

1 **Functional groups of Sahelian trees in a semiarid agroforestry system of**
2 **Senegal**

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17

18 **Abstract**

19 Addressing plant responses to water stress is critical to understand the structure of plant
20 communities in water-limited environments and to forecast their resilience to future changes in
21 climate. In a semiarid agroforestry system in the Sahelian savannah of Leona (Senegal), we
22 selected nine common tree species and explored their stress-resistance mechanisms. These
23 species represent a variety of life forms and are of high regional socio-economic importance.
24 We hypothesized that different species would show different suites of traits to cope with water
25 stress, and expected to identify functional groups differing in strategies to withstand water
26 shortage. Along a dry and a wet season we monitored four traits reflecting above- and below-
27 ground strategies of resource acquisition such as: predawn leaf water potential (Ψ_{pd}), specific
28 leaf area (SLA), leaf thickness, and leaf area index (LAI). We also measured two morphological
29 traits: trunk diameter and tree height. LAI and Ψ_{pd} were measured six times during the dry and
30 rainy seasons, and the other traits were measured once. We identified two functional classes
31 subdivided into two functional groups each class. The first class included deciduous and semi-
32 deciduous species that generally had large SLA, low leaf thickness, and small to intermediate
33 inter-seasonal variations in Ψ_{pd} . The second class included evergreen species of two functional
34 groups that differ in SLA, leaf thickness and the magnitude of inter-seasonal variations of Ψ_{pd}
35 throughout the year. The four functional groups identified in this study represent plant strategies
36 differing in their response to changing environmental conditions.

37

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

41 **Introduction**

42 Tropical seasonally-dry forests and savannahs are subjected to rainfall regimes that greatly vary
43 in frequency and intensity across years where rainfall is unevenly distributed among seasons
44 within a year. Therefore, water availability is one of the most limiting factors for plants in such
45 tropical systems, influencing plant productivity and community structure across large-scale
46 regional gradients and small-scale, topographic gradients (Ogle and Reynolds 2004). The
47 relative success of tree species along these gradients and their fate under potential changes in
48 water availability will depend on the mechanisms through which they respond to water shortage
49 (Markestijn 2010). Research on plant responses to water stress is critically important as most
50 climate-change scenarios suggest an increase in aridity in many areas of the globe, including
51 the tropics (Petit et al. 1999; Dai 2013; Diop et al. 2016) which may result in shifts in the
52 composition of current plant communities and their distribution range. For instance, the severe
53 droughts in the Sahel from the 1970s to the 1990s, followed by relatively low annual rainfall
54 afterward (Funk et al. 2012), changed the ecological baselines in the region (Nicholson 2005;
55 Bell and Lamb 2006). In fact, in this area there are already significant declines in tree density
56 and species richness as a consequence of increased temperature and decreased rainfall
57 (Gonzalez et al. 2012).

58 Functional traits may result from evolutionary processes (Flores et al. 2014) and are
59 used as indicators of eco-physiological function. For example, they may be used to anticipate
60 plant responses to environmental factors (Lavorel and Garnier 2002; Cornelissen et al. 2003a)
61 including water shortage (Knevel et al. 2005), to highlight adaptive strategies (Grime 2001),
62 and, overall, their analysis help us explain species effects at ecosystem level (Vendramini et al.
63 2002; Wright et al. 2005).

64 Species differ in drought tolerance and associated traits (Valladares and Sánchez-Gómez
65 2006; Markestijn 2010, Lohbeck et al. 2015). Plant sensitivity to water shortage may be

66 evaluated through different indicators of plant physiological status, such as leaf water potential,
67 stomatal conductance, or chlorophyll fluorescence (Armas and Pugnaire 2005; Gómez-
68 Aparicio et al. 2006; Armas and Pugnaire 2009; Quero et al. 2011) and therefore measuring key
69 drought-resistance traits may provide powerful tools to examine inter-specific responses to
70 drought (Engelbrecht and Kursar 2003).

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

81 Plant species segregate along natural gradients of water availability according to their
82 capacity to withstand water stress. However, species with contrasting ecological requirements
83 coexist (Valladares and Sánchez-Gómez 2006), as in the semiarid Sahelian zone of Senegal,
84 where evergreen and deciduous species co-occur. Such contrasted functional groups certainly
85 reflect different strategies of the different species in a plant community to deal with water
86 shortage (Fournier 1995), a feature that still puzzles the scientific community (Westoby et al.
87 2002).

88 Here we focus on drought resistance mechanisms in nine Sahelian tree species of high
89 socio-economic importance for local populations. We hypothesized that 1) in the semi-arid area
90 of Sahel, different woody species will evidence trade-offs between water uptake traits and use

91 conservation, and 2) the presence of similar water use strategies will allow the grouping of
92 different tree species into the same plant functional group.

93

94 **Materials and methods**

95 *Study site and species*

96 The study was conducted in the Sahelian savannah of Leona, northwest Senegal, a semiarid
97 environment with Sub-Canarian climate (Wade 1997). It is under the influence of oceanic winds
98 and currents that reduce the extreme seasonal contrasts of the Sudano-Sahelian climate.
99 Therefore, this region has a smooth, atypical climate whose influence diminishes away from
100 the coast. Between February and May, the area is dominated by the *Harmattan* (hot and dry
101 winds) with huge sand storms and high desiccating effect. The wet monsoon season occurs
102 between June and October with an average annual rainfall that varies between 220 and 350 mm
103 (Gaye and Edmunds 1996) followed by a dry season between November and May.
104 Temperatures are high during most of the year. The hottest periods generally correspond to the
105 months of May and October. Minimum temperatures range between 22 and 28 °C and
106 maximum temperatures between 31 and 37 °C (Wade 1997). However, temperatures have
107 increased steadily since the 50s while rainfall has decreased (Sagna et al. 2015), in agreement
108 with IPCC scenarios.

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

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

123

124 *Plant traits*

125 We selected four plant traits that are indicators of different functions related to resource use by
126 the plant, and are also complementary in representing water use strategies. They were predawn
127 leaf/twig water potential (Ψ_{pd}), specific leaf area (SLA), leaf area index (LAI) and leaf thickness
128 (Niinemets 2001). Predawn leaf water potential (Ψ_{pd}) provides information on plant water status
129 as well as on its capacity to take up soil water. Its value range is species-specific and depends,
130 among others, on rooting depth, root architecture, and root physiological properties (Pérez-
131 Harguindeguy et al. 2013). Predawn leaf water potential provides data comparable among
132 species and is less variable than mid-day water potential, which is affected by temperature,
133 radiation, vapour pressure deficit, and other environmental variables. Although mid-day
134 Ψ could make a better index of a species tolerance to water shortage, mid-day Ψ is quite
135 variable as hydraulic properties of highly stressed leaves and twigs may vary significantly from
136 point to point (Turner et al. 1984; Koide et al. 1989). We used a pressure chamber (PMS
137 Instruments, Santa Barbara, California) to measure Ψ_{pd} . Specific leaf area (SLA) is one of the
138 most widely used leaf traits to analyse plant responses to the environment. SLA is strongly
139 linked to relative growth rate and the plant resource-use strategy (Poorter and Garnier 2007),

140 and can be used to estimate resource availability (Pérez-Harguindeguy et al. 2013). A related
141 trait is leaf-thickness, linked to leaf construction costs, leaf lifespan and gas exchange (Loranger
142 and Shipley 2010). Leaf thickness is one of the key components of SLA. Finally, we also
143 measured the leaf area index (LAI), or the total leaf area of the plant per unit ground area
144 (Jonckheere et al. 2004) with a LAI 2000 (Li-Cor Biosciences, Lincoln, Nebraska, USA). LAI
145 is a dimensionless index (m^2/m^2) and reflects the capacity of the plant to intercept radiation.
146 Predawn leaf water potential and LAI may be inversely related (Bréda et al. 1995), as higher
147 LAI means higher evaporative surface which may lead to a decrease in Ψ_{pd} . In summary, these
148 four traits reflect plant strategies in resource capture and use. Two tree-level morphological
149 traits, diameter at breast height (DBH) and plant height were additionally measured to control
150 for variability associated to tree size. Trait data were collected following the protocols in
151 Cornelissen et al. (2003b), Knevel et al. (2005) and Pérez-Harguindeguy et al. (2013).

152 We measured these traits in six randomly selected healthy, mature trees of each of nine
153 species, all growing in the field. Leaf measurements were performed on six intact, fully
154 developed leaves from a well-lit branch (ca. 1 cm in diameter and at least 1 m long) per
155 individual tree. Predawn leaf water potential was measured on one leaf or twig (depending on
156 the species) per branch. Leaf water potential and LAI measurements were carried out five times,
157 two during the dry season (November 2010 and April 2011) and three during the rainy season
158 (July 2010, August and September 2011), whereas SLA and leaf thickness were measured once
159 when leaves were at their best during the rainy season for all species except for *Faidherbia*; for
160 this species leaves were collected in the dry season, as it is a rainy-season deciduous species.
161 The 2010 wet season was well above average, which in July reached 230 mm, while the dry
162 season was quite below average, with no precipitation in November 2010 and April 2011—our
163 sampling dates. The sampling dates in the 2011 wet season (August and September) were about
164 average.

165

166 *Data analysis*

167 Differences in plant traits among species, seasons, and months were analysed with repeated
168 measures general linear mixed models. Main fixed factors were species, season/month and the
169 interaction between them. Each tree (identified with a unique ID) was the repeated-measured
170 unit across months, and we set a compound symmetry correlational structure to account for the
171 relation among repeated measures. We also tested several variance structures to avoid
172 heteroscedasticity. In the case of Ψ_{pd} and LAI we selected varExp, which represents an
173 exponential structure of a variance-covariate function structure (Galecki and Burzykowski
174 2013). For the others traits (SLA, thickness, DBH and height) we used varIdent, which
175 represents a variance structure with different variances for different strata (Galecki and
176 Burzykowski 2013). We selected the best model according to the Akaike Information Criterion
177 (Akaike 1974), choosing the one with lowest value. Post-hoc differences were tested with
178 Fisher LSD test. We also performed multivariate analyses (Principal Component and Cluster
179 Analyses) of all functional traits in order to identify groups of individuals with common
180 functional characteristics.

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

183

184 **Results**

185 There were significant changes in the seasonal course of Ψ_{pd} in most species (Fig. 1a). It was
186 highest (i.e., less negative) for all species in July 2011, after the onset of the rainy season, when
187 values ranged -0.24 to -0.65 MPa. *Adansonia*, *Sclerocarya* and *Neocarya* showed rather steady
188 Ψ_{pd} during both the rainy and dry seasons. In most species, however, there was a decrease in
189 Ψ_{pd} during the dry season, which remained low for the whole period (Fig. 1b). We recorded

190 important intra-specific variability in November 2010 and April 2011 (both months in the dry
191 season), especially in *Acacia*, *Balanites* and *Tamarindus*.

192 Similarly, LAI changed across seasons (Fig. 1), but differences between dry and wet
193 seasons were only significant for *Faidherbia* and *Sclerocarya*. *Faidherbia* was the only species
194 in our dataset that was deciduous during the rainy season and it showed higher LAI values
195 during the dry season than the rainy season (Fig. 2d). *Sclerocarya* showed high LAI in the dry
196 season, likely due to a long rain season in 2010. During the dry season the evergreen species
197 *Neocarya* and *Combretum* had the highest LAI. Large intra-specific variation was observed in
198 *Adansonia* (April 2011), *Combretum* and *Celtis* in August 2010, and also in *Neocarya*
199 (November 2010 and August 2011) (Fig. 1c).

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

207 We aimed to identify functional groups according to variations in traits by principal
208 component analysis (PCA) and performed a hierarchical clustering, both considering the
209 following variables: Ψ_{pd} , LAI, SLA and height of all species. We excluded leaf thickness as we
210 had no values for one species. The PCA showed that the absolute value of Ψ_{pd} (i.e., without
211 sign) was positively correlated with LAI, and inversely correlated with SLA and tree height
212 (Fig. 3); i.e., the lower the SLA and tree height, the higher the LAI and the absolute value of
213 Ψ_{pd} (thus, the more negative the water potential). Thus, *Balanites* and *Combretum*, which had
214 more negative Ψ_{pd} values than most of the species, had also low SLA. Species like *Acacia* and

215 *Adansonia* were characterized by high SLA, while *Neocarya*, *Celtis* and *Tamarindus* showed
216 comparatively higher LAI.

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

228

229 **Discussion**

230 A combination of physiological and morphological traits enabled the grouping of our
231 nine Sahelian tree species into different functional types. This classification implies that species
232 in the same functional group, sharing similar features, will likely display similar responses to
233 the environment (Garnier and Navas 2012) i.e., they are “functional response groups” (Lavorel
234 et al. 1997). We used traits easy to monitor and quantify (Garnier et al. 2004), measured using
235 standardised protocols (Cornelissen et al. 2003b; Knevel et al. 2005; Pérez-Harguindeguy et al.
236 2013), which are indicators of the mechanisms by which plants make use of water and tolerate
237 water stress.

238 Tropical savannahs are important biomes across the world (Williams et al. 1997) with a
239 high diversity of species and life forms in both the herbaceous and woody layers (Wilson et al.

240 1996). Numerous woody species in savannahs, dominant and subdominant, are drought-
241 deciduous but have developed additional strategies to cope with seasonal, chronic and erratic
242 dry spells. Larcher (1995) described two wide groups that appear to display “drought-avoiding”
243 and “drought-tolerant” strategies, and our data lend support to classifications that sort out
244 drought avoidance and drought tolerance strategies.

245 Tree species in our study avoid water stress by different means. Our analyses grouped
246 species into two classes with two functional groups each. One of these classes could be
247 considered as that of the water stress avoiders, and, overall, included the deciduous and semi-
248 deciduous species, which were divided into two functional groups. One group included *Acacia*,
249 *Adansonia*, *Faidherbia* and *Sclerocarya*, all deciduous species, and another group included
250 *Celtis* (semi-deciduous). The two functional groups decrease evaporative surfaces by shedding
251 leaves during the unfavourable season (except *Faidherbia*) contributing to preserve water
252 within the plant; but these species are also deep rooted (Logan et al. 2010), which suggests
253 access to deep water storages as a complementary measure to avoid water stress (Logan et al.
254 2010). In addition, these two functional groups share large SLA and generally low leaf
255 thickness, traits associated with low leaf longevity (i.e., deciduousness) and low construction
256 costs (Westoby et al. 2002; Flores et al. 2014) and are indicative of rapid resource capture or
257 exploitative strategy (Flores et al. 2014).

258 The first functional group of water stress avoiders included the deciduous *Acacia*,
259 *Adansonia*, and *Sclerocarya* characterized by small-to-intermediate inter-seasonal variations in
260 water potential, suggesting that they have access to permanent water sources. Overall, this
261 functional group includes species that avoid water stress first by maximizing water uptake
262 through extended root systems, except *Faidherbia*, and, when water stress accentuates, by
263 minimizing water loss by progressively shedding their leaves, again, except *Faidherbia*.
264 Shallow roots in *Adansonia* occupy up to 0.7 ha while lateral roots in *Sclerocarya* extend up to

265 58 m (mean 40 m) and 20-25 m in *Acacia* (Soumaré et al. 1994; Breman and Kessler 1995).
266 *Faidherbia*, also included in this group, has the unique character of losing its leaves in the wet
267 season. Roupsard et al. (1998) proposed that this behaviour is intended to avoid competition
268 with herbs. However, *Faidherbia*'s strategy may be better regarded as a response that provides
269 protection against herbivores and diseases, as some studies have suggested for other species
270 (William and Thomas 1986). This explanation would be supported by the fact that *Faidherbia*
271 showed high SLA, which is related to soft, less-defended leaves against herbivores. *Faidherbia*
272 thrives in the dry season based on the efficiency of its root system, able to take up water 30 m
273 deep (Breman and Kessler 1995). As the taproots of adult *Faidherbia* individuals reach the
274 water table, they ensure water supply all year round.

275 In the same group of water stress avoiders is *Acacia*, displaying a moderate inter-
276 seasonal variation in Ψ_{pd} . Many authors have characterized water relations in *Acacia* (Do et al.
277 1998; Otieno et al. 2005; Gebrekirstos et al. 2011). Its wide spatial distribution is indicative of
278 a remarkable adaptability to different environmental conditions which can be attributed to three
279 basic elements: water uptake from deep soil layers, low water consumption, and optimization
280 of the ratio between assimilation and transpiration (i.e., high water use efficiency; Do et al.
281 1998). In addition, the bulk of gas exchange does occur in the rainy season where potential
282 water losses are lower (Do et al. 1998). Therefore, the drought-avoidance strategy of *Acacia* is
283 based on two mechanisms, maximization of water uptake and minimization of water loss. Both
284 mechanisms keep turgor high and, as shown by our data, maintain relatively high water
285 potential all year round.

286 Regarding *Adansonia* and *Sclerocarya*, in addition to losing their leaves under water
287 stress, they have relatively short taproots (reaching depths of 2.4 m in *Sclerocarya*; Orwa et al.
288 2009) and robust lateral roots. *Adansonia* roots are relatively shallow (down to ca. 1.8 m), but
289 spread out to a distance greater than the height of the tree (Fenner 1980). Robust lateral roots

290 allow these species to explore the upper soil horizons and extract the maximum of rainwater
291 before infiltration. Such an extensive shallow root system suggests it is adapted to exploiting
292 erratic rainfall (Pugnaire et al. 2006; Hodge 2010; February et al. 2013). Water may be stored
293 in the trunk and, along with leaf shedding during the dry season, enable the tree to have access
294 to water supplies. Storage organs in *Adansonia* are large woody stems more or less lignified,
295 with succulent tissue (Arbonnier 2004). Baobab trees have long been assumed to depend on
296 water stored in their large, swollen stems (Wickens 1983) but recent reports indicate that only
297 a limited amount of stored water is used for physiological processes buffering daily water
298 deficits (Chapotin et al. 2006b). In contrast, stem water reserves are used by the tree to support
299 new leaf growth and cuticular transpiration, but not to support stomatal opening in the dry
300 season (Chapotin et al. 2006a) since leaves are present only during the rainy season.

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

314 strategy instead of investing more resources in strong, sclerophyll leaves to stand climatic
315 adversity.

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

326 During the dry season leaf water potential decreased in all evergreen species in our study
327 (except *Neocarya*), thereby reducing their ability to supply water to cells. Such imbalance
328 between water provision and needs may be explained by a very high resistance to the passage
329 of water in the soil-plant interface (Sobrado 1986). Evergreen species lose their turgor pressure
330 at a total water potential much lower than deciduous species (Fournier 1995). Thereby, the leaf
331 tissue of evergreen species is adapted to stand higher turgor pressure than deciduous species
332 when the water potential decreases, although there is variability (e.g., *Balanites* and
333 *Combretum*; Fournier 1995). The species in this group have developed several strategies to
334 withstand water stress. *Balanites*, one of Sahelian trees with higher tolerance to water stress
335 (Depierre and Gillet 1991), in addition to have deep root system (Hall and Walker 1991) has
336 long spines and sclerophyllous leaves. *Tamarindus* seems the less water stress-resistant species
337 in the group, as it reduces transpiration through a gradual loss of leaves to almost total
338 defoliation under stressful conditions, but maintains water potentials (Bourou 2012). The last

339 functional group included only *Neocarya*, a species which experienced small Ψ_{pd} variations
340 throughout the year, with high LAI, leaf thickness and low SLA. Low SLA tend to correspond
341 with high structural defences and long leaf lifespan (Cornelissen et al. 2003b; Wright et al.
342 2004), which is characteristic of a resource conservative strategy (Flores et al. 2014). Indeed,
343 *Neocarya* has leathery and hairy leaves that decrease transpiration and allow coping with water
344 stress (Arbonnier 2004).

345

346 **Conclusion**

347 Our data show that different tree species display contrasting suites of traits reflecting different
348 mechanisms to cope with water stress even within an apparently homogeneous environment,
349 suggesting that they evolved under different environmental conditions. Functional traits
350 allowed us to identify plant strategies and group species into four functional groups based on
351 their responses to water stress. Overall, evergreen and semi-deciduous species root deeper than
352 deciduous species, and rely on deep-stored water reserves during the dry period. Changes in
353 rainfall amount and the length of drought spells will likely be critical for these species, being
354 the species with high LAI more sensitive to these changes. On the other hand, deciduous and
355 semi-deciduous species cope with drought by avoiding activity in the periods of water shortage.
356 They make a less efficient use of water and have low capacity to control water losses. Changes
357 in the length of the wet season and of drought spells within the wet season will likely be the
358 most critical for the persistence of these species.

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594

595

596 Table 1. Selected woody species of the Sahelian zone of Senegal and habits

597

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 macrophyla</i> (sabine) Prance	Chrysobalanaceae	Evergreen
<i>Sclerocarya birrea</i> (A. Rich) Hochst	Anacardiaceae	Deciduous
<i>Tamarindus indica</i> L.	Fabaceae	Evergreen to deciduous

598

599

600 FIGURE LEGENDS

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

609

610 Figure 2. Specific Leaf Area (SLA) (a), leaf thickness (b), plant height (c) and Diameter at
611 Breast Height (DBH) (d) of the nine Sahelian tree species (species legend as in Figure 1).
612 Data are mean values \pm SE, n=6. Bars with different letters are significantly different (Fisher
613 LSD post-hoc tests).

614

615 Figure 3. Principal Component Analysis (PCA) of SLA, absolute value (with no sign) of
616 predawn leaf water potential (Ψ_{pd}), and tree LAI and height of the nine Sahelian tree species.

617

618 Figure 4. Cluster analysis of three physiological traits (predawn leaf water potential (Ψ_{pd}),
619 specific leaf area (SLA) and Leaf Area Index (LAI)) of the nine Sahelian tree species
620 (Cophenetic correlation = 0.925).