1 FUNCTIONAL RESPONSES OF FOUR SAHELIAN TREE SPECIES TO

2 RESOURCE AVAILABILITY

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20   **Abstract**

21   Plants experience a fluctuating environment in time and space that affects resource supply.

22   As human impacts on the environment directly and indirectly alter resource availability, it is

23   important to address plant responses to changing resources to be able to anticipate impacts of

24   these changes on plant communities. We analyzed plant traits to assess responses to resource

25   limitation in four Sahelian tree species of wide ecological and socio-economic importance.

26   We used species already adapted to harsh conditions (high temperatures, low rainfall) to

27   anticipate how climate change could affect their growth patterns and, indirectly, their spatial

28   distribution and the services they provide. Seedlings grew under two levels of water and

29   nutrient additions in a factorial design. Our results showed differences among species,

30   watering regimes, and nutrient supply in three key functional traits related to the plant's

31   resource-use strategy, relative growth rate (RGR), root-to-shoot ratio (R/S), and specific leaf

32   area (SLA). On average, RGR was responsive to the amount of water and nutrients, with

33   species with high RGR showing the largest response to resource supply. RGR in the species

34   with a conservative resource-use strategy (evergreen leaves, lowest RGR) remained

35   unchanged with different levels of water and nutrients. Overall, large RGR was supported by

36   large SLA. All species allocated more biomass to roots than to shoots, particularly under low

37   resource supply, reflecting adaptive strategies to keep RGR leveled to resource supply. Not

38   all species showed similar plasticity in their functional traits responses; however, *Acacia*

39   *tortilis* and *Faidherbia albida* showed the greatest plasticity, which may explain their large

40   geographical distribution range in Africa. Our data suggest that the different Sahelian species

41   will respond differently to future environmental changes, likely affecting their geographical

42   distribution, the structure of plant communities, and the services they provide.

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44   **Keywords**: Plant functional traits, phenotypic plasticity, Relative growth rate, Root-to-shoot

45   ratio, specific leaf area, resource-use strategies, water and nutrient availability.

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1. Introduction

Climate alterations over the last decades may be already responsible for changes in tree species ranges (Song et al., 2016) and warming and altered precipitation patterns may profoundly alter savannas worldwide (Volder et al., 2013). Future climate projections predict severe droughts in the African savanna (Boko et al., 2007; Brooks, 2004) and the Sahel is expected to experience a combination of increased temperatures and modified precipitation regimes, which will intensify seasonal droughts (MacCracken et al., 2003; Pope et al., 2000; Wetherald and Manabe, 1995) potentially altering the function, growth, and distribution of plant functional groups (Hungate et al., 2002; Knapp et al., 2008a, b). Since drought tolerance ability is one of the strongest predictors of tree species distribution in seasonally-dry tropical environments (Box, 1995; Condit et al., 2013), understanding differences in plant adaptive responses to resource availability is important to better understand possible outcomes of these changes (Cuni-Sanchez et al., 2011; Garnier et al., 2018; Lang et al., 2018).

Seedlings are the most vulnerable stage of the plant life cycle, being particularly sensitive to water limitation during drought (Chaturvedi et al., 2013; Khurana and Singh, 2001; Montgomery and Chazdon, 2002; Padilla and Pugnaire 2007; Yavitt and Wright, 2008). Seedling survival is strongly dependent on the severity of drought, as water stress is the main factor affecting seedling mortality in dry environments (Comita and Engelbrecht, 2009; Engelbrecht et al., 2005; Pugnaire et al., 2006; Slot and Poorter, 2007). Watering experiments in tree species of tropical moist forests also reveal that water availability controls species seasonal growth patterns and that drought stress limits seedling growth rates (Engelbrecht et al., 2006; Engelbrecht and Kursar, 2003; Paine et al., 2008; Yavitt and Wright, 2008). Hence, assessing seedlings responses to water availability, and how they modify their traits, will help understand the long-term response of forest species to

72   environmental change (Capers et al., 2005; Jump et al., 2007; Pedersen, 1998; Peñuelas et al.,

73   2007).

74   Further, understanding the role of plasticity in response to resource availability will

75   bring insights into plant growth and persistence of species in their current environments

76   under novel conditions (Nicotra et al., 2010). While drought is acknowledged as a crucial

77   climatic factor that would likely undermine tree survival in the future (Allen and Breshears,

78   1998; Hanson and Weltzin, 2000), progressive drought-induced stress is a non-linear process

79   largely dependent on the interaction between temperature and water availability, and to

80   plants' adaptability to higher temperatures in terms of morphology and physiology (Adams et

81   al., 2009). The ability of plant species to cope with environmental change will depend on the

82   capacity to adapt physiological and other functional responses to these changes; but, for an

83   effective prediction of the capacity of populations to persist in a certain environment,

84   empirical studies that aim to assess intra-specific response variability under controlled

85   environmental conditions are necessary. Therefore, examination of trait variability in

86   heterogeneous environments that reflect population-level responses to the environment can

87   provide deeper insights into how species might respond to future environmental changes

88   (Oke and Wang, 2015). In addition, identifying trade-offs that underlie the diversity of a

89   species' morphology and function is important because trade-offs constrain demographic

90   change rates and their linkages to ecosystem processes (Díaz et al., 2016; Shipley et al.,

91   2016).

92   Growth rate is a prominent indicator of plant strategies that deals with environmental

93   stress and disturbance (Pérez-Harguindeguy et al., 2013), and substantial volume of theory

94   and data support the correspondence between functional traits and growth rate (Hunt and

95   Cornelissen, 1997; Reich et al., 1998; Shipley, 2006). However, variation in individual-level

96   access to resources can cause trait correlations within species to differ from inter-specific

97   correlations (van Noordwijk and de Jong, 1986) due to phylogenetic constraints.

98   Here we analyzed functional responses of seedlings to simultaneous effects of

99   moisture stress and nutrient variability in four Sahelian tree species of wide ecological and

100   socio-economic importance. Target species were selected as representative of functional

101   groups of the highly diverse agroforestry ecosystems in the Sahel (Diémé et al., 2018). We

102   linked RGR and biomass allocation patterns with functional traits deemed relevant to plant

103   persistence (Kleyer et al., 2008). We addressed responses in relative growth rate (RGR), root-

104   to-shoot ratio (R/S) and specific leaf area (SLA) of seedlings growing under two levels of

105   water and nutrient availability in a full factorial greenhouse experiment and explored

106   potential trade-offs among traits. We hypothesize that 1) RGR will increase with resource

107   supply but the magnitude of the response will depend on resource use strategies (Grime et al.,

108   1997). We expected that 2) fast-growing species, i.e. with exploitative strategy, will show

109   high RGR under high water and nutrient supply, but RGR will decline strongly with low

110   resource supply levels; in contrast, 3) plants with conservative resource-use strategy will have

111   a less plastic response to changes in water and nutrient supply, i.e., stable RGR regardless

112   resource levels, with more biomass allocated to roots at low levels of water and nutrient

113   supply (Meier et al., 2018). And 4) SLA, a trait strongly associated to the plant resource-use

114   strategy, will respond in parallel to RGR.

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116   **2. Methods**

117   A greenhouse experiment was established in 2012–2013 at the University of Almería (36º 50'

118   N, 2º 27' W), Spain using four Sahelian tree species, two dry-season deciduous species,

119   *Acacia tortilis* (Savi) Brenan and *Adansonia digitata* L., one wet-season deciduous species

120   (*Faidherbia albida* (Del.) Chev.), and one evergreen species, *Tamarindus indica* L. Seeds of

121   these species were obtained in Senegal (PRONASEF, Senegal National Project of Forestry

122   Seeds, Dakar) and subjected to a pre-germination treatment using concentrated sulfuric acid

123   for 10 min (*T. indica*), 60 min (*A. tortilis* and *F. albida*) and 12 h (*A. digitata*). Seeds of each

124   species were harvested in the same area so that their mother plants were subjected to the same

125   environmental (soil and climatic) conditions. Two seeds per species were sown in a sand and

126   vermiculite mixture (1:1 in volume) in 50 cm long, 10 cm wide PVC tubes and thinned to one

127   after germination. Plants were watered every morning and received fertilizer (commercial

128   NPK fertilizer [Mg-S]; 19-19-19 [2-8]) once a month between November 2012 and March

129   2013, just before the experiment started. In March 2013, treatments were set in a factorial

130   design with nutrient (low and high nutrient supply) and water (low and high level of

131   watering) as factors (2 × 2 factorial design; n = 6–9 plants per treatment and species). At the

132   start of the experiment, plant size differed depending on the species. It was <5 cm in *A.*

133   *albida, A. digitata*, and *T. indica,* and <15 cm in *F. albida*. Half the plants per species

134   received a high nutrient solution (N+) of 0.5 g fertilizer per liter of water, and the other half

135   received a low nutrient solution (N-; 0.05 g of fertilizer per liter of water). In addition, half of

136   the plants were watered once a week with 100 ml (low water supply; W-) and the other half

137   was watered twice a week with 100 ml each time (high water supply; W+, 200 ml of water

138   per week). So, four treatments were established according to nutrient and water regime,

139   W+N+, W+N-, W-N+, and W-N-. Treatments were applied for four months and pots were

140   randomly redistributed in the greenhouse once a month. Temperature within the greenhouse

141   ranged 16–22ºC during the course of the experiment, with natural daylight length (10.30 to

142   14 hours of light).

143   At harvest, nine months after sowing, plants were sorted into above- and below-

144   ground parts, and the aboveground parts were subdivided into leaves and stem. Plant parts

145   were dried at 70 ºC for 48 h and weighed. Plant traits were calculated following standard

146   protocols (Pérez-Harguindeguy et al., 2013). In brief, six fully expanded and undamaged

147   leaves per plant were scanned with a flatbed scanner to determine the Specific Leaf Area

148   (SLA; the ratio of leaf area to dry mass). Total Plant Biomass (TPB) was obtained by adding

149   the dry mass of the different plant parts. Root-to-Shoot ratio (R/S) was calculated by dividing

150   root mass by shoot mass. Relative growth rate was estimated as $RGR = (\ln TPB_2 - \ln$

151    $TPB_1)/(t_2 - t_1)$, where t is the elapsed time in days between sowing (t_1) and harvest (t_2). To

152   calculate TPB_1, we selected 10 seeds per species, extracted and dried the embryos in an oven

153   for at least 72 h at 70 ºC, and weighed their dry mass with a precision balance (to 10^{-6} g). We

154   used the mean TPB_1 value per species. We also recorded plant height (measured with a ruler

155   to 0.1 cm).

156   The effect of water and soil nutrient addition on plant functional traits (RGR, SLA,

157   R/S, biomass, plant height, and allocation patterns) was analyzed with general linear models

158   including a full-factorial design. Fixed-factors were species (as we were interested in inter-

159   specific responses of species belonging to different functional groups; Dieme et al., 2018),

160   nutrient addition (low and high level), and watering (low and high level) and the interaction

161   across factors. Assumptions of normal distribution of residuals and homogeneity of variances

162   were tested and met. Differences in means across treatment levels were analyzed with

163   Fisher's least significance difference (LSD) post-hoc test. Statistical analyses were conducted

164   in R (R Development Core Team, 2013) using the interface implemented in InfoStat-

165   Statistical Software (Di-Rienzo et al., 2013). Reported values throughout the text and figures

166   are means ±1 standard error.

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3. Results

There were differences in RGR, R/S and SLA among species in response to water and nutrient addition regimes (Table 1). There were significant differences in RGR among all species; RGR was greatest in *Acacia tortilis* and lowest in *Tamarindus indica* (Fig. 1). All species increased RGR with water supply except *T. indica* (significant species × water interaction, Table 1), whose RGR remained unchanged irrespective of water and nutrient addition. Growth of the other 3 species reacted similarly to both water and nutrient availability, and RGR in the two extreme treatments (W+N+ *vs*. W-N-) were always different (higher with higher resource supply) regardless of species. RGR response at intermediate resource supply (W+N- or W-N+) was in between above extreme treatments (Fig. 1).

>>insert Table 1 here

>>insert Fig. 1 here

SLA varied among species as well (Table 1), being greatest in *Adansonia digitata* (Fig. 2). SLA responded similarly to the addition of nutrient and water in all species; i.e., there were no significant interaction Species × N; Species × W or Species × N × W (Table 1).

>>insert Fig. 2 here

All species had, on average, R/S values above 1 (Fig. 3), meaning they allocated more biomass to roots than to aboveground parts (Fig. 4). There were significant differences in R/S among species, and R/S allocation responded also to the nutrient and water levels (Table 1). R/S generally increased as resources became limiting (Fig. 3), and the significant interaction N × W indicated that allocation to roots or shoots responded non-additively to nutrient and water levels (i.e., significantly lower and higher responses than average in W-N- and W+N+ treatments). At the same time, R/S responses to nutrient and water levels depended on the

species (significant interaction S × N and S × W; Table 1). The highest differences in R/S response to the treatments was observed in *F. albida,* whereas R/S in *T. indicus* remained unchanged regardless treatment (Fig. 3). Overall, *A. tortilis* and *F. albida* were the most responsive species to differences in water supply (i.e., differences in R/S were greatest between W- and W+ treatments). However, R/S values are size-dependent and therefore change with plant size. To check whether it was the case we compared the slopes of ln root vs ln shoot among treatments within a species (Fig. 1.A). We found that there was true plasticity (*e.g.,* McCarthy and Enquist 2007) only in *Adansonia digitata*, but *Faidherbia albida* showed plasticity with respect to watering treatments.

>>insert Fig. 3 here

>>insert Fig. 4 here

Nutrient levels affected different morphological traits (Table 2). Plants in the high nutrient treatment were taller and had higher shoot and leaf mass than plants in the low nutrient treatment except *T. indica*, but there was no effect of nutrient regime on root mass of the different species (Table 2). Hence, plant size in general was much larger in the high-nutrient treatment (Table 2) except for *T. indica*. Water also had a significant effect on plant size. Low water availability decreased overall plant height and mass (Table 3). Total plant mass was much higher in the high-water regime (Table 3), except in *A. digitata* and *T. indica*. Overall, *T. indica* was the only species that did not show a significant response in biomass or allocation patterns in response to nutrient or water addition (Fig. 4).

>>insert Table 2 here

>>insert Table 3 here

4. Discussion

215

216   The four Sahelian tree species in our study differed significantly in RGR, and as
217 expected, plant size and growth rate responded positively and consistently to both nutrient
218 and water levels (Cornelissen et al., 1998), although the response to water levels was species-
219 specific (significant interaction S × W). RGR was significantly higher when both resources
220 were high compared to low, in agreement with published reports (e.g., Poorter, 1989). In
221 general, species maintained a RGR ranking across resource availability levels, i.e. *A. tortilis,*
222 *F. albida, A. digitata* and *T. indica* showed highest to lowest RGRs regardless of resource
223 supply. *Acacia tortilis* maintained high RGR under all treatments except with the lowest
224 levels of nutrient and water supply, while RGR in *T. indica* remained unchanged
225 notwithstanding nutrient and water levels. These results support our prediction of a larger
226 plasticity in response to varying levels of water and nutrient supply in species with high RGR
227 (resource exploitative strategy) and low plastic capacity in species with low RGR
228 (conservative resource strategy). Our results are also indicative that maintaining an optimal
229 RGR (i.e., according with environmental conditions) seems to be an important plant strategy
230 irrespective of resource supply level, since high RGR is critical for plants to grow and occupy
231 space, both below- and above-ground, to get a larger share of resources (Grime, 1998; Ruiz-
232 Robleto and Villar, 2005). All species except *T. indica* are deciduous species and show RGR
233 values between 0.005 and 0.023 g g^{-1} d^{-1}, which is a rather high range compared to tree
234 species from other dry environments (Atta et al., 2012; Hoffmann and Franco, 2003; Lamers
235 et al., 2006). Overall, species with high RGR generally have high rates of photosynthesis and
236 respiration per unit mass, requiring high nutrient levels to sustain such physiological activity
237 and high leaf turnover. Slow-growing species show opposite patterns (Reich et al., 1997;
238 Wright et al., 2004). In contrast to the deciduous species in our study, the evergreen *T. indica*

239   did not respond to resource addition. It is a slow-growing species (Diallo et al., 2008; El-

240   Siddig et al., 2006) native to dry, subtropical environments and may have, over evolutionary

241   time, adjusted a low resource demand to a low supply to avoid exhausting limiting resources.

242   This way the low RGR is closer to its optimum (Chapin, 1980; Grime and Hunt, 1975). The

243   lack of a stronger response of species with a resource exploitative strategy to resource

244   shortage indicates the presence of trade-offs between traits and with biophysical constraints

245   that result in convergence of resource acquisition strategies (Reich, 2014).

246   The RGR is a product of net assimilation rate (NAR) and leaf area ratio (LAR)

247   (Evans, 1972). LAR in turn can be partitioned into specific leaf area (SLA) and leaf mass

248   ratio (LMR), or the dry mass of leaves relative to total plant dry mass. Most studies show that

249   LAR is the factor that best explains differences in RGR, and the most important component

250   of LAR is SLA (Antúnez et al., 2001; Hoffmann and Franco, 2003; Ruiz-Robleto and Villar,

251   2005) further reflecting a trade-off in plant resource-use strategy tightly coupled to resource

252   availability (Grime et al., 1997). In our experiment, SLA differed among species and across

253   water and nutrient supply levels (Coley et al., 1985; Evans, 1972; Lavorel and Garnier,

254   2002). Therefore, changes in RGR paralleled variations in SLA, suggesting that SLA was a

255   key factor sustaining RGR (Poorter and Garnier, 2007).

256   Biomass allocation patterns vary among species and are sensitive to environmental

257   clues (Atkin et al., 2006). Many reports have shown that drought influences allocation

258   patterns (Ledo et al., 2018; Liu and Stützel, 2004; Poorter et al. 2015; Spollen et al., 1993)

259   particularly R/S values (Poorter et al., 2012; Turner, 1997). Plants with a higher allocation to

260   roots can compete more effectively for soil resources while those with a higher proportion of

261   shoots can collect more radiation (Bloom et al., 1985; Tilman, 1988). In our experiment, R/S

262   values were generally well above 1 irrespective of the species, suggesting a genetically-fixed

263   higher biomass allocation to roots in saplings of species adapted to infertile environments

264   (Aerts and Chapin, 2000; Chapin, 1980; Lambers et al., 2008) or with severe water shortage

265   (Fernández and Reynolds, 2000; Lambers et al., 2008; Padilla et al., 2009; Wright and

266   Westoby, 1999). Since initial growth is an important life history trait, critical for plant

267   survival and establishment in water limited environments, we expect traits in early

268   ontogenetic stages to contribute significantly to the species' adaptive capacity. It is worth to

269   note that R/S changes with plant development, as seedlings allocate more biomass to roots

270   (Gedroc et al., 1996), and therefore our results may be consequence of differences in plant

271   size (Husáková et al., 2018). In our dataset, however, there was true plasticity (*sensu* Weiner,

272   2004) in *Adansonia digitata* and *Faidherbia albida* showed plasticity with respect to watering

273   treatments. Therefore, we can say that, for these species, the differential allocation to roots

274   can be interpreted as a strategy response to water limitation (Ledo et al., 2018). R/S was

275   highest in *F. albida*, reaching a value of 4 under low water and nutrient levels and reflecting

276   its ability to strongly alter allocation patterns. It fact, *F. albida* is a species very sensitive to

277   drought (Roupsard, 1997) and its ability to quickly reach deeper, moist soil horizons may be

278   critical in coping with drought at such an early stage, as has been shown for other woody

279   species in dry conditions (Padilla and Pugnaire, 2007). Opposite to its dramatic response

280   concerning R/S, RGR did not change much in *F. albida*, and SLA tended to decrease only

281   under reduced water, but high N availability.

282   In our experiment, R/S in baobab *(A. digitata)* responded to N addition but only when

283   water was added. This may be because, while adult baobab trees accumulate water in their

284   stem, baobab seedlings use the taproot as main storage organ (Wickens and Lowe, 2008)

285   allocating more resources to belowground structures than adults (Cuni-Sanchez et al., 2011),

286   particularly when water is limiting. A similar strategy has also been observed in other tropical

287 tree species (Poorter and Markesteijn, 2008). Given the importance of the taproot for seedling

288 survival under dry spells (Padilla and Pugnaire, 2007; Poorter and Markesteijn, 2008),

289 seedlings with relatively larger taproots have a higher chance of survival in drought-prone

290 regions than seedlings with relatively smaller taproots, because they can store both more

291 water and carbohydrates (Kabeya and Sakai, 2003) and keep the root in contact with moist

292 soil horizons (Padilla and Pugnaire, 2007).

293   A characteristic of plants in arid environments such as the Sahelian savanna is to

294 show high temporal and spatial variation in growth patterns, which depends on environmental

295 variability, particularly soil moisture (Abdelrahman and Krzywinski, 2008). Leaf habit, i.e.

296 whether a species is evergreen or deciduous, has been linked to divergent plant strategies in

297 seasonal climates (Markesteijn and Poorter, 2009; Tomlinson et al., 2012) as the Sahel.

298 Deciduous species may allocate more resources to roots than evergreen species in any

299 seasonal environment, defining distinct biomass partitioning patterns between leaf habits

300 (Espelta et al., 2005). Within our species, *F. albida* and *A. tortilis* showed high plasticity in

301 their functional traits responses allowing them to cope with water and nutrient variability,

302 which may be a reason behind their large geographical spread in Africa, as they are able to

303 cope with contrasted supply levels of water and nutrients.

304

305 **5. Conclusions**

306 Our data show that important plant functional traits changed strongly in response to changing

307 resource availability, and that higher RGR was supported by larger SLA. Overall, seedlings

308 of the Sahelian species in our study allocated more biomass to roots than to shoots, reaching

309 4-fold at times, reflecting adaptive strategies to keep RGR leveled to resource supply.

310 Overall, functional traits other than R/S responded more to nutrient than to water addition,

311   and two species, *A. tortilis* and *F. albida*, showed high phenotypic plasticity, which may

312   underlie their large distribution area. Our data suggest that the different Sahelian species will

313   respond differently to future environmental changes, which will likely affect their geographic

314   distribution and therefore the structure of the plant communities they are part of.

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601 **Figure 1**

602 Relative growth rate (RGR) of *Acacia tortilis, Adansonia digitata, Faidherbia albida* and

603 *Tamarindus indica* individuals growing at two levels of nutrient availability (high, N+ and low,

604 N-) and two water regimes (W+ and W-). Data are mean ± 1SE (n = 6–9). Different letters show

605 significant differences among species and treatments (post-hoc comparisons among species ×

606 water × nutrient levels).
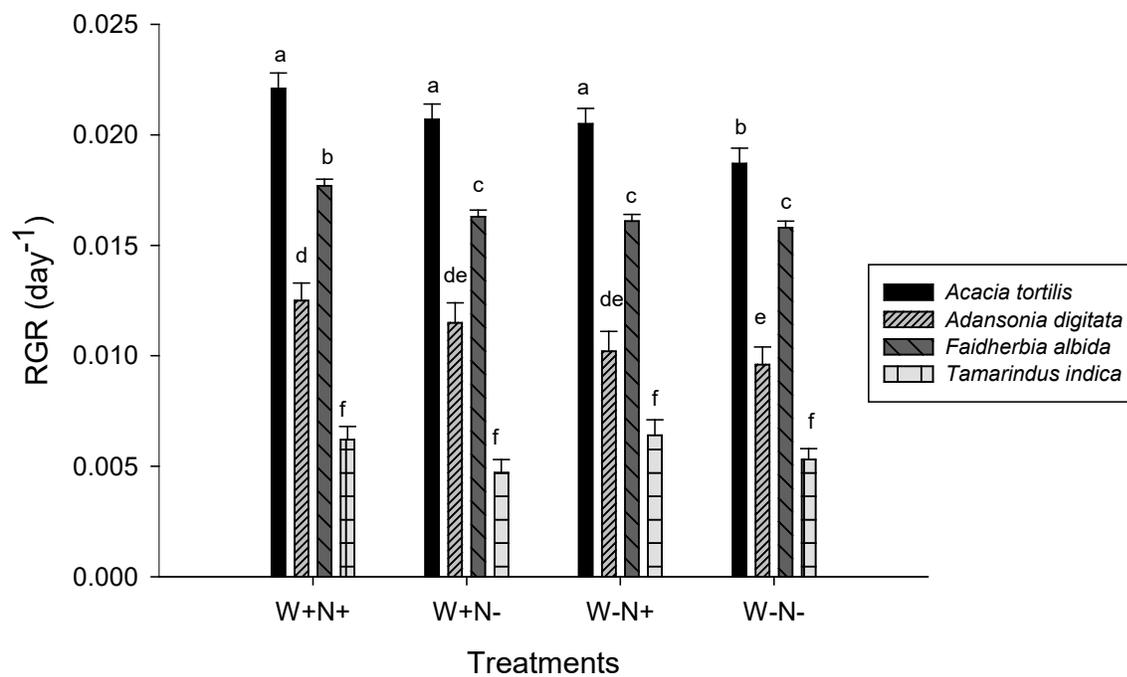
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608   **Figure 2**

609   Specific leaf area (SLA) of *Acacia tortilis*, *Adansonia digitata*, *Faidherbia albida* and

610   *Tamarindus indica* individuals growing at two levels of nutrient availability (high, N+ and low,

611   N-) and two water regimes (W+ and W-). Data are mean ± 1SE (n = 6–9). Different letters show

612   significant differences (post-hoc comparisons among species × water × nutrient levels).

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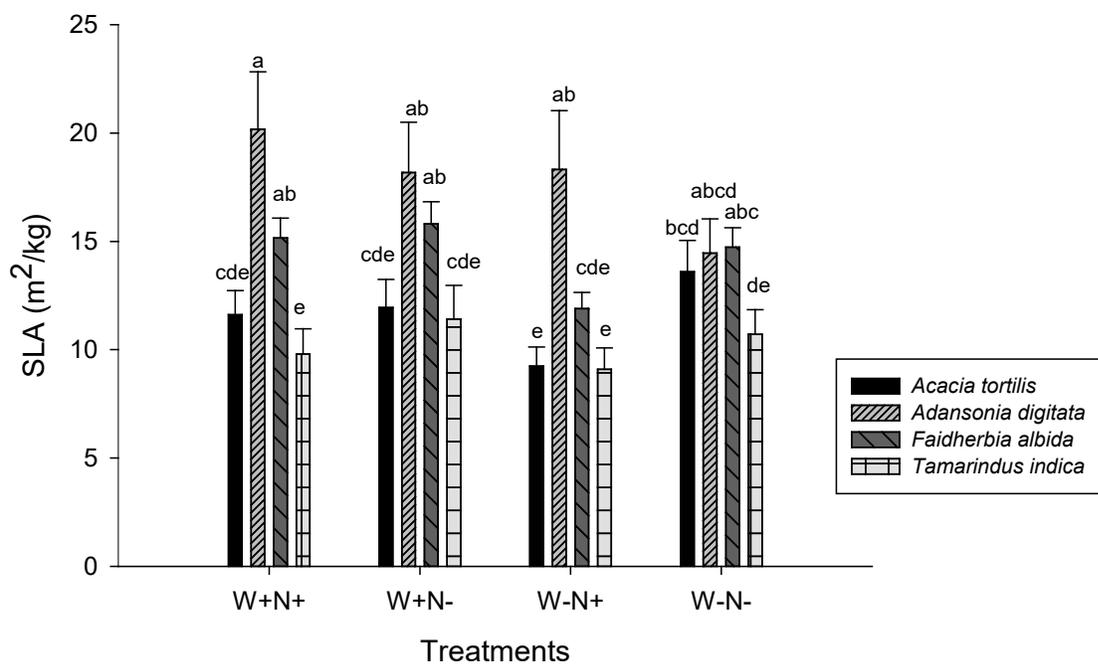
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615 **Figure 3**

616 Root shoot ratio (R/S) of *Acacia tortilis*, *Adansonia digitata*, *Faidherbia albida* and *Tamarindus*

617 *indica* individuals growing at two levels of nutrient availability (high, N+ and low, N-) and two

618 water regimes (W+ and W-). Data are mean ± 1SE (n = 6–9). Different letters show significant

619 differences (post-hoc comparisons among species × water × nutrient levels).

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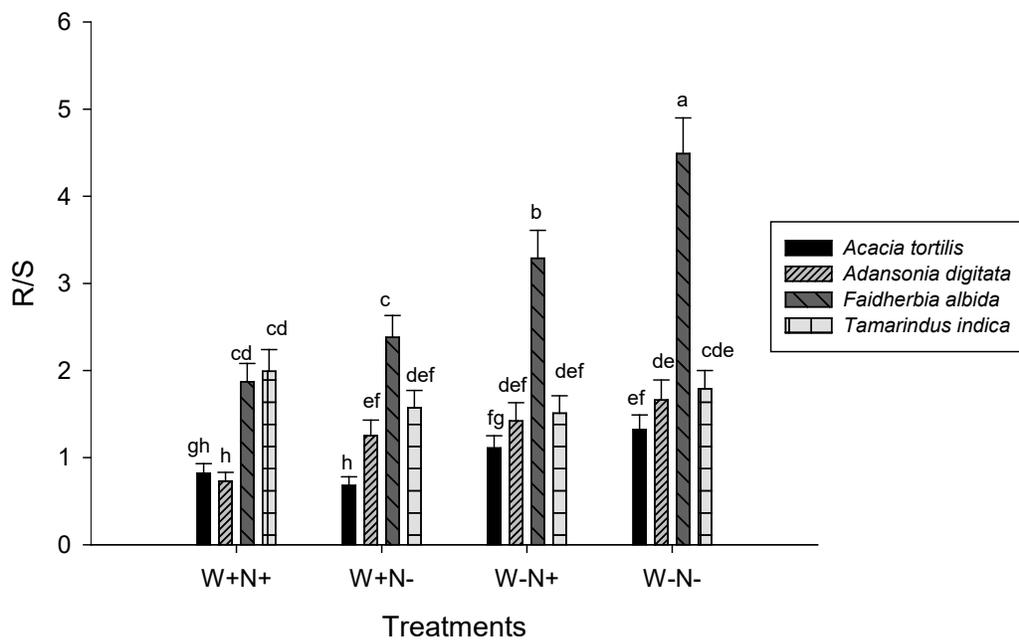
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Figure 4

Mean relative biomass allocation (%) to roots, shoots and leaves of *Acacia tortilis, Adansonia digitata, Faidherbia albida* and *Tamarindus indica* plants grown at two levels of nutrient availability (high: N+, and low: N-) and two water regimes (W+ and W-). Different letters show significant differences in biomass allocation across plant organs and treatments for each species separately (post-hoc comparisons among plant organs × water × nutrient levels).
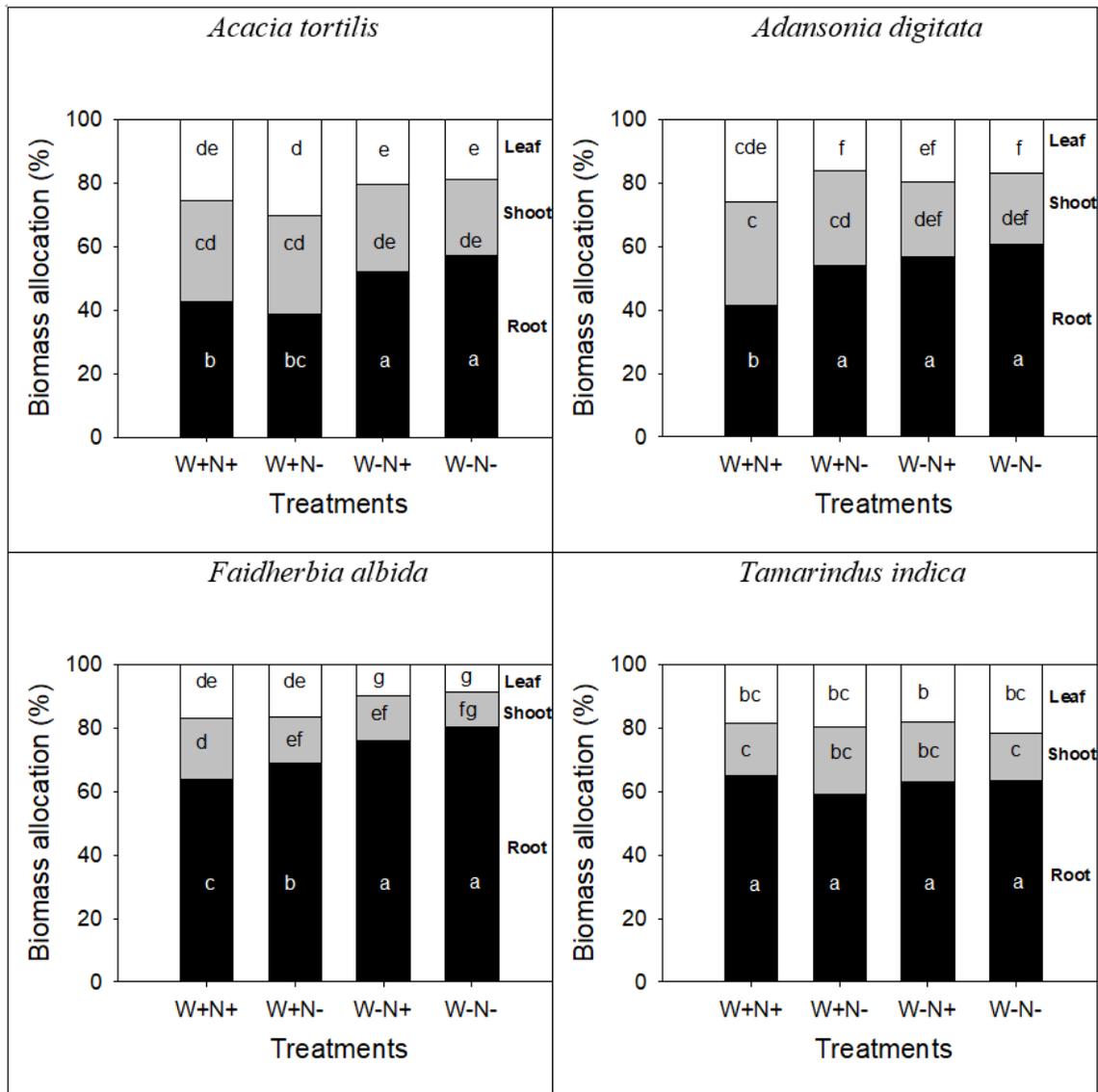
629   **Table 1.** Results of linear models analysing differences in relative growth rate (RGR), root to shoot ratio (R/S) and specific leaf area

630   (SLA) of four Sahelian tree species growing under different soil water and nutrient regimes (n = 6–9). Species, level of fertilizer or

631   water treatments were included in the model as fixed factors with a full-factorial design. Significant p values are highlighted in bold.

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	d.f.	RGR		R/S		SLA	
		F-value	p-value	F-value	p-value	F-value	p-value
(Intercept)	1	6832.59	**<0.0001**	1001.79	**<0.0001**	503.3	**<0.0001**
Species (S)	3	463.65	**<0.0001**	53.24	**<0.0001**	4.01	**0.0094**
Nutrient (N)	1	12.37	**0.0006**	7.39	**0.0076**	4.16	**0.0437**
Water (W)	1	12.34	**0.0007**	36.42	**<0.0001**	6.38	**0.0129**
S × N	3	0.47	0.7020	2.81	**0.0428**	1.78	0.1557
S × W	3	2.87	**0.0398**	8.58	**<0.0001**	0.71	0.5472
N × W	1	0.31	0.5804	8.58	**<0.0001**	0.71	0.5472
S × N × W	3	0.38	0.7709	1.2	0.3136	0.64	0.5934

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635 **Table 2.** Responses of our four target tree species to nutrient addition. Data are mean ± 1SE (n = 6–9); different letters in a row show

636 significant differences between species ($p < 0.05$).

	Acacia tortilis		*Adansonia digitata*		*Faidherbia albida*		*Tamarindus indica*	
	High	Low	High	Low	High	Low	High	Low
Shoot mass (g)	1.61±0.22[a]	0.73±0.06[b]	1.34±0.23[a]	0.55±0.05[c]	1.22±0.12[a]	0.66±0.04[bc]	0.19±0.02[d]	0.18±0.02[d]
Root mass (g)	2.17±0.3[b]	1.60±0.19[b]	2.12±0.42[b]	1.46±0.21[b]	4.58±0.29[a]	4.18±0.27[a]	0.71±0.09[c]	0.76±0.09[c]
Leaf mass (g)	1.27±0.14[a]	0.56±0.05[bc]	0.97±0.25[ab]	0.44±0.06[c]	1.19±0.13[a]	0.47±0.04[c]	0.22±0.03[d]	0.26±0.03[d]
Total plant mass (g)	5.05±0.56[b]	2.86±0.26[cd]	4.44±0.76[bc]	2.44±0.32[d]	6.99±0.47[a]	5.30±0.31[b]	1.12±0.13[e]	1.20±0.13[e]
Plant height (cm)	44.67±3.16[a]	29.97±1.70[c]	24.45±2.85[c]	14.62±1.43[d]	46.96±2.33[a]	35.55±1.57[b]	10.22±0.78[e]	9.23±0.74[e]

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643 **Table 3.** Responses of our four target tree species to water addition. Data are mean ± 1SE (n = 6–9); different letters in a row show

644 significant differences between species (p < 0.05).

	Acacia tortilis		*Adansonia digitata*		*Faidherbia albida*		*Tamarindus indica*	
	High	Low	High	Low	High	Low	High	Low
Shoot mass (g/plant)	1.44±0.21[a]	0.89±0.09[b]	1.15±0.22[ab]	0.74±0.09[bc]	1.19±0.12[a]	0.69±0.05[c]	0.21±0.02[d]	0.16±0.02[d]
Root mass (g/plant)	2.18±0.30[b]	1.58±0.20[b]	1.79±0.30[b]	1.79±0.36[b]	4.73±0.30[a]	4.03±0.26[a]	0.82±0.10[c]	0.65±0.09[c]
Leaf mass (g/plant)	1.07±0.12[a]	0.76±0.08[bc]	0.92±0.25[ab]	0.49±0.07[d]	0.98±0.12[ab]	0.68±0.06[c]	0.26±0.04[d]	0.22±0.03[d]
Total plant mass (g/plant)	4.70±0.52[bc]	3.21±0.32[d]	3.86±0.67[cd]	3.02±0.47[d]	6.90±0.47[a]	5.40±0.31[b]	1.29±0.14[e]	1.04±0.12[e]
Plant height (cm)	38.14±2.4[b]	36.49±2.67[b]	22.86±2.73[c]	16.21±1.66[d]	45.33±2.26[a]	37.17±1.68[b]	10.16±0.8[e]	9.29±0.71[e]

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651   **Annex A**

652   To see true plasticity in response to different water and nutrient supply, there should be significant

653   differences in R/S between treatments for the same species but also changes in the allometric

654   relationships between biomass of roots and shoot, independent of size. To test this, we plotted Ln(root)

655   *vs.* Ln(shoot) for every species and treatment to check for differences in allocation patterns taking into

656   consideration plant size (Fig. A.1). In this case, we considered each species independently.

657
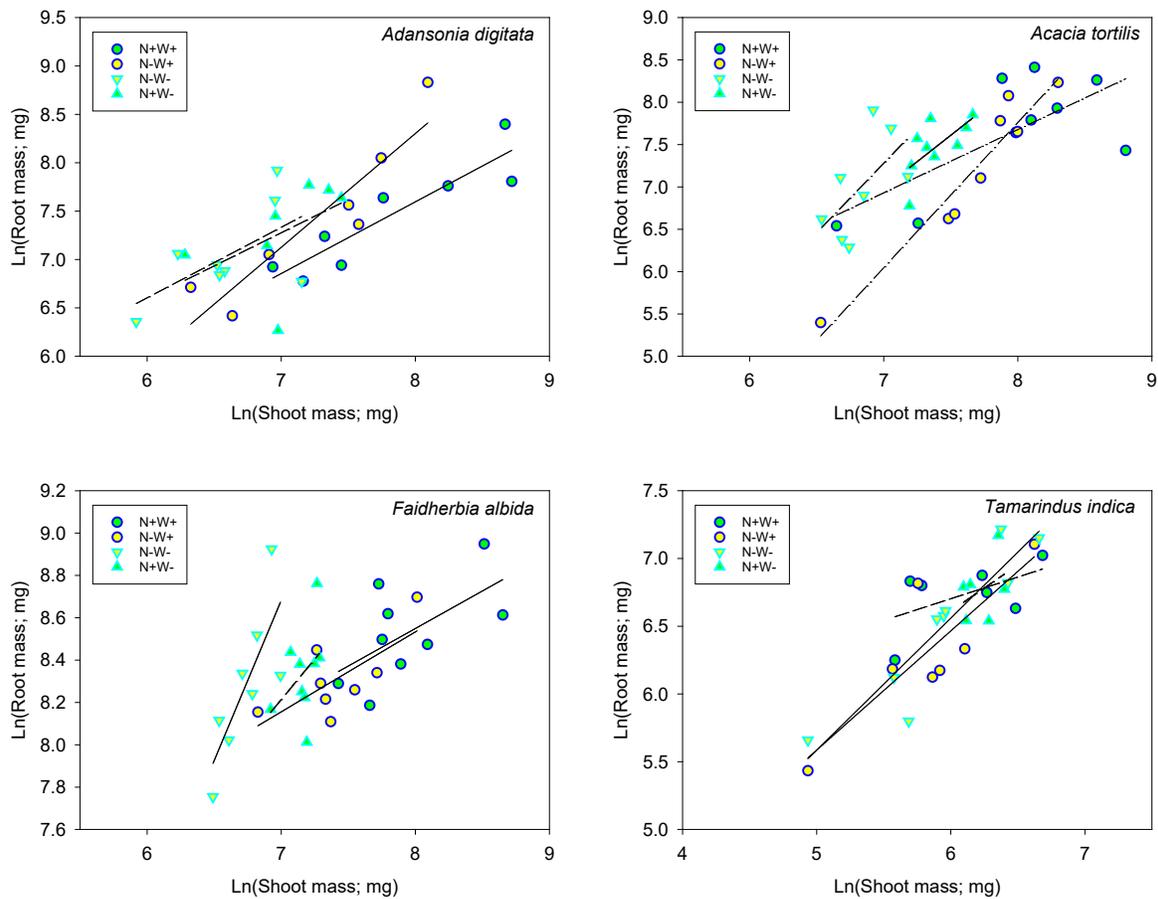
658   **Figure A.1.** Linear regressions between Ln(root mass) and Ln(shoot mass) for each species and treatment. Solid

659   lines show significant linear trends (overall, $r^2 > 0.7$ and $p \leq 0.01$, except in *Acacia tortilis* in N+ treatments and

660   *Faidherbia albida* in N- treatments, where $r^2 > 0.5$ and $p \leq 0.05$); dashed lines are non-significant linear relations

661   ($p > 0.05$).

662

663   Although plants differ in size among treatments, the relationship between total biomass and root
664   biomass held constant across treatments (data not shown). In *Adansonia digitata* R/S was similar in all
665   treatments except for the W+N+ treatment, which had a significantly lower R/S (Fig.3 in the main text).
666   There were no significant relationships between lnR and lnS in the drought treatments (W-) but they
667   were significant in the W+ treatments. Therefore, there is true plasticity (*sensu* Weiner 2004) for this
668   species in response to high resource availability. *Faidherbia albida* plants responded similarly to
669   different water availability; the allometric relationships shown in Fig. A.1 differed between W+ and W-
670   treatments. In *Tamarindus indica* there were no differences in R/S(Fig. 3). Finally, in *Acacia tortilis* the
671   low-resource treatment (W-N-) had a R/S greater than the W+ treatments and the relationship between
672   lnS and LnR were also different between these treatments (no significant vs. significant linear relation
673   for W- vs W+ treatments, respectively).