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The influence of vegetation pattern on the productivity, diversity and stability of vegetation: The case of 'brousse tigrée' in the Sahel

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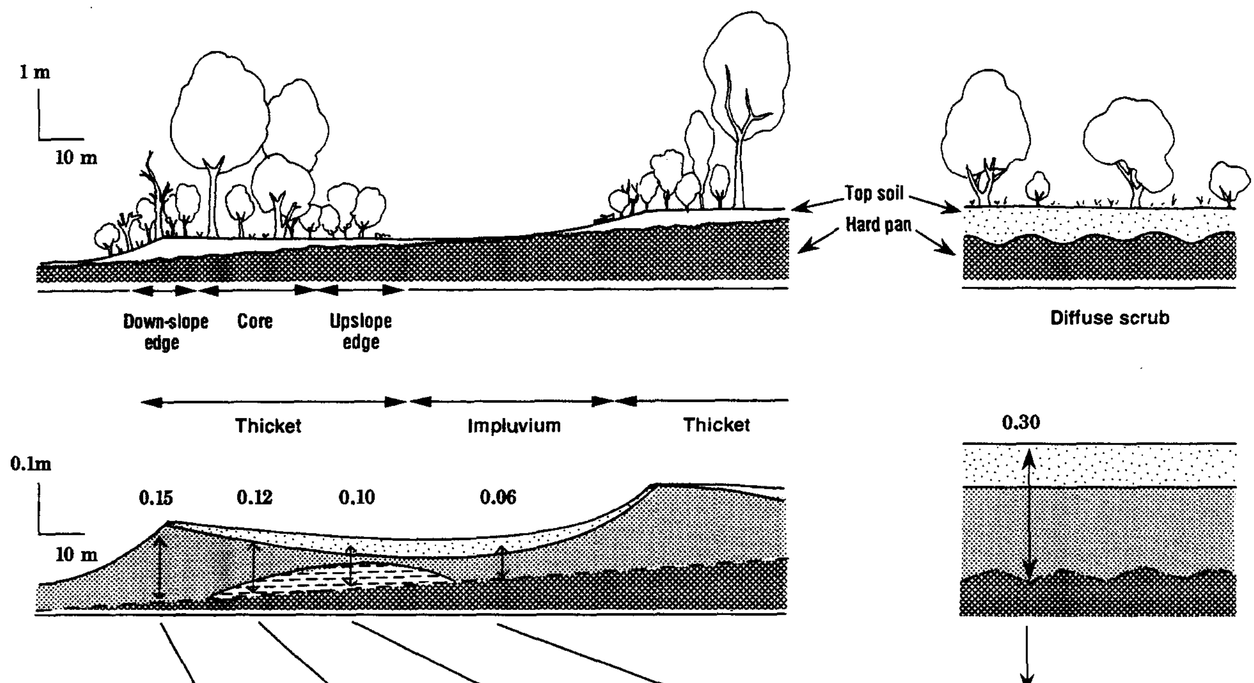
Abstract — Sample sites of 'brousse tigrée' and related vegetation types are described for Mali and Niger. Species composition and physical structure of the herbaceous layer as well as woody plant population were recorded at all sites together with data on soils and natural resource management. Herbage yield was measured whereas foliage yield and wood mass were calculated using allometry equation calibrated for each species. 'Brousse tigrée' is characterized by the regularly alternating bare-soil stripes with dense linear thickets arranged perpendicularly to the slope. There was no clear superiority in total plant production of 'brousse tigrée' when compared to neighbouring site with diffuse vegetation. However, the pattern of 'brousse tigrée' tended to favour woody plant yield to the detriment of herbage yield. The number of herbaceous species recorded per site (22–26) was slightly above Sahelian vegetation average despite low number of species per 1-m^2 quadrat (6–9), bare soil excluded. This species richness reflects the diversity in edaphic niches resulting from the redistribution and local concentration of water resources and shade. The high spatial heterogeneity and species richness of the herbaceous layer in 'brousse tigrée' did not attenuate the interannual variation in herbage yield despite low yields. Except for the herb layer, little evidence was found of grazing influence on the vegetation structure and yield a few hundred metres away from livestock concentration points. On the other hand, the clearing of thickets for cropping led to severe soil erosion which threaten the resilience of 'brousse tigrée'. These observations and the well-defined climatic, soil and topographic situations under which the 'brousse tigrée' occurs invalidate the hypothesis of an anthropic origin of that vegetation pattern. © Elsevier, Paris

Vegetation pattern / patchiness / diversity / herbage yield / wood mass / vegetation dynamics / Sahel

1. INTRODUCTION

'Brousse tigrée' differs from other Sahelian vegetation types by the dominance of woody plants and a pattern characterized by the regularly alternating bare soil stripes with linear and dense thickets (*figure 1*). The bare stripes act as impluvium for the thickets which are linear shaped following the contours. 'Brousse tigrée' develops naturally in the Sahel between the isohyets 400 and 600 mm on poorly permeable soils, often composed of a very thin silty horizon that caps the bedrock or an indurated pan, located on uniform and very gentle slopes [10]. Variants of 'brousse tigrée' have been distinguished based on pattern characteristics such as width and shape of the thickets and bare stripes [2] and on the dominant woody species [17]. Locally, the vegetation pattern can range from uniform 'diffuse scrub' to well patterned 'brousse tigrée' of variable impluvium and thickets width, all with similar woody species composition. Neighbouring sites with diffuse scrub and 'brousse tigrée' sampled in Mali and Niger were analysed to test the following hypotheses: higher spatial heterogeneity of the vegetation pattern increases: 1) vegetation diversity; 2) vegetation productivity [21]; 3) higher spatial heterogeneity and species diversity of the herbaceous layer attenuate interannual fluctuations in herbage yields [1, 26]; 4) 'brousse tigrée' has an anthropic origin; 5) clearing, wood cutting and grazing by livestock cause the 'brousse tigrée' pattern to degrade [4].



Soil horizons	A			B			C			D			E		
	S	L	C	S	L	C	S	L	C	S	L	C	S	L	C
0 - 6 cm	63	35	02	73	23	04	69	29	02	76	23	01	74	25	01
6 - 12 cm	62	33	06	60	30	10	67	31	02	60	31	09	71	26	03
12 - 25 cm	63	41	06	37	36	27	28	54	18	50	32	18	63	29	08
25 - 50 cm	56	34	10	37	36	27	33	37	30	42	32	26	55	33	12

Figure 1. Scheme of the vegetation pattern, terrain topography and soil texture profiles (loose soil only) for neighbouring 'brousse tigrée' and diffuse scrub sites in Nampala (Mali).

2. METHODS

Data from three different studies by the International Livestock Centre for Africa (ILCA, now ILRI) in collaboration with the Malian Institute of Rural Economy (IER) and the National Institute of Agriculture Research in Niger (INRAN) have been used in this paper. 'Brousse tigrée' and related vegetation sites were characterized in the regional assessment and mapping of pastoral resources conducted in a region of Mali centred on the flood plain of the Niger River, known as Macina, and extending to adjacent uplands to the west and north (*figure 2*). Other sites were characterized in the Gourma study which extended to the south of the Niger river between Timbuktu and Gao down to the border with Burkina Faso. The objective of that study was to monitor changes in vegetation (1984–1993) following the major drought in 1983–84 [11]. The third group of 'brousse tigrée' sites were described and monitored (1994–1998) in western Niger (Fakara) in a study on the role of livestock in nutrient cycling within Sahelian agro-ecosystems.

2.1. Field measures

Herbage yields, pattern and species composition, as well as woody plant population density and species composition were recorded at all sites together with data on soils and resource management. However, because of differences in scale and aims, the sampling designs differed between studies. In the Macina study, the classification of the vegetation types was based on a correspondence analysis of descriptors including the list of herbaceous species, recorded in 400 plots, 10 × 10 m in size, distributed over the area stratified by climatic zones subdivided by edaphic units based

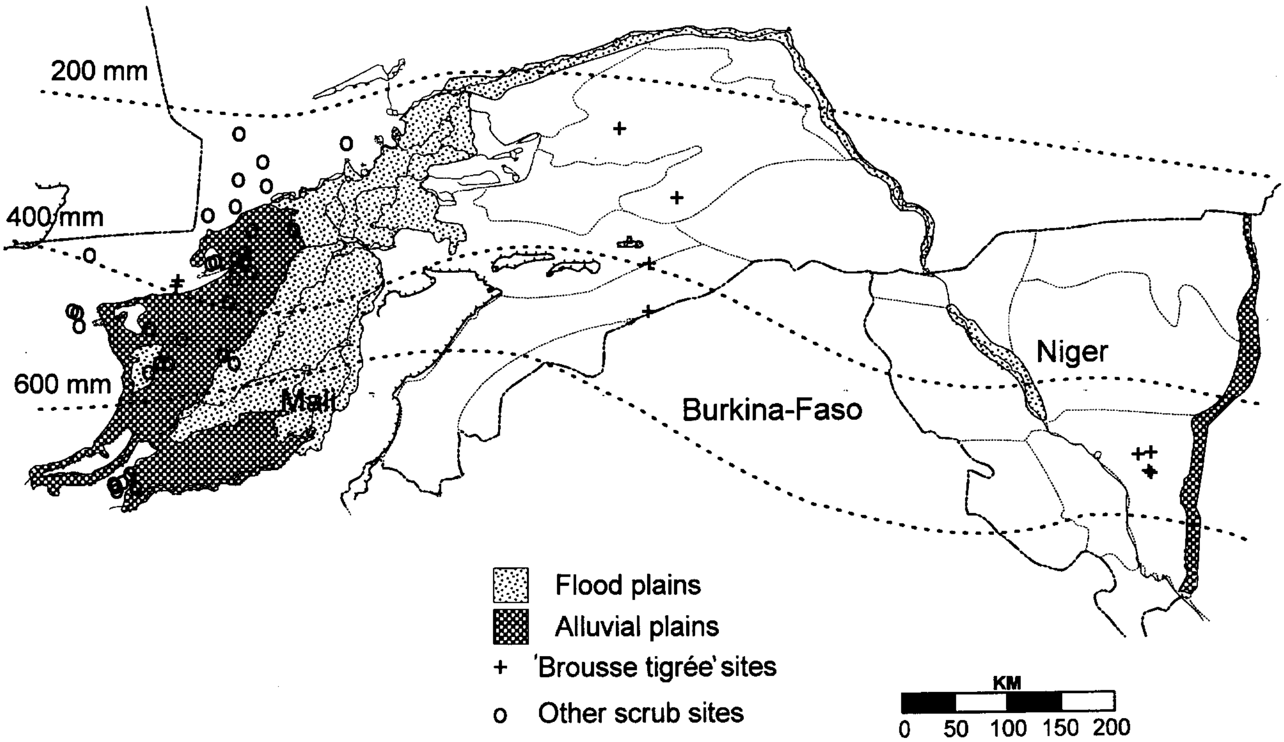


Figure 2. Situation map of the 'brousse tigrée' and related vegetation sites studied within the Sahel of Mali and Niger.

on soil texture and flood regime, in turn subdivided by the type of land use [31]. Herbaceous standing mass at the end of the growing season was destructively measured in 1 × 1 m plots placed in each facies whose area within the 10 × 10 m plot was visually assessed. To better characterize the woody plant population complementary observations were made in 100 of these sites. They consisted of exhaustive counting of the woody plants encountered in each of sixteen adjacent 10 × 10 m plots arranged in a 160-m long transect band [15]. Less frequent species were also recorded in bands adjacent to one side of the transect band and of increasing width (10, 20, 40, 80 m) so that the total area investigated was 160 × 160 m. Each plant recorded was characterized by its species name, canopy dimensions, number and trunk circumference.

The same woody plant descriptors were observed in the Gourma and Fakara studies but in a different sampling design. The plots were circular and centred on four points located randomly along a linear transect of 1 000 m (Gourma) or 200 m (Fakara) long, set perpendicular to the major ecological gradient in the site. The radius of the circular plot was chosen depending on the density of the species in the stand. As a result the size of the individual plots ranged between 1/64 and 1 ha. In patterned vegetation, thickets and impluvium were sampled separately. At all sites, foliage yield and wood mass were estimated using allometric relations established, for each species, between yield or mass and the basal circumference of the stems [6, 18, 28].

In the Gourma and Fakara studies, herbage cover, standing mass and species composition were recorded using a two-level stratified random sampling design: major differences in vegetation induced by terrain features (such as impluvium and thicket often subdivided into upstream, core and downstream bands) were identified as facies sampled individually. Four strata were systematically distinguished within each facies on the base of the apparent density of the vegetation: bare soil, low, medium and high density. The areas covered by each strata within facies were measured along linear transects of 1 000 m (Gourma) or 200 m (Fakara), which were used to weigh the vegetation parameters. Weighed averages and variances were calculated for each site following Cook and Stubbendieck [7]. In the Gourma study, a virtual sample of fifty plots was created using a random generator for normal distribution applied to each strata in proportion of the area it covered, each strata being characterized by the mean and variance of the herbage mass measured in quadrats. The mean and variance of the virtual random sample were calculated and the coefficient of variation of that mean used to estimate spatial heterogeneity. Interannual variability was estimated by the coefficient of variation of the interannual means calculated over 10 years [16].

2.2. Remote sensing

To better characterize the vegetation pattern of 'brousse tigrée', aerial photographs were scanned at a resolution of 300 dpi for panchromatic prints whereas colour slides were processed and transferred to CD-ROM at a Kodak laboratory. After correction for contrasts, pixel brightness was used to classify vegetation and soils using Adobe Photoshop software. In the case of colour slides, the analysis was done on the red band reflectance data in order to enhance the contrast between vegetation and soils [14]. Neighbouring 'brousse tigrée' and 'diffuse scrub' sites located less than 5 km from large water points and across a major and historical transhumance track were studied to assess the effect of high intensity of trampling and grazing by livestock on the vegetation pattern. An aerial photograph (IGN mission 75 MAL 32/500, photo 875) was scanned over an area of 3×3 km centred on the transhumance track. Isolated trees and thicket were identified by a classification of pixel brightness. The image was then vectorized and imported in Atlas GIS. The mean and total areas occupied by tree crowns or thickets were derived for 100-m wide corridors drawn parallel to the central axis of the transhumance path and at distances ranging from 0 to 600 m on either side of the track.

3. RESULTS

3.1. Woody species composition

From the results of the correspondence analysis of the Macina data [17] and observations in Gourma and Niger, species composition of 'brousse tigrée' was related to average rainfall and to the texture of the top soil (*figure 3*). A few species including *Combretum micranthum*[1], *Pterocarpus lucens* (although absent in eastern Burkina Faso, Niger and northern Nigeria), *Boscia senegalensis*, *B. angustifolia*, *Grewia flavescens*, *G. bicolor*, *Acacia ataxacantha* and *Guiera senegalensis* constituted the core of what could be considered as the archetype 'brousse tigrée' (*figure 3A*). This archetype was found between the isohyets 400 and 600 $mm \cdot yr^{-1}$, on poorly permeable soils with a thin silty horizon overlaid on ferralitic hardpans (*figure 1*). Variants were found when top soil was more loamy (*figure 3B*) or more sandy (*figure 3C*). Below 400 mm mean annual rainfall, 'brousse tigrée' was gradually replaced by open scrubs whose species composition depended on top soil texture (*figure 3D, E, F*), while above 600 mm there was gradual transition towards the 'low trees and shrub savannah' found on the shallow soils of the northern sub-humid zone (*figure 3H*). Whatever the variant considered, the woody species composition of 'brousse tigrée' was not distinctive of that particular vegetation pattern. Diffuse scrubs with similar woody species composition were found in environment very similar to those of 'brousse tigrée' except for the terrain slope (*figure 1*). Moreover, vegetation with similar species composition also occurred on deep alluvial soils of the fossil flood plain of the Niger river in Mali (*figure 2*). The flatness of the terrain and the low permeability of the alluvial soils resulted in ecological niches equivalent to the niches found on the shallow soils of 'brousse tigrée' [17].

3.2. Vegetation pattern

Patchy patterns are common in arid and semi-arid vegetation [8, 12, 30] among them the 'brousse tigrée' pattern is characterized by regularly alternating bare soil stripes with linear and dense thickets set perpendicular to the direction of the gentle slope. In the studied sites, the impluvium to thicket area ratio increased when annual rainfall decreased (*table I*). The average width of the pattern period (impluvium + thicket) varied with slope and top soil texture. In the dryer situations, sand may deposit across the bare strips and, depending on the orientation of the thicket relative to the dominant winds, sand may accumulate on the windward side of the thicket [20].

Two of the range sites monitored in northern Gourma between the isohyet 300 and 200 mm (indicated as 'very open scrub' in *figure 5*) were patterned and functioned as 'brousse tigrée' although their thickets were few and far apart at the onset of

[1] Taxa are named after the second edition of the *Flora of West Tropical Africa, 1954-1972*, by J. Hutchinson and J.M. Dalziel, re-edited by R.W.J. Keay and F.N. Hepper, Crowns Agents for Overseas Governments and Administrations, London, vol. 1–3.

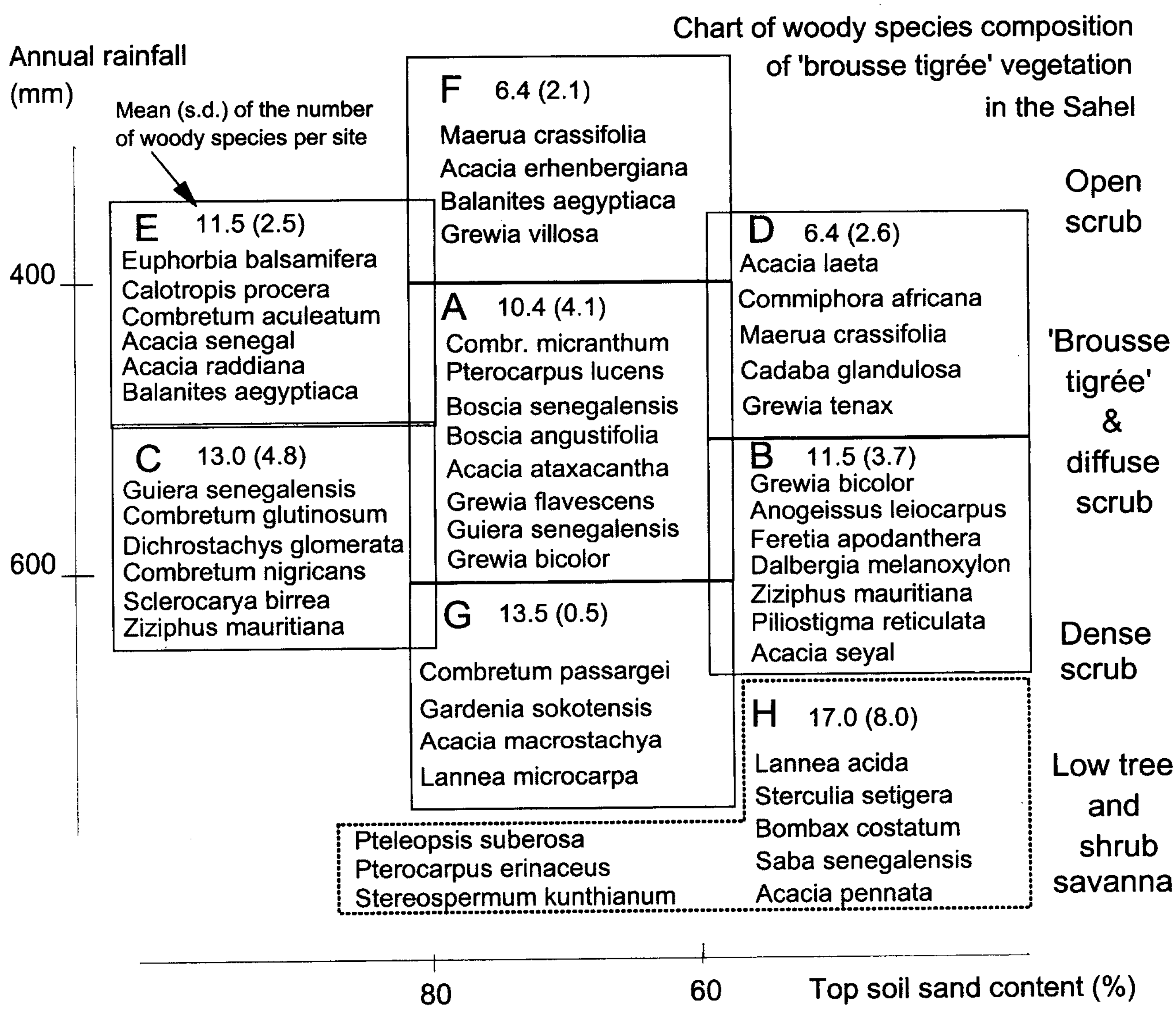


Figure 3. Species composition of 'brousse tigrée' and related vegetation in relation to climatic and soil texture conditions.

observations in 1984. Ten years later, the spatial pattern and composition of the vegetation were totally modified and the vegetation could not be considered part of 'brousse tigrée' any longer. The herbaceous layer has been the first to suffer from a succession of dry years. Herbaceous cover and yield declined and the herbaceous layer fragmented into scattered patches. However, herbaceous species diversity was maintained in a few refuge niches. Then, as the dry condition persisted, most of the woody plants died with the exception of *Boscia senegalensis* and *Maerua crassifolia* shrubs. A few species such as *Acacia erhenbergiana* and *Commiphora africana* for the woody plants, *Microchloa indica*, *Tragus berteronianus* and *Schoenefeldia gracilis* for the grasses started to establish with better rains in 1988 and 1990. However, these new comers spread in linear patterns along the new network of gullies that resulted from the change from sheet run-off to concentrated run-off.

'Brousse tigrée' and related diffuse scrub are distributed on shallow soils irrespective to rural popula-

Table I. Parameters of the vegetation pattern of 'brousse tigrée' (BT) and diffuse scrub (DS) sites observed along transects in the field and on aerial photographs.

Region Pattern	Rainfall (mm)	Slope (%)	Top soil texture	Period width[1] (m)		Thicket (%)			Impluvium (%)		
				mean	s.d.	Dense stand	Open stand	Total	Gravels or herbs	Silty flats	Total
Macina											
BT	320	0.6	silty sand	102	20	7.9	9.6	17.5	65	17.5	82.5
BT	510	0.3	silty sand	160	31	36.3	8.2	44.5	36.4	19.1	55.5
BT	510	0.4	silty sand	109	22	41	17	58	39.1	2.9	42
BT	510	0.5	silty sand	80	20	11.9	40.9	52.8	18.7	30.5	49.2
DS	510	0.1	Silty sand	–	–	5.7	29.9	35.6	53.7	10.7	64.4
BT	580	0.2	sandy silt	72	10	25.3	30.9	56.2	9.6	34.2	43.8
Gourma											
BT	390	0.5	sandy loam	126	29	10.6	2.8	13.4	69.8	16.8	86.6
DS	390	< 0.1	sandy loam	–	–	11.6	3.4	15	56.9	28.1	85
Fakara											
BT	440	0.4	silty sand	73	17	23.8	6.5	30.3	57.2	12.5	69.7
BT	440	0.5	silty sand	55	10	10.9	10	20.9	21.6	57.5	79.1
DS	440	< 0.1	sandy silt	–	–	54.6	9.3	63.9	19.2	16.9	33.8

[1] Period width = width of impluvium + downstream thicket.

tion density and livestock stocking rates. The vegetation pattern of neighbouring sites of 'brousse tigrée' and diffuse scrub located along a major transhumance track was very much affected in the first 50-m from the central axis of a major transhumance track: the relative area covered by scattered shrubs and thickets, as well as density of thickets largely decreased (*figure 4*). Further away from the axis but within 200 m, the density of thickets was still affected but the area covered by thickets (or individual shrubs) decreased or increased depending on the local orientation of slope relative to the transhumance track. Further away, no evidence was found of grazing influence on the vegetation pattern whether the track traversed the 'brousse tigrée' or the diffuse scrubs. On the contrary, a widespread and large reduction of the area covered by thickets and thicket fragmentation was observed when comparing 1995 to 1950 aerial photographs of 'brousse tigrée' and diffuse scrub sites located in a densely populated area of the Fakara region (*table II*). The decrease in woody plant cover was accompanied by a severe reduction of the herbaceous cover with the exception of newly formed thin sand deposits on the impluvium which were colonized by *Zornia glochidiata* and *Sida cordifolia*.

3.3. Flora diversity

In 'brousse tigrée', the average number of woody species recorded per site ranged between eight and nine (*table III*) which is below most of the other Sahelian natural vegetation types except for tempo-

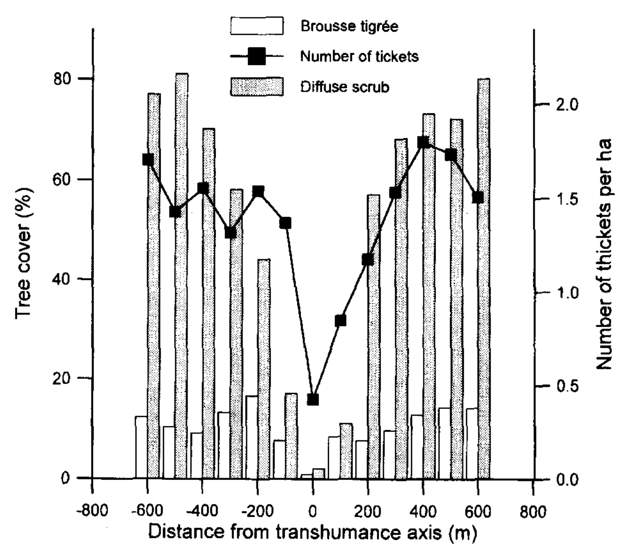


Figure 4. Effects of grazing on the number and area of thickets in a 'brousse tigrée' site and on the woody plant cover in a neighbouring diffuse scrub site, both located across a major transhumance track (Nampala, Mali).

Table II. Changes from 1950 to 1995 of the area covered by thickets and bare soil impluviums in two 'brousse tigrée' sites from the Fakara region (Kodey, Niger) subjected to intense forestry and pastoral use and partially cleared for shifting millet and sorghum crops.

Site	Year	Period width (m)		Thicket relative area (%)			Impluvium relative area (%)		
		mean	s.d.	Dense stand	Open stand	Total thicket	Gravels or herbs	Bare silty or sandy soils	Total impluvium
Peyrel	1950	55	10	10.7	45.9	56.6	27.1	16.3	43.4
	1995			10.9	10.0	20.9	21.6	57.5	79.1
Raneo	1950	95	21	19.0	30.7	49.7	15.0	35.3	50.3
	1995			3.6	6.3	9.9	4.8	85.3	90.1

rarily flooded sites. The direction of differences between neighbouring diffuse and patterned vegetation was not constant. The average numbers of herbaceous species recorded per site (flora richness) in 'brousse tigrée' and diffuse scrub were comparable and ranged between 22 and 26 (*table III*), while average numbers of species recorded per quadrat, excluding bare patches, ranged between 6.7 to 9.0. In contrast to woody plants, the flora richness of the herbaceous layer of 'brousse tigrée' and related diffuse scrub was slightly superior to Sahelian vegetation average, while the average number of species per quadrat was inferior.

3.4. Herbaceous plant production

In the Macina study, the herbaceous yield of 'brousse tigrée' was 489 kg DM·ha^{-1} compared to 1 194 kg DM·ha^{-1} for neighbouring diffuse scrub (*table IV*). In the Gourma, from 1984 to 1993, the annual herbage yields of the 'brousse tigrée' site averaged 177 (SE 42) kg·ha^{-1} compared to 927 (SE 203) kg·ha^{-1} for the neighbouring diffuse scrub and the average of the coefficient of variation of the mean herbage mass (virtual random sampling of fifty quadrats) were 441 % (SE 63) and 131 % (SE 11) respectively. The interannual variability of the herbage production was assessed by the coefficient of variation of the interannual production mean which was 76 % in 'brousse tigrée' and 69 % in the diffuse scrub. In the Fakara, from 1994 to 1996, the average herbage yield of the heavily grazed 'brousse tigrée' site was 363 (SE 137) kg DM·ha^{-1} compared to 507.3 (SE 134.7) kg·ha^{-1} in the heavily grazed diffuse scrub site, and the averages of the coefficient of variation of the mean herbage mass were 124 and 90 %, respectively. There was thus a large superiority of the herbage yield in diffuse scrub compared to 'brousse tigrée' in all sites and years. There also was a difference of magnitude in the spatial heterogeneity of the herbaceous layer as indicated by the coefficient of variation of the herbage mass which was much larger in 'brousse tigrée' than in diffuse scrub, at least when the site was not too heavily grazed.

Table III. Woody and herbaceous species richness per site, and average number of herbaceous species recorded per 1-m^2 quadrat in 'brousse tigrée' (BT) and diffuse scrubs (DS) sites from three study zones in the Sahel.

Study zone	Vegetation pattern	Woody plants				Herbaceous plants					
		Area sampled × replicates (m^2)	Sites × years	Species recorded per site		Area sampled × replicates (m^2)	Sites × years	Species recorded /m^2		Species recorded /site	
				mean	s.d.			mean	s.d.	mean	s.d.
Macina	BT	1 600 × 4	1	9	–	–	–	–	–	–	–
	DS	1 600 × 4	4	8.5	2.5	–	–	–	–	–	–
Gourma	BT	312.5/2 500 × 4	3	7.7	0.5	1 × 12	9	7.7	0.9	22.5	3
	DS	2 500 × 4	3	15	2.2	1 × 12	10	9	1.1	23.2	1.4
Fakara	BT	312.5/1 250 × 4	2	8.5	0.5	1 × 12	2	6.7	2.5	22.5	1.5
	DS	625 × 4	2	5.5	0.5	1 × 12	4	7.8	1.3	26.5	5.8

Table IV. Contribution of herbaceous species grouped by life-type and palatability classes to the herbage mass of the structural units of 'brousse tigrée' compared to the diffuse scrub (Macina sites, Mali).

Grasses and forbs palatibility	'Brousse tigrée'						Diffuse scrub
	Thicket				Impluvium	Total 'brousse tigrée'	
	Upstream edge	Core	Downstream edge	Total thicket			
Area (%)	17	17	16	50	50	100	100
Good	3.3	1.8	4.4	2.8	10.4	6.6	2.3
Mediocre	3.6	5.2	8.8	5.2	5.2	5.2	3.7
Poor	10.7	1.8	1.1	3.9	26.8	15.4	6
Total grasses	**17.6**	**7.8**	**14.3**	**11.9**	**42.4**	**27.1**	**12**
Good	0.4	0	1.1	0.4	35.3	17.9	59.7
Mediocre	77.9	80.4	70.3	77.6	10.5	44	16.5
Poor	4.1	10.8	14.3	10.1	11.8	10.9	11.8
Total forbs	**82.4**	**91.2**	**86.7**	**88.1**	**57.6**	**72.8**	**88**
Herbage yield (kg DM·ha^{-1})	2 618	430	332	952	25	489	1 194

As illustrated by the Macina site data (*table IV*), the species composition of the herbaceous layer of 'brousse tigrée' was generally dominated by dicotyledons, especially in the thicket where they were better adapted to dense shade. Among the grasses, most of the species were found at the upstream edge of the thicket and were adapted to temporary soil water logging. The feed quality and palatability of the herbage was usually low with the exception of a few plants that colonize the sandy deposits such as *Zornia glochidiata*, an annual legume promoted by heavy grazing, *Schoenefeldia gracilis* and *Brachiaria xantholeuca*, annual grasses, or *Andropogon gayanus*, a perennial grass.

3.5. Woody plant production

The patterned structure of 'brousse tigrée' translated into contrasting densities and composition of woody plants between impluvium and thicket, and also between the upstream edge, core and downstream edge of the thicket (*table V*). Compared to neighbouring diffuse scrub, the high density of the woody plants in the thicket approximately compensated for the very low density in the impluvium. With the exception of

Table V. Density of woody plant species per structural units of the 'brousse tigrée' compared to diffuse scrub (Macina sites, Mali).

Woody species	Density of woody plants in 'brousse tigrée' (ha^{-1})						Density in diffuse scrub (ha^{-1})
	Thicket				Impluvium	Total 'brousse tigrée'	
	Upstream edge	Core	Dowstream edge	Total thicket			
area (%)	17	17	16	50	50	100	100
Pterocarpus lucens	206	439	150	308	38	173	250
Combretum micranthum	219	811	925	691	8	350	281
Boscia senegalensis	156	321	325	281	39	160	200
Dichrostachys glomerata	31	–	–	8	–	4	12
Grewia flavescens	–	–	25	6	–	3	50
Acacia ataxacantha	6	–	50	14	–	7	19
Guiera senegalensis	656	473	25	407	15	211	–
Grewia tenax	25	–	–	6	–	3	–
All species	**1 300**	**2 044**	**1 500**	**1 721**	**81**	**901**	**812**

Table VI. Woody plant density, foliage and wood masses of ‘brousse tigrée' (BT) and diffuse scrub (DS) sites in three regions of the Sahel.

Study zone	Vegetation type	Component facies	Area (%)	Woody plant density (ha^{-1})	Wood mass (kg DM ha^{-1})	Leaf mass (kg DM·ha^{-1})
Macina	BT	thicket	50	1 721	11 095	1 402
		impluvium	50	81	68	8
		all	**100**	**901**	**5 030**	**705**
	DS	–	100	812	11 621	1 263
Gourma	BT	thicket	13	2 091	47 366	4 213
		impluvium	87	210	143	11
		all	**100**	**207**	**4 388**	**389**
	DS	–	100	220	1 938	123
Fakara	BT	thicket	30	4 519	53 820	4 109
		impluvium	70	151	572	79
		all	**100**	**2 335**	**27 196**	**2 094**
	DS	–	100	2 243	6 037	2 221

the Macina site, foliage and wood masses were higher in the 'brousse tigrée' than in diffuse scrub even at lower density of woody plants (*table VI*). The larger size of individual plants and longer span of the growing season allowed by the spatial concentration of resources in the thicket, could explain the superiority of 'brousse tigrée' foliage production and wood mass despite inferior plant density. Indeed, the partition of the wood mass per size of logs: large logs from the trunks and main branches, and small wood from branches, showed a higher proportion of large logs in 'brousse tigrée' than in associated diffuse scrubs. 'Brousse tigrée' and related diffuse scrub rank among the more productive vegetation types in the Sahel in term of woody plant products. In the studied 'brousse tigrée' sites, woody plant production spanned widely from 689 to 2 094 kg DM·ha^{-1}·yr^{-1} for foliage while the standing wood mass varied from 4 388 to 27 196 kg DM·ha^{-1} (*table VI*). Production in 'brousse tigrée' was not systematically superior to the production in diffuse scrub despite the close density of woody plant observed within each pair of neighbour sites. The palatable fraction of the foliage production of 'brousse tigrée' varied largely depending on species composition from 44.5 and 46.8 % palatable foliage in the Macina and Gourma, respectively, to only 1.3 % in the Fakara. The use of these browse resources was further limited by the difficulty of access for the animals, due to the height of some trees and the high density of the thickets. Standing wood in 'brousse tigrée' was composed of about 70 % of trunks and large branches and 30 % of minor branches, and number of species such as *Pterocarpus lucens* and *Combretum* ssp. provided good quality fuel wood.

4. DISCUSSION

4.1. Flora richness and diversity

The wide array of ecological niches created by the spatial concentration of water, nutrients and shade could explain the relatively rich herbaceous flora recorded in the 'brousse tigrée' and diffuse scrub sites (hyp. 1 validated). However, the larger contrasts between niches in 'brousse tigrée' compared to diffuse scrub did not result in a richer flora (hyp. 1 invalidated), perhaps because of the high fragmentation of the herbaceous layer in 'brousse tigrée'. The lower mean number of species per quadrat in 'brousse tigrée' supports this argumentation but the edaphic specialization of each niche (xeric in the bare soil impluvium; hydromorphic at the upstream edge of the thicket; sciaphyllous within thicket) could also contribute to explain the limited number of species recorded per quadrat. The same principles should apply to the woody plants. However, the woody flora was relatively poor whatever the pattern of the vegetation (hyp. 1 invalidated). This could indicate that niche diversification is less effective for woody plants, perhaps because competition is more severe as plant size increases [1].

4.2. Herbage and woody plant yields

Large extent of bare soils in the impluvium is the main reason for low herbage yields in 'brousse tigrée' compared to neighbouring diffuse scrubs (hyp. 2 invalidated). The impluvium is very hostile to plant development because of the shallowness of the top soil, associated to surface crusting. This causes sheet

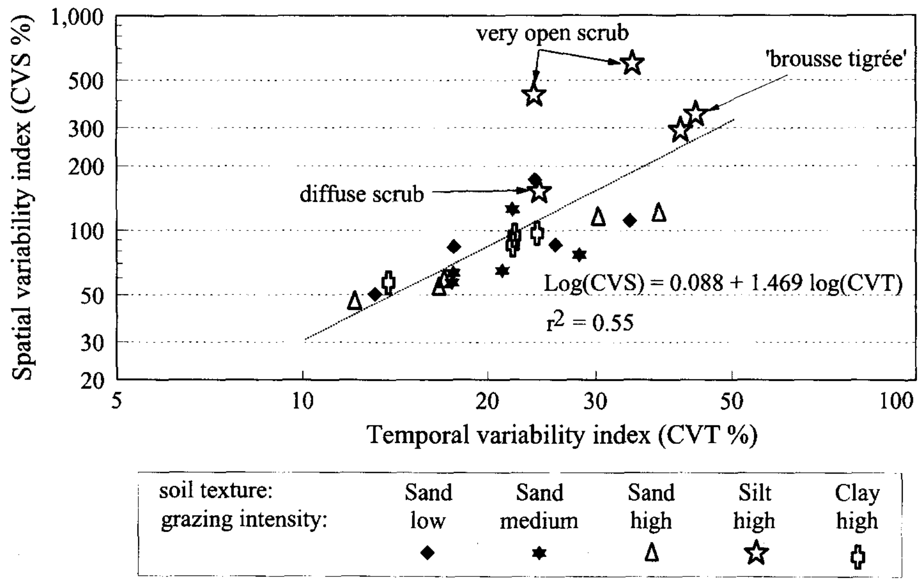


Figure 5. Relationship between spatial heterogeneity and temporal variability in herbage mass for 24 Sahelian sites (Gourma, Mali). The regression is established between the logarithm of average coefficient of variation of annual mean herbage mass (CVS) and the logarithm of the coefficient of variation of the 10 years interannual mean of the herbage mass (CVT).

run-off to redistribute most rainfall downstream to the detriment of the impluvium soil moisture [25]. In addition, the herbaceous layer is very sparse in the core of the thicket because of the dense shade. The spatial redistribution of water and nutrients benefits perennial plants, especially woody plants, allowing for the development of dense and multi-layered forest islands instead of a diffuse scrub. Annual wood production has not been measured, however; only annual foliage production compensated for inferior herbage yields in 'brousse tigrée' (hyp. 2 validated). The standing wood mass was superior in 'brousse tigrée' than in the neighbouring diffuse scrub in the Gourma and Fakara sites as observed in another site in western Niger [19], but not in the Macina site (hyp. 2 partially validated). The concentration of resources on a portion of the area extends the duration of the growing season in that spot to the benefit of the productivity of long-cycle plants and reduces the risk of plant mortality in that niche [21]. On the other hand, redistribution of resources may also increase losses through run-off spill over out of the patterned vegetation unit during large rain events or through deep percolation and leaching under the thickets [13]. The effect of patterning on the overall vegetation productivity will depend on trade-offs between productivity benefits for the woody plants in the thicket and resource losses by run-off and deep percolation.

4.3. Vegetation stability

Contrary to expectations, the high spatial heterogeneity and species diversity of the herbaceous layer of 'brousse tigrée' did not attenuate the interannual variation in herbage yield despite much lower average yields (hyp. 3 invalidated). The coefficient of variation of the 10-year mean herbage yield was consistently higher for 'brousse tigrée' than diffuse scrub found in the same climatic zone. Moreover, considering the 24 range sites monitored for 10 years in the Gourma, there was a positive linear regression between this coefficient of variation which is an indicator of the interannual variability and the average coefficient of variation of annual mean herbage mass which is an indicator of spatial heterogeneity (*figure 5*). Therefore, it appears that the higher the spatial heterogeneity of the vegetation pattern, the larger the susceptibility of the herbaceous layer production to vary from year to year [16].

4.4. The origin of 'brousse tigrée'

The transformation of two 'brousse tigrée' sites into very open scrubs following two decades of poor rains in a region that receives between 300 and 200 mm of rain annually on average confirms the climatic limit of 'brousse tigrée'. The very open scrub that resulted from these changes cannot be considered part of 'brousse tigrée' any longer because of the mutation in species composition, vegetation pattern and, above all, the change in the mode of water redistribution from sheet run-off to concentrated run-off [9]. The well-defined climatic, and also soil and topographic situations under which the 'brousse tigrée' occurs irrespective of population density [2, 10] does not support the anthropic origin of that vegetation pattern although it does totally exclude influences of grazing, selective wood cutting or burning practices on the onset of the pattern and its dynamics.

4.5. The degradation of 'brousse tigrée'

Grazing by livestock and wood cutting or clearing for cropping are often implicated in the set-up of the patchy pattern of 'brousse tigrée' as well as in its degradation [4]. Indeed, selective and intensive grazing of annual herbs during the growing season help the dominance of woody plants (hyp. 5 validated). In addition, the patchiness of the vegetation cover reduces the risk of fire which could have balanced the influence of grazing in the competition between herbs and woody plants. However, except for species composition of the herb layer [29], no evidence was found of an influence of a long history of grazing by transhumant livestock on the structure of vegetation across grazing pressure gradients established from livestock concentration points such as water points, cattle paths or resting sites (hyp. 5 invalidated). This was confirmed by the narrow limits of the influence of livestock along major transhumance tracks such as the Diafarabé track that connect the Macina flood plains to the upland rangelands 600 km away in southern Mauritania [5]. Centuries of seasonal heavy grazing and trampling along the path only affected the pattern of the 'brousse tigrée' and that of neighbouring diffuse scrubs within 200 m from the central axis of the track (*figure 4*). On the contrary, the thicket clearing and subsequent cropping, because wood cutting, tillage and weeding maintain the soil loose and denudated during the wet season, affects the spatial redistribution of water which drives the pattern and functioning of 'brousse tigrée' [22]. The concentration of run-off, gully formation and mobilization of the sand deposits rapidly led to severe soil erosion which threatens the resilience of the 'brousse tigrée' (hyp. 5 validated) as observed in two sites in Niger (*table II*).

5. CONCLUSION: IMPLICATIONS FOR NATURAL RESOURCE MANAGEMENT

The pastoral value of 'brousse tigrée' is limited by low herbage yields and feed quality with the exception of the patches found on the thin sandy deposits which exist in some of the dryer or degraded 'brousse tigrée' [20]. However, depending on the species composition of the woody vegetation, browse could provide an important animal feed resources [24]. Selective cutting that would favour the growth of selected best-value browse species, such as *Pterocarpus lucens* and *Ziziphus mauritiana* is one option for improved management. Planting best-value species could even be envisaged in the poorest stands.

The main production of 'brousse tigrée' is forestry [23]. Because of the spatial concentration of water and nutrients, the ecological conditions in the thicket are appropriate for a forest system to develop despite limited rainfall and long lasting dry season. Based on the annual foliage production, the productivity of this discontinuous forest at least equals the productivity of neighbouring diffuse scrubs, and it yields a larger proportion of higher value timbers [19]. Forestry management should aim at maintaining this productivity in organizing selective cutting of live wood, chiefly as building material and fuel, although fuel wood harvest in the Sahel consist mainly in collecting dead wood [3] which has limited impact on the ecosystem.

The increasing practice of thicket clearing for shifting crop of sorghum, in southern Sahel, and millet, in northern Sahel, puts the 'brousse tigrée' at risk as it affects the spatial redistribution of water which drives the pattern and functioning of that biome. The concentration of run-off that result from clearing for cropping rapidly aggravates erosion on poorly permeable soils and increases water flows outside the 'brousse tigrée'. This causes sudden floods that threaten downstream cropping lands and may further justify costly reclamation operation on degraded 'brousse tigrée' [27].

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