

# Functional groups of Sahelian trees in a semiarid agroforestry system of Senegal

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## Abstract

### Aims

Addressing plant responses to water stress is critical to understand the structure of plant communities in water-limited environments and to forecast their resilience to future changes in climate. In a semiarid agroforestry system in the Sahelian savannah of Leona (Senegal), we selected nine common tree species and explored their stress-resistance mechanisms. These species represent a variety of life forms and are of high regional socio-economic importance. We hypothesized that different species would show different suites of traits to cope with water stress and expected to identify functional groups differing in strategies to withstand water shortage.

### Methods

Along a dry and a wet season, we monitored four traits reflecting above- and below-ground strategies of resource acquisition such as predawn leaf water potential ( $\psi_{pd}$ ), specific leaf area (SLA), leaf thickness and leaf area index (LAI). We also measured two morphological traits: trunk diameter and tree height. LAI and  $\psi_{pd}$  were measured six times during the dry and rainy seasons, and the other traits were measured once.

### Important Findings

We identified two functional classes subdivided into two functional groups of each class. The first class included deciduous and semi-deciduous species that generally had large SLA, low leaf thickness and small-to-intermediate inter-seasonal variations in  $\psi_{pd}$ . The second class included evergreen species of two functional groups that differ in SLA, leaf thickness and the magnitude of inter-seasonal variations of  $\psi_{pd}$  throughout the year. The four functional groups identified in this study represent plant strategies differing in their response to changing environmental conditions.

**Keywords:** *Acacia tortilis*, *Adansonia digitata*, *Balanites aegyptiaca*, *Celtis integrifolia*, *Combretum glutinosum*, *Faidherbia albida*, functional traits, *Neocarya macrophylla*, *Sclerocarya birrea*, *Tamarindus indica*, water stress

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## INTRODUCTION

Tropical seasonally dry forests and savannahs are subjected to rainfall regimes that greatly vary in frequency and intensity across years where rainfall is unevenly distributed among seasons within a year. Therefore, water availability is one of the most limiting factors for plants in such tropical systems, influencing plant productivity and community structure across large-scale regional gradients and small-scale, topographic gradients (Ogle and Reynolds 2004). The relative success of tree species along these gradients and their fate under potential

changes in water availability will depend on the mechanisms through which they respond to water shortage (Markesteijn 2010). Research on plant responses to water stress is critically important as most climate change scenarios suggest an increase in aridity in many areas of the globe, including the tropics (Dai 2013; Diop *et al.* 2016; Petit *et al.* 1999), which may result in shifts in the composition of current plant communities and their distribution range. For instance, the severe droughts in the Sahel from the 1970s to the 1990s, followed by relatively low annual rainfall afterward (Funk *et al.* 2012), changed the ecological baselines in the region (Bell and Lamb

2006; Nicholson 2005). In fact, in this area, there are already significant declines in tree density and species richness as a consequence of increased temperature and decreased rainfall (Gonzalez *et al.* 2012).

Functional traits may result from evolutionary processes (Flores *et al.* 2014) and are used as indicators of ecophysiological function. For example, they may be used to anticipate plant responses to environmental factors (Cornelissen *et al.* 2003a; Lavorel and Garnier 2002), including water shortage (Knevel *et al.* 2005), to highlight adaptive strategies (Grime 2001), and, overall, their analysis help us explain species effects at ecosystem level (Vendramini *et al.* 2002; Wright *et al.* 2005).

Species differ in drought tolerance and associated traits (Lohbeck *et al.* 2015; Markesteijn 2010; Valladares and Sánchez-Gómez 2006). Plant sensitivity to water shortage may be evaluated through different indicators of plant physiological status, such as leaf water potential, stomatal conductance, or chlorophyll fluorescence (Armas and Pugnaire 2005, 2009; Gómez-Aparicio *et al.* 2006; Quero *et al.* 2011), and therefore, measuring key drought-resistance traits may provide powerful tools to examine interspecific responses to drought (Engelbrecht and Kursar 2003).

Such trait measurements, and the trade-offs they may show, can explain much about species performance and community composition (Poorter *et al.* 2010). Although there are many plant traits reflecting sensitivity to water stress, most studies on trait–environment linkages have focused on leaf traits (Reich 2014) as they reflect strategies of resource uptake and use. For example, species with high specific leaf area (SLA), low-density tissues and high leaf nitrogen content tend to have rapid resource capture (Poorter and Garnier 2007; Ruiz-Robledo and Villar 2005; Wright and Westoby 2001), allowing these plants to be dominant in moist and fertile areas (Grime *et al.* 1997; Reich *et al.* 1999). By contrast, species with efficient resource conservation (Chapin *et al.* 1993; Wright *et al.* 2004) minimize nutrient loss and increase their competitive abilities in dry and nutrient-poor environments (Aerts 1995; Hobbie 1992).

Plant species segregate along natural gradients of water availability according to their capacity to withstand water stress. However, species with contrasting ecological requirements coexist (Valladares and Sánchez-Gómez 2006), as in the semiarid Sahelian zone of Senegal, where evergreen and deciduous species co-occur. Such contrasted functional groups certainly reflect different strategies of the different species in a plant community to deal with water shortage (Fournier 1995), a feature that still puzzles the scientific community (Westoby *et al.* 2002).

Here, we focus on drought-resistance mechanisms in nine Sahelian tree species of high socio-economic importance for local populations. We hypothesized that (i) in the semiarid area of Sahel, different woody species will evidence trade-offs between water uptake traits and use conservation and (ii) the presence of similar water-use strategies will allow the grouping of different tree species into the same plant functional group.

## MATERIALS AND METHODS

### Study site and species

The study was conducted in the Sahelian savannah of Leona, northwest Senegal, a semiarid environment with Sub-Canarian climate (Wade 1997). It is under the influence of oceanic winds and currents that reduce the extreme seasonal contrasts of the Sudano-Sahelian climate. Therefore, this region has a smooth, atypical climate whose influence diminishes away from the coast. Between February and May, the area is dominated by the *Harmattan* (hot and dry winds) with huge sand storms and high desiccating effect. The wet monsoon season occurs between June and October with an average annual rainfall that varies between 220 and 350 mm (Gaye and Edmunds 1996), followed by a dry season between November and May. Temperatures are high during most of the year. The hottest periods generally correspond to the months of May and October. Minimum temperatures range between 22 and 28°C and maximum temperatures between 31 and 37°C (Wade 1997). However, temperatures have increased steadily since the 1950s while rainfall has decreased (Sagna *et al.* 2015), in agreement with the Intergovernmental Panel on Climate Change scenarios.

Soils are mostly sandy, little-leached ferruginous tropical soils with poor structure and usually occupied by peanut, cowpea, millet crops and grasslands. There are some areas under intensive cropping all year round, leading to impoverished soils that require large inputs of fertilizer before new crops are sowed. Nonetheless, a large proportion of the area is covered with grassland used for livestock. Being sandy soils, they have low water-holding capacity, low organic matter content and are often subject to wind erosion.

The natural landscape is a savannah where scattered big trees and shrubs grow in a matrix of a continuous herbaceous/grass species layer that thrives during the rainy season. Most woody species of this Sahelian savannah ecosystem are thorny. Harvesting of trees and shrubs, grazing, cropping and rainfall all contribute to shape the vegetation regionally (Konaté 2010). We selected nine dominant and ecologically and socio-economically important tree species with multiple uses in these areas: *Acacia tortilis* spp. *raddiana*, *Adansonia digitata* (baobab), *Balanites aegyptiaca*, *Celtis integrifolia*, *Combretum glutinosum*, *Faidherbia albida*, *Neocarya macrophylla*, *Sclerocarya birrea* and *Tamarindus indica* (Table 1).

### Plant traits

We selected four plant traits that are indicators of different functions related to resource use by the plant and are also complementary in representing water-use strategies. They were predawn leaf/twig water potential ( $\psi_{pd}$ ), SLA, leaf area index (LAI) and leaf thickness (Niinemets 2001). The  $\psi_{pd}$  provides information on plant water status as well as on its capacity to take up soil water. Its value range is species specific and depends, among others, on rooting depth, root architecture and root physiological properties (Pérez-Harguindeguy *et al.* 2013). The  $\psi_{pd}$  provides data comparable among species and

**Table 1:** selected woody species of the Sahelian zone of Senegal and habits

Species	Families	Leaves habit
<i>Acacia tortilis</i> subsp. <i>raddiana</i> (Savi) Brenan	Fabaceae	Deciduous
<i>Adansonia digitata</i> L.	Malvaceae	Deciduous
<i>Balanites aegyptiaca</i> (L.) Del.	Balanitaceae	Evergreen
<i>Celtis integrifolia</i> Lam.	Ulmaceae	Evergreen to deciduous
<i>Combretum glutinosum</i> Perr. Ex DC.	Combretaceae	Evergreen
<i>Faidherbia albida</i> (Del.) Chev.	Fabaceae	Deciduous
<i>Neocarya macrophylla</i> (sabine) Prance	Chrysobalanaceae	Evergreen
<i>Sclerocarya birrea</i> (A. Rich) Hochst	Anacardiaceae	Deciduous
<i>Tamarindus indica</i> L.	Fabaceae	Evergreen to deciduous

is less variable than midday water potential, which is affected by temperature, radiation, vapour pressure deficit and other environmental variables. Although midday water potential could make a better index of a species tolerance to water shortage, midday water potential is quite variable as hydraulic properties of highly stressed leaves and twigs may vary significantly from point to point (Koide et al. 1989; Turner et al. 1984). We used a pressure chamber (PMS Instruments, Santa Barbara, CA, USA) to measure  $\psi_{pd}$ . SLA is one of the most widely used leaf traits to analyse plant responses to the environment. SLA is strongly linked to relative growth rate and the plant resource-use strategy (Poorter and Garnier 2007) and can be used to estimate resource availability (Pérez-Harguindeguy et al. 2013). A related trait is leaf thickness, linked to leaf construction costs, leaf lifespan and gas exchange (Loranger and Shipley 2010). Leaf thickness is one of the key components of SLA. Finally, we also measured the LAI or the total leaf area of the plant per unit ground area (Jonckheere et al. 2004), with an LAI 2000 (Li-Cor Biosciences, Lincoln, NE, USA). LAI is a dimensionless index ( $m^2/m^2$ ) and reflects the capacity of the plant to intercept radiation, and LAI and  $\psi_{pd}$  may be inversely related (Bréda et al. 1995), as higher LAI means higher evaporative surface, which may lead to a decrease in  $\psi_{pd}$ . In summary, these four traits reflect plant strategies in resource capture and use. Two tree-level morphological traits, diameter at breast height (DBH) and plant height were additionally measured to control for variability associated with tree size. Trait data were collected following the protocols in Cornelissen et al. (2003b), Knevel et al. (2005) and Pérez-Harguindeguy et al. (2013).

We measured these traits in six randomly selected healthy, mature trees of each of the nine species, all growing in the field. Leaf measurements were performed on six intact, fully developed leaves from a well-lit branch (~1 cm in diameter and at least 1 m long) per individual tree. The  $\psi_{pd}$  was measured on one leaf or twig (depending on the species) per branch. LAI and  $\psi_{pd}$  measurements were carried out five times, two during

the dry season (November 2010 and April 2011) and three during the rainy season (July 2010, August and September 2011), whereas SLA and leaf thickness were measured once when leaves were at their best during the rainy season for all species except for *Faidherbia*; for this species, leaves were collected in the dry season, as it is a rainy season deciduous species. The 2010 wet season was well above average, which in July reached 230 mm, while the dry season was quite below average, with no precipitation in November 2010 and April 2011—our sampling dates. The sampling dates in the 2011 wet season (August and September) were above average.

### Data analysis

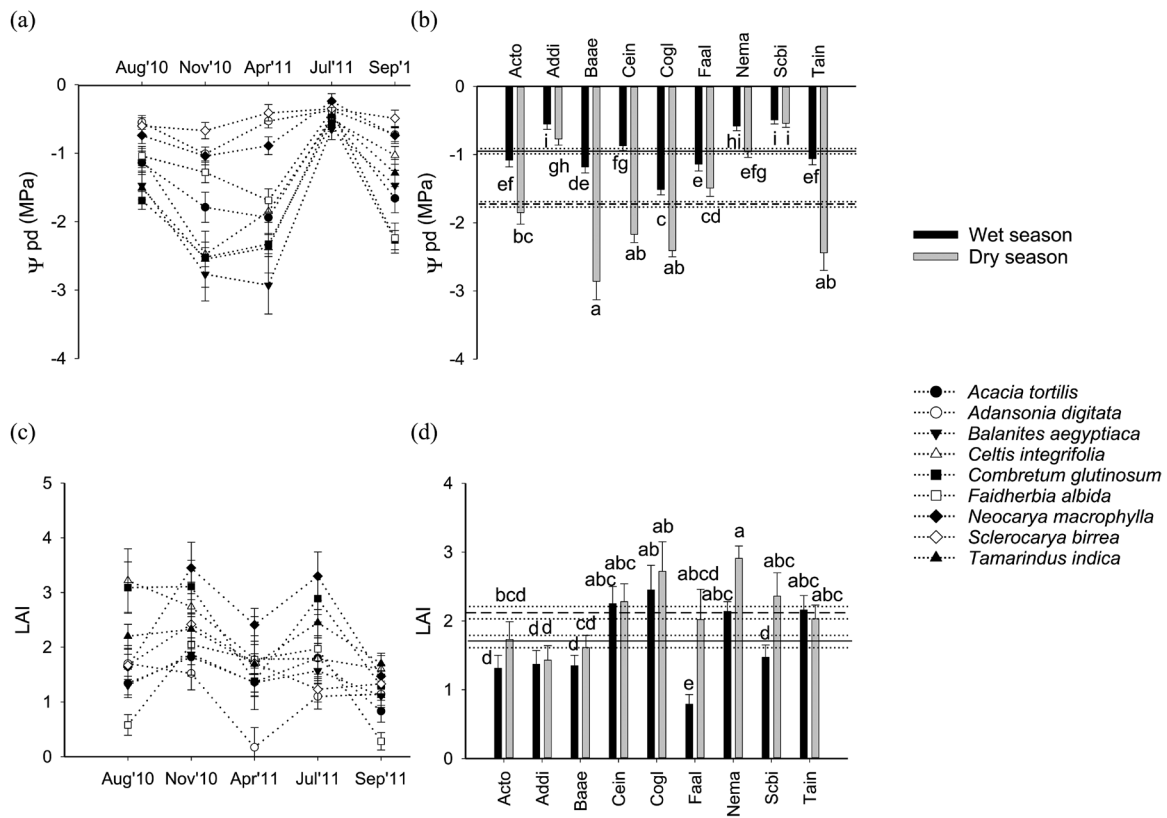
Differences in plant traits among species, seasons and months were analysed with repeated-measures general linear mixed models. Main fixed factors were species, season/month and the interaction between them. Each tree (identified with a unique ID) was the repeated-measured unit across months, and we set a compound symmetry correlational structure to account for the relation among repeated measures. We also tested several variance structures to avoid heteroscedasticity. In the case of  $\psi_{pd}$  and LAI, we selected varExp, which represents an exponential structure of a variance-covariate function structure (Galecki and Burzykowski 2013). For the other traits (SLA, thickness, DBH and height), we used varIdent, which represents a variance structure with different variances for different strata (Galecki and Burzykowski 2013). We selected the best model according to the Akaike information criterion (Akaike 1974), choosing the one with lowest value. Post hoc differences were tested with Fisher's least significant difference test. We also performed multivariate analyses (principal component analysis [PCA] and cluster analysis) of all functional traits, in order to identify groups of individuals with common functional characteristics.

Statistical analyses were performed with Infostat (Di-Rienzo et al. 2015). Reported values throughout the text and figures are means  $\pm$  1 standard error (SE).

## RESULTS

There were significant changes in the seasonal course of  $\psi_{pd}$  in most species (Fig. 1a). It was highest (i.e. less negative) for all species in July 2011, after the onset of the rainy season, where values ranged from  $-0.24$  to  $-0.65$  MPa. *Adansonia*, *Sclerocarya* and *Neocarya* showed rather steady  $\psi_{pd}$  during both the rainy and dry seasons. In most species, however, there was a decrease in  $\psi_{pd}$  during the dry season, which remained low for the whole period (Fig. 1b). We recorded important intraspecific variability in November 2010 and April 2011 (both months in the dry season), especially in *Acacia*, *Balanites* and *Tamarindus*.

Similarly, LAI changed across seasons (Fig. 1), but differences between dry and wet seasons were only significant for *Faidherbia* and *Sclerocarya*. *Faidherbia* was the only species in our data set that was deciduous during the rainy season, and it showed higher LAI values during the dry season than during



**Figure 1:** seasonal changes in  $\Psi_{pd}$  (a) and LAI (c) and mean  $\Psi_{pd}$  (b) and LAI (d) along the rainy and dry seasons of nine tree species in the Sahelian region of Senegal: *Acacia tortilis* (Acto), *Adansonia digitata* (Addi), *Balanites aegyptiaca* (Baae), *Celtis integrifolia* (Cein), *Combretum glutinosum* (Cogl), *Faidherbia albida* (Faal), *Neocarya macrophylla* (Nema), *Sclerocarya birrea* (Scbi) and *Tamarindus indica* (Tain). Data are mean values  $\pm 1$  SE,  $n = 6$ . Post hoc letters in panels (a) and (c) are not included to improve clarity (see supplementary Tables S1 and S2 for post hoc tests). Mean seasonal values shown by horizontal lines (solid, wet; broken, dry)  $\pm 1$  SE (dotted lines).

the rainy season (Fig. 2d). *Sclerocarya* showed high LAI in the dry season, likely due to a long rainy season in 2010. During the dry season, the evergreen species *Neocarya* and *Combretum* had the highest LAI. Large intraspecific variation was observed in *Adansonia* (April 2011), *Combretum* and *Celtis* in August 2010 and also in *Neocarya* (November 2010 and August 2011) (Fig. 1c).

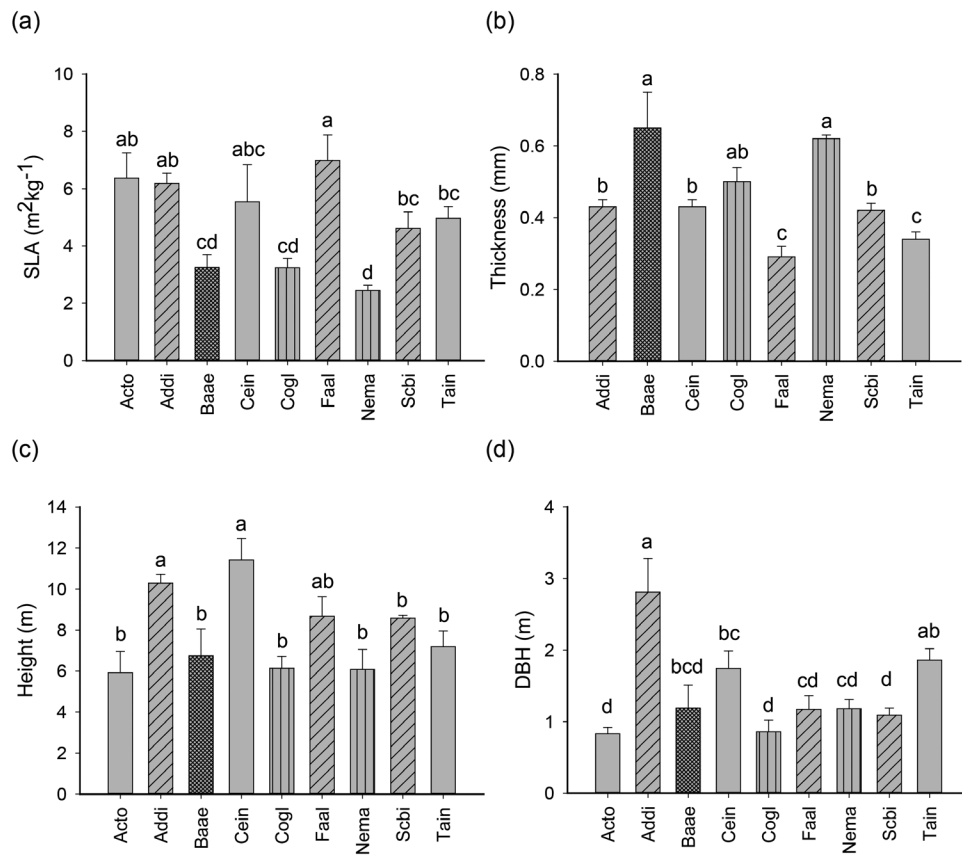
SLA differed across species, being smallest in *Balanites*, *Combretum* and *Neocarya* and highest in *Faidherbia* (Fig. 2a). Leaf thickness (Fig. 2b) also differed among species and, not surprisingly, was highest in the evergreens *Balanites*, *Neocarya* and *Combretum*, whereas it was low in the deciduous and semi-deciduous species *Faidherbia* and *Tamarindus*, the other species displaying intermediate values. Finally, the tallest (tree height, Fig. 2c) individuals were those of *Celtis* and *Adansonia*, and there was large intraspecific variation in *Balanites* and *Celtis*.

We aimed to identify functional groups according to variations in traits by PCA and performed a hierarchical clustering, both considering the following variables:  $\Psi_{pd}$ , LAI, SLA and height of all species. We excluded leaf thickness as we had no values for one species. The PCA showed that the absolute value of  $\Psi_{pd}$  (i.e. without sign) was positively correlated with LAI and inversely correlated with SLA and tree height (Fig. 3); i.e. the lower the SLA and tree height, the higher the

LAI and the absolute value of  $\Psi_{pd}$  (thus, the more negative the water potential). Thus, *Balanites* and *Combretum*, which had more negative  $\Psi_{pd}$  values than most of the species, had also low SLA. Species like *Acacia* and *Adansonia* were characterized by high SLA, while *Neocarya*, *Celtis* and *Tamarindus* showed comparatively higher LAI.

The hierarchical classification (Fig. 4) allowed us to group species into two classes with two functional groups each. The first class included deciduous and semi-deciduous species and generally had large SLA and low leaf thickness, showing small-to-intermediate inter-seasonal variations in  $\Psi_{pd}$ . This first class was split into two functional groups, the first group was formed by four deciduous species, *Acacia tortilis*, *Adansonia digitata*, *Faidherbia albida* and *Sclerocarya birrea*, while the second group only included one species, the evergreen-to-semi-deciduous *Celtis integrifolia*. The second class included all evergreen species and one semi-deciduous, all with overall low SLA, high leaf thickness and generally large inter-seasonal variations of  $\Psi_{pd}$  throughout the year. This class was also subdivided into two groups, one formed only by *Neocarya macrophylla* while the other by *Balanites aegyptiaca*, *Combretum glutinosum* and *Tamarindus indica* (this last species was the only semi-deciduous in this class).





**Figure 2:** SLA (a), leaf thickness (b), plant height (c) and DBH (d) of the nine Sahelian tree species (species legend as in Fig. 1). Data are mean values  $\pm$  SE,  $n = 6$ . Bars with different letters are significantly different (Fisher's LSD post hoc tests).

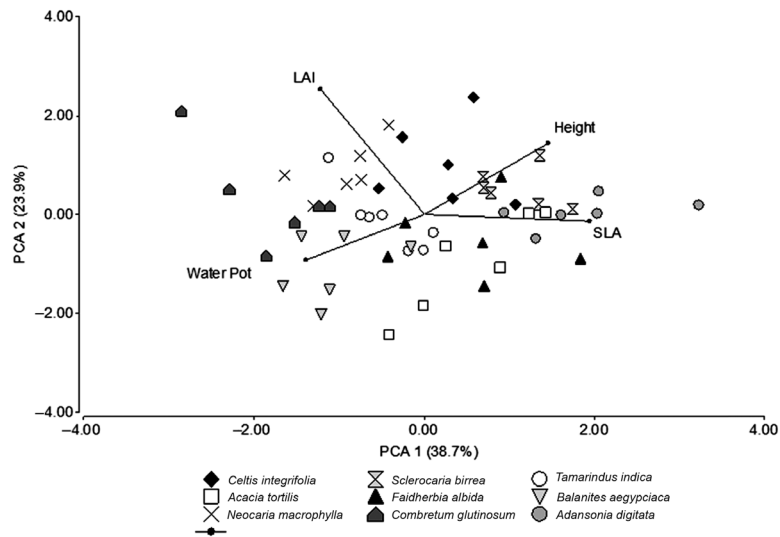
## DISCUSSION

A combination of physiological and morphological traits enabled the grouping of our nine Sahelian tree species into different functional types. This classification implies that species in the same functional group, sharing similar features, will likely display similar responses to the environment (Garnier and Navas 2012) i.e. they are 'functional response groups' (Lavorel et al. 1997). We used traits easy to monitor and quantify (Garnier et al. 2004), measured using standardized protocols (Cornelissen et al. 2003b; Knevel et al. 2005; Pérez-Harguindeguy et al. 2013), which are indicators of the mechanisms by which plants make use of water and tolerate water stress.

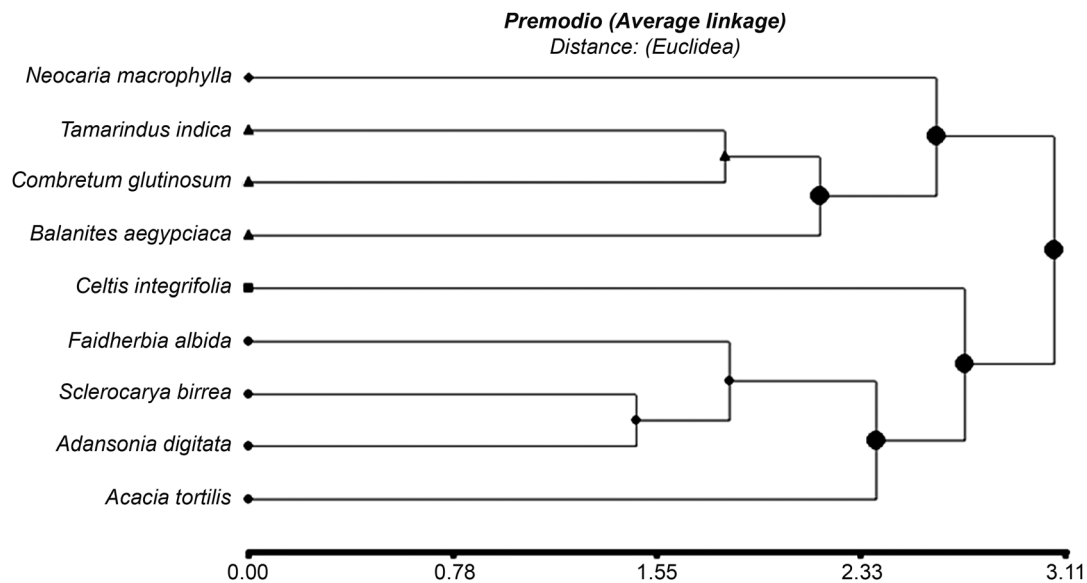
Tropical savannahs are important biomes across the world (Williams et al. 1997), with a high diversity of species and life forms in both the herbaceous and woody layers (Wilson et al. 1996). Numerous woody species in savannahs, dominant and subdominant, are drought deciduous but have developed additional strategies to cope with seasonal, chronic and erratic dry spells. Larcher (1995) described two wide groups that appear to display 'drought-avoiding' and 'drought-tolerant' strategies, and our data lend support to classifications that sort out drought avoidance and drought-tolerance strategies.

Tree species in our study avoid water stress by different means. Our analyses grouped species into two classes with two functional groups each. One of these classes could be considered as that of the water stress avoiders and, overall, included the deciduous and semi-deciduous species, which were divided into two functional groups. One group included *Acacia*, *Adansonia*, *Faidherbia* and *Sclerocarya*, all deciduous species, and another group included *Celtis* (semi-deciduous). The two functional groups decrease evaporative surfaces by shedding leaves during the unfavourable season (except *Faidherbia*), contributing to preserve water within the plant; but these species are also deep-rooted (Logan et al. 2010), which suggests access to deep water storages as a complementary measure to avoid water stress (Logan et al. 2010). In addition, these two functional groups share large SLA and generally low leaf thickness, traits associated with low leaf longevity (i.e. deciduousness) and low construction costs (Westoby et al. 2002; Flores et al. 2014) and are indicative of rapid resource capture or exploitative strategy (Flores et al. 2014).

The first functional group of water stress avoiders included the deciduous *Acacia*, *Adansonia*, and *Sclerocarya* characterized by small-to-intermediate inter-seasonal variations in water potential, suggesting that they have access to permanent



**Figure 3:** PCA of SLA, absolute value (with no sign) of  $\Psi_{pd}$ , and tree LAI and height of the nine Sahelian tree species.



**Figure 4:** cluster analysis of three physiological traits ( $\Psi_{pd}$ , SLA and LAI) of the nine Sahelian tree species (Cophenetic correlation = 0.925).

water sources. Overall, this functional group includes species that avoid water stress first by maximizing water uptake through extended root systems, except *Faidherbia*, and, when water stress accentuates, by minimizing water loss by progressively shedding their leaves, again, except *Faidherbia*. Shallow roots in *Adansonia* occupy up to 0.7 ha, while lateral roots in *Sclerocarya* extend up to 58 m (mean 40 m) and 20–25 m in *Acacia* (Breman and Kessler 1995; Soumaré *et al.* 1994). *Faidherbia*, also included in this group, has the unique character of losing its leaves in the wet season. Roupsard *et al.* (1998) proposed that this behaviour is intended to avoid competition with herbs. However, *Faidherbia*'s strategy may be better regarded as a response that provides protection against

herbivores and diseases, as some studies have suggested for other species (William and Thomas 1986). This explanation would be supported by the fact that *Faidherbia* showed high SLA, which is related to soft, less defended leaves against herbivores. *Faidherbia* thrives in the dry season based on the efficiency of its root system, able to take up water 30 m deep (Breman and Kessler 1995). As the taproots of adult *Faidherbia* individuals reach the water table, they ensure water supply all year round.

In the same group of water stress avoiders is *Acacia*, displaying a moderate inter-seasonal variation in  $\psi_{pd}$ . Many authors have characterized water relations in *Acacia* (Do *et al.* 1998; Gebrekirstos *et al.* 2011; Otieno *et al.* 2005). Its wide spatial

distribution is indicative of a remarkable adaptability to different environmental conditions that can be attributed to three basic elements: water uptake from deep soil layers, low water consumption and optimization of the ratio between assimilation and transpiration (i.e. high water use efficiency; Do *et al.* 1998). In addition, the bulk of gas exchange does occur in the rainy season where potential water losses are lower (Do *et al.* 1998). Therefore, the drought-avoidance strategy of *Acacia* is based on two mechanisms: maximization of water uptake and minimization of water loss. Both mechanisms keep turgor high and, as shown by our data, maintain relatively high water potential all year round.

Regarding *Adansonia* and *Sclerocarya*, in addition to losing their leaves under water stress, they have relatively short tap-roots (reaching depths of 2.4 m in *Sclerocarya*; Orwa *et al.* 2009) and robust lateral roots. *Adansonia* roots are relatively shallow (down to ~1.8 m) but spread out to a distance greater than the height of the tree (Fenner 1980). Robust lateral roots allow these species to explore the upper soil horizons and extract the maximum of rainwater before infiltration. Such an extensive shallow root system suggests it is adapted to exploiting erratic rainfall (February *et al.* 2013; Hodge 2010; Pugnaire *et al.* 2006). Water may be stored in the trunk and, along with leaf shedding during the dry season, enable the tree to have access to water supplies. Storage organs in *Adansonia* are large woody stems more or less lignified with succulent tissue (Arbonnier 2004). Baobab trees have long been assumed to depend on water stored in their large, swollen stems (Wickens 1983), but recent reports indicate that only a limited amount of stored water is used for physiological processes buffering daily water deficits (Chapotin *et al.* 2006b). In contrast, stem water reserves are used by the tree to support new leaf growth and cuticular transpiration, but not to support stomatal opening in the dry season (Chapotin *et al.* 2006a) since leaves are present only during the rainy season.

The second group in the class of water stress avoiders is monospecific and formed by *Celtis*, the only evergreen-to-semi-deciduous species (Arbonnier 2004). It has intermediate-to-high SLA values and the highest height along with *Adansonia*. However, it has high LAI, and water loss is minimized by a progressive loss of leaves as water stress intensity progresses (Bourou 2012; Maes *et al.* 2009). Depending on the environmental conditions where this species grows, it can show an evergreen or semi-deciduous syndrome. As Bai *et al.* (2015) described, when unfavourable conditions (temperature, water and nutrient) are relatively short, the retention of evergreen leaves in evergreen-to-semi-deciduous species is beneficial for carbon fixation. However, when unfavourable conditions become longer, the maintenance of leaves requires a vast investment of nutrients and energy for these species. Thus, a species such as *Celtis integrifolia* with high LAI under high water availability tends to have more leaves with higher SLA (Ogaya and Peñuelas 2007), which is a more efficient strategy to maximize photosynthetic gain. Under lower water availabilities, however,

*Celtis* adopts a deciduous strategy instead of investing more resources in strong, sclerophyll leaves to stand climatic adversity.

The other functional class is split into two functional groups that showed a drought-tolerance strategy by being able to maintain low leaf water potentials (Valladares *et al.* 2004). Tolerant species have tissues resistant to dehydration and xylem cavitation, show osmotic adjustment and high cell wall elasticity (Marshall and Dumbroff 1999; Pereira *et al.* 2004; Villar-Salvador *et al.* 2013). With the exception of *Tamarindus*, which is semi-deciduous, species in this class (*Balanites*, *Combretum*—Group III) and *Neocarya* (Group IV) are all evergreen, maintain high LAI all the year round and show low  $\psi_{pd}$  even during the rainy season, but particularly during the dry season, allowing high rates of light interception (Kool and Lenssen 1997). Maintaining a higher LAI, however, increases transpiration, leading to higher inter-seasonal variations in  $\psi_{pd}$  which is characteristic of this group.

During the dry season, leaf water potential decreased in all evergreen species in our study (except *Neocarya*), thereby reducing their ability to supply water to cells. Such imbalance between water provision and needs may be explained by a very high resistance to the passage of water in the soil–plant interface (Sobrado 1986). Evergreen species lose their turgor pressure at a total water potential much lower than deciduous species (Fournier 1995). Thereby, the leaf tissue of evergreen species is adapted to stand higher turgor pressure than deciduous species when the water potential decreases, although there is variability (e.g. *Balanites* and *Combretum*; Fournier 1995). The species in this group have developed several strategies to withstand water stress. *Balanites*, one of Sahelian trees with higher tolerance to water stress (Depierre and Gillet 1991), in addition to have deep root system (Hall and Walker 1991), has long spines and sclerophyllous leaves. *Tamarindus* seems the less water stress-resistant species in the group, as it reduces transpiration through a gradual loss of leaves to almost total defoliation under stressful conditions but maintains water potentials (Bourou 2012). The last functional group included only *Neocarya*, a species that experienced small  $\psi_{pd}$  variations throughout the year, with high LAI, leaf thickness and low SLA. Low SLA tend to correspond with high structural defences and long leaf lifespan (Cornelissen *et al.* 2003b; Wright *et al.* 2004), which is characteristic of a resource-conservative strategy (Flores *et al.* 2014). Indeed, *Neocarya* has leathery and hairy leaves that decrease transpiration and allow coping with water stress (Arbonnier 2004).

## CONCLUSION

Our data show that different tree species display contrasting suites of traits reflecting different mechanisms to cope with water stress even within an apparently homogeneous environment, suggesting that they evolved under different environmental conditions. Functional traits allowed us to identify

plant strategies and group species into four functional groups based on their responses to water stress. Overall, evergreen and semi-deciduous species root deeper than deciduous species and rely on deep-stored water reserves during the dry period. Changes in rainfall amount and the length of drought spells will likely be critical for these species, being the species with high LAI more sensitive to these changes. On the other hand, deciduous and semi-deciduous species cope with drought by avoiding activity in the periods of water shortage. They make a less efficient use of water and have low capacity to control water losses. Changes in the length of the wet season and of drought spells within the wet season will likely be the most critical for the persistence of these species.

## SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Plant Ecology* online.

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