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Adaptative above-ground biomass, stand density and leaf water potential to droughts and clearing in *Guiera senegalensis*, a dominant shrub in Sahelian fallows (Niger)

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Abstract: *Guiera senegalensis* tolerates repeated cutting and pruning to which it is increasingly subjected at the onset of each cropping period, and one to three times during the annual cropping period (June–September). It responds by profusely branching at the shrub base. The topographic and geomorphic influences, and the effect of clearing on the relationships between shrub density, mean individual above-ground biomass and leaf water status were analysed for seven fallow sites. They were sampled 75 km east of Niamey in Niger. Surprisingly, shrub density and mean individual above-ground biomass were highest in the sites that had been recently in fallow and intensively cultivated prior to crop abandonment. Stand above-ground biomass was also positively related to mean predawn and daily minimum leaf water potentials. Consequently, in the studied *G. senegalensis* stands, above-ground biomass appeared to be controlled by water availability – rainfall, runoff, infiltration – rather than by cropping intensity. Anisohydric stomatal regulation, resulting in large safety margins from critical transpiration, was inferred from the diurnal amplitude of leaf water potential during the dry season. The plant physiological resistance to water stress combined with its population adjustment in density and growth contributes to the sustainable dominance of *G. senegalensis*.

Key Words: biomass, coppices, fallow, functional traits, *Guiera senegalensis*, water status

INTRODUCTION

The expansion and intensification of cropping activities is increasingly altering the species composition of large areas of West Africa. A better understanding of the ecophysiology and population adaptations of plant species that are promoted by changing land use is therefore needed. This information should lead to an improved management of these semi-arid zone lands that are subject to harsh and variable climatic conditions and to very high agriculture pressure. In addition, an accurate evaluation of the physiological functioning of the plant species that dominate in a large area is required to model the present and future carbon, energy and water transfers between soil, vegetation and atmosphere (Chehbouni *et al*. 1997, Dolman *et al*. 1997, Hanan 2001, Mougin *et al*. 1995, Nicholson *et al*. 1997).

Fallowing is the main practice used by farmers to restore soil productive potential on land cropped with little or no fertilizer inputs in West Africa south of the Sahara (Floret & Pontanier 2001, Floret & Serpantié 1993, Wezel & Boecker 1998). Fallowing also provides fodder for grazing animals as well as fuel, medicines, food and building material for human populations. The duration of alternating crop and fallow periods varies, depending on soil type and on the human land pressure (Loireau *et al*. 2000). During the fallow period, native vegetation re-establishes from trees and coppices that survive the cropping period and from self-propagating herbaceous and woody plants (Floret & Pontanier 2001,

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Ruthenberg 1971, Wezel & Schlecht 2004). In the southern Sahel, and especially in southern Niger, the fallow vegetation is a complex structure comprised of an herbaceous layer dominated by annual plants, a layer of shrubs dominated by *Guiera senegalensis* J.L. Gmel. (Hutchinson & Dalziel 1954) and scattered trees spared in the clearing process. *Guiera senegalensis* is a shrub from the Combretaceae, indigenous to the Sahel (Aubreville 1950, Breman & Kessler 1995) and its home range extends over a large range of climatic and soil conditions. This species is commonly found in lands with between 300–1200 mm annual rainfall, on soils ranging from deep sandy or sandy-loam soils to shallow soils, hard pans and eroded slopes. *Guiera senegalensis* tolerates repeated cutting and pruning to which it responds by profusely branching at the shrub base, often from below the ground surface, conferring on the shrub its common multi-stemmed appearance (Bellefontaine 1997). *Guiera senegalensis* stands are subject to increasingly frequent clearing at the onset of each cropping period. In addition they must tolerate being slashed from one to three times each year during the cropping period. The length of the cropping period generally increases relative to the duration of the accumulated fallow period (Loireau *et al.* 2000, Wezel & Boecker 1998).

Plants adapted to water stress do so at the cost of some photosynthetic and growth performance (Lambers *et al.* 2000, pp. 1–7). Plants tolerant to drought are able to maintain turgor pressure at low (more negative) water potentials (Rundel 1995). However, high leaf mass results in high transpiration rates leading to the rapid exhaustion of soil moisture reserves. Inadequate water supply to the foliage due to dry soil or deep water resources, or because of plant architecture, xylem traits or stomatal behaviour, can trigger partial or complete leaf dieback (Sperry *et al.* 2002). Thus, in response to soil moisture deficit, individual plants or whole populations may reduce leaf area and shorten their growth period resulting in a decreased yield and mass (Rundel 1995). The trade-off between shrub population growth and the water stress they experience is controlled to some extent by rainfall and water redistribution by runoff and infiltration. However, plant competition, including factors such as density and size of the shrubs, also affects plant growth. Frequency and severity of past clearing and coppicing can influence size of the shrubs (Bellingham & Sparrow 2000).

Few studies have documented the ecophysiology of woody plants in the Sahel (Berger *et al.* 1996, Nizinski *et al.* 1994, Seghieri & Galle 1999). The success of *G. senegalensis* in establishing, surviving and dominating over a large range of soil moisture conditions in western Niger implies an effective strategy with respect to drought stress. Depending on local topography or on seasonal conditions, *Guiera senegalensis* is either evergreen or is deciduous with a long leafless period (Seghieri & Simier 2002). The high plasticity in its leaf phenology suggests that *G. senegalensis* optimizes its leaf area in relation to the available soil water resources at any location (Breman & Kessler 1995, Hiernaux *et al.* 1994, Piot *et al.* 1980, Poupon 1979, Seghieri & Galle 1999). To further analyse the mechanism behind this adaptation, the population structure and plant physiological features were studied in seven fallow sites chosen and instrumented in Niger by Delabre (1998). These fallow sites differed primarily in their age and cropping history. They also differed in their topographic and geomorphic positions, and then in their relative degradation state estimated visually (magnitude of soil encrusting, shrub turgescence). Finally shrub sizes and density varied between them. The main hypothesis is that differences among sites and years in stand above-ground biomass are a simple function of the age of the fallow and available water supply. The objectives of the study are (1) to characterise the daily and seasonal changes in leaf water status of the seven *G. senegalensis* populations, because they are related to variation in water stress the shrubs suffer; (2) to assess the relationships between the temporal magnitude of the variations in leaf water status of the populations and their landscape location; (3) to relate shrub density, mean individual above-ground biomass and stand above-ground biomass to the age of the fallow and to the cropping history of the site; (4) to explain the part of physiology adaptations which contributed to *G. senegalensis* success in the studied fallows.

MATERIAL AND METHODS

Sites and shrub populations

The seven fallow sites were included in the central site of the HAPEX-Sahel experiment (Hydrological and Atmosphere Pilot Experiment in the Sahel, 1990–1992, Goutorbe *et al.* 1997). They are located in the vicinity of Banizoumbou village in Western Niger (13°32′N, 2°42′E), 75 km north-east from Niamey. The local climate is semi-arid tropical with mean annual rainfall estimated to be 560 mm at the HAPEX central site over the period 1905–1989 (Le Barbé & Lebel 1997). The rainy season extends from June to September (90% of the annual rainfall). Long-term average potential evaporation exceeds rainfall in all months except August, when it approximately equals rainfall. Soils are composed of aeolian sandy deposits from fossil ergs, 50 000 to 15 000 y old (Delabre 1998), overlaying a lateritic hardpan (several metres deep), below which lies a sequence of Continental Terminal Miocene sandy-clay deposits (Gaze *et al.* 1998). Soils in Banizoumbou are classified as an Arenosol in the FAO system (Gaze *et al.* 1998). They have sand contents exceeding 90%, and silt content is higher than

Table 1. Topographic and geomorphic situation, fallow age, cropping intensity (R), density and mass of *Guiera senegalensis* in seven fallow sites from Banizoumbou (Western Niger).

Site code	Fallow age$^{(1)}$ (y)	R$^{(2)}$ (%)	Topographic location	Geomorphic condition	*G. senegalensis* density (SD/mean) (shrubs m^{-2})	*G. senegalensis* contribution to the total shrub density (%)	Number of shrub species	Mean individual above-ground biomass (kg)
P1	1	≈ 100	Down-slope gully web	Loamy-sand pediment	0.36 (0.22)	85	9	12.67 ± 21.90
S2a	2	55	Mid-slope gully web	Thick sand deposit	0.13 (0.23)	95	3	26.66 ± 30.09
S2b	2	55	Mid-slope	Thick sand deposit	0.10 (0.40)	94	3	16.83 ± 29.82
H3	3	42	Mid-slope	Sand Hill-slope	0.11 (0.55)	100	1	3.22 ± 3.33
S4	4	44	Mid slope	Thick sand deposit	0.04 (0.10)	58	2	11.18 ± 11.62
P19	19	12	Erosion surface$^{(3)}$	Loamy-sand pediment$^{(4)}$	0.18 (0.22)	97	2	5.16 ± 5.60
P23	23	≈ 0	Erosion surface	Loamy-sand pediment	0.11 (0.45)	98	2	1.96 ± 2.68

(1) After Delabre (1998).
(2) Ruthenberg ratio (1971) number of y of cultivation over total duration of crop-fallow cycle in percent.
(3) A gentle slope pediment (Goudie *et al.* 1994, p. 233).
(4) A smooth planoconcave upward erosion surface (Goudie *et al.* 1994, p. 377).

clay content in the top 30 cm. Organic matter does not exceed 0.3% (Rockström & de Rouw 1997).

The seven sites (Table 1) were chosen to represent diversity of fallows within the HAPEX-Sahel central site following the typology established by Delabre (1998). The typology is based on the degree of dominance by *G. senegalensis* and on structure and composition of the herbaceous under-layer. Each fallow site covers about 1 ha and was fenced to exclude grazing animals in 1993. All the data were collected from June 1994 to December 1995. This period includes two rainy seasons and an intermediate dry season. Rainfall was measured in three rain gauges placed within or close to the sites from 1992 on. These rain gauges were part of a network monitored by the EPSAT Program (an ORSTOM program assessing rainfall by remote sensing).

The seven fallows were located on the geomorphologic units most commonly chosen by farmers to grow millet in the studied area (Rockström & de Rouw 1997). The sites were located close enough to each other (in a 5 km radius) to assume that the incident climate was similar. At all sites, the shrub population was dominated by *G. senegalensis*. Some shrubs of *Combretum micranthum* G. Don and *Combretum glutinosum* Perrott. ex DC. (Hutchinson & Dalziel 1954) are present in most sites. Annual plants, such as the legume *Zornia glochidiata* (short life cycle) and the grass *Ctenium elegans* (long life cycle, Hutchinson & Dalziel 1954), dominated the herbaceous layer. The cropping history of each site was documented by Delabre (1998) based on farmer testimony. Farmer information established the age of the fallow, and the approximate duration of previous cropping and fallowing periods as far back as the farmer could remember. Based on this information, the ratio duration of the cropping periods over duration of the crop-fallow cycle was calculated and expressed in per cent. It is known as the Ruthenberg ratio, R (Ruthenberg 1971) that was used as an indicator of cropping intensity.

The typical crop-fallow cycle is initiated by the clearing of a pristine savanna, or more commonly, a fallow. Clearing is practised during the dry season, and consists in cutting trees and shrubs at or near the base of the stems. Only a few selected trees are spared, either because of their useful products, or to provide shade, or to delineate tenures on the edge of fields (Loireau 1998). Stumps are never removed, thus most of the woody plants resprout more or less intensively from the base of the stump. Wood is partially harvested for on-farm use or sale, but the smallest branches are often gathered in heaps and burned, and sometimes left scattered on the soil as mulch. In western Niger, no till is the most common system, thus millet is sown on mounds raised with a hoe 0.5–2 m apart, depending on soil fertility, at the onset of the rains. Resprouting shrubs may be slashed back just before sowing or later during the rainy season (to first offer protection from wind erosion) when their development is thought to compete with the crop. The small branches resulting from this cut are left as mulch. Crop harvest is organized in two steps. Panicles are first harvested at maturity and stalks lefts on the field either standing or cut at the base and laid on the soil. Stalks are then either harvested for forage or building purposes or left in the field to be grazed by livestock during most of the dry season. When the field is cropped the following year, coppice resprouts are cut back during the dry season and burned with the remnants of crop residues, or left as mulch. Shrubs are submitted to repeated slashing once or twice, exceptionally three times a year during the whole cropping period. They may eventually die if the cutting regime is too severe or extends over many years.

Mean individual above-ground biomass estimates from allometric relationships

During the study, no destructive sampling was undertaken to avoid affecting the site shrub populations. Above-ground leaf and wood masses were estimated using allometric relationships established on *G. senegalensis* multi-stemmed shrubs from fallows in Mali (Cissé 1980, Franklin & Hiernaux 1991, Hiernaux *et al.* 1994).

Foliage mass of each stem of each shrub, Bl_{stem} (g), was related first to the basal circumference of the stem, C_{stem} (cm):

$$Bl_{\text{stem}} = 1.09 \times C_{\text{stem}}^{1.89} \tag{1}$$

(all stems of $n = 20$ shrubs, $r^2 = 0.82$, $P < 0.001$)

The same approach was used to estimate each stem wood dry mass, Bw_{stem} (kg):

$$Bw_{\text{stem}} = 0.0037 \times C_{\text{stem}}^{2.40} \tag{2}$$

(36 stems among $n = 15$ shrubs, $r^2 = 0.90$, $P < 0.001$)

Leaf and wood masses were then aggregated for each multi-stemmed (i is the number of stems) shrub:

$$Bl_{\text{shrub}} = \Sigma_{\text{i}}\, Bl_{\text{stem (i)}} \tag{3}$$

$$Bw_{\text{shrub}} = \Sigma_{\text{i}}\, Bw_{\text{stem (i)}} \tag{4}$$

with Bl_{shrub} = shrub leaf mass (kg),

Bw_{shrub} = shrub wood mass (kg)

These relationships were validated in Western Niger on fallows of different ages (P. Hiernaux, unpubl. data). Mean individual above-ground biomass was then related to the basal circumference of the shrub (i.e. of each clump of stems corresponding to each multi-stemmed shrub), C_{shrub} (cm):

$$Bl_{\text{shrub}} = (1.09 \times C_{\text{shrub}}^{1.89})/10000 \tag{5}$$

($r^2 = 0.63$, $P = 0.05$)

$$Bw_{\text{shrub}} = (0.0037 \times C_{\text{shrub}}^{2.4})/50 \tag{6}$$

($r^2 = 0.54$, $P = 0.05$)

These last regressions were used to estimate the individual shrub leaf and wood masses in the seven fallow sites. The basal circumference of the shrubs was measured for a subsample of 10% of the *G. senegalensis* found within 10 quadrats 31.6 × 31.6 m in size placed systematically at each site. These subsamples counted 44–175 individuals depending on sites. Finally, the leaf-plus-wood mean individual above-ground biomass value and the extrapolated value of the stand above-ground biomass to the area sampled were calculated to characterize the pattern of the *G. senegalensis* population at each fallow site.

Monitoring leaf water potential of *Guiera senegalensis* across seasons

The leaf water potential (LWP) of *G. senegalensis* was monitored from June 1994 to December 1995. This was done fortnightly during the rainy season and monthly during the dry season as long as the shrubs had leaves. The LWP was measured on a permanent sample of three shrubs per fallow site, one for each of the three dominant classes of shrub size for each site. The measurements were performed with a hydraulic press (HP, Objectif K model, France). It was found to be sturdier, more convenient and less dangerous than a pressure chamber using compressed air. Significant correlations had already been established between data obtained with HP and reference pressure chamber data (Hicks *et al.* 1986, Jones & Carabaly 1980, Sojka *et al.* 1990). For each sampled shrub the measurements were performed on a piece of leaf (0.5–1.0 cm^2 size) and repeated on two different leaves per shrub. Leaf pieces were taken from mature leaves exposed to full sunlight at about 1.30 m above the ground. Measurements were made every hour from predawn and until the daily minimum of LWP (the most negative) was reached in the afternoon.

Data analysis

Analysis of covariance (ANCOVA) was used to test the linear relationship between log-transformed shrub density and log-transformed mean individual above-ground biomass for the fallow sites, considering two groups of sites: thick sands *versus* other geomorphic situations. Three models were compared: with different slopes and intercepts for the two groups of sites (model 1), same slope but different intercepts, i.e. removing interaction effect (model 2), and same slope and intercept, i.e. removing group effect (model 3).

At each site and each date of measurement, mean LWP values were calculated for two leaf replicates of the three shrubs sampled. The least negative mean LWP observed before 08h00 was set as the predawn LWP (Ψ_{PD}) for the corresponding site and date. With no direct measurements of the soil water content, Ψ_{PD} was considered as an indicator of the water supply for the plant. Indeed, Ψ_{PD} is a function of water availability in the rooting zone of the soil since it is assumed that during the night, low atmospheric demand for water and stomatal closure minimizes transpiration (Ritchie & Hinkley 1975, Rundel 1995). This approximation implies that the soil next to the roots can provide sufficient water during the night to recharge dehydrated plant tissues. It also implies that there is no limitation in water transport within the plant. The most negative mean LWP value recorded over the day was considered as the daily minimum LWP (Ψ_{DM}) and taken as an indicator of the maximum water stress that the shrubs suffered from the combined effects of the atmospheric demand and soil moisture.

The seasonal courses of Ψ_{PD} and Ψ_{DM} were compared between sites. To account for the different rain distributions recorded over three rain gauges, rainy and dry periods were defined according to the specific rainfall distribution recorded at each site. The rainy periods were defined as the time intervals between the first and the last rain of the year. The dry period was defined as the period with no rain in between but only as long as sampled shrubs had leaves.

Analyses of variance (ANOVAs) were then performed on Ψ_{PD} and Ψ_{DM} values to test the differences (1) between dry and rainy periods, (2) between sites within the dry period and (3) between sites within the rainy period. Multiple comparison tests were performed *a posteriori* using Scheffe's pairwise comparison method because of its compatibility with the overall ANOVA results. The results of the between-sites tests performed on Ψ_{PD} and Ψ_{DM} within the dry period (2) were used to classify the sites.

Finally, the relationship between the by-site mean Ψ_{PD} and Ψ_{DM} and the log-transformed stand above-ground biomass was quantified.

RESULTS

Across sites, on average, rainfall was more abundant and the rainy season longer in 1994 (649 mm, SD = 56 mm, over more than 4 mo) than in 1995 (527 mm, SD = 17 mm, over less than 4 mo), but both were close to long-term average.

Mean individual above-ground biomass and densities

Despite the fact that no correlation has been found significant, the higher shrub densities and higher mean individual above-ground biomasses were observed in young fallow sites compared to fallows 23 y old or 19 y old that had been the least intensively cultivated before abandonment (Table 1).

The linear relationship between the natural logarithm (Ln) of mean individual above-ground biomass and shrub density was not significant when all sites were combined (Table 2 – model 3), but was highly significant when the geomorphologic situation was included in the model considering two groups: sites on thick sand deposit and sites on loamy-sand pediments or on sandy hill-slope. The slopes of the relationships were not significantly different (Table 2 – model 2) but the intercepts were (Table 2 – models 2 and 3), with mean individual above-ground biomass significantly lower on the loamy-sand pediment than on the thick sand deposits at similar shrub density (Figure 1).

Table 2. Results from the covariance analysis (ANCOVA) testing the linear models ($Y = aX + b$) between the log transformed mean shrub mass (Y) and the log transformed shrub density (X) of seven fallow sites for two groups (G) depending on geomorphic condition, either on loamy-sand pediment and sandy hillslope, or on thick sand deposit.

Model 1: different slope (a) and intercept (b) for the two groups of stations: $Y_{gk} = a_g X_{gk} + b_g + e_{gk}$

Model 2: same slope (a′) but different intercept (b′), i.e. removing interaction effect: $Y_{gk} = a' X_{gk} + b'_g + e'_{gk}$

Model 3: same slope (a″) and same intercept (b″), i.e. removing group effect: $Y_{gk} = a'' X_{gk} + b'' + e''_{gk}$

Model		df	F	P
1	Shrub density	1	35.8	0.009
	Group of sites	1	7.2	0.075
	Shrub density × group	1	3.4	0.163
	Residual	3		
2	Shrub density	1	26.4	0.007
	Group of sites	1	66.1	0.001
	Residual	4		
3	Shrub density	1	0.01	0.913
	Residual	5		

Seasonal variation in leaf water potential

Significant differences ($P < 0.001$) between seasons were observed for Ψ_{PD} and Ψ_{DM} (Table 3a). However, the total variances in Ψ_{PD} and Ψ_{DM} were only partially explained by the period (respectively 20% and 26%), indicating large within-season variability. Between-sites ANOVAs that were performed separately for rainy and dry periods showed different patterns. During the rainy period, Ψ_{PD} values ranged between 0 and −1 MPa while Ψ_{DM} did not drop below −1.5 MPa (Figure 2) and did not vary significantly between sites (Table 3b). In contrast, during the dry period, differences between sites were significant for both Ψ_{PD} and Ψ_{DM} (Table 3c). From the Scheffe's pairwise comparison test, LWPs between sites H3, S4 and P23 during the dry period (Group 1, Table 4c) were not significantly different, and the greatest variability in LWP during the dry season were recorded in these sites (SD, Figure 2). Similarly, LWPs were not significantly different between sites S2a, P19 and P1 (Group 2 – Table 4c). This group had the lowest inter-shrub variation in dry-season LWP (SD, Figure 2). The differences in LWPs between sites from the two groups were always significant. Site S2b being part of both groups, it was considered as an intermediate situation.

The difference between Ψ_{DM} and Ψ_{PD} recorded the same day at each site, was systematically calculated as diurnal amplitude of the LWP and used to characterize *G. senegalensis* water regulation strategy (Bonal & Guehl 2001, Tardieu & Simonneau 1998). The decrease in Ψ_{PD} during the dry season was associated with a more pronounced decrease in Ψ_{DM} (Figure 2). Significant positive linear correlation ($R = 0.86$, $P < 0.0001$) was found between Ψ_{PD} and Ψ_{DM} over all sites and sampling dates. Finally, the decrease in Ψ_{DM} was less pronounced

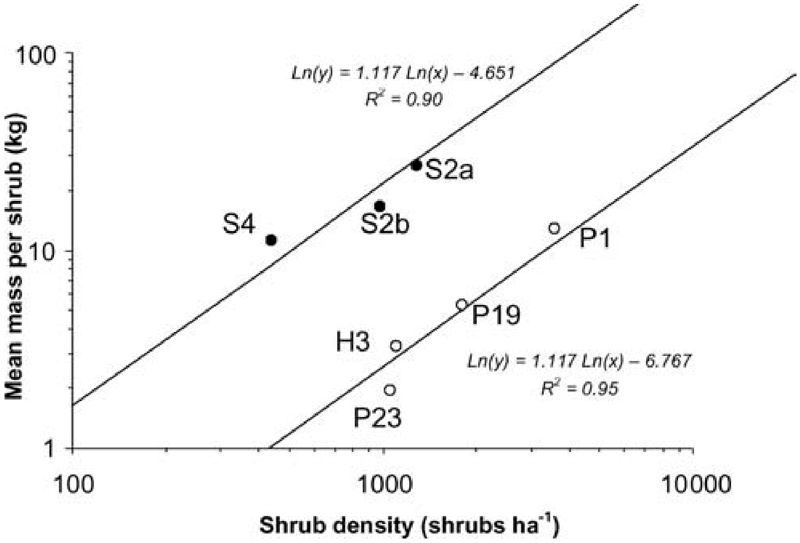

Figure 1. Linear relationships between the log-transformed shrub density and mean above-ground mass for fallow sites on loamy sand pediment and sandy hillslope (open symbols), and on thick sand deposit (solid symbols).

during the 1995 dry season (the drier year), than in 1994 except for sites H3 and S4 (Figure 2).

Relationship between leaf water potential and stand mass

The mean Ψ_{PD} and Ψ_{DM} calculated over the whole sampling period were significantly and positively correlated with the logarithm of the stand above-ground biomass ($R = 0.95$, $P = 0.0008$ for Ψ_{PD}, $R = 0.96$, $P = 0.0007$ for Ψ_{DM}). The standard deviation of the mean Ψ_{PD} and Ψ_{DM} also decreased with increasing stand above-ground biomass (Figure 3). Therefore, less negative and less variable LWP were recorded in sites S2a and P1 that had the highest stand above-ground biomasses. Conversely, the most negative and most variable LWP were measured in sites with the lowest shrub stand above-ground biomass. The intermediate position of site P19, in spite of being an old fallow (19 y) could be explained by the relatively high density of the shrubs that compensated for low mean individual above-ground biomass (Table 1).

DISCUSSION

Mass distribution in relation to local productivity and cropping history

For a given geomorphic situation, shrub density and mean individual above-ground biomass of *G. senegalensis* are confirmed as indicators of site productivity but not of clearing intensity (Figure 1). Indeed, even a very young fallow – such as site P1 which has been almost continuously cultivated in living memory (R value, Table 1) – supported the highest shrub density in accordance with its

Table 3. ANOVA results for predawn and daily minimum leaf water potential (a) difference between dry (287 observations) and rainy (254 observations) periods as defined in the text, (b) difference between stations during the rainy period and (c) difference between stations during the dry period.

			df	F	P	r^2
(a) Difference between dry and rainy periods	Ψ_{PD}	Model : period	1	133	< 0.0001	0.20
		Residual	539			
	Ψ_{DM}	Model : period	1	186	< 0.0001	0.26
		Residual	539			
(b) Difference between stations during the rainy period	Ψ_{PD}	Model : station	6	1.15	0.34	0.03
		Residual	247			
	Ψ_{DM}	Model : station	6	2.04	0.06	0.05
		Residual	247			
(c) Difference between stations during the dry period	Ψ_{PD}	Model : station	6	15.1	< 0.0001	0.25
		Residual	280			
	Ψ_{DM}	Model : station	6	18.2	< 0.0001	0.28
		Residual	280			

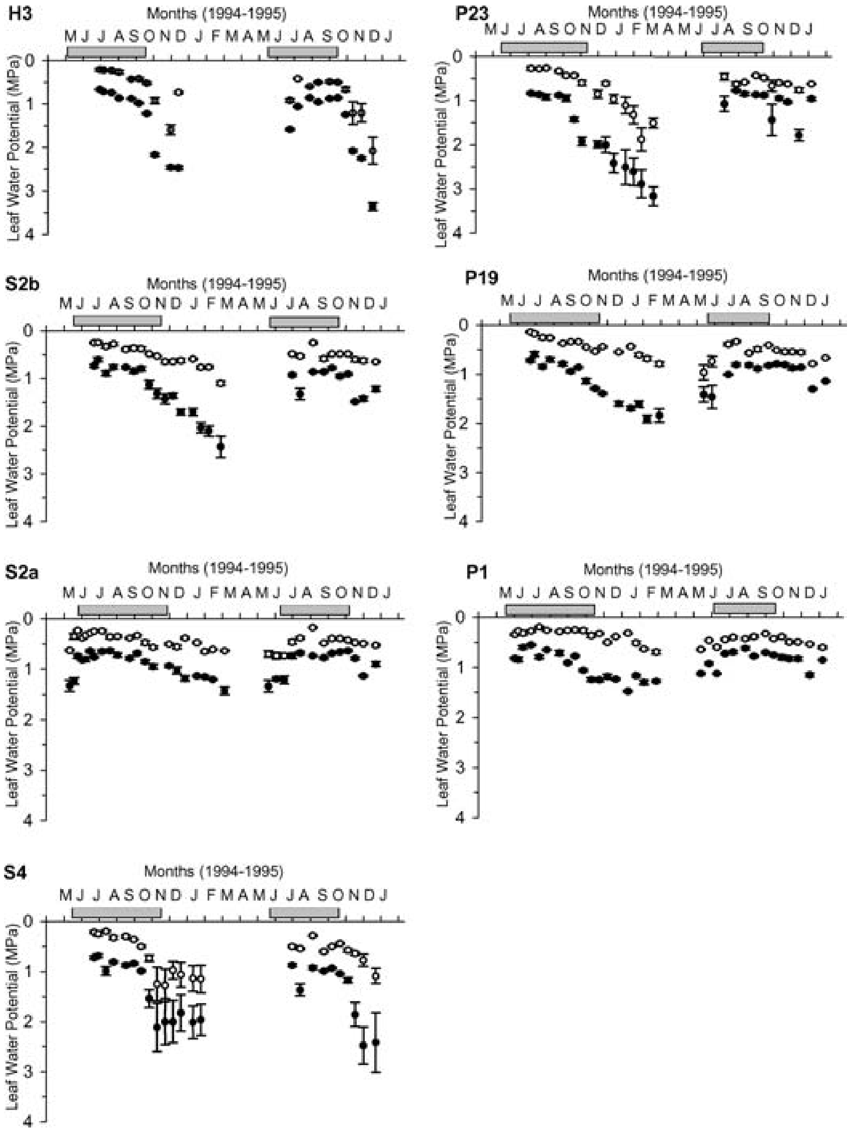

Figure 2. Seasonal course of the predawn ($\Psi_{PD} \pm$ SD, open symbols) and daily minimum ($\Psi_{DM} \pm$ SD, solid symbols) leaf water potential (MPa, negative values) in the seven *Guiera senegalensis* stands (mean of six leaves, i.e. two leaves per shrub on three shrubs per stands). The grey bar represents the rainy period.

favourable topographic situation (down-slope in a water catchment). Site S2a, was also a young fallow taking benefit from the water run-on from a web of gullies, and it supports the highest mean individual above-ground biomass (Table 1). On the other hand, mean individual above-ground biomass was minimal in the oldest fallow site P23 (23 y), a site that had been cleared and not cropped after this clearing (Delabre 1998). This could be interpreted as being caused by early shrub senescence due to the low potential productivity of the site. Since farmers leave shrubs in the millet field, their density must be closely linked with the potential productivity of the site before cropping rather than with their actual productivity after cropping. The Ruthenberg ratio is not a robust indicator of the site productivity, since farmers do not systematically select the location of crop fields where shrubs grow dense and big. The high productivity of such habitats gives farmers too much work for field clearing and coppice slashing during the cropping period. These sites are thus used for cultivation only when the productivity of the others falls too low (Loireau 1998).

Relationship between shrub density and mean individual above-ground biomass

The positive relationship found between shrub density and mean individual above-ground biomass (Figure 1)

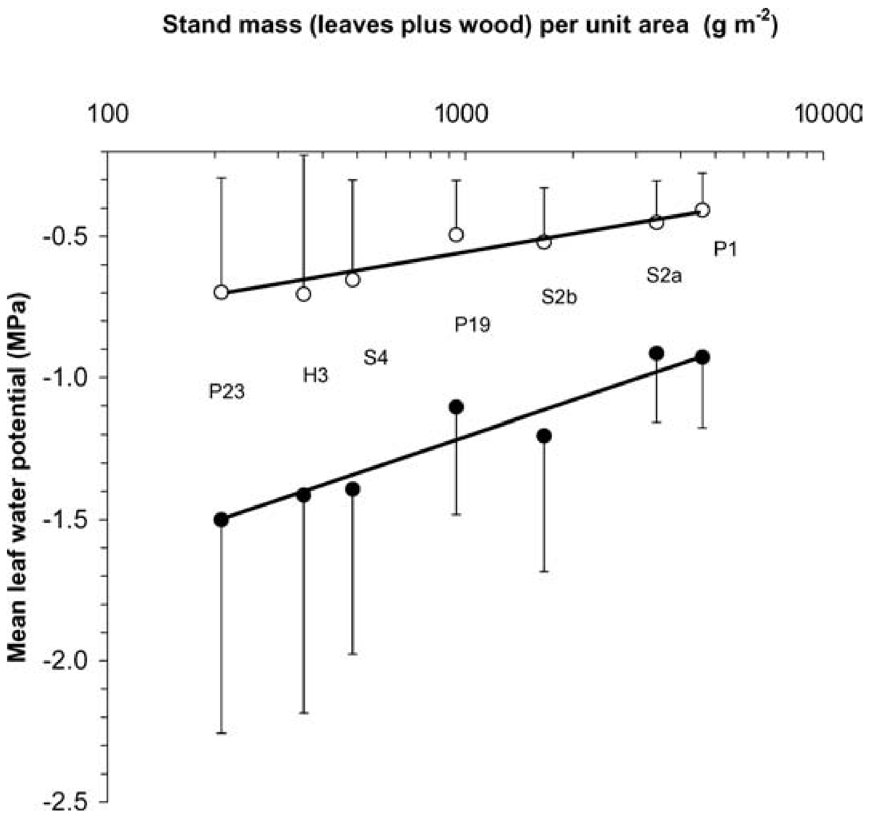

Figure 3. Linear relationships between mean leaf water potentials (Ψ_{PD} open symbols, Ψ_{DM} solid symbols, the standard deviations of the means are shown) and the stand above-ground biomass per unit area.

has to be confirmed on other sites before generalization. It probably reflects the dynamic equilibrium between the availability of soil resources to plants and the total above-ground mass of the vegetation. The age, pattern and mass of the shrub roots are not known, except that roots reach at least to 3 m depth (J. Seghieri unpubl. data). Resource uptake depends both on root extension and resource availability in the rooting zone. Castell *et al.* (1994) showed that the speed and magnitude of regrowth of *Quercus ilex* and *Arbutus unedo* are positively related to the mass of the root system. Active resprouting is encouraged by an extended root system together with reduced shoot mass after disturbance due to enhanced water availability (Fleck *et al.* 1995). This process obviously applies to the young fallows located down-slope in water catchments, as in sites S2a and P1 that had either the highest mean individual above-ground biomass (site S2a) or the highest shrub density (site P1). *Guiera senegalensis* stands regenerate rapidly after cutting when located in well-watered conditions. Similarly, it was found in chaparral (evergreen) shrubs that moisture was not limiting resprouting, providing that deep roots remained intact (Rundel 1995).

Table 4. Number of observations (n), mean values of predawn (Ψ_{PD}) and daily minimum (Ψ_{DM}) leaf water potential (MPa) of *Guiera senegalensis* (a) per period (b) per site over the rainy period (c) per site over the dry period. Means are not significantly different within a group (Scheffe test, P = 0.05).

	n	Ψ_{PD}	Ψ_{DM}	Group
(a) Period				
Dry period	287	− 0.67	− 1.45	1
Rainy period	254	− 0.38	− 0.83	2
(b) Site (rainy period)				
H3	27	− 0.41	− 0.90	1
S4	30	− 0.38	− 0.92	1
P23	24	− 0.41	− 0.82	1
S2b	36	− 0.38	− 0.84	1
S2a	63	− 0.41	− 0.82	1
P19	32	− 0.34	− 0.83	1
P1	42	− 0.34	− 0.74	1
(c) Site (dry period)				
H3	30	− 0.98	− 1.90	1
S4	31	− 0.89	− 1.82	1
P23	41	− 0.89	− 1.93	1
S2b	45	− 0.62	− 1.47	3
S2a	42	− 0.51	− 0.98	2
P19	47	− 0.58	− 1.29	2
P1	51	− 0.46	− 1.08	2

The zone of influence of a living shrub includes the physical space occupied by the shrub itself and the immediate environment it influences by its presence and activity (Li *et al.* 2000). When resources are scarce, this zone of influence enlarges through root development of individual plants and thus limits stand density.

Root development results in scarcer water availability and higher below-ground competition between shrubs, while low aerial development reduces above-ground competition between shrubs for space or light (such as in sites H3, S2b, S4, P23 and P19). Therefore sites can then be ranked from the lower density or lower mean individual above-ground biomass, probably related to poorer water availability for the shrubs (site S4, H3 and P23; Figure 1), to the higher density or mean individual above-ground biomass for the sites that benefit from run-off (sites S2a and P1).

Seasonal variation in the leaf water potential

Leaf water potential measured during the rainy period did not differ between sites. Water availability was probably sufficient in all sites to buffer the spatial heterogeneity in other production factors (topography, chemical fertility, etc.). The abundance of water resource removes the water stress at the shrub population scale as well as at the meta-population scale, decreasing between-site variability. This explains the full leaf development during the rainy period and the absence of phenological differences between sites as observed by Seghieri & Simier (2002). During the dry period, some *G. senegalensis* populations were exposed to a wide range of water-stress conditions, thus explaining the differential decreases in leafing magnitude between sites reported previously (Seghieri & Galle 1999, Seghieri & Simier 2002). The group of sites H3, S4 and P23, characterized by the lowest and most variable leaf water status during the dry season (Table 4) correspond also to the fallow sites with lower shrub density or mean individual above-ground biomass (Table 1, Figure 1). At the other extreme, the group of sites S2a, P1 and P19 that maintained highest LWP during the dry season had the highest shrub densities or mean individual above-ground biomass. Since sites S2a and P1 benefit from water run-off, while site P23 is a source of run-off, the site ranking confirms that water availability in the soil is more important in predicting the shrub stand above-ground biomass in western Niger than coppicing intensity, fallow age or cropping history.

In the absence of inter-annual data on mean individual above-ground biomass, the interpretation of the more pronounced decreases in Ψ_{DM} during the 1995 dry season compared to the 1994 one remains uncertain (Figure 2). However reduced leaf development due to lower water resources during the 1995 rainy season may have improved the water status of the individual shrubs during the following dry season by reducing leaf area and thus transpiration. Indeed, reduced leaf area index was observed in coppices of *Arbutus unedo* and *Coriaria myrtifolia* allowing stomata to remain open under stressful conditions without dehydration (Fleck *et al*. 1995).

Guiera senegalensis physiological strategy

When drought increases, the more pronounced decrease in Ψ_{DM} than in Ψ_{PD} confirmed, *a posteriori*, that Ψ_{DM} is a good indicator of the water stress experienced by the shrubs. As with Mediterranean coppices (Rundel 1995), *G. senegalensis* is tolerant to drought stress since it is able to maintain positive turgor and open stomata at low water potentials. (His behaviour conforms to the anisohydric strategy (Bonal & Guehl 2001, Tardieu & Simonneau 1998) for which stomatal regulation results in very large safety margins from critical transpiration rate when soil water potential is high (Sperry *et al*. 2002). That strategy is consistent with high values of potential stomatal conductance measured for *G. senegalensis* by Hanan & Prince (1997). However, the same authors observed high sensitivity of the stomata to decreasing soil moisture, incident PAR (Photosynthetically Active Radiation) and vapour pressure deficit. This sensitivity argues for some stomatal regulation taking place in *G. senegalensis* leaves confirming its isohydric behaviour. This behaviour would protect the shrub against lethal xylem cavitation at low water potential (Bonal & Guehl 2001, Tardieu & Simonneau 1998). The decrease in leaf water potential in response to aridity is thus probably regulated up to a threshold depending on *G. senegalensis* resistance to xylem cavitation. This combination of strategies in *G. senegalensis* would increase the period of photosynthetic activity during the dry season compared with shrubs that have a strict isohydric strategy such as *Combretum micranthum* for which active photosynthesis is strictly limited to the rainy season (Seghieri & Galle 1999).

CONCLUSION

(1) Seasonal and daily variations in leaf water status of the seven studied *G. senegalensis* populations follow an anisohydric strategy. It allows the species to remain active under severe water stress.

The magnitude of the daily and seasonal variations in leaf water status of the populations was linked to the topographic location, i.e. to the water supply.

Shrub density, mean individual above-ground biomass and stand above-ground biomass differed according also to the topographic location, rather than to the fallow age or to the cropping history of the site. In shrub populations with abundant soil water supply, growth is faster even in young fallows intensively cultivated before abandonment, since shrubs benefit from rejuvenation of tissues and favourable root to shoot ratio.

Guiera senegalensis anisohydric behaviour allowing active photosynthesis during part of the dry season, has certainly contributed to the maintenance of this shrub species as a dominant in the Sahelian landscape. Its adaptation to habitats with widely varying water resources should confer a high resilience to the present populations, and leaves little chance for less-opportunistic species.

The severe disturbances generated by the unprecedented changes in land use and management in the Sahel opens up new habitats for colonization, for which the plasticity of their water requirements should confer a decisive competitive advantage to opportunistic species such as *G. senegalensis*.

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