Functional responses of four Sahelian tree species to resource availability☆

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ABSTRACT

Plants experience a fluctuating environment in time and space that affects resource supply. As human impacts on the environment directly and indirectly alter resource availability, it is important to address plant responses to changing resources to be able to anticipate impacts of these changes on plant communities. We analyzed plant traits to assess responses to resource limitation in four Sahelian tree species of wide ecological and socio-economic importance. We used species already adapted to harsh conditions (high temperatures, low rainfall) to anticipate how climate change could affect their growth patterns and, indirectly, their spatial distribution and the services they provide. Seedlings grew under two levels of water and nutrient additions in a factorial design. Our results showed differences among species, watering regimes, and nutrient supply in three key functional traits related to the plant's resource-use strategy, relative growth rate (RGR), root-to-shoot ratio (R/S), and specific leaf area (SLA). On average, RGR was responsive to the amount of water and nutrients, with species with high RGR showing the largest response to resource supply. RGR in the species with a conservative resource-use strategy (evergreen leaves, lowest RGR) remained unchanged with different levels of water and nutrients. Overall, large RGR was supported by large SLA. All species allocated more biomass to roots than to shoots, particularly under low resource supply, reflecting adaptive strategies to keep RGR leveled to resource supply. Not all species showed similar plasticity in their functional traits responses; however, *Acacia tortilis* and *Faidherbia albida* showed the greatest plasticity, which may explain their large geographical distribution range in Africa. Our data suggest that the different Sahelian species will respond differently to future environmental changes, likely affecting their geographical distribution, the structure of plant communities, and the services they provide.

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

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seedlings responses to water availability, and how they modify their traits, will help to understand the long-term response of forest species to environmental change (Capers et al., 2005; Jump et al., 2007; Pedersen, 1998; Peñuelas et al., 2007).

Further, understanding the role of plasticity in response to resource availability will bring insights into plant growth and persistence of species in their current environments under novel conditions (Nicotra et al., 2010). While drought is acknowledged as a crucial climatic factor that would likely undermine tree survival in the future (Allen and Breshears, 1998; Hanson and Weltzin, 2000), progressive drought-induced stress is a non-linear process largely dependent on the interaction between temperature and water availability, and to plants' adaptability to higher temperatures in terms of morphology and physiology (Adams et al., 2009). The ability of plant species to cope with environmental change will depend on the capacity to adapt physiological and other functional responses to these changes; but, for an effective prediction of the capacity of populations to persist in a certain environment, empirical studies that aim to assess intra-specific response variability under controlled environmental conditions are necessary. Therefore, examination of trait variability in heterogeneous environments that reflect population-level responses to the environment can provide deeper insights into how species might respond to future environmental changes (Oke and Wang, 2015). In addition, identifying trade-offs that underlie the diversity of a species' morphology and function is important because trade-offs constrain demographic change rates and their linkages to ecosystem processes (Díaz et al., 2016; Shipley et al., 2016).

Growth rate is a prominent indicator of plant strategies that deals with environmental stress and disturbance (Pérez-Harguindeguy et al., 2013), and substantial volume of theory and data support the correspondence between functional traits and growth rate (Hunt and Cornelissen, 1997; Reich et al., 1998; Shipley, 2006). However, variation in individual-level access to resources can cause trait correlations within species to differ from inter-specific correlations (van Noordwijk and de Jong, 1986) due to phylogenetic constraints.

Here we analyzed functional responses of seedlings to simultaneous effects of moisture stress and nutrient variability in four Sahelian tree species of wide ecological and socio-economic importance. Target species were selected as representative of functional groups of the highly diverse agroforestry ecosystems in the Sahel (Diémé et al., 2018). We linked RGR and biomass allocation patterns with functional traits deemed relevant to plant persistence (Kleyer et al., 2008). We addressed responses in relative growth rate (RGR), root-to-shoot ratio (R/S) and specific leaf area (SLA) of seedlings growing under two levels of water and nutrient availability in a full factorial greenhouse experiment and explored potential trade-offs among traits. We hypothesize that 1) RGR will increase with resource supply but the magnitude of the response will depend on resource use strategies (Grime et al., 1997). We expected that 2) fast-growing species, i.e. with exploitative strategy, will show high RGR under high water and nutrient supply, but RGR will decline strongly with low resource supply levels; in contrast, 3) plants with conservative resource-use strategy will have a less plastic response to changes in water and nutrient supply, i.e., stable RGR regardless resource levels, with more biomass allocated to roots at low levels of water and nutrient supply (Meier et al., 2018). And 4) SLA, a trait strongly associated to the plant resource-use strategy, will respond in parallel to RGR.

2. Methods

A greenhouse experiment was established in 2012–2013 at the University of Almería (36° 50′ N, 2° 27′ W), Spain, using four Sahelian tree species, two dry-season deciduous species, *Acacia tortilis* (Savi) Brenan and *Adansonia digitata* L., one wet-season deciduous species (*Faidherbia albida* (Del.) Chev.), and one evergreen species, *Tamarindus indica* L. Seeds of these species were obtained in Senegal (PRONASEF,

Senegal National Project of Forestry Seeds, Dakar) and subjected to a pre-germination treatment using concentrated sulfuric acid for 10 min (*T. indica*), 60 min (*A. tortilis* and *F. albida*) and 12 h (*A. digitata*). Seeds of each species were harvested in the same area so that their mother plants were subjected to the same environmental (soil and climatic) conditions. Two seeds per species were sown in a sand and vermiculite mixture (1:1 in volume) in 50 cm long, 10 cm wide PVC tubes and thinned to one after germination. Plants were watered every morning and received fertilizer (commercial NPK fertilizer [Mg-S]; 19-19-19 [2–8]) once a month between November 2012 and March 2013, just before the experiment started. In March 2013, treatments were set in a factorial design with nutrient (low and high nutrient supply) and water (low and high level of watering) as factors (2×2 factorial design; n = 6–9 plants per treatment and species). At the start of the experiment, plant size differed depending on the species. It was < 5 cm in *A. albida, A. digitata*, and *T. indica,* and < 15 cm in *F. albida.* Half the plants per species received a high nutrient solution (N+) of 0.5 g fertilizer per liter of water, and the other half received a low nutrient solution (N-; 0.05 g of fertilizer per liter of water). In addition, half the plants were watered once a week with 100 ml (low water supply; W-) and the other half was watered twice a week with 100 ml each time (high water supply; W+, 200 ml of water per week). So, four treatments were established according to nutrient and water regime, W + N +, W + N-, W-N+, and W-N-. Treatments were applied for four months and pots were randomly redistributed in the greenhouse once a month. Temperature within the greenhouse ranged 16–22 °C during the course of the experiment, with natural daylight length (10.5–14 hours of light).

At harvest, nine months after sowing, plants were sorted into above- and below-ground parts, and the aboveground parts were subdivided into leaves and stem. Plant parts were dried at 70 °C for 48 h and weighed. Plant traits were calculated following standard protocols (Pérez-Harguindeguy et al., 2013). In brief, six fully expanded and undamaged leaves per plant were scanned with a flatbed scanner to determine the specific leaf area (SLA; the ratio of leaf area to dry mass). Total plant biomass (TPB) was obtained by adding the dry mass of the different plant parts. Root-to-shoot ratio (R/S) was calculated by dividing root mass by shoot mass. Relative growth rate was estimated as RGR = (ln TPB_2 - ln TPB_1)/(t_2 - t_1), where t is the elapsed time in days between sowing (t_1) and harvest (t_2). To calculate TPB_1, we selected 10 seeds per species, extracted and dried the embryos in an oven for at least 72 h at 70 °C, and weighed their dry mass with a precision balance (to 10^{-6} g). We used the mean TPB_1 value per species. We also recorded plant height (measured with a ruler to 0.1 cm).

The effect of water, soil nutrient addition on plant functional traits (RGR, SLA, R/S, biomass, plant height, allocation patterns) was analyzed with general linear models including a full-factorial design. Fixed-factors were species (as we were interested in inter-specific responses of species belonging to different functional groups), nutrient addition (low, high), watering (low, high), and the interaction across factors. Assumptions of normal distribution of residuals, homogeneity of variances were tested, met. Differences in means across treatment levels were analyzed with Fisher's least significance difference (LSD) post-hoc test. Statistical analyses were conducted in R (R Development Core Team, 2013) using the interface implemented in InfoStat-Statistical Software (Di-Rienzo et al., 2013). Reported values throughout the text, figures are means ± 1, standard error.

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 (significant species × water interaction, Table 1) except *T. indica*, whose RGR remained unchanged irrespective of water and nutrient addition. Growth of the other 3 species

Table 1
Results of linear models analysing differences in relative growth rate (RGR), root to shoot ratio (R/S) and specific leaf area (SLA) of four Sahelian tree species growing under different soil water and nutrient regimes (n = 6–9). Species, level of fertilizer or water treatments were included in the model as fixed factors with a full-factorial design. Significant p values are highlighted in bold.
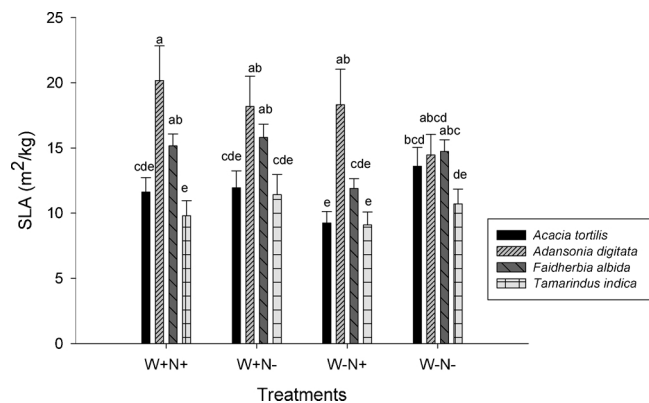
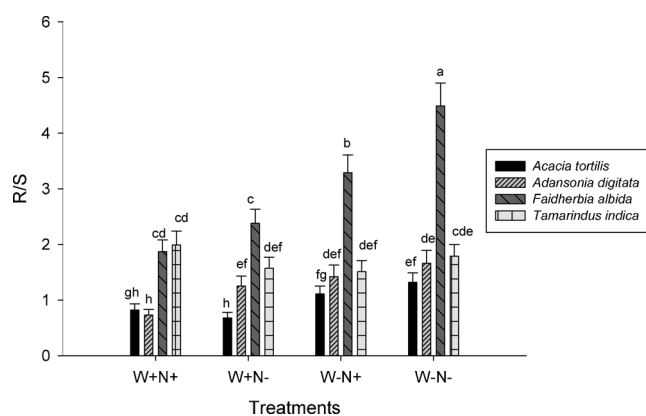|	d.f.	RGR		R/S		SLA	
		F-value	p-value	F-value	p-value	F-value	p-value
(Intercept)	1	6832.59	**< 0.0001**	1001.79	**< 0.0001**	503.3	**< 0.0001**
Species (S)	3	463.65	**< 0.0001**	53.24	**< 0.0001**	4.01	**0.0094**
Nutrient (N)	1	12.37	**0.0006**	7.39	**0.0076**	4.16	**0.0437**
Water (W)	1	12.34	**0.0007**	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
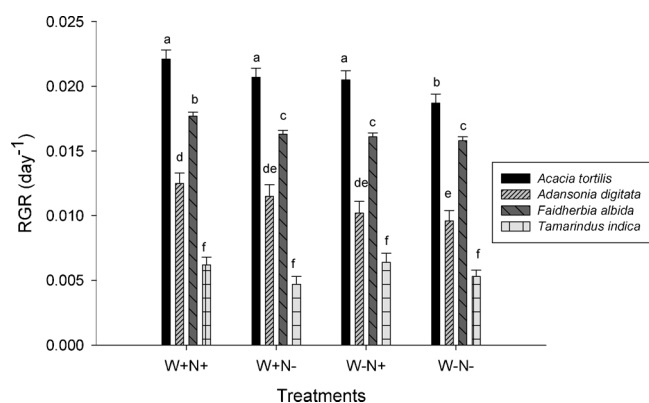
Fig. 1. Relative growth rate (RGR) of *Acacia tortilis, Adansonia digitata, Faidherbia albida* and *Tamarindus indica* individuals growing at two levels of nutrient availability (high, N + and low, N-) and two water regimes (W + and W-). Data are mean ± 1SE (n = 6–9). Different letters show significant differences among species and treatments (post-hoc comparisons among species × water × nutrient levels).

Fig. 3. Root shoot ratio (R/S) of *Acacia tortilis, Adansonia digitata, Faidherbia albida* and *Tamarindus indica* individuals growing at two levels of nutrient availability (high, N + and low, N-) and two water regimes (W + and W-). Data are mean ± 1SE (n = 6–9). Different letters show significant differences (post-hoc comparisons among species × water × nutrient levels).

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).

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

Fig. 2. Specific leaf area (SLA) of *Acacia tortilis, Adansonia digitata, Faidherbia albida* and *Tamarindus indica* individuals growing at two levels of nutrient availability (high, N + and low, N-) and two water regimes (W + and W-). Data are mean ± 1SE (n = 6–9). Different letters show significant differences (post-hoc comparisons among species × water × nutrient levels).

interaction Species × N; Species × W or Species × N × W (Table 1).

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 of the 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. A1). We found that there was true plasticity (*sensu* e.g., Weiner, 2004) only in *Adansonia digitata*, but *Faidherbia albida* showed plasticity with respect to watering treatments.

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
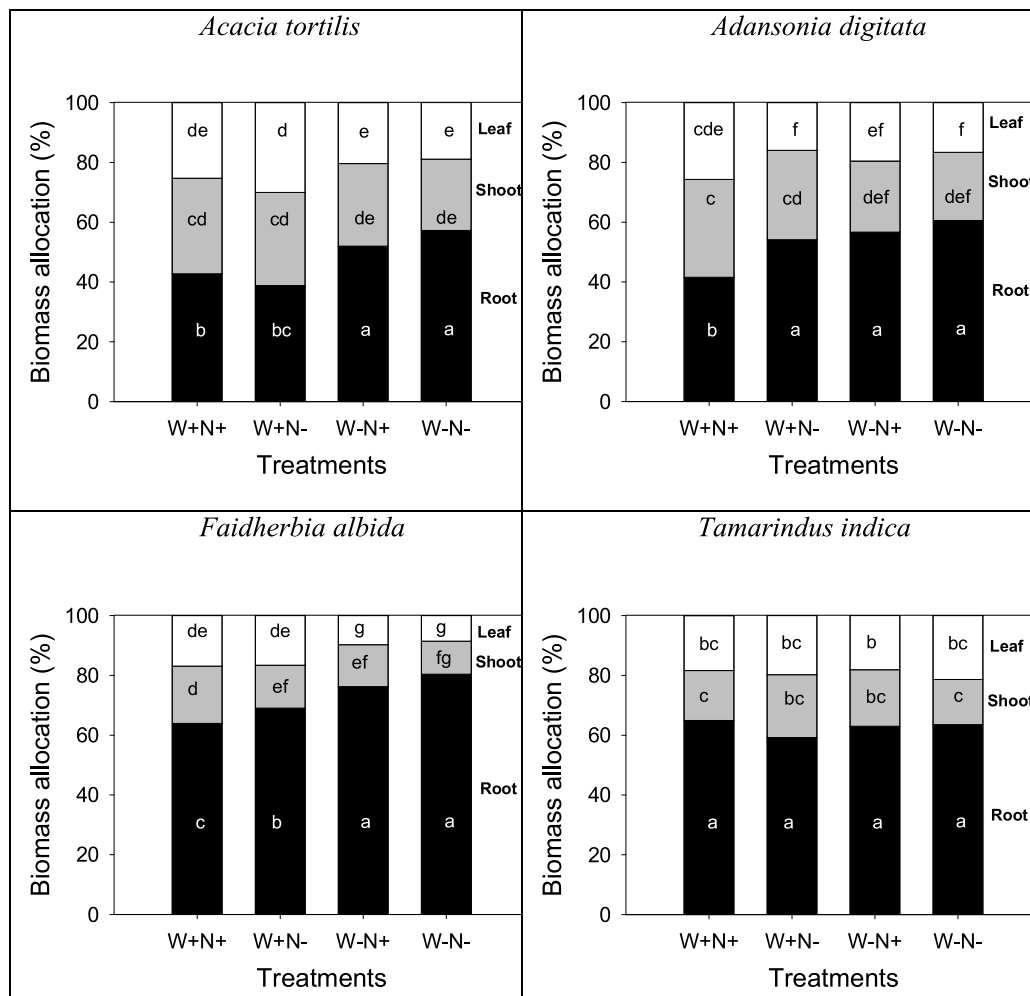
Fig. 4. Mean relative biomass allocation (%) to roots, shoots and leaves of *Acacia tortilis, Adansonia digitata, Faidherbia albida* and *Tamarindus indica* plants grown at two levels of nutrient availability (high: N +, and low: N-) and two water regimes (W + and W-). Different letters show significant differences in biomass allocation across plant organs and treatments for each species separately (post-hoc comparisons among plant organs × water × nutrient levels).

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 regarding biomass or allocation patterns in response to nutrient or water addition (Fig. 4).

4. Discussion

The four Sahelian tree species in our study differed significantly in RGR, and as expected, plant size and growth rate responded positively and consistently to both nutrient and water levels (Cornelissen et al., 1998), although the response to water levels was species-specific (significant interaction S × W). RGR was significantly higher when both

resources were high compared to low, in agreement with published reports (e.g., Poorter et al., 1989). In general, species maintained a RGR ranking across resource availability levels, i.e., *A. tortilis, F. albida, A. digitata* and *T. indica* showed highest to lowest RGRs regardless of resource supply. *Acacia tortilis* maintained high RGR under all treatments except with the lowest levels of nutrient and water supply, while RGR in *T. indica* remained unchanged notwithstanding nutrient and water levels. These results support our prediction of a larger plasticity in response to varying levels of water and nutrient supply in species with high RGR (resource exploitative strategy) and low plastic capacity in species with low RGR (conservative resource strategy). Our results are also indicative that maintaining an optimal RGR (i.e., adjusted to environmental conditions) seems to be an important plant strategy

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 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]

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 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]

irrespective of resource supply, since a high RGR is critical for plants to grow and occupy space, both below- and above-ground, to get a larger share of resources (Grime, 1998; Ruiz-Robleto and Villar, 2005). All species except *T. indica* are deciduous species and show RGR values between 0.005 and 0.023 g g^{-1} d^{-1}, which is a rather high range compared to tree species from other dry environments (Atta et al., 2012; Hoffmann and Franco, 2003; Lamers et al., 2006). Overall, species with high RGR generally have high rates of photosynthesis and respiration per unit mass, requiring high nutrient levels to sustain such physiological activity and high leaf turnover. Slow-growing species show opposite patterns (Reich et al., 1997; Wright et al., 2004). In contrast to the deciduous species in our study, the evergreen *T. indica* did not respond to resource addition. It is a slow-growing species (Diallo et al., 2008; El-Siddig et al., 2006) native to dry, subtropical environments and may have, over evolutionary time, adjusted a low resource demand to a low supply to avoid exhausting limiting resources. This way the low RGR is closer to its optimum (Chapin, 1980; Grime and Hunt, 1975). The lack of a stronger response of species with a resource exploitative strategy to resource shortage indicates the presence of trade-offs between traits and with biophysical constraints that result in convergence of resource acquisition strategies (Reich, 2014).

The RGR is a product of net assimilation rate (NAR) and leaf area ratio (LAR) (Evans, 1972). LAR in turn can be partitioned into specific leaf area (SLA) and leaf mass ratio (LMR), or the dry mass of leaves relative to total plant dry mass. Most studies show that LAR is the factor that best explains differences in RGR, and the most important component of LAR is SLA (Antúnez et al., 2001; Hoffmann and Franco, 2003; Ruiz-Robleto and Villar, 2005) further reflecting a trade-off in plant resource-use strategy tightly coupled to resource availability (Grime et al., 1997). In our experiment, SLA differed among species and across water and nutrient supply levels (Coley et al., 1985; Evans, 1972; Lavorel and Garnier, 2002). Therefore, changes in RGR mostly paralleled variations in SLA, suggesting that SLA was a key factor sustaining RGR (Poorter and Garnier, 2007).

Biomass allocation patterns vary among species and are sensitive to environmental clues (Atkin et al., 2006). Many reports have shown that drought influences allocation patterns (Ledo et al., 2018; Liu and Stützel, 2004; Poorter et al., 2015; Spollen et al., 1993) particularly R/S values (Poorter et al., 2012; Turner, 1997). Plants with a higher allocation to roots can compete more effectively for soil resources while those with a higher proportion of shoots can collect more radiation (Bloom et al., 1985; Tilman, 1988). In our experiment, R/S values were generally well above 1 irrespective of the species, suggesting a genetically-fixed higher biomass allocation to roots in seedlings of species adapted to infertile environments (Aerts and Chapin, 2000; Chapin, 1980; Lambers et al., 2008) or with severe water shortage (Fernández and Reynolds, 2000; Lambers et al., 2008; Padilla et al., 2009; Wright and Westoby, 1999). Since seedling growth rate is an important life history trait, critical for plant survival and establishment in water-limited environments, we expect traits in early ontogenetic stages to contribute significantly to the species' adaptive capacity. It is worth to note that R/S changes with plant development, as seedlings allocate more biomass to roots (Gedroc et al., 1996), and therefore our results

may be consequence of differences in plant size (Husáková et al., 2018). In our dataset, however, there was true plasticity (*sensu* Weiner, 2004) in *Adansonia digitata*, while *Faidherbia albida* showed plasticity with respect to watering treatments. Therefore, we can say that, for these species, the differential allocation to roots can be interpreted as a strategy response to water limitation (Ledo et al., 2018). R/S was highest in *F. albida*, reaching a value of 4 under low water and nutrient levels and reflecting its ability to strongly alter allocation patterns. In fact, *F. albida* is a species very sensitive to drought (Roupsard, 1997) and its ability to quickly reach deeper, moist soil horizons may be critical in coping with drought at such an early stage, as has been shown for other woody species in dry conditions (Padilla and Pugnaire, 2007). Opposite to its dramatic response concerning R/S, RGR did not change much in *F. albida*, and SLA tended to decrease only under reduced water, but high N availability.

In our experiment, R/S in baobab (*A. digitata*) responded to N addition but only when water was available. This may be because, while adult baobab trees accumulate water in their stem, baobab seedlings use the taproot as main storage organ (Wickens and Lowe, 2008) allocating more resources to belowground structures than adults (Cuni-Sanchez et al., 2011), particularly when water is limiting. A similar strategy has also been observed in other tropical tree species (Poorter and Markesteijn, 2008). Given the importance of the taproot for seedling survival under dry spells (Padilla and Pugnaire, 2007; Poorter and Markesteijn, 2008), seedlings with relatively larger taproots have a higher chance of survival in drought-prone environments than seedlings with relatively smaller taproots, because they can store more water and carbohydrates (Kabeya and Sakai, 2003) and keep the root in contact with moist soil horizons (Padilla and Pugnaire, 2007).

A characteristic of plants in arid environments such as the Sahelian savanna is to show high temporal and spatial variation in growth patterns, which depends on environmental variability, particularly soil moisture (Abdelrahman and Krzywinski, 2008). Leaf habit, i.e. whether a species is evergreen or deciduous, has been linked to divergent plant strategies in seasonal climates (Markesteijn and Poorter, 2009; Tomlinson et al., 2012) as the Sahel. Deciduous species may allocate more resources to roots than evergreen species in any seasonal environment, defining distinct biomass partitioning patterns between leaf habits (Espelta et al., 2005). Within our species, *F. albida* and *A. tortilis* showed high plasticity in their functional traits responses allowing them to cope with water and nutrient variability, which may be a reason behind their large geographical spread in Africa, as they are able to cope with contrasted supply levels of water and nutrients.

5. Conclusions

Our data show that important plant functional traits changed strongly in response to changing resource availability, and that higher RGR was supported by larger SLA. Overall, seedlings of the Sahelian species in our study allocated more biomass to roots than to shoots, reaching 4-fold at times, reflecting adaptive strategies to keep RGR leveled to resource supply. Overall, functional traits other than R/S responded more to nutrient than to water addition, and two species, *A.*

tortilis and *F. albida*, showed high phenotypic plasticity, which may underlie their large distribution area. Our data suggest that the different Sahelian species will respond differently to future environmental changes, which will likely affect their geographic distribution and therefore the structure of the plant communities they are part of.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.flora.2018.10.009.

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