

# Change in water loss regulation after canopy clearcut of a dominant shrub in Sahelian agrosystems, *Guiera senegalensis* J. F. Gmel

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**Abstract** This paper analyzes the effect of the canopy age of *Guiera senegalensis* J.F. Gmel on water regulation processes and adaptative strategy to drought over a period of 2 years. The species is widespread in the agricultural Sahel. Before sowing, farmers cut back the shrubs to limit competition with crops. The stumps resprout after the millet harvest. Leaf water potential and stomatal conductance were measured in two fallows and in the two adjacent cultivated fields. Leaf transpiration rate and soil-to-leaf hydraulic conductance were deduced. The decrease in both stomatal and plant hydraulic conductance caused by seasonal drought was greater in mature shrubs than in current year resprouts. The decrease in predawn and midday leaf water potentials in response to seasonal drought was isohydrodynamic, and it was greater in mature shrubs,

suggesting that current year resprouts are under less stress. In resprouts, the leaf transpiration rate stopped increasing beyond a hydraulic conductance threshold of  $0.05 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ . Vulnerability to cavitation was determined on segments of stems in the laboratory. The leaf water potential value at which stomatal closure occurred was  $-2.99 \pm 0.68 \text{ MPa}$ , which corresponded to a 30 % loss in xylem conductivity. Thanks to its positive safety margin of 0.6 MPa, *G. senegalensis* can survive above this value. The observed strategy places *G. senegalensis* among the non-extreme xeric plants, leading us to suppose that this species will be vulnerable to the expected increase in regional drought.

**Keywords** Adaptation · Embolism · Functional limits · *Guiera senegalensis* · Hydraulic conductance · Transpiration rate

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## Introduction

In arid and semi-arid regions like the Sahel, water is the main constraint for plant growth and production (Le Houerou et al. 1988). The rainy season lasts three to 4 months during summer and is subject to high seasonal variations, with frequent dry spells occurring during the rainy season (Breman and Kessler 1995; Sultan et al. 2005). The growth and survival of woody plants during dry periods depend as much on water availability as on physiological control by the plant (Breman and Kessler 1995; Eamus and Prior 2001).

Based on variations in leaf water potential during drought, Tardieu and Simonneau (1998) defined two contrasting plant strategies for dealing with water limitation. According to these authors, anisohydric plants can

withstand a highly negative water potential, while isohydric plants maintain their leaf water potential above a specific threshold by actively regulating water loss by closing their stomata. Recently, Franks et al. (2007) identified an isohydrodynamic plant ideotype in which stomatal closure is insufficient to prevent midday leaf water potential from falling to values at which xylem embolism occurs during the driest periods but helps maintain a constant difference between predawn and midday leaf water potentials. Even more recently, Quero et al. (2011) observed that the stomatal regulation mechanism can act in both isohydric and anisohydric plants. It is now accepted that regulation of water loss caused by drought interacts with both hydraulic and stomatal functions (Cochard et al. 1996, 2002; Cruiziat et al. 2002; Beikircher and Mayr 2009). There is a trade-off between stomatal opening, which allows transpiration and photosynthesis to occur, and stomatal closing to protect the integrity of the water transport system from the soil-to-root interface to the substomatal cavity (Aranda et al. 2000; Sperry et al. 2002). Zimmermann (1983), e.g., showed that, after soil drying, the decrease in the xylem water potential caused embolism in vessels. The decrease in hydraulic conductance throughout the soil-to-leaf continuum is thought to be involved in the decrease in transpiration (Meinzer et al. 1995; Cochard et al. 2002; Limousin et al. 2009). Water regulation strategies and specific functional limits need to be investigated to understand how vulnerable woody plants face drought today, and how they will be affected by predicted drier environmental conditions in the future (Sperry et al. 1998, 2002). While many such studies have been conducted in temperate and Mediterranean environments (Granier and Colin 1990; Cochard et al. 1996; Lu et al. 1996; Cruiziat et al. 2002; Beikircher and Mayr 2009; Limousin et al. 2010), only a few studies have addressed Sahelian species (Berger et al. 1996; Roupsard et al. 1999; Do et al. 2008).

*Guiera senegalensis* J. F. Gmel is a semi-evergreen shrub (*Combretaceae*) (Seghieri et al. 2012) that is abundant in the Sudano-Sahelian region and may be locally dominant (Arbonnier 2001). The species plays an important role in socio-economic and agroforestry activities in this region (Louppe 1991; Wezel et al. 2000; Larwanou and Saâdou 2011). It is dominant in south-western Niger, where it grows on sandy, leached or exhausted soils, in fallows and in millet fields (Saâdou 1990). It is a major resource for livestock browsing, medicinal purposes and firewood, and is consequently subject to increasing anthropic pressure. As it is ubiquitous and tolerant to cutting and pruning, it is sometimes the only surviving species of the woody cover (Seghieri and Simier 2002). Determining its functional limits is crucial in the context of less favourable water conditions predicted in this region,

particularly an increase in rainfall variability and a decrease in soil infiltrability (Hély et al. 2006; Leblanc et al. 2008, Frappart et al. 2009; Lebel and Ali 2009).

The aim of this study was to (1) investigate the processes that regulate water loss in *G. senegalensis*, (2) determine their functional limits under drought conditions, and (3) check if the regulation processes are affected by canopy clearcut by comparing mature shrubs in fallows and current year resprouts in millet fields. The results improve our mechanistic understanding of hydric functioning of an agroforestry species that grows throughout the agricultural Sahelian belt, where such knowledge is still rare.

## Materials and methods

### Study area and selection of sample plots

The study area is located in the southern part of the Sahel, in the Dantiandou “kori” (temporary river) catchment in south-western Niger (Cappelaere et al. 2009). Mean annual rainfall, calculated for the 1905–2004 period is 560 mm (Balme et al. 2006). Mean daily temperatures range from 20 °C in January to 35 °C in April (Ramier et al. 2009). Mean daily vapor pressure deficit is below 1 kPa in the rainy season (July–August) and above 5 kPa in early May, but drops shortly after the boreal winter solstice (December–January) due to lower temperatures (Ramier et al. 2009). The region is dominated by the sedimentary formations of the Iullemeden Basin (Ambouta 1984). The landscape consists of a series of laterite plateaus of the Continental Terminal surrounded by sandy slopes (1–10 km<sup>2</sup>) whose soils are poor in organic matter (0.3 %), with mainly rainfed crops such as pearl millet, *Pennisetum glaucum*, and fallows. Fallows are shrubby steppes dominated by *G. senegalensis* and a sparse annual stratum (Saâdou 1990; Boulain et al. 2009).

Our experiment was conducted from April 2009 to February 2011 on four 0.25-ha plots located midslope (see Table 1 for characteristics). The plots were (1) a 22-year-old fallow in favorable water conditions near the village of Banizoumbou, (2) a young fallow (~5-year-old) in less favorable water conditions near the village of Wankama, and (3) two millet fields adjacent to the two above-mentioned fallows. Shrubs in the millet fields were cut before sowing and several times during the millet growing season. The young fallow was open and was used for grazing and to harvest fuel wood. The old fallow was protected by a fence, because it is a permanent reference plot for ecological monitoring by the national ROSELT network (*Réseau d'Observatoire et de Surveillance Ecologique à Long Terme*). Soil and historical management were homogeneous within each plot. A structural analysis of the

*G. senegalensis* cover was performed in each plot. Height and basal area classes were crossed to enable sampling of 10 % of individuals representing the most abundant classes.

#### Microclimatic variables

Air temperature and relative humidity were measured at 1-min intervals by Vaisala HMP45C and Campbell CS215 probes. These sensors were mounted on 2-m masts, with one sensor in the young fallow and one in the neighboring field, and one sensor for the old fallow and its adjacent field. Half-hourly means were recorded using Campbell CR1000 and CR800 data loggers. Atmospheric pressure was measured with a Casio Protrek barometer watch. An automatic YOUNG rain gauge was set up in the four plots.

#### Leaf water potential and stomatal conductance

Leaf water potential and stomatal conductance were measured simultaneously on the 10 % sample of shrubs representing the most abundant size classes in each plot (Table 1). Two leaves were excised to measure their water potential. Stomatal conductance was measured on two other leaves that remained on the shrub. All measurements were completed within a single sunny day. The first measurements were taken before dawn (5:00–6:00 a.m.) and then every 2 h until the minimum values of leaf water potential and the maximum values of stomatal conductance were exceeded (5:00–6:00 p.m.). For both parameters, the mean of the two sample leaves per shrub was calculated to obtain one result per shrub, and the mean of all the leaves sampled from all the sample shrubs was calculated to obtain one result at the whole population in each plot. This daily protocol was repeated monthly, except in periods of bud break or defoliation during which the frequency was increased to twice a month.

Leaf water potential was measured with a hydraulic press (HP, Objectif K model, France) chosen for its

robustness and portability (Seghieri 2010). Predawn leaf water potential ( $\Psi_{PD}$  MPa) is the value measured before sunrise. Minimum leaf water potential ( $\Psi_{DM}$  MPa) is the most negative value measured during the day.  $\Psi_{PD}$  is an indicator for the water potential of the soil in the root zone, based on the assumption that stomatal closure during the night allows equilibrium to be reached between soil and plant water potential (Ritchie and Hinkley 1975). According to Donovan et al. (2001), disequilibrium may exist. However, Berger et al. (1996) observed in several Sahelian shrub species that disequilibrium never exceeded 0.1–0.3 MPa. Hence, we chose to disregard the possibility of disequilibrium in this study. Stomatal conductance was measured using an AP4 transit-time porometer (Delta-T Devices) on the lower surface of mature leaves (two leaves per shrub), since *G. senegalensis* is hypostomatous.

#### Hydraulic traits

Segments were collected from ten branches in each of the four plots during the dry season (February 2011), and rapidly dispatched to the BIOGECO laboratory in Bordeaux. To avoid embolism before measurements started, the segments were collected very early in the morning, and the leaves immediately removed to limit transpiration. The segments were then rolled in moist newspaper and kept moist and cool (3 °C) until cavitation resistance was measured at the laboratory within 3 weeks after collection. It has been shown that samples can be stored for up to a month without altering the measurements (Herbette et al. 2010). Prior to measurement, all segments were cut to a standard length of 27 cm under water, and the bark was removed with a razor blade. The native embolism of the segments was measured with the XYL'EM apparatus (INRA license, <http://www.instrutec.fr>); the segments were then flushed with degassed water at low pressure until maximum water conductance was obtained (Cochard et al. 2002).

Xylem cavitation was assessed with a Cavitrion (Cochard 2002, 2005), at the new high-throughput phenotyping

**Table 1** Structural characteristics of woody vegetation in the four study areas in the southern Sahel (Niger)

Plot	Number of shrubs monitored (10 % of total number of <i>G. senegalensis</i> sampled for monitoring of leaf water potential and stomatal conductance)	Mean height (m) of <i>G. senegalensis</i> shrubs	Mean area of the crown (m <sup>2</sup> ) of <i>G. senegalensis</i> shrubs	Total shrub density (N/ha)
Crop field close to the young fallow (72 shrubs)	7	1.54 (±0.59) <sup>a</sup>	3.10 (±1.67) <sup>a</sup>	288
Young fallow (164 shrubs)	16	2.02 (±0.45)	5.91 (±2.05)	656
Crop field close to the old fallow (92 shrubs)	9	1.31 (±2.7) <sup>a</sup>	2.7 (±1.9) <sup>a</sup>	368
Old fallow (96 shrubs)	9	3.47 (±0.88)	12.39 (±3.95)	384

<sup>a</sup> Maximum values measured on shrubs in the plots at the stage of maximum shoot development after the last cutting

platform for hydraulic traits (CavitPlace, University of Bordeaux, Talence, France; <http://sylvain-delzon.com/caviplace>). Centrifugal force was used to establish negative pressure in the xylem and to trigger water-stress induced cavitation using a custom-built honeycomb rotor (Precis 2000, Bordeaux, France) mounted on a high-speed centrifuge (Sorvall RC5, USA). This technique enables measurement of the hydraulic conductance of a branch segment under negative pressure. Xylem pressure was first set to a reference pressure ( $-0.5$  MPa), and the corresponding hydraulic conductance  $k_{\max}$  was determined. To expose the sample to more negative pressure, the centrifugation speed was then set higher for 3 min. Conductance  $k_i$  corresponding to each pressure step was determined using the average flux of a reference ionic solution ( $10 \text{ mmol dm}^{-3}$  KCl and  $1 \text{ mmol dm}^{-3}$  CaCl<sub>2</sub> in deionized water) through the sample which was measured three times. The percentage loss of xylem conductance PLC was calculated at each pressure step using the following equation:

$$\text{PLC} = 100 \times \left(1 - \frac{k_i}{k_{\max}}\right). \quad (1)$$

The procedure was repeated for at least eight pressure values with a  $-0.5$  MPa step increment until PLC reached at least 90 %. Rotor velocity was monitored with a 10-rpm resolution electronic tachymeter, and xylem pressure was adjusted to about  $-0.02$  MPa. We used Cavisoft software (version 2.0, Biogeco, University of Bordeaux) for conductance measurements and computation of all vulnerability to cavitation (VC) curves.

The percentage loss of xylem conductance as a function of xylem pressure (MPa) represents the VC of the sample. A sigmoid function, or “s”-shaped curve (Pammenter and Van der Willigen 1998) was fitted to the VC curve of each sample using the following equation:

$$\text{PLC} = \frac{100}{[1 + \exp\{\frac{S}{25} * (P - P_{50})\}]} \quad (2)$$

where  $P_{50}$  (MPa) is the xylem pressure that caused 50 % loss of conductance and  $S$  (%MPa<sup>-1</sup>) is the slope of the vulnerability curve at the inflexion point. The xylem-specific hydraulic conductance  $k_s$  (m<sup>2</sup> MPa<sup>-1</sup> s<sup>-1</sup>) was calculated by dividing  $k_{\max}$  by the sapwood area of the sample. To obtain an “s”-shaped curve, the sampled segment must be longer than the length of the xylem vessel, otherwise an “r”-shaped curve is obtained, and this is considered abnormal when the centrifugal method is used (Cochard et al. 2010). Because some vessels had been cut open during preparation of the sample, proper “s”-shaped VC curves were obtained only for five branch segments, while “r”-shaped curves were obtained for 35 segments. Recent studies indicated that there is limited genetic diversity of  $P_{50}$  in a conifer (*Pinus pinaster*, Lamy et al. 2011) and in an

angiosperm (*Fagus sylvatica*, Wortemann et al. 2011). Other studies mentioned low intraspecific variation in  $P_{50}$  across rainfall gradients (Pammenter and Vander Willigen 1998; Maherali et al. 2004; Cornwell et al. 2007; Martinez-Vilalta et al. 2009) and showed that, when grown in the same conditions, subspecies maintained their native embolism resistance (Kolb and Sperry 1999). Thus, we felt confident using the average and standard error of the five proper “s”-shaped curves to provide *G. senegalensis* VC.

The safety margin was defined as the difference between the leaf water potential value  $\Psi_{SC}$  (MPa) corresponding to the lowest stomatal conductance measured in the field, and  $P_{50}$  measured in the laboratory (Beikircher and Mayr 2009).

#### Data analysis

The vapor pressure deficit (VPD, kPa) was calculated from the relative humidity value (RH, %) and the air temperature ( $T$ , °C) using Jones' (1992) equation.

The leaf transpiration rate ( $E$ , mmol. m<sup>-2</sup> s<sup>-1</sup>) was calculated from stomatal conductance ( $g_s$ , mmol. m<sup>-2</sup> s<sup>-1</sup>), saturation vapor pressure ( $e_s$ ), air vapor pressure ( $e$ ), and atmospheric pressure ( $P_{\text{atm}}$ , kPa) using McDermitt's (1990) equation:

$$E = g_s \left( \frac{e_s - e}{P_{\text{atm}}} \right). \quad (3)$$

We considered that relative humidity is close to 100 % in the leaf, so leaf vapor pressure is surrogated by  $e_s$  and  $\text{VPD} = e_s - e$ , then transpiration rate  $E$  is given by

$$E = \frac{g_s * \text{VPD}}{P_{\text{atm}}}. \quad (4)$$

which means that  $E$  varies during the day according to the two variables  $g_s$  and VPD.  $E_{\max}$  is thus the daily maximum transpiration rate obtained.

Soil-to-leaf hydraulic conductance ( $K_{S-L}$ , mol. m<sup>-2</sup> s<sup>-1</sup> MPa<sup>-1</sup>) was calculated for each field measurement date, as the slope of the line representing intradiurnal variation in the leaf water potential as a function of the leaf transpiration rate, after checking that this relationship was linear. The absolute value of the slope equals  $1/K_{S-L}$  (Schulze et al. 1985), and hence,  $K_{S-L}$  is expressed by Darcy's law as follows:

$$K_{S-L} = \frac{dE}{\Delta\Psi} \quad (5)$$

where  $\Delta\Psi$  is the gradient between soil and daily minimum water potentials proxied by  $\Psi_{PD}$  and  $\Psi_{DM}$ , respectively.

Analysis of variance (ANOVA, Systat 12 Software, Inc., Chicago, IL, USA) was performed to evaluate the effects of

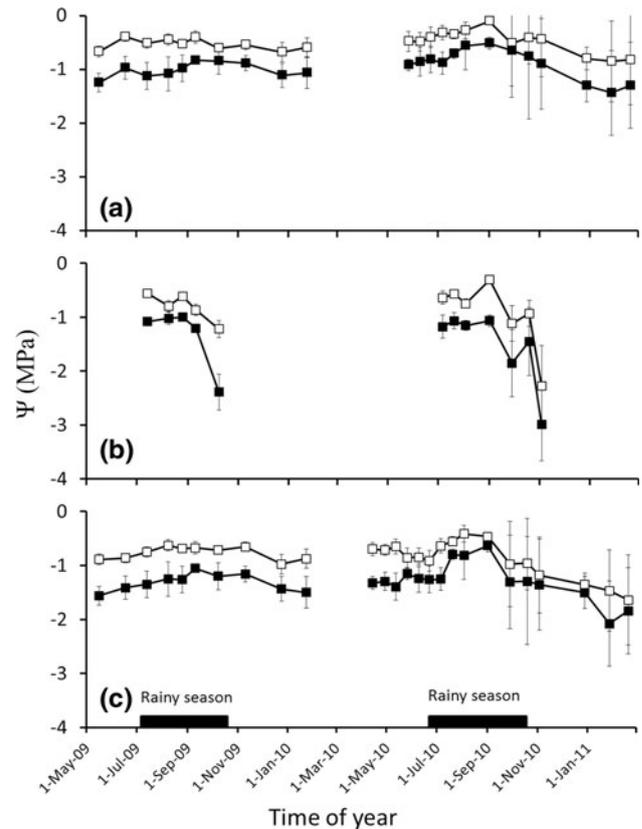
the plot on  $\Psi_{PD}$ ,  $\Psi_{DM}$ , and  $K_{S-L}$ , and their means were compared using R–E–G–W test at a 0.05 probability level. Homogeneity of variance and distribution of normality were checked previously with the Levene test. Data were log-transformed for all nonlinear trends among variables, and the relationship was considered significant at  $p < 0.05$ .

## Results

Seasonal changes in  $\Psi_{PD}$  and  $\Psi_{DM}$  in *G. senegalensis* are presented in Fig. 1. During the dry season, the leaf water potential decreased more in the two fallows than in the crop fields, but the difference between the two remained fairly constant with an average of 0.46 MPa. There was a significant difference in  $\Psi_{PD}$  and  $\Psi_{DM}$  between the three types of cover ( $F = 40.60$ ,  $p < 0.0001$  and  $F = 37.56$ ,  $p < 0.0001$ , respectively), with more negative values of  $\Psi_{PD}$  recorded in the young and old fallows ( $-2.27$  and  $-1.67$  MPa respectively), indicating severe water stress in the young fallow due to less favourable water conditions.

Figure 2 shows the magnitude of native embolism, vulnerability to cavitation (VC), and variation in maximum daily stomatal conductance ( $g_{smax}$ ) as a function of  $\Psi_{DM}$  in *G. senegalensis*. In the dry season, native embolism was significantly lower in the crop fields ( $2.2 \pm 1.7$  %) than in the fallows ( $34.2 \pm 7.0$  % in the young fallow and  $26.4 \pm 6.2$  % in the old fallow). The mean value of  $P_{50}$  obtained from VC was  $-3.59 \pm 0.19$  MPa. The value of  $g_{smax}$  was obtained between 9.00 and 10.00 a.m. in the dry season (data not shown) and around 12.00 a.m. in the rainy season. The highest value of  $g_{smax}$  measured in the field was  $687 \pm 234$  mmol. m<sup>-2</sup> s<sup>-1</sup>. This value was considered as full stomatal opening (100 %, Fig. 2). The lowest value of  $g_{smax}$  ( $106 \pm 52$  mmol. m<sup>-2</sup> s<sup>-1</sup>) was measured in the field in the dry season. This corresponds to 85 % of stomatal closure (15 %  $g_{smax}$ , Fig. 2), which we considered to be almost full stomatal closure. This stomatal closure value corresponded to a potential pressure of  $-3$  MPa assumed to be  $\Psi_{SC}$ . The safety margin of *G. senegalensis* was thus 0.59 MPa.  $\Psi_{SC}$  corresponded to a 30 % loss in hydraulic conductance PLC, which was slightly below the value of native embolism measured in the two fallows (34 %, Fig. 2).

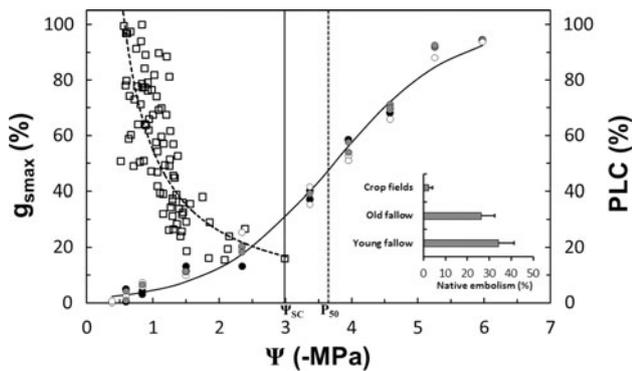
Figure 3 shows the relationship between  $g_{smax}$  and  $VPD_{max}$  under the three land covers.  $g_{smax}$  declined significantly with an increase in VPD only in mature shrubs in the two fallows, although  $g_{smax}$  variability explained by VPD remained low (29–37 %).  $g_{smax}$  decreased more rapidly in young fallow than in the old, and the minimum value for the two was 100 mmol. m<sup>-2</sup> s<sup>-1</sup> corresponding to a VPD of 6 kPa. Our results (Fig. 4) confirmed that in *G.*



**Fig. 1** Seasonal changes in predawn (open squares) and midday (solid squares) leaf water potential ( $\Psi$ ) over a 2-year period in *G. senegalensis* in the southern Sahel (Niger) in **a** current year resprouts in the two crop fields, **b** mature shrubs in a 5-year-old fallow and **c** in a 22-year-old fallow. The rainy season is indicated by black rectangles along the time axis. Vertical bars represent the standard errors

*senegalensis*, the leaf transpiration rate,  $E$ , varies linearly as a function of leaf water potential  $\Psi$  during the day ( $R^2 = 0.7\text{--}0.9$ ,  $p < 0.05$ ). The steepest slope ( $-0.33$ ) and the most negative values of  $\Psi_{PD}$  ( $-2.27$  MPa) and  $\Psi_{DM}$  ( $-3.12$  MPa) were obtained in mature shrubs in the young fallow during the dry season (Fig. 4), probably because conditions in this fallow were drier than in the old fallow and also due to the fact the canopy was older than that of the current year resprouts.

In all sites,  $K_{S-L}$  and  $g_{smax}$  decreased logarithmically with a decrease in  $\Psi_{PD}$  (Fig. 5). When values were log-normalized, significant linear relationships ( $p < 0.05$ ) were found, except for  $K_{S-L}$  in the current year resprouts (Fig. 5a). A better relationship was observed for  $g_{smax}$  than for  $K_{S-L}$  and for the fallows than for the crop fields. Variance analysis showed that  $g_{smax}$  varied seasonally between plots ( $F = 66.87$ ,  $p < 0.0001$ ). During the dry season, minimum values of  $g_{smax}$  were 165, 106, and 110 mmol. m<sup>-2</sup> s<sup>-1</sup> in crop fields, young, and old fallows, respectively.  $K_{S-L}$  varied



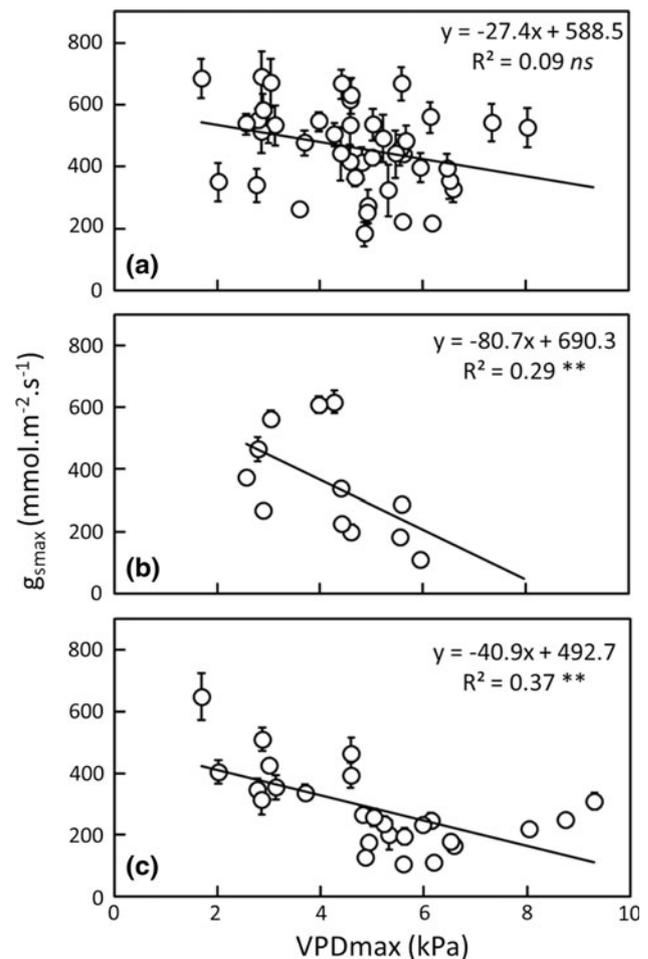
**Fig. 2** Vulnerability to cavitation (VC) of *G. senegalensis* (percentage loss of hydraulic conductance (PLC) versus xylem pressure ( $\Psi$ )) obtained using the Cavitrone on branches collected in the southern Sahel (Niger) between May 2009 and February 2011 in current year resprouts (*open circles*) and in mature shrubs in young fallow (*solid circles*) and old fallow (*grey circles*). Variation in daily maximum stomatal conductance (%  $g_{smax}$ , open squares) expressed as a function of daily minimum leaf water potential ( $\Psi$ ) measured in situ ( $g_{smax} = 54.83 \Psi^{-1.08}$ ,  $R^2 = 0.62$  and  $p < 0.05$  with log transformed data). For  $g_{smax}$  data, all plots were pooled (9–16 shrubs per plot, two or three leaves per shrub). The *solid vertical line* represents the water potential ( $\Psi_{SC}$ ) value corresponding to the minimum stomatal conductance measured in situ. The *dotted vertical line* represents the value of xylem pressure that caused 50 % loss of hydraulic conductance ( $P_{50}$ ). The difference between  $\Psi_{SC}$  and  $P_{50}$  corresponds to the species' safety margin. Mean values ( $\pm$ SE) of native embolism are presented in the inset ( $n = 10$  for each type of cover)

significantly between the three types of cover ( $F = 19.96$ ,  $p < 0.001$ ) and the maximum value ranged from  $0.05 \text{ mol. m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$  in mature shrubs to  $0.11 \text{ mol. m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$  in current year resprouts.

Figure 6 shows the trends in the daily maximum leaf transpiration rate  $E_{max}$  as a function of the soil-to-leaf hydraulic conductance  $K_{S-L}$  according to the age of the canopy. Daily maximum leaf transpiration ( $E_{max}$ ) ranged from  $2.67$  to  $22.4 \text{ mmol. m}^{-2} \text{ s}^{-1}$  over the study period and across the four plots.  $E_{max}$  increased linearly up to a limit of  $20 \text{ mmol. m}^{-2} \text{ s}^{-1}$  in all plots with increasing  $K_{S-L}$  up to  $0.05 \text{ mol. m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$  (Fig. 6). This threshold was the maximum value of  $K_{S-L}$  in mature shrubs in the two fallows but not in the current year resprouts, where, beyond that threshold, there was no longer a correlation between  $E_{max}$  and  $K_{S-L}$ , and  $E_{max}$  fluctuated around  $16 \text{ mmol. m}^{-2} \text{ s}^{-1}$ .

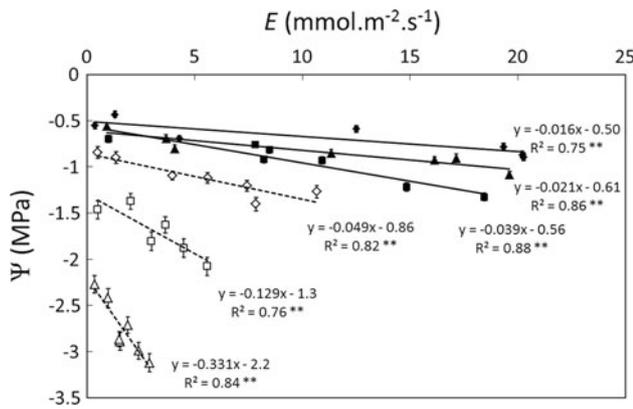
## Discussion

A species can survive if the water regime of the soil is compatible with its functional limits (Sperry et al. 1998; Hacke et al. 2000). In our study conditions, results demonstrate that soil water limitation remained below the functional limits of *G. senegalensis*, as indicated by



**Fig. 3** Relationship between daily maximum stomatal conductance ( $g_{smax}$ ) and daily maximum vapor pressure deficit ( $VPD_{max}$ ) in *G. senegalensis* in the southern Sahel (Niger) in current year resprouts in two crop fields (a), mature shrubs in a 5-year-old fallow (b) and in a 22-year-old fallow (c). Each *dot* represents the mean measurements of two leaves on each shrub for a total of 9–16 shrubs. *Bars* represent the standard errors

the positive safety margin. The species displayed a low-cavitation rate under the drought conditions of its environment. Because of the relatively constant value of  $\Delta\Psi$  across seasons, *G. senegalensis* must be considered to be isohydrodynamic according to the classification of Franks et al. (2007). The relative stability of  $\Delta\Psi$  was already reported by Seghieri and Galle (1999) in the same species in tiger bush under artificially induced water stress. However, in *Acacia senegal* and *Ziziphus mauritiana* in the northern Sahel, marked variations in  $\Delta\Psi$  ranging from  $0.54$  to  $2.4 \text{ MPa}$  and  $0.46$  to  $2.1 \text{ MPa}$ , respectively, were reported (Berger et al. 1996). Less variation was reported in *Faidherbia albida* in the more humid Sudanese zone ( $2 \text{ MPa}$ , Rouspard et al. 1999) and in *Acacia xanthophloea*

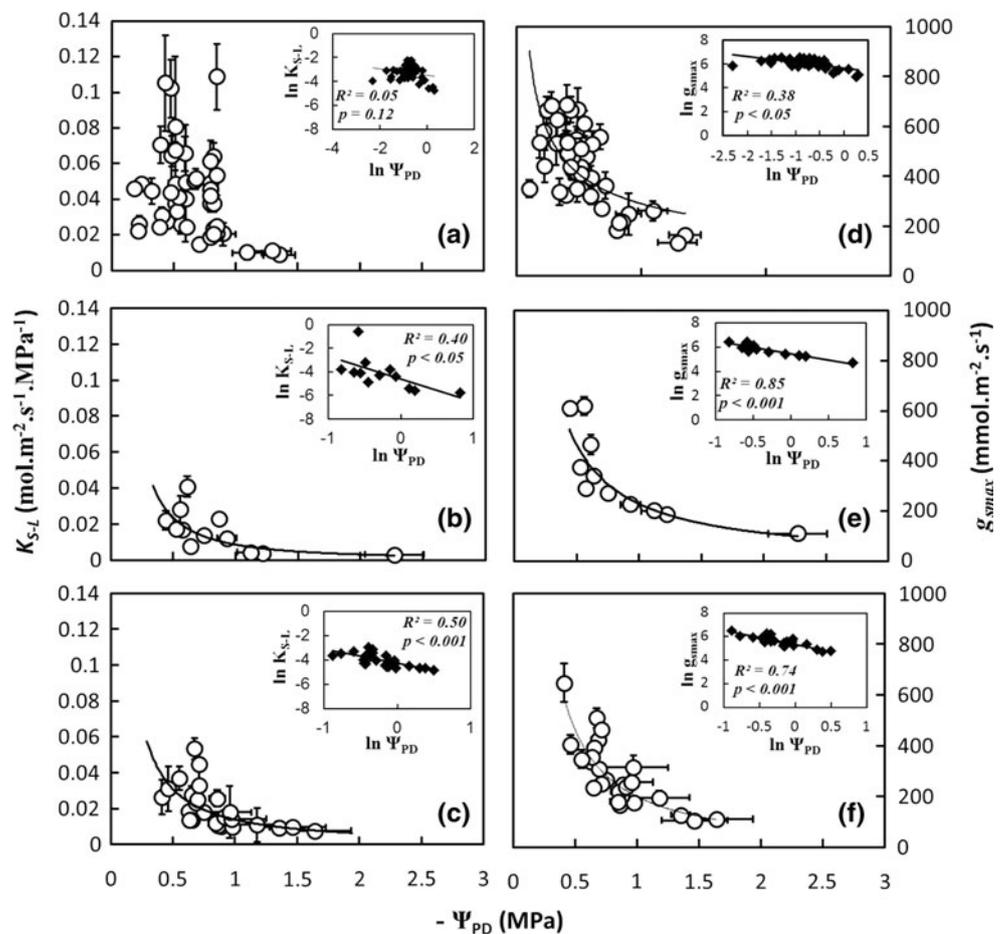


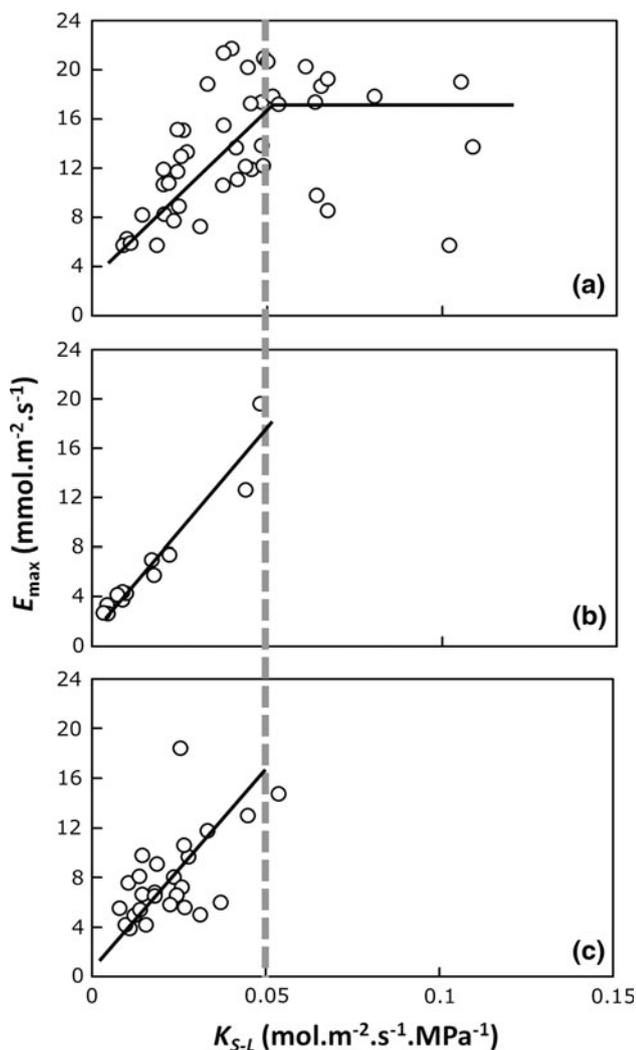
**Fig. 4** The daily variations in leaf transpiration rate ( $E$ ) as a function of leaf water potential ( $\Psi$ ) in *G. senegalensis* in all study plots measured over several days are representative of the range obtained between May 2009 and February 2011. *Solid symbols* show measurements made during the wet season, and *open symbols* those made during the dry season (*diamond shapes* for the current year respouts in the two crop fields ( $n = 16$  shrubs), *triangles* for the mature shrubs in young fallow ( $n = 16$  shrubs), and *squares* for the mature shrubs in old fallow ( $n = 9$  shrubs). *Bars* represent standard errors. These linear relationships are significant ( $p < 0.05$ )

(2 MPa) and *Acacia tortilis* saplings (1.4 MPa) in semi-arid Kenya (Otieno et al. 2005).

The maximum value of stomatal conductance measured in situ was similar to that measured by Hanan and Prince (1997,  $661 \text{ mmol. m}^{-2} \text{ s}^{-1}$ ) in the same species in the same area. However, it was higher than the range of values ( $260\text{--}540 \text{ mmol. m}^{-2} \text{ s}^{-1}$ ) reported by Berger et al. (1996) in *Combretum glutinosum*, *Acacia senegal*, *Z. mauritiana*, *A. tortilis*, *Balanites aegyptiaca*, and *Boscia senegalensis* in the northern Sahel. Our results also highlight the efficient stomatal control of transpiration in *G. senegalensis*. Stomatal regulation has been reported in other species in water-limited environments (Acherar and Rambal 1992; Diagne 2003; Limousin et al. 2009; Quero et al. 2011). Chapotin et al. (2006) reported that stomatal control of transpiration occurred suddenly at a leaf water potential of  $-1$  MPa in baobab trees (*Adansonia* spp.) in Malagasy tropical dry forest. Berger et al. (1996) observed low leaf water potential ( $\Psi_{DM}$  between  $-2$  and  $-3$  MPa) but high stomatal conductance throughout the year in *C. glutinosum*, in contrast to our results in *G. senegalensis*. However, in

**Fig. 5** Relationship between soil-to-leaf hydraulic conductance ( $K_{S-L}$ ) and maximum stomatal conductance ( $g_{Smax}$ ) as a function of daily predawn leaf water potential ( $\Psi_{PD}$ ) in *G. senegalensis* in the southern Sahel (Niger) in current year respouts in the two crop fields (a, d), mature shrubs in the young fallow (b, e), and mature shrubs in the old fallow (c, f). *Insets* show a linear relationship of log-transformed data. Each *dot* represents the mean of 9–16 shrubs (two to three leaves were measured on each shrub). *Bars* represent the standard errors





**Fig. 6** Maximum rate of leaf transpiration ( $E_{\max}$ ) versus soil-to-leaf hydraulic conductance ( $K_{S-L}$ ) in *G. senegalensis* in the southern Sahel (Niger) between May 2009 and February 2011 in the current year respouts in the two crop fields (a), mature shrubs in the young fallow (b), and mature shrubs in the old fallow (c). The dotted vertical line indicates the value of  $K_{S-L}$  at which  $E_{\max}$  stops increasing

their study, populations of *C. glutinosum* were reported to be regressing. The hydromechanical stomatal control observed in *G. senegalensis* in the Sahel explains why there is no contradiction between fluctuating leaf water potential and stomatal regulation, which is an adaptive strategy to enable the plant to function in dry but variable environmental conditions (Quero et al. 2011). The low variability of  $g_{\text{smax}}$  explained by VPD indicates that other physical variables than VPD, such as soil water content, may be stronger drivers of stomatal conductance in *G. senegalensis*.

The value of VPD at which we measured the lowest value of  $g_{\text{smax}}$  in *G. senegalensis* was within the range (5–8 kPa) reported by Grouzis et al. (1998) in six woody

species (*C. glutinosum*, *A. senegal*, *Z. mauritiana*, *A. tortilis*, *B. aegyptiaca*, and *B. senegalensis*) in the northern Sahel, relatively close to the VPD observed in *F. albida* in the Sudanese zone (5 kPa, Roupsard et al. 1999) but higher than that found in *A. xanthophloea* in a semi-arid zone in Kenya (4 kPa, Otieno et al. 2005). In the desert in California, a more arid environment than that of *G. senegalensis*, the lowest values of stomatal conductance were recorded with higher VPD (7.5 kPa, Meinzer et al. 1988). For many species growing in temperate and Mediterranean climates (Breda et al. 2006) and in tropical rainforest (Bonal and Guehl 2001), stomatal conductance was minimum with VPD values ranging between 2 and 3 kPa. Low sensitivity of stomata to high VPD is common in drought-tolerant species (Aranda et al. 2000). In environments where temperatures are high, such as in the Sahel, stomata that close when VPD values are high can cause heat stress of leaves even if the leaves are turgid (Tardieu 2005).

The maximum stomatal closure and the corresponding value of leaf predawn water potential measured in *G. senegalensis* is comparable to that found in *Quercus ilex* in a Mediterranean environment (90 % of stomatal closure for a predawn potential of  $-4$  MPa, Limousin et al. 2009). However, our results also showed that in *G. senegalensis*, xylem water potential can decrease beyond the value of leaf water potential corresponding to almost 100 % of stomatal closure, owing to the species' positive safety margin. In our study conditions, the loss of xylem conductivity that triggered maximum stomatal closure in *G. senegalensis* was lower than that measured in *Adansonia* spp (40–65 %) in Malagasy tropical dry forest that corresponds to higher leaf water potential ( $-1$  MPa, Chapotin et al. 2006). It was also only half the stomatal closure measured in *Q. ilex* in a Mediterranean environment (64 %, Limousin et al. 2010) and in *Ligustrum vulgare* and *Viburnum lantana*, two temperate forest species (65 %, Beikircher and Mayr 2009). However, in the two latter species, the corresponding leaf water potential was less negative ( $-3.3$  MPa). According to the classification of Bréda et al. (2006), the positive value of the safety margin we measured in *G. senegalensis* classifies it as a xeric species, although not one of the most extreme. When Cruiziat et al. (2002) linked vulnerability to cavitation and the degree of stomatal closure, they identified three distinct strategies. In the first strategy (the most common among the species tested), the water potential value that caused 10 % conductivity loss corresponded to a theoretical stomatal closure of at least 90 %. In the second strategy, the water potential value that caused 10 % loss of conductivity triggered stomatal closure at levels well below 90 %. In the third strategy, closure of more than 90 % of stomata was caused by water potential that was much less negative than the value corresponding to 10 % loss of conductivity. Our

results show that *G. senegalensis* clearly belongs to the first group.

At global scale, Maherali et al. (2004) showed that, in angiosperms,  $P_{50}$  tends to increase with an increase in climate aridity. The  $P_{50}$  value obtained for *G. senegalensis* in our study conditions is more negative than the average value for angiosperms calculated by these authors ( $-3.15 \pm 0.19$  MPa). However, the value is less negative than the median values they found in evergreen shrubs ( $-5.09$ ) and in desert plants ( $-4.5$  MPa) and relatively close to the value ( $-3.64$  MPa) found in *Q. ilex* by Limousin et al. (2010). These results are in agreement with the semi-evergreen nature of the species (Seghieri et al. 2012) and confirm its non-extreme xeric nature, suggesting that it may suffer in a more arid environment.

The linearity of the relationship between daily variations in the intensity of leaf transpiration and leaf water potential, rather than a curvilinear pattern, indicates a negligible contribution to transpiration of water possibly stored in the shrub's tissues (Schulze et al. 1985; Meinzer 2002). Linearity appears to be widespread in many species in which  $K_{S-L}$  decreases with water stress. For example, in *F. albida* growing in a Sudanian environment, i.e., moister than our study area, Roupsard et al. (1999) showed that the value of  $K_{S-L}$  dropped by 50 % at the end of the dry season when  $\Psi_{DM}$  decreased from  $-2$  to  $-2.7$  MPa. Lu et al. (1996) measured a drop in the  $K_{S-L}$  value to close to zero in *Picea abies* in a temperate environment, when  $\Psi_{PD}$  fell from  $-0.5$  to  $-1.5$  MPa. In contrast, in *A. tortilis* in the northern Sahel, Otieno et al. (2005) and Do et al. (2008) found no significant difference between  $K_{S-L}$  values measured during the dry season and those measured during the rainy season because of the phreatophytic nature of the species.  $K_{S-L}$  values estimated for *G. senegalensis* ( $0.05$ – $0.11$  mol.  $m^{-2} s^{-1} MPa^{-1}$ ) are lower than those estimated by Roupsard et al. (1999) in *F. albida* in a Sudanian environment ( $0.4$ – $1.2$  mol.  $m^{-2} s^{-1} MPa^{-1}$ ), but higher than those reported by Berger et al. (1996) for north Sahelian species ( $0.0084$ – $0.0016$  mol.  $m^{-2} s^{-1} MPa^{-1}$ ) and by Limousin et al. (2009) for *Q. ilex* ( $0.003$  mol.  $m^{-2} s^{-1} MPa^{-1}$ ). Thanks to its high inter-regional variation, the range of values observed in  $K_{S-L}$  could be a good indicator of the relative water conditions under which a species grows, i.e., medium conditions (mesic) in the case of *G. senegalensis* in our study conditions.

The mechanisms by which stomatal conductance, and hence transpiration are linked to variations in soil-to-leaf hydraulic conductance are not yet well understood (Sperry and Pockman 1993). In a given species, the decrease in  $K_{S-L}$  may be due either to xylem cavitation (Zimmermann 1983) or to increased resistance to water transfer at the soil-root interface because of the decrease in water availability (Sperry et al. 1998; Lu et al. 1996). Our results confirm that, in *G. senegalensis*, there is active stomatal response to

a decrease in hydraulic conductance that is primarily due to increasing resistance at the soil-root interface with the decrease in soil water availability, since xylem cavitation was only 30 % when the stomata were almost completely closed. Monteny et al. (1997) and Boulain et al. (2009) showed that in *G. senegalensis* plots in the same area as ours, evapotranspiration was controlled by atmospheric conditions up to a threshold value of relative soil water content corresponding to 70 %. Below this threshold, evapotranspiration was linearly controlled by soil water content. Similarly, our results confirm that, in the shrub itself, transpiration, indicated by increasing  $K_{S-L}$ , increases linearly with soil water content, but only up to a limit of approximately  $0.05$  mol.  $m^{-2} s^{-1} MPa^{-1}$ , which corresponds to a value of  $\Psi_{PD}$  of  $-0.6$  MPa. Above this limit, atmospheric conditions may control variations in  $K_{S-L}$ , and hence in transpiration in the current year resprouts in the crop fields. A  $K_{S-L}$  threshold was also found by Meinzer et al. (1995) in trees in tropical rainforests, which were later (Meinzer 2003) explained by the physiological limits specific to the plant (stage of foliation, leaf size, dimension and frequency of stomata). In our case, the small size of the aboveground part of the current year resprouts may limit their leaf area and consequently their capacity to evaporate. Transpiration is thus adjusted not only to the plant's transport capacity but also to its leaf transpiration capacity.

The lower  $\Psi_{DM}$  and  $\Psi_{PD}$  in tall mature shrubs than in small current year resprouts reflects the lack of stress undergone by the current year resprouts. Indeed, more soil water was available in the crop fields than in the fallows at the end of the rainy season after the millet harvest (Ramier et al. 2009), probably thanks to lower shrub density in the crop fields, which also means that more water was available per shrub while they resprouted. In addition, the current year resprouts carried young leaves that were consequently more turgid, again contributing to a less negative leaf water potential than in mature shrubs. Finally, the current year resprouts do not have a cuticle (personal observation), which limits water loss from old leaves on mature shrubs. This lack of cuticle on leaves helps increase  $K_{S-L}$  beyond the threshold reached by mature shrubs, while the canopy is regenerating, and the leaf surface increases.

In response to seasonal drought, water conducting capacity ( $K_{S-L}$ ) decreased more in mature shrubs than in current year resprouts. In current year resprouts, leaf water potential was maintained lowly negative by high hydraulic conductance. This change with canopy rejuvenation in the same species has not been previously reported, although an anisohydric to isohydric transition has been already reported in two varieties of *Vitis vinifera* cultivars of the same age and linked to differences in their hydraulic conductance (Schultz 2003). Small current year resprouts on old stumps probably had a higher root/shoot ratio favoring

more water conducted to the aboveground part of the plant than in taller older canopies, as shown in *Arbutus unedo* in Mediterranean environments (Castell and Terradas 1994). Furthermore, after removal of the canopy, current year resprouts only contain vessels with negligible native embolism. This explains why their hydraulic conductance was higher than that of mature shrubs.

It is becoming increasingly clear that, to resist drought, a plant's capacity for water loss through its leaves is associated with its capacity to supply its leaves with water (Cruziat et al. 2002). Consequently, the suspected close link between foliation and the species resistance to cavitation needs more detailed studies. We compared the results obtained by Seghieri and Simier (2002) for foliation and by Seghieri and Laloe (2004) for variations in leaf water potential on a sample of seven populations of *G. senegalensis* in our study area. The first shrubs started to defoliate when the minimum water potential reached between  $-2.5$  and  $-3.5$  MPa, a range that included the value of  $\Psi_{SC}$  we found, i.e., at which 80 % of stomata were closed. This link now needs to be confirmed.

## Conclusion

The maximum water stress experienced by *G. senegalensis* during dry periods in situ in the conditions of our study corresponded to a relatively small decrease in the plant's water transport capacity. Stomatal closure protects the xylem from embolism. Closure of the stomata regulated transpiration before the leaf water potential reached  $-3$  MPa, a probable threshold at which leaf fall begins. Beyond this threshold, a positive safety margin enabled the species to survive in good conditions as long as water potential remained below the critical value of  $-3.6$  MPa, the lethal value being  $-6$  MPa. The decrease in shrub density and the yearly canopy clearcut reduced water stress in the current year resprouts and increased the capacity of the plants to transport water. However, their intense transpiration is ultimately limited by the meager development of their canopy. Further research will be undertaken to describe the role of foliation and defoliation in the maintenance of the internal water balance in *G. senegalensis*.

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## References

- Acherar M, Rambal S (1992) Comparative water relations of four Mediterranean oak species. *Vegetatio* 99:177–184
- Ambouta KJM (1984) Contribution à l'édaphologie de la brousse tigrée de l'ouest nigérien. PhD dissertation, Nancy I University, France, Nancy
- Aranda I, Gil L, Pardos JA (2000) Water relations and gas exchange in *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. *Trees* 14:344–352
- Arbonnier M (2001) Arbres, arbustes et lianes des zones sèches d'Afrique de l'Ouest, vol 2. CIRAD, MNHN, Paris
- Balme M, Vischel T, Lebel T, Peugeot C, Galle S (2006) Assessing the water balance in the Sahel: impact of small scale rainfall variability on runoff. Part 1: rainfall variability analysis. *J Hydrol* 331:336–348
- Beikircher B, Mayr S (2009) Intraspecific differences in drought tolerance and acclimation in hydraulics of *Ligustrum vulgare* and *Viburnum lantana*. *Tree Physiol* 29:765–775
- Berger A, Grouzis M, Fournier C (1996) The water status of six woody species coexisting in the Sahel (Ferlo, Senegal). *J Trop Ecol* 12:607–627
- Bonal D, Guehl J-M (2001) Contrasting patterns of leaf water potential and gas exchange responses to drought in seedlings of tropical rainforest species. *Funct Ecol* 15:490–496
- Boulain N, Cappelaere B, Ramier D, Issoufou HBA, Halilou O, Seghieri J, Guillemin F, Oi M, Gignoux J, Timouk F (2009) Towards an understanding of coupled physical and biological processes in cultivated Sahel-2. Vegetation and carbon dynamics. *J Hydrol* 375:190–203
- Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann For Sci* 63:625–644
- Breman H, Kessler J (1995) Woody plants in agro-ecosystems of semi-arid regions, with an emphasis on the Sahelian countries. Berlin Springer-Verlag, Berlin
- Cappelaere B, Descroix L, Lebel T, Boulain N, Ramier D, Laurent JP, Favreau G, Boubkraoui S, Boucher M, Bouzou Moussa I, Chaffard V, Hiernaux P, Issoufou HBA, Le Breton E, Mamadou I, Nazoumou Y, Oi M, Otlé C, Quantin G (2009) The AMMACATCH experiment in the cultivated Sahelian area of southwest Niger—Investigating water cycle response to a fluctuating climate and changing environment. *J Hydrol* 375:34–51
- Castell C, Terradas J (1994) Effects of water and nutrient availability on water relations, gas exchange and growth rate of mature plants and resprouts of *Arbutus unedo* L. *Ann Bot* 73:595–602
- Chapotin SM, Razanameharizaka JH, Holbrook NM (2006) Water relations of baobab trees (*Adansonia* spp. L.) during the rainy season: does stem water buffer daily water deficits? *Plant Cell Environ* 29:1021–1032
- Cochard H (2002) A technique for measuring xylem hydraulic conductance under high negative pressures. *Plant Cell Environ* 25:815–819
- Cochard H, Breda N, Granier A (1996) Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evident for stomatal control of embolism? *Ann For Sci* 53:197–206

- Cochard H, Coll L, Le Roux X, Améglio T (2002) Unraveling the effects of plant hydraulics on stomatal conductance during water stress in walnut. *Plant Physiol* 128:282–290
- Cochard H, Damour G, Bodet C, Tharwat I, Poirier M, Améglio T (2005) Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. *Physiol Plant* 124:410–418
- Cochard H, Herbette S, Barigah T, Badel E, Ennajeh M, Vilagrosa A (2010) Does sample length influence the shape of xylem embolism vulnerability curves? A test with the Cavitrone spinning technique. *Plant Cell Environ* 33:1543–1552
- Cornwell WK, Bhaskar R, Sack L, Cordell S, Lurch CK (2007) Adjustment of structure and function of *Metrosideros polymorpha* at high versus low precipitation. *Funct Ecol* 21:1063–1071
- Cruziat P, Cochard H, Améglio T (2002) The hydraulic architecture of trees: main concepts and results. *Ann For Sci* 59:723–752
- Diagne AL (2003) Transpiration globale et fonctionnement hydrique unitaire chez *Acacia tortilis* en conditions de déficit pluviométrique. *Sècheresse* 14:235–240
- Do FC, Rocheteau A, Diagne AL, Goudiaby V, Granier A, Lhomme JP (2008) Stable annual pattern of water use by *Acacia tortilis* in Sahelian Africa. *Tree Physiol* 28:95–104
- Donovan LA, Linton MJ, Richards JH (2001) Predawn plant water potential does not necessarily equilibrate with soil water potential under well watered conditions. *Oecologia* 129:328–335
- Eamus D, Prior L (2001) Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. *Adv Ecol Res* 32:113–197
- Franks PJ, Drake PL, Froend RH (2007) Anisohydric but isohydrodynamic: seasonally constant plant water potential gradient explained by stomatal control mechanism incorporating variable plant hydraulic conductance. *Plant Cell Environ* 30:19–30
- Frappart F, Hiernaux P, Guichard F, Mougouin E, Kergoat L, Arjounin M, Lavenu F, Koité M, Paturol JE, Lebel T (2009) Rainfall regime across the Sahel band in the Gourma region, Mali. *J Hydrol* 375:128–142
- Granier A, Colin F (1990) Effets d'une sécheresse édaphique sur le fonctionnement hydrique d'*Abies bornmulleriana* en conditions naturelles. *Ann Sci For* 47:189–200
- Grouzis M, Diouf M, Rocheteau A, Berger A (1998) Fonctionnement hydrique et réponses des ligneux sahéliens à l'aridité. In Campa Claudine, Grignon C, Gueye M, Hamon Serge (eds) *L'acacia au Sénégal*. Paris : ORSTOM pp 47–61 (Colloques et Séminaires). *L'Acacia au Sénégal : Réunion Thématique, 1996/12/03-05, Dakar*
- Hacke UG, Sperry JS, Ewers BE, Ellsworth DS, Schafer KVR, Oren R (2000) Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124:495–505
- Hanan NP, Prince SD (1997) Stomatal conductance of west-central supersite vegetation in HAPEX-Sahel: measurements and empirical models. *J Hydrol* 188–189:536–562
- Hély C, Bremond L, Alleaume S, Smith B, Sykes MT, Guiot J (2006) Sensitivity of African biomes to changes in the precipitation regime. *Global Ecol Biogeogr* 15:258–270
- Herbette S, Wortemann R, Awad H, Huc R, Cochard H, Barigah TS (2010) Insights into xylem vulnerability to cavitation in *Fagus sylvatica* L. phenotypic and environmental sources of variability. *Tree Physiol* 30:1448–1455
- Jones HG (1992) *Plant and microclimate: a quantitative approach to environmental plant physiology*, 2nd edn. Cambridge University Press, Cambridge
- Kolb KJ, Sperry JS (1999) Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). *Ecology* 80:2373–2384
- Lamy JB, Bouffier L, Burrett R, Plomion C, Cochard H, Delzon S (2011) Uniform selection as a primary force reducing population genetic differentiation of cavitation resistance across a species range. *PLoS One* 6:e23476. doi:10.1371/journal.pone.0023476
- Larwanou M, Saïdou M (2011) The role of human interventions in tree dynamics and environmental rehabilitation in the Sahel zone of Niger. *J Arid Environ* 75:194–200
- Le Houerou HN, Bingham RL, Skerbek W (1988) Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *J Arid Environ* 15:1–18
- Lebel T, Ali A (2009) Recent trends in the central and western Sahel rainfall regime 4 (1990–2007). *J Hydrol* 375:52–64
- Leblanc M, Favreau G, Massuel S, Tweed S, Loireau M, Cappelaere B (2008) Land clearance and hydrological change in the Sahel: SW Niger. *Glob Planet Change* 61:135–150
- Limousin JM, Rambal S, Ourcival JM, Rocheteau A, Joffre R, Rodriguez-Cortina R (2009) Long-term transpiration change with rainfall decline in a Mediterranean *Quercus ilex* forest. *Glob Change Biol* 15:2163–2175
- Limousin JM, Longepierre D, Huc R, Rambal S (2010) Change in hydraulic traits of Mediterranean *Quercus ilex* submitted to long-term throughfall exclusion. *Tree Physiol* 30:1026–1036
- Louppe D (1991) *Guiera senegalensis*: espèce agroforestière? Micro-jachère dérobée de saison sèche et approvisionnement énergétique d'un village du centre-nord du bassin arachidier sénégalais. *Bois et Forêts des Tropiques* 228:41–47
- Lu P, Biron P, Granier A, Cochard H (1996) Water relation of adult Norway spruce (*Picea abies* (L.) Karst) under soil drought in the Vosges Mountains: whole-tree hydraulic conductance, xylem embolism and water loss regulation. *Ann For Sci* 53:113–121
- Maherali H, Pockman WT, Jackson RB (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85:2184–2199
- Martinez-Vilalta J, Cochard H, Mencuccini M, Sterck F, Herrera A, Korhonen JFJ, Llorens P, Nikinmaa E, Nollé A, Poyatos R, Pipillone F, Sass-Klaassen U, Zweifel R (2009) Hydraulic adjustment of Scots pine across Europe. *New Phytol* 183:353–364
- McDermitt DK (1990) Sources of error in the estimation of stomatal conductance and transpiration from porometer data. *HortScience* 25:1538–1548
- Meinzer FC (2002) Co-ordination of vapour and liquid phase water transport properties in plants. *Plant Cell Environ* 25:265–274
- Meinzer FC (2003) Functional convergence in plant responses to the environment. *Oecologia* 134:1–11
- Meinzer FC, Sharifi MR, Nilsen ET, Rundel PW (1988) Effects of manipulation of water and nitrogen regime on the water relations of the desert shrub *Larrea tridentata*. *Oecologia* 77:480–486
- Meinzer FC, Goldstein G, Jackson P, Holbrook NM, Gutiérrez MV, Cavelier J (1995) Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic conductance properties. *Oecologia* 101:514–522
- Monteny BA, Lhomme JP, Chehbouni A, Troufleau D, Amadou M, Sicot M, Verhoef A, Galle, Said F, Lloyd CR (1997) The role of the Sahelian biosphere on the water and the CO<sub>2</sub> cycle during the HAPEX-Sahel experiment. *J Hydrol* 188–189:516–535
- Otieno DO, Schmidt MWT, Kinyamario JL, Tenhunen J (2005) Responses of *Acacia tortilis* and *Acacia xanthophloea* to seasonal changes in soil water availability in the savanna region of Kenya. *J Arid Environ* 62:377–400
- Pammenter NW, Vander Willigen C (1998) A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiol* 18:589–593
- Quero JL, Sterck FJ, Martínez-Vilalta J, Villar R (2011) Water-use strategies of six co-existing Mediterranean woody species during a summer drought. *Oecologia* 166:45–57

- Ramier D, Boulain N, Cappelaere B, Timouk F, Rabanit M, Lloyd CR, Boubkraoui S, Métayer F, Descroix L, Wawrzyniak V (2009) Towards an understanding of coupled physical and biological processes in the cultivated Sahel-1. Energy and water. *J Hydrol* 375:204–216
- Ritchie GA, Hinkley TM (1975) The pressure chamber as an instrument for ecological research. *Adv Ecol Res* 9:165–254
- Roupsard O, Ferhi A, Granier A, Pallo F, Depommier D, Mallet B, Joly HI, Dreyer E (1999) Reverse phenology and dry-season water uptake by *Faidherbia albida* (Del.) A. Chev. in an agroforestry parkland of Sudanese West Africa. *Funct Ecol* 13:460–472
- Saâdou M (1990) La végétation des milieux drainés nigériens à l'est du fleuve Niger. PhD dissertation, Abdou Moumouni University, Niger, Niamey
- Schultz HR (2003) Differences in hydraulic architecture account for near-isohydric and anisohydric behaviour of two field-grown *Vitis vinifera* L. cultivars during drought. *Plant Cell Environ* 26:1393–1405
- Schulze ED, Cermak J, Matyssek R, Penka M, Zimmermann R, Vasicek F, Gries W, Kucera J (1985) Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea* trees—a comparison of xylem flow, porometer and cuvette measurements. *Oecologia* 66:475–483
- Seghieri J (2010) Comparison of the measurements of leaf water potential between a hydraulic press and a pressure chamber in six Sahelian woody species. *Agrofor Syst* 80:185–190
- Seghieri J, Galle S (1999) Contribution to a Sahelian two-phase mosaic system: soil water regime and vegetation life cycles. *Acta Oecol* 20:209–218
- Seghieri J, Laloe F (2004) Characterization of the variability of the daily course of leaf water potential in the dominant shrub species within Sahelian fallows in South-West Niger. *Ecol Model* 173:271–281
- Seghieri J, Simier M (2002) Variations in phenology of a residual invasive shrub species in Sahelian fallow savannas, south-west Niger. *J Trop Ecol* 18:897–912
- Seghieri J, Do FC, Devineau JL, Fournier A (2012) Phenology of woody species along the climatic gradient in west tropical Africa. In: Zhang X (ed) Phenology and climate change InTech. <http://www.intechopen.com/books/phenology-and-climate-change/phenology-of-woody-species-along-the-climatic-gradient-in-west-tropical-africa-> doi:10.5772/33729
- Sperry JS, Pockman WT (1993) Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant Cell Environ* 16:279–287
- Sperry JS, Adler FR, Campbell GS, Comstock JP (1998) Limitation of plant water use by rhizosphere and xylem conductance: results from model. *Plant Cell Environ* 21:347–359
- Sperry JS, Hacke UG, Oren R, Comstock JP (2002) Water deficits and hydraulic limits to leaf water supply. *Plant Cell Environ* 2:251–263
- Sultan B, Baron C, Dingkuhn M, Sarr B, Janicot S (2005) La variabilité climatique en Afrique de l'Ouest aux échelles saisonnière et intra-saisonnière. II: applications à la sensibilité des rendements agricoles au Sahel. *Sècheresse* 16:1–10
- Tardieu F (2005) Plant tolerance to water deficit: physical limits and possibilities for progress. *CR Geoscience* 337:57–67
- Tardieu F, Simonneau T (1998) Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modeling isohydric and anisohydric behaviour. *J Exp Bot* 49:419–432
- Wezel A, Rajot JL, Herbrig C (2000) Influence of shrubs on soil characteristics and their function in Sahelian agro-ecosystems in semi-arid Niger. *J Arid Environ* 44:383–398
- Wortemann R, Herbette S, Barigah TS, Fumanal B, Alia R, Ducouso A, Gomory D, Roedel-Drevet P, Cochard H (2011) Genotypic variability and phenotypic plasticity of cavitation resistance in *Fagus sylvatica* L. across Europe. *Tree Physiol* 31:1175–1182
- Zimmermann MH (1983) Xylem structure and the ascent of sap in plants. Springer, New York