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Research paper

Is the WBE model appropriate for semi-arid shrubs subjected to clear cutting?

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It is crucial to understand the adaptive mechanisms of woody plants facing periodic drought to assess their vulnerability to the increasing climate variability predicted in the Sahel. *Guiera senegalensis* J.F.Gmel is a semi-evergreen Combretaceae commonly found in Sahelian rangelands, fallows and crop fields because of its value as an agroforestry species. We compared canopy leafing, and allometric measurements of leaf area, stem area and stem length and their relationships with leaf water potential, stomatal conductance (g_s) and soil-to-leaf hydraulic conductance ($K_{S–L}$), in mature and current-year resprouts of *G. senegalensis* in Sahelian Niger. In mature shrubs, seasonal drought reduced the ratio of leaf area to cross-sectional stem area ($A_L : A_S$), mainly due to leaf shedding. The canopy of the current-year resprouts remained permanently leafed as the shrubs produced leaves and stems continuously, and their $A_L : A_S$ ratio increased throughout the dry season. Their $K_{S–L}$ increased, whereas g_s decreased. West, Brown and Enquist's (WBE) model can thus describe allometric trends in the seasonal life cycle of undisturbed mature shrubs, but not that of resprouts. Annual clear cutting drives allometric scaling relationships away from theoretical WBE predictions in the current-year resprouts, with scaling exponents 2.5 times greater than those of mature shrubs. High $K_{S–L}$ (twice that of mature shrubs) supports this intensive regeneration process. The adaptive strategy described here is probably common to many woody species that have to cope with both severe seasonal drought and regular disturbance over the long term.

Keywords: adaptive mechanism, allometry, *Guiera senegalensis*, resource allocation, resprouts, water-limited environment.

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Introduction

The Sahel is a semi-arid region located directly south of the Sahara between isohyets 200 and 600 mm, where woody plants have to cope with unpredictable water availability and with a dry season that lasts 6–8 months, during which little or no soil water is available, and evaporative demand is high (2000 mm year^{-1}). In the 1970–80s, the region was affected by severe droughts, but since the late 1990s, there has been a trend toward rainfall recovery, although with a higher frequency of extreme events such as drought and floods (Lebel and Ali 2009, Descroix et al. 2012, GIEC 2013, Roehrig et al. 2013). In addition, the extent of cultivated land has increased rapidly in recent decades due to continuous population growth (especially in Niger), with a resulting decline in natural vegetation (Guengant and Banoin 2003, Cappelaere et al. 2009). Although part of the regeneration success of natural vegetation has been linked to the recent increase in rainfall (Anyamba and Tucker 2005), its specific adaptive traits, especially those responsible for its

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resilience in rapidly expanding cultivated areas, have not yet been identified.

Traditional Sahelian agriculture is characterized by rotation of crops and fallows with fallows ranging from a few months in the winter off-crop season to several decades, and by the presence of woody species spared by farmers because of their value (Breman and Kessler 1991, Mubarak et al. 2012). *Guiera senegalensis* J. F. Gmel is a multipurpose semi-evergreen (Seghieri et al. 2012) arido-active shrub sensu Evenari (1985) that has to cope with a highly variable water supply (Seghieri and Galle 1999, Seghieri and Simier 2002, Issoufou et al. 2013). It is one of the most abundant shrub species in rangelands, fallows and crop fields in the Sudanian–Sahelian belt (Louppe 1991, Wezel et al. 2000, Lahmar et al. 2012). Every year, before sowing and during the millet growth period, shrubs growing in farmers' fields are cut back but not uprooted, providing an experiment in itself. The cut shrubs immediately resprout. The processes involved in allometric adjustment during the seasonal cycle of mature shrubs and during current-year resprouting after cutting need to be addressed to understand its ability to adapt both to drought and to yearly cutting back. West, Brown and Enquist's theoretical model (hereafter referred to as WBE) derivation predicts that leaf area scales as the two power of diameter based on the assumption that a plant's gross photosynthetic rate is determined by its potential rates of resource uptake across the absorbing surface and resource redistribution throughout the entire plant (West et al. 1999, Enquist 2002, Enquist and Niklas 2002, Coomes 2006). Thus the WBE model provides a framework for predicting how plant functioning and morphology vary with scale. Hydraulic traits and allometric scaling laws vary with tree ontogeny and competitive interactions (Mencuccini 2002, Muller-Landau et al. 2006). However, the relevance of the WBE model predictions has not yet been tested in disturbed environments, particularly in Sahelian agrosystems.

In semi-evergreen species, water loss is assumed to be regulated not only by stomatal closure but also by a decrease in leaf area (Sperry et al. 2002). The strategies the plant uses to allocate resources during growth and during regrowth after being cut back determine its ability to maintain its water balance, and hence to survive under drought conditions (Gotsch et al. 2010). In the present study, variations in *G. senegalensis* leaf area were compared with variations in its conducting sapwood area because these are useful indicators of the species' ability to maintain gas exchange and to continue to grow during periodic droughts (White et al. 1998). In chaparral angiosperms, Ackerly (2004) showed that the specific ratio of leaf-to-sapwood area (the inverse of this ratio, sapwood area to leaf area referred to as the Huber Value) decreased with an increase in the intensity of drought in the environment in which a species grows. This has also been demonstrated in conifers in European temperate and Mediterranean regions (Mencuccini and Grace 1995, Martínez-Vilalta et al. 2009). The leaf-to-sapwood area ratio was also reported to decrease with tree age and with an increase in plant height (Ryan and Yoder 1997, Delzon et al. 2004).

The main objective of this study was to evaluate the WBE prediction when applied to the functional response of *G. senegalensis* to seasonal drought in mature shrubs (in fallows) and in shrubs resprouting after yearly cutting back (in crop fields) in the Sahelian region in Niger. The second aim was to determine the appropriate allometric relationships in Sahelian shrubs for which observations are scarce, but crucial to scale up carbon and water fluxes from the leaf, or whole plant, to the ecosystem. The study answers the two following questions: (i) What are the relationships between leaf growth, shoot growth and plant water status in mature shrubs in fallows? (ii) What are the impacts of yearly cutting on these relationships in the current-year resprouts in crop fields? Our results contribute to the ongoing debate on the biological relevance of the WBE model (Kozlowski and Konarzewski 2004, Meinzer et al. 2005).

Materials and methods

Data were collected in the field from April 2009 to February 2011.

Study area and sample plots

The study area is located in southwestern Niger, ~70 km northeast of the capital Niamey (13.4°N, 2.4°E) (Cappelaere et al. 2009). It is representative of the southern agricultural Sahel. Average annual rainfall is 560 mm, with rain falling from June to September (1905–2004, Balme et al. 2006). During the dry season from November to April, no rain falls at all, and May and October are transition periods during which small quantities of rain may fall. The average annual temperature is 24 °C. Geology, soils and vegetation cover are described in Issoufou et al. (2013).

The experiment was conducted in four 0.25 ha plots located in the middle of a sand deposit (average slope of 2% and 0.3% organic matter content) surrounding a laterite plateau of the Continental Terminal. The plots were (i) a fallow in relatively favorable soil water conditions that has been fenced for 22 years (Seghieri et al. 2005, Mahamane et al. 2007), (ii) an unfenced 5-year-old fallow located at a distance of 15 km from the previous one with drier soil conditions (Cappelaere et al. 2009) and (iii) two crop fields, one adjacent to each fallow.

Climatic variables and soil water content

Climatic variables and soil water content (SWC) were monitored in the young fallow and its adjacent crop field from April 2009 until February 2011, and in the 22-year-old fenced fallow and its adjacent crop field from December 2009 until February 2011. Details on the probes, sensors, frequencies and data loggers used to measure rainfall, air temperature (T, °C) and air relative humidity (RH, %) are given in Issoufou et al. (2013).

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The vapor pressure deficit (VPD, kPa) was deduced from RH and T following Jones (1992).

Volumetric SWC θ (%) was measured with reflectometer probes. In the younger unfenced fallow and its adjacent crop field, measurements were taken at depths of 0.1, 0.5 and 1 m with three Campbell Scientific CS616 probes. In the older fenced fallow and its adjacent crop field, measurements were taken at depths of 0.05, 0.25, 0.65 and 1.25 m with four EnviroSCAN probes. Semi-hourly means were recorded by Campbell Scientific CR1000 and CR800 data loggers. Following the observations of Kizito et al. (2006) concerning the depth of *G. senegalensis* roots, the daily mean soil water content (SWC, mm) of the 0–1 m soil layer in each plot was calculated as follows:

$$\mathrm{SWC} = \sum_{i=1}^{n} h_i \times \theta_i, \quad (1)$$

where θ_i is volumetric SWC measured in a given soil layer and h_i is the height of the layer.

To buffer possible differences between the soils in the four plots, we approximated the water available to the plants (WAP, mm) as follows:

$$\mathrm{WAP} = \mathrm{SWC} - \mathrm{SWC}_{\mathrm{min}}, \quad (2)$$

where $\mathrm{SWC}_{\mathrm{min}}$ is the minimum SWC measured during the dry season, a value that did not change over the 2-year experimental period in any of the plots.

Leaf water potential, stomatal conductance and soil-to-leaf hydraulic conductance

Leaf water potential and stomatal conductance (g_s, mmol m^{-2} s^{-1}) were measured simultaneously on 10% of shrubs representative of the most abundant classes of height and basal area combined (see details in Issoufou et al. 2013). Two leaves were excised to measure their water potential. g_s was measured on two other leaves that were left on the shrub. All the measurements were completed within a single sunny day. The first measurements were made before dawn (5:00–6:00 a.m.) and then at 2-hourly intervals until the minimum values of leaf water potential and the maximum values of g_s were exceeded (5:00–6:00 p.m.). For both parameters, the mean of two sample leaves per shrub was calculated to give one result per shrub, and the mean of all leaves sampled from all the sampled shrubs was calculated to give one result at the scale of the whole population in each plot. This daily protocol was repeated monthly, except during periods of bud break or of defoliation, when the frequency was increased to twice a month.

Leaf water potential was measured with a hydraulic press (HP, Objectif K model, Sols Mesures, Elancourt, France) chosen for its robustness and portability (Seghieri 2010). Predawn leaf water potential (Ψ_{PD}, MPa) is the value measured before sunrise. Minimum leaf water potential (Ψ_{DM}, MPa) is the most negative value measured during the course of the day. Ψ_{PD} is an indicator of 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 potentials (Ritchie and Hinckley 1975). According to Donovan et al. (2001), disequilibrium may exist, but Berger et al. (1996) observed that disequilibrium did not exceed 0.1–0.3 MPa in several Sahelian shrub species. We therefore chose to disregard the possibility of disequilibrium in this study. g_s was measured with an AP4 porometer (Delta-T Devices Ltd, Cambridge, UK) on the lower surface of mature leaves, as *G. senegalensis* is hypostomatous.

Soil-to-leaf hydraulic conductance ($K_{\mathrm{S-L}}$, mol m^{-2} s^{-1} MPa^{-1}) was calculated from the leaf water potential and g_s measured each time the daily courses of these variables were monitored. After checking that the relationship was linear, $1/K_{\mathrm{S-L}}$ is the absolute value of the slope of the intradiurnal variation in leaf water potential as a function of the leaf transpiration rate (Schulze et al. 1985). We first calculated the leaf transpiration rate (E, mmol m^{-2} s^{-1}) from g_s, VPD and atmospheric pressure (P_{atm}, kPa) using McDermitt's (1990) equation:

$$E = \frac{g_s \times \mathrm{VPD}}{P_{\mathrm{atm}}} \quad (3)$$

According to Darcy's law, $K_{\mathrm{S-L}}$ is then expressed as follows:

$$K_{\mathrm{S-L}} = \frac{dE}{\Delta\Psi} \quad (4)$$

where $\Delta\Psi$ is the gradient between soil and leaf water potential, as proxied by Ψ_{PD} and Ψ_{DM} respectively.

Canopy phenology and variations in leaf area and stem cross-sectional area

The canopy phenology of all the shrubs was monitored in all four plots. A shrub was considered as being in leaf as soon as >10% of the canopy was covered with mature leaves up to when 50% of the canopy was covered by senescent leaves. Next, we calculated the percentage of shrubs in leaf in each plot and plotted it as a function of the date (Figure 1c).

In 2010, on all shrubs on which leaf water potential and g_s were monitored in mature shrubs in the two fallows and in resprouts in the two crops fields, three current-year shoots per shrub were tagged to monitor changes in leaf and cross-sectional shoot areas and in shoot length. Current-year shoot lengths were measured with tailor's tape and their diameter with calipers, and the leaves were counted. After having calculated their basal cross-sectional area, we calculated their mean cross-sectional area and their mean length (A_S and L_S, respectively). To obtain the average leaf area without disturbing the monitored shrubs, two or three current-year shoots were removed from

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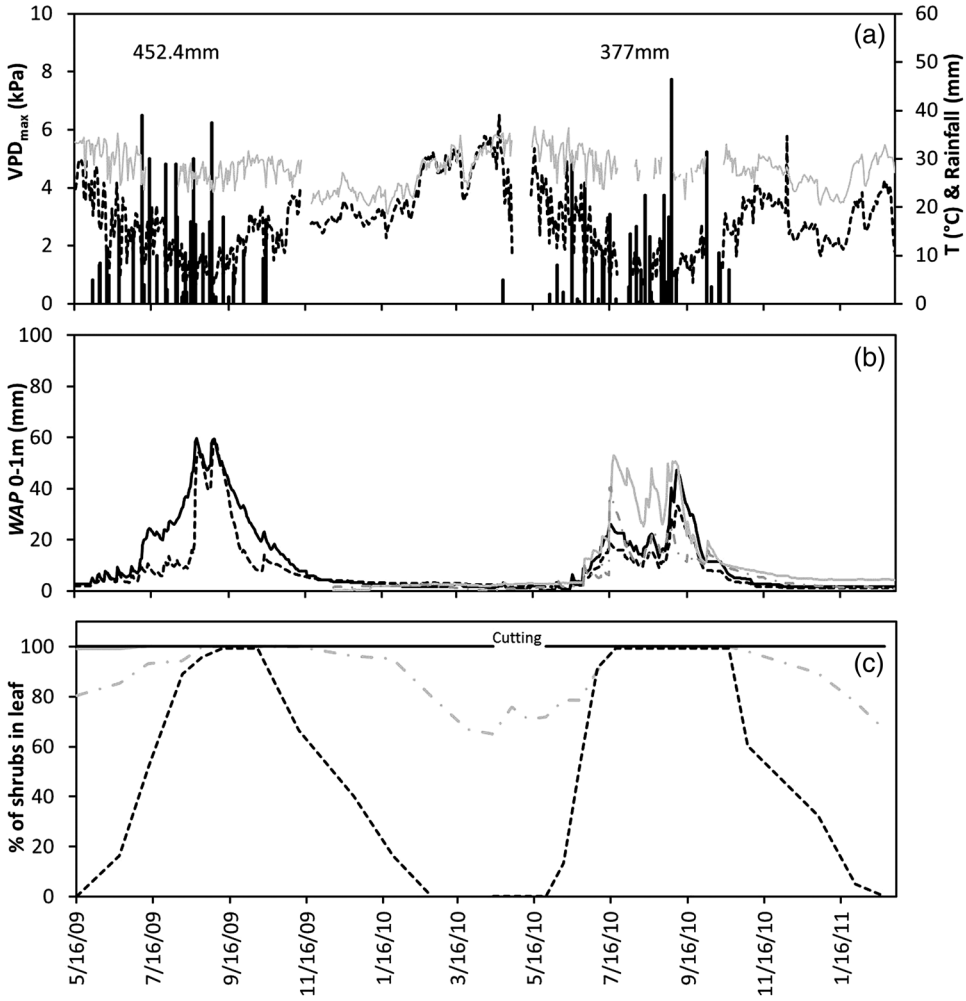

Figure 1. Variations in the environmental conditions and shrub canopy leaf phenology of *G. senegalensis* growing in the southern Sahel in Niger over two growing seasons. Daily rainfall (bar chart), temperature *T* (solid gray line) and VPD (dashed black line) (a), water available for plants at a depth of 0–1 m (b), in a young fallow (dashed black line), in the crop field adjacent to the young fallow (solid black line), in an old fallow (dash-dot gray line) and in the crop field adjacent to the old fallow (solid gray line), and canopy leafing (symbols are the same as for water available for plants) (c).

other shrubs in the same plot. All the leaves were harvested, counted and scanned, and their area was estimated using ImageJ image processing and analysis software (v1.43). We estimated the leaf area (A_L) of the monitored shrubs by multiplying the number of leaves on each tagged shoot by the average area of the leaves harvested on shoots on the other shrubs. The ratio of leaf-to-cross-sectional areas of the current-year shoot ($A_L : A_S$) was deduced. Shoot basal area is likely to be a valid proxy of sapwood area only when the proportion of non-conducting heartwood is insignificant (Brenner et al. 1991). In the cross-section areas of the current-year shoots we monitored, we found that heartwood was insignificant both in the mature shrubs in the fallows and in the current-year resprouts in crop fields.

Measurement of the length of longer vessels

The length of the longer vessels was determined using the method of Ewers and Ficher (1989). Ten unbranched stems were harvested in each plot. The apical part of the stem was cut and immediately immersed in water. An air pump was used to inject air at low pressure (2 kPa) into the distal part of the stem. If no air bubbles appeared, the stem was shortened by removing one centimeter from the distal end. As soon as air bubbles appeared, implying that at least one vessel had been opened, the stem length was measured, the value corresponding to the length of the longer vessel to within 1 cm.

Data analyses

Analysis of variance was performed to test the plot effects on Ψ_{PD}, Ψ_{DM} and g_{smax} using SYSTAT 12.0 software (Systat Software, Inc., Chicago, IL, USA). Homogeneity of variance and distribution of normality were checked using Levene's test. Post hoc pairwise mean comparisons were performed using the REGW test, and differences between plots ($P < 0.05$) were tested using the least squares means method. The relationships between $A_L : A_S$ and Ψ_{PD} and between $A_L : A_S$ and g_{smax} were assessed using linear regression. Allometric relationships

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between A_L and A_S and between A_L and L_S were derived from standard major axis (SMA) regressions of log-transformed variables using 'smatr' software in an R package. SMA regressions are particularly appropriate for estimating the best line describing the scatter of X and Y for allometries (Warton et al. 2006). We compared the slope and the intercepts of the regressions according to the type of cover and season (rainy vs dry). According to the WBE hypothesis, the leaf area is predicted to scale with the square of shoot diameter based on the area-preserving branching rule (Enquist and Niklas 2002, Coomes 2006). This means the leaf area and the cross-sectional shoot area scale isometrically. That is why we also tested the isometry of the regression between A_L and A_S and between L_S and A_S to evaluate possible allometric deviations from the theory.

Results

Figure 1 shows the leaf canopy phenology of *G. senegalensis* during two growing seasons in the two fallows and their two adjacent crop fields in relation to variations in daily rainfall (mm), T, VPD and WAP. In 2009 and 2010, cumulative annual rainfall was below the long-term mean annual rainfall in the study site, with a 20% rainfall deficit in 2009 and a 30% deficit in 2010 (Figure 1a). Mean daily VPD was 2 kPa during the rainy season when mean T was ~28 °C (Figure 1a), moderate (between 2 and 4 kPa with a mean T of ~20 °C, Figure 1a) during the early cold dry season and high during the late hot dry season (6–8 kPa and mean T ~35 °C, Figure 1a).

During the rainy season, WAP in the 0–1 m layer tended to vary as expected (Boulain et al. 2009). The soil in the crop fields became wet earlier and dried out later than in the fallows in 2009 (Figure 1b) and maximum WAP was higher in 2010 (Figure 1b). These differences can be attributed to the less dense populations of the shrub, and hence reduced water use in the crop fields (see Table 1 in Issoufou et al. 2013). The less favorable water conditions in the younger fallow were confirmed (Figure 1b). As a consequence of the more favorable water conditions in the crop fields, unlike the shrubs in the fallows, the canopy of the current-year resprouts remained fully leafed throughout the dry season, except just after cutting (Figure 1c).

In the older fallow, mature shrubs started coming into leaf 2 months before the rainy season but in the younger fallow, leafing only began after the onset of the rainy season (Figure 1c), i.e., when the WAP began to increase (Figure 1b). During the dry season, the decrease in the percentage of leafed shrubs with WAP was more progressive in the old than in the young fallow, and at the end of the season, all the shrubs in the young fallow had lost their leaves, whereas 60% of the shrubs in the older fallow remained in leaf.

Table 1 shows that the maximum stomatal conductance (g_{smax}) and the two leaf water potentials (Ψ_{PD} and Ψ_{DM}) varied significantly between the plots ($P < 0.0001$). Table 2 shows that the means of g_{smax}, Ψ_{PD} and Ψ_{DM} did not vary significantly between the two crop fields but that there was a significant difference between the crop fields and the older fallow (group 2, Table 2) and between the crop fields and the younger fallow (group 3, Table 2). Based on these results, the data collected in the two crop fields were pooled to make a single data set.

Table 1. Results of the one-way analysis of variance with the plot effect as a factor to test the difference between the following dependent variables: predawn (Ψ_{PD}, MPa) and minimum (Ψ_{DM}, MPa) leaf water potential and maximum stomatal conductance (g_{smax}, mmol m^{-2} s^{-1}) in *G. senegalensis* in crop fields and in young and old fallows in the southern Sahel in Niger. *$P > 0.05$ not significant, $P < 0.05$ weakly significant, $P < 0.01$ significant and $P < 0.001$ highly significant.

Dependent variables	Df	*F*-value	*P*-value*	R^2
Ψ_{PD}	3	83.776	<0.0001	0.376
Ψ_{DM}	3	96.25	<0.0001	0.402
g_{smax}	3	44.899	<0.0001	0.260

Table 2. Results of a post hoc test using the Ryan–Einot–Gabriel–Welsch method to check for differences among plots by comparing mean predawn (Ψ_{PD}, MPa) and minimum (Ψ_{DM}, MPa) leaf water potential and maximum stomatal conductance (g_{smax}, mmol m^{-2} s^{-1}) in *G. senegalensis* in the southern Sahel in Niger. Means followed by the same letter are not significantly different within a group (Q test, $\alpha = 0.05$, n = number of observations).

Plots	*N*	Ψ_{PD}	Ψ_{DM}	g_{smax}	Group
Crop field adjacent to young fallow	408	−0.56a	−0.99a	462.9a	1
Crop field adjacent to old fallow	409	−0.50a	−0.93a	441.6a	1
Young fallow	258	−1.37b	−2.16b	244.0b	2
Old fallow	437	−0.84c	−1.28c	283.9c	3

Figure 2 shows variations in $A_L : A_S$, in A_L and in A_S as a function of Ψ_{DM} in the two fallows and their adjacent crop fields. There was a significant decrease in $A_L : A_S$ and A_L ($P < 0.01$) with Ψ_{DM} in the mature shrubs, whereas these values increased in the current-year resprouts. A_S increased significantly as a linear function of Ψ_{DM} in the current-year resprouts ($P < 0.05$) but did not vary significantly in mature shrubs ($P > 0.05$). The minimum value of Ψ_{DM} in the current-year resprouts was −1.5 MPa, including the entire dry season, which was less negative than the values reached in mature shrubs in both the young fallow and the old fallow (−2 and −3 MPa, Figure 2).

Figure 3 shows that relationships between $A_L : A_S$ and g_{smax} and K_{S-L} were more significant ($P < 0.01$) and the higher variability of $A_L : A_S$ was explained ($R^2 \geq 0.6$) by g_{smax} and K_{S-L} in the mature shrubs rather than in the current-year resprouts. As expected, the ratio $A_L : A_S$ decreased with g_{smax} and K_{S-L} in the mature shrubs (the minima being reached in the dry season); however, the ratio tended to increase when g_{smax} and K_{S-L} decreased in the current-year resprouts, minimum and maximum values of the ratio $A_L : A_S$ and for g_{smax} being observed during the dry season during which

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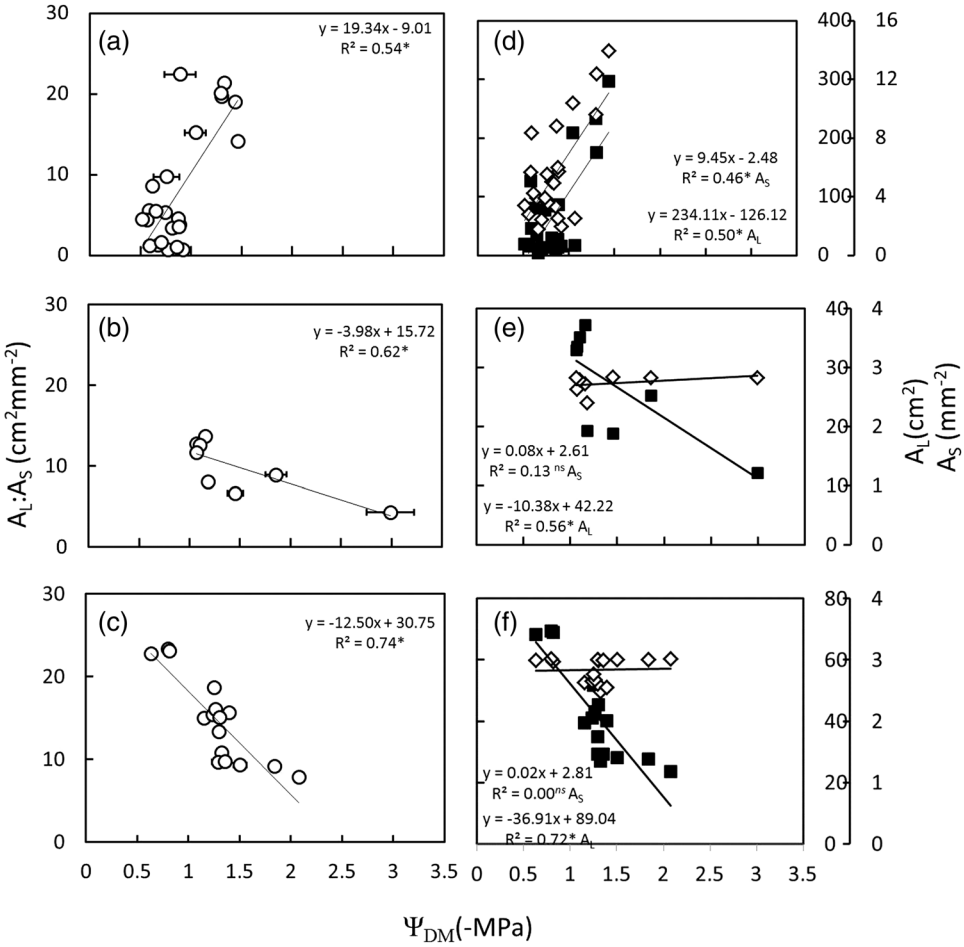

Figure 2. Ratio of leaf area to cross-sectional area $A_L : A_S$ of the current-year shoot (empty circles) as a function of the minimum leaf water potential Ψ_{DM} (left) and leaf area A_L of current-year shoots (black squares) and cross-sectional area A_S (empty diamonds) of current-year shoots as a function of minimum leaf water potential Ψ_{DM} (right) in *G. senegalensis* in the southern Sahel (Niger) in two crop fields (a and d), a young fallow (b and e) and an old fallow (c and f).

the range of K_{S-L} values increased. In addition, minimum g_s was slightly higher in the resprouts (134 mmol m^{-2} s^{-1}) than in mature shrubs (110 mmol m^{-2} s^{-1}, Figure 3a–c), and the maximum value of K_{S-L} was almost three times higher (0.11 mol m^{-2} s^{-1} MPa^{-1} vs 0.04 mol m^{-2} s^{-1} MPa^{-1}) while its minimum value (observed during the dry season) was almost 10 times higher (0.023 mol m^{-2} s^{-1} MPa^{-1} vs 0.003–0.007 mol m^{-2} s^{-1} MPa^{-1}, Figure 3d–f).

The allometric regression of the $A_L : A_S$ and $A_L : L_S$ ratios (Table 3) confirmed the results shown in Figure 4. Slopes and intercepts of the regressions of both $A_L : A_S$ and $A_L : L_S$ were similar in the two crop fields. Likewise, the slopes of the equivalent regressions were similar in the two fallows, but for the same A_S, in the old fallow A_L was 20% higher than in the young fallow while for the same L_S, it was 30% lower. Conversely, the slopes of the regressions of $A_L : A_S$ and $A_L : L_S$ were highly significantly ($P < 0.001$, Table 3a) higher in the crop fields than in their respective adjacent fallow, as shown in Figure 4. In addition, the slopes of allometric regressions of $A_L : A_S$ and $A_L : L_S$ were generally similar in the dry and rainy season in the fallows, although the slopes were only slightly significantly different from the regression of $A_L : A_S$ in the old fallow (Table 3b). For the same A_S and for the same L_S, A_L was, respectively, 12 and 31% higher in the young fallow (Figure 4b and e), and, respectively, 21 and 24% higher in the old fallow, in the rainy season than in the dry season (Figure 4c and f). Conversely, differences between the dry and rainy seasons were highly significant in the crop fields (Table 3b, Figure 4). There was a highly significant difference in the slopes of the allometric regression of $A_L : A_S$ compared with the isometric model in the two field crops whatever the season, and in the old fallow during the rainy season (Table 4, Figure 4). The slopes of the allometric regression of $L_S : A_S$ differed highly significantly from the isometric model in all the situations whatever the season (data not shown).

Figure 5 shows that the mean length of the longer vessels was significantly shorter in the current-year resprouts than in the mature shrubs in both the young fallow (*t*-test, $P = 0.041$) and the old fallow (*t*-test, $P = 0.006$). The length of the longer vessel

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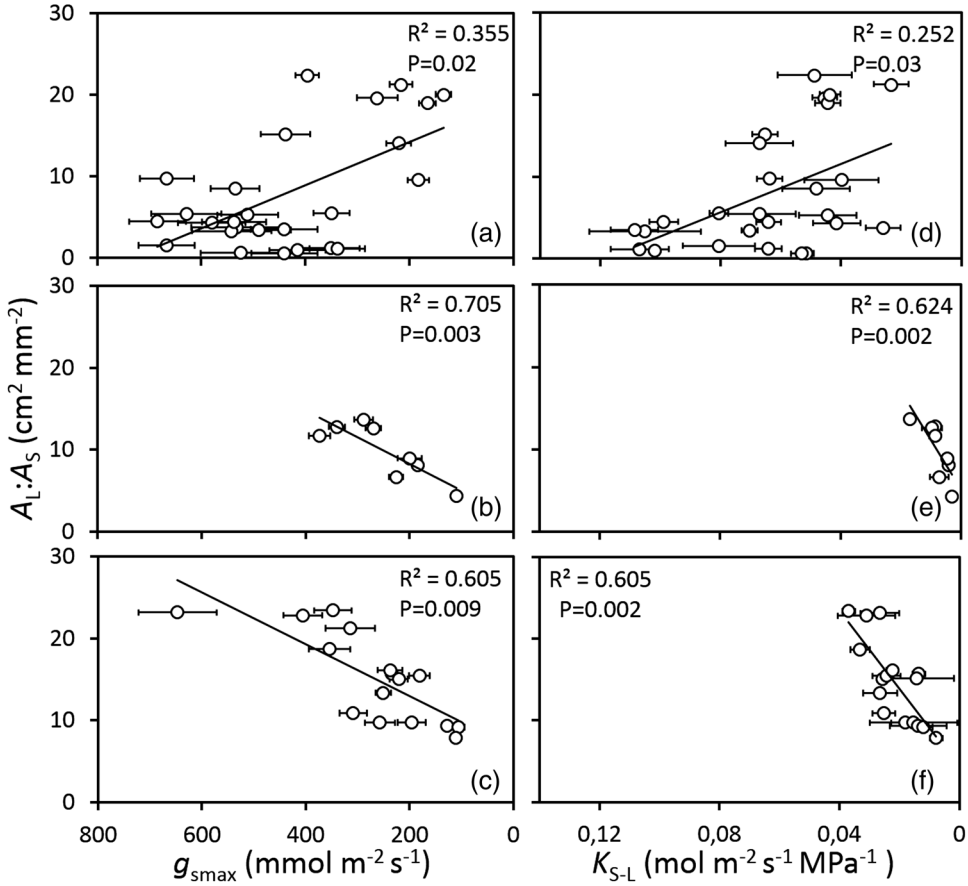

Figure 3. Ratio of leaf area to cross-sectional area of the current-year shoots $A_L : A_S$ as a function of daily maximum stomatal conductance g_{smax} (left) and soil-to-leaf hydraulic conductance K_{S-L} (right) in *G. senegalensis* in the southern Sahel in Niger in two crop fields (a and d), a young fallow (b and e) and an old fallow (c and f). The horizontal bars represent the standard error.

did not differ significantly between the two fallows (*t*-test, $P = 0.219$).

Discussion

Our findings revealed a positive correlation between biomass growth and plant water status in mature undisturbed *G. senegalensis* shrubs. Yearly cutting back decoupled this relationship and drove the current-year resprout allometry away from the WBE model predictions. In the conditions of our study in Niger, compared with undisturbed shrubs, the changes in hydraulic functioning of the *G. senegalensis*—when cut back every year—are consistent with the changes described in Mencuccini (2002) for relationships between plant size and plant hydraulic efficiency, which helped us interpret them (see below).

Scaling relationships of annual stem growth in mature shrubs were consistent with WBE model predictions

The scaling slope of the allometry between A_L and A_S we found in mature shrubs of *G. senegalensis* showed an isometric relationship, as predicted by the theoretical WBE scaling model (Enquist and Niklas 2002) and like in other species and environments. For instance, in North American forests, Brouat et al. (1998) found an isometric relationship between A_L and A_S in gymnosperms and in evergreen and deciduous angiosperms. Mature *G. senegalensis* shrubs responded to seasonal drought (when WAP declined and VPD increased) by decreasing leaf area (A_L) and by stopping the increase in the diameter of the current-year shoots with a decrease in leaf water potential and a decrease in stomatal and hydraulic conductance. Similar results were found in conifers under hydraulic constraints by Magnani et al. (2002), whose model predicted lower allocation to transpiring foliage with increasing VPD and soil drought. Devineau (1997) reported that in *G. senegalensis* and other Sahelian species, mature shrubs showed little between-season variation in their trunk diameters, confirming the relative stability of the plant's capacity to transport water we observed in the stems of mature *G. senegalensis* shrubs. In Australian *Eucalyptus* spp., Prior and Eamus (2000) reported that drought had the effect of decreasing shoot hydraulic conductance (conductivity per unit of leaf surface area), leading to the death of leaves and shoots, similar to the tendency we observed in mature *G. senegalensis* shrubs. From the outset of the rainy season, we found that *G. senegalensis* leafing was coupled with an increase in the

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Table 3. Allometric regression parameters and test for common slope and equal intercepts between two lines ($\alpha = 0.05$), dry and rainy seasons, fitted with the SMA regression in *G. senegalensis* shown in Figure 4. The slope test was used to test if the slope of SMA equals 1. $P > 0.05$ not significant, $P < 0.01$ significant and $P < 0.001$ highly significant.

	Site	Slope	Common slope	*P*	Intercept	*P*
(a) Allometry according to site						
Log (leaf area of current-year shoot) vs log (cross-sectional area of current-year shoots)	Crop field adjacent to the young fallow	2.55	2.53	0.8085	0.77	0.2532
	Crop field adjacent to the old fallow	2.52			0.73	
	Young fallow	1.10	1.21	0.0520	1.87	0.0000
	Old fallow	1.24			2.34	
	Crop field adjacent to the young fallow vs young fallow		1.81	0.0000		0.0000
	Crop field adjacent to the old fallow vs old fallow		1.81	0.0000		0.0002
Log (area of current-year shoot leaf) vs log (length of current-year shoot)	Crop field adjacent to the young fallow	2.53	2.50	0.6417	−5.37	0.2038
	Crop field adjacent to the old fallow	2.47			−5.31	
	Young fallow	0.94	0.93	0.8090	2.00	0.0000
	Old fallow	0.92			1.39	
	Crop field adjacent to the young fallow vs young fallow		2.13	0.0000		0.0000
	Crop field adjacent to the old fallow vs old fallow		1.87	0.0000		0.0000

	Site	Slope		Common slope	*P*	Intercept		*P*
		Dry season	Rainy season			Dry season	Rainy season	
(b) Allometry according to season								
Log (area of current-year shoot leaf) vs log (cross-sectional area of current-year shoots)	Crop fields	2.53	2.13	2.35	0.0005	1.15	0.97	0.0000
	Young fallow	0.98	1.11	1.04	0.3864	1.97	2.23	0.0000
	Old fallow	1.09	0.85	0.95	0.0041	2.34	2.97	0.0000
Log (area current-year shoot leaf area) vs log (length of current-year shoot)	Crop fields	2.52	1.97	2.29	0.0000	−4.35	−4.59	0.0000
	Young fallow	0.89	0.99	0.96	0.3879	1.09	1.59	0.0000
	Old fallow	0.71	0.61	0.65	0.1040	2.14	2.83	0.0000

diameter of the current-year shoots, and with an increase in stomatal and plant hydraulic conductance. In semi-arid areas in Australia, Gleason et al. (2012) also showed that high plant conductivity allowed woody plants to increase their $A_L : A_S$ ratio. Finally, in the Brazilian savanna, Gotsch et al. (2010) reported that trees that allocated more resources to sapwood had higher conductivity. However, this basic model is no longer applicable in *G. senegalensis* subjected to yearly cutting back.

Scaling relationships of current-year resprouts were not consistent with WBE model predictions

For the same shoot growth, we observed more leaf area produced than predicted by the WBE model. Leaves were clearly favored in all seasons, but particularly during the dry season, with lower leaf water potential than in mature shrubs, after the millet had been harvested when there was no longer any competition between the crop and the shrub. Cutting affects the trade-off between hydraulic safety and efficiency via changes in the morphology of aerial systems (Savage et al. 2010, Sperry et al. 2012). Substantial resources were allocated to the conductive apparatus and even more to the leaves thanks to high K_{S-L}. Ackerly (2004) also demonstrated that in chaparral woody plants, species with less negative Ψ_{DM} (lower stress) had higher $A_L : A_S$ ratios, like the *G. senegalensis* resprouts we monitored in Niger. Nardini (2002) and Cochard et al. (2005) reported strong correlations between shoot hydraulic conductance and shoot and leaf growth in several species. Winkel and Rambal (1993), Castell et al. (1994) and Cochard et al. (2005) demonstrated that the growth of woody plants depends on their ability to maintain cell turgidity, which is enhanced by hydraulic conductivity. In the *G. senegalensis* studied here, continuous leaf turgidity (low negative values of Ψ_{DM}) and high shoot conductivity enabled continuous growth (leaves and stems) decoupling allometric adjustment from hydraulic control in resprouts, unlike in mature shrubs. Cutting disturbs the plant life cycle by increasing leaf area and intensifying leaf activities during the dry season, which underlies intensive regeneration in *G. senegalensis*.

One of the most important assumptions of the WBE model is that the conducting system of the plant tapers toward the top of the tree, thereby optimizing vascular transport under environmental constraints (Enquist 2002, Petit and Anfodillo 2009, Sperry et al. 2012). We showed that the longer vessels in the current-year resprouts of *G. senegalensis* were shorter than in the mature shrubs. Bucci et al. (2009) and Hacke et al. (2006)

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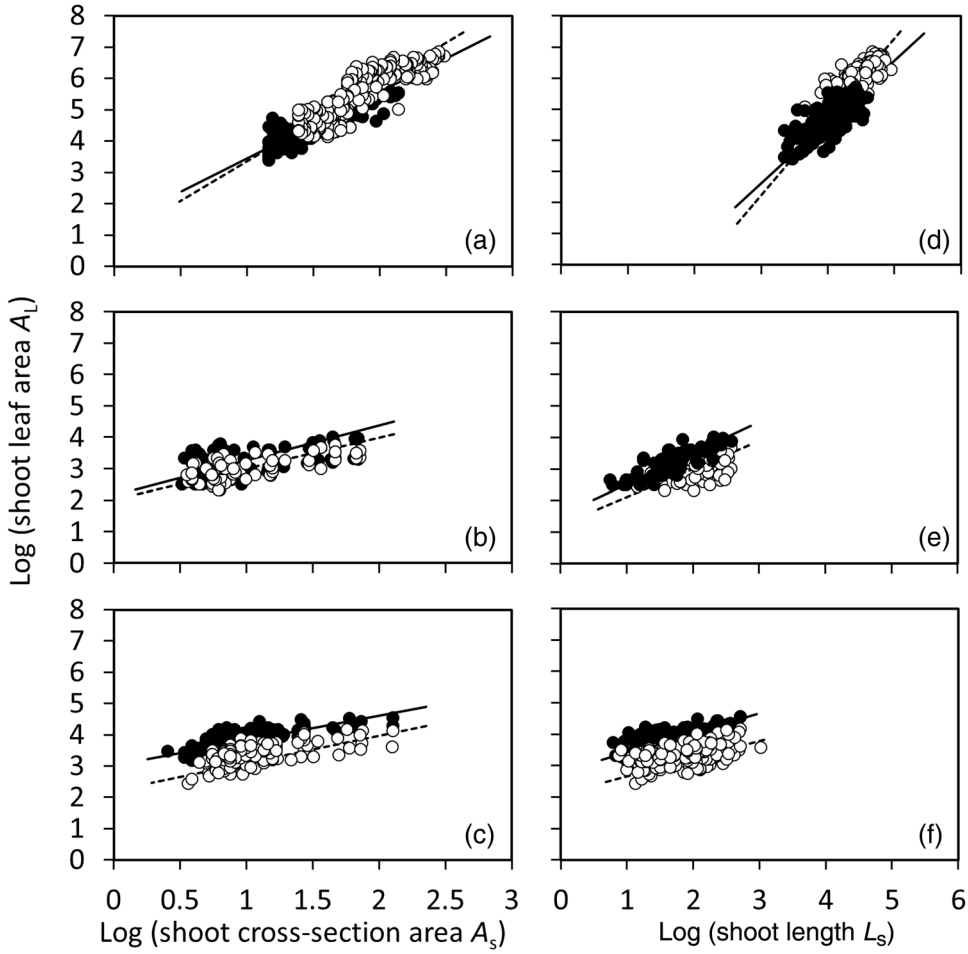

Figure 4. Allometric regressions of the leaf area A_L, cm^2 of the current-year shoot versus the cross-sectional area of the current-year shoot A_S, mm^2, (left) and versus the length of current-year shoot L_S, cm, (right) in *G. senegalensis* in the southern Sahel in Niger in two crop fields (a and d), a young fallow (b and e) and an old fallow (c and f) (rainy season: black circles and solid regression line; dry season: empty circles and dashed regression line).

Table 4. Comparison of the slopes of the SMA regressions of the stem leaf areas and cross-sectional stem areas, according to season (rainy vs dry season) and type of cover, and the slopes of the theoretical WBE model predicting a slope equal to 1. *P* is the probability that the slope of the regression is equal to 1.

Allometry	Site	Season	Slope	*P*
Log (leaf area of current-year shoot) vs log (cross-sectional area of current-year shoots)	Crop fields	Dry season	2.53	0.0000
		Rainy season	2.13	0.0000
	Young fallow	Dry season	0.98	0.8551
		Rainy season	1.11	0.3202
	Old fallow	Dry season	1.09	0.1587
		Rainy season	0.85	0.0067

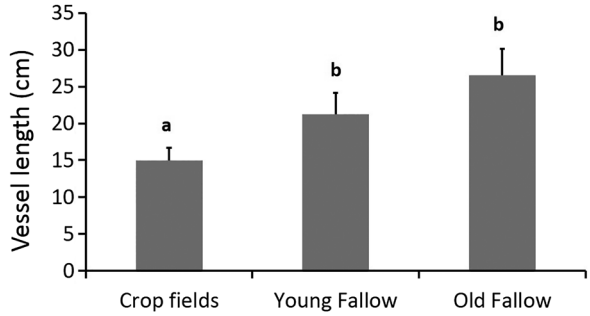

Figure 5. Average length of the longer vessels in *G. senegalensis* in the southern Sahel (Niger) in crop fields, a young fallow and an old fallow. Means followed by the same letter are not significantly different ($P < 0.05$) and the vertical bars represent the standard error.

showed that the shorter vessels also had a larger diameter, which is not consistent with the tapering of the conducting system hypothesized in the WBE model. The 'bottleneck effect' due to tapering of xylem conduits, which occurs in undisturbed shrubs and helps them minimize hydraulic resistance to bottom-up flow in new shoots and leaves regardless of path length, is compensated in resprouts by high hydraulic conductance. Consequently, the increase in the transpiration rate in resprouts enables intensive regeneration and thus explains why the scaling slope of relationship between A_L and A_S is higher than the slope predicted by the WBE model. These results confirm the hypothesis that in savannas, long-term adaptation to frequent intensive disturbance regimes—cutting for cropping as well as fire and herbivory—drives allometric scaling relationships away from

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theoretical WBE predictions (Moncrieff et al. 2011, Tredennick et al. 2013). WBE predictions are based on a theoretical tree that is not subject to disturbance or to limited resources, which supposes that vascular networks have evolved to minimize hydrodynamic resistance and to maximize the scaling of exchange surface such as leaves (West et al. 1999, Enquist 2002). To generalize the WBE model to woody plants in the Sahelian agrosystem requires taking the regeneration processes inherent to disturbance into account (Kozlowski and Konarzewski 2004).

Analysis of allometric relationships by Mencuccini (2002) showed how hydraulic functioning varied with the morphology and size of *G. senegalensis* shrubs, and explained the specific resource allocation strategy. Our results support the hypothesis that savanna woody plants that are tolerant to long-term regular cutting practices have acquired the ability to rebuild their aboveground part at the expense of optimizing resource transport (Sarmiento et al. 1985). This suggests a general trade-off between resilience to cutting and optimization of resource transport in shrubs in Sahelian agroforestry systems. Cutting modifies the overall plant structure in favor of the root system, which may help reduce the disequilibrium between aboveground and belowground parts through rapid regrowth of the aboveground system thanks to mobilization of the resources in their roots.

In the long-term, promoting hydraulic efficiency could make current-year resprouts more vulnerable to the predicted climate change than mature shrubs in fallows, which now appear to be better adapted to environments with limited resource availabilities. Previous studies in tropical forests (Coomes 2006, Muller-Landau et al. 2006) showed that variations in allometric patterns could also be linked to light limitation, competition for nutrients and other ecological drivers that modify the specific photosynthetic rate and the allocation of plant resources to growth either above or belowground. Concerning *G. senegalensis* in the Sahel, further investigation is required (i) on the role of the probable change in the root-to-shoot ratio as a result of cutting back of the shrub in the decoupling between allometric adjustment and hydraulic control when the current-year resprouts start growing, and (ii) on the role of roots in the growth of resprouts over a period of several years to determine the threshold at which the growth pattern again becomes consistent with the WBE.

Conclusion

This paper describes how cutting stimulates a major investment in vegetative regeneration in *G. senegalensis*. The decoupling of allometric adjustment from hydraulic control in shrubs that are cut back every year may be explained by the drastic change in plant structure and the rejuvenation of the canopy leading to the intensification of the water flow through the plant. This process enables intensive regrowth of their photosynthetic apparatus, driving the allometric scaling relationships away from the theoretical WBE model. The high soil-to-leaf hydraulic conductance of the current-year resprouts supported the continuous production of leaves and stems throughout the dry season, even when stomata closed in response to soil drying and to an increase in atmospheric demand. These intensive regeneration processes combined with potential evergreenness may be an adaptive strategy used by plants that have to cope with both severe seasonal drought and regular disturbance, irrespective of the type of disturbance (fire, grazing or cutting).

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Conflict of interest

None declared.

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