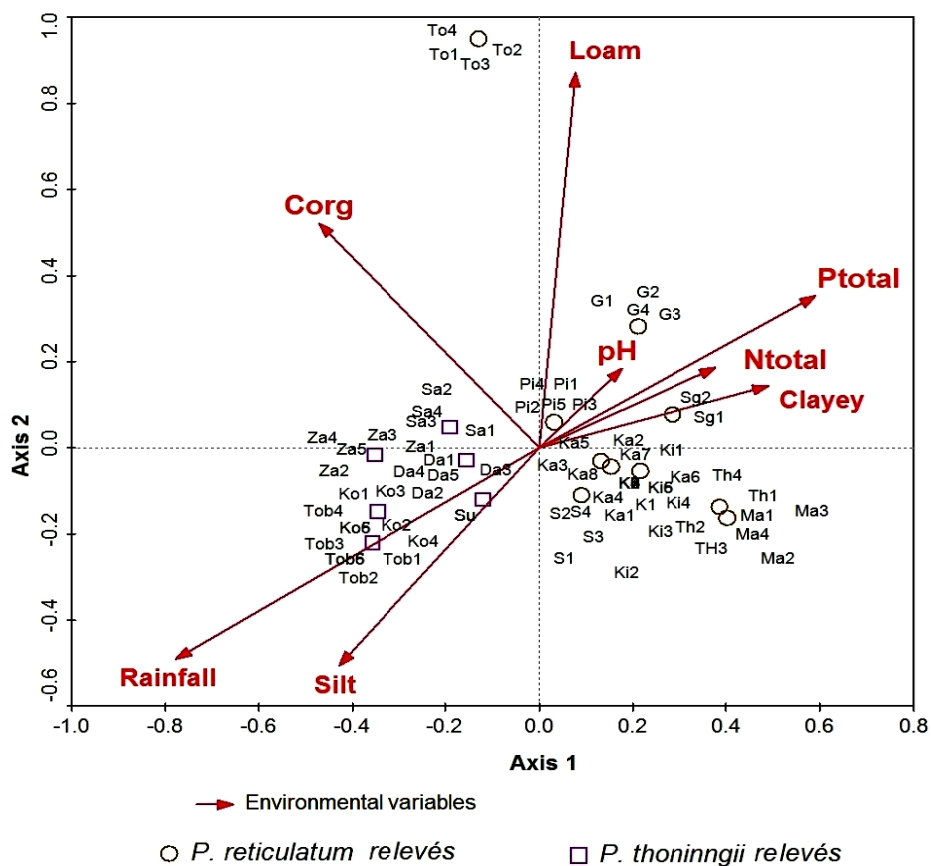
Marginal effects			Conditional effects		
Variables	Lambda 1(λ_1)	Variables	Lambda A(λ_A)	P	F-value
Rainfall	0.3	Rainfall	0.3	0.002	5.41
P_{total}	0.23	Silt	0.2	0.002	3.88
C_{org}	0.2	Sand	0.19	0.002	3.8
Clay	0.19	Clay	0.12	0.002	2.3
Sand	0.18	P_{total}	0.11	0.002	2.18
Silt	0.18	$\text{pH}(\text{H}_2\text{O})$	0.08	0.01	1.67
N_{total}	0.13	C_{org}	0.08	0.008	1.69
pH_{water}	0.1	N_{total}	0.08	0.002	1.92

C_{org} = organic carbon, P_{total} = total phosphorus, N_{total} = total nitrogen.

Table 8. Matrix of relationships species - canonical axes - pedoclimatic variables.

	Sp. Axis 1	Sp. Axis 2	Sp Axis 3	Sp. Axis 4	Env. Axis 1	Env. Axis 2	Env. Axis 3	Env. Axis 4
Sp. Axis 1	1							
Sp. Axis 2	-0.05	1						
Sp. Axis 3	-0.03	0	1					
Sp. Axis 4	-0.04	0.09	0.05	1				
Env. Axis 1	0.94	0	0	0	1			
Env. Axis 2	0	0.88	0	0	0	1		
Env. Axis 3	0	0	0.70	0	0	0	1	
Env. Axis 4	0	0	0	0.69	0	0	0	1
Clay	0.46	0.13	-0.42	-0.14	-0.49	0.14	-0.60	-0.20
Sand	-0.40	-0.44	0.47	-0.1	-0.43	-0.51	0.67	-0.14
Silt	0.07	0.77	-0.28	0.14	0.08	0.87	-0.40	0.20
pH _{water}	0.07	0.16	0.04	0	0.18	0.18	0.05	0
C _{org}	-0.44	0.46	0.03	-0.26	-0.47	0.52	0.05	-0.38
N _{total}	0.35	0.16	0.20	-0.28	0.38	0.19	0.29	-0.40
P _{total}	0.55	0.31	-0.08	-0.3	0.59	0.35	-0.11	-0.43
Rainfall	-0.73	-0.43	-0.16	-0.07	-0.78	-0.49	-0.22	-0.11

Sp= species, Env.= environment, C_{org}= organic carbon, N_{total}= total nitrogen, P_{total}= total phosphorus.

**Fig. 4.** The species-environment variables biplot of CCA with pedoclimatic variables jointly reflecting species distributions along gradient of environmental variables.

low carbon content. The *P. thonningii* association was more related to clay soil with high total N and P.

Discussion

Richness and diversity of the Piliostigma associations

The overall species richness reported in this study accounts for nearly one third of native woody species found in the country. Fontes & Guinko (1995) have reported that the woody flora of the country comprises 188 species. Six of the 79 species encountered (*Adansonia digitata*, *Anogeissus leiocarpa*, *Bombax costatum*, *Parkia biglobosa*, *Prosopis africana*, *Vitellaria paradoxa*) are classified as “vulnerable” according to their conservation status at the national level. Three of the species (*Pterocarpus lucens*, *Vitex diversiflora*, *Ximenia americana*) are “threatened” while four are listed as “overexploited” and at risk of extinction in the north (*Annona senegalensis*, *Daniellia oliverii*, *Diospyros mespiliformis*, *Entada africana*, *Securidaga longepedunculata*). The abundance of these species in our plots was very low, indicating a need of reintroduction to save them from local extinction and to maintain a viable population size. These results differed from those reported by Traoré (2008) for the Eastern part of Burkina Faso in the south-sahelian to south-sudanian phytogeographic zones; he reported 3 to 7 species in 900 m² in *Acacia* populations. The differences in species composition between sites might be due to micro-site factors. Indeed, in semiarid ecosystems species occurrence is determined by moisture, soil characteristics, landscape position (Menaut *et al.* 1995; Scholes & Walker 1993) and species-specific growth requirements. *Piliostigma* species are of shrubby shape with low branches which act like a windbreak to stop some of the soil particles driven by the wind, or by surface run-off. In addition, because of the canopy structure, the soil humidity under *Piliostigma* individuals remains higher thanks to leaf litter accumulation under canopies. Such conditions create a specific biotope and allow the establishment of shade-tolerant species (Girvinish 1999). Association of species with those factors and specialization for particular microhabitats contribute to explaining the observed species diversity. This may contribute to the high floristic diversity under *Piliostigma* canopies and in consequence the high species richness of the *Piliostigma* associations.

Species diversity was higher in the *P. thon-*

ningii association at low latitudes. The values of the diversity indices reported for the *Piliostigma reticulatum* association was 1.56 for the Shannon diversity index and 0.61 for the equitability index. For *P. thonningii*, the corresponding values were respectively 1.92 and 0.63. *Piliostigma* associations have low Shannon diversity indices, according to the Magurran (2004) threshold. The latitudinal variation is in agreement with previous studies which indicate a gradual increase in species richness from north to south in most parts of the country (Schmidt *et al.* 2005). This gradient corresponds to an increase in precipitation. The values of *Piliostigma* diversity indices found in the present study were low compared to other studies, notably those reported by Paré *et al.* (2010) for the south-soudanian zone - 1.73 and 0.87 on protected sites and 1.83 and 0.88 on non-protected sites. Nikiéma (2004) reported values of 1.95 and 0.86 for sub-sahelian sites in Burkina Faso. In the north-sudanian zone (Tiogo forest, State Forest Reserve), Savadogo *et al.* (2007) reported values of Shannon diversity ranging from 1.33 and 4.34 in different landscapes patches. Such differences could be explained by the effect of site-specific conditions and heterogeneity (soil mosaic), which influence the woody diversity in the savanna (Menaut *et al.* 1995). In seasonal dry forest, local site factors such as the presence and size of canopy gaps, soil properties, anthropogenic disturbance, and total annual precipitation, may have important effects on tree species richness, composition, abundance, and structure in seasonal dry forest (Gillespie 1995; Segura *et al.* 2003). In addition, anthropogenic disturbances such as fire, grazing and fuel-wood collection can cause spatial variability in the woody diversity (Paré *et al.* 2010). For Lescuyer (2005), the first reason for depletion of biological diversity is over-exploitation, which leads to landscape and habitat fragmentation. *Piliostigma reticulatum* is a robust species, persistent in drought conditions, well adapted to the degraded soil, and pioneer in old fallows (Yélémou *et al.* 2007). *Piliostigma thonningii*, in its ecological zone, shows the same relation to the other plant species. The high diversity values obtained for *P. thonningii* could be explained by the fact that the environmental conditions were favourable in the south-sudanian zone, which received more rainfall as compared with the other zones.

The number of diagnostic species of the *Piliostigma* associations increases with the rainfall gradient. The *P. reticulatum* association which extends from the south sahelian to the north

sudanian zone had 10 diagnostic species, whereas 30 diagnostic species were recorded for the *P. thonningii* association, situated in the south sudanian zone. Furthermore, the *P. thonningii* association is marked by a higher differential value of species than for those of the *P. reticulatum* association. The combination of a weak beta diversity and high species richness could explain the narrow fidelity of most species recorded in the relevés, as indicated by Traoré (2008).

The DCA indicated a clear floristic distinction between relevés of the *P. reticulatum* and *P. thonningii* associations, which translates into an individualization of these different associations. However, like all ecological phenomena, the fidelity of a species to an association and the concept of diagnostic species are especially linked to the scale of the study, particularly if the length of the gradients is short (Traoré 2008). Furthermore, diagnostic species at a local level can lose their consistency when a regional scale is considered (Kuzelova & Chytrý 2004).

The *P. reticulatum* association, situated in the south sahelian and north sudanian zones, is characterized by only a few diagnostic species. The low number of diagnostic species could be explained by the fact that generally this environment is relatively dry, which leads to competition for water; the woody species remain sparsely distributed, increasing the water-use efficiency (Ozinga *et al.* 2004). The substantial number of diagnostic species for the *P. thonningii* association and their dependence on *P. thonningii* could be explained by the greater clustering of *P. thonningii* individuals southwards. Also, the litter accumulation under the *Piliostigma* canopy improves the regeneration conditions for many species by increased levels of moisture and nutrients.

The *P. reticulatum* and *P. thonningii* associations include dominant species, as indicated by the *Phi* coefficient values. The *Piliostigma* associations often host a large cohort of species. *Combretum micranthum* is dominant in the south-soudanian and north-soudanian zones, and *Annona senegalensis*, *Dichrostachys cinerea*, *Securinega virosa* and *Strychnos spinosa* abound in the south-sudanian zone (Ouédraogo 2006; Thiombiano 1996). The scale of our study and the impact of man-made disturbances could also explain the weak fidelity of these species. The concept of species fidelity is dynamic in time and space, and seems linked with species adaptation to the disturbed environment. However, *Piliostigma* associations have *Phi* coefficients above 18,

indicating that they are again relatively clearly defined despite an increasingly hostile environment.

Vegetation-environment relationship

Piliostigma associations are characterized by low beta diversity (length of the gradients) and moderate alpha diversity values. DCA analyses of the relevés show the floristic heterogeneity of the *Piliostigma* associations. The *P. reticulatum* relevés extend over a vast zone along the first gradient (the rainfall axis), from the south-sahelian to the south-sudanian zone. This is an indication of a high tolerance of this species to drought. The great importance of rainfall seasonality as well as decrease in the annual rainfall and increase in evapotranspiration reduces the occurrence of some species particularly on a broad scale where there is a strong south-north rainfall gradient from the south-sudanian zone to the sahelian zone associated with vegetation changes (Schmidt *et al.* 2005).

The floristic relevés To1 to To3 (Fig. 3), with values on the Axis 1 comparable with those of *P. thonningii* relevés, were found in a flooded environment along a billabong of the Mouhoun river. The particular edaphic conditions (moisture and nutrient status) there could explain the presence of *P. reticulatum* relevés close to *P. thonningii* relevés. Previous studies have shown that microhabitat specialization with regard to topography and soil characteristics can affect the distribution of several plant groups, including tropical trees (Swaine 1996). Indeed different species can be specialized along moisture gradients (Hubbell 1995). *Piliostigma thonningii* relevés were found under high rainfall in the south-soudanian zone. Two variants of *P. thonningii* floristic relevés were identified toward the south. In the south-soudanian zone, *P. thonningii* individuals are mixed with numerous other species. However, in the extreme south *P. thonningii* individuals are found with large canopy and large foliage and often constitute a monospecific population.

The analysis of floristic relevés by the CCA method taking into account the amount of rainfall shows that only 42 % of species variance is determined by the climatic gradient. In addition, only the first axis showed a clear relationship with the climatic variable. Climate plays a major role in determining vegetation distribution and composition in the tropical zones generally (Hahn-Hadjali 1998), and similarly in the structure and

composition of the *Piliostigma* associations. However, in the CCA analysis, only 26 % of the species variance was explained by pedoclimatic variables - 16 % less than the effect of rainfall variability. Despite this observed difference, all pedoclimatic variables had significant effects on species variation. The rainfall was the factor with the greatest influence, followed by the soil texture and chemical elements. This observation is in agreement with Devineau (2001), who reported that the soil nutrient content and water availability among habitats was an important factor in species distribution in the savanna. However, the pre-eminence of soil nutrients as a controlling factor for the distribution of savanna species is often emphasized (Klop & Prins 2008). Indeed, rainfall, through the different physical and chemical changes that it creates, is at the origin of sand constitution at the surface, and the deposition of silt and clay. These different phenomena could explain the positive correlation of rainfall with sand content, and the negative relationship with silt and clay.

Soil organic carbon and total nitrogen had weak relationships with soil texture. These variables are consequences of the influence of the plant canopy on soil features (Traoré 2008). Total phosphorus is highly correlated with total nitrogen and the clay fraction, although they are very often carried away by rainwater. Further, according the ORSTOM soils map of 1968 and 1973, the *Piliostigma* associations in our study zone are found on tropical ferruginous soils. These soils are representative of large tracts of the sudanian zone in Burkina Faso, and are characterized by a low content of carbon and nitrogen (Pallo 1998); they are shallow and often present harsh environmental conditions limiting seedling emergence and survival. The limited variation in soil type could also explain the marginal effects of soil texture and their low importance in species variance.

Conclusions

Piliostigma associations are characterized by a relatively high specific diversity despite the environmental conditions. They often consist of pioneer species on degraded land, and enhance the establishment of other species. Considering the extent of our investigated area, spreading from the north to the south of the country, and through several isohyets from the subsahelian zone to the south sudanian zones, the climate constitutes the

most important variable affecting the floristic composition of the associations studied. Because of the similarity of edaphic variables recorded for the *Piliostigma* associations studied, these factors explain little of the variance in the species data. In addition, when combined with the rainfall variable, the analysis of the CCA shows that some edaphic variables have a negative relationship with the dominant gradient. Despite the over-exploitation to which they are often subject, due to their sociocultural value, *Piliostigma* species are well present in the different ecological zones. This is an indication of a good adaptation which makes these species resilient to environmental variability. Due to the high biodiversity that they attract after their establishment these species are ecologically important and contribute to the resilience and maintenance of diversity in the ecosystems studied.

References

- Adekunle, V. A. J., A. O. Olagoke & S. O. Akindele. 2013. Tree species diversity and structure of a Nigerian strict nature reserve. *Tropical Ecology* **54**: 275-289.
- Bognounou, F., A. Thiombiano, P. Savadogo, J. I. Boussim, P. C. Oden & S. Guinko. 2009. Woody vegetation structure and composition at four sites along latitudinal gradient in Western Burkina Faso. *Bois et Forêt des Tropiques*, **300**: 29-44.
- Bognounou, F., M. Tigabu, P. Savadogo, A. Thiombiano, I. J. Boussim, P. C. Oden & S. Guinko. 2010. Regeneration strategies of five Combretaceae species at four latitudinal gradients in Sahelo-Sudanian zones of West Africa. *Annals of Forest Sciences* **67**: 306-315.
- Bosma, R. H., L. C. Zongo, A. Sané, C. Zoungrana & A. Soudré. 2004. Comparaison participatoire de trois méthodes d'engraisement des porcs dans les provinces du Sanguié et du Boulkiemdé au Burkina Faso. *Livestock Research for Rural Development* **16**: 2.
- Bruehlheide, H. 2000. A new measure of fidelity and its application to defining species groups. *Journal of Vegetation Science* **11**: 167-178.
- Chytry, M., L. Tichy, J. Holt & Z. Botta-Dukat. 2002. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science* **13**: 79-90.
- Dalle, S. P. & S. de Blois. 2006. Shorter fallow cycles affect the availability of noncrop plant resources in a shifting cultivation system. *Ecology and Society*

- 11(2) art 2 (on line).
- Darkoh, M. B. K. 2003. Regional perspectives on agriculture and biodiversity in the drylands of Africa. *Journal of Arid Environments* **54**: 261-279.
- Day, P. R. 1965. Particles fractionation and particle size analysis. pp. 545-567. In: C. A. Black (ed.) *Method of Soil Analysis*. Part 1: *Physical and Mineralogical Properties*. American Society of Agronomy, Inc., Publisher, Madison, Wisconsin, USA.
- Devineau, J.-L. 2001. Les espèces ligneuses indicatrices des sols dans les savanes et jachères de l'Ouest du Burkina Faso. *Phytocoenologia* **31**: 325-351.
- Dufrène, M. & P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monograph* **67**: 345-366.
- FAO. 2010. *Global Forest Resources Assessment 2010*. Main report: Food and Agriculture Organization of the United Nations, Rome. FAO Forestry paper 163.
- Fontes, J. & S. Guinko. 1995. Carte de la végétation et de l'occupation du sol du Burkina Faso. Ministère de la Coopération Française : projet campus (88 313 101).
- Gaston, J. K. 2007. Latitudinal gradient in species richness. *Current Biology* **17**: R574.
- Gauch. 1979. Variants of polar ordination. *Vegetatio* **40**: 147-153.
- Gillespie. 1995. Diversity, composition and structure of tropical dry forest in Central America. *Plant Ecology* **147**: 37-47.
- Girvnish, T. J. 1999. On the causes of gradients in tropical tree diversity. *Journal of Ecology* **87**: 193-210.
- Hahn-Hadjali, K. 1998. Les groupements végétaux des savanes du sud est du Burkina Faso (Afrique de l'Ouest). *Etudes Flore et Végétation du Burkina Faso* **4**: 3-79.
- Harrison, S. & E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* **22**: 225-232.
- Higgins, I. S., M. C. Shackleton & R. E. Robinson. 1999. Changes in woody community structure and composition under contrasting landuse systems in semi-arid savanna, South Africa. *Journal of Biogeography* **26**: 619-627.
- Hill, M. O. & H. G. Gauch. 1980. Detrended correspondence analysis - an improved ordination technique. *Vegetatio* **42**: 47-58.
- Houba, V. J. G., J. Vander Lee, I. Novozamky & I. Walinga. 1988. *Soil and Plant Analysis*. Part 5: Soil Analysis Procedures. Department of Soil Science and Plant Nutrition. Wageningen Agricultural Univ., the Netherlands.
- Hubbell, S. P. 1995. Towards a theory of biodiversity and biogeography on continuous landscapes. pp. 173-201. In: G. R. Carmichel, G. E. Folk & J. L. Schnoor (eds.) *Preparing for the Global Change: A Midwestern Perspective*. SPB Academic Publishing, Amsterdam, Netherlands.
- Hutchinson, J., J. M. Dalziel, F. N. Hepper & R. W. J. Keay. 1954. *Flora of West Tropical Africa: All Territories in West Africa South of Latitude 18° N and to the West of Lake Chad, and Fernando Poo*. Crown Agents for Oversea Governments and Administrations, London.
- Jongman, R. H. G., C. J. F. Ter Braak & O. F. R. V. Tongeren. 1995. *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, New York.
- Klop, E. & H. H. T. Prins. 2008. Diversity and species composition of West African ungulate assemblages: effects of fire, climate and soil. *Global Ecology and Biogeography* **17**: 778-787.
- Kumar, Suresh & Manish Mathur. 2014. Impact of invasion by *Prosopis juliflora* on plant communities in arid grazing lands. *Tropical Ecology* **55**: 33-46.
- Kuzelova, L. & M. Chytrý. 2004. Interspecific association in phytosociological data sets: how do they change between local and regional scale? *Plant Ecology* **173**: 247-357.
- Lambin, E. F., H. J. Geist & E. Lepers. 2003. Dynamics of land-use and land-cover change in tropical regions. *Annual Review of Environment and Resources* **28**: 205-241.
- Legendre, P. & E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* **129**: 271-280.
- Lehmann, A., J. M. Overton & M. P. M. Austin. 2002. Regression models for spatial prediction: their role for biodiversity and conservation. *Biodiversity and Conservation* **11**: 2085-2092.
- Lescuyer, G. 2005. La valeur économique de la biodiversité: Fondements, méthodes et usages, IEPF. Liaison Energie Francophone No 66- 87 1er et 2e trimestre, 66-68.
- Lortie, C. J., R. W. Brooker, P. Choler, Z. Kikvidze, R. Michalet, F. I. Pugnaire & R. M. Callaway. 2004. Rethinking plant community theory. *Oikos* **107**: 433-438.
- Magurran, A. E. 2004. *Measuring Biological Diversity*. Blackwell Science Ltd, USA.
- Marks, E., G. K. S. Aflakpui, J. Nkem, R. M. Poch, M. Khouma, K. Kokou, R. Sagoe & M. T. Sebastia. 2009. Conservation of soil organic carbon, biodiversity and the provision of other ecosystem services along climatic gradients in West Africa.

- Biogeosciences* **6**: 1825-1838.
- Menaut, J. C., M. Lepage & L. Abbadiel. 1995. Savanna, Woodlands and dry forest in Africa. pp. 64-92. *In: Seasonally Dry Tropical Forests*. Cambridge University Press, UK, USA.
- Nikiéma, P. 2004. *Establishment and Indigenous Management of Vitellaria paradoxa Gaerth. F. Parkland Systems in South-western Part of Burkina Faso: A Case Study of Torokoro Village*. M.Sc. Thesis, Kwame N'krumah University of Science and Technology, Kumasi, Ghana.
- Nyadoi, P., P. Okori., J. B. L. Okullo, J. Obua, S. Fluch, K. Burg & R. Jamnadass. 2014. *Tamarindus indica* L. patterns of diversity from the genetic to the niche-species level in East Africa. *Tropical Ecology* **55**: 19-32.
- Oliveira-Filho, A. T., N. Curi, E. A. Vilela & D. A. Carvalho. 1998. Effects of canopy gaps, topography, and soils on the distribution of woody species in a central Brazilian deciduous dry forest. *Biotropica* **30**: 362-375.
- Ouédraogo, A. 2006. *Diversité et Dynamique de la Végétation Ligneuse de la Partie Orientale du Burkina Faso*. Vol. Thèse de Doctorat unique, 195 Université de Ouagadougou.
- Ozinga, W. A., R. M. Bekker, J. H. J. Schaminée & J. M. Van Groenendael. 2004. Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology* **92**: 767-777.
- Pallo, F. 1998. La biomasse microbienne des sols sous formation naturelle dans la zone du Centre-Ouest du Burkina Faso, Séminaire International sur l'Amenagement Integre des forêts Naturelles des Zones Tropicales Sèches en Afrique de l'Ouest, Ouagadougou, Burkina Faso.
- Paré, S., M. Tigabu, P. Savadogo, P. C. Odén & J. M. Ouadba. 2010. Does designation of protected areas ensure conservation of tree diversity in the Sudanian dry forests of Burkina Faso? *African Journal of Ecology* **48**: 347-360.
- Savadogo, P., M. Tigabu, L. Sawadogo & P. C. Odén. 2007. Woody species composition, structure and diversity of a Sudanian savanna in Burkina Faso, West Africa. *Bois et Forêts des Tropiques* **294**: 5-17.
- Schemske, D. W. 2002. Ecological and evolutionary perspectives on the origins of tropical diversity. pp. 163-173. *In: R. Chazdon & T. Whitmore (eds.) Foundations of Tropical Forest Biology: Classic Papers with Commentaries*. University of Chicago Press, Chicago, IL.
- Schmidt, M., H. Kreft, A. Thiombiano & G. Zizka. 2005. Herbarium collections and field data-based plant diversity maps for Burkina Faso. *Diversity and Distributions* **11**: 509-516.
- Scholes, R. J. & B. H. Walker. 1993. *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge University Press, Cambridge.
- Segura, G., P. Balvanera, E. Duran & A. Perez. 2003. Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. *Plant Ecology* **169**: 259-271.
- Slot, M. & L. Poorter. 2007. Diversity of tropical tree seedling responses to drought. *Biotropica* **39**: 683-690.
- Sokal, R. R. & F. J. Rohlf. 1995. *Biometry. The Principles and Practice of Statistics in Biological Research*. 3rd edn. Freeman, New York, NY, US.
- Somé, A., J. S. Ouédraogo & D.-Y. Alexandre. 2000. Biodiversité et fonctionnement des écosystèmes post-cultureux de la zone soudanienne (Burkina Faso). pp. 422-430. *In: Floret et Pontanier (éd.) Vol. I*.
- Swaine, M. D. 1996. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *Journal of Ecology* **84**: 419-428.
- Ter Braak, C. J. F. & P. Smilauer. 2002. *CANOCO Reference Manual and CANODRAW for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. New York: Microcomputer Power, Ithaca.
- Ter Braak, C. J. F. & P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* **57**: 254-289.
- Thiombiano, A. 1996. *Contribution à l'étude des Combretaceae dans les Formations Végétales de la Région est du Burkina Faso*. Thèse de Doctorat 3^e cycle. Université de Ouagadougou.
- Tichy, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science* **13**: 451-453.
- Tichy, L. & M. Chytrý. 2006. Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science* **17**: 809-818.
- Traoré, S. 2008. *Les Formations à Acacia de l'Est du Burkina Faso: Typologie en Relation avec les Facteurs Pedoclimatiques, Prédictiones Spatiales et Fonctions sur la Dynamique du Carbone et de L'azote*. Thèse de Doctorat, Université de Ouagadougou.
- Vincke, C., I. Diedhiou & M. Grouzis. 2010. Long term dynamics and structure of woody vegetation in the Ferlo (Senegal). *Journal of Arid Environments* **74**: 268-276.
- Walkley, A. & I. A. Black. 1934. An examination of the degtjareff method for determining soil organic matter arid a proposed chromic acid titration

- method. *Soil Science* **37**: 29-38.
- Willig, M. R., D. M. Kaufman & R. D. Stevens. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics* **34**: 273-309.
- Wilmanns, O. 1989. *Ökologische Pflanzensoziologie*. 4th edn. Quelle & Meyer, Heidelberg.
- Yaméogo, G., B. Yélémou & D. Traoré. 2005. Pratique et perception paysannes dans la création de parc agroforestier dans le terroir de Vipalogo (Burkina Faso). *Biotechnologie Agronomie, Sociétés et Environnement* **4**: 241-248.
- Yélémou, B., B. Bationo, G. Yaméogo & J. Millogo-Rasolodimby. 2007. Gestion traditionnel et usage de *Piliostigma reticulatum* (D.C.) Hochst., dans le plateau central du Burkina Faso. *Bois et Forêt des Tropiques* **291**: 55-65.

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Appendix Table 2. List of all species recorded in the relevés, with authorities.

Species	Species
<i>Acacia dudgeoni</i> Craib.	<i>Gliricidia sepium</i> (Jacq.) Kunth.
<i>Acacia macrostachya</i> Rchb. ex G.Don	<i>Grevia flavescens</i> A. Juss.
<i>Acacia nilotica</i> (L.) Wild.ex Del.	<i>Grewia bicolor</i> Juss.
<i>Acacia pennata</i> Willd.	<i>Grewia flavescens</i> Juss.
<i>Acacia polyacantha</i> Willd.	<i>Grewia mollis</i> Juss.
<i>Acacia seyal</i> Del.	<i>Guiera senegalensis</i> J.F. Gmel.
<i>Acacia sieberiana</i> DC.	<i>Lannea acida</i> A. Rich.
<i>Adansonia digitata</i> L.	<i>Lannea microcarpa</i> Engl. & K.Krause
<i>Azelia africana</i> Person	<i>Lannea velutina</i> A. Rich.
<i>Albizia malacophylla</i> Walp.	<i>Lonchocarpus laxiflorus</i> Guill.& Perr.
<i>Albizzia chevalieri</i> Harms	<i>Maytenus senegalensis</i> (Lam.) Exell
<i>Annona senegalensis</i> Pers.	<i>Mimosa pigra</i> L.
<i>Anogeissus leiocarpus</i> (DC.) G.& Perr.	<i>Mitragyna inermis</i> (Willd.) O.Kuntze.
<i>Azadirachta indica</i> A. Juss.	<i>Nauclea latifolia</i> Sm.
<i>Balanites aegyptiaca</i> (L.) Del.	<i>Ozoroa insignis</i> Del.
<i>Bombax costatum</i> Pellegr.& Vuill.	<i>Parkia biglobosa</i> Benth.
<i>Bridelia ferruginea</i> Benth.	<i>Pericopsis laxiflora</i> (Benth.) Van Meeuwen.
<i>Burkea africana</i> Hook.	<i>Piliostigma reticulatum</i> (DC.) Hochst.
<i>Capparis corymbosa</i> Roxb.	<i>Piliostigma thonningii</i> (Schumach.) Milne-Redh.
<i>Cassia sieberiana</i> DC.	<i>Prosopis africana</i> (G.& Perr.) Taub.
<i>Cassia singueana</i> Del.	<i>Prosopis juliflora</i> (Sw.) DC.
<i>Combretum aculeatum</i> Vent.	<i>Pseudocedrela kotschy</i> (Schweinf.) Harms
<i>Combretum fragrans</i> F. Hoffm.	<i>Pteleopsis suberosa</i> Engl.& Diels
<i>Combretum glutinosum</i> Hochst. ex A.Rich.	<i>Pterocarpus erinaceus</i> Lam.
<i>Combretum micranthum</i> G. Don	<i>Pterocarpus lucens</i> Lepr.
<i>Combretum molle</i> R. Br.	<i>Saba senegalensis</i> (A.DC.) Pichon
<i>Combretum nigricans</i> Lepr. ex Guill.& Perr.	<i>Sclerocarya birrea</i> (A.Rich.) Hochst.
<i>Crossopteryx febrifuga</i> (G.Don) Benth.	<i>Securidaca longipedunculata</i> Fres.
<i>Daniellia oliveri</i> (Rolfe) Hutch.& Dalz.	<i>Securinega virosa</i> (Roxb. ex Willd.) Baill.
<i>Detarium microcarpum</i> Guill.& Perr.	<i>Sterculia setigera</i> Del.
<i>Dichrostachys cinerea</i> (L.) Wight & Arn.	<i>Stereospermum kunthianum</i> Cham.
<i>Diospyros mespiliformis</i> Hochst.	<i>Strychnos spinosa</i> Lam.
<i>Entada africana</i> Guill. & Perr.	<i>Tamarindus indica</i> L.
<i>Eucalyptus camaldulensis</i> Dehnh.	<i>Terminalia avicennoides</i> Guill. & Perr.
<i>Faidherbia albida</i> (Del.) A. Chev.	<i>Terminalia macroptera</i> Guill. & Perr.
<i>Feretia apodanthera</i> Del.	<i>Vitellaria paradoxa</i> C.F.Gaertn.
<i>Ficus gnaphalocarpa</i> (Miq.) Steud. ex A.Rich.	<i>Vitex simplicifolia</i> Oliv.
<i>Gardenia erubescens</i> Stapf & Hutch.	<i>Ximenia americana</i> L.
<i>Gardenia sokotensis</i> Hutch.	<i>Ziziphus mauritiana</i> A.Rich.
<i>Gardenia ternifolia</i> Schumach.	<i>Ziziphus mucronata</i> Willd.

A note "The complete data set is available from the authors."