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Differences between banded thickets (tiger bush) at two sites in West Africa

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Abstract. This paper deals with the influence of edaphic conditions on the spatial structure of banded thickets or tiger bush (*brousse tigrée*). It is based on two sites in West Africa, with similar climatic conditions but located on contrasting substrates. The spatial structure was described with standardized characteristics including thicket spacing, thicket/inter-thicket contrast, upslope/downslope asymmetry and species zonation throughout the vegetation band. Recruitment and senescence features of woody stands were emphasized in order to understand current dynamics. Data were collected on transects oriented perpendicular to the contours and so to the thickets as well. A standardized analytical procedure was applied to data from both sites to ensure consistent and thorough delineation of thickets.

The overall periodicity of thickets, the woody flora and the dominant species *Combretum micranthum* were similar at the two sites. However, thicket spacing, thicket/inter-thicket contrast and upslope/downslope floristic asymmetry of the thickets were higher in the less favourable site. Also seedlings were less abundant, with a greater dependence on pre-existing thickets.

Not all banded vegetation systems show sharp contrasts and are strongly asymmetric, since such characteristics are likely to be reinforced by adverse environmental conditions. As a consequence, current dynamics may be more diverse than expected. Quantified inter-site comparisons can greatly help to classify African banded vegetation systems and to discuss potential dynamic outcomes.

Keywords: Burkina Faso; Mortality; Niger; Recruitment; Seedling; Spatial pattern.

Nomenclature: Hutchinson & Dalziel (1954-1972).

Abbreviations: BD = site in Burkina Faso; BN = site in Niger; TBA = Total Basal Area; WR = Water Reserve.

Introduction

In Africa, tiger bush or '*brousse tigrée*' has been reported from Mauritania to Somalia and Sudan (MacFadyen 1950; Clos-Arceduc 1956; Boaler & Hodge 1964; Boudet 1972; White 1970; Wickens & Collier 1971; Lawesson 1995; Leprùn 1999). This vegetation type is composed of alternating, densely vegetated bands and bare areas

oriented parallel to the contour. Banded patterns have also been studied in Mexico (Cornet et al. 1992) and Australia (Mabbutt & Fanning 1987; Ludwig & Tongway 1995).

Vegetated bands accumulate scarce resources (soil, water, nutrients) that run off bare areas (Cornet et al. 1992; Ludwig & Tongway 1995; Seghieri et al. 1997). This process can be analysed in terms of a positive feedback loop that vegetation may exert on itself in arid climates (Wilson & Agnew 1992; Dunkerley 1997). However, the consequences of resource re-allocation in terms of patch structure and subsequent dynamics are less straightforward, even if several studies reported banded systems with: (1) strong contrast between thicket and inter-thicket; (2) strong asymmetry between upslope and downslope parts of a thicket; (3) clear ecological zonation with distinct species (and/or life stages) occurring along the slope.

From these elements certain papers inferred peculiar vegetation dynamics such as thicket migration against the slope (Cornet et al. 1992; Montaña 1992; Thiéry et al. 1995), whereas other authors remain sceptical (White 1970; Wickéns & Collier 1971; Mabbutt & Fanning 1987; Couteron et al. 1996) or at least circumspect (López-Portillo 1996; López-Portillo & Montaña 1999). Most available field characterizations nevertheless dealt with banded systems that were located under rather arid situations – annual rainfall 150-400 mm and values for ETP (potential evapotranspiration according to Penman) of ca. 2000 mm – whereas extensive areas of West African tiger bush are encountered when the annual rainfall is between 400 and 700 mm, for similar ETP-values (Hiernaux & Gérard 1999). A more favourable climate may determine different spatial structures and dynamic outcomes. Furthermore, banded systems were also observed on contrasting substrata (White 1971; Wickens & Collier 1971; Hiernaux & Gérard, 1999), the properties of which may influence the actual water balance experienced by vegetation.

The aim of this paper is to compare the spatial structure of two West African banded vegetation systems with similar rainfall conditions (> 400 mm/yr),

flora and human uses, but located on different substrates. The question addressed is whether contrast, asymmetry and species zonation (with related potential dynamics) are influenced by edaphic conditions. A consistent inter-site pattern quantification was attempted in terms of overall structure (thicket periodicity and size), thicket characteristics (contrast and asymmetry) and species distribution. Special attention was paid to spatial patterns of seedlings and dead trees, to obtain insights into present thicket dynamics.

Material and Methods

Study sites

One site (referred to below as BN) is located in South West Niger (13°30' - 13°40' N and 2°40' - 2°50' E), near Banizoumbou village (75 km east of Niamey). The second site (referred to below as BD) is located in northern Burkina-Faso (around 14° N and 2°30' W), near Bidi village (about 30 km north of Ouahigouya). The climate at both sites is semi-arid tropical with a long dry season (from October to May), alternating with a short rainy season (June to September). In Niamey the average annual rainfall was 613 mm between 1950 and 1967 but decreased with 20% between 1968 and 1985; during the same period Ouahigouya experienced a 30% decrease (Morel 1992).

The two study sites are located in the 'Sahelian transition zone', where most of the woody species are related to the 'Sudanian centre of endemism' (White 1983). Most of the woody plants were multi-stemmed. In both sites there were no perennial grasses, and the herbaceous cover was composed of annual grasses and forbs. *Cyanotis lannata* and *Microchloa indica* were dominant in BN, while *Andropogon pseudapricus* and *M. indica* were the most abundant in BD. Pastoral use was moderate in BN and low in BD. Both study sites displayed typical banded patterns with no indication of previous clearing or regular woodcutting.

In Niger, the banded pattern occurs only on the laterite-capped plateaux of 'terminal continental' sandstones, which are virtually flat (angle < 0.5% for the study site). The soils (27% clay and 56% sand) are thin, poorly developed with petroferric gravels originating from a cemented iron-pan that limit root penetration (Ambouta 1984; Seghieri et al. 1997). These soils have a low potential Water Reserve (WR) of 17 mm in the 0-60 cm layer (water content between 3.0 pF units and 4.2 pF units times soil depth; Hillel 1988). Soil moisture content was monitored over the 1991-1995 period by neutron probe (Galle et al. 1999). A temporary deep drainage occurred within thickets every year down to more than a depth of 5.60 m while the infiltration front extended barely beyond

50 cm in the inter-band zone; intermediate figures (1.60 m and 0.60 m) were found, respectively, for the upslope and downslope fringes of the thicket.

In northern Burkina Faso, tiger bush patterns occur either on old Palaeozoic sandstones or on granites of the Precambrian 'Mossi' shelf (Leprun 1999). We investigated tiger bush on deep granitic alterite (often more than 2 m), presuming that we would have more favourable edaphic conditions than on the iron-capped plateaux of Niger. The site is located on the upper part of a gentle slope (about 0.8%). Soils (10% clay and 70% sand) are poorly developed on the deep sandy-clay alterite, which is easily penetrated by roots. The potential WR of the substratum appeared higher than in BN (about 25 mm in 0-60 cm layer plus 40 mm in 60-130 cm; Guillet 1991), due to a deeper penetrable volume. Moisture within the first 30 cm of the soil was monitored gravimetrically during the 1994 rainy season. Only slight differences were found between the thicket and its fringes (Ouedraogo 1997).

Methods

Observations were carried out along parallel transects 2 m wide and 700 m long, with a spacing of 25 m and oriented perpendicular to the contours (i.e. a sampling strategy similar to the 'gradsect' approach; Gillison & Brewer 1985). Censuses were performed at the end of the rainy season (September). The height and the girth of the biggest stem (40 cm above the ground) were measured for all woody plants in each of the contiguous 2 m × 2 m quadrats. The state (dead or live) of each tree was noted. The herbaceous cover was visually estimated in each quadrat (in %). We considered individuals of more than 1.5 m in height as mature, i.e. a threshold that corresponds roughly to the ability for producing diaspores. Additional data on mature individuals of the less frequent woody species were recorded in 12 m × 12 m quadrats along the same transects to obtain representative samples of their populations. The total basal area of each species was calculated directly from the girth for mono-stemmed trees, and through specific regressions based on the girth of the biggest stem. (r^2 ranged from 0.7 to 0.8 with respect to species, for samples of 194 to 490 individuals.)

A standardized procedure for thicket delineation was necessary to enable consistent inter-site comparisons. Ludwig & Tongway (1995) used an objective procedure to locate discontinuities (i.e. boundaries) from transect data. However, in order to cope with low contrast band/inter-band patterns (as in BD), we emphasized peaks of local density of woody vegetation (i.e. the 'core' of thickets). From a data-processing standpoint, it meant using smoothing filters instead of edge detection

ones (Niblack 1986). Thicket identification was based on the distribution of mature woody individuals expressed into binary data (occupied quadrats vs. empty), for the sake of robustness. A median filter for binary data was used to identify stretches of the transect with a high frequency of occupied quadrats, subsequently referred as 'thickets'. (A median filter is well-known as a tool for reducing general noise while preserving the edges (Niblack 1986: 78).) Filtering was based on a moving window of five consecutive quadrats (10 m in the field). For each thicket, the location of the centroid was deduced from the distribution of all individuals found in the constituent quadrats. Quadrats not belonging to a thicket were assigned to either the downslope or upslope margins according to their relative distance to the nearest thicket edge. A thicket and its two margins constituted an 'element' of the overall banded pattern.

Margins and thickets were characterized according to the densities of woody individuals of a given category (species or size class). Results were illustrated by plotting elements into an equilateral triangle whose sides expressed the relative proportion of density or cover (%) in each of the three components. – This is an analogy of the soil texture class triangle. – Highly contrasting elements with higher vegetation proportions in the thicket were closer to the upper apex. Asymmetrical elements with higher proportions in the upslope margin were closer to the lower right apex, and *vice versa* for the downslope margin (see Fig. 1). Elements with homogeneous vegetation distribution tended to be located around the 'centre' of the triangle. For the two dominant species in each site, emphasis was placed on the density distribution of trees below 0.5 m tall, regarded as seedlings.

27 permanent plots (5 m × 5 m) were established on each site to assess the survival rate of new seedlings during their first rainy season. Three thickets were randomly selected along the transects, with three plots on the upslope margin, three inner plots and three plots on the downslope margin. New seedlings were tagged and registered at the end of one rainy season (in October 1993 in BD and 1994 in BN) from the presence of their cotyledon traces. Plots were revisited at the onset of the next rainy season (June).

For most of the results, two-way contingency tables resulting from cross-classifications of plant numbers according to site, height, species, location or condition (dead/alive), and sometimes age, were tested for independence between rows and columns using 'Fisher's exact test' (Sokal & Rohlf 1995). This test is based on the hypergeometrical distribution and on the number of individuals in the cells of the tables, although it enables indirect comparisons between proportions. Mean values of a quantitative variate (e.g. height) have been compared through *t*-test (Sokal & Rohlf 1995).

Results

Comparison of the overall woody cover

There were 11 thickets per transect in BN and 12 in BD. Along the slope, the mean width of thickets was 9.5 m (S.D. = 7 m) in BN and 11 m (S.D. = 8.5m) in BD. The mean width of bare area was 50m (S.D. = 28 m) in BN and 41 m (S.D. = 21) in BD. Thicket centroids were located 60m apart (S.D. = 28m) in BN and 52m apart (S.D. = 32m) in BD. Consequently the two sites showed a pattern scale of similar size. *Combretum micranthum* dominated the woody cover in the two sites (Table 1), accounting for 69% of mature individuals in BN (72% in BD), and for 60% and 57% respectively of the total basal area (TBA). The mean height of its mature individuals (2.4 m in BN and 2.6 m in BD) did not differ significantly according to a *t*-test.

Woody vegetation was denser in BN than in BD. The most abundant species after *C. micranthum* were *Guiera senegalensis* (13% of TBA) and *Combretum nigricans* (14% of TBA) in BN, and *Pterocarpus lucens* in BD (28% of TBA). Its mature trees were 4.2 m tall on average (S.D. = 2.2 m). Trees taller than 5 m were scarcer in BN than in BD, accounting respectively for 0.8% and 17% of the TBA. Also seedlings (below 0.5m in height) were less abundant in BN than in BD. In BN, 49% of them were *C. micranthum* and 43% were *Guiera*. In BD 48% were *P. lucens* and 40% were *C. micranthum*. Finally, *P. lucens* was not found at all in BN, although all other species were found in both sites.

Species distribution within 'elements' of the pattern

Mature individuals were cross-classified according to species and location within the pattern. Some species, were too scarce to yield significant results (Fisher's exact test) whatever the site (*Cadaba farinosa, Lannea acida, Maerua angolensis, Pterocarpus erinaceus*). Five species yielded significant results on both sites. In BN (Table 2a), the relative distributions discriminated species that were more frequent in the upslope margin (mainly *Boscia salicifolia*) vs. species that were more frequent

Table 1. Main characteristics of woody stands. Specific densities refer to mature individuals.

	BN	BD
Total basal area (m²/ha)	7.9	3.1
Density of mature individuals (N/ha)	1565	550
Density of trees with height > 5 m (N/ha)	8	15
Density of *Combretum micranthum* (N/ha)	1080	413
Density of *Guiera senegalensis* (N/ha)	247	20
Density of *Combretum nigricans* (N/ha)	81	< 1
Density of *Pterocarpus lucens* (N/ha)	-	43
Density of seedlings for all species (N/ha)	5800	9100

Table 2. Contingency table of species distributions within elements of the pattern (based on mature individuals). Each cell is tested for independence between rows and columns (i.e. a similar distribution whatever the species) using Fisher's exact test. Symbols + and − express the sign of the departure from the null assumption; $p < 0.001$ unless otherwise stated: ** $= p < 0.01$; * $= p < 0.05$. In bold: species yielding significant results on both sites.

	Upslope margin	Thicket	Downslope margin
a. BN site			
Boscia salicifolia	+	− **	−
Guiera senegalensis	+	−	−
Combretum nigricans	NS	NS	− *
Commiphora africana	− *	+	−
Acacia macrostachya	NS	+ *	NS
Boscia angustifolia.	−	NS	NS
Grewia flavescens	−	+	NS
Combretum micranthum	−	+	+
Acacia ataxacantha	NS	+	+
Gardenia sokotensis	NS	+ *	+
b. BD site			
Boscia senegalensis	+	−	+
Guiera senegalensis	+	−	NS
Pterocarpus lucens	+	−	NS
Piliostigma reticulatum	+	−	NS
Gardenia sokotensis	+ *	+	− **
Acacia ataxacantha	−	+	− **
Combretum micranthum	−	+	NS
Grewia flavescens	−	+	NS
Dichrostachys glomerata	NS	NS	+ *
Grewia bicolor	NS	− *	+ *

in both the thicket and the downslope margin (*Acacia ataxacantha, C. micranthum, Gardenia sokotensis, Grewia flavescens*). Only one rather scarce species (*Commiphora africana*) was clearly more frequent in the thicket than in either margin. In BD (Table 2b), certain species appeared more frequently in the upslope margin, whilst others had a relatively higher frequency in the thicket. However, most species had similar relative frequency in the downslope margin. There was no floristic similarity between thicket and downslope margin, whereas some similarity could be observed between the two margins.

Spatial distribution of seedlings within 'elements' of the pattern

Triangles of vegetation proportions were used to compare the distribution of the density of the dominant species seedlings (below 0.5 m) and the herbaceous cover between the two sites. Points concerning the density of *C. micranthum* seedlings were concentrated in the upper apex of the triangle for both sites (densities were higher in the thicket than in the margins; Fig. 1a). However, for BD, most points were located at a greater distance from the upper apex than for BN, denoting less

contrasted densities between thickets and margins. Furthermore, some 'elements' had seedlings only in the margins of the thickets. In BN, *Guiera* had denser seedling populations in the upslope margin of most elements (Fig. 1b), although 9% of them contained no seedlings. In BD, *Guiera* seedlings (not plotted) tended to be on both margins but their density was low (only 320 individuals/ha). In BD, seedlings of *P. lucens* were quite evenly distributed (Fig. 1b), with no preferential pattern. The herbaceous cover tended to be higher in the upper margins in BN, whilst evenly distributed in both margins in BD (Fig. 1c).

To confirm these results, the relative distributions of seedlings of the dominant species were compared from a contingency table (Table 3). In BN, the relative distribution of *C. micranthum* seedlings had a significant peak within the thicket and a significant depression outside ($p<0.001$). In BD, the relative distribution of *C. micranthum* seedlings had significant peaks in upslope and downslope margins. Consequently, the proportion of *C. micranthum* seedlings inside the thicket was much higher in BN (52%) than in BD (22%). In BN, the absolute distribution of *Guiera* seedlings decreased from the upslope to the downslope margin, whereas the relative distribution was significantly higher upslope of the centroid, than downslope ($p<0.001$). Furthermore,
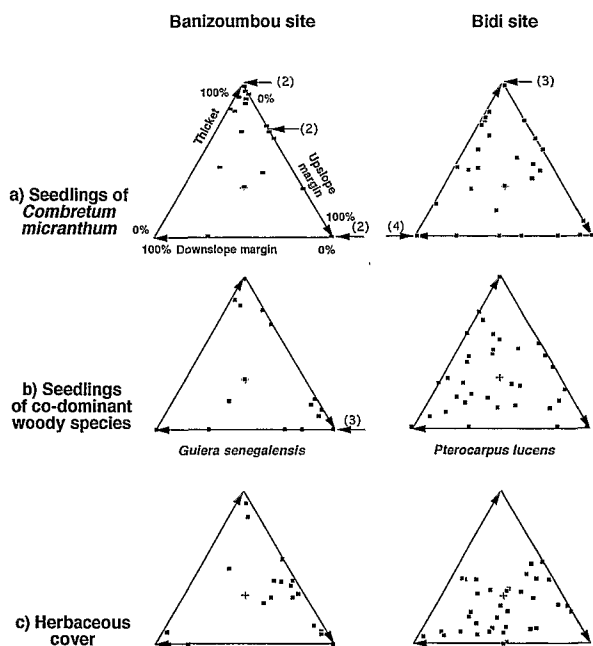

Fig. 1. Triangular classification of the elements according to vegetation distribution in thicket and margins. Overlapping elements are indicated by an arrow, the number of elements involved is in brackets. Comparison between BN and BD for seedlings of dominant species (i.e. *C. micranthum*) (**a**), seedlings of co-dominant species (**b**), and herbaceous vegetation (**c**).

Table 3. Contingency table of seedling distributions within elements. Each cell is tested for independence between rows and columns (i.e. similar distribution whatever species and site) using Fisher's exact test. Symbols + and − express the sign of the departure from the null assumption ($p < 0.001$ unless otherwise stated: [1]$p = 0.24$; [2]$p = 0.41$).

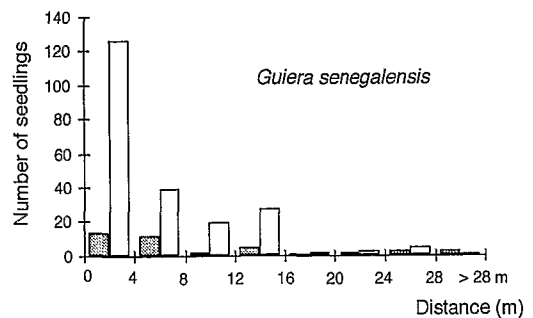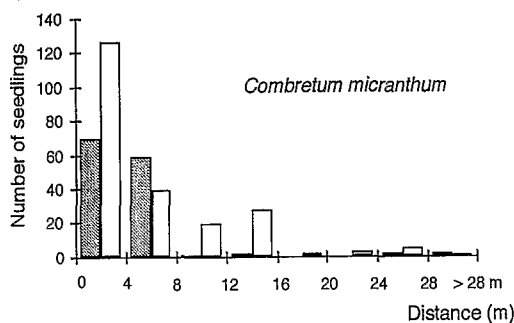|	In downslope margins	Inside thickets downslope the centroid	Inside thickets upslope the centroid	In upslope margins	Total number of seedlings sampled
Combretum micranthum (BN)	135 −	196 +	186 +	222 −	739
Guiera senegalensis (BN)	42 −	53 −	192 +	365 +	652
Combretum micranthum (BD)	340 +	132 − [1]	96 + [2]	492	1060
Pterocarpus lucens (BD)	434 +	96 −	60 −	598 +	1188

57% of the *Guiera* seedlings were located in an upslope margin against 37% inside a thicket. The relative distribution of *P. lucens* seedlings in BD was significantly higher outside and lower inside the thickets ($p<0.001$; Table 3).

The number of seedlings outside the thickets was plotted against the distance from the nearest thicket edge (Fig. 2). In BN, *C. micranthum* had 82% of its seedlings located within 8 m from a thicket edge against only 37% in BD. Seedlings of *P. lucens* had the most scattered distribution, with 53% of them at more than 8 m from a thicket edge. In BN, 42% of *Guiera* seedlings were located at more than 8 m from a thicket edge.

New seedling survival and mortality of mature trees

For each dominant species, Fisher's exact test was applied separately in BN and in BD to contingency tables that compare the distributions of surviving seedlings, with respect to the distribution of all new seedlings tagged one year before in 5 m × 5 m plots (Table 4). In BN, *C. micranthum* showed a lower proportion of surviving seedlings in upslope margins ($p < 0.05$). The survival rate of *Guiera* was 61%, from 28 tagged seedlings which were found exclusively in upslope margins. New seedlings of *C. micranthum* were denser within the thickets in both sites, but their initial number and survival rates were
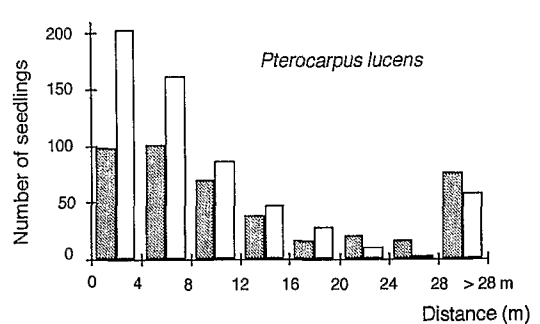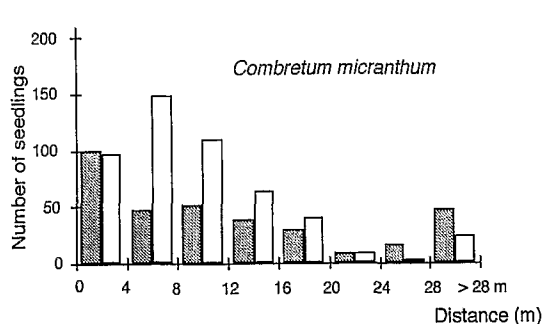
a) Banizoumbou site

b) Bidi site

Fig. 2. Histograms of the total number of seedlings sampled outside the thickets according to the distance from the nearest thicket edge in BN (**a**) and in BD (**b**). Grey = in downslope margins; white = in upslope margins.

Table 4. Contingency tables for the distribution of *Combretum micranthum* new germinants after one dry season. Each cell is tested for independence between rows and columns using Fisher's exact test. Symbols + and – = sign of the departure from the null assumption, in bold when significant.

Location	Total number of new germinants tagged	Number of surviving germinants	Survival rate
a) *Combretum micranthum* in BN site			
Upslope margins	47	8	17%
		– *p* = **0.013**	
Thickets	76	27	36%
		+ *p* = 0.09	
Downslope margins	20	8	40%
		+ *p* = 0.22	
b) *Combretum micranthum* in BD site			
Upslope margins	20	2	10%
		+ *p* = 0.34	
Thickets	62	4	7%
		– *p* = 0.60	
Downslope margins	17	0	0%
		– *p* = 0.31	

lower in BD than in BN whatever the location. In BD, the relative distribution of surviving *C. micranthum* displayed no significant difference in relation to location (Table 4). The same result was observed for *P. lucens* (not presented), but this species had a higher survival rate than *C. micranthum* (33% vs. 5%).

The same independence test was applied for each of the two sites to a contingency table that compared the distributions of dead and live mature *C. micranthum* (> 1.5 m tall). The number of dead trees of the other species was too low to be analysed. In BN the proportion of dead mature *C. micranthum* was significantly higher (*p* < 0.05) in the downslope margin, with no significant difference between the upslope margin and the thicket. In BD, the relative distribution of dead individuals was significantly depressed within the thicket (*p* < 0.01) and slightly higher in the upslope margin (*p* = 0.05). At BN, many dead stumps of unidentifiable species were localized near the downslope edge of the thickets (visual observation), where they constituted 'a senescence zone' *sensu* Ambouta (1984) and Seghieri et al. (1997). In BD, no similar feature was observed, since dead stumps were scarce and scattered all over the banded pattern (pers. obs.).

Discussion

Zonal similarities vs. inter-site differences

In spite of distinct substrata, the two vegetation systems shared several broad characteristics, both floristic and structural. They were dominated by the same species, *Combretum micranthum*, which is the backbone of these banded patterns. All other woody species were present on both sites, except *Pterocarpus lucens*. However, the absence of this species in BN can be related to a chorological limit, corresponding roughly to the Niger river, with no obvious ecological cause (Bortoli 1983).

In BN, thicket spacing was slightly higher than in BD (60 m vs. 52 m). According to field results (White 1971; Hiernaux & Gérard 1999), and theoretical modelling (Lejeune et al. 1999), there is a decreasing relationship between thicket spacing and mean annual rainfall. However, the observed spacing values were very similar, compared to more arid situations (e.g. 160 m found in Somalia for ca. 150-300 mm of rainfall; MacFadyen 1950). This corroborated the conclusion, deduced from rainfall and floristic data, that the two sites belonged to the same zonally distributed vegetation type. The shorter spacing in BD was, nevertheless, in agreement with other results, such as the greater importance of large trees, and the more extended herbaceous cover, which confirmed more favourable edaphic conditions (deep root penetrability and more sandy topsoil). Nonetheless, density of woody individuals and basal area were higher in BN, in spite of harsher soil conditions and of a less extended vegetation cover. These results may be explained by the efficiency of a more contrasted pattern to trap scarce resources (Noy-Meir 1973; Ludwig & Tongway 1995), with an adaptable balance between the inter-patch area (runoff source) and the patch size/ biomass (runoff sink). Hence, not only patch size and inter-patch distance (White 1971), but also contrast and asymmetry may be reinforced by adverse edaphic conditions. A similar conclusion may be drawn as to homogeneous soils along rainfall gradients, although this has never explicitly been stated in the literature.

Spatial dynamics of species

In BN, seedlings of *C. micranthum* were more frequent inside thickets and had rather high survival rates. In BD, seedlings were more frequent outside, but their survival rates were lower than in BN. In the two sites, regeneration from seeds did exist within the thickets at a level that can easily compensate the observed mortality rates. Recruitment may be limited by existing adults in thickets and by low survival rates outside, a kind of intra-specific control that might explain the persistence

of a fragmented woody cover (Winkler & Klotz 1997). Seedlings of *C. micranthum* did not appear along sharp transitions ('ecotone dependent') as did those of *Flourensia cernua* in Mexican banded vegetation (Mauchamp et al. 1993). Thicket extension on their periphery appeared possible during very favourable years, as occurred in the early 1990s. But there was no clear asymmetry in favour of the upslope side. In BD, the trend toward extension was bidirectional and weak, due to low survival rates. In BN, the upslope edge had a lower survival rate than that observed downslope. On both sites, the spatial pattern of dead individuals matched pretty well the distribution of seedlings, suggesting a kind of balance between trends toward extension and contraction (dead individuals occurred frequently in places where seedlings were abundant and/or had a high survival rate). All the above observations support a vision of stable, highly persistent, thickets of *C. micranthum*.

Most individuals belonging to other important species such as *P. lucens* and *Guiera* were located outside the thickets, despite a less favourable water budget. This distribution denoted lower water requirements than *C. micranthum*, and low competitive ability (hence the exclusion from the best places). In BN, *Guiera* was restricted to the upper margin, whilst, in BD, *P. lucens* was able to establish on both sides of the bands, sometimes far from the thickets. This species displayed abundant seedlings, high survival rates and few dead trees. Hence there was a trend toward an increase in density of *P. lucens* all over the area, which did not mean an extension of the thicket itself. Indeed, spatial distribution of mature *P. lucens* generally displays little aggregation (Couteron & Kokou 1997), and closed canopy stands have never been observed. Other woody species are too scarce to be thought of as influencing the overall vegetation dynamics.

Potential overall dynamics

In BN, seedlings of dominant woody species were highly dependent on the existing thickets, i.e. a strong patch/inter-patch contrast, but only *Guiera* showed a clear asymmetry in favour of the upslope side, as did the herbaceous cover. Conversely, the distribution of dead individuals proved asymmetric in favour of the downslope side. In BD, the contrast was weaker, and no substantial asymmetry was detected for either seedlings, herbaceous cover or dead individuals. Ecological zonation of species was observed on both sites, but this followed a slope oriented asymmetry in BN whereas it expressed a thicket vs. margin opposition in BD.

A slope-oriented zonation of species within the banded system was sometimes considered as supporting the hypothesis of thicket migration (Cornet et al. 1992;

Thiéry et al. 1995). A light-demanding species (e.g. *Guiera*) located on the upper edge has been supposed to pave the way to more water-demanding and shade-tolerant species (as *C. micranthum*). However, spatial zonation may also be interpreted in terms of persistent niche separation in a previously established pattern – see Keddy (1989) for examples – with minor change i.e. extension/contractions, resulting from rainfall fluctuation (Jeltsch et al. 1997). Results from the BN site did not allow such an interpretation to be discarded in favour of upslope migration. In BD, due to the absence of any obvious slope oriented asymmetry, the pattern is probably static. Several reasons can explain why woody patches may not move upslope, such as: (1) greater water infiltration in the core of the thicket than in the upslope zone (Cornet et al. 1992; Seghieri & Galle 1999); (2) sufficient water availability without runoff compensation, due to high rainfall and favourable edaphic conditions (as in BD); (3) extension of the rhizosphere of trees in the upslope zone (argument proposed by White 1970). Indeed, the size of adult trees may enable them to exert significant influences (favourable/adverse) on both sides of a patch, so 'trees could have become self-stabilizing' (Wickens & Collier 1971). Furthermore, certain theoretical models demonstrated that static banded systems may exist (Dunkerley 1997; Lejeune & Tlidi 1999). As a consequence, upslope migration should not be considered as an intrinsic property of all banded systems (White 1971; López-Portillo & Montaña 1999), since alternative dynamics are possible.

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