



Relationships between soil moisture and growth of herbaceous plants in a natural vegetation mosaic in Niger

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The 'tiger bush' is a particular vegetation pattern in which densely vegetated bands alternate with bare areas. In general, bare areas are working as impluvium for the downslope vegetated stripes. The intraseasonal regimes of soil moisture are quantified during a rainy season, and their influence on the growth of the annual vegetation is analysed.

Data were collected along the line of maximum slope crossing two vegetated bands. Density and phenology of herbaceous layer are related to the changes of soil moisture and to the associated soil surface features.

The herbaceous layer comprises only annual species, mainly composed of the tiny grass *Microchloa indica* and *Cyanotis lanata* (Commelinaceae). Both are indicators of long-term overgrazing. The distribution of *Microchloa indica* is well correlated with the sedimentary crusts located immediately upslope of the thicket. *Cyanotis lanata* is the only species recorded in the downslope part of the transect. Its distribution is well correlated with the biological crusts located in the core of the thicket, where infiltration first occurs and high infiltration rates are seen, as long as shade and litter are not limiting for seedling development. As the rainy season progresses, infiltration also increases upslope of the thicket which, until then, remains bare and where only *Microchloa indica* germinates provided the seed stock is not limiting.

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Introduction

The 'tiger bush' or 'vegetation arcs' is characterised by parallel stripes of thicket alternating with stripes of bare soil, and is clearly recognisable on aerial photographs (Clos-Arceuduc, 1956). Such a vegetation pattern has been reported in many arid and semi-arid regions of the world (Ives, 1946; Worrall, 1959; Boaler & Hodge, 1962; Audry & Rossetti, 1962; Hemming, 1965; White, 1971; Wickens & Collier, 1971;

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Boudet, 1972; Cornet *et al.*, 1988; Le Houérou, 1989; Tongway & Ludwig, 1990; Barker, 1992; Leprun, 1992).

Three major processes have been proposed to explain the origin and the functioning of the tiger bush pattern: (1) vegetation stripes develop along wind blown material so that the vegetation arcs are perpendicular to the direction of the dominant winds (Ives, 1946; White, 1971); (2) the vegetation arcs form natural obstacles that can slow or even stop soil surface runoff from the upslope bare soil impluviums; the obstruction is reinforced by the deposit in the vegetation of aeolian material (Worrall, 1959; Audry & Rossetti, 1962; Leprun, 1992); (3) finally, the influence of aeolian erosion is negligible and water flow is the essential factor (Boaler & Hodge, 1964; Cornet *et al.*, 1988).

In the tiger bush of the Sahelian zone of Niger, vegetated bands generally are not oriented according to the main wind direction but perpendicularly to the main slope, i.e. to the runoff/runon flow. Ambouta (1984) did not notice any large differences in soil constitution between the bare and vegetated zones. More recently, differences in soil profiles have been tested by Barker (1992) who found no structural difference between the bare soil zone and the vegetated zone and found no evidence of aeolian material accumulation in the vegetated area. So our hypothesis is that the tiger bush studied is mainly controlled by the water flow (third process) as shown by Cornet *et al.* (1988) in Mexico. In this paper the soil moisture flows and the growth of the annual layer were quantified in the transition zone between the intervening bare soil and the core of the thicket. It is expected that annual plants would respond faster than woody plants to any changes. In a synthesis of studies related to banded vegetation occurring on sheet wash surface, White (1971) mentioned that trees and shrubs tend to be established in more stable stripes in the higher rainfall zones but that the grasses are the essential component in most cases. Furthermore, the transition zone can be considered as a spatial analogue of temporal changes in vegetation (Delcourt & Delcourt, 1992), so that its dynamics can be regarded as an indicator of the longer-term evolution of the whole ecosystem.

Study area

In Niger tiger bush occurs in a zone about 250 km wide extending from approximately 13° N to 15° N (Ambouta, 1984). Within this zone, the annual rainfall varies from 400 mm in the north to 750 mm in the south, 95% of the total annual rainfall occurring between May and September. The banded vegetation pattern occurs exclusively on shallow gravelly soils developed at the top of plateaux capped with a thick Pliocene ironpan (Gavaud, 1965). The regular slope of the plateaux is less than 0.2%. The size, form and space between the vegetated stripes change with the climatic gradient and with local variations in topography and soils. From an economic point of view, the tiger bush contributes to the livestock forage resources as well as woody products, especially fuel.

The study site was selected near Banizoumbou, 60 km east of Niamey. The mean annual rainfall is 560 mm calculated from 1905 to 1989 (Lebel & Le Barbé, 1997). Data were collected from the nearest meteorological station to the study site (Niamey) for which rainfall has been recorded since the beginning of this century. The soil has a sandy clay loam texture (after the USDA classification) with 56% sand and 27% clay (Galle, unpubl. data). The site is in a typical tiger bush (Fig. 1). The stripes are arranged in a 'rosette' concentric pattern (Ambouta, 1984). The thickets are about 50 m apart and are 10 m wide. The vegetation covers 25% of the study area as shown on the digitised photograph (Fig. 1).

The woody population is mainly composed of *Combretum micranthum* G. Don (69% of mature individuals; Couteron *et al.*, submitted) and *Guiera senegalensis* J.F. Gmel. Associated species are *Gardenia sokotensis* Hutch., *Acacia macrostachya* Reichenb.,

Combretum nigricans Lepr., *Grewia flavescens* Juss., and *Commiphora africana* Engl. At the downslope boundary of the thicket, the presence of dead stumps constitutes the senescence zone first reported by Gavaud (1965). *Boscia angustifolia* A. Rich., a low shrub surviving in that zone, is often associated with abandoned termitaria. The herbaceous layer is preferentially concentrated at the upslope boundary of the thicket (Couteron *et al.*, submitted). The functional elementary unit of the tiger bush system is composed of both a thicket and the upslope bare zone.

Methods

Two elementary units (two thickets and two bare zones) were sampled and studied during the 1992 rainy season (Fig. 1). The objective was to identify the general processes involved; particularly soil moisture regime and herbaceous growth were quantified. Six transects 20 m long (three per unit) were set along the slope, from the bare zone to the core of the thicket. The number of vegetative, flowering and fruiting plants were counted per species in a sliding rectangle 5×20 cm moved along the transects. Monitoring of annual plant density and phenology was repeated every 20 days, from the beginning of the growth period (from when we were able to identify the species) to total drying out of the plants. At the end of herbaceous growth, in order to analyse the similarity of the two units, correlations were calculated between the distribution of species density in the two units.

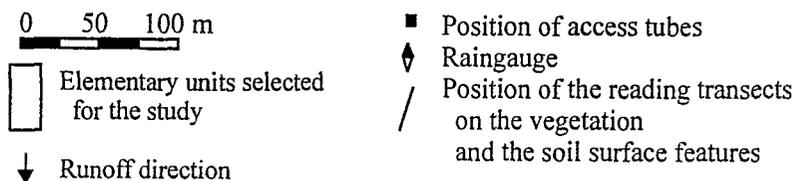


Figure 1. Field device on the tiger bush site.

To confirm the interpretation of the results, two supplementary investigations were conducted. The first consisted of an estimate of the seed bank in the thicket soil and in the bare zone soil to judge the influence of the seed bank on the upslope extent of the herbaceous plants. Four quadrats 10×10 cm and 5 cm deep were randomly sampled in the middle of the bare zone and five others in the core of the thicket. Soil samples were sieved and all the seeds found were counted. The second investigation consisted of an analysis of the preferential location of the two main species in the herbaceous population. Two hundred and ten quadrats (10×10 cm) were randomly sampled under the tree canopy and away from it. Dominant species were noted in each of them. Fisher's exact test was used to analyse the relationship between the species that dominated the downslope transects and the tree canopy and the species that dominated the upslope transects and the open environment.

Distribution of the soil surface crusts was recorded in September along the transects. Crusts were described and correlations were then calculated between the distribution of the crust cover in the two units. At the end of the herbaceous growth, the relationship between the distribution of the crust cover and the species density along the transects were analysed by statistical correlations. Spatial distributions of the species and the crusts from upslope to downslope of the transects, and their relationships, are presented for an average transect calculated from the six field transects. To reduce noise due to local variations a moving average of five points size was used.

Soil moisture profiles to depths down to 1 m or 5.60 m were monitored, using neutron probes (Nardeux Solo 25s). Access tubes were set in each of the main types of soil surface feature (crusts) occurring from upslope to downslope of each unit: (1) in the bare zone, (2) at the upslope boundary of the thicket, (3) in the core of the thicket, and (4) at the downslope boundary of the thicket, in the 'senescence' zone. A rain gauge was installed on the site. Soil moisture profile were monitored at rain dependant time steps. A first measurement is performed as soon as possible after each rain (typically 5 to 10 h), and following measurements were taken 1, 2 and 4 days later if no rain occurs. After 4 days without rain, measurements are made once a week during the rainy season, and once a month during the dry season. A principal component analysis (PCA) was done on the time evolution of soil moisture to verify the similarity of the water behaviour of the soil located in the same surface crust area. For each group of access tube (three per group), i.e. for each crust type or for each relative location along the transects, profiles showed the intraseasonal variations in infiltration. The evolution of the soil water moisture in the 0–40 cm horizon was then analysed in relation to the changes in the density and phenology of herbaceous plants during the rainy season.

Results

Vegetation composition and distribution

The annual plant cover extends into the dry season although by then the plants are all dead. At maturity (early September), the herbaceous layer was composed of 23 annual species. Only a few seedlings (less than 1-year-old) were found of the two woody species that dominate the ecosystem (*Combretum micranthum* and *Guiera senegalensis*). Among the 25 species, 67% of the total number of individuals were *Microchloa indica* (L. f.) P. Beauv. and 21% were *Cyanotis lanata* Benth. (Fig. 2). Their distribution in the transition zone was compared for the two sample sites. Due to their low frequency, no consistency was found in the spatial distribution of the other species.

The distribution of the two main species along the transects was consistent between the two sampled units and at all the reading dates, $0.64 < r^2 < 0.81$ and $0.47 < r^2 < 0.64$

for *Microchloa indica* and *Cyanotis lanata*, respectively. When the plant cover was maximum, the distribution of the two species characterised the structure of the herbaceous layer (Fig. 3). *Microchloa indica* occurred along the 20 m transect but showed peak density (2500 plants m^{-2}) in the middle of the transects. *Cyanotis lanata* was more abundant downslope with peak density much lower than that of *M. indica* (maximum of 1000 plants m^{-2}). The density distributions of all the species showed a spatial arrangement from upslope to downslope. *Microchloa indica* and *C. lanata* were dominant (first rank in density) upslope and downslope of the transects, respectively. Furthermore, the dominance of *C. lanata* under the woody canopy and the dominance of *M. indica* away from it were confirmed by the statistical analysis of the data collected from the 10×10 cm quadrats (Table 1). The dominance of *C. lanata* was significantly more frequent under the tree canopy than away from it ($p < 10^{-20}$, Fisher's exact test). The dominance of *M. indica* was significantly more frequent away from the woody canopy ($p < 10^{-27}$, Fisher's exact test). The dominance of *Spermacoce ruelliae* DC., the third most abundant species, was not significantly more frequent in either case (the probability of the null hypothesis is 0.125). *Spermacoce ruelliae* and the remaining species were distributed along the transects but their density reached locally a maximum of four plants m^{-2} . No species grew along the upslope and downslope boundary of the transects except *M. indica* and *C. lanata*, respectively.

The soil seed bank (all species) averaged 9000 seeds m^{-2} at the core of the thicket and 50 seeds m^{-2} at the centre of the bare zone. Moreover, as these were all annual

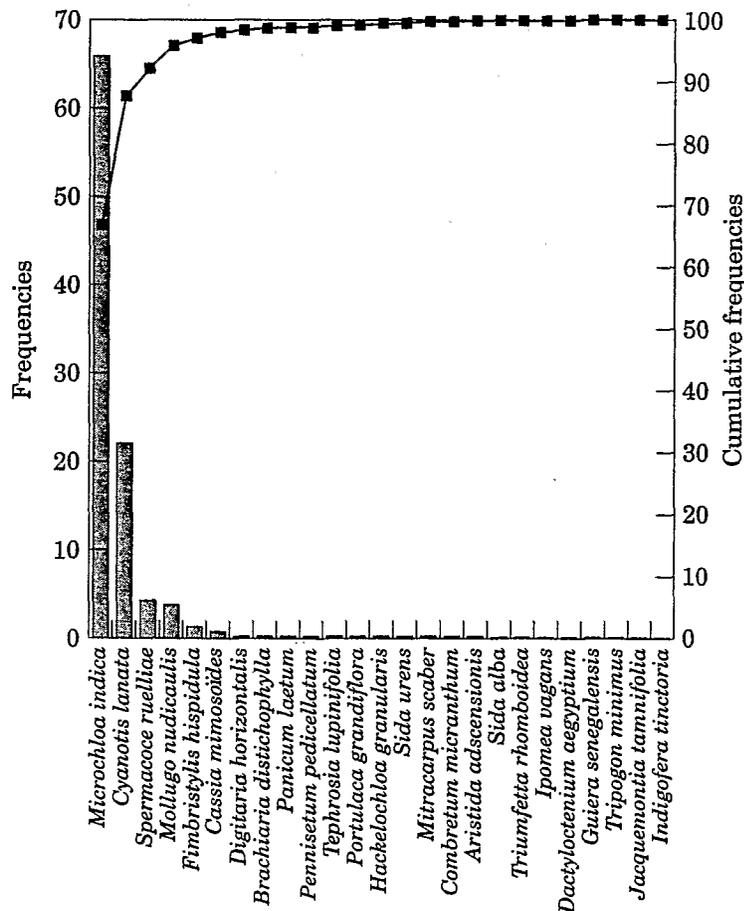


Figure 2. Frequency bars and cumulative frequencies (■) of the whole species inventoried in 1992 ($N = 25$ species).

seeds, only a part of this seed stock was viable. This confirms a potential limitation of the annual plant development by the seed bank in the bare zone.

Soil surface features and vegetation relationships

At the soil surface thin crusts, more compact and hard when dry than the material

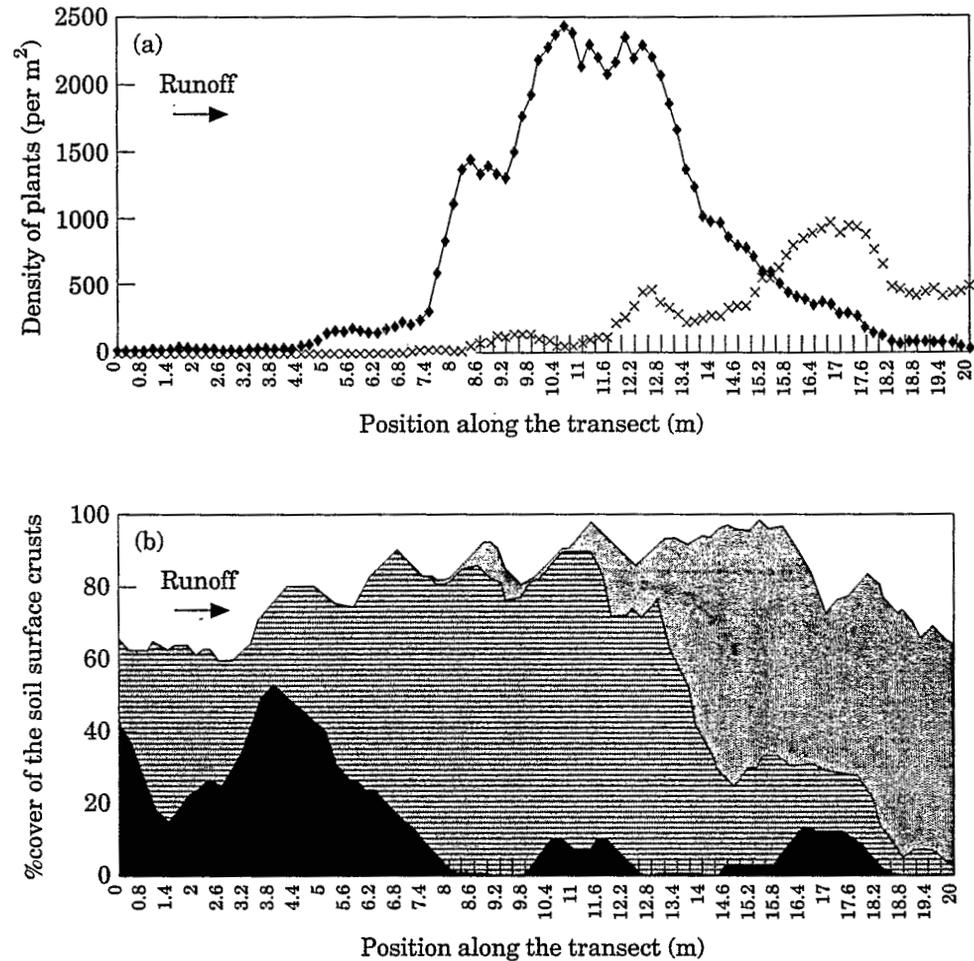


Figure 3. (a) Distribution of the two main species and (b) the types of crusts along the transect. (◆) = *Microchloa indica*; (×) = *Cyanotis lanata*. (■) = pavement crusts, G; (▨) = erosion crusts, ERO; (▩) = sedimentary crusts, SED; (▧) = biological crusts, BIO; (□) = runoff depositional crusts, RUI.

Table 1. Number of $10 \times 10 \text{ cm}^2$ quadrats in which dominant species were found

	<i>Cyanotis lanata</i>	<i>Microchloa indica</i>	<i>Spermacoce ruelliae</i>	Total
Under the tree canopy	96	7	23	126
Out of the tree canopy	10	65	9	84
Total	106	72	32	210

directly beneath (Valentin, 1993), are one of the most important features influencing soil infiltration in the Sahel (Casenave & Valentin, 1989). Five crust types were identified (Fig. 3). They have been related to runoff ability by Casenave & Valentin (1992); in Table 2 they are ranked by increasing infiltration rate.

The pavement crusts (G) are composed of ironpan fragments included in the soil surface. They form small mounds of 1 m diameter, and up to 5 cm thick. Erosion crusts (ERO) are smooth bumps 1 cm thick, due to the high clay content, and are developed where B horizon comes to the surface as a result of runoff flow events (Casenave & Valentin, 1989). Runoff depositional crusts (RUI) are composed of stacks of thin layers deposited by the runoff flow or are located in shallow runoff channels. They are assumed to have the same infiltration rate as structural crusts (ST3) as defined by Casenave & Valentin (1992). In the studied site, the RUI crusts include small ironpan fragments (< 5 mm in diameter). Sedimentary crusts (SED) recorded in the studied site often are covered by a mat of cryptogams (algae, mosses and lichens). They fragment into curled up plates more than 5 cm in diameter in the presence of cryptogam, and smaller otherwise. Biological crusts (BIO) are typically covered by a mat of cryptogams. They crack on drying into polygons 5 cm wide and 2 mm apart. The soils covered by biological crusts are submitted to intense termite activity that increases with plant and litter cover, resulting in a high density of macropores opened at the soil surface. Consequently, they are classed as termite and earthworm surface type (TW) in terms of infiltration rate (Casenave & Valentin, 1992).

The five crust types are not randomly distributed (Fig. 3). They tend to be organised in accordance with the following sequence: most of the ERO and G crusts occur upslope, SED dominates in the area covered by herbaceous layer, then, downslope, BIO dominates in the core of the thicket. RUI crusts are present here and there: upslope as flat sheet flow deposition, and downslope in runoff channels. The SED and BIO spatial distributions vary little between the two sampled zones ($r^2 = 0.64$ and 0.75 , respectively). On the other hand G, ERO and RUI crust distributions changed a lot between the two sample zones ($r^2 = 0.12$, -0.01 , and -0.46 , respectively). G crusts are confined to scarce niches positioned differently in the two sampled areas. Our sampled zone included the downslope boundary of the ERO crust area (upslope the transects). This takes into account only the part where the cover of the ERO crusts is low and randomly sparse. It may be the cause of the very low correlation between the two sampled zones. A significant part of RUI crusts recorded in the sampled zones correspond to small runoff channels going through the vegetated bands, which are not located at the same places in the two sampled units. However, the downslope part of the transects is a particular zone where BIO crusts are absent, SED crusts decrease, but the cover of G, ERO and RUI crusts are at the maximum as compared to the remaining part of the transects (Fig. 3).

Because of the good accordance between the pattern of both crusts and vegetation features, spatial correlations were calculated between the spatial distributions of the two main species and the crust types. The distribution of the two species was not correlated with the crusts G, ERO and RUI. However Fig. 4 shows the relationships established between *Microchloa indica* and SED ($r^2 = 0.52$ but only 0.02 between *M. indica* and BIO). The relationship found between *Cyanotis lanata* and BIO is stronger ($r^2 = 0.68$ against 0.26 between *C. lanata* and SED). These correlations express overall trends rather than close relationships, indeed the coefficient of correlation calculated for each of the six transects individually are no more than 0.23 . In addition the relationships between *Microchloa indica* and SED, and between *Cyanotis lanata* and BIO depend on the position on the average transect calculated from the six transects (Figs 3 and 4). The population of *Microchloa indica* is very sparse on the upslope of the transect, probably due to the lack of seeds, while SED percentage already is high (up to 73%, Fig. 4). In contrast, at the upslope boundary of the thicket, the density of *M.*

indica increases from 250 to almost 2500 plants m^{-2} while the percentage of SED crusts fluctuates between 73 and 86%. Further downslope on the transect, the two variables decrease. BIO and *C. lanata* fluctuate in the same direction further upslope on their occurrence area where BIO reaches its maximum cover of 76% (Fig. 4). Farther downslope the population of *C. lanata* continues to increase to its maximum while BIO crusts cover decreases to 44%. Lastly, *C. lanata* density decreases towards the lower part of the transect while BIO crusts cover increases again up to 70%.

Soil water content, soil surface features and vegetation relationships

The consistency of the soil moisture changes between the two sample sites was verified, according to the position where they were recorded: a principal component analysis (PCA) was carried out for all the access tubes on the changes of the soil moisture content during the rainy season. The soil layer considered was the 0–40 cm top layer, as the root depth of the herbaceous layer is hardly ever more than 40 cm. The analysis confirmed the homogeneity between the two sampled areas of the soil moisture regime at the same topographic position, in relation to the type of crust that dominated. Three statistical groups appeared (Fig. 5). The first group corresponded to bare ground where ERO, G or RUI crusts were dominant. The second group corresponded to the place where SED was dominant. The last one corresponded to the core of the thicket where BIO was dominant.

The moisture regime at each place was illustrated by the soil moisture status for

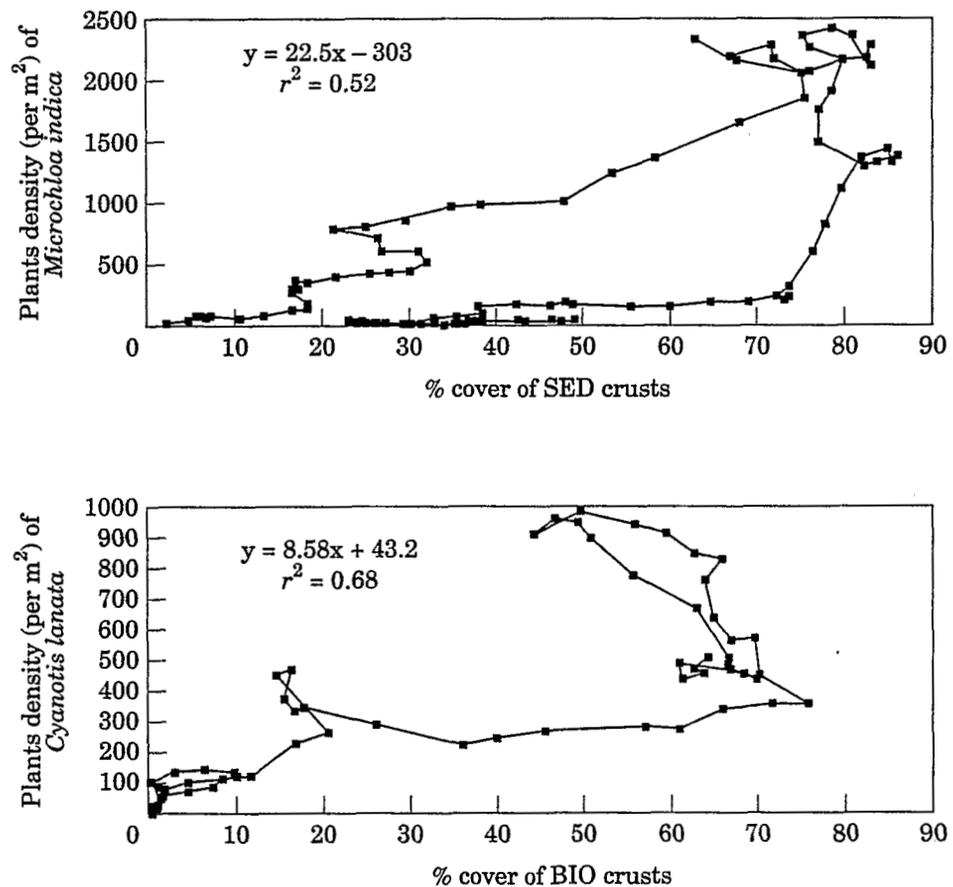


Fig. 4. Plants densities of the two main species in relation to the percentage of the sedimentary (SED) and biological (BIO) crust cover, for which the strongest correlations occur along the transect.

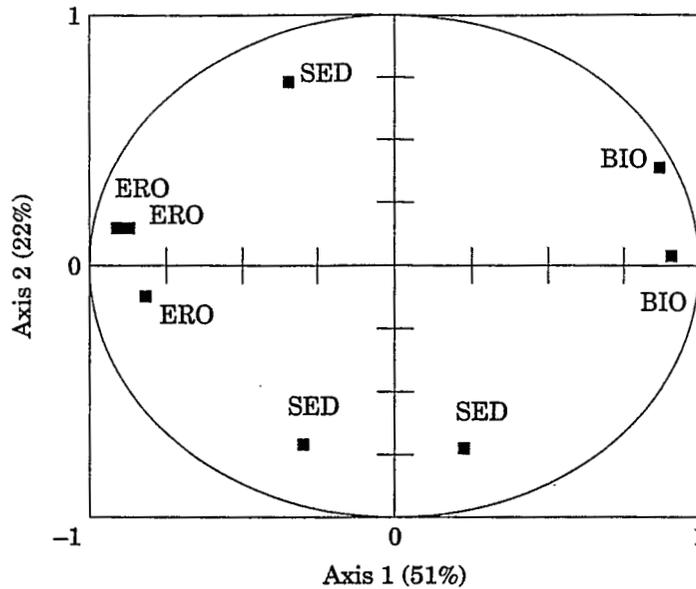


Figure 5. Results of the principal component analysis (PCA) on the soil moisture changes during the rainy season 1992. Annotations refer to place covered by erosion (ERO), sedimentary (SED), or biological (BIO) crusts.

three dates corresponding to vegetation observations and by the maximum and the minimum moisture profiles (Fig. 6(a-c)). During the dry season, drainage and evapotranspiration exhausted the profile throughout the measured depth. The remaining water was tightly bound to the soil and corresponded to the minimum profile. The

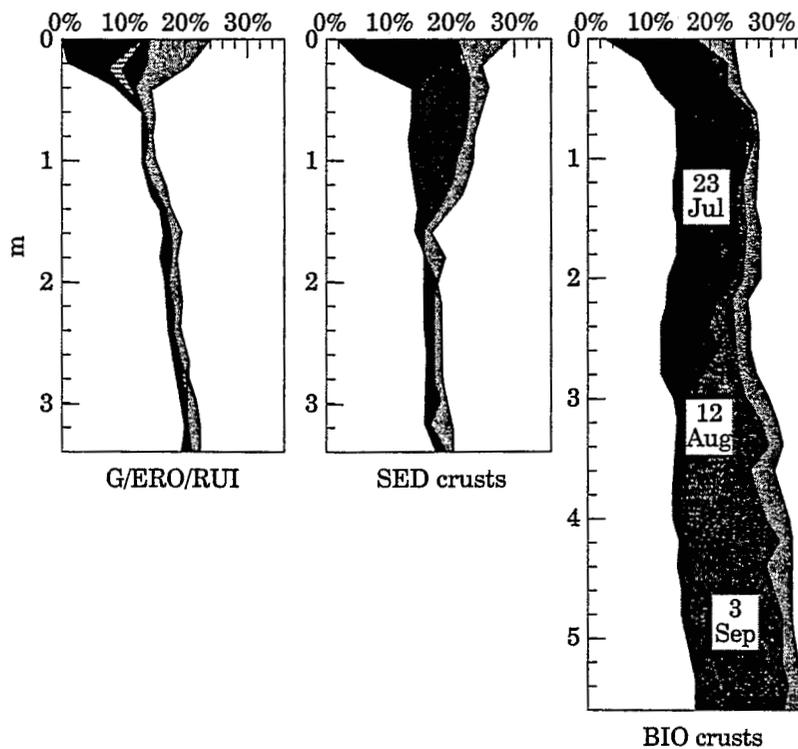


Figure 6. Maxima, minima and seasonal changes (three dates) in soil moisture profiles in three zones of the tiger bush, during the rainy season 1992. The zones are covered by pavement (G), erosion (ERO), runoff depositional crusts (RUI), sedimentary (SED), or biological (BIO) crusts.

maximum profile was drawn using the maximum water content observed at each depth. Unlike the minimum profile, it did not correspond to a single day and it could change from one rainy season to another. Available water is the soil water content subtracted of minimum soil water content.

In 1992, rain began on 6 May (first rain of 4 mm), but no heavy rain occurred until late June (30 June with 41 mm). Considering the evolution of moisture profiles during the rainy season, the earliest, deepest and most abundant infiltration took place in the core of the thicket where BIO crusts dominated (Fig. 6(c)). On 23 July, cumulative rainfall reached 130 mm and the wetting front reached a depth of 3 m in the core of the thicket, whereas it did not wet deeper than 60 cm elsewhere on the transect. On 12 August, 70 mm additional rain fell but the soil water content was the same as for July, except for the core of the thicket where the wetting front went deeper. On 3 September, following a period of heavy rain, the cumulative rainfall was 420 mm. The soil moisture profile was about its maximum all along the transect. The thicket soil was saturated down to 5.60 m, and deeper drainage occurred. Water infiltration in the area covered by SED crusts began to differ from bare soil and senescence zones, with a wetting front down to 1.50 m compared with 60 cm on other locations.

If we focus on the 0–40 cm top layer, where most herbaceous roots were found, the soil moisture was available everywhere from 23 July. During the rainy season, the soil moisture content did not vary much in the core of the thicket. From 23 July it already reached more than 20% at 20 to 40 cm depth and on the 0–40 cm layer it kept roughly constant from 23 July to 3 September. In the area covered by SED crusts, in the 0–20 cm layer soil moisture reached 20% as early as 23 July and did not vary until 3 September. However, in the 20–40 cm layer soil moisture reached more than 20% only on 3 September. Water was available before that date but there was a strong decreasing gradient from 20 to 40 cm of depth. In the bare soil zone water was significantly available only in the upper part of the profile but it was not more than 12%, with a strong decreasing gradient from the top to 40 cm of depth. In the 0–40 cm soil layer, soil moisture only exceeded 12% in early September. During the growth period of annual plants (from early June to early September), in the 0–40 cm soil layer there was always more moisture in the core of the thicket and always less in the bare soil zone than somewhere else. Although its amplitude could vary, the occurrence of a spatial increasing gradient from the upslope bare soil to the core of the thicket during the whole growing season was confirmed by the evolution of the soil moisture content in the 0–40 cm soil layer (Fig. 7).

Soil moisture content increased very quickly after the first rains in the thicket core where BIO crusts dominate, whereas it increased more gradually in the SED crusts area, and did not change in the ERO crust area (Fig. 7). From 15 July to the mid-August, soil water of the 0–40 cm layer fluctuated with rain along the transect, showing a slight increasing trend. Increasing soil moisture content was almost immediate after rainfalls, but the soil dried out and drained very quickly. Only from 22 August, after a 50 mm rain on a wet soil, to the end of the rainy season, were water contents of the soil covered by BIO and SED crusts about equal and near the maximum. During this period, moisture of the soil covered by ERO crusts increased quickly from 20 to 40 mm, but available water remained lower than in soil covered by BIO and SED crusts. However, *M. indica*, mainly occurring on SED crusts, did not settle later than *C. lanata*. Furthermore the ERO area was colonised only by *M. indica* late in August (Fig. 8) when water content increased to 40 mm (Fig. 7). We did not observe late seedlings of *C. lanata* upslope of the area covered by BIO crusts (Fig. 8), despite the moisture content increase to 80 mm during the same period in the soil covered by SED crusts (Fig. 7). However, the intervals between readings on vegetation growth were too large to conclude that *M. indica* requires less water than *C. lanata*. The density of *M. indica* is much higher than that of *C. lanata* (up to 700 plants m⁻² compared with less than 225 plants m⁻²). However, although we did not compare their biomass, the first

species is a very small and thin Gramineae (less than 10 cm high), while *C. lanata* is a taller Commelinaceae (often more than 10 cm high) that would provide thrice the ground cover of *M. indica*. Soil water content decreased exponentially after the last rain. For the 0–40 cm top layer, 55% of available water vanished 1 month after the last rain (occurring on 14 September) and 100% 8 months later. One month after the last rain around 500 plants m⁻² of *M. indica* were counted on 14 October, i.e. 73% of the maximum. Over the same time *C. lanata* population decreased faster (around 125 plants m⁻², i.e. only 50% of the maximum were observed at the same date). The reproduction phase of *M. indica* started before the soil water content in SED crust area

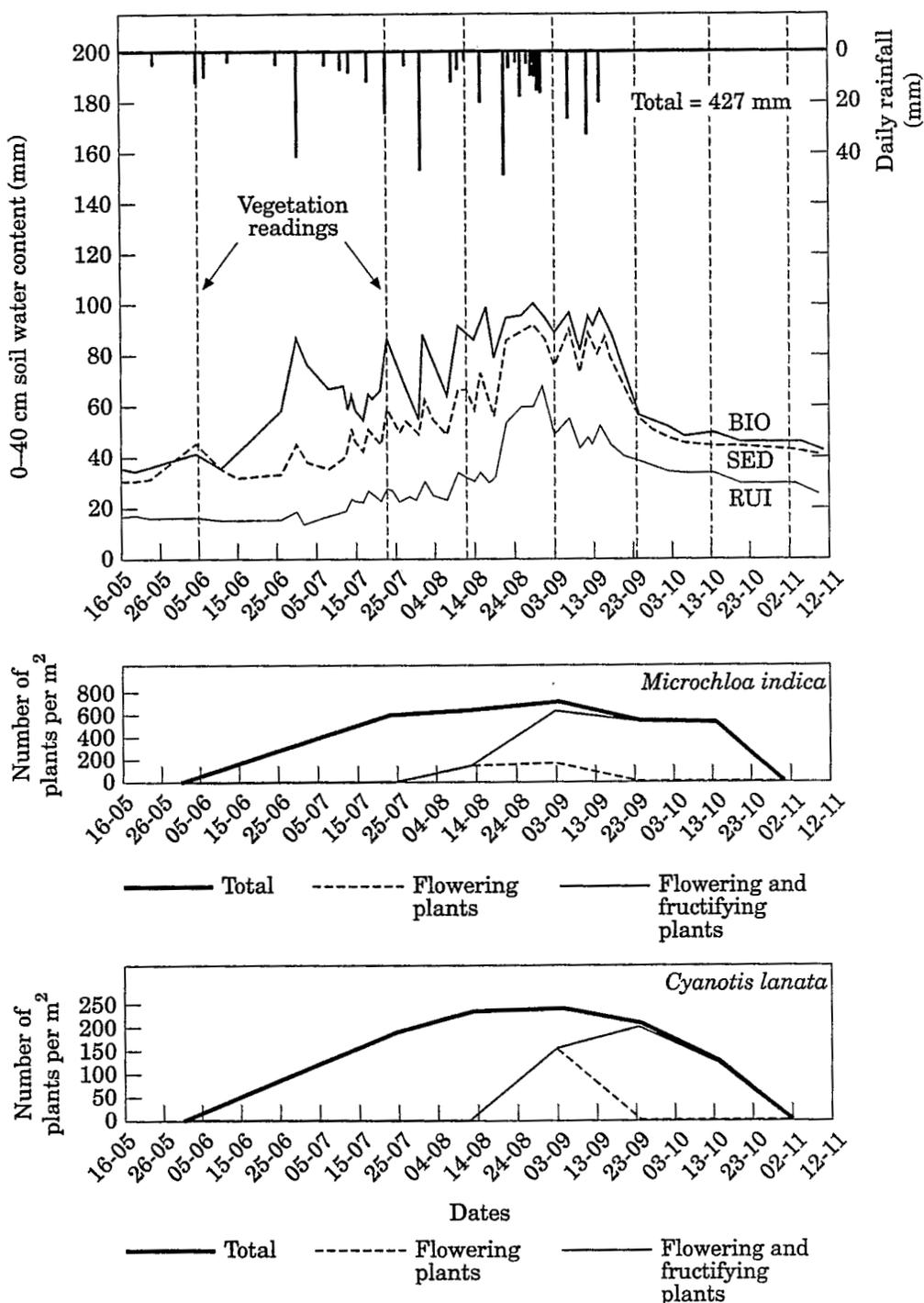


Figure 7. Rainfall distribution, intraseasonal changes in soil water content between 0–40 cm of depth and in plant density of the two main species.

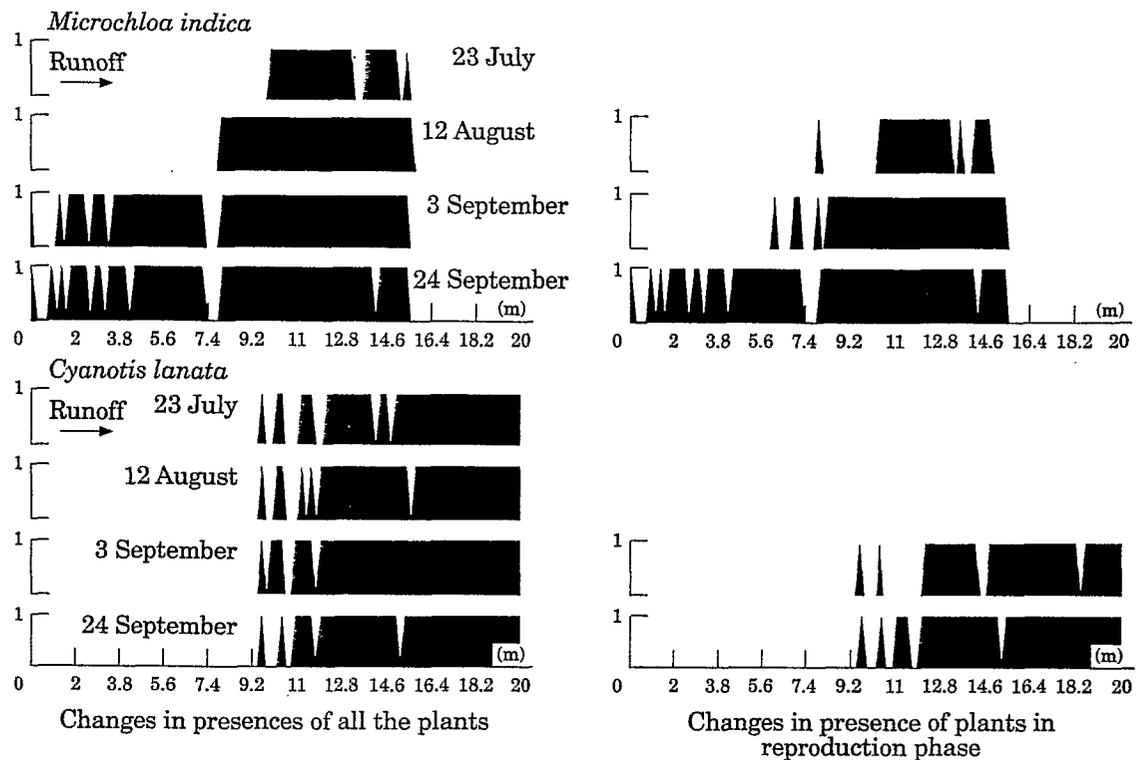


Figure 8. Changes in presence distribution of the two main species along the transect at four dates in the rainy season 1992.

was at its maximum. This is not the case for *C. lanata* which showed a later and a shorter life cycle in BIO crust area (Figs 7 and 8). At least a part of the population of *M. indica* that germinated later during the last 2 weeks of August in soil covered by ERO crusts reproduced (Fig. 8). This contributed to lengthening the reproductive period of this species in comparison to *C. lanata*.

Discussion

Three zones have been identified where the type of crust, water dynamics and annual vegetation development constitute homogeneous and coherent functional units on the two sample sites studied (Fig. 9). Intra-seasonal variations in soil moisture content are related to the soil surface conditions and to the overall topography. Spatial distribution of the annual species across the tiger bush is associated with redistribution of rain water by topography and soil surface features that control infiltration rates, i.e. the available water for plants.

From the bare zone upslope to the core of the thicket, firstly gravel, erosion and depositional crusts on the bare zone (G, ERO, RUI) are the sign of a strong runoff (Table 2). In relation to the low and late infiltration recorded, few plants occur in this zone, and only when water becomes significantly available (above 40 mm) in the 0–40 cm layer in the beginning of September. The very low density of seedlings observed from this period in this area is due to the very low density of viable seeds in the bare soil. This is because the seeds would be washed away by the runoff flows before they could be buried in the soil. Only a few seeds of *Microchloa indica* germinated and reproduced. At the upslope boundary of the thicket, a sedimentary crust (SED), 3–5 m wide, reveals the existence of water stagnation at the soil surface before infiltration. Slow water penetration due to water persistence on the surface for relative long periods

Table 2. Infiltration rates corresponding to the tiger bush crusts (after Casenave & Valentin, 1992, modified)

Crust types	Infiltration rates (KI %)
Pavement (G)	5-15
Erosion (ERO)	10-20
Runoff depositional (RUI) or structural (ST3)	15-25
Sedimentary (SED)	20-35
Biological (BIO) or termite and earthworm (TW)	85-100

was already noted by White (1970). Also a high surface evaporation certainly occurs during this period (Peugeot, 1995). A population of *Microchloa indica* grows and colonises a great part of this area from the beginning of the rainy season. This species is known to be adapted to grazed and open environments, where other species have been eliminated, and even occurs on squelettic soils in the southern savannas (Boudet, 1972; Breman & Cisse, 1977; Seghieri *et al.*, 1994). In the upper fringe of the thicket, there is a decreasing gradient of available soil moisture away from upslope fringe, seed stock decreases and plant distribution becomes more and more sparse. Consequently, the synergy and competition for available water should be less and less active when moving upslope from the thicket despite water availability decreasing.

Downslope, where entering the thicket, sedimentation crusts are increasingly broken due to emerging plants during the rainy season and termite activity. Progressive dominance of *Cyanotis lanata* replaces dominance by *Microchloa indica*, while the cover of biological crusts (BIO) increases with porosity and infiltration. The high water

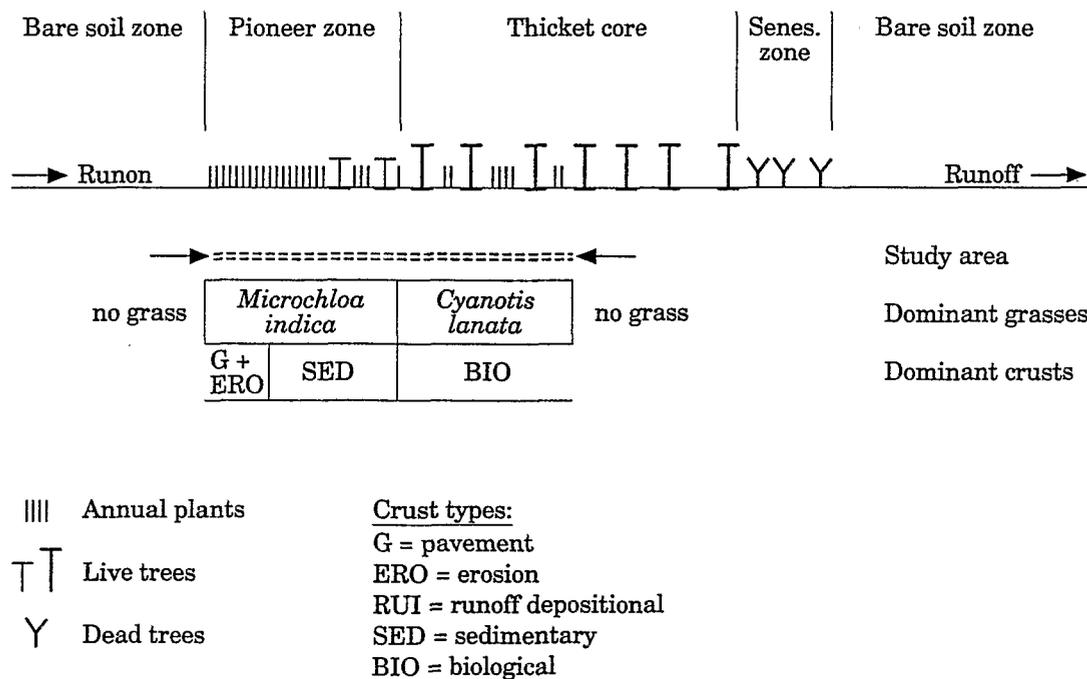


Figure 9. Scheme of a cross-section through an elementary unit of the studied tiger bush. The very gentle slope (0.2%) is not visible on the scheme.

content and deep moisture profile allows a dense woody vegetation to develop. *Cyanotis lanata* is shade tolerant, although it is also able to grow in open environments; it is avoided by grazing cattle (Hiernaux, unpubl. data). From 23 July, available water is not limiting for *Microchloa indica* in the SED crust area but it is for *Cyanotis lanata*, despite the small size of its roots (at the most 10 cm, pers. observ.). When the soil moisture of the SED crust area in the 0–40 cm soil layer has increased up to the amount of moisture in the BIO crust area (about mid August), *Microchloa indica* has already grown and covered the area. Consequently, the reason for the absence of *Cyanotis lanata* in the SED crusts area is water requirement in the early rainy season and competition for space later. Hiernaux (unpubl. data) also suggested intolerance of the species to the sharp variations of the water regime in the further top soil layers (alternation of water stagnation and soil drying). Furthermore, in the core of the thicket, the dense woody cover and the continuous cover of litter impede the development of seedlings. Accordingly, the richness of herbaceous species decreases so that only one species, best adapted to the shade, survives (*Cyanotis lanata*), and further downslope its density decreases despite large water availability. The non-random arrangement of the species along a line crossing from upslope to downslope the thicket has already been observed in other banded vegetation ecosystems. Worrall (1959) noted in herbaceous stripes of Butana (Sudan) that the distribution of the upslope herbs and downslope grasses appeared to be due to the lower moisture requirement of the former ('pioneer') and their inability to compete for light with the tall grasses. Worrall (1960) observed too that the grass became thicker and continuous at the forefront of the bands of acacia trees in Western Sudan, but became thin and patchy under the trees. Furthermore, if the bands were wide, the grass may disappear entirely. Competition for light could be an important factor determining the species spatial arrangement in the banded ecosystems but it has not been taken into account in biological models such as that of Mauchamp *et al.* (1994).

Despite the low specific richness of the studied site, the species arrangement is that expected in an ecotone, with a specific richness progressively decreasing at the further upslope and downslope boundaries of the herbaceous layer area. The specific poorness would be the consequence of strong variations in space and time of the upslope boundary of the thicket (Di Castri & Hansen, 1992). The irregularity of rainfall and human disturbances combine to induce an unstable environment during growth of the herbaceous layer.

Conclusion

The two dominant species recorded in the herbaceous layer are indicators of a long standing heavy grazing regime (Boudet, 1972; Le Houérou, 1989) in the study area. The spatial arrangement from the bare soil stripe to the core of the thicket and the growth of annual species during the rainy season are mainly controlled by the top soil moisture regime in relation to the distribution of soil surface crusts along the slope. The influence of the soil moisture regime on the annual plant growth is combined with other factors that increasingly predominate towards the upslope and downslope boundaries of the herbaceous layer area. The lack of viable seeds upslope and the density of trees downslope limit the extent of the annual vegetation cover despite the occurrence of water availability.

The spatial arrangement of the species and the soil moisture gradient recorded along the slope are consistent with observations on other banded vegetation patterns (Cornet *et al.*, 1988; Tongway & Ludwig, 1990; Montana, 1992). Examples of grass zoning were given in former studies such as Audry & Rossetti (1962), Boaler & Hodge (1964) and Worrall (1959) where pioneer communities occupied the front positions or advanced edges of the stripes. This type of ecotone pattern is regularly associated with

an upslope migration of the vegetation, either in relation to the primary succession prefigured by the spatial arrangement of the plants (Ambouta, 1984; Montana, 1992; Mauchamp *et al.*, 1994), or based on the gradient of water resource related to the runoff direction and the relative position of the plants compared to each other, independent of the species (Thiéry *et al.*, 1995). However, in Niger, no field study has shown any evidence of such a dynamic adjustment, although Leprun (1992) estimated the vegetated bands of the tiger bush in Mali migrated upslope at a speed of 20–75 cm per annum. Irregularity of the rainy season is spatially and temporally high in the area where tiger bush occurs (Lebel & Le Barbé, 1997). The regeneration processes of the woody vegetation are not clear (Couteron *et al.*, submitted). Lastly, the annual vegetation layer is strongly affected by the grazing and regulation mechanisms observed in this small-scale study and should be very sensitive to degradation from grazing pressure (Tongway & Ludwig, 1994). Moreover, to improve the bare soil of degraded banded landscape in Niger, Orr (1995) proposed to plant the early successional grasses in open areas rather than planting trees alone. This should reduce reclamation and erosion control.

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