

Run-on contribution to a Sahelian two-phase mosaic system: Soil water regime and vegetation life cycles

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Received April 1, 1997; revised February 12, 1999; accepted March 16, 1999

Abstract — An experiment was carried out from 1992 to 1995, in south-western Niger on a banded vegetation pattern which dominates on a laterite-capped plateau in the region. We quantified the changes in infiltration and vegetation in a thicket from which run-on from the upslope bare soil zone was artificially divested. A concrete wall (40 m long, 60 cm high, 20 cm thick, with a foundation 25 cm deep) was constructed at its upslope boundary. Infiltration was measured to a depth of 5.4 m by a neutron probe, and densities of annual plants were monitored along transects crossing perpendicularly a control thicket and the thicket deprived of run-on. Phenological phases and leaf water potential of the two dominant shrub species were recorded from stratified sampling according to their preferred location along the water resource gradient. Results indicated that run-on contributed the most to infiltration in the central zone, but the water content available to the annual plants (layer 0–10 cm) was not affected by run-on deprivation. Significant differences were found in the water content available to the shrubs (layer 0–100 cm) both between zones (upslope and central), and between thickets after the wall was built. However, in the thicket deprived of run-on, life cycle and physiology of the shrubs were severely disturbed upslope, while much smaller effects were observed in the centre. Surprisingly, within the study interval, run-on contribution was not found to be as essential to shrubs' life cycle at the location where it contributed the most to the infiltration. © Elsevier, Paris

Banded vegetation pattern / leaf water potential / phenology / life history strategy / water resource / water flow / gradient

1. INTRODUCTION

Several hypotheses have been proposed to explain the functioning of banded vegetation pattern and most refer to the influence of overland water flow [3, 15, 16, 17]. In Niger, 4 years of monitoring soil water content and run-off demonstrated that about 70 % of heavy rain (54 % of annual rainfall) falling on bare surfaces produces sheet run-off [20]. It moved downslope to be intercepted and to pond over the thicket where the average infiltration was equal to four times the incident rainfall [8]. Seghieri et al. [21] showed that the distribution of the vegetation changed characteristically along this soil-water gradient. In this study, we sought to quantify the changes in infiltration and

vegetation response when no water flow reaches the thicket.

We prevented water flow into a thicket by building a concrete wall on its upslope border. We compared the soil moisture regime, the density of plants in herbaceous layer, and the phenology and leaf water potential of the two dominant species in the woody cover between a control thicket, and the thicket deprived of run-on. The leaf water potential indicated the physiological responses of the shrubs to drought periods induced by seasonal variations in water availability. It allowed us to quantify the level of shrub water stress [10, 24]. Leaf water potential represents the integration of both atmospheric stress and soil water

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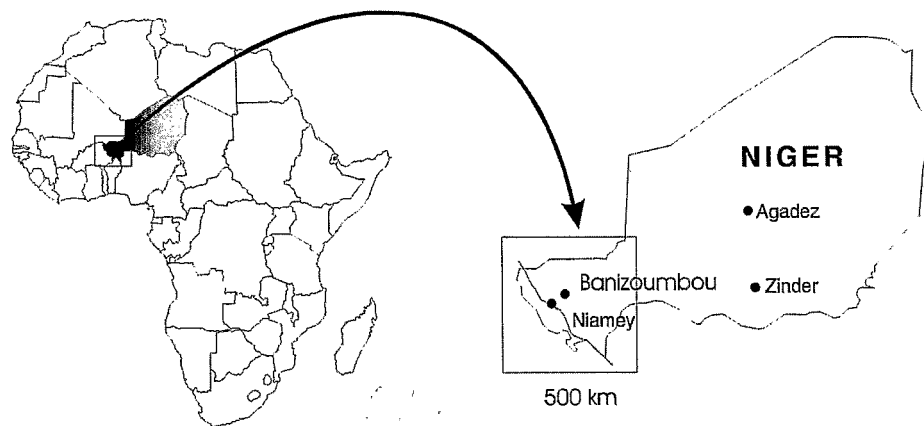


Figure 1. Geographical location of Banizoumbou site, south-western Niger.

stress in the whole rooting zone of the plants, and it is the basic measurement to which other plant functions are related [22].

2. MATERIALS AND METHODS

The nomenclature used throughout is that of Hutchinson and Dalziel [11].

2.1. Study site

The site was located in south-western Niger (13°32' N and 2°42' E) near Banizoumbou village (75 km north-east of Niamey) in the Tillabery department (figure 1).

Climate is semi-arid tropical with a long dry season (from October to May), alternating with a short rainy season (June to September) characterised by high intensity storms. Mean annual rainfall (1905–1989) is 560 mm [13]. A rain gauge recorder was installed at the site during the entire study period (1992–1995, figure 2). The study period included both relatively dry years and wet years (from –25 % to +21 % of the mean). The longest rainy season, the highest amount of rainfall and the most regular distribution of the showers occurred in 1994. 1992, 1993 and 1995 were drier and distribution of the first rains were more irregular (figure 2).

In Niger, banded vegetation patterns occur only on the laterite-capped plateau composed of 'continental terminal' sandstone, with a gentle slope (range 0.06–0.5 %). The shallow soil (60–110 cm thick) is underlain by ferricretes, located over a laterite gravel-land, with hardening of the plinthite to ironstone. The soil is sandy clay loam (after USDA scheme) with

56 % sand and 27 % clay in 0–250 cm layer; the 250–550 cm layer is loam and more homogeneous [8, 21].

The study site showed a typical 'tiger bush' vegetation with thickets arranged in a concentric pattern (figure 3). They were 5 to 20 m in width while the bare zones were 25 to 80 m wide. The vegetation covered 25 % of the study area, according to an aerial photograph assessment (figure 3). The woody population was mainly composed of *Combretum micranthum* G. Don (60 % of total basal area) and *Guiera senegalensis* J.F. Gmel (13 % of total basal area). *Combretum micranthum* dominated the central zones of the thickets and *Guiera senegalensis* was almost the only shrub of the upslope zone. In the centre of the thickets, associated species were *Gardenia sokotensis*, *Acacia macrostachya* Reichenb., *Combretum nigricans* Lepr., *Grewia flavescens* Juss., *Commiphora africana* Engl. At the downslope boundary of the thicket, the dominance of dead stumps indicated a 'senescence zone' [1]. Only the annual species formed the herbaceous layer of which the densest part covered the upslope half of the thickets.

2.2. Methods

Two areas (50 × 40 m each) including thicket and its upslope bare soil zone were monitored from 1992 to 1995 (figure 3). At the upslope boundary of one thicket, a concrete wall (40 m long, 60 cm high, 20 cm thick with a foundation 25 cm deep) was built perpendicularly to the slope before the 1993 rainy season. Deflectors at its ends prevented the monitored area from receiving potential lateral water flows (figure 3). The boundary of the thicket was defined as the upper limit of the area colonised by the annual plants during 1992. Consequently, the 'upslope zone' dominated by

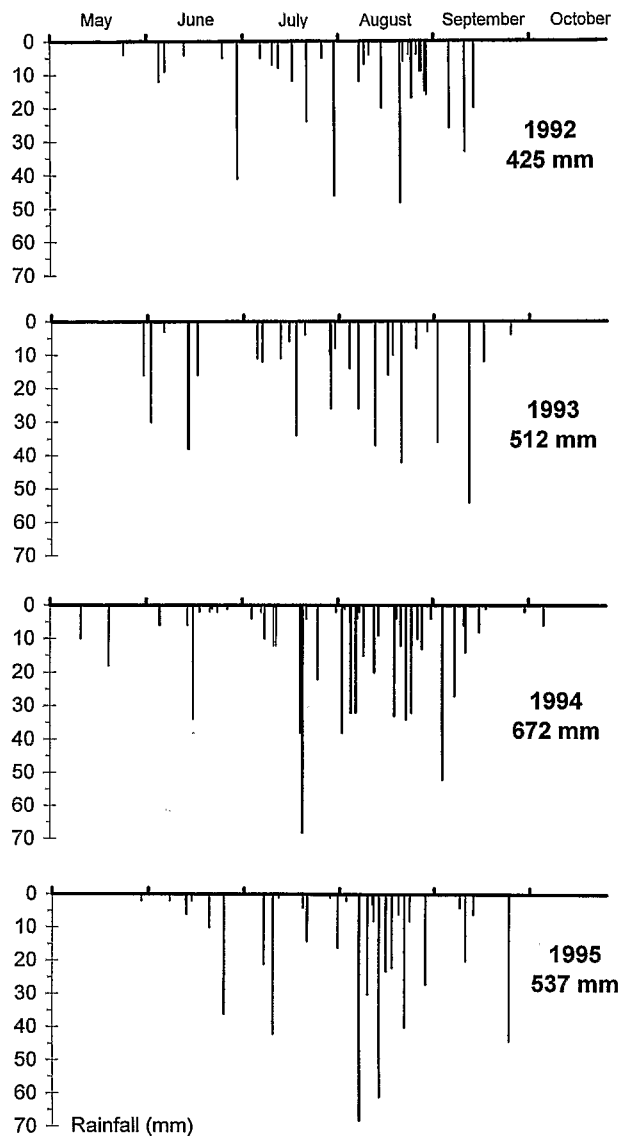


Figure 2. Rainfall distribution in Banizoumbou during the 1992, 1993, 1994 and 1995 rainy seasons.

Guiera senegalensis and annual cover, the 'central zone' dominated by *Combretum micranthum* and the 'senescence zone' of the thicket were divested of run-on. We collected data on infiltration and annual plant density before and after the wall was built, which allowed comparisons using a time control as well as a spatial control.

2.2.1. Infiltration and available moisture for vegetation

Soil moisture profiles (min. 1 m and max. 5.40 m deep) were monitored over 4 years, using Solo-25s neutron probes (Nardeux, Saint-Avertin, France). Access tubes were installed in each of the two thickets as follows: 1) one in the upslope bare zone; 2) one in the upslope zone of the thicket; 3) one in the central zone; and 4) one in the senescence zone. Soil moisture was monitored according to a rain-dependent time series, i.e. 1, 2 and 4 d after rainfall. Frequency progressively decreased to once a month during the dry season. For calibration, two soil samples, 500 g each, were used from the 0–250 and 250–550 cm layers. They were analysed using the nuclear absorption-desorption technique described in Couchat et al. [4]. The calibration equation was a function of the dry bulk density. It was measured with a gamma-ray probe (Nardeux Solo40), with values ranging from $1.65 \text{ g}\cdot\text{cm}^{-3}$ in the 0–20 cm top layer, to $1.8 \text{ g}\cdot\text{cm}^{-3}$ in deeper layers. Further details on the calibration specific to banded vegetation are available in Cuenca et al. [5].

During the dry season, deep drainage and evapotranspiration exhausted the moisture in the profile to the depth measured [8]. Whatever the previous rainy season, the driest profile observed remained the same every year. Tightly bound to the soil, this remaining water was unavailable for plants and for redistribution. The retention curve indicated that a volumetric soil water content of 12 % corresponds to a 10-MPa soil water pressure head. Unlike the minimum water profile, the maximum water profile observed depended on the rainy season. The annual range of variation of soil water content characterised the infiltration processes during each year in each zone.

In a given soil layer, the available water for the plants at any time was calculated as the difference between the measured stored soil water at this time and the minimum stored soil water (in mm). At the end of the experiment, extractions of plants from the three herbaceous groups considered below indicated that their roots were never deeper than 10 cm and generally above 5 cm. Uprooted shrubs of *Guiera senegalensis* in the upslope zone and of *Combretum micranthum* in the central zone had 90 % of their major roots above 60 and 100 cm deep, respectively. Means of stored water available for the plants were calculated over a period from July to September for each year, in upslope and in central zones of the thickets. The two soil layers considered corresponded to two rooting depths: one for annual plants (0–10 cm) and the other for woody plants (0–100 cm).

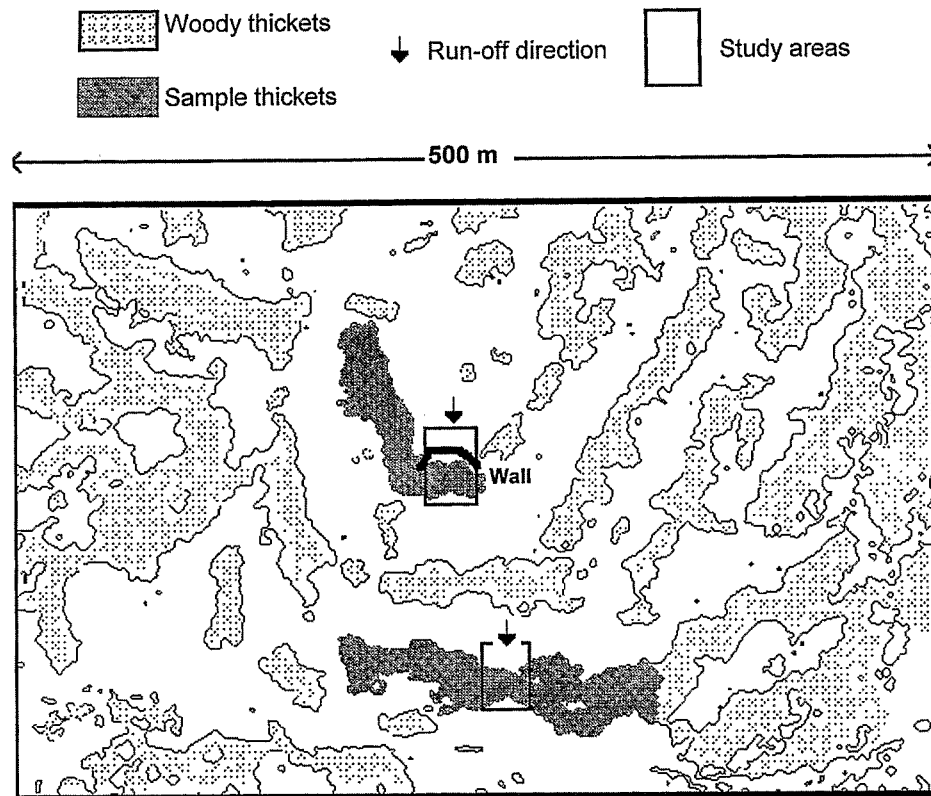


Figure 3. Experimental lay-out.

Analysis of variance (software Genstat 5, release 3.2 PC/Windows NT) was used to test the significance level of the differences observed in available water for the plants between two thickets (control and thicket deprived of run-on in 1993), two periods (before and after the wall was built), 3 years (1992, 1993 and 1994), and two zones (upslope and central).

2.2.2. Vegetation

Data on the herbaceous layer were recorded during 1992, 1993 and 1994, from upslope boundaries to the centre of the thickets, along six transects (three per thicket), 20 m long, and perpendicular to the thickets. The number of plants were counted for each species in a sliding rectangle (5×20 cm). Data were collected once or twice a week, from the beginning of the growth period (when seedlings became identifiable) until the plants withered. Species were divided into three groups: one group for each of the two dominant species and one group for all remaining species. The two dominant herbaceous species were identified in

1992. Among the 25 species registered, 67 % of individuals were *Microchloa indica* (L.F.) P. Beauv. (Gramineae) and 21 % were *Cyanotis lanata* Benth. (Commelinaceae). They were dominant respectively upslope and downslope of the six transects. Their spatial distributions were consistent between the two thickets on the six transects at all dates of observations [21]. For this work, mean densities of each group of plants were calculated for the two zones (upslope and central zones of the thickets) on the six transects over the period of July to September every year. Analysis of variance was used to test the significance level of the differences observed between thickets (control and thicket behind the wall), two periods (before and after the wall was built), 3 years (1992, 1993 and 1994), and two zones (upslope and central zones).

The phenology and the leaf water potential of the woody species were recorded, after the wall was built, during 1994 and 1995 for *Guiera senegalensis* and only 1995 for *Combretum micranthum*. In each

Table I. Classification of the phenological stages observed on each individual shrub sampled.

	Foliation	Flowering	Fruiting
Stage 0	Absent	Absent	Absent
Stage 1	Swelling buds, no leaf development	Floral buds only	Early setting stage
Stage 2	Leaf buds and open buds (over 10 and less than 50 % of these organs in each individual)	Floral buds and open flowers (over 10 but less than 50 %)	Development of fruits to normal size
Stage 3	Leaves mostly open	Over 50 % of organs carrying open flowers	Maturity
Stage 4	Leaves and dry leaves, or leaves which have changed colour (over 10 but less than 50 %)	Open flowers and dry flowers (over 10 and less than 50 %)	Ripe fruits and onset of dissemination (fall of fruits)
Stage 5	Over 50 % in each individual with dry leaves and falling leaves*	A majority of dry flowers and shedding of flower elements	Fruits dried and fallen

* This is a difficult stage to monitor since it may extend over several months according to the species (e.g. *Guiera senegalensis*).

thicket, ten *Guiera senegalensis* located in the upslope zone and twenty *Combretum micranthum* located in the central zone were selected. Data on phenology were collected according to the method of Grouzis and Sicot [9]. Each shrub was classified as shown in *table I* after Le Floc'h [14]. Data were collected weekly during the rainy season, and monthly during the dry season.

Among the individuals for which phenology was monitored, three *Guiera senegalensis* and five *Combretum micranthum* per thicket were sampled for the leaf water potential recordings. We used a hydraulic press (HP, Objectif K model, France) rather than conventional methods, because it was more convenient to implement in the field. Good correlations have been found between HP and conventional methods such as psychrometric and pressure chamber techniques [2, 10, 12, 23]. We measured the pressure when water was first exuded from a piece of leaf. Diurnal variation in leaf water potential of each shrub was recorded every week or every two weeks. It was measured on two leaves per shrub, every hour from predawn to the time the minimum value was overtaken. The mean water potentials were calculated from six sampled leaves per thicket for *Guiera senegalensis* and ten sampled leaves per thicket for *Combretum micranthum* at each time of measurement. For each species, seasonal courses of predawn and daily minimum means were plotted for the two thickets. Predawn leaf water potential was an indicator of the soil water availability in the rooting zone. Daily minimum potential was related to the daily maximum of both atmospheric stress and soil water stress from which the shrubs suffered.

3. RESULTS

3.1. Similarities remaining between the two thickets after construction of the wall

The increasing infiltration gradient from the bare soil zone to the centre of the thicket, and the decreasing one from the centre of the thicket to the senescence zone remained in the thicket deprived of run-on (*figure 4*). Indeed, there was a statistically significant difference in available water for the shrubs between upslope and central zone in layer 0–100 cm within the two thickets ($P < 0.05$), with a mean of 2.4 times more water in the central zone. In the two thickets and the four zones, abundant rainfalls during 1994 produced the highest amount of infiltration (*figure 4*). For the superficial layer 0–10 cm, the same difference occurred in available water for the plants between thickets before and after the wall was built ($P > 0.05$). Consequently, the difference observed could not be due to the erection of the wall but only to a natural spatial heterogeneity. There was no statistical difference in available water of this layer between upslope and central zone within the two thickets.

Densities of *Microchloa indica* in the upslope and the central zones were the same ($P > 0.05$) within the two thickets over the study time in the six transects. There was a difference between the two thickets ($P < 0.001$) in the mean densities of *Cyanotis lanata*. However, it was of the same order before and after the wall was built (103 plants·m⁻² in the control and 409 plants·m⁻² in the other thicket). Consequently, it was not due to run-on deprivation. Unlike *Microchloa indica*, there was a difference ($P < 0.001$) in densities of *Cyanotis lanata* between upslope and the centre of the thickets (twelve times more plants·m⁻² in the

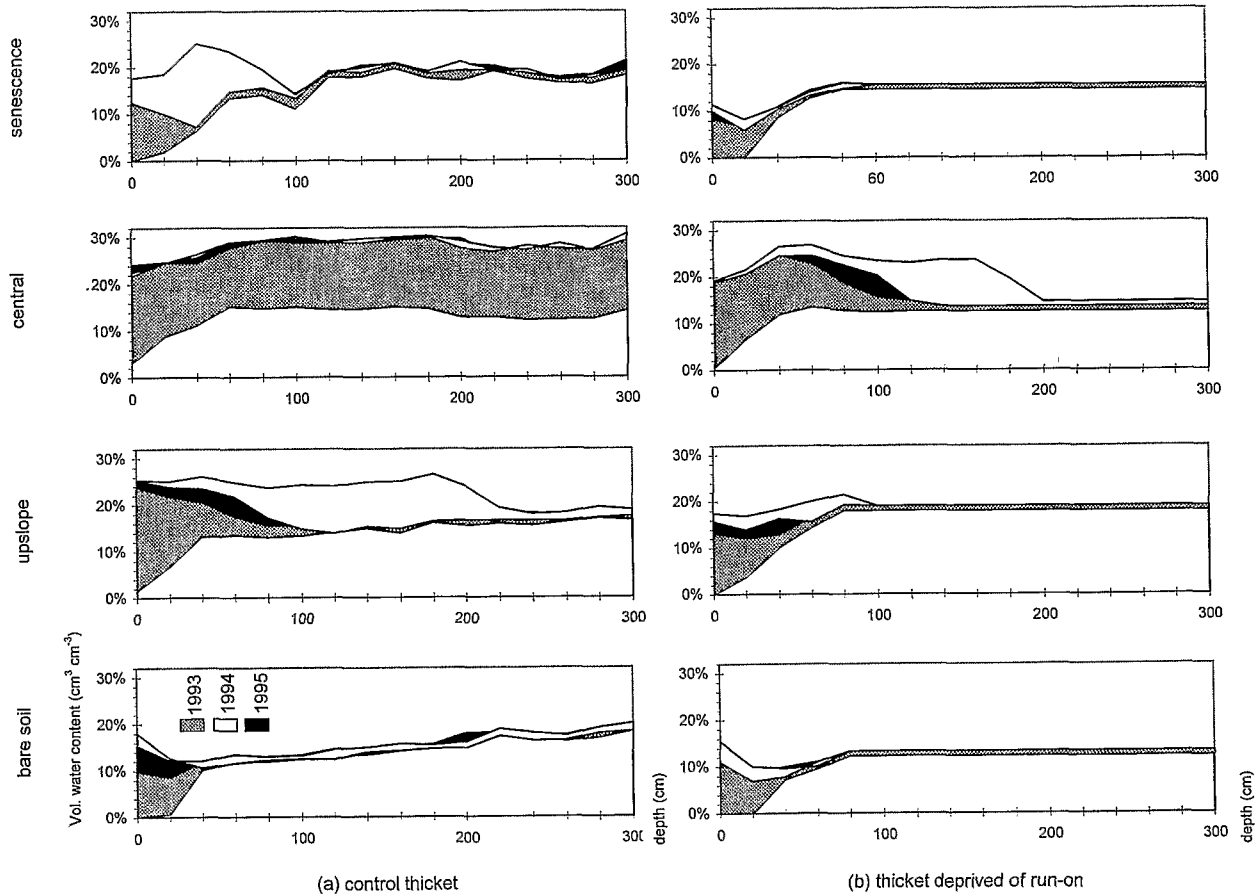


Figure 4. Minimum and maximum moisture profiles over 3 years in four vegetation zones in (a) the control thicket and (b) the thicket deprived of run-on.

centre on the six transects over the whole study time). Also, there were more plants belonging to the group 'remaining species' in the centre than the upslope of the two thickets ($P < 0.05$).

Virtually no difference occurred between the two thickets in *Combretum micranthum* phenology (figure 5b).

3.2. Changes resulting from the construction of the wall

An obvious wall effect was observed in the amount of total water stored. Maximum moisture percentage was lower and infiltration depth was shallower every year in all zones of the thicket deprived of run-on than in the control one (figure 4). The greatest decrease of infiltration due to the wall effect occurred in the centre

of the thicket. Indeed, the moisture front was more than 5.40 m deep in the control thicket (not plotted on figure 4 because of its scale) against 1.40, 1.20 and 2 m in 1993, 1995 and 1994, respectively, without run-on contribution. The moisture front passed the bottom of the tube, which indicated that a deep drainage occurred. This drainage was completely suppressed in the thicket deprived of run-on during the monitoring years (figure 4). The senescence zone was hardly supplied with run-on water except during the wet year (1994) during which it benefited greatly. In the layer 0–100 cm, the amount of stored water available for the plants was similar in the two thickets before the wall was constructed, and was greater in the control thicket after the wall was built ($P < 0.05$). This indicated the effect of run-on deprivation on water availability for the shrubs.

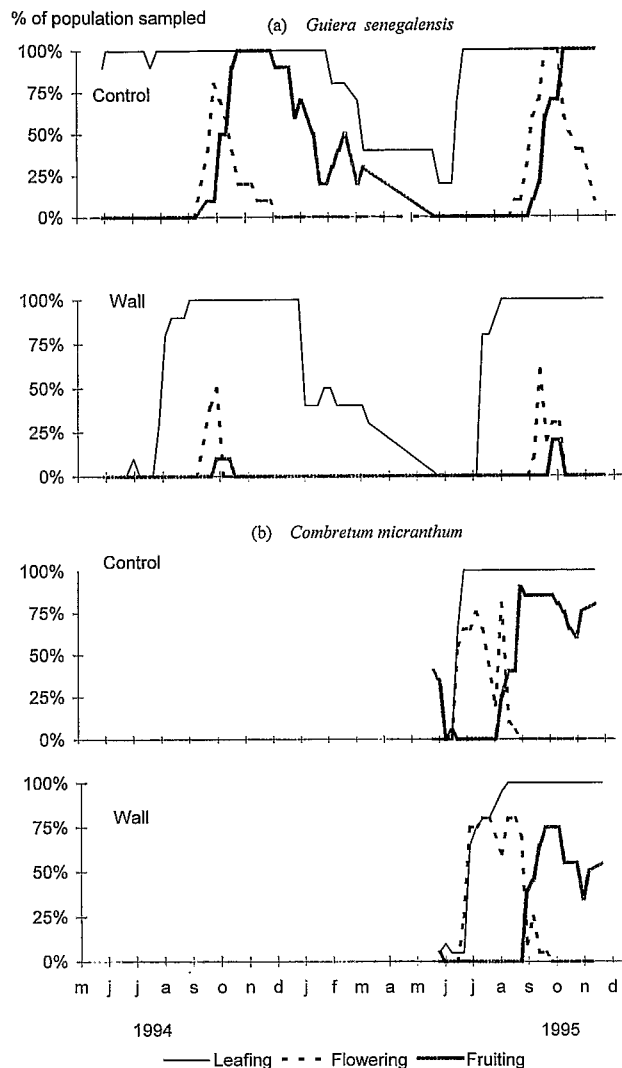


Figure 5. Phenological spectra over 2 years in the control thicket (Control) and the thicket deprived of run-on (Wall) of (a) *Guiera senegalensis* and (b) *Combretum micranthum*.

The difference in mean densities of *Microchloa indica* between thickets were significantly reversed before and after the wall was built ($P < 0.001$). Indeed, the means were 195 plants·m⁻² in the control thicket and 862 plants·m⁻² in the other one before the wall was built, and they shifted to 430 and 361 plants·m⁻² respectively over the two following years. Consequently, the wall appeared as the probable cause of the drop in the thicket deprived of run-on since the difference between thickets remained the same every year after construction ($P > 0.05$). Before the wall was built, mean densities of the group 'remaining species'

were significantly lower in the control thicket than in the other, but significantly higher after ($P = 0.002$). The density dropped almost to 50 % behind the wall while it increased in the control thicket. Construction of the wall could be the main cause since the difference between thickets remained statistically stable during the 2 years following construction (1993, 1994).

Figure 5a indicated that population of *Guiera senegalensis* suffered from a strong reduction in the number of shrubs flowering and fruiting in the thicket deprived of run-on compared to the population in the control thicket. The maximum percentage of reproducing shrubs and the duration of the two sexual reproduction phases, that took place at the beginning of the dry season, strongly decreased behind the wall. Although the leafing phase was less disturbed, it suffered a reduction in amplitude and duration of the period when maximum percentage of the population was leafing. For the same species, the two leaf water potential (daily minimum and predawn) decreased quickly after the break of the rains in the thicket behind the wall compared to control (figure 6a, b). This indicated plant stress linked to a reduction in availability of water in the rooting zone of the thicket deprived of run-on. Although reduced, a similar effect was recorded in *Combretum micranthum* physiology (figure 6c).

4. DISCUSSION

In the study site, at the scale of the bare zone and the thicket just downslope, obviously the run-on flow from the bare zone contributed mainly to the total infiltration in the central zone of the thicket. Its contribution was much less in the upslope vegetated zone. It was negligible downslope of the thicket except when a long and abundant wet season, with regular distribution of rains, occurred as was the case in 1994. The central zone benefited from the highest infiltration capacity that could reach 500 mm during a single rainy event [8]. Cracks in the rooting zone as well as activity of foraging termites mainly contribute to this high infiltration rate [6, 19]. The infiltration capacity in the central zone was so high that even a considerable reduction of water input by run-on did not induce a great deficit of water content available to the shrub, i.e. in layer 0–1 m. In this zone, the rainfall and the negligible run-off taking place in the upslope vegetation zone (about 2 % of total rain [8]) provided enough water to *Combretum micranthum* for it to complete its life cycle, especially as it overlapped with the rainy season ('arido-passive' species, i.e. metabolically inactive during the dry season [7]). If *Combretum micranthum* was affected, the consequences were not

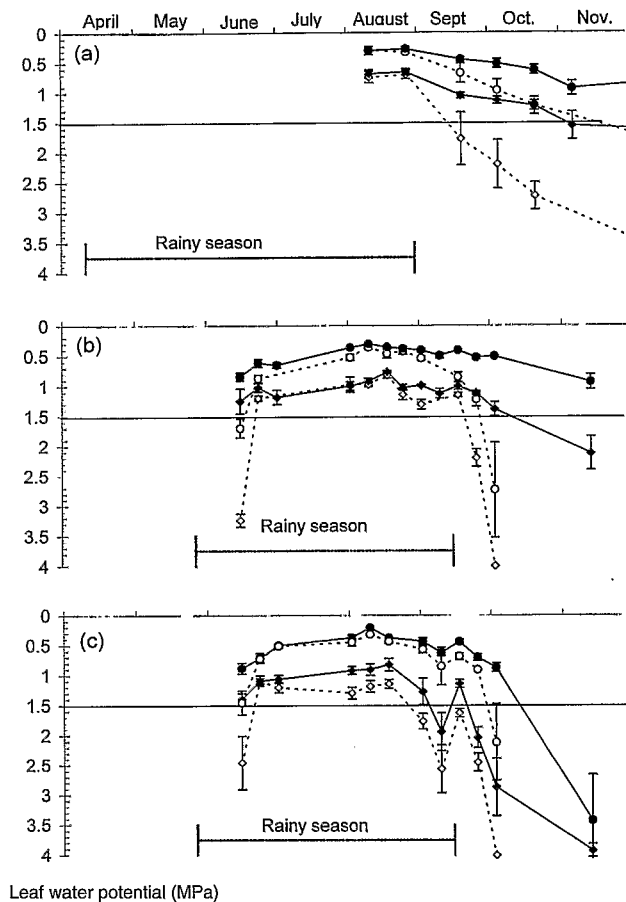


Figure 6. Seasonal changes in the predawn and daily minimum leaf water potentials over 2 years in the control thicket and the thicket deprived of run-on: (a) *Guiera senegalensis* during 1994, (b) *Guiera senegalensis* during 1995, (c) *Combretum micranthum* during 1995. The rainy period is indicated. Solid line and symbols, control thicket; dashed line and open symbols, thicket deprived of run-on; circles, predawn potential; diamonds, daily minimum potential; error bars, confidence intervals ($P = 5\%$).

visible (within 3 years) in the whole plant functioning, despite some disturbance observed at the organ scale. Unlike *Combretum micranthum*, *Guiera senegalensis* suffered seriously from a lack of water in the upslope zone of the thicket deprived of run-on. That led to a delay and a concentration of the leafing-out stage and to a drastic decrease in the reproductive rate. A combination of two probable causes can be suggested: its reproduction started at the end of the rainy season, when the soil was drying ('arido-active' species [7]) and the species was located in an area (upslope) where there was 2.4 times less available water for the plants than in the central zone of the thicket. When this zone

was supplied only with precipitation providing less than 20% of overall moisture, and corresponding to a drop of 45% in soil moisture as compared to the control thicket, shrubs were strongly affected. Response of shrubs to run-on deprivation depended both on the life cycle and the location of the species along the water resource gradient.

Contrary to the shrub rooting zone, there was neither a 'wall effect' nor a 'zone effect' in the rooting layer of annual plants. There, water resource was mainly controlled by direct rainfall and evaporation. Consequently, decreases in mean densities of *Microchloa indica* and 'remaining species' in the dammed thicket could not be caused by a decrease in soil water content available to the plants. The wall has probably stopped the possible input of plant seeds carried by the runoff flows from the upslope zone in natural conditions [21]. The presence of annual plants located along the upslope border of the wall where an irregular and thin covering of sand and dust had gradually accumulated supports this interpretation.

Microchloa indica was as abundant in the central zone than upslope (no zone effect). That means its domination upslope [21] was due to the significant lower densities of the other species compared to the central zone (significant zone effect).

5. CONCLUSION

Run-on did not contribute to water storage in layer 0–10 cm, and thus did not supply the annual herbaceous cover which probably depends mainly on microheterogeneity of the bumpy soil surface.

The central zone of the study thickets benefited the most from run-on. Even so, most of the supply from run-on to this zone was lost for the woody vegetation through deep drainage; despite this, the zone was a favourable habitat for vegetation as it supported the greater number of species. For instance, some Sudanian woody species were observed there (*Gardenia sokotensis* Hutch., *Combretum nigricans* Lepr.). It had such a high infiltration capacity that rainfall input, without run-on contribution, was sufficient to maintain dominant shrubs in quite good conditions at least for a long while (several years). This suggested that the run-off/run-on pattern was not as essential to vegetation performance in the central zone than in the upslope one. Although the run-on contribution was much less to the upslope zone than to the central one, it seemed of primary importance for the survival of shrubs which are located upslope (*Guiera senegalensis*). The result on the upslope zone fully supports the

conventional opinion that a banded pattern is necessary for optimal vegetation function [18].

Acknowledgments

We are very grateful to D. Freudenberger (CSIRO, Div. Wildlife and Ecology, Canberra, Australia) for his help in statistics, and J. Aronson (CEFE-CNRS Montpellier, France) for the improvement in the English. This research was partially supported by SAVanna on the Long Term (SALT), centre-project of the Global Change Terrestrial Ecosystems project, and the programme Hydrological and Atmospheric Pilot Experiment in Sahel (HAPEX-Sahel).

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