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Catena 37 (1999) 231–256

CATENA

## Niger tiger bush as a natural water harvesting system

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Received 16 September 1996; received in revised form 5 December 1996; accepted 10 February 1998

### Abstract

Tiger bush in Niger has been often hypothesised to act as a natural water-harvesting system. The interband:band ratio (IBR) and the related efficiency of the system in terms of water concentration and woody biomass production appeared as crucial questions to be addressed and documented. This study focused on the role of annual rainfall upon the structure and the functioning of the tiger bush system. A regional transect, totalling approximately 200 km in length was established north/south across the rainfall gradient. It included 10 local transects each spanning five interbands and bands. Along the local transects, surface features were carefully recorded as well as woody biovolume. One of these local transects was completely harvested so that biovolume could be related to biomass. Annual woodcutting was estimated after a detailed regional study. In addition to field measurements performed in 1995, the IBR was measured on sequential aerial photographs (1950, 1955, 1962, 1975, 1992), using a 16 × binocular magnifier combined with a stage micrometer with 0.1 mm division. A simple model of rainwater redistribution was designed based on surface conditions properties. The best correlation of IBR was obtained with annual rainfall averaged over the last 15 yr ( $R_{a_{15}}$ ). This ratio was dramatically increased where  $R_{a_{15}}$  declined below a threshold of approximately 350 mm. The ratio between the water shedding zone (RZ) and the infiltration zone (IZ), RZ:IZ, based on field crust type survey, was a better predictor for the water-harvesting efficiency of the system than was IBR. The water harvesting model could be used as a satisfactory predictor for woody biomass ( $R^2 = 0.83$ ). Best simulations were obtained when wood cutting during the last 8 yr was accounted for. The water harvesting and concentration enables wood production which equals that of the forest in much more humid southern zones. The thicket production in the banded patterned systems succeeds in over-compensating the barrenness of the interbands, even exceeding woody biomass of industrial plantations in the same region. Due to the gradual thickening of the infiltration zone, the water-harvesting system becomes no longer effective at the wetter southern end of the tiger bush

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domain ( $Ra_{15} = 685$  mm). Conversely, the decreasing favourable conditions to infiltration should lead to a dry limit of ( $Ra_{15} = 155$  mm). Therefore, woody biomass production of the tiger bush is controlled by two opposing trends linked to mean rainfall. The result is that the production of these structures reaches a maximum at 550 mm mean annual rainfall. The sustainable use of tiger bush in the longer term requires the careful maintenance of this natural water harvesting system, with no attempts of afforestation in the interbands, no agriculture, and only moderate wood harvesting in the vegetation bands. Rehabilitation strategies which mimic the natural tiger bush ecosystem are the most appropriate under these climatic circumstances. © 1999 Elsevier Science B.V. All rights reserved.

*Keywords:* Surface conditions; Surface crusting; Runoff; Water harvesting; Banded vegetation patterns; Drought

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## 1. Introduction

Under arid and semi-arid conditions, the concentration of resources into patches results in a higher plant productivity (Noy-Meir, 1973). Such patches occur frequently in the form of dense vegetation bands aligned perpendicular to slope, interspersed with bare soil. These banded vegetation patterns, which support distinctive communities of grasses, shrubs and trees, have been reported throughout the Sahelian zone from Mauritania (Audry and Rossetti, 1962) to Somalia (MacFayden, 1950), in East African (Belsky, 1989) and South African semi-arid regions (Van der Meulen and Morris, 1979) as well as in the Middle East (Vezev-FitzGerald, 1957; White, 1969); Mexico (Cornet et al., 1988) and Australia (Slatyer, 1961). Many authors considered overland flow as an essential factor in the formation and the maintenance of these banded systems (e.g., Ambouta, 1984; Mabbut and Fanning, 1987; Tongway and Ludwig, 1990; Greene, 1992; Dunkerley and Brown, 1995; Thiéry et al., 1995).

In these environments, often referred to as 'tiger bush' in West Africa (in French 'brousse tigrée', Clos-Arceud, 1956), the capture and storage of limited water resource appeared to be optimized through a spatial partitioning between run-off, run-on and infiltration, the bare interband acting as a source, and the vegetation band as a sink (Noy-Meir, 1973; Ludwig et al., 1998). In support of this natural water harvesting theory, infiltration input in the bands was found to exceed 1.5–2.5 times the local precipitation (Hemming, 1965; Cornet et al., 1988; Bromley et al., 1997).

In a given site, the amount of run-on to the vegetation bands is generally assumed to be controlled by the surface conditions of the interband. Hydrologic characters of the two main system components, often broken into subzones, have been assessed using rings method (Slatyer, 1961; Ambouta, 1984), rainfall simulation tests (Tongway and Ludwig, 1990; Delhoume, 1996) and disk infiltrometers (Greene, 1992; Vandervaere et al., 1997; Bromley et al., 1997). However, relatively little is known about factors controlling water shedding and trapping efficiencies and run-off models are still needed to predict redistribution within the system.

If the vegetated run-on band requires a certain area of interband to shed run-off water, the relative dimensions of these two components must be an essential factor to the maintenance of the system. It has been thus postulated that the width of the interbands

should increase relative to that of the bands as rainfall decreases. (Gavaud and Boulet, 1967; Ambouta, 1984). The interband intervals can range from one to four times as wide as the bands (Gavaud and Boulet, 1967; Mabbut and Fanning, 1987). However, no factor has been clearly shown to influence the width of the vegetation area as compared to the run-off contributing area (Dunkerley and Brown, 1998).

Even less documented is the plant biomass production within the band. Because water inflow is the first critical factor for production under these climatic conditions (Noy-Meir, 1973), it seems reasonable to speculate that productivity should be affected by the factors controlling run-off from the bare band and infiltration into the vegetation band.

The objectives of this study were (1) to investigate the factors influencing the interband width:band width ratio, (2) to design a simple predictive model of rainwater redistribution based upon surface conditions, (3) to relate woody phytomass to the efficiency of the tiger bush regarded as a water-harvesting system.

## 2. Methods

### 2.1. *The tiger bush domain in Niger*

In south western Niger, the plateaux where tiger bush patterns may occur covers an area estimated at 22000 km<sup>2</sup> (Ambouta, 1984) and located between 13°N and 15°N (Gavaud and Boulet, 1967). This region shares many characteristics of sites where vegetation banding has been reported. The annual rainfall is characterized by a strong temporal and spatial variability. This is due to periodic regional droughts and the randomness of local convective storms. However, in the long-term, annual rainfall clearly decreases from approximately 750 mm in the south to 400 mm in the north (Gavaud and Boulet, 1967). Rainfall distribution is monomodal, starting usually in June and lasting until mid-September. Intensive dry spells occur from late September until the subsequent rainy season in June. In Niamey, most rainfall occurs in storm events. The median rainfall intensity being 35 mm h<sup>-1</sup> and 35% of the total rainfall falling with an intensity exceeding 50 mm h<sup>-1</sup> (Lebel et al., 1997). Mean monthly maximum and minimum air temperatures are 36.0°C and 22.2°C, respectively with the maximum in April (40.9°C) and the minimum in January (15.9°C). Mean annual potential evapotranspiration is 2294 mm (Sivakumar et al., 1993).

The region is underlain by the Birrimian crystalline basement complex, part of the Precambrian pan-African shield. The overlying rocks consist of a complex formation of loamy sandstone of Miocene deposits called the Continental Terminal. These highly weathered materials are covered with sand deposits of late Quaternary age which tend to plug the dry valley systems and in the north form dunes oriented ENE–WSW (Gavaud and Boulet, 1967; Wilding and Daniels, 1989; d'Herbès and Valentin, 1997). The gentle undulating landscape is disrupted by broad, nearly flat-topped, ironstone-capped plateaux of the Continental Terminal. The tiger bush patterns occur only on these plateaux. However, where thin, discontinuous aeolian sands survive on the plateaux, there is typically no vegetation banding probably due to an insufficient surface for production of

run-off. In the tiger bush systems, the bare interbands are generally steeper (slope gradient = 1.3%) than the vegetated bands (0.8%; Ambouta, 1984).

In this region, the differences in the topsoils of the interbands and bands have been ascribed to the influence of the vegetation itself through accumulation of litter and rooting (White, 1971; Ambouta, 1984; Barker, 1992). In general, these soils exhibit between 0.1 and 0.9 m of gravely loam (35–60% silt and clay) over ubiquitous ironstone gravel and more or less cemented sesquioxide sheets. Mineral reserves in these acidic soils (pH < 5.0) are low. Due to the iron pan and the gravel, these soils offer a low water-holding capacity. According to the reference base of the International Society of Soil Science et al. (1994), most of these soils have been classified as Skeletic Leptosols (d'Herbès and Valentin, 1997). Detailed physical and pedologic descriptions have been given by Ambouta (1984), Wilding and Daniels (1989), Barker (1992) and Legger and van der Aa (1994).

Typically, the thickets of the Nigerien tiger bush are contour-aligned and arranged in more or less concentric rings surrounding the slightly convex tops of the plateaux, forming more parallel arcs than straight bands. The downslope distance between arcs ranges from 35 to 150 m, and the width of the thickets from 10 m to 40 m (Gavaud and Boulet, 1967; White, 1970; Bromley et al., 1997). These arcs may extend up to 100–300 m. The wavelength, i.e., interband width plus band width, is mainly controlled by slope (d'Herbès and Valentin, 1998; Eddy et al., 1998).

The interbands are completely devoid of vegetation. Starting from the bare area, a sequence of three zones is more or less systematically encountered in a downslope direction through the arc (Ambouta, 1984; Thiéry et al., 1995; Bromley et al., 1997): (1) a grassy open bush consisting of a nearly total grass cover of annual plants, such as *Microchloa indica* (Linn. f.) (Seghier et al., in press), associated with the shrub *Guiera senegalensis* J.F. Gmel; (2) a closed bush with a canopy cover between 60 and 100% of tall shrubs and trees, up to 8 m, dominated by *Combretum* spp., with an understorey of small shrubs, such as *Gardenia sokotoensis* Stapf et Hutch, and a very sparse grass cover (< 5%); (3) a bare open bush with a cover declining from 40 to 0% contributed mainly by *Combretum micranthum* and small shrubs as *Boscia angustifolia* A. Rich. and *B. senegalensis* (Pers.) Lam.

## 2.2. Regional transect and field measurements

To investigate the effect of rainfall upon the geometry and the woody biomass production of the tiger bush pattern, a regional transect, was established north/south across the rainfall gradient (Fig. 1). Nearly 200 km long, it included nine study sites at intervals as regular as possible depending on tiger bush occurrence and accessibility for a four-wheel drive vehicle. Zoukouara was the southernmost plateau with tiger bush that could be recognized on the panchromatic SPOT images of February 1991 (field resolution 10 m). Only one selected site, located north of Farantara, our northernmost site, was not sampled due to safety reasons, the region north of the 14° parallel being out of governmental control. Each site consisted of a local line transect spanning five wavelengths of the banding. One site, Dingazi, encompassed two transects, one with typically patterned and one with large bands and interbands.

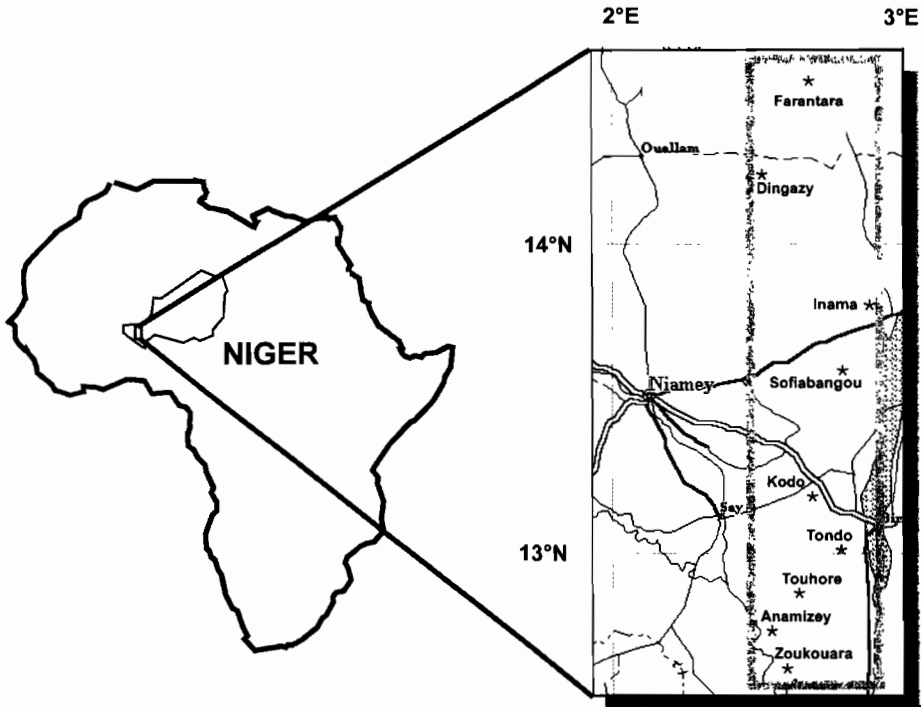


Fig. 1. Location map of the regional transect including the nine selected sites.

The location of each local transect was assessed using a Global Position System and recorded on aerial photographs at 1:50 000. The transect started in the down-slope portion of the uppermost band, a degraded zone (D, Fig. 2), crossed the bare run-off area (R), into the leading edge of the next band, a sedimentation zone (S) and a pioneer zone (P) and the core of this band (C), crossed the same sections in the second, third and fourth bands and stopped at the boundary of the down-slope portion of the fifth band (D). Detailed topographic profiles along these transects were derived from careful survey with an optical theodolite. Steel measuring tapes were laid on the ground to demarcate the boundaries of the tiger bush elements as characterized by vegetation cover and soil surface features using the method presented by Thiéry et al. (1995).

Along the line transects, surface features were carefully recorded after the crust typology of Valentin and Bresson (1992) and the run-off capability classification of Casenave and Valentin (1992). The portions of areas of the surface covered by these classes (%) were visually assessed at intervals varying from 0.5 m to 15 m depending on the heterogeneity of the soil surface. The main features of the different classes of surface conditions identified in the tiger bush transects are presented in Table 1.

In tandem with the topographical survey, the woody vegetation was visually assessed along the line transect, in terms of soil cover ( $Sc$ , %), mean shrub height ( $Msh$ , m) and dominant species. The combination of vegetation and surface features survey resulted in the definition of the five typical zones presented in Fig. 2 and in Table 2.

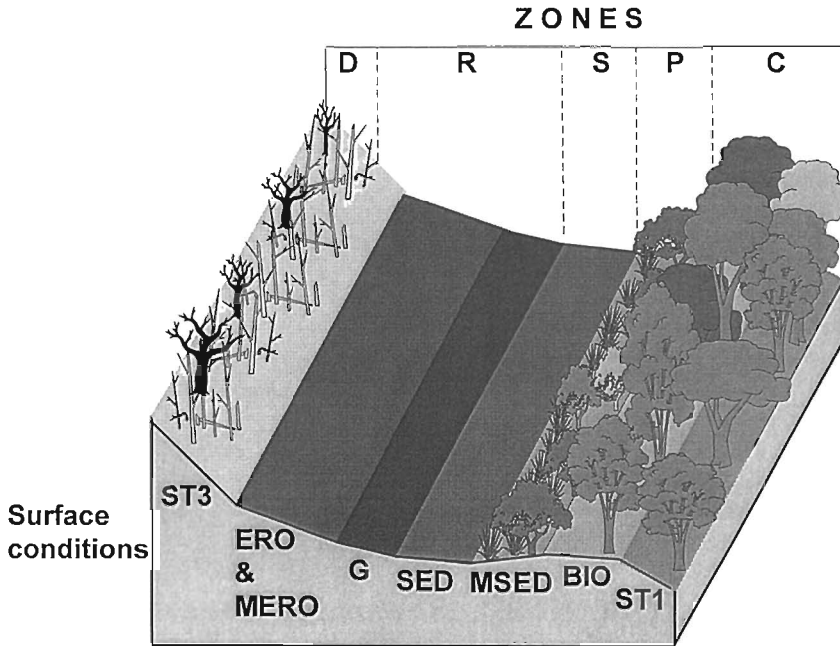


Fig. 2. Schematic cross-section across a tiger bush wavelength showing the different zones (see Tables 1 and 2 for definitions of zones and surface conditions).

The phytovolume ( $Pv_z$ ,  $m^3$ ) was computed for any given zone  $z$ , as

$$Pv_z = sl_z Sc_z Msh_z \quad (1)$$

where  $s$  is the width of the transect (1 m),  $l_z$  (m) is the length of the zone  $z$  along the transect,  $Sc_z$  (%) is the soil cover and  $Msh_z$  the mean height of woody vegetation (m) in zone  $z$ .

### 2.3. Estimation of aboveground woody phytomass

To assess the aboveground woody phytomass, woody plants were exhaustively harvested along a 20-m wide transect spanning six thickets in Sofiabangou, the most central site of the regional transect (Fig. 1). The dry woody phytomass (WM) was then assessed including leaves, branches and timbers for the six thickets (Ichaou, 1995). Since the phytovolume (PV) of these thickets had been assessed, a relation with WM could be established, enabling the conversion of PV ( $m^3$ ) into WM (kg) through the multiplicative coefficient of  $1.64$  ( $kg\ m^{-3}$ ). Assuming that this relation was valid for similar plant communities, it was applied to the ten transects.

In the view of relating WM to water supply, one must distinguish woody phytomass per hectare of thicket core (WMt) from the woody phytomass per hectare of patterned plateau ( $WMp = WMt Iz$ , where  $Iz$  is the percentage of the transects occupied by thicket cores). WMp had to be broken into two categories: WMo that was observed in situ and

Table 1

Main features and properties of the different surface conditions in the Nigerien tiger bush (adapted from Valentin and Bresson, 1992; Casenave and Valentin, 1992)

Type	Structure	Thickness (mm)	Infiltrability (mm ha <sup>-1</sup> )	Mean run-off coefficient <sup>a</sup> (Rc, %)	Zone <sup>b</sup>
<i>Structural crusts</i>					
Slaking (ST1)	rough surface, weak textural differentiation, weak void interconnection	1–3	5–8	35	C
Sieving (ST3)	coarse sandy layer at the top, vesicular fine sandy layer, seal of fine particles at the bottom	2–10	0–5	50	R
Coarse pavement (G)	similar to the sieving crust including coarse fragments and much pronounced vesicular porosity	2–30	0–2	90	R
Erosion crusts (ERO)	smooth exposed seal made of fine cemented particles, possible vesicles	< 1	0–2	85	R
Microphytic erosion (MERO)	similar to ERO but colonised by microphytes as algae	< 1	0–2	85	R
<i>Depositional crusts</i>					
Run-off (ROF)	interbedding of sandy layers and seals of finer particles, possible vesicles	2–20	1–5	50	R
Sedimentary (SED)	larger particles at the top, finer particles at the bottom, possible vesicles, frequent curled-up plates	2–50	0–2	72.5	S
Microphytic sedimentary (MSED)	similar to S but more platy in structure and colonised by microphytes as algae and mosses	2–50	4–7	50	P
No crust (BIO)	continuous and evolved forest litter, high termitic porosity	–	25–40	7.5	C

<sup>a</sup>Rc: mean cumulative run-off/rainfall ratio, as assessed through rainfall simulation tests.<sup>b</sup>Main zone of occurrence. D: degraded, R: run-off, S: sedimentation, P: pioneer, C: central (after Thiéry et al., 1995).

Table 2

Main characteristics of the zones across the Nigerien tiger bush (see Fig. 2)

Zone	Shrubs/trees cover	Main surface features	Slope gradient	Microtopographic features
Degraded	low	ST3	moderate	common microsteps
Run-off	nil	ERO, MERO, G, ROF	low	
Sedimentation	nil	SED	nil–very low	
Pioneer	low	MSED	very low	frequent micro-counterslopes
Central	high	BIO, ST1	very low	

WMC that had been cut for fuelwood over a certain period of time. We have therefore  $WMP = WMO + WMC$ .

The estimation of woodcutting has been carried out within a circle centred in Niamey with a 150-km radius (Project Energie II, 1991). During the year 1990, every day, 24 h a day, every wood transport entering Niamey was enquired about the wood amounts and its origin. The whole area was divided into squares of 3240 ha. Considering that local wood cutting on the plateaux is insignificant compared to the export to Niamey, the annual wood cutting was assessed for each of these squares. This annual rate of wood cutting was then categorized into five gross classes from < 500 tons to > 6000 tons. The original data from the squares encompassing our nine sites were provided by one of the investigators of the woodcutting study (Montagne, personal communication). However, the proportion of each square occupied by tiger bush was unknown. Therefore, we have held constant the proportion of dense vegetation on the plateaux to equal 5.2% which is the mean value for this soil cover as assessed through satellite image analysis of the square degree of Niamey (lat.: 2–3°E; long.: 13–14°N; d'Herbès and Valentin, 1997). Because we had no indication of the long term response of woody biomass to wood cutting, we used different levels of wood cutting intensity from 5 to 15 yr to evaluate WMC.

#### 2.4. Estimation of interband:band ratio from sequential aerial photographs

To investigate the possible effect of rainfall upon the interband:band ratio (IBR) of the banded patterns, we studied sequential aerial photographs at approximately 1:50000-scale taken in 1950, 1955, 1962, 1975 and 1992 (Table 3). For each photograph, we pinpointed the transect sampled in the field, and measured the total length of the transect and the width of the thickets using a 16 × binocular magnifier combined with a stage micrometer with 0.1 mm divisions. We estimated the error to be < 10%, given the marked contrast between thicket and bare interband.

#### 2.5. Estimation of annual rainfall in space and in time

A simple model had to be designed to estimate the annual rainfall over a given period at a given location along the regional transect. In Niamey, rainfall data are available for

Table 3  
Aerial photography specifications (see Fig. 1 for site location)

Date	Nov. 1950	Nov.–Dec. 1955	Sept.–Nov. 1962	Jan.–Apr. 1975	Sept. 1992	Oct.–Nov. 1992
Mission	IGN-AOF	IGN-ND-31-II	IGN, ND, 31-XV	IGN, 75 NIG 40/600	NASA, Hapex–Sahel	DG-DA/IGNN-JICA
Approx. scale	1:50 000	1:50 000	1:50 000	1:50 000	1:50 000	1:60 000
Farantara	011–318		230	3297		1–21
Dingazi	011–153		352	3143		4–19
Inama	016–163		255	2635		9–21
Banizoumbou	016–338		337	2767	88	
Kodo	016–596		603	2961		
Tondo	016–723	506	698	3090		
Touhore		485		4846		
Anamizey		416		4892		
Zoukouara		353		4943		

the period 1905–1995. However we limited ourselves to a period of 20 yr preceding the oldest aerial photograph, i.e., 1930. Long-term annual rainfall patterns were plotted using  $n$ -years moving averages,  $n$  being varied from 5 to 20 yr. Relating the dates of the aerial photographs to the annual rainfall in Niamey averaged over the period 1930–1995 (556 mm), and to the 10-yr and the 20-yr moving averages, it appeared that photographs of 1950, 1955 and 1975 were taken after a period of about average rainfall, 1962 of above average rainfall, and 1992 of pronounced below average rainfall.

As shown by many authors (e.g., Lebel et al., 1992; Sivakumar et al., 1993), the Niamey region is characterized by strong latitudinal variation of annual rainfall. Over the period 1950–1989, Lebel et al. (1992) estimated the increasing north-to-south gradient as approximately constant and equal to 100 mm per degree of latitude. Using the data set of Sivakumar et al. (1993) over the period 1931–1990, including five locations along the gradient, the mean annual rainfall ( $R_a$ ) could be regressed onto latitude ( $L$ ) through the equation

$$R_a = 2930.8 - 179.12L \quad (2)$$

where  $R_a$  is mm and  $L$  is degrees (Fig. 3;  $R^2 = 0.96$ ).

Because large scale averages retain this general climatic gradient (Lebel et al., 1992), we assumed that this latitudinal relation held constant over time. Considering the mean annual rainfall in Niamey Ran (Latitude  $13.5^\circ$ , Fig. 4) over a given period we had:

$$R_{a_{sp}} = R_{a_{np}} - 179.12(L_s - 13.5) \quad (3)$$

where  $R_{a_{sp}}$  (mm) was the mean annual rainfall at the latitude  $L_s$  (in degrees), over the time-period  $p$ .

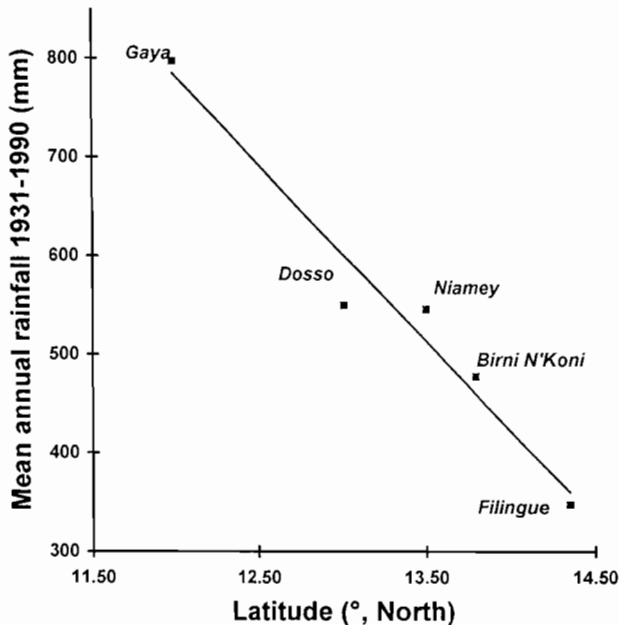


Fig. 3 Influence of latitude upon annual rainfall averaged over the period 1931–1990 (after Sivakumar et al., 1993) for five Nigerien cities as affected by latitude ( $R^2 = 0.96$ ).

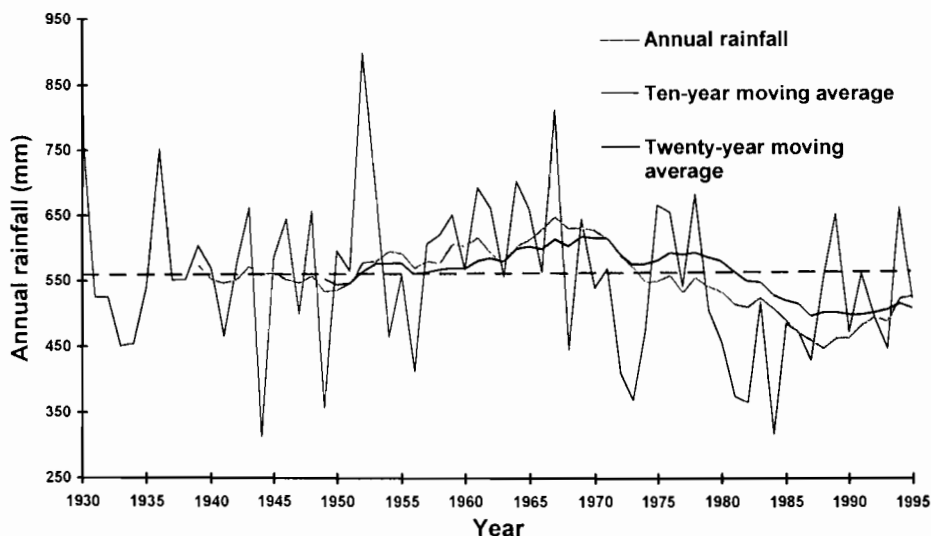


Fig. 4. Annual rainfall in Niamey (1930–1995).

Due to the high temporal and spatial variability of rainfall in the region, such a rough model was unable to estimate annual rainfall, but was postulated to reflect the shifts of the isohyets commonly observed over a long period in the region (Sivakumar et al., 1993).

## 2.6. The water harvesting model

Three simplifications and assumptions were made.

1. The five wavelengths of each local transect were broken into ten distinct parts including five identical run-off zones (RZ) and five identical infiltration zones (IZ). The run-off zones were characterized by the percentages of surface types ST3, ERO, G, SED and MSED (Table 1) averaged over the five wavelengths. Due to their similarities, the ST3 and ROF (Table 1) types were merged into a single category. Similarly, no distinction has been made between surfaces ERO and MERO. The infiltration zone was defined by the percentages of ST1 and BIO surface types.

2. For each of these ten zones, the amounts of run-off (Off), run-on (On), and infiltration (In) was calculated using the model proposed by Casenave and Valentin (1992), and recently validated at similar scales in the region (Peugeot, 1995; d'Herbès and Valentin, 1997). Water flows were assumed to be additive which means that flows in one zone were the sums of flows for each type of surface identified in the zone (Valentin and Casenave, 1992). For each type of surface, the values of the run-off coefficient ( $R_c$ ) and hence of its infiltration coefficient ( $I_c = 1 - R_c$ ) are presented in Table 1.

3. The first run-off zone was assumed to receive no run-on from upslope, in other words to be the uppermost of the whole hillslope.

Table 4  
Main characteristics of the ten local transects along the regional transects

Site	Latitude	Longitude	SG(%)	MWL(m)	VC <sub>50</sub> (%)	VC <sub>55</sub> (%)	VC <sub>62</sub> (%)	VC <sub>75</sub> (%)	VC <sub>92</sub> (%)	VC <sub>95</sub> (%)	Ra <sub>15–1995</sub>
Farantara	14°28.87'	2°38.61'	0.40	55.3	0.44		0.47	0.39	0.31	0.30	310
Dingazi1	14°13.18'	2°30.20'	0.18	131.5	0.45		0.51	0.46	0.36	0.44	360
Dingazi2	14°11.71'	2°30.87'	0.21	64.4	0.89		0.52	0.53	0.44	0.39	363
Inama	13°44.97'	2°49.12'	0.25	66.2	0.46		0.50	0.47	0.37	0.38	441
Sofiabangou	13°33.04'	2°46.44'	0.41	89.7	0.44		0.51	0.53	0.45	0.47	476
Kodo	13°12.52'	2°40.88'	0.41	86.1	0.51		0.57	0.47		0.45	537
Tondo	13°01.60'	2°43.19'	0.30	77.8	0.57	0.58	0.56	0.54		0.46	570
Touhore	12°53.56'	2°39.12'	0.28	71.3		0.60		0.60		0.58	594
Anamizey	12°46.83'	2°34.92'	0.71	55.5		0.64		0.56		0.51	614
Zoukouara	12°38.25'	2°40.20'	0.48	55.0		0.66		0.66		0.64	641
Mean	13°47.50'	2°64.69'	0.36	75.3				0.53		0.46	491

SG: slope gradient; MWL: mean length of a cycle including bare interband and vegetated band (1995); VC<sub>n</sub>: vegetation cover in the year *n* as assessed from aerial photographs and in the field in 1995; Ra<sub>15–95</sub>: estimated annual rainfall averaged over the 15 yr prior to 1995.

Based on these simplifications and assumptions, the basic equations for Off, On, and In could be written as

$$\text{Off}_z = \text{Ra} \sum_{s=1}^{s=n} \text{Rc}_s C_s \tag{4}$$

$$\text{On}_z = \text{Off}_{z-1} (1_{z-1} / 1_z) \tag{5}$$

$$\text{In}_z = \text{Ic}_z (\text{Ra} + \text{On}_z) \tag{6}$$

where  $\text{Off}_z$  (mm) is the run-off production of the length percentage  $l_z$  (%) along the local transect occupied by the zone  $z$ , Ra is annual rainfall (mm),  $\text{Rc}_s$  (%) is the run-off coefficient of the surface type  $s$  and  $C_s$  (%) the percentage of surface occupied by the surface type  $s$ .

The component  $\sum_{s=1}^{s=n} \text{Rc}_s C_s$  is the mean run-off coefficient of the zone  $z$  ( $\text{Rc}_z$ )

$\text{On}_z$  (mm) is the run-on received by the zone  $z$  from the upstream adjacent zone  $z - 1$ .

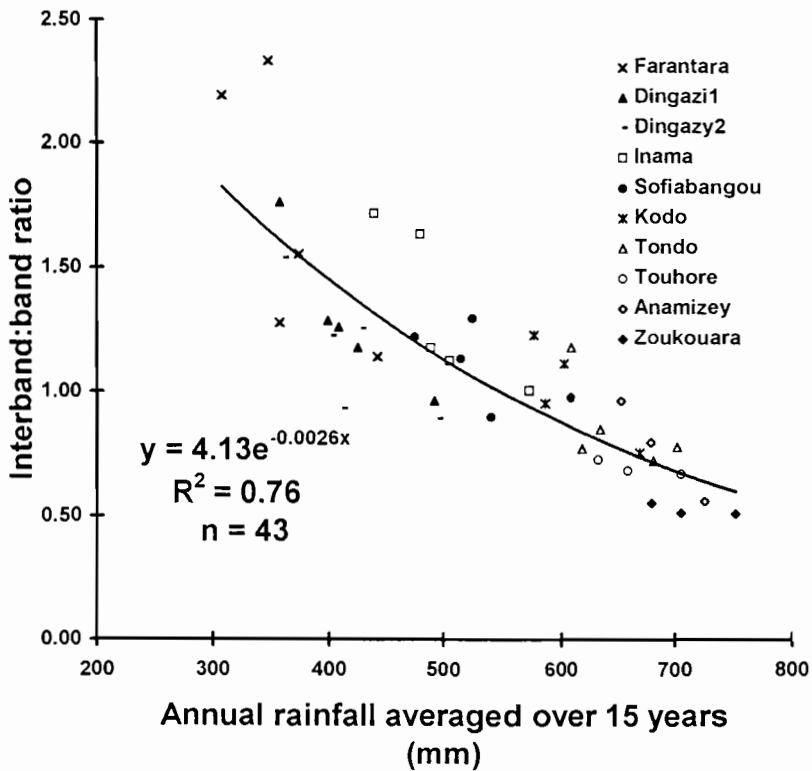


Fig. 5. The influence of annual rainfall averaged over 15 yr upon interband:band ratio after field measurements (1995) and aerial photographs of 1950, 1955, 1962, 1975, and 1992 from ten local transects across a regional transect in Niger

$Ic_z$  (%) is the infiltration coefficient of the zone z.

The water harvesting efficiency (WHE) of the system is assessed by the ratio  $In/Ra$  calculated for the infiltration zone, combining Eqs. (5) and (6):

$$WHE = Ic_{iz}(1 + Rc_{rz}Rz/Iz) \tag{7}$$

where  $Ic_{iz}$  (%) is the infiltration coefficient of the infiltration zone,  $Rc_{rz}$  (%) the run-off coefficient of the run-off zone,  $Rz$  (%) the length of the run-off zone and  $Iz$  (%) the length of the infiltration zone.

### 3. Results

#### 3.1. The impact of rainfall upon interband:band ratio

The main characters of the ten local transects are presented in Table 4. We combined the data on interband:band ratio (IBR) measured on the sequential aerial photographs over the period 1950–1992 and the field observations of 1995. IBR ranged from 0.51 to 2.33 depending on climatic conditions. Best correlation of IBR with  $Ra_p$  ( $R^2 = 0.76$ ) was found for a time period of  $p = 15$  ( $R^2 = 0.60, 0.64$  and  $0.68$  for  $p = 5, 10$  and  $20$ , respectively). Fig. 5 clearly portrays the impact of temporal and spatial variations of  $Ra_{15}$  upon IBR. This figure suggests that IBR was dramatically increased where  $Ra_{15}$

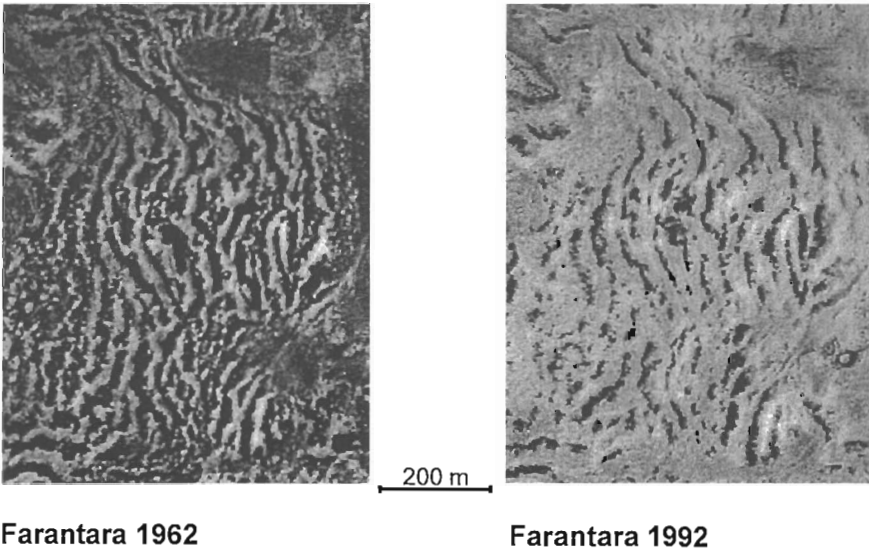


Fig. 6. Aerial photographs from Farantara site. The interband:band ratio was increased from 1.13 in 1962 ( $Ra_{15} = 426$  mm) to 2.3 in 1992 ( $Ra_{15} = 315$  mm).

Table 5  
Main surface characteristics and run-off properties of each site

Site	ST3(%)	ERO(%)	MERO(%)	G(%)	SED(%)	MSED(%)	BIO(%)	ST1(%)	RZ(%)	IZ(%)	RZ:IZ	Rc <sub>rz</sub> (%)	Ic <sub>iz</sub> (%)
Farantara	0.15	0.44	0.00	0.00	0.15	0.12	0.10	0.03	0.87	0.13	6.83	0.52	0.87
DingaziY	0.23	0.23	0.00	0.11	0.09	0.15	0.06	0.13	0.81	0.19	4.18	0.55	0.73
DingaziL	0.25	0.10	0.00	0.08	0.14	0.24	0.13	0.06	0.81	0.19	4.37	0.46	0.84
Inama	0.21	0.18	0.07	0.02	0.21	0.15	0.10	0.06	0.84	0.16	5.32	0.42	0.82
Sofiabangou	0.22	0.11	0.03	0.09	0.13	0.11	0.15	0.15	0.70	0.30	2.37	0.44	0.78
Kodo	0.18	0.11	0.08	0.18	0.09	0.06	0.16	0.14	0.70	0.30	2.38	0.58	0.80
Tondo	0.06	0.08	0.13	0.06	0.18	0.16	0.18	0.16	0.67	0.33	2.00	0.38	0.80
Touhore	0.31	0.06	0.04	0.07	0.12	0.07	0.17	0.15	0.68	0.32	2.13	0.40	0.80
Anamizey	0.19	0.08	0.02	0.24	0.06	0.11	0.18	0.11	0.70	0.30	2.37	0.62	0.82
Zoukouara	0.19	0.15	0.07	0.00	0.06	0.02	0.22	0.28	0.50	0.50	0.99	0.30	0.77
Mean	0.21	0.15	0.05	0.08	0.12	0.12	0.15	0.13	0.72	0.27	3.29	0.47	0.80

The surface types are listed in Table 1.

RZ is the proportion of surface occupied by the run-off zones, IZ by the infiltration zones; Rc<sub>rz</sub> is the run-off coefficient of the run-off zones, Ic<sub>iz</sub> the infiltration coefficient of the infiltration zones.

Table 6

Results from five iterations of the rainwater redistribution model, including run-off amount ( $Off_n$ , mm) in the run-off zone and infiltration amount ( $In_n$ , mm) in the core of the thicket for the wavelength  $n$ ; mean infiltration amount (MIn, mm) and water-harvesting efficiency (WHE = MIn/Ra15)

Transect	Off <sub>1</sub>	In <sub>1</sub>	Roff <sub>2</sub>	In <sub>2</sub>	Roff <sub>3</sub>	In <sub>3</sub>	Roff <sub>4</sub>	In <sub>4</sub>	Roff <sub>5</sub>	In <sub>5</sub>	MIn	WHE
Farantara	160	1218	173	1299	174	1305	174	1305	174	1305	1287	4.15
Dingazi1	197	862	239	990	245	1009	246	1012	246	1012	977	2.71
Dingazi2	168	925	186	992	187	997	187	997	187	997	982	2.70
Inama	186	1171	206	1260	208	1267	208	1267	208	1267	1246	2.83
Sofiabangou	210	765	250	838	253	845	254	846	254	846	828	1.74
Kodo	309	1016	372	1134	379	1148	380	1150	380	1150	1119	2.08
Tondo	216	797	254	859	257	864	258	864	258	864	850	1.49
Touhore	239	882	281	953	284	959	284	960	284	960	943	1.59
Anamizey	383	1250	455	1389	463	1405	464	1407	464	1407	1371	2.23
Zoukouara	195	644	253	689	257	692	257	692	257	692	682	1.06
Mean	226	953	267	1040	271	1049	271	1050	271	1050	1028	2.26

declined below a threshold of approximately 350 mm. For example, in Farantara (Fig. 6) IBR was twice as large in 1992 than in 1962 whilst it remained virtually unchanged in Zoukouara since 1955 (Table 4).

### 3.2. Surface properties and hydrologic simulations

Aerial photographs alone could not provide accurate data on the areal proportion of run-off and infiltration zones along the local transects since some sections of the vegetated bands contribute significantly to run-off, (Fig. 2; Table 1). Specific data on soil surface conditions are thus necessary. Table 5 lists the areal proportion occupied by each surface type along the local transects. No clear climatic influence was shown for run-off coefficients of the run-off zones ( $Rc_{tz}$ ) or for the infiltration coefficient of the

Table 7

Woody phytomass per hectare of thicket core (WMt) and per hectare of patterned plateau (WMP) as the sum of the biomass evaluated in the field (WMO) and the biomass cut over a period of 8 yr (WMC)

Site	WMt (ton ha <sup>-1</sup> )	WMP (ton ha <sup>-1</sup> )	WMO (ton ha <sup>-1</sup> )	WMC (ton ha <sup>-1</sup> )
Farantara	74.35	9.49	9.49	0.00
Dingazi1	54.26	10.47	6.65	3.83
Dingazi2	58.64	10.91	7.09	3.83
Inama	81.20	12.85	4.82	8.02
Sofiabangou	48.05	14.26	14.26	0.00
Kodo	60.78	17.98	6.21	11.77
Tondo	44.75	14.93	11.05	3.88
Touhore	34.40	10.98	9.03	1.95
Anamizey	67.08	19.90	12.20	7.70
Zoukouara	17.12	8.59	8.59	0.00
Mean	54.06	13.04	8.94	4.10

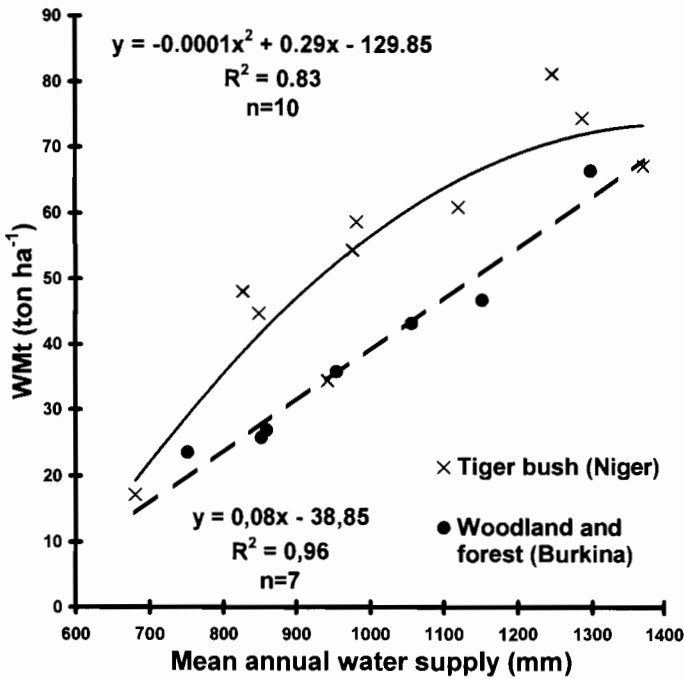


Fig. 7. Influence of mean annual water infiltrated in the thicket core upon the woody above-ground phytomass (WMT) of tiger bush in Niger ( $R^2 = 0.83$ ) compared to the influence of mean annual rainfall upon the woody above-ground phytomass of unpatterned woodland and forest of southern Burkina (after Guinaudeau, 1984).

infiltration zones. More conspicuous was the favourable influence of  $Ra_{15}$  upon the thickening of the thicket core ( $ST1 + BIO$ ,  $R^2 = 0.75$ ) resulting more from increasing  $BIO$  ( $R^2 = 0.78$ ) than  $ST1$  ( $R^2 = 0.53$ ). The ratio between the water shedding zone (RZ) and the infiltration zone (IZ),  $RZ:IZ$  decreased linearly with  $Ra_{15}$  ( $R^2 = 0.79$ ), within a much wider range (0.99–6.83) than the interband:band ratio (0.51–2.33). These two ratios are strongly correlated ( $R^2 = 0.84$ ).

Simulated run-off amount ( $Off_n$ ) in the run-off zone, infiltration amount ( $In_n$ ) in the core of the thicket for the wavelength  $n$ , mean infiltration amount ( $MIn$ ) and water harvesting efficiency ( $WHE = MIn/Ra_{15}$ ) are shown in Table 6 for the five wavelengths of each local transect. These data suggest that even though run-off from the first thicket can attain the second run-off zone, its effect upon the run-off and infiltration of the next zones remains very limited. Consequently, water uptake in the fifth thicket did not largely differ from the water intake in the first thicket due to the very effective trapping effect of the infiltration zone. Results from five iterations of the rainwater redistribution model are shown by  $WHE$  values (Table 6). The infiltration in the thicket core was found higher than precipitation, especially in the most arid sites.  $WHE$  decreased linearly with increasing  $Ra_{15}$  ( $R^2 = 0.72$ ).

$$WHE = -0.0064Ra_{15} + 5.386 \quad (8)$$

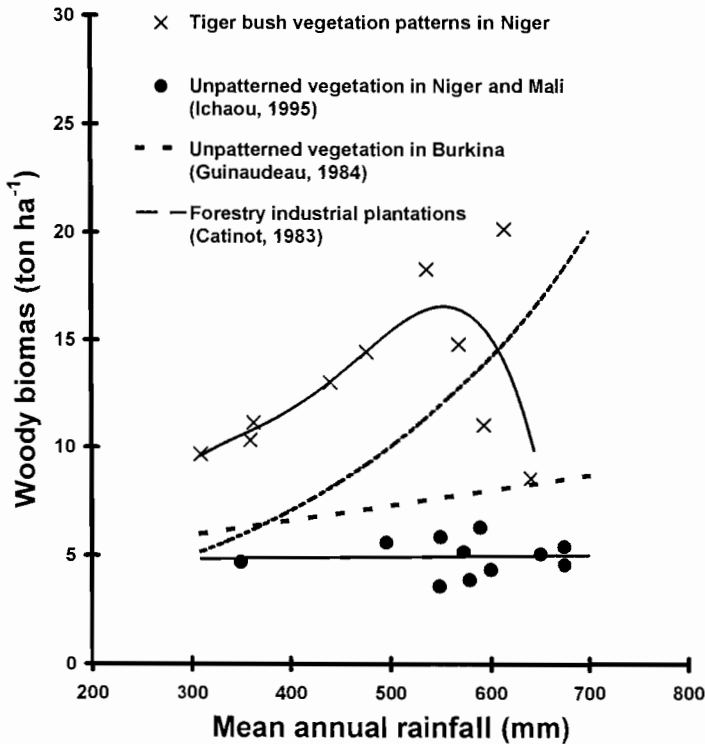


Fig. 8. Influence of mean annual rainfall upon the tiger bush woody above-ground phytomass per hectare of plateau in Niger (WMP), compared to unpatterned vegetation in Niger, Mali and Burkina and forestry industrial plantations in the Sahelian and Sahelo-Sudanian regions.

### 3.3. Woody phytomass as influenced by mean annual rainfall and water intake

The best fit ( $R^2 = 0.83$ ) between  $WM_t$  and  $MI_n$  was obtained when 8 yr of wood cutting was considered (Table 7; Fig. 7):

$$WM_t = -0.0001MI_n^2 + 0.29MI_n - 129.85 \quad (9)$$

$R^2$  was respectively 0.71, 0.81, 0.82 and 0.73 for 5, 7, 10 and 15 yr of wood cutting, respectively.

Wood cutting was the most severe in the two sites located next to tarred roads (Inama and Kodo, Fig. 1) where  $WM_c$  exceeded  $WM_o$ . According to this curve fitting, a maximum of  $WM_t = 80.4 \text{ ton ha}^{-1}$  should be obtained for  $MI_n = 1450 \text{ mm}$  which was very similar to the  $MI_n$  value calculated for Farantara, the northernmost site with  $WHE = 4.15$ .

The ratio  $Rz:Iz$  appears to be crucial for prediction of  $WM_t$  and  $WMP$ . Because this ratio may be tedious and difficult to evaluate in the field, it may be more attractive (especially for foresters) to predict  $Rz:Iz$  from rainfall data, using the regression equation ( $R^2 = 0.79$ ):

$$Rz:Iz = -0.0136Ra_{15} + 9.96 \quad (10)$$

The percentage area covered with thicket cores ( $I_z$ ) increased with rainfall ( $R^2 = 0.75$ ):

$$I_z = 0.0008Ra_{15} - 0.1237 \quad (11)$$

This equation suggested that  $I_z = 0$  for  $Ra_{15} = 155$  mm.

Combining Eqs. (6), (7), (9) and (10) demonstrates that the influence of  $Ra_{15}$  on the production of the thicket cores ( $W_{Mt}$ ) is complex but can be fit with a fourth order polynomial function of  $Ra_{15}$ . Eq. (8) suggested that the water harvesting system should not be efficient ( $W_{HE} < 1$ ) for  $Ra_{15} > 685$  mm.

Since  $W_{Mp} = W_{Mt} I_z$ , the tiger bush domain should fall within the rainfall range defined by the two minima of  $I_z$  (155 mm) and  $W_{HE}$  (685 mm). As shown in Fig. 8,  $W_{Mp}$  had a tendency to increase with rainfall up to threshold and then to plummet dramatically and to become as low as for unpatterned vegetation. This reflected the fact that  $W_{Mp}$  was controlled by two opposing trends ( $W_{Mt} I_z$ ) linked to mean rainfall. The result was that  $W_{Mp}$  reaches a maximum for 550 mm mean annual rainfall as indicated by the adjusted polynomial function of  $Ra_{15}$  of the fifth order (Fig. 9). Best fits were obtained for the increasing section of the curve ( $R^2 = 0.99$ ). Predictions are less robust for the plummeting section of the curve.

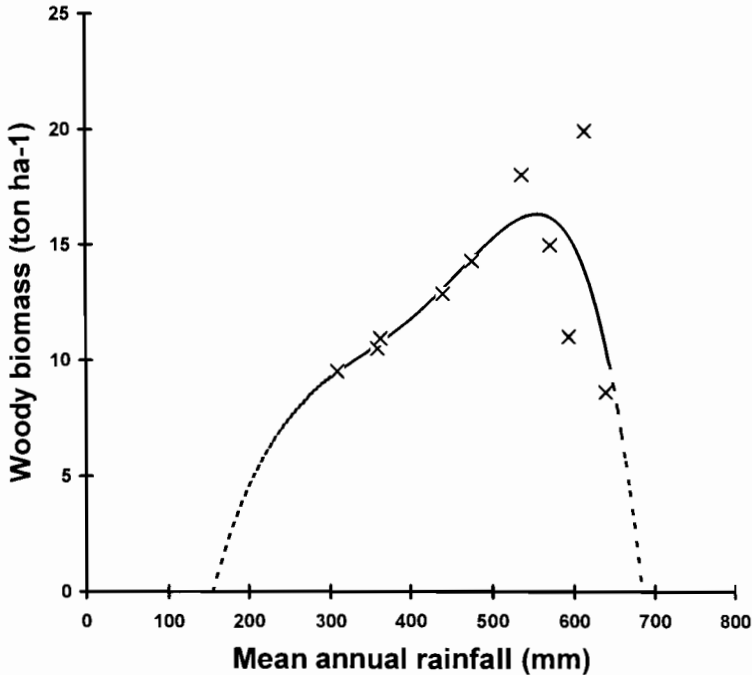


Fig. 9. Climatic tiger bush domain as inferred from the observed (squares) and adjusted (dotted line) influence of mean annual rainfall upon the tiger bush woody above-ground phytomass per hectare of plateau in Niger ( $W_{Mp}$ ). Note that the mean annual rainfall has been averaged over the period 1980–1994.

## 4. Discussion

### 4.1. The efficiency of the natural water harvesting system for woody biomass production

As might intuitively be anticipated, vegetated bands in more humid regions require smaller catchment areas to shed run-off water, hence a marked decline of the interband:band ratio with increasing rainfall. Our results are consistent with the observations of Ambouta (1984) in the same region (IBR = 2.1 for 400–450 mm, 1.2 for 450–600 mm and 0.9 for 600–800 mm). IBR values as high as 5 to 20 have been reported by White (1969) in the very arid region of Jordan ( $R_a = 50\text{--}100$  mm). In fact, comparisons with other regions are made difficult due to the different nature of the interband areas. For example, under an annual rainfall of 250 mm in Australia, IBR was found to range from 3 to 5 (Slatyer, 1961) but the water-shedding efficiency of the interbands was presumably hampered by the presence of perennial grass, annual forbs and even isolated trees. In our case, the clearness of the relationship between IBR and  $R_{a15}$  was favoured by the fact that the bare interband zones exhibited invariably the same succession of crust types associated with a high run-off coefficients.

Our results suggest that the run-off zone:infiltration zone ratio based on field crust type survey was a better predictor for the water-harvesting efficiency (WHE) of the system than was IBR. A part of the vegetated surface, especially in the most arid region, generates significant run-off. Only the thicket core can therefore be considered as a sink for overland flow. As a result WHE showed a wider range than IBR and a more pronounced decline with rainfall increase. The simulated values of WHE are consistent with the few data available in the literature (1.5–2.5 in northern Mexico, Cornet et al., 1988; 1.38 in eastern Australia, Greene, 1992). In Niger these simulated values of WHE agree well with the data obtained from field measurements which fall in the range 1–2 for the thicket core in a region south of Niamey (Bromley et al., 1997). However, this redistribution model of rainwater along the transects across the banded patterns may suffer some exception due to local heterogeneity. This variability can be associated with local landscape concavities and salients of the pioneer zone (Thiéry et al., 1995). Slight counterslopes may force run-off to accumulate and to preferably infiltrate in these zones. This may explain why a higher water storage (WHE = 3.2, compared to 1.6 in the thicket core) could be locally simulated and corroborated by field measurements in this pioneer zone (Bromley et al., 1997). Heterogeneity in local microroughness may also result in higher run-off concentration into the thicket core (Peugeot, 1995; Galle et al., 1998).

Due to the prevailing role of crusts in hampering infiltration, field survey of surface crusts appears to be a useful tool for predicting the spatial variation in soil moisture as shown by the consistency between simulations and field measurements. The very simple model derived from the hydrological characters of these crusts (Casenave and Valentin, 1992) has proven to also be efficient to predict water redistribution along cultivated hillslope in the region (Rockström and Valentin, 1997).

As pointed by our many authors (e.g., Noy-Meir, 1973; Schreiber et al., 1995), understanding run-off offers a key to biotic processes in arid and semi-arid regions. A satisfactory relation could be obtained between the simulated water intake in the thicket

core and woody biomass despite the numerous coarse simplifications and assumptions on the amount of cut wood. The very high values of simulated WMt ( $17\text{--}81\text{ ton ha}^{-1}$ ) were consistent with field data from tiger bush in West Africa ( $21\text{--}88\text{ ton ha}^{-1}$ , Hiernaux and Gérard, submitted). As illustrated in Fig. 7, the mean annual water infiltrating into the thicket cores to produce such biomass under Sahelian conditions are very similar to the mean annual rainfall required to support woodland and forest in the Sudanian zone. Thus this water concentration enables wood production which equals that of a forest in much more humid southern zones. This implies that local high production is made possible but not that the tiger bush system would be invariably more effective than vegetation with no tiger bush patterns under the same climatic conditions. To tackle this issue, we need to compare woody biomass per hectare not of thicket but of plateau (WMP) with unpatterned vegetation in the same region. WMP of the patterned plateau was found three times higher than plateau in Niger and Mali with no tiger bush patterns (Fig. 8; Ichaou, 1995). However these latter values have not been corrected by the amount of cut wood (WMC). Even though the mean value of WMC considered for the tiger bush ( $5.1\text{ ton ha}^{-1}$ ) is systematically added to WMP, the woody biomass of unpatterned vegetation remains approximately half of that of the tiger bush. The thicket production in the banded patterned systems succeeds therefore in overcompensating the barrenness of the interbands, as much as even exceeding woody biomass of industrial plantations in the same region (Fig. 8). This is corroborated by the WMP values available for Burkina Faso (Fig. 8). Similarly, banded vegetation systems in Australia have a net primary production about double that of landscape systems with no patterns (Ludwig et al., 1998).

#### 4.2. *The climatic domain of the tiger bush*

This regional transect also gives some insight on the climatic domain of tiger bush. In addition to slope conditions (d'Herbès and Valentin, 1998), this domain appears to be limited in the south by the water-harvesting efficiency of the system ( $WHE = 1$  for  $R_{a_{15}} = 685\text{ mm}$ ). In the most arid zone, the decline in rainfall is over-compensated by an increase of the run-off zone:infiltration zone ratio. However, such a system requires the existence of an infiltration zone  $I_z$  which tends to disappear below  $R_{a_{15}} = 155\text{ mm}$  (Eq. (11)). This may explain why similar formations may occur under  $200\text{--}250\text{ mm}$  in Mali, north of the  $15^\circ\text{N}$  parallel (Leprun, 1998; Hiernaux and Gérard, submitted) and under  $150\text{--}200\text{ mm}$  north of the  $17^\circ\text{N}$  parallel in Mauritania (Audry and Rossetti, 1962). The disappearance of tiger bush in Niger, north of the  $15^\circ\text{N}$  parallel seems therefore more related to a change in geomorphic than to rainfall conditions. No lateritic plateaux covered with shallow gravelly soils occur north of this limit. The climatic optimum ( $R_{a_{15}} = 550\text{ mm}$ ) for woody biomass production from banded vegetation patterns is comparable to the rainfall optimum for run-off production under natural conditions at the scale of West Africa (Valentin, 1996). Along a regional transect from the Sahara to the tropical forest, run-off coefficient was found to decline regularly whilst rainfall increases. The result of these two opposed trends is a maximum of mean annual run-off amount for an annual rainfall of approximately  $600\text{ mm}$ . Such a consistency among the

two optima tend to confirm the strong relation between the tiger bush patterns and run-off. Because of the frequent shift of the isohyets in the region, the rainfall figures ( $Ra_{15}$ ) should be taken for their relative and not absolute values. In particular,  $Ra_{15}$  may overemphasize the drought of the 1980's.

#### 4.3. Maintenance and rehabilitation of the tiger bush system

Lack of understanding of this system has led to poor management in the past. Foresters considered the bare interbands to be a sign of degradation, and reafforestation attempts were initiated. In Niger, the main technology was the construction of half-moon shaped furrows in the interbands. The reafforestation attempts were spectacular failures. Not only did the seedlings in the interbands receive insufficient rainfall to survive, the furrows and seedlings trapped overland flow necessary for the maintenance of the downslope vegetation, which consequently began to decay. With further disturbance, such as intensive fuelwood harvesting or ephemeral cropping of sorghum or millet, the spatial pattern of water redistribution was altered, run-off increased, and serious gully erosion resulted (Hiernaux and Gérard, submitted). Our simulations suggest that the tiger bush is a nearly hydrologically closed system, acting as a very effective buffer; overland flow was only very slightly incremented from the first to the fifth wavelength (Table 6). Moreover, the vegetated bands form natural benches which enhance soil conservation (d'Herbès and Valentin, 1998). Therefore breakdown of the banded patterns of woody vegetation caused a marked degradation of the landscape.

As emphasized by many authors (Thiéry et al., 1995; Orr, 1995; Ludwig et al., 1998), rehabilitation strategies which mimic the natural tiger bush ecosystem are the best appropriate. Tree planting alone is not expected to be sufficient without restoring surface conditions. As suggested by our results, the restoration of the BIO surface type is essential for improving infiltration, and thus the chance of success for vegetation regrowth. BIO is characterized by decomposed litter and intensive bioturbation, i.e., by the absence of crusts and of crusting hazards. Therefore branch mulching, which protects soil surface from erosion and attract termites, has great promise in terms of acceptance and cost effectiveness as shown in the Nigerien tiger bush by Chase and Boudouresque (1987).

#### 4.4. Climatic variations

As shown in Fig. 5, the synchronic study of a regional transect provides information on diachronic evolution. Our observations indicated that shifts in rainfall isohyets have been associated with a shift in the interband:band ratio. Better correlations were found for a rainfall averaging period of 15 yr, suggesting that such a period was necessary for the vegetation to response to rainfall changes. It is noteworthy that a 10 to 15-yr cycle is used by foresters in the region to enable woody plant regrowth between two successive harvests (Orr, 1995).

Ambouta (1984) described the process of thinning of bands subjected to drought. A drought period should accelerate the decay of the downslope edge of the band, while the

pioneering process of the upslope edge should be seriously reduced if not stopped. As a result the IBR increases, still enabling sufficient water to be shed from the bare interband and trapped into the thicket core. The contrast between band and interband is enhanced resulting in a thinned thicket, and an even thinner thicket core. In years of return to normal, or above average, the bottom edge of the band should receive enough water from the overland flow to develop again whilst the pioneer zone should extend. However this process is limited by the water-harvesting efficiency of the system which tends to decrease with the IBR.

As simulated by Thiéry et al. (1995), these alternating periods should result in a net migration of the vegetation bands. After caesium-137 measurements (Chappell et al., 1998) this upslope migration rate should be of few 0.1 m per year. These results have been obtained near the Sofiabangou site, i.e., in the central part of the regional transect. Because rainfall and associated IBR are subject to more pronounced variations in the northern part of the transect, slightly higher rates are speculated in the most arid zone. However, even on scanned and enlarged aerial photographs, such migrations are very difficult to perceive (Fig. 6).

Despite major rainfall variations, especially in the north, no transformation of pattern type was observed on the aerial photographs. This suggests that the limits between the banded vegetation pattern (tiger bush) and other patterns in the region (spotted, diffuse, etc., Ambouta, 1984) are mainly topographic in nature (d'Herbès and Valentin, 1998).

## 5. Conclusion

Based on a detailed survey of surface conditions on ten sites along a regional transect, simulation modelling indicated that the tiger bush in Niger functions as a natural water-harvesting system. The major critical factor for the efficiency of this system is the ratio between the run-off zone, which includes a part of the vegetated band, and the infiltration zone, limited to the thicket core. The soil surface acts as a regulator controlling the partitioning of rainwater between run-off, run-on, infiltration and runout. Due to the very effective buffering effect of the bands for the overland flow, the banded systems on the plateaux, albeit not utterly hydrologically closed, limits considerably the risks of degradation of the adjoining hillslopes and valleys. The tiger bush system has a very effective buffer for overland flow not only at the interband–band scale but also at the landscape scale. Although this natural water-harvesting system has proved to be robust and productive, its sustainable management requires some care. In particular it is essential to maintain high run-off production in the run-off zone (afforestation of the bare interbands are meaningless) and high infiltration rate in the infiltration zone (no-cultivation, no complete clearing, but perhaps some selective wood-cutting).

The observation of sequential aerial photographs from 1950 to 1992 highlighted the great plasticity of the tiger bush system which adjusted its geometry (IBR) to the fluctuating mean annual rainfall averaged over the last 15 yr. In the face of drought conditions, IBR was dramatically increased, enlarging therefore the catchment area to

shed run-off to maintain the remaining vegetation. Upon the return of more favourable conditions, the initial geometry recovered. Such variations in time were validated in space along the regional transect. The possible adjustment of geometry to rainfall conditions confer a great robustness to the system even under arid conditions.

The concentration of run-on into thicket cores favours high local woody biomass production (20–80 tons ha<sup>-1</sup>) similar to that of woodland and forest in the wet savannah zone, reflecting the infiltration depth in the thicket (as high as 1450 mm in the northernmost site). Even converted into value per hectare of plateau, namely accounting for the run-off zone, the woody biomass production was found to exceed that of forestry industrial plantations under the same climatic conditions.

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Valentin Christian, D'Herbès Jean-Marc (1999)

Niger tiger bush as a natural water harvesting system

In : Valentin Christian (ed.), Poesen J. (ed.) The  
significance of soil, water and landscape processes in  
banded vegetation patterning

Catena, 37 (1-2), 231-256

ISSN 0341-8162