FLORISTIC AND STRUCTURAL PATTERN AND CURRENT DISTRIBUTION OF TIGER BUSH VEGETATION IN BURKINA FASO (WEST AFRICA), ASSESSED BY MEANS OF BELT TRANSECTS AND SPATIAL ANALYSIS

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Abstract. In semi-arid regions of West Africa, tiger bush vegetation is a striking example of a self-organised, banded vegetation pattern. It consists of regularly arranged woody stripes alternating with areas free of vegetation, whereby the distance between the vegetation stripes increases with decreasing precipitation. In this study, the floristic and structural pattern of tiger bush in Burkina Faso, its current distribution and the relationship between floristic and structural pattern were studied. Five subareas within the study area were chosen for a systematic field survey. Data collection took place along nine continuous belt transects. Occurance of ligneous species was recorded. Diversity indices, the relative frequency and the Importance Values of these species were calculated. For frequent species, quadrate variance and new local variance values (TLQV and NLV) were calculated, and the relationship between habitat factors and the occurrence of dominating woody species was tested. The scales of the underlying pattern varied and re-occurring patch sizes were not detectable. In many areas, tiger bush vegetation had completely disappeared or had been dramatically reduced over the last 50 years probably as a result of increased anthropogenic pressure and grazing. Still existing tiger bush stands are often degraded. 27 ligneous species from 11 plant families were recorded, *Pterocarpus lucens*, *Combretum micranthum*, *Guiera senegalensis* and *Boscia senegalensis* being most frequent species. Coverage of the woody layer was between 8 and 90%, with mean heights between 5 to 8m and low diversity indices. Soil crusts and the occurrence of woody species were always negatively associated with each other. *G. senegalensis* showed high coverage in the herb zone where rejuvenation of woody plants occurred. Where present, the ground layer of tiger bush vegetation was highly differentiated. Variance values for *P. lucens* were always higher than those of *C. micranthum* and *G. senegalensis*. With one exception, the size pattern in the different transects was not uniform. The variances of the diversity indices were small. Studying pattern of tiger bush has a potential to monitor further climatic and human impacts in semi-arid ecosystems; this study can be used as baseline documentation for future studies in the same area. Future studies should also look at seedling establishment and biomass distribution and at the plant-to-plant relationship and its role for the pattern organisation.

Keywords: *Sahel, Oudalan, vegetation structure, phytodiversity, quadrate variance analysis*

Introduction

Tiger bush

Landscape-scale patterns of stripes of vegetation alternate with bare soil attracted the attention of researchers early in the 20th century. Macfadyen (1950) was the first who scientifically described such landscape patterns vegetation in Africa, and Clos-Arceduc (1956) defined the term tiger bush (French *brousse tigrée*) for these patterns in semi-arid regions in West Africa. Today, tiger bush vegetation is often studied e.g. to analyse non-linear dynamics or to answer basic ecological questions such as self-organisation

(Barbier et al., 2006). West African tiger bush vegetation is one of the most striking examples of such self-organised, banded vegetation, although similar formations exist also in America, Asia and Australia (e.g. Cornet et al., 1992; Ludwig and Tornway, 1995; Dunkerley and Brown, 2002). In West Africa, tiger bush consists of regularly arranged woody vegetation stripes alternating with areas free of vegetation (see Valentin et al., 1999 and Couteron et al., 2000 for very good introductions and overviews). It has attained a very high attention in the Sahelian bioclimatic zone (see e.g. Kusserow and Haenisch, 1999; Leprun, 1999; Ludwig et al., 1999; Tongway et al., 2001). The vegetation stripes (bands) are typically oriented along the contours of gentle slopes. This zonation is not symmetric in relation to species composition or spatial structure.

The origin and dynamics of tiger bush vegetation have long been discussed controversially. Clos-Arceduc (1956) mentioned the role of termite hills during its genesis; however termite hills are not necessarily involved since they do not lead automatically to strip structures. Janke (1976) mentioned the influence of fluvio-morphodynamic processes. Early models showed that the spatial differentiation of tiger bush is the result of endogenous dynamics in combination with external (edaphic and climatic) factors (Thiéry et al., 1995; Lefever and Lejeune, 1997; Lejeune and Tlidi, 1999; Couteron et al., 2000); an anthropogenic origin is considered less probable (Couteron et al., 2000). In contrast, Barbier et al. (2006) found a strong interaction between human activities, in particular the grazing of domestic animals, and the appearance of periodic vegetation patterns. In more recent years mathematical models were developped to explain the genesis of tiger bush. Whereas these models were at the beginning based on competition for water (Klausmeier, 1999), more recent models included the dynamics of water, re-distribution of sediment in runon-runoff areas and seed dispersal and their following re-distribution (Saco et al., 2007). The density of the vegetation depends on the hydrology (Zonneveld, 1999), whereby the distance between the vegetation stripes increases with decreasing precipitation and vice versa. In contrast, Dunkerley and Brown (2002) showed for oblique vegetation banding in Australia that there was no correlation between the width of the vegetation-free area and the width of the woody stripes receiving run-off water from it. Not only water and its availability but also the accumulation and re-allocation of soil particles, soil surface features and nutrients are used to explain the structure and dynamics of tiger bush vegetation. Once established, tiger bush vegetation is self-modifying (Cornet et al., 1992). Some authors reported a gradual uphill migration of the vegetation stripes (see Sherratt, 2005), although this migration did not remain unchallenged (see Couteron et al., 2000; Dunkerley and Brown, 2002). Sherratt and Lord (2007) used a bifurcation model analysis to show that in semi-arid environments, such patterns exist for a wide range of rainfall levels, and that the pattern selection depends on the rainfall history. Lefever et al. (2009) highlighted the importance of root/crown ratio and demonstrated that the allometric relationship between this ratio and plant development played an essential part for the vegetation dynamics under limited water resources.

Zonation of tiger bush in West Africa

In the tiger bush of the Sahel zone in tropical West Africa, several zones are differentiated. The "run-off zone" is free of vegetation. Its top soil has erosion crusts which prevent the infiltration of precipitation water to a large extent, although this zone can not automatically be considered degraded. Precipitation water runs off superficially, following the slightly inclined surface and taking soil particles with it. The following "herb zone" is divided by some authors into a sedimentation and a pioneer zone. In this zone, soil particles from the run-off zone are deposited, while water penetrates still further into the woody stripes. Sedimentation crusts prevail. Annual plant species such as *Microchloa indica*, *Cyanotis lanata*, *Zornia glochidiata*, or *Schoenefeldia gracilis* dominate the vegetation aspect, the shrub *Guiera senegalensis* regenerates vegetatively (Thiéry et al., 1995). Benefitting particularly from the sedimentation and water input, the "herb zone" moves slowly upwards into the "run-off zone". Leprun (1999) measured the speed of this movement at 0.2 to 0.7 m per year. Phanerophytes follow the grasses during the succession (Thiéry et al., 1995). The "central zone" (or woody zone) represents the actual woody stripe of the tiger bush; the most common species is *Combretum micranthum* (Couteron et al., 2000). Run-off water penetrates into the centre of the stripe where woody plants are tallest and where water consumption is highest (Cornet et al., 1992). In fact, the woody plants receive an amount of water which corresponds to up to the quadruple amount of precipitation per area ("water harvesting system"). As a result, woody plants grow more luxuriantly and produce more biomass than they do outside the tiger bush under the same local climatic conditions (Valentin and d'Herbés, 1999). The ground layer in the central zone is developed only scarcely. Termites are very active in the soil and cause a high bioturbation. The silt proportion, humus and carbon contents are relatively high ("fertility islands" after Guillaume et al., 1999). The clay content is lower than outside of the central zone. Microbiotic soil crusts, composed of cyanobacteria (e.g. of the genus *Schizothrix*), eukaryotic algae, lichens, or liver mosses enhance the resistance against erosion. These microorganisms are responsible for the increased carbon content of these soils. Downwards from the central zone, the "senescence zone" (or degraded zone) follows, bearing structural soil crusts. The water supply is insufficient as no run-off precipitation water penetrates into this zone. The proportion of dying or already dead woody plants increases, the density of woody plants decreases accordingly. Fine soil material is washed off from the then open surface, at the same time aeolic material is deposited in the intermediate area.

This paper will present quantitative data about tiger bush vegetation in Burkina Faso. It tries to answer the following three questions: 1) what is the current distribution of tiger bush vegetation in northern Burkina Faso, 2) what can be said about the small-scale floristic and structural pattern of ligneous species in the different zones of tiger bush and 3) what are the most characteristic plant species building the vegetation bands? The dataset is used to show the relationship between plant diversity and spatial pattern of tiger bush and might be used as a baseline documentation against which changes in the same area can be detected in future studies.

Materials and methods

Study area

In Burkina Faso, tiger bush vegetation has been recorded only from the northermost provinces (Couteron and Kokou, 1997; Leprun, 1999; Couteron et al., 2000). Our study area comprised the two political provinces Soum and Oudalan in the Sahelian part of the country (*Fig. 1A*). The climate is tropical semi-arid with a long dry season (October to June) and a short rainly season (July to September). The mean annual precipitation with large fluctuations from year to year is 320mm (period 1968-1985, station Markoye;

Morel, 1992); mean annual temperature is about 30 °C. The water scarcity is increased by high evapotranspiration rates and surface run-off. Open savannas with often thorny shrubs and small trees prevail. Taller growing and denser vegetation exists only near watercourses. The poor, shallow soils of tiger bush habitats are slightly inclined and have a high portion of silt, clay and fine particles lying over sedimentary rocks or lateritic crusts. Below the sandy-loamy topsoil a coarse-grained sandstone or fine lateritic gravel follows usually in a sandy-loamy matrix. Outside the woody stripes, the pH value is < 5, within the woody stripes it is between 5 and 6 (Chappell et al., 1999).

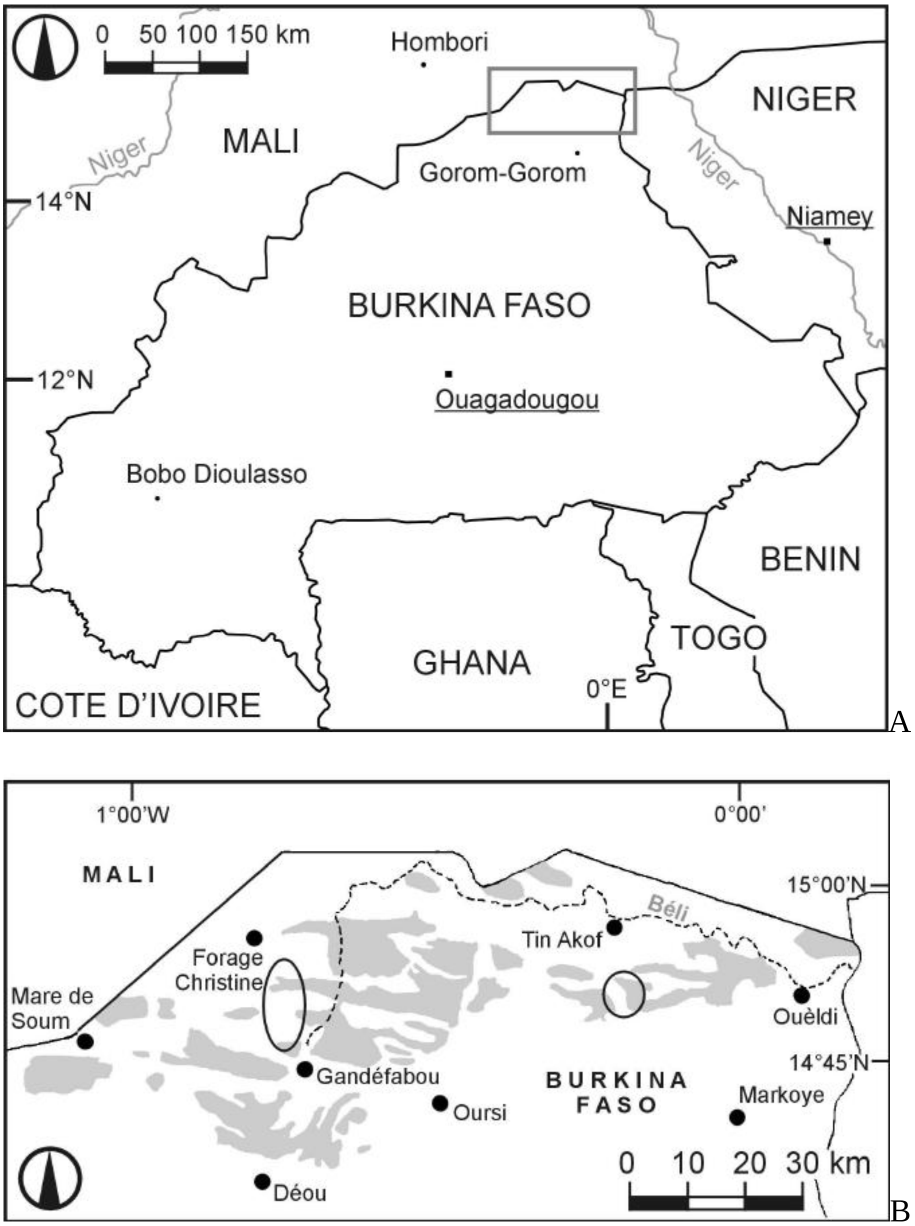

Figure 1. *A. Location of the study area in the north of Burkina Faso (grey rectangle). B. Study area with name of villages and locations as mentioned in the text. Grey areas show tiger bush vegetation, as shown on the most recent topographical maps, based on aerial photographs taken between 1958 and 1960. The black circles indicate the sub-areas which were selected for data collecting*

Data collecting

In preparation for the field survey, tiger bush vegetation in Burkina Faso's Oudalan province and the easternmost parts of Soum province was identified on the most recent topographic maps dating back to 1958 to 1960 (ND-30-XVII Djibo, ND-30-XVIII Dori, ND-30-XXIV In-Tillit, ND-31-XIII Téra; scale 1:200 000) which are based on black / white aerial photographs from the 1950s. The vegetation map of Burkina Faso produced by Fontès et al. (1994), based on satellite images, turned out to be not precise enough for our purposes. Certain areas within the study area where tiger bush vegetation was likely to be found were chosen for a systematic field campaign (subarea 1 between the villages Gandéfabou and Déou, subarea 2 south of Tin Akof, subarea 3 between Tin Akof and Ouèldi, subarea 4 in the triangle between Gandéfabou, Mare Soum and Forage Christine, and subarea 5 north-east of Gandéfabou (*Fig. 1B*). Other areas showing tiger bush vegetation on the topographic maps, for example north of the river Béli and south of Mare Soum, were excluded from further analysis for logistic reasons.

The subsequent field survey showed that tiger bush vegetation in subareas 1, 3 and 5 had completely disappeared or its extent had been dramatically reduced. The following data collecting concentrated therefore on the two subareas 2 south of Tin Akof and 4 in the triangle between Gandéfabou, Mare Soum and Forage Christine. In subarea 2, tiger bush vegetation existed mainly in degraded form, subarea 4 was the least anthropogenically influenced of the studied subareas with no permanent settlements nearby.

Data were collected along nine continuous belt transects in intact and degraded stands of tiger bush (*Table 2*), following a transect approach adapted from Couteron et al. (2000). The transects were positioned perpendicular to the central zone of a woody stripe, starting in the upper run-off zone and ending in the run-off zone further down. All transects were divided into continuous sampling plots of 2m length × 1m width. The total area sampled on 441 plots was 882 sqm. In each plot, all ligneous species, the number of individuals of each species and their maximum height (rounded to 50cm) were documented. Branches of neighbouring individuals growing over into the plots were included into the analysis. The following habitat parameters were recorded: presence of dense herbaceous/grass vegetation, termite hills and soil sealing / crusts.

Data analysis

For each transect, the total number of woody plant species as a measure of the α-diversity of a plant community (Whittaker, 1972) was calculated. For each transect plot, the number of woody plant species, the SHANNON diversity index H (Shannon, 1948) and the SIMPSON diversity index D (Simpson, 1949) were calculated. The SHANNON index is affected by the number of species and the dominance structure. It increases with an increasing number of species and with an increasing uniformity of the species' distribution. With only one species, H is 0. Its highest value is reached if all species are evenly distributed.The SIMPSON index takes values between 0 and 1; the higher it is, the more a particular species dominates the sample. Species area relationships were calculated.

The Importance Values of all recorded woody plant species were calculated. The Importance Value of a species is the sum of the relative density and the relative frequency of that species, divided by 2 (Maingi and Marsh, 2006). The Importance Value does not include the relative dominance, as this was not measured in the field.

Relative frequencies of the woody plant species were calculated in each transect and across all nine transects. It can be assumed that those plant species that have high frequencies in the transects display strong spatial patterns. Therefore, these species were selected for quadrate variance analyses (three-term local quadrate variance 3TLQV, new local variance NLV; Dale, 1999), using PASSAGE 1.0 (Rosenberg, 2001). Quadrate variance analyses determine the scale and size of the underlying spatial patterns and their variance: 3TLQV determines the patch size with the largest variance; 3NLV indicates the mean size of the smaller phase of the pattern. Random tests with 1000 iterations determined the 95% confidence intervals.

The association between grass cover, soil crusts and the occurrence of dominating woody species were tested with chi-square-tests for those transects where the number of samples was > 10. I followed Lebrun and Stork (1991-1997) for names of plant species.

Results

Current distribution of tiger bush in the study area

The field survey showed that tiger bush vegetation in northern Burkina Faso is far less widespread than compared to the situation in the middle of the 20th century. Although no quantitative data were available for all five subareas which would have allowed a more precise analysis, it became clear that between Gandéfabou and Déou (subarea 1), between Tin Akof and Ouèldi (subarea 3) and north-east of Gandéfabou (subarea 5), tiger bush vegetation had completely disappeared or had been dramatically reduced. In particular the former stands between Gandéfabou and Déou and between Tin Akof and Ouèldi do no longer exist; the areas previously occupied by tiger bush turned out to be in many cases either bare of vegetation, or individual trees and shrubs remain as remnants of the continuous woody stripes. Where tiger bush vegetation could still be found, it often exhibits signs of degradation (for example south of Tin Akof, subarea 2), with degraded tiger bush showing a lower vegetation cover in the central zone and being poorer in species. In the triangle between Gandéfabou, Mare Soum and Forage Christine (subarea 4), tiger bush forms a broad ecotone with the surrounding savanna vegetation on dune ridges. *Figures 2* and *3* show the different seasonal aspect of tiger bush near Gandéfabou in the dry and rainy seasons.

Figure 2. *Mid rainy season aspect of a tiger bush north of the village Gandéfabou; the dominant land-use form is extensive grazing by semi-nomadic herdsmen, hunting and fire wood collecting. The run-off zone is covered by a soil crust and for the most part free of vegetation. Individual grassy patches of vegetation, dominated by annual grasses such as Schoenefeldia gracilis are characteristic for the herb zone in which soil particles are deposited. Few woody species such as Guiera senegalensis may colonise this section. The actual woody stripe (central zone) can be seen in the background and on the right hand sight of the picture*

Figure 3. *Tiger bush near Gandéfabou towards the end of the dry season. In the dry season, the landscape aspect changes dramatically. Annual grasses have dried back, and most of the ligneous species have lost their leaves. The woody stripes of the tiger bush are more clearly visible, the interspace between two vegetation bands appears to be wider than during the rainy season; it can reach few hundred meters*

Floristic composition and diversity

In total, 27 ligneous species belonging to eleven plant families were documented in the transect plots and their direct vicinity. These 27 ligneous species constitute 39 percent of all phanerophytes occurring in whole region (Claude et al., 1991). Only seven species occurred in both sampling areas, the most frequent species (relative frequency > 5%) being *Pterocarpus lucens*, *Combretum micranthum*, *Guiera senegalensis* and *Boscia senegalensis*. Other ligneous species did not occur with high frequency or constancy. Five species were exclusive to one of the two sampling areas (*Table 1*). The four most frequent families were Combretaceae, Mimosaceae, Capparidaceae, and Tiliaceae. The total number of ligneous plant species per transect varied between 3 (transects 1 and 7) and 8 (transects 3, 4 and 9). There is a strong positive relationship between the length of the transects (= area sampled) and the number of ligneous species found in the transect plots. The species-area relationship is illustrated by Figure 4a and b, which show in double logarithmic presentation the cumulative number of species as a function of the area. The mean values of the SHANNON index of the transects were between 0,04 and 0,41 which is very low (*Table 2*). Transect 4 showed the highest SHANNON diversity value. The SIMPSON index was generally close to 1 indicating the dominance of only one species. Transect 4 showed the highest value.

Table 1. *List of ligneous plant species recorded in transects 1 to 9 of two subareas in the study area in the Sahelian zone of Burkina Faso. RF = relative frequency. Values from 1.49 to 55.22 in columns 4 to 12 are Importance Values, based on the relative density and the relative frequency of the species*

		RF	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Number of species			**3**	**6**	**8**	**8**	**6**	**4**	**3**	**6**	**7**
Species present in both sampling areas											
Pterocarpus lucens	Papilionaceae	41,3		7,69	3,70	20,00	40,00	52,73	44,12	28,00	55,22
Combretum micranthum	Combretaceae	25,0	33,33		7,41	20,00	53,33	20,00			17,91
Guiera senegalensis	Combretaceae	7,6			1,85		4,44	16,36			23,88
Boscia senegalensis	Capparidaceae	5,9	1,96	15,38	3,70	6,67				8,00	
Boscia angustifolia	Capparidaceae	2,7	1,96		3,70	3,33			5,88		1,49
Grewia bicolor	Tiliaceae	2,3				1,67	2,22		5,88	4,00	
Grewia tenax	Tiliaceae	2,2		3,85	1,85					8,00	
Species only present in subarea 2 (south of Tin Akof)											
Combretum aculeatum	Combretaceae	3,5		7,69	5,56	8,33					
Acacia spec. (winding)	Mimosaceae	3,0		11,54		6,67					
Grewia villosa	Tiliaceae	2,5		15,38							
Anogeissus leiocarpa	Combretaceae	0,6			3,70						
Feretia apodanthera	Rubiaceae	0,3				1,67					
Species only present in subarea 4 (Gandéfabou-Mare Soum-Forage Christine)											
Acacia laeta	Mimosaceae	1,5						1,82		6,00	1,49
Ziziphus mauritiana	Rhamnaceae	0,6					2,22				1,49
Acacia tortilis subsp. *raddiana*	Mimosaceae	0,4					2,22				
Commiphora africana	Burseraceae	0,3								2,00	
Piliostigma reticulatum	Caesalpiniaceae	0,2									1,49
Species in immediate vicinity of the transect plots											
Acacia erythrocalyx	Mimosaceae										
Acacia senegal	Mimosaceae										
Balanites aegyptiaca	Balanitaceae										
Bauhinia rufescens	Caesalpiniaceae										
Cadaba farinosa	Capparidaceae										
Calotropis procera	Asclepiadaceae										
Combretum glutinosum	Combretaceae										
Dalbergia melanoxylon	Papilionaceae										
Grewia flavescens	Tiliaceae										
Maerua crassifolia	Capparidaceae										

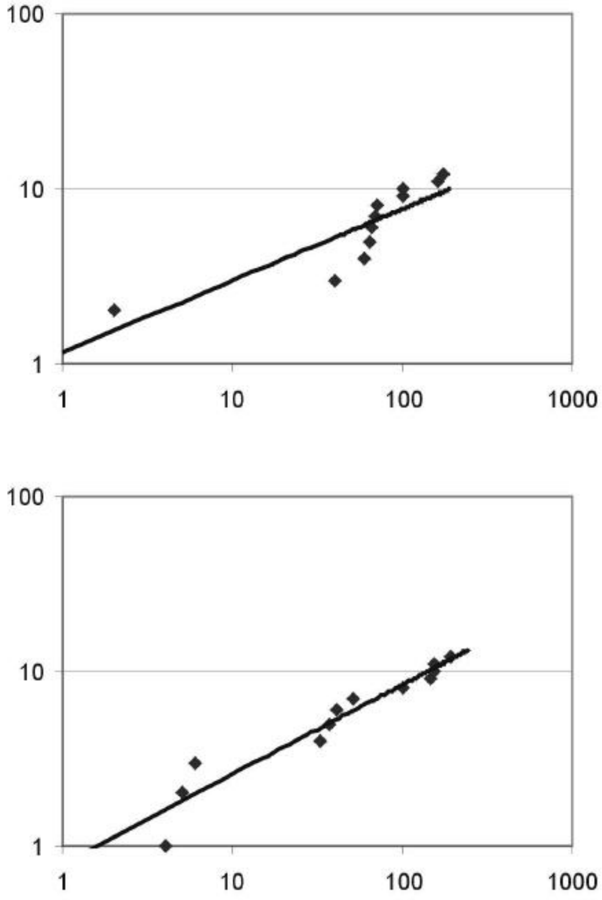

Figure 4. *Ligneous species-area relationships for the two subareas 2 (A) and 4 (B) on double logarithmic axes. In both subareas, there is a strong positive relationship between the number of ligneous species and the size samples area, although the stepping is a sign of a discontinuous habitat [R²(A)=0,7412; R²(B)=0,9197]*

Spatial structure

A clear zonation of the transects into four zones as described in the literature (run-off zone with soil crusts, herb zone with the pioneering ligneous plant species, central zone with high coverage of ligneous plants, and senescence zone) was identified only for transect 9. Transects 3, 5, 6, and 8 showed the initial stages of such a zonation, whereas the spatial structure of transects 1, 2, 4 and 7 did not correspond to this zonation at all. *Pterocarpus lucens* and *Combretum micranthum* were the dominant phanerophytes. Depending upon site conditions, the coverages of the woody layer varied between 8 and 90%, with a mean height of the vegetation between five to eight meters. In the centre of the woody strips (= central zone), which form at some localities impenetrable scrubs, the tiger bush reached heights of up to ten meters. The mean height of those vegetation plots which contained ligneous plant species was between 2,4m (transect 1) and 6,2m (transect 9). Soil crusts and the occurrence of woody species were always negatively associated with each other; the occurrence of woody species was not associated with high coverages of the herb layer (*Table 1*). Even in the otherwise bare areas of the run-off zone, some isolated bushes were present. Areas of abandoned, eroded termite hills were to a large extent free of vegetation.

Even if it may not be expected due to its name, the run-off zone was at least partly covered by vegetation. A high cover of the herbaceous ground layer and the soil crusts were always mutually exclusive. *Guiera senegalensis* achieved high coverage particularly in the herb zone. Towards the central zone, the vegetation became denser and taller. It reached maximum heights of 160cm and a maximum coverage of 95%. Protected by a dense ground layer, rejuvenation of woody plants, particularly of *Guiera senegalensis*, occurred. In the ground layer, the grasses *Panicum laetum* and *Eragrostis pilosa* were present, and *Schoenefeldia gracilis*, *Pennisetum pedicellatum*, *Enteropogon prieurii* and *Dactyloctenium aegyptium* were co-dominating.

In the central zone, a dense herbaceous cover or soil crusts were only rarely found. Species typical for the adjacent peneplain such as *Acacia tortilis* subsp. *raddiana*, *Balanites aegyptiaca* and *Calotropis procera* penetrated into the stands. In many cases, the central zone was open and impoverished in woody species, so that it became difficult to differentiate this zone from the senescence zone. In the senescence zone, the cover of woody species and the total number of species decreased and the stands were lower than in the central zone. In the ground layer, the vegetation reached coverages of maximally 95% and culmed up to 40cm. *Panicum laetum*, one of few Sahelian endemics and an important fodder plant for grazing lifestock, was constantly present.

Where present, the ground layer of tiger bush vegetation was highly differentiated. *Panicum laetum* was the most important species and dominant in all locations. Other important species in the ground layer were *Cassia obtusifolia* and *Eragrostis pilosa*. The floristic composition (*Panicum laetum*, *Cassia obtusifolia*, *Eragrostis pilosa*, and *Schoenefeldia gracilis*, *Enteropogon prieurii*, *Dactyloctenium aegyptium*, *Cenchrus biflorus*, *Tragus racemosus* and less frequently *Pennisetum pedicellatum*) allowed assigning it to the typical subcommunity of the *Schoenefeldia gracilis*-community (Müller, 2008). The vegetation culmed up to 65cm and covered up to 100%. In a few cases on silty substrate of the open areas, the floristic composition could be assigned to the phytosociological association Eragrostietum pilosae which is typical for low-lying areas of the peneplain in contact to depressions and the edges of seasonal ponds (Müller and Wezel, 2006)

Table 2. *Floristic and structural characteristics of the nine transects in the study area*

transect number	number of transect squares	number of squares with phanerophytes	total number of species	mean height [m]	Shannon-index		Simpson-index		number of species per square		association between woody species and	
					mean	**s.d.**	**mean**	**s.d.**	**mean**	**s.d.**	**dense herb cover**	**soil crusts**
1	51	17 (= 33%)	3	2,4	0,08	0,22	0,94	0,16	1,1	0,32	n.t.	n.t.
2	26	11 (= 42%)	6	2,8	0,24	0,34	0,84	0,22	1,5	0,66	2,2	n.t.
3	54	15 (= 28%)	8	2,9	0,08	0,2	0,95	0,14	1,1	0,34	n.t.	18,5
4	60	24 (= 40%)	8	3,8	0,41	0,37	0,72	0,24	1,7	0,68	3,3	17,5
5	45	35 (= 78%)	6	4,3	0,22	0,3	0,85	0,21	1,3	0,48	n.t.	n.t.
6	55	43 (= 78%)	4	4,7	0,1	0,27	0,93	0,17	1,2	0,37	n.t.	n.t.
7	34	18 (= 53%)	3	4,2	0,04	0,15	0,97	0,11	1,1	0,23	1,5	6,4
8	50	23 (= 46%)	6	2,8	0,13	0,26	0,91	0,18	1,2	0,41	3,7	n.t.
9	67	48 (= 72%)	7	6,2	0,28	0,33	0,81	0,23	1,4	0,54	n.t.	16,6

Abbreviation: n.t. = not tested. The Hypothesis H_0 *(A is not associated with presence of B) is rejected if* $Chi^2 > 3.8$ *at* $\alpha = 0.05$ *(one degree of freedom)*

Table 3. *Summary of the results of the quadrate variance analyses. Abbreviation: TLQV = three-term local quadrate variance, NLV = new local variance, and statistical correlation between structural indices and diversity indices, s.p.: size pattern [meter], *: variance within the 95% confidence interval*

A

transect number	**species**	**3TLQV**		**3NLV**	
		s.p.	**variance**	**s.p.**	**variance**
1	*Combretum micranthum*	20	2,64	18	1,60
4	*Combretum micranthum*	22	3,79	24	1,54
	Pterocarpus lucens	22	15,62	24	6,17
5	*Combretum micranthum*	28	14,91	26	4,08
	Pterocarpus lucens	28	44,22	10	18,86
6	*Combretum micranthum*	36	10,90	34	3,58
	Pterocarpus lucens	36	151,09	34	26,90
	Guiera senegalensis	36	3,52	8	1,15
7	*Pterocarpus lucens*	14	16,11	12	9,45
8	*Pterocarpus lucens*	32	8,87	32	4,16
9	*Pterocarpus lucens*	44	341,78	42	26,83
	Guiera senegalensis	44	10,02	8	3,43

B

transect number	**diversity index**	**3TLQV**		**3NLV**	
		s.p.	**variance**	**s.p.**	**variance**
1	Shannon-index	.	*	.	*
	Simpson-index	.	*	4	0,31
2	Shannon-index	16	0,32	12	0,15
	Simpson-index	10	0,29	8	0,32
3	Shannon-index	.	*	.	*
	Simpson-index	34	0,94	8	0,26
4	Shannon-index	6	0,12	.	*
	Simpson-index	34	0,54	34	0,23
5	Shannon-index	6	0,10	10	0,12
	Simpson-index	.	*	28	0,12
6	Shannon-index	.	*	.	*
	Simpson-index	36	0,54	.	*
7	Shannon-index	.	*	.	*
	Simpson-index	14	0,55	.	*
8	Shannon-index	.	*	30	0,04
	Simpson-index	6	0,30	6	0,35
9	Shannon-index	12	0,15	14	0,10
	Simpson-index	44	0,21	.	*

Results of the quadrate variance analyses

The scales of the patterns of Combretum micranthum and Pterocarpus lucens corresponded to each other, however the variance varied much (*Table 3*). Pterocarpus lucens showed its highest variance values in transects 5, 6 and 9. Its values were always higher than those of Combretum micranthum and Guiera senegalensis. With one exeption, the size pattern in the different transects was not uniform; only in the case of Guiera senegalensis the size pattern lied at 8m. The variances of both, the Shannon and the Simpson indices, were altogether small; in many cases they were within the 95% confidence interval (in *Table 3* marked with an asterix). For the Shannon index, the variance peaks were between 6 and 16 meters and for the Simpson index between 6 and 44 meters. The size of the diversity patterns (3NLV) varied between 10 and 30 meters (for the Shannon index) and between 4 and 34 meters (for the SIMPSON index).

Discussion

Current distribution of tiger bush in the study area

A direct comparison of historic aerial photographs of the study area with current ground-truthed satellite imagery (see e.g. Paré et al., 2008 for southern Burkina Faso; Brink and Eva, 2009) would have allowed quantifying the dynamics of tiger bush vegetation on a landscape scale and over a sufficiently long time span. However, this was not the focus of the presented study. Even with our chosen semi-quantitative approach, comparing extensive field work data with topographic maps from the mid 1950s, some interesting trends were recognisable. Our results showed a dramatic loss of total area occupied by tiger bush. This finding is in line with results from neighbouring areas which are based on remote sensing data only (e.g. Niger; Kusserow and Haenisch, 1999). In a future study, a quantitative analysis of current aerial photographs and satellite imagery would reveal the full scope of the actual loss (or potential recovery) of tiger bush vegetation in the study area and beyond. So far, there have been no studies that causally link the disappearance of these tiger bush stands with either climatic conditions (prolonged dry periods in the second half of the 20th century) and / or human (over) utilisation for e.g. timber use or fire wood collections. Barbier et al. (2006) showed a shift from homogeneous savanna in Niger to a spotted vegetation pattern in the second half of the 20th century, with the interaction between human activities and increased aridity as the triggering factor. Kusserow and Haenisch (1999) and Leprun (1999) interpreted the loss of tiger bush vegetation in the Sahel in recent years and the increasing signs of degradation largely as a result of increased anthropogenic pressure and grazing by domestic animals. A degradation of other woody vegetation types in northern Burkina Faso was documented by Lykke et al. (1999).

Floristic composition

Compared to other tropical regions, tiger bush vegetation in Burkina Faso is poor in woody species. This fact is in line with the general relative floristic poverty of Sahelian vegetation. The number of woody species in tiger bush in Burkina Faso does not differ from tiger bush in other countries. Valentin et al. (1999) found eight to nine woody species per tiger bush stand in adjacent areas of Niger. The graphic presentation of the species-area relationship reveals that, although an increase in sampling size would result in additional species to be found, the sampling effort would be disproportionally high and therefore not be justified. However, harbouring about 40% of the region's woody species pool, tiger bush in Burkina Faso has a significant importance for the botanic diversity of the region. Although none of these woody species are exclusive to tiger bush, with dispersal barriers such as longitudinal dune ridges, its populations are contributing to the overall genetic diversity of the species. The very low values of the SHANNON index point to the low species numbers and the dominance of individual species. SIMPSON index values point likewise to the dominance of certain individual species which form the backbone of the tiger bush formation. These results confirm findings by Leprun (1999) and Couteron et al. (2000) who found *Combretum micranthum*, *Pterocarpus lucens*, and *Commiphora africana* dominating the woody layer of tiger bush stands in Mali and Burkina Faso (although present in our plots, *Commiphora africana* did not play an important role). Hiernaux and Gérard (1999) and Couteron et al. (1996) mentioned *Combretum micranthum*, *Pterocarpus lucens* (whose distribution is independent from the spatial structure of tiger bush, contrary to those of

Combretum micranthum; Couteron et al., 1996), *Boscia senegalensis, Boscia angustifolia*, *Grewia flavescens*, *Grewia bicolor*, *Acacia ataxacantha*, *Balanites aegyptiaca*, *Boscia senegalensis*, *Boscia salicifolia*, *Cadaba farinosa*, *Combretum nigricans* and *Guiera senegalensis*. In the tiger bush in southwest Niger, the woody layer is primarily formed of *Combretum micranthum*, *Combretum nigricans*, *Combretum glutinosum*, *Acacia senegal*, *Acacia macrostachya* and *Guiera senegalensis* (Couteron et al., 2000). In a study by Seghieri et al. (1997), *Boscia angustifolia* and to a lesser extent *Combretum micranthum* and *Acacia macrostachya* were often associated with abandoned termite hills.

For the ground layer, Leprun (1999) mentioned as dominating species the grasses *Andropogon gayanus*, *Pennisetum pedicellatum* and *Cenchrus biflorus*. Although *Andropogon gayanus* was missing in our plots, the observed dominance of *Panicum laetum* has so far not been described in the literature. Barral (1977) called *Pennisetum pedicellatum* the dominating species of the ground layer. The ground layer of tiger bush stands in Niger consists in particular of *Ctenium elegans* and *Pennisetum pedicellatum* as well as many ephemeral species. The presence of the typical subcommunity of the *Schoenefeldia gracilis*-community and a plant community which is typical for water edges and inundated areas (Eragrostietum pilosae) is in so far remarkable as the tiger bush occurs in close vicinity to dune ridges and its woody layer consists of typical dune species.

Spatial structure

The recorded heights of the woody vegetation in the tiger bush correspond to other published data. Thiery et al. (1995) and Valentin and d'Herbès (1999) recorded heights up to eight meters in the centre of the central zone. Under comparable climatic conditions, the mean width of the woody stripes within the central zone amounts to only about ten meters (Couteron et al., 2000) and is thus substantially less than in the presented study. In other geographical areas, there is some evidence for stable bands. Dunkerley and Brown (2002) could not find any upward movement in Australian vegetation bands, the boundaries of vegetation to stripes bare of vegetation remained fixed for several years. The spatial anisotropy affects the motion of run-off water between the vegetation bands. It becomes clear that the effects of spatial anisotropy are much more complex than it had been presented in early models (Lefever et al., 2009). Such effects have been poorly studied so far.

The question of seed dispersal and spatial patterns of seedlings establishment should be studied in more detail to answer the question about spatial dynamics of the tiger bush formation. Seed dispersal obviously plays a role in the propagation of individual species. However, it seems quite unlikely that it plays a role in the formation of the specific band pattern. Lefever et al. (2009) concluded that an increase of the efficiency of seed production and/or propagation could only lead to the suppression of large-scale banded vegetation structures and would lead to the restoration of a uniform vegetation cover.

Results of the quadrate variance analyses

Leprun (1999) described three zones in the tiger bush in northern Burkina Faso; woody stripes which run perpendicular to the main wind direction, sandy micro-dunes covered with grasses as well as stripes bare of vegetation. A distinction of these three zones was not possible in our case. The dynamic connection of these three individual zones is not clear, and other authors emphasized the self-organisation of the formation (Barbier et al., 2006). We interpret the variance peaks of the 3 TLQV analyses as the corresponding scale of the investigated pattern (Rosenberg, 2001). The individual dominating species and the diversity indices behave inconsistently in the individual transects. The studied tiger bush in Burkina Faso turned out to be less clearly structured than it had been expected. The scales of the underlying pattern varied and re-occurring patch sizes were not detectable. This result corresponds to the observation that the tiger bush vegetation along the transects did not show uniformity or a firm, repetitive zonation.

However, within the same transect, the uniform variance patterns of the SHANNON and SIMPSON index (*Table 3*) point to a very uniform dominance structure of certain species, of which *Pterocarpus lucens* showed the highest variance values. The question arises what the reason for this inconsistency between the observed non-uniformity and the dominance structure evaluated from the diversity indices might be. We interpret the dissolution of clearly distinct patterns as described in the literature as a direct consequence of the degradation of these stands mainly by an opening of the central zone.

Tiger bush and human use

The fact that many stands of tiger bush are today degraded or have completely disappeared shows the negative influence of human use (Kusserow and Haenisch, 1999). Strictly speaking, tiger bush is well adapted to harsh and changing environmental conditions and stable patterns exists for a wide range of rainfall levels (Sherratt and Lord, 2007). That means that climatic changes like declining precipitation does not automatically lead to its disappearing, but to a change of the type of pattern, e.g. to a widening of the bare zones (Serpantié et al., 1992). But wood collection and browsing thin out the woody stripes and create discontinuities (Saco et al., 2007). A well-structured tiger bush is correlated with an average grazing intensity (d'Herbès et al., 1997). The pastural value of tiger bush is limited. In Burkina Faso, tiger bush is mainly grazed by goats, which penetrate also into the dense areas of the woody zone, cattle - on the contrary - limit their activity to the marginal areas and to already existing corridors. Not only is the vegetation structure along cattle paths less dense and more fragmented, the clearing in the woody stripes also leads to soil erosion and degradation, which diminishes the system’s resiliance against further disturbances (Hiernaux and Gérard, 1999) and represents at the same time degradation on the landscape level. Equally, an opened ground layer gives less protection for rejuvenating woody species which influences the future growth and dynamics of the woody stripes, with already low survival rates outside the stripes (Couteron et al., 2000).

Future studies

With our dataset, we cannot make any statement about the dynamics of the vegetation bands and its potential up-ward moving. Field observations spanning several years would be necessary (e.g. Leprun, 1999). Future studies should look at the below ground biomass and compare the ratio of above ground and below ground biomass with the pattern of vegetation bands and areas free of vegetation (Lefever et al., 2009). Such studies, ideally performed on a coenotic level, could give valuable insights into the self-organisation and dynamics of tiger bush. Equally, it would be interesting for future field studies to clarify the relationship between plant-to-plant interactions (competition and facilitation) and its role for the vegetation organisation.

Studying vegetation patterns has a potential to monitor further climatic and human impacts in semi-arid and arid ecosystems (Barbier et al., 2006). For example, the extension of bare ground is known to influence the atmospheric energy and water budget in a non-linear way.

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Appendix: original transect data available on request from the author, shows presence-absence data of ligneous species along the nine transects.

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Appendix 1. *Original data set, showing the distribution of all ligneous plant species found along the nine samples transect in two subareas of the study area, data centred*

Sub-area	Tran-sect no.	Transect plot Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67
2	1	*Combretum micranthum*										X				X	X	X			X							X	X			X	X			X	X		X											X					X	X		X		X									
		Boscia senegalensis										X																																																								
		Boscia angustifolia																																																X																			
	2	*Pterocarpus lucens*																																						X		X																											
		Boscia senegalensis																						X											X			X	X																														
		Grewia tenax																																								X																										
		Combretum aculeatum																																			X			X																													
		Acacia spec. (winding)																																	X		X	X																															
		Grewia villosa																												X	X	X			X																																				
	3	*Pterocarpus lucens*																		X										X																																									
		Combretum micranthum																																																X			X	X	X																
	|*Guiera senegalensis*|																												|X|																																									
		Boscia senegalensis																		X																						X																											
		Boscia angustifolia												X																																		X																					
		Grewia tenax																																																X																			
		Combretum aculeatum																																				X	X	X																													
		Anogeissus leiocarpa																															X	X																																					
	4	*Pterocarpus lucens*																						X	X	X																				X	X	X		X				X	X	X	X													X			
		Combretum micranthum																		X																								X	X		X	X		X	X	X	X	X	X	X	X																	
		Boscia senegalensis												X	X	X																								X																															
		Boscia angustifolia																							X									X																																						
		Grewia bicolor																																				X																															
		Combretum aculeatum												X			X			X		X											X																																						
		Acacia spec. (winding)																		X						X																							X							X																
		Feretia apodanthera																																														X																					
4	5	*Pterocarpus lucens*																X					X	X	X		X			X	X	X	X	X	X	X						X	X	X	X			X	X																				
		Combretum micranthum																	X	X		X	X	X		X	X	X	X	X				X		X	X	X	X	X	X	X	X	X	X	X	X			X	X																			
		Guiera senegalensis															X	X																																																				
		Grewia bicolor																																											X																							
		Ziziphus mauritiana																																																X																			
		Acacia tortilis subsp. *raddiana*																																																			X															
	6	*Pterocarpus lucens*																					X	X	X		X	X	X		X	X	X	X	X	X	X	X	X	X	X					X	X	X		X	X	X	X	X		X	X	X													
		Combretum micranthum															X										X	X			X								X				X	X	X	X	X	X																								
		Guiera senegalensis								X	X			X	X	X	X	X																																									X	X										
	|*Acacia laeta*|										|X|																																																									
	7	*Pterocarpus lucens*																				X	X			X	X	X	X	X	X	X	X	X	X						X	X																													
		Boscia angustifolia																		X																												X																					
		Grewia bicolor																																														X	X																				
	8	*Pterocarpus lucens*														X	X		X	X	X					X	X	X	X	X																										X	X												
		Boscia senegalensis																									X							X	X																																						
		Grewia bicolor													X																	X																																								
		Grewia tenax																																	X	X							X				X																						
		Acacia laeta																																							X	X	X																										
	|*Commiphora africana*|																												|X|																																								
	9	*Pterocarpus lucens*																	X	X			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X			X	X	X	X			X			X	X	X	X	X	X					
		Combretum micranthum																					X	X	X	X	X	X										X	X	X							X	X														X								
		Guiera senegalensis							X	X			X	X	X					X																			X	X										X	X		X	X				X	X	X		X										
		Boscia angustifolia																																							X																											
		Acacia laeta														X																																																							
		Ziziphus mauritiana							X																																																														
		Piliostigma reticulatum													X																																																							