

Tree Shade Effects on Soils and Environmental Factors in a Savanna of Senegal

L.-É. Akpo¹, V. A. Goudiaby¹, M. Grouzis², H.-N. Le Houerou³

¹*Département de Biologie végétale, FST/UCAD, BP 5005 Dakar, Sénégal*

²*Mission IRD, Route d'Ambohipo, BP 434 101 Antananarivo, Madagascar*

³*327, rue A.L. De Jussieu, F-34090 Montpellier, France*

Abstract

The influence of tree shade on soils and microclimatic features was investigated in a Sahelian savanna of Ferlo, Senegal, in West Africa by measuring soil and environmental parameters under trees (i.e. shade) and in the open. Moisture content and the levels of carbon, nitrogen and phosphorus were greater in the surface soil layers (0–10 cm) under trees than in the open. Air temperature and incoming radiation were lower under trees, which contributed to a lower level of evaporation compared to the open. Water interception and stem-flow were associated with more water in the soil, hence, an increased available water.

Introduction

Savannas include a wide range of vegetation types and can be characterized by more or less continuous herbaceous undergrowth and an intermittent cover of shrubs and trees. The herbs, shrubs and trees are of economic importance to livestock and crop production.

Many authors including Vetaas (1992) have shown that in dry seasons trees influence the diversity and productivity of herbaceous plants as well as properties of the soil environment. For example, distribution of water between trees and grasses is very vital in the structure and in designing management practices in savannas (Belsky, 1990).

In the semi-arid regions of Africa, the effects of trees on environmental factors have mainly been studied in agroforestry context (Akpo & Grouzis, 1996a). It has been shown in northern Senegal, which is characterized by a long dry season (9–10 months) alternating with a short rainy season

(2–3 months), a low annual rainfall (< 300 mm), which falls mainly between 16–25 days, high solar radiation (the daily mean insolation is 8–11 h/day), and a high temperature, that trees have favourable effects on exuberant flora, lengthening of the period of plant development, and consequently, biomass production of the herbaceous undergrowth (Akpo, 1993; Akpo, & Grouzis 1993; Grouzis & Akpo, 1997).

The present study was undertaken to identify differences in micro-environmental factors (microclimate and soil properties) which could be the causes of changes observed in herbaceous undergrowth. In order to ascertain whether soil fertility is improved by the presence of trees in the study area, a semi-arid climate, we investigated physical, chemical and hydraulic properties of soils under trees and in the open. This study was important because the dominant management practice in these agro-pastoral systems is removal of

trees to improve grass production.

Materials and methods

Study area

The survey was carried out near Souilène, a village located at about 16° N and 15° W in Ferlo, North-Senegal (Fig. 1). The climate is tropical arid with an average

formations (slope < 0.05%) with enclosed depressions. Even small changes in altitude play a significant role in the distribution of plant species. The vegetation is composed of thorny shrubs, annual grasses and herbs. Within a hectare of land, there were 128 shrubs, which covered about 37.6% of the total area. The dominant shrubs were

Balanites aegyptiaca (L.) Del. (38 shrubs per ha with a crown coverage of 12.5%), *Acacia tortilis* (Forsk.) Hayne ssp. *raddiana* (Savi) Brenan (27 shrubs per ha with a crown coverage of 23.5%) and *Boscia senegalensis* (Pers.) Lam. (54 shrubs per ha with a crown coverage of 1.6%). The mean diameter of the tree crown is 4 m with a height of 7.2 m (Akpo & Grouzis, 1996b).

Microclimate

Direct solar radiation in the North, South, East and West, under a canopy at 1 m from the stem and in the open, was measured between 10 and 15 h with a pyranometer (Licor 200S, Lincoln NE, USA) on the dominant species, *Acacia tortilis*, *Balanites aegyptiaca* and *Ziziphus maritiana* (Akpo, 1993). The coefficient of light transmission through the tree cover was determined with these data. The sample was made up of 25 *Acacia*, 20 *Balanites* and six *Ziziphus*.

Air temperature at 40 cm (above ground) of the

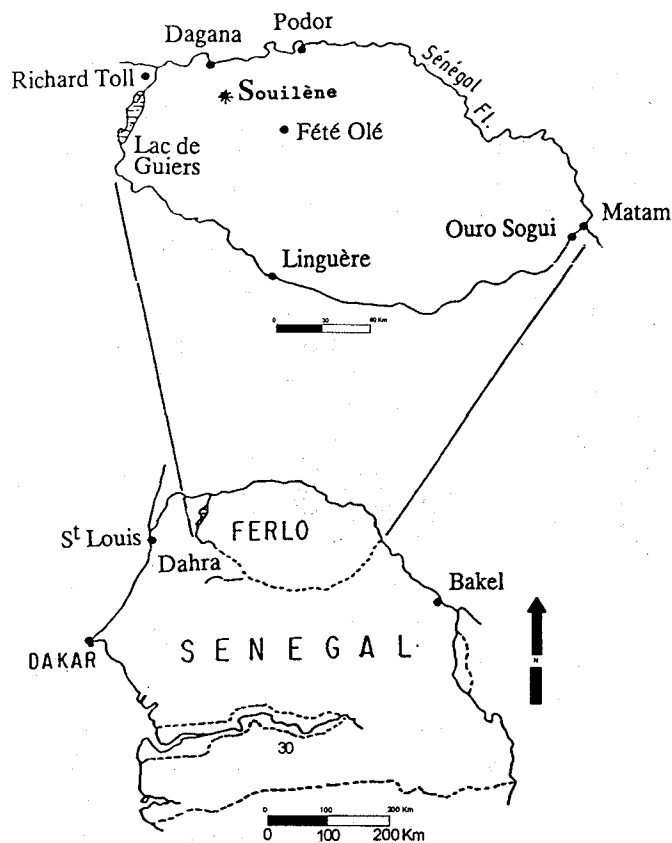


Fig. 1. Map of the study area

annual rainfall of 282 mm (data covering 1918-1990), distributed mainly over 16-25 days (Akpo, 1993) between June and October (90% of rains fall between July and September). Annual rainfall is variable, with a coefficient of variation of 37% (Le Houérou, 1989).

The topography of the study area is characterized by multi-directional small dune

herbaceous undergrowth and the photosynthetic photon density (PPF) was measured with a porometer (Licor 1600) under the *Acacia* and *Balanites* trees. Daily observations were conducted both under trees and in the open. Soil temperatures were taken 1 m under shade, 3.2 m beneath the end of the crown and 16 m away from the trunk of *Acacia tortilis* at a depth of 10 cm using a mercury thermometer.

Soil properties

Soil properties were determined on samples taken at two depths, 0-10 and 45-55 cm, from different vegetation types (Table 1). Three vegetation types under the same pastoral use were examined. The

Soil moisture

The sampling system comprised 11 permanent access tubes on similar lines installed in the soils at a depth of 4.75 m. Soil moisture content was determined with a neutron probe (Solo 25, Nardeux, France) on weekly basis during the growing season (July-October) and once a month during the dry season (November-June) in the herbaceous undergrowth. The neutron probe was calibrated gravimetrically. Measurements were taken at every 10 cm to a depth of 100 cm, then every 20 cm to 200 cm and then every 50 cm up to 475 cm.

Data processing

The mean and standard error (SE) were

TABLE 2
Location and distribution of soil samples

Situations	PA4	G8A	PS4	Total
Under tree	15	10	5	35
<i>Acacia raddiana</i>		10	5	15
<i>Balanites aegyptiaca</i>		5	5	15
Open	10	6	6	22
Total	25	16	16	57

three vegetation types were G8A, PS4 and PA4 rangelands (Valenza & Diallo, 1972). The rangeland, PA4, was chosen for the monitoring of soil moisture because of its large expanse (covered >35% of the total area of study).

Before the texture of the soils was determined, the soil samples were oxidized with heated sulfochromate (Anne method) to obtain their C content. Total N and P were determined colourimetrically (Technicon Autoanalyser). t-distribution was used to compare soil properties under canopies to those in the open.

calculated for the physical and chemical properties of the soils from each vegetation type. Under the trees, the access tubes were set under two species (*Acacia tortilis* and *Balanites aegyptiaca*) and at different distances from the trunk. Analysis of variance (ANOVA) was carried out on soil moisture content in order to determine (1) the effect of shrubs, and (2) the soil depths that had comparable moisture content. Thus, soil water storage in the different layers under trees and in the open were compared. In order to characterize the dynamics of soil water content, measurements were taken in the dry season (April), in the mid-rainy

season (September) and towards the growing season (November).

Results

Microclimatic conditions

Annual rainfall in the study period (1989-1994) varied from 112 mm to 261 mm. The mean annual rainfall for this period was 202 mm, which was 28% below the long term. No year had amounts higher than the long-term average. Stem-flow, measured on only *A. raddiana*, was 2.8% of the total amount of rainfall in 1990 and 1991. Rainfall measured under the canopy in 1993 and 1994 was 84% of the total amount of rainfall in the great *Acacia tortilis* grove of Souilène. Thus, individual variability occurred. Generally for the Sahelian zone, a linear regression relating rainfall amounts under shade (P_{in}) to that in the open (P_{ou}) was

$$P_{in} = 0.85 P_{ou} - 1.5, (R^2 = 0.95, n = 24).$$

The amount of rainfall intercepted by the canopy of *A. raddiana* in Ferlo could be

estimated to about $16.5 \pm 5\%$, i.e. the amount of water lost due to the presence of the canopy is

$$\frac{(P_{ou} - P_{in})}{P_{ou}}$$

Temperature and direct solar radiation

Air temperatures (Fig. 2) were higher in the open (26-42 °C) than under the tree (29-36 °C). At a depth of 10 cm, soil temperature under the tree ranged from 27 to 30 °C and from 29 to 34 °C at 3.2 m (i.e. in transition zone) from the tree. Soil temperature ranged between 25.5 and 35 °C in the open (Fig. 3). Daily variation in temperature increased from under the tree to the open. It was 3 °C under the tree and 9 °C in the open. A mean difference of 5 °C was recorded between the shaded (i.e. 1 m away from the trunk) and in the open (i.e. 16 m away from trunk) areas at mid-day. It is interesting to note that early in the morning, temperature under the shade was higher than in the open by about 1.5 °C. These results indicate that trees reduce temperature fluctuations by

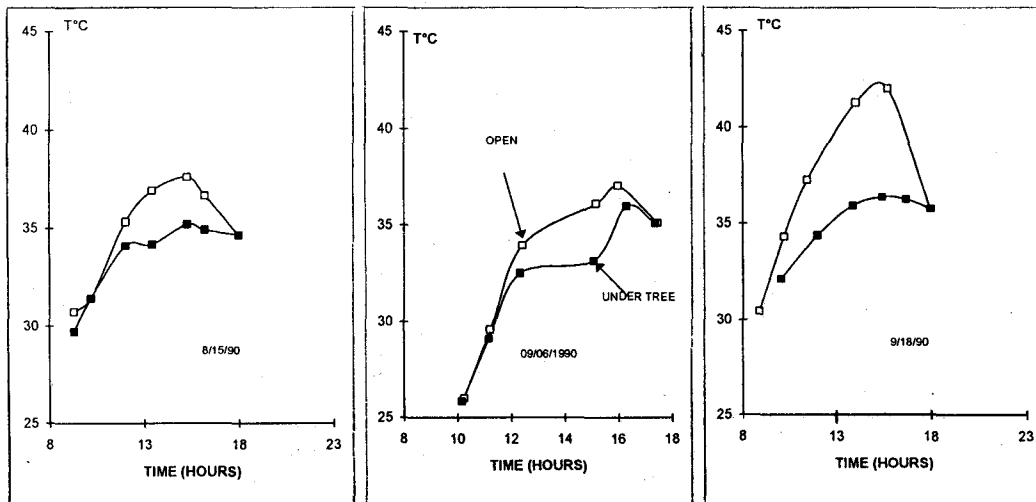


Fig. 2. Daily air temperature (°C) measured at 50 cm above ground in the herbaceous undergrowth and in the open grassland at different stages of growth at Souilène, Senegal.

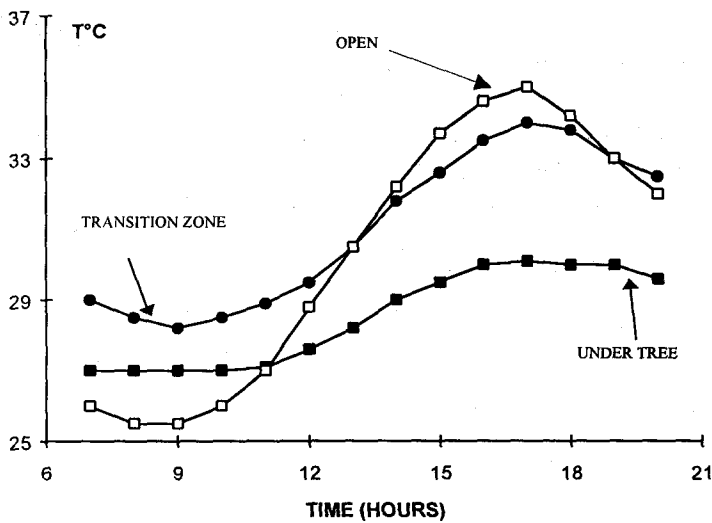


Fig. 3. Daily temperature ($^{\circ}\text{C}$) measured at 10 cm depth at different distances from the trunk of the tree in Ferlo, Senegal. The tree canopy has a radius of 4 m in Ferlo, Senegal (Akpo and Grouzis, 1996b).

decreasing the maxima and increasing the minima. The transmission of direct solar radiation through tree canopies at midday differed a little across species: *Acacia raddianna*: $21.3 \pm 6.8\%$, *Balanites aegyptiaca*: $16.8 \pm 5.5\%$, *Ziziphus*

radiation were 540 Wm^{-2} under the canopy as compared to 1100 Wm^{-2} in the open.

Physico-chemical properties of soils

Particle-size distribution. All the soils were sandy in texture and contained small

mauritania: 20.1 ± 2.9 . Although the shapes of the crowns were different, the levels of solar radiation were similar.

During the vegetative cycle of the herbaceous species, photosynthetic photon flux density ranges between 600 and $1400 \mu\text{M m}^{-2} \text{ s}^{-1}$ under the shade of *Acacia tortilis* and between 1500 and $2400 \mu\text{M m}^{-2} \text{ s}^{-1}$ in the open (Fig. 4). The daily mean values for solar

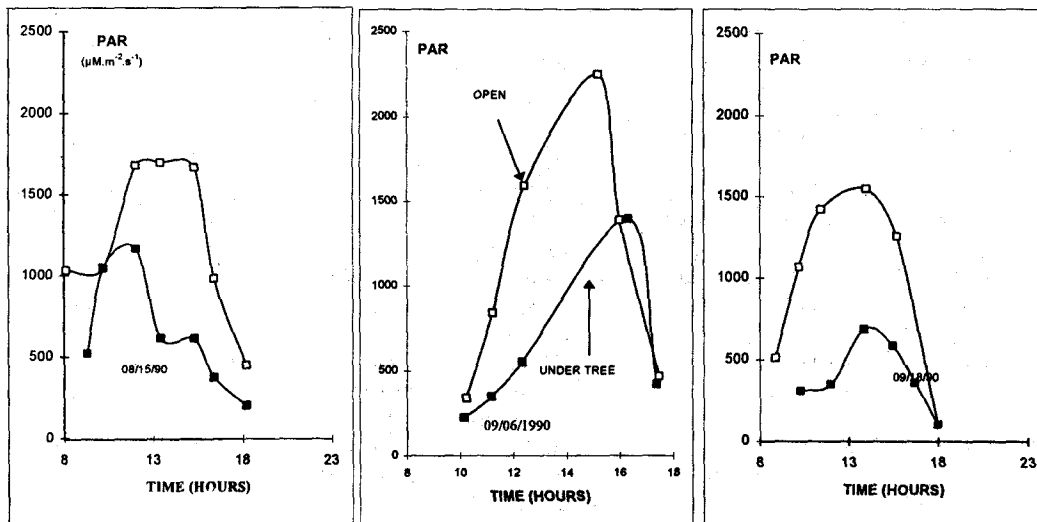


Fig. 4. Daily photosynthetic active radiation (PAR: $\mu\text{M m}^{-2} \text{ s}^{-1}$) under the tree canopy and in the open grassland at different stages of the vegetative season.

amounts of silt and clay (12-18%). The amount of clay in the soils increased with depth whereas the amount of silt decreased. The sand fraction showed no particular trend with soil depth but under shade its content was more than that in the open.

Chemical properties. Organic matter level (Table 2) was higher in the surface soils under shade than in the open. Organic matter content of the surface soil under shade was about two to three times higher than in the open for all the rangelands.

TABLE 2.
Selected chemical properties of soil samples

Types of rangelands	0 -10 cm		45-55 cm			
	Under	Open	Under	Open		
<i>Organic matter (%)</i>						
PA4	0.73±0.23	0.34±0.12	0.27±0.05	0.30±0.07		
G8A	0.65±0.13	0.24±0.06	0.30±0.03	0.19±0.02		
PS4	0.47±0.13	0.35±0.05	0.23±0.02	0.18±0.01		
<i>Nitrogen (%)</i>						
**PA4	0.42	** 0.15	0.18	0.22		
*** G8A***	0.38	*** 0.17	0.15	*** 0.13		
PS4*	0.27	0.24	0.14	* 0.12		
<i>Carbon (%)</i>						
PA4	3.70±1.20	2.00±0.70	1.40±0.30	1.50±0.39		
G8A	3.20±0.59	1.40±0.40	1.50±0.20	*** 1.10±0.08		
PS4	2.40±0.70	2.00±0.30	1.10±0.10	1.10±0.07		
<i>Organic matter quality (C:N)</i>						
PA4	8.7	8.3	7.6	6.8		
G8A	8.5	8.1	8.9	8.3		
PS4	8.7	8.5	8.1	8.8		
<i>Phosphorus (%)</i>						
PA4**	0.26	** 0.19	0.19	0.19		
***G8A*	0.29	***0.16	0.23	* 0.18		
PS4	0.16	0.14	0.14	0.12		
Situation	Pa4	PS4	G8A	PA4	PS4	G8A
<i>Clay (%)</i>						
Under	3.72±0.3	3.45	3.90	4.70±0.4	4.95	2.75
Open	3.65±0.2	2.85	2.75	5.15±0.2	4.30	5.25
<i>Fine silt (%)</i>						
Under	3.57±0.3	3.90	4.05	2.93±0.4	2.60	2.25
Open	3.44±0.3	3.50	3.65	3.28±0.3	2.70	2.85
<i>Coarse silt (%)</i>						
Under	8.63±0.7	6.45	10.40	6.40±0.5	4.75	6.05
Open	8.45±0.9	6.95	8.30	7.29±0.3	4.55	6.15
<i>Fine earth (%)</i>						
Under	53.30±3.10	43.45	55.25	53.70±5.01	46.85	52.05
Open	54.50±2.50	43.40	52.70	52.90±2.00	45.80	54.50
<i>Coarse sand (%)</i>						
Open	30.00±2.50	43.90	26.70	31.40±3.89	40.95	29.35
Under	27.68±2.70	43.00	31.80	30.79±4.29	43.05	28.55

The symbol * before or after rangeland types indicates the level of significance of tiers 0/10 cm (before) and 45/55 cm (after), respectively (*: $P_{0.05}$, **: $P_{0.01}$, ***: $P_{0.001}$).

Organic matter content in the sub-soils under shade was nearly twice as much as in the open. Carbon:Nitrogen (C:N) ratio was very low (6.8:1-8.9:1) which indicates a high rate of mineralization of N as compared to humification. This represents 5-8% of total N on annual basis. Total P content was also higher under shade than in the open. Nitrogen content of the soils under shade and in the open tended to decrease with the soil depth. In the surface soils under shade N content was three times greater than in the open. However, in the sub-soils N content under shade was not different from that in the open. For all the soils, C:N and P levels were about two to three times greater in the surface soils than in the sub-soils.

cm.

Dynamics of soil moisture profile. In the height of the dry season (April) and towards the end of the growing season (i.e. November), the soil did not show any changes in moisture content in the upper layers (Fig. 5). On the other hand, layers within soil depth of 70-350 cm were markedly dry. At the end of the rainy season in September, increased moisture content was observed under the shade in three layers: 0-150 cm; 150-300 cm and 300-450 cm.

Soil water storage. Changes in water storage were similar in all the soil depths (Fig. 6). During the dry season (from January to close to the end of June), storage of soil

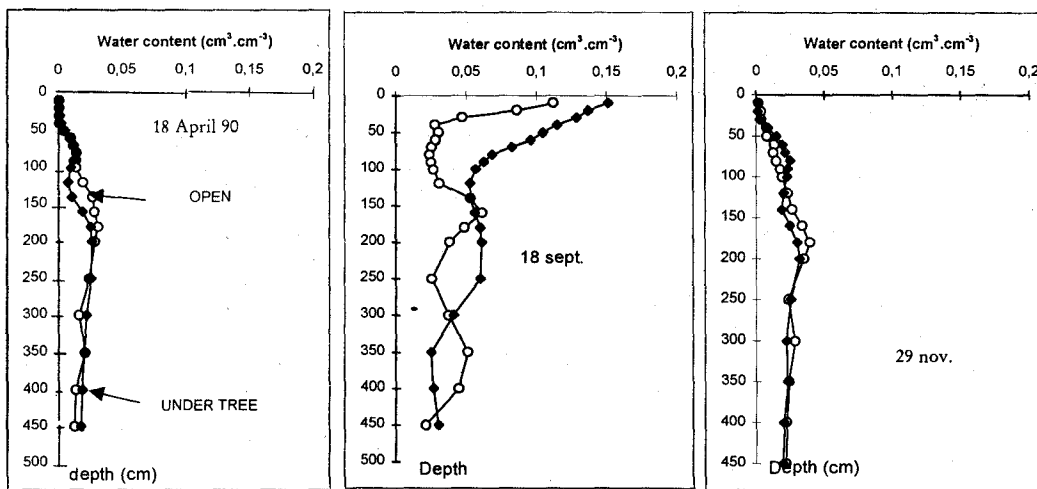


Fig. 5. Volumetric soil-water content ($\text{cm}^3.\text{cm}^{-3}$) for the three main seasons under the tree canopy and in the open grassland.

Soil moisture regime

Soil moisture under shade was not significantly different under *Acacia* and *Balanites* trees, suggesting that there was no effect of tree species on soil moisture content. Thus, under shade there were four soil depths in terms of moisture content: 0-70 cm; 70-140 cm, 140-250 cm and 250-500

water was the same under the shade and in the open. In the first half of the growing season (June- September), soil moisture content was higher in the open than under the shade. This was due to a more efficient use of water by the tree/grass system. During the same period, Nizinsky & Grouzis (1991) reported that the actual

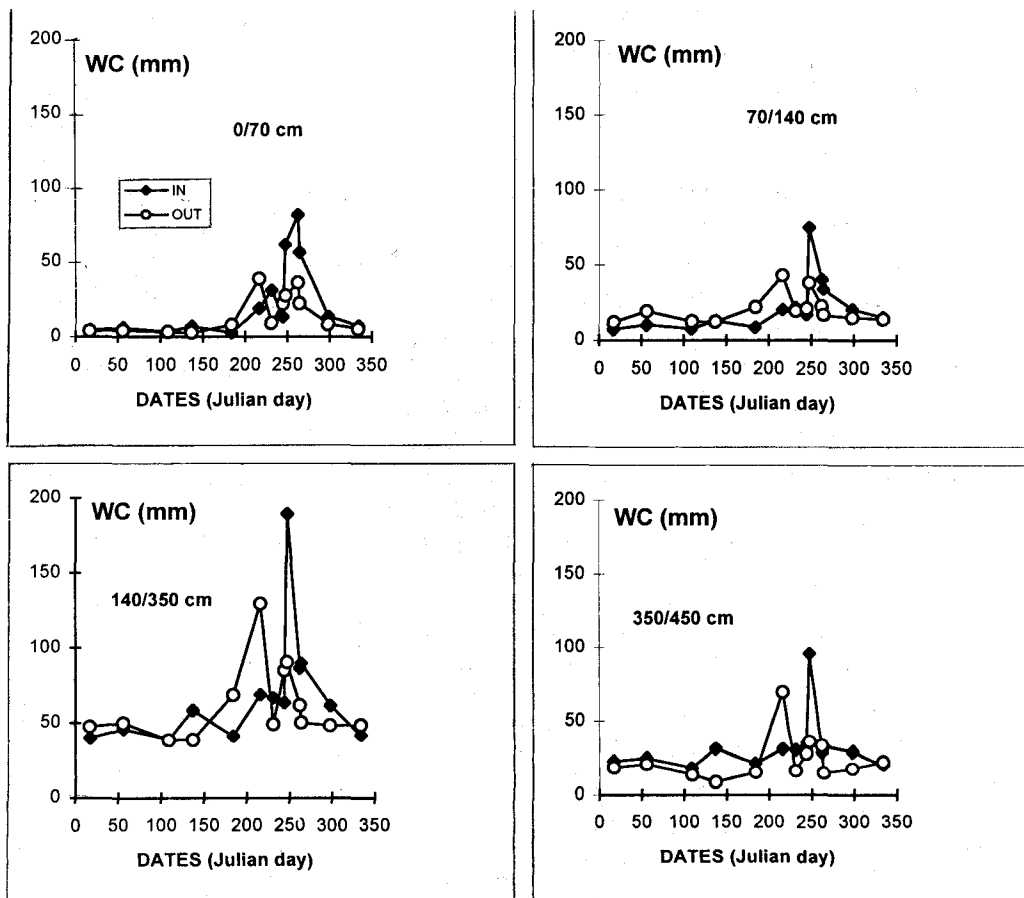


Fig. 6. Seasonal variation of the soil water storage at different depths under the canopy and in the open.

evapotranspiration was higher for the tree/grass system (4.47 mm j^{-1}) than for the grass system alone (3.31 mm j^{-1}).

Between the second half (i.e. September-October) and the end of the vegetative season, and at the beginning of the next dry season (i.e. November-December), soil moisture content was high in the shade. This enabled the continuation of various phenological phases of the trees (foliage production, flowering and fruiting). At the beginning of the rainy season (i.e. July-August), the soil moisture increased and reached 129.4 mm . During this period, biomass production was low in the open.

This showed that the efficiency of the available soil water was not always proportional to its amount but to the microclimatic conditions.

Discussion

The study area is a typical Sahelian climate characterized by arid conditions, mainly a long dry season followed by a short rainy season, high solar radiation, high temperatures and intense evapotranspiration. These conditions give rise to the unfavourable water balance that prevails in the area. The influence of the arid conditions was revealed in the results obtained in the

shade: (1) decreased temperature and solar radiation which gave rise to reduced evaporation, (2) improvement in the amount of nutrients in all the soil layers. The levels of organic matter and nutrients were significantly greater in the shade than in the open, (3) there was a 16.5% reduction in rainfall due to net interception, but stem-flow probably induced a better penetration. Consequently, the sub-soil retained more water than in the upper layers.

These results showed that trees enhanced soil fertility and water availability which is consistent with results obtained in other semi-arid regions of the world. With respect to soil fertility, the results were similar to those of Charreau & Vidal (1965), Radwanski & Wickens (1967) and Belsky *et al.* (1989). The results, however, did not agree with those obtained by Tiedemann & Klemmedson (1979) and O'Connor (1983) who found no difference in P content under shade and in the open. The results were also lower than those of Bernhard-Reversat (1982, 1986) and Weltzin & Coughenour (1990). Bernhard-Reversat reported higher values 5.6% and 11.3% in the surface soil under *Acacia senegal* and *A. seyal*, respectively.

In addition to the vertical gradient obtained in this study, many authors (Bernhard-Reversat, 1982; Belsky *et al.*, 1989; Weltzin & Coughenour, 1990) have reported horizontal gradient from tree trunk to the periphery. Kessler (1992) reported that improved availability of water under tree canopies was due to a decrease in actual evapotranspiration as well as better water infiltration. Under certain conditions in the upper soil layers, water availability is improved by the absorption and transfer of water by roots located at lower horizons to

the surface horizons (Richards & Cadwell, 1987).

Increases in soil fertility under or near the trees were reported to be related to tree litter (Bernhard-Reversat, 1986; Belsky *et al.* 1989). Organic matter accumulation under trees was due to a better stability of litter from tree leaves (Bernhard-Reversat, 1982). In Ferlo (i.e. the study area), foliage production represented 3% of the total aerial biomass, i.e. 109 kg ha⁻¹ yr⁻¹ (Poupon, 1980), with high spatial variations (from 25 kg ha⁻¹ yr⁻¹ on hill dunes to 658 kg ha⁻¹ yr⁻¹ in depressions). Other authors pointed out the ability of certain indigenous trees such as, *Acacia*, to fix N in order to explain increased levels of N under shade. Even if this is true, it could not be the only explanation since comparable results were obtained under other trees of different families and species (e.g. *Acacia albida*, *A. raddiana*, *Balanites aegyptiaca*, *Adansonia digitata*, *Delonix* sp. and *Faidherbia albida*). Although it is believed that mature Sahelian *Acacia* (*A. senegal* and *A. raddiana*) might have high N fixing abilities, the amounts fixed are yet to be documented. CTFT (1988) reported that the increase in soil fertility under *F. albida* due to relatively low N fixation was observed only in the seedlings and in barren soils.

Apart from N fixation, other ways of increasing nutrients could be through precipitation (Kellman, 1979), redistribution of nutrients from lower to upper horizons (Charley & Cowling, 1986) and the droppings of domestic and wild animals resting under trees. Tréca *et al.* (1996) noted that birds had recycled 12.8 kg of N and 0.9 kg of P ha⁻¹. The birds also produced about 186 kg ha⁻¹ of organic matter from the grasses utilized for their nests.

Trees and shrubs may reduce solar radiation under canopies by 45-60% in the Sahelian zone and by 85-95% in the Sudan savanna (Akpo & Grouzis, 1996a). However, Gonzalez-Bernaldez *et al.* (1969) reported that *dehesas* undergrowth received a high amount of solar radiation because the *Quercus* sp. canopy could reduce it by only 20-30%.

Only few investigations have been conducted on rainfall interception in the Sahelian zone. Investigations done in other ecological zones under *Acacia seyal* yielded values ranging from 30-60% for net interception and 40% for stem-flow (Leyton, 1987). The values obtained, 16.5% for net interception and 3% for stem-flow, under *A. tortilis* were far lower than those of Leyton (1987). High moisture was obtained in the open than under the canopy at the beginning of the rainy season, which agreed with the results reported by Belsky *et al.* (1989) and Jackson *et al.* (1990). During the rainy season, the situation reversed and moisture content became higher under the canopy than in the open. It was also observed that roots of trees and herbs exploited different depths of soils. Grouzis & Akpo (1997) reported higher root biomass under trees in the same year this study was conducted. Knoop & Walker (1985) also observed the selective soil depth exploitation by roots.

Conclusion

From the results of the study, the influence of trees on the environment could be summarized as follows: (1) no effect on soil texture, (2) an increase in nutrients and moisture content especially in the surface soil layers, (3) a favourable effect on the microclimate as shown by a reduction in air temperature and solar radiation, hence, a

reduction in evaporation, (4) an improvement in soil conditions through water interception and stem-flow which led to better infiltration into the soil and, thus, increased available water, and (5) the presence of trees caused important microclimatic conditions that had strong influences on the herbaceous undergrowth.

As stated earlier, the favourable soil fertility and moisture conditions that prevailed under the trees were the major factors that enhanced the diversity and growth of the undergrowth vegetation. The results of the study showed that trees enhance the development of undergrowth vegetation, thereby, increasing the long-term potential productivity of arid climates and improve conditions for animal husbandry

Acknowledgement

The research was sponsored by grants from Institut Français de Recherche Scientifique pour le Développement en Coopération (IRD).

References

- Akpo L. E. (1993). *Effet de l'arbre sur la structure et le fonctionnement de la strate herbacée en milieu sahélien. Les déterminants écologiques*. Orstom éd., TDM, 93F, 174 p.
- Akpo L. E. (1997). Phenological interactions between tree and herbaceous vegetation of a sahelian semi-arid savanna. *Pl. Ecol.* **131**: 241-248.
- Akpo L. E. & Grouzis M. (1993). Etude comparée de la phénologie de la végétation herbacée sous et hors couvert ligneux en milieu sahélien. *Webbia* **47**(2): 387-401.
- Akpo L. E. & Grouzis M. (1996a). Interactions Arbre/Herbe en zones arides et semi-arides d'Afrique : état des connaissances. *Rev. di Agric. subtrop. e trop.* **90**: 95-106.
- Akpo L. E. & Grouzis M. (1996b). Influence

- du couvert sur la régénération de quelques espèces ligneuses sahéliennes (Nord-Sénégal, Afrique occidentale). *Webbia* 50: 247-263.
- Belsky, A. J.** (1990). Tree/grass ratios in East African savannas: a comparison of existing models. *J. Biogeogr.* 17: 483-489.
- Belsky A. J., Amundson R. G., Duxbury J. M., Riha S. J., Ali A. R. & Mwonga S. M.** (1989). The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. *J. appl. Ecol.* 26: 1005-1024.
- Bernhard-Reversat F.** (1982). Biogeochemical cycle of nitrogen in a semi-arid savanna. *Oikos.* 38: 321-332.
- Bernhard-Reversat F.** (1986). Le recyclage des éléments minéraux par la strate herbacée dans un peuplement naturel à *Acacia* et dans une plantation d'*Eucalyptus* au Sénégal. *Oecol. Gener* 7: 353-364.
- Charley J. L and Cowling SW** (1986). Changes in soil nutrient status resulting from overgrazing and their consequence in plant communities of semi-arid areas. *Proc. ecol. Soc. Aust.* 3: 28-38.
- Charreau C. and Vidal R.** (1965). Influence de l'*Acacia albid* sur le sol, la nutrition minérale et les rendements des mils *Pennisetum* du Sénégal. *Agron. trop.* 20: 600-626.
- CTFT** (1988) *Faidherbia albida* Del, Monographie. CTFT, Nogent sur Marne, 72 pp.
- Gérakis P. A. & Tsangarakis C. E.** (1970). The influence of *Acacia senegal* on fertility of sand sheet soil in the central Sudan. *Pl. Soil.* 33: 81-86.
- Gonzalez-Bernaldez, F. Morey M. and Velasco F.** (1969). Influences of *Quercus ilex angustifolia* on the herb layer at the Parado forest (Madrid). *Biol. Rael. Soc. Esp. Hist. Nat.* 67: 265-284.
- Grouzis M. and Akpo L. E.** (1997) Influence of tree cover on herbaceous layer above and below ground phytomass in Sahelian zone. *J. Arid Envir.* 35: 285-296.
- Jackson L. E, Strauss R. B, Firestone M. K. and Bartolome J. W.** (1990). Influence of tree canopies on grassland productivity and nitrogen dynamics in deciduous oak savanna. *Agr. Ecosyst. Envir.* 32: 89-105.
- Kellman M.** (1979). Soil enrichment by neotropical savanna trees. *J. Ecol.* 67: 565-577.
- Kessler J. J.** (1992). The influence of karité (*Vitellaria paradoxa*) and néré (*Parkia biglobosa*) trees on sorghum production in Burkina Faso. *Agrof. Syst.* 17: 97-118.
- Knoop W. T. and Walker B. H.** (1985). Interactions of woody and herbaceous vegetation in a southern African savanna. *J. Ecol.* 73: 235-253.
- Le Houerou H. N.** (1989). The grazing land ecosystems of the African Sahel. Springer-Verlag, Berlin.
- Leyton L.** (1987). Crop water use. In Huxley P.A. (ed). *Plant Research and Agroforestry.* ICRAF, Nairobi. pp. 379-400.
- Nzinsky J. and Grouzis M.** (1991). Bilan d'eau d'une steppe à *Acacia tortilis* (Forsk.) Hayne ssp. *raddiana* (Savi) Brena et *Balanites aegyptiaca* (L.) Del. (Nord-Sénégal). In *Actes du IVème congrès international des Terres de parcours, Montpellier* (Le Houéron et al., ed.)
- O'conor K. F.** (1983). Nitrogen balances in natural grassland and extensively grassland systems. *N. Z. Jl Ecol.* 6: 1-18.
- Poupon H.** (1980). *Structure et dynamique de la strate ligneuse d'une steppe sahélienne au nord du Sénégal.* Orstom éd.
- Radwanski S. A. and Wickens G. E.** (1967). The ecology of *Acacia albid* on mantle soils in Zalingei, Jebel Marra, Sudan. *J. appl. Ecol.* 4: 477-487.
- Richards J. H. and Caldwell M. M.** (1987). Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisa tridentata* roots. *Oecologia.* 73: 486-489.
- Tiedeman A. R, & Klemmedson J. O.** (1979). Effect of Mesquite trees on vegetation and soil in the desert grassland. *J. Range Mgmt* 30: 361-367.

- Tréca B, Tamba Z, Akpo L. E. and Grouzis M.** (1996). Importance de l'avifaune sur les apports en azote et en phosphore dans une savane sahélienne du Nord-Sénégal. *Terre Vie*. 51: 359-373.
- Valenza J. & Diallo A. K.** (1972). *Etude des pâturages naturels du Nord-Sénégal. Etudes agrostologiques*. IEMVT, Maisons Alfort. 311 pp. + 3 cartes.
- Vetaas O. R.** (1992). Micro-sites effects of trees and shrubs in dry seasons. *J. Veg. Sci.* 3:337-344.
- Weltzin J. F. and Coughenour M. B.** (1990). Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *J. Veg. Sci.* 1:325-334.