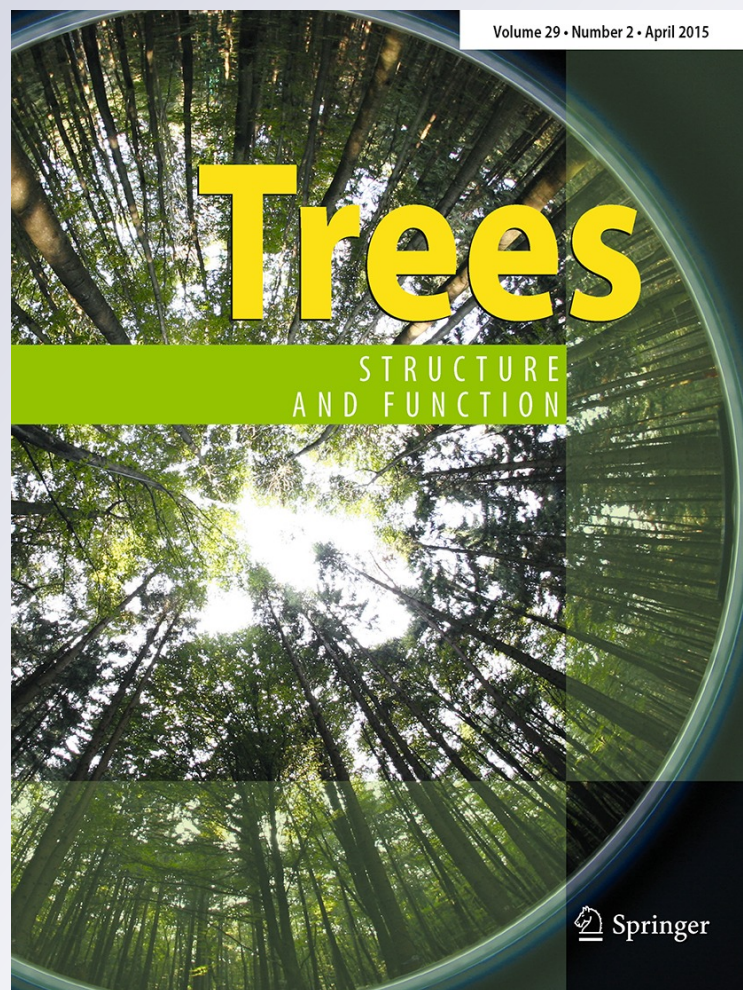# Effects of water stress and substrate fertility on the early growth of Acacia senegal *and* Acacia seyal *from Ethiopian Savanna woodlands*

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Effects of water stress and substrate fertility on the early growth of *Acacia senegal* and *Acacia seyal* from Ethiopian Savanna woodlands

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Abstract

Key message ***Acacia senegal*** **and** ***Acacia seyal*** **present different drought stress coping mechanisms that are independent of substrate fertility. Higher substrate fertility increased aboveground plant growth, even with low watering.**

Abstract   The potential of native African tree species for agriculture and forestry have not yet been thoroughly investigated. In this experiment, we studied the early growth of *Acacia senegal* and *Acacia seyal* plants in an experiment with two substrates of contrasting fertility (low/high) and two watering frequency regimes (low = 24.40 l/m^2 per month, high = 48.80 l/m^2 per month). Our objectives were: (1) to study whether the mechanisms by which nutrients affect plant growth at the seedling stage operate differently when water availability varies, and (2) to look for differences in the growth strategies of the two species in early stages. Higher substrate fertility increased aboveground plant growth at the expense of roots in both water regimes. Though water stress significantly limited growth under both soil conditions, substrate fertility effects were relatively higher in plants with low water supply than in those with high water supply. However, even with low resources the root-to-shoot ratio was between 0.7 and 0.9, plants presented adequate nutrition and no mortality was observed. This indicates opportunistic mechanisms for water and nutrient use. *A. seyal* showed the lowest negative pre-dawn stem water potential value (−0.15 MPa) and shed nearly all leaves in the hottest month of the assay, which suggests a different drought avoidance strategy and adaptation to water stress than *A. senegal*. Both species can be produced successfully in local nursery conditions and can survive and thrive with low watering. The study also demonstrated that fast growing genotypes can be effectively isolated in nursery conditions.

Keywords   Arid land · Biomass · Nutrient uptake · Soil fertility · Vigor · Water potential

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Introduction

Although Africa has a huge array of indigenous legumes which can be used for crops and wood, there has been a tendency to use exotic species in agriculture and forestry for these purposes. Thus, even though indigenous species are better adapted to their environment and even though legumes have been used by indigenous peoples for

centuries, their full potential has not yet been realized (Sprent et al. 2010). *Acacia senegal* (L.) Willd. and *Acacia seyal* Del. are a very economically important species for the production of gum Arabic, for reforestation and reclamation of marginal lands, for high-protein forage, for fuel wood, timber, shelterbelts and soil fertility improvement thanks to their root symbiotic nitrogen-fixing bacteria (Palmberg 1981, Harrier et al. 2000; Midgley and Bond 2001; Otieno et al. 2005; Raddad et al. 2005; Raddad 2007), and they are present in many social and cultural facets of African local communities. In addition, acacias have a reputation for moderate-to-high tolerance to water stress and for biomass production even under extreme drought conditions (Oba et al. 2001; Otieno et al. 2005) and cold spells (Raddad et al. 2005).

Soil water availability is the key factor in the growth, development, species composition and distribution of savanna trees (Otieno et al. 2005). However, when annual rainfall is below 500 mm in savanna ecosystems, soil properties determine natural vegetation growth (Walter 1997). Water thus constrains plant growth and survival directly (Hooper and Johnson 1999; Song et al. 2010), but also indirectly by influencing how plants subjected to water stress respond to nutrients (Song et al. 2010). Plant growth, primary production and survival rates decline significantly under water stress due to the nutrient deficit that accompanies water shortage (Chapin 1991). Some have suggested that nutrient stress may enhance plant tolerance to drought (Chapin 1991; Wu et al. 2008). However, information is still scarce concerning the effects of nutrient supply on water-stressed plants in arid lands, under nursery conditions or at the seedling stage. Fertilization provides a practical way to stimulate plant growth: it increases nutrient availability, enhances stress tolerance and encourages more efficient use of limited resources in infertile or dry environments (Wu et al. 2008). In contrast, many studies have associated increased N under drought conditions with lower biomass allocation to root, increased leaf sensitivity to stress (Tan and Hogan 1997; Wu et al. 2008), stunted plant growth and high seedling mortality (see literature in Wu et al. 2008).

Acacia savanna woodlands in African tropical and subtropical dry forests have undergone heavy deforestation in recent years (Argaw et al. 1999; Zida et al. 2008), resulting in the degradation of vegetation cover, primary production, and soil fertility. Better understanding of the interplay between water use strategies and nutrient stress tolerance in seedlings is essential for restoration programs in these environments. Afforestation plans to re-establish vegetation cover with N-fixing species such as *Acacia* species in degraded areas (Larwanou et al. 2010) will depend on accurate knowledge of their growth and productivity and their performance in the environment

selected. For example, results on seed, seedling and tree traits show that *A. senegal* from clay provenances can be quite distinct from those originating from sandy soil areas (Raddad et al. 2005, 2006; Raddad and Luukkanen 2006; Raddad 2007; Gray et al. 2013). Increasing the chances of producing and successfully establishing vigorous seedlings is a vital first step in improving re-vegetation (Li et al. 2008). For instance, height is usually considered an important variable in the evaluation of genetic variation in tree species and provenances. Height may also be seen as a measure of the adaptation of the tree to its environment (Raddad et al. 2006). More over, tree height, basal diameter and the number of branches have been proposed to be used as criteria in selection of *A. senegal* for reforestation and agroforestry in the clay part of the gum belt in Sudan (Raddad 2007).

Plant adaptation in arid climates generally involves great tolerance to drought, highly efficient utilization of water and nutrients, and greater biomass allocation to roots (Otieno et al. 2005; Wu et al. 2008; Gray et al. 2013). Knowledge about shoot and root responses to water and nutrient stress may provide basic information for assessing differences among species in productivity, survival and distribution, and could shed more light on the functioning of dry-land ecosystems (Otieno et al. 2005). We investigated the influence of substrate fertility and water stress on the early growth of two important drought deciduous and N-fixing (Gebrekirstos et al. 2006) species from the southeastern Ethiopian savannas: *A. senegal* and *A. seyal*. There has been a recent global revision of *Acacia* that has seen the genus name *Acacia* being retained only for Australian species. African species have all been renamed and *A. senegal* is now known as *Senegalia senegal* (L.) Britton and *A. seyal* is now in a different genus *Vachellia seyal* (Delile) P.J.H. Hurter (referee's contribution). However, we have retained the use of *A. senegal* and *A. seyal* here for continuity with previous literature and general communication, and because of the widespread familiarity of the African people with the former names (Gray et al. 2013). Our objectives were: (1) to study whether the mechanisms by which nutrients affect plant growth at the seedling stage operate differently when water availability varies, and (2) to look for differences in the growth strategies of the two species in early stages. We expected to find significant species-dependent differences, higher aboveground biomass production in plants with high nutrient and water availability, and higher root growth in plants with low nutrient and water availability. Our two main questions were: (1) How do morphology and biomass production react when water stress is combined with higher soil nutrient content? (2) Which species is the most tolerant to water and nutrient stress?

Materials and methods

Study species and seed origin sites

In this study we used *A. seyal* and *A. senegal* plants 2–5 months of age obtained from seeds germinated in mid-April 2010 under controlled conditions in a culture chamber belonging to the University of Valladolid in Palencia (Spain). Seeds were obtained from the National Forest Research Centre of Ethiopia: the *A. seyal* seeds came from *Acacia* woodlands located in the Abijatta-Shalla National Park (7°32′N–38°40′E) and the *A. senegal* seeds came from Langano (7°26′N–38°47′E). The altitude of these locations ranges from 1,540 to 2,075 m.a.s.l. and soils are classified as phosphate-deficient Andosols with low organic matter content (Argaw et al. 1999). These silty, coarse, alkaline (pH = 7.6–8.2) clay loam and rather infertile soils developed over ancient lake deposits. Maximum and minimum temperatures are 26.9 and 11.7 °C, respectively (Argaw et al. 1999) in the areas where the seeds were collected. Some 500–600 mm of rain falls between March and September. In Ethiopia the main rainy season (Kiremt season) usually lasts from June to September, affecting everywhere except in the water-deficient southern and southeastern parts of the country (Seleshi and Zanke 2004; Cheung et al. 2008). There, the light rainy season (Belg season) from March to May provides most of the rainfall (Seleshi and Zanke 2004; Cheung et al. 2008). The dry season (Bega season) usually lasts from October to February in the whole country, with the exception of occasional rainfall in the central sections (Seleshi and Zanke 2004; Cheung et al. 2008). In the Rift Valley watershed (where seed origin sites are located), around 23 % of the total rain falls during the light rainy season, and 66 % during the main rainy season (Cheung et al. 2008).

Plant material and experimental design

Seeds were germinated on mid-April, 2010. Germination was carried out in a culture chamber in plastic Petri dishes (25 seeds per dish), on the top of three sterile filter-papers discs moistened with sterile distilled water. Petri dishes position in the growth chamber was randomly distributed, where seeds were incubated with a 12-h light/12-h dark photoperiod, and at an alternate temperature of 30 °C and 80 % of relative humidity. The seeds were pretreated by immersing them in water at 100 °C and leaving them to soak overnight as the water cooled. Most seeds germinated on the third day. After germination and initial growth (a 1- to 1.5-cm-long radicle), plants from the two species were transferred (May, 2010) to Arnabat® 48-cavity forest trays (308 cm³). Each cavity was 18 cm² with vertical anti-spiraling ribs along the inside walls.

The experimental design was developed to test the effects of species, substrate fertility and water stress on early plant growth. Growth measurements were carried out from June to September 2010. Plants were harvested at 2, 3, 4 and 5 months after sowing, and two plants were randomly selected from each combination (species, substrate, watering and block) for a total of 64 plants per harvest. The test was established using two different split-plot designs with a factorial combination of species (2), substrate (2) and watering regime (2). Design Phase 1 consisted of a randomized four-block split-plot experiment. Species and watering were associated with the plot or main unit (forest tray), while substrate was associated with the subplot (two substrates per forest tray). The 32 plants sown on the borders and in the center of the forest tray (edge between the two substrates employed per forest tray) were discarded from measurements to avoid the edge effect; so a total of 256 plants (8 plants × 2 substrates × 2 watering × 2 species) were available in this first design phase. After the first harvest (plant age 2 months), the six plants that had been kept in each of the two substrate compartments per tray were transplanted to individual forest pots (16 cm diameter, 23 cm deep). Design Phase 2 thus consisted of 192 plants, following a randomized three-block split-plot design with a factorial combination of species, substrate and watering. In this case, watering was associated with the main unit while species and substrate factors were randomly distributed within the blocks. Each block consisted of 4 forest trays/m² (Design Phase 1) and 32 forest pots/m² (Design Phase 2).

Treatments and culture conditions

Substrate treatments

Two substrates of contrasting fertility were used (Table A1 in the ESM). Substrate 1 (Su1, rich nutrient content) was a 3:1 (v:v) mixture of commercial peat (0–10 mm), black peat (0–5 mm) and vermiculite. Substrate 2 (Su2, poor nutrient content) was prepared according to Ethiopian local practices, with a 2:1:1 mixture of vegetable patch soil, compost and sand.

Watering treatments

A low-watering unit (W1) was defined as the application of 12.20 l/m² every 15 days; while a high-watering unit (W2) was defined as the application of 12.20 l/m² every 7 days. During the 5 months of the experiment, W1 plants received a total of 122 l/m² of water, and W2 plants received a total of 244 l/m². W2 plants received water, at once, every 7 days; while W1 plants were watered as follows: from May 1 to June 15 (first harvest) water was delivered at once, every 15 days. Then, from July 1 to August 15

(the hottest period), 2/3 of the total amount of water was delivered at once after the first 7 days, and the 1/3 remaining after the second 7 days. The final watering amount was delivered at once, on September 1 (the last harvest was carried out on September 15).

The study was conducted under common garden experiment conditions in a greenhouse belonging to the University of Valladolid, in Palencia (Spain), (42°01′N-4°32′W, 739 m.a.s.l). Relative air humidity (RH, %) and air temperature (T, °C) were measured and recorded throughout the experiment using field data loggers (Testo 175-H2; Testo S.A., Spain). In the greenhouse the average, maximum and minimum T (May to September) were 26; 45 and 9 °C, respectively. Average, maximum and minimum RH were 43, 84 and 9 %, respectively.

Data collection and measured variables

Harvested plants were hermetically stocked in plastic bags and kept frozen at −5 °C for later measurement. Stem height (length of the main stem measured to the nearest 5 mm with a hand tape) and basal diameter (root collar measured with a caliper to the nearest 0.01 mm) of each plant were recorded. Plants were divided into their components (stem, leaves, and roots). Leaf area and specific leaf area were based on the average of three representative leaves from the upper, middle and lower parts of the plant (significant differences were not observed among them). These species have pinnate leaves divided into small leaflets. Sample leaves were scanned using an EPSON EXPRESSION 1640XL scanner, with a resolution of 300 dots/in. The average area of one-side of an individual leaf was estimated using Winfolia 2002 image analysis software. Plant components were oven-dried for 48 h at 70 °C and weighed to the nearest 0.001 g. The weight of the scanned leaf subsets after drying was used to calculate the average specific leaf area (leaf area/leaf dry weight). Dry weights of leaves, stem and roots were used to compute the relative allocation to plant components: leaf mass fraction (LMF, leaf dry weight/total plant dry weight), stem mass fraction (SMF, stem (main shoot + branches) dry weight/total plant dry weight) and root mass fraction (RMF, root dry weight/total plant dry weight).

Nutrient content was analyzed in the different plant components (leaves, stem and root) after the final harvest at 5 months. The Kjeldahl method was used to extract N and determine leaf N concentration, along with colorimetric detection of N in a Technicon auto analyzer. To analyze Mg, P and K (along with Ca in soil analyses), the samples were burnt to char at 450 °C and the ashes dissolved in concentrated HCl. Ca and Mg levels were then measured by atomic absorption spectrometry and K was measured by emission spectrometry, using a Perkin Elmer AAnalyst 100. P was

measured by UV–visible spectrometry at 882 nm with a Biochrom Libra S22 spectrometer. All nutrient contents are expressed as % of leaf, stem and root dry mass. Chemical analyses were conducted at Itagra.ct in Palencia (Spain).

Prior to the final three harvests, pre-dawn water potential in the xylem was measured in 2–4 plants of adequate size per combination of treatments. A 1000 MMS Scholander (0–70 bars) pressure chamber was used to estimate water availability for the plant (Bowie and Ward 2004).

Statistical analyses

A total of nine variables were classified into three groups for analysis: (1) vigor and total biomass production: stem height (H, cm), basal diameter (D, mm), number of branches or lateral stems (LS, number) and total plant dry weight (TDW, g); (2) leaf structure: average leaf area (LA, cm^2) and specific leaf area (SLA, cm^2 g^{-1}); and (3) biomass partitioning (stem mass fraction, SMF; leaf mass fraction, LMF, and root mass fraction, RMF). A descriptive analysis of all variables was done for each species in each harvest. Variables that did not meet normality and homoscedasticity assumptions were transformed to their natural logarithms or the root square of $X + 1$ before analysis. Multifactor analyses of variance (GLMs), using sum of squares Type III, were used to analyze the effects of species, substrate, watering and harvest on morphological and biomass traits. Post hoc multiple comparisons were carried out using the Tukey HSD test. Watering was the factor associated with the main unit (forest tray in Design 1 and plot in Design 2) while species and substrate factors were randomly distributed within the blocks. The watering effect was tested against the block due to the split-plot designs.

Design model 1 is expressed as:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + \tau_{ij} + \gamma_k + \beta\gamma_{jk} + \delta_l + \beta\delta_{jl} + \gamma\delta_{kl} + \beta\gamma\delta_{jkl} + \varepsilon_{ijkl}, \tag{1}$$

where Y_{ijkl} is the dependent variable; μ is the mean; α_i Block effect; β_j watering effect; γ_k species effect; $\beta\gamma_{jk}$ species × watering interaction; δ_l substrate effect; $\beta\delta_{jl}$ substrate × watering interaction; $\gamma\delta_{kl}$ species × substrate interaction; $\beta\gamma\delta_{jkl}$ species × watering × block triple interaction; $\tau_{ij} \rightarrow N (0, \omega^2)$ error among trays; $\varepsilon_{ijkl} \rightarrow N (0, \sigma^2)$ error among plants.

Design model 2 is expressed as:

$$Y_{ijklm} = \mu + \alpha_i + \beta_j + \tau_{ij} + \gamma_k + \delta_l + \gamma\delta_{kl} + \beta\gamma_{jk} + \beta\delta_{jl} + \beta\gamma\delta_{kjl} + \theta_m + \beta\theta_{jm} + \gamma\theta_{km} + \delta\theta_{lm} + \gamma\delta\theta_{klm} + \beta\gamma\theta_{kjm} + \beta\delta\theta_{jlm} + \beta\gamma\delta\theta_{jklm} + \varepsilon_{jklm}, \tag{2}$$

where Y_{ijklm} is the dependent variable; μ is the average mean; α_i block effect; β_j watering effect; γ_k species effect; δ_l substrate effect; $\gamma\delta_{kl}$ species × substrate interaction; $\gamma\beta_{jk}$

species × watering interaction; $\beta\delta_{jl}$ watering × substrate interaction; θ_m harvest effect; $\beta\theta_{jm}$ watering by harvest interaction; $\gamma\theta_{km}$ species × harvest interaction; $\delta\theta_{lm}$ substrate × harvest interaction; $\gamma\delta\theta_{klm}$ species × substrate × harvest triple interaction; $\theta\gamma\beta_{mkj}$ species × watering × harvest triple interaction; $\beta\delta\theta_{jlm}$ watering × substrate × harvest triple interaction; $\beta\gamma\delta\theta_{jklm}$ watering × species × substrate × harvest quadruple interaction; $\tau_{ij} \rightarrow N(0, \omega^2)$ error among trays; $\varepsilon_{ijkl} \rightarrow N(0, \sigma^2)$ error among plots.

Significant differences in initial morphological and biomass traits (1st harvest, plant age 2 months) were identified using multifactor analyses of variance, specifically General Linear Models (GLMs) and Eq. 1. Significant differences in morphological and biomass traits in the 2nd, 3rd and 4th harvests were analyzed using a GLM. With plants from the final harvest we tested for significant differences in nutrient accumulation in the root, stem and leaves among the different combinations of species, substrate, watering and plant compartments (leaf, stem and root). This analysis was done with a GLM and a model similar to Eq. 2. Likewise, the effects of species, substrate and watering on the water potential in the stem xylem of the plants were investigated by GLM, using sum of squares Type III and a model similar to Eq. 2, but with the age or harvest factor as covariable.

Statistical analyses of morphological and biomass traits and water potential in the stem xylem were carried out with the STATISTICA (StatSoft 2002) program, while (SAS 2012) was used to analyze nutrient uptake.

Results

Growth

Four of the eight traits studied (*H*, *D*, TDW and LA) at 2 months were affected by substrate fertility and watering interaction effects (Table 1). Species significantly differed in total dry weight, leaf area and specific leaf area, while the species varied in stem height depending on the substrate by watering effects (Table 1). In the final harvest (5 months), 5 out of 9 traits (*D*, TDW, SLA, LMF and RMF) were found to be affected by substrate fertility and watering interaction effects (Table 2a). Substrate fertility effects on total plant dry weight, root mass fraction and leaf area varied with plant age (Table 2a), but plant age did not significantly affect watering and species interaction effects, except in the number of lateral stems or branches (Table 2a). Plant stem height increased from 3 to 4 months, but not from 4 to 5 months; while diameter did not increase from 3 to 4 months but did increase from 4 to 5 months (Table 3 and Tables A2, A3 in ESM). At

2 months *A. seyal* presented significantly higher total dry weight in the high-fertility substrate/high-watering regime combination (1.3 g ± 0.13) than *A. senegal* (0.92 g ± 0.11) (Table 3a). However, the total dry weight of *A. seyal* did not increase in plants from subsequent harvests (Table 3b; Tables A2 and A3 in ESM). In fact, total plant dry weight did not increase for any high-fertility substrate plants in subsequent harvests. However, total dry weight significantly increased month after month in plants with low-fertility substrate (Table 3b and Tables A2, A3 in ESM).

Under a high-watering regime, higher nutrient supply increased stem height by 108 % (11.85–24.7 cm) in *A. senegal* and 57 % (15.33–24 cm) in *A. seyal*, compared to the local substrate. Higher nutrient supply and low watering did not significantly increase stem height in *A. senegal*, but a 77 % increase (10.5–18.61 cm) was observed in *A. seyal* (Table 3a). Basal diameter followed a similar pattern. Specific leaf area varied between species, but was not influenced by substrate and watering effects. Leaf area was greater with high watering and high-substrate fertility, indicating a higher response under better environmental conditions. Leaf area varied according to species, substrate and watering regime, but with no significant interactions except for substrate by watering. For example, the leaf area of *A. seyal* grown in low-fertility substrate doubled under the high-watering treatment. The influence of the different treatments on allometric relations was of minor importance compared to other variables at 2 months.

After the final harvest (Table 3b), corresponding to a plant age of 5 months, *A. seyal* showed the highest stem height (67.23 cm ± 5.12), while *A. senegal* plants showed the highest basal diameter values (5 mm ± 0.45). *A. senegal* presented the highest total dry weight value (8.67 g ± 1.21) but the difference between it and *A. seyal* (7.93 g ± 1.21) was not significant. The substrate fertility effect on plant growth was positive for both watering levels. Predictably, high nutrient with high water availability significantly increased growth in both species. Under these conditions, *A. senegal* stem height increased 43 % (37–53 cm) and *A. seyal* stem height increased 29 % (52–67.23 cm) with respect to the low-nutrient treatment (Table 3b). However, high nutrient with low water availability resulted in a much greater stem height increase of 113 % (24–51 cm) in *A. senegal* and 97 % (24.31–48 cm) in *A. seyal*, compared to plants in the low-watering/low-nutrient regime. Similar effects were observed for total dry weight. With low-watering/high-nutrient supply, total dry weight increased by 269 % in *A. senegal* and 235 % in *A. seyal*. However, with high-watering/high-nutrient supply total plant dry weight increased importantly but with a smaller effect: 171 % in *A. senegal*, and 71 % in *A. seyal*, compared to low water/low nutrient plants. The same

Table 1 Effects of: species (Sp), substrate fertility (Su) and water stress (W) on morphology and biomass in *Acacia senegal* and *Acacia seyal* plants at 2 months of age

Variable	Bl	Sp	Su	W	Sp × Su	Sp × W	Su × W	Sp × Su × W
H	ns	*	***	**	ns	ns	**	*
D	ns	ns	***	*	ns	ns	**	ns
TDW	ns	***	***	*	ns	ns	***	ns
LA	ns	***	***	*	ns	ns	*	ns
SLA	ns	*	ns	ns	ns	ns	ns	ns
LMF	ns	ns	ns	ns	ns	ns	ns	ns
SMF	ns	ns	ns	**	**	ns	ns	ns
RMF	ns	ns	**	*	ns	ns	ns	ns

Bl block, *H* stem height, *D* basal diameter, *TDW* total plant dry weight, *LA* average leaf area, *SLA* specific leaf area, *LMF* leaf mass fraction, *SMF* stem mass fraction, *RMF*, root mass fraction, *TDW* LA, and SLA were transformed Log_{10} (X) prior to analysis, *ns* not significant ($p > 0.05$)

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

pattern was observed for basal diameter, which increased by 74 % in *A. senegal* and 53 % in *A. seyal* with low water/high nutrient availability, though average basal diameter values were significantly higher with high water/high nutrient availability (Table 3b). Less lateral branch growth was observed in both species with the combination of low water availability and low-fertility substrate, but more so in *A. seyal* (Table 3b).

Leaf and stem mass fractions did not vary significantly among treatments (Table 3b), but high-fertility substrate decreased root mass fraction under both watering regimes (22 % for high watering and 55 % for low watering) (Table 3b). The root-to-shoot ratio (data not shown) did not vary significantly among plants 3–5 months old in high-fertility substrate, but was very low (around 0.35) compared to plants cultivated in low-fertility substrate (0.8 in 5-month plants). Root mass fraction followed the same pattern. In high-fertility/high-watering plants the number of leaves decreased by 46 % in *A. senegal* and 57 % in *A. seyal*. In fact, *Acacia seyal* in high-fertility substrate shed almost all its leaves in the hottest month of the study. Average leaf area increased 90 % in *A. seyal* when higher substrate fertility was combined with low watering; but the same combination reduced leaf area in *A. senegal* by 10 % with respect to low-fertility substrate (Table 3b). Specific leaf area was significantly higher in *A. senegal* but low in both species with the high-fertility/low-watering combination. Similar values were observed when plants grown with high-fertility/high-watering were compared to plants grown with low-fertility/low-watering (Table 3b).

Plant nutrition

Total plant N, P, Mg and K uptake varied primarily according to substrate fertility and plant compartment or part (leaves, stem or root), and to a lesser degree

according to watering and species simple effects (Table 2b). Adequate nutrient concentrations were observed in plants with low nutrient substrate (Table 4), indicating that nutrient-poor substrate did not limit growth. P and N uptake were higher in plants cultivated with high-fertility substrate and high water availability. K and Mg were high, especially in low-fertility substrate plants (Table 4). The highest N concentration was always observed in leaves (>3 %), and then in root and stem (leaf > root > stem). P concentration was significantly higher in stem and leaves in both species, but no significant differences were observed between leaf-P and root-P in high-fertility substrate/low-watering plants (Table 4). K concentration was highest in leaves, especially in plants grown with low-fertility substrate. K concentrations were leaf > stem > root and higher in *A. senegal* under both watering regimes; but especially lower in *A. seyal* plants with higher water availability. Mg concentrations were leaf > stem = root in many of the treatments, but Mg was high with leaf = stem = root in *Acacia seyal* (Table 4).

Stem water potential

Acacia senegal presented higher stem water potential (higher negative average value of −1.40 MPa (±0.14), than *A. seyal* (average −0.9 MPa (±0.13). The most negative water potential value (−5 MPa) was recorded for *A. senegal* plants cultivated with high-fertility substrate and low water availability, while *A. seyal* plants cultivated with high-fertility substrate and high water availability presented the lowest negative value of −0.15 MPa. The analysis of variance to test differences in pre-dawn stem water potential (data not shown) revealed that watering level had a significant effect ($p < 0.001$; $df = 1$; $F = 38.10$), as did the species factor ($p < 0.01$; $df = 1$; $F = 10.52$). In other words, the average water potential values were higher

Table 2 Effects of species (Sp), substrate fertility (Su), water stress (W), plant age (Age) and plant part or component (Part: leaves, stem and root) on the morphology and biomass (Model 2a), and nutrient uptake (Model 2b) of two *Acacia* species

Model 2a Significant effects of: species (Sp), substrate fertility (Su), water stress (W) and plant age (Age) on morphology and biomass traits in 3- to 5-month-old *Acacia senegal* and *Acacia seyal* plants

Variables	Bl	Sp	Su	W	Age	Sp × Su	Sp × W	Sp × Age	Su × W	Su × Age	W × Age	Sp × Su × W	Sp × Su × Age	Sp × W × Age	Su × W × Age	Sp × Su × W × Age
H	ns	***	***	**	***	ns	***	ns	ns	ns	ns	ns	ns	ns	ns	ns
D	ns	***	***	**	***	**	ns	ns	**	ns	ns	ns	ns	ns	ns	ns
LS	ns	***	***	ns	***	*	ns	ns	ns	ns	ns	ns	ns	ns	***	**
TDW	ns	***	***	**	***	***	**	ns	**	***	ns	ns	ns	ns	***	ns
LA	ns	***	***	ns	**	ns	ns	ns	ns	***	ns	***	ns	ns	***	ns
SLA	ns	***	ns	ns	***	ns	ns	ns	***	ns	ns	ns	ns	ns	ns	ns
LMF	ns	ns	***	ns	***	ns	*	ns	***	ns	ns	ns	ns	ns	ns	ns
SMF	ns	*	***	**	***	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns
RMF	ns	ns	***	ns	***	ns	ns	ns	***	**	ns	ns	ns	ns	ns	ns

Model 2b Significant effects of the species (Sp), substrate fertility (Su), water stress (W) and plant component (Part) on nutrient uptake, based on total dry weight, in 5-month-old *A. senegal* and *A. seyal* plants

Variables	Bl	Sp	Su	W	Part	Sp × Part	Sp × Su	Sp × W	Part × Su	Part × W	Su × W	Sp × Part × Su	Sp × Part × W	Sp × Su × W	Part × Su × W	Sp × Su × W × Part
N (%)	–	ns	***	ns	***	*	**	ns	ns	ns	ns	ns	ns	ns	ns	ns
P (%)	–	ns	***	**	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
K (%)	–	***	***	ns	***	ns	ns	**	*	ns	ns	ns	ns	ns	ns	ns
Mg (%)	–	***	***	ns	***	**	*	ns	***	*	ns	ns	ns	ns	**	ns

Some variables were transformed using $Log_{10}(X + 1)$, (LS) and using $Log_{10}(X)$, (TDW and LA) prior to analysis. Part refers to leaves, stem and root

Bl block, *H* stem height, *D* basal diameter, *LS* lateral stems or branches, *TDW* total plant dry weight, *LA* average leaf area, *SLA* specific leaf area, *LMF* leaf mass fraction, *SMF* stem mass fraction, *RMF* root mass fraction, *N* nitrogen, *P* phosphorous, *K* potassium, *Mg* magnesium, *ns* not significant ($p > 0.05$)

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

Table 3 Mean values and standard error (in brackets) of functional traits of two Acacias cultivated with different substrates and water stress levels (W1 = 12.20 l/m² water administered every 15 days; W2 = 12.20 l/m² water administered every 7 days)

Variable	Acacia senegal				Acacia seyal			
	W1-low watering		W2-high watering		W1-low watering		W2-high watering	
	Su1-high fertility	Su2-low fertility	Su1-high fertility	Su2-low fertility	Su1-high fertility	Su2-low fertility	Su1-high fertility	Su2-low fertility
(a) 2 months age								
H (cm)	13.5 (4.09) ac	8.7 (0.8) a	24.7 (1.56) b	11.85 (1) a	18.61 (1) bc	10.5 (1.36) a	24 (2) b	15.33 (2) ac
D (mm)	1.6 (0.26) a	1.3 (0.1) a	2.26 (0.16) b	1.65 (0.15) a	1.64 (0.05) a	1.33 (0.05) a	2.11 (0.1) b	1.52 (0.07) a
TDW (g)	0.43 (0.13) ad	0.23 (0.04) a	0.92 (0.11) b	0.38 (0.07) ad	0.78 (0.05) bd	0.43 (0.05) ae	1.3 (0.13) c	0.58 (0.09) de
LA (cm²)	0.19 (0.03) a	0.21 (0.03) a	0.42 (0.05) ab	0.23 (0.04) a	0.55 (0.07) b	0.31 (0.02) ab	0.87 (0.10) c	0.49 (0.05) b
SLA (cm² g⁻¹)	12.53 (3.84) a	13.69 (1.27) a	11.43 (1.48) a	10.45 (1.31) a	12.46 (0.69) a	14.47.2 (0.43) a	14.41 (1.26) a	15.52 (0.72) a
LMF (g g⁻¹)	0.48 (0.03) a	0.43 (0.03) a	0.45 (0.04) a	0.43 (0.02) a	0.48 (0.01) a	0.41 (0.02) a	0.46 (0.02) a	0.49 (0.02) a
SMF (g g⁻¹)	0.21 (0.06) ab	0.24 (0.01) ab	0.28 (0.02) ab	0.30 (0.01) a	0.24 (0.01) ab	0.21 (0.02) b	0.28 (0.01) ab	0.21 (0.01) b
RMF (g g⁻¹)	0.31 (0.04) ac	0.33 (0.04) bc	0.21 (0.02) a	0.28 (0.02) abc	0.27 (0.01) abc	0.37 (0.03) c	0.26 (0.02) ab	0.31 (0.02) abc
(b) 5 months age								
H (cm)	51 (4.44) ac	24 (2) b	53 (4.23) ade	37 (2) bc	48 (4) cd	24.31 (2) b	67.23 (5.12) e	52 (3) ace
D (mm)	4 (0.4) ad	2.3 (0.15) c	5 (0.45) b	3 (0.22) cd	3.1 (0.25) ac	2.03 (0.1) c	4.04 (0.34) ab	3 (0.11) ac
LS (n°)	10.6 (1.46) a	2.16 (1.6) bc	10.42 (1.9) a	3.5 (3.4) bc	9.1 (5.11) a	1 (0.0) c	7.0 (4.4) ab	4.87 (0.66) ab
TDW (g)	4.8 (0.65) ac	1.3 (0.25) b	8.67 (1.21) a	3.2 (0.59) cd	5.70 (0.83) ac	1.7 (0.22) bd	7.93 (1.21) a	4.63 (0.37) ac
LA (cm²)	0.36 (0.09) ac	0.40 (0.06) ac	0.62 (0.07) abc	0.41 (0.04) ac	0.93 (0.19) b	0.49 (0.05) c	0.82 (0.13) bc	0.69 (0.06) abc
SLA (cm² g⁻¹)	8.67 (2.39) a	13.59 (1.44) a	13.68 (0.84) a	10.20 (1.08) a	7.17 (2.13) a	10.59 (0.68) a	11.6 (1.08) a	10.34 (0.46) a
LMF (g g⁻¹)	0.35 (0.04) ab	0.3 (0.03) a	0.3 (0.02) a	0.3 (0.03) a	0.5 (0.05) b	0.3 (0.02) a	0.3 (0.03) a	0.33 (0.02) ab
SMF (g g⁻¹)	0.44 (0.03) ac	0.27 (0.01) b	0.4 (0.01) ac	0.28 (0.02) b	0.34 (0.03) bc	0.25 (0.01) b	0.5 (0.03) a	0.3 (0.02) b
RMF (g g⁻¹)	0.21 (0.03) a	0.45 (0.02) b	0.32 (0.02) ac	0.41 (0.04) bc	0.2 (0.04) a	0.47 (0.02) b	0.23 (0.01) a	0.4 (0.02) bc

Letters indicate differences among treatments and species ($p < 0.05$)

(higher negative tension value) in plants grown with low water availability (-1.63 MPa ± 0.14) than with high water availability (-0.66 MPa ± 0.14), and higher in *A. senegal* (min. $= -0.3$ MPa; max. $= -5$ MPa) than in *A. seyal* (min. $= -0.15$ MPa; max. $= -2.2$ MPa). Pre-dawn stem water potential was not affected by substrate fertility or plant age, which was used as the covariable in the analysis.

Discussion

We studied the early growth (2–5 months) of *A. senegal* and *A. seyal* plants in an experiment with two substrates of contrasting fertility and two watering regimes. Both species presented rapid and high early growth along with opportunistic mechanisms for water and nutrient use. This may explain lower growth with low resource availability, but morphological plasticity, higher vigor and higher investment in dry biomass production—especially leaves and stem mass—when resource availability was higher. The results suggest that despite the fact that water was the most important factor in limiting growth, both watering regimes combined with high nutrient supply significantly influenced growth (especially aboveground growth, at the expense of root growth). Of particular interest here is the indication that high-fertility substrate combined with low watering resulted in a much greater productivity compared to plants in the low watering/low nutrient regime. In terms of aboveground growth potential, *A. senegal* showed high basal diameter increment potential; while *A. seyal* demonstrated a clear tendency toward height increment potential. This difference in growth strategy among the two species has been reported in other studies (Aref et al. 2003).

Despite lower growth, all plants of both species survived on the low watering regime of 24.40 l/m^2 per month. Some species studied from the African savanna woodlands, such as *Acacia nillotica* (L.) Delile and *Mundulea sericea* Willd. were unable to grow and successfully become established when seedlings were watered to field capacity once every 12 or 15 days (Wilson and Witkowski 1998). Other studies have reported that Ethiopian species such as *Acacia horrida* (L.) Willd. were able to survive and cope with drought stress (no watering and high evaporation conditions) for 24 days (Sánchez-Bayo and King 1994). With the low-watering/low-fertility substrate combination, *A. senegal* presented higher numbers of branches and slightly higher relative biomass allocation to root than *A. seyal*. This suggests that although plant growth was lower than in the high-fertility substrate/high-watering regime with respect to total dry weight, basal diameter and height (Ogbonnaya et al. 1998), plants were able to survive by means of other

morphological adaptations; especially by increasing the *R:S* ratio, which varied between 0.7 and 0.9, under water and nutrient stress. Otieno et al. (2005) reported a dry mass reduction of 45 % in water-stressed plants of *Acacia xanthophloea* Benth. and of 40 % in *Acacia tortilis* Forsk. Hayne, and a *R:S* ratio of 0.67 (± 0.04) in *A. tortilis* compared with 0.52 (± 0.01) in the control plants. Li et al. (2008) observed that water stress significantly limited growth, biomass production and biomass partitioning of *Bauhinia faberi* var. *microphylla* Oliv. Ex Craib. (leguminous shrub from arid regions of China). Water stress also altered biomass allocation to root system, resulting in a higher R:S ratio. Our study is consistent with these and other findings (Singh and Singh 2006; Zida et al. 2008). Many other studies show the significant influence of soil fertility and water stress on the growth and biomass allocation of species from arid zones (Hooper and Johnson 1999; Zainudin et al. 2003). For example, Wu et al. (2008) observed better growth in stem height and basal diameter, but decreased root length for *Sophora davidii* (Franch.) Skeels (shrub found in arid zones) in high N soils with good drainage. Some studies show negative effects of fertilization in drought conditions because less biomass is allocated to the root system, since higher N fertilization can accelerate top growth, creating an imbalance between the crown and root system (Zainudin et al. 2003), which makes plants more susceptible to stress (Tan and Hogan 1997; Snyman 2002). Field trials are necessary to test this.

Nutrient uptake was determined principally by substrate fertility and plant parts or components (leaves, branches, stem and roots) interaction effects. Significant differences between *A. senegal* plant components have been observed previously in the P and K values (Raddad et al. 2006). Nutrient concentrations in plant tissues, based on dry weight, indicated adequate nutrition even in local or low-nutrient substrate, and with low watering. The results presented in this study coincide with values for *Acacia* spp. presented in Reuter and Robinson (1997). Singh and Singh (2006) reported on macronutrient concentrations for *Dalbergia sissoo* Roxb. at different watering levels. They observed that N, P, Ca and K decreased with water stress, while P, K and Ca increased in the root. In our study, P and N concentrations were higher in the high-fertility substrate plants and increased with more water; while K and Mg were higher in low-fertility substrate plants. We observed that K accumulation was similar to that of N (both were higher in leaves) and much higher than that of P. This also coincides with typical nutrient accumulation values in plants, where K and N accumulation tends to be 5–10 times greater than P (Brady and Well 2002). In both species, P concentration was significantly higher in stem and leaves. The highest N concentration was always observed in leaves (>3 %) which coincides with previous results on *A.*

Table 4 Mean nutrient concentration values in 5 month-old *Acacia senegal* and *Acacia seyal* plants cultivated with different levels of substrate fertility and water stress (W1 = 12.20 l/m^2 water administered every 15 days; W2 = 12.20 l/m^2 water administered every 7 days)

Concentration (%)	Part	Su1-high fertility				Su2-low fertility			
		W1-low watering		W2-high watering		W1-low watering		W2-high watering	
		A. senegal	*A. seyal*	*A. senegal*	*A. seyal*	*A. senegal*	*A. seyal*	*A. senegal*	*A. seyal*
N	Leaf	4.00 a	3.62 ad	3.56 ab	3.63 ad	2.80 abcde	2.40 abce	3.24 abc	2.40 abce
	Stem	1.70 ce	2.82 abce	1.65 ce	2.34 abce	1.93 bce	1.48 c	1.75 ce	1.41 e
	Root	1.87 bce	2.87 abce	2.28 bcd	2.57 abce	1.68 ce	1.75 ce	2.10 bcde	2.01 bcde
P	Leaf	0.26 a	0.24 a	0.23 a	0.20 a	0.19 a	0.15 a	0.14 a	0.15 a
	Stem	0.30 a	0.28 a	0.24 a	0.20 a	0.18 a	0.26 a	0.12 a	0.13 a
	Root	0.21 a	0.20 a	0.14 a	0.16 a	0.12 a	0.14 a	0.14 a	0.17 a
K	Leaf	2.05 ae	1.86 adef	1.97 ade	1.56 deg	2.39 ab	2.64 ab	3.18 b	2.15 ae
	Stem	1.28 ce	1.19 ceg	1.31 ce	0.94 cfg	2.07 ae	2.05 ae	1.85 adef	1.32 ce
	Root	0.65 c	0.59 c	0.67 cg	0.54 c	0.99 cf	0.83 cg	1.12 cd	0.67 cg
Mg	Leaf	0.27 abde	0.34 afgh	0.31 ade	0.24 bceg	0.32aef	0.36 agh	0.39af	0.46 fh
	Stem	0.10 c	0.17 bc	0.11 c	0.15 bc	0.18 bcd	0.34 afg	0.16 bc	0.23 cefg
	Root	0.15 bcde	0.13 c	0.15 bc	0.15 bc	0.15 afg	0.35 afg	0.35 afg	0.35 afg

Letters indicate differences among treatments and species ($p < 0.05$)

N nitrogen, *P* phosphorous, *K* potassium, *Mg* magnesium concentrations based on tissue dry weight

senegal (Raddad et al. 2006), followed by root and then stem (leaf > root > stem). K concentration was highest in leaves, result that contrasts with those presented by Raddad et al. (2006), who observed that K levels in *Acacia senegal* trees were higher in the roots. In this study, *A. seyal* plants cultivated under the high-watering regime presented lower amounts of K. This key element for helping plants adapt to environmental stress is also associated with water stress tolerance (Brady and Well 2002). The low concentration of this nutrient under high-watering conditions could be related to leaf shedding and the low water potential observed (higher water availability needed in *A. seyal*). As a component of cellular cytoplasm, K plays a key role in reducing osmotic water potential, decreasing water loss through leaf stomata, and increasing root cell capacity to obtain water from the soil (Brady and Well 2002). K also facilitates N fixation (Brady and Well 2002).

Results indicate that both species can tolerate high water stress, which coincides with previous results (Argaw et al. 1999; Raddad et al. 2005; Gaafar et al. 2006; Gebrekirstos et al. 2006), but may present different adaptive responses to water availability. *A. senegal* presented higher stem water potential than *A. seyal*, indicating less efficient water extraction from substrate and transport through the xylem by this species. Studies carried out in field conditions confirm that *A. seyal* has difficulty extracting water from deep soil layers (Traoré et al. 2012). However, *A. seyal* may have presented other characteristics that permit it to withstand the water stress, for example shedding of leaves. In the present work, *A. seyal* shed more leaves under higher

nutrient and high water availability conditions (virtually all of them) than *A. senegal* in the hottest month of the experiment. The leaf shedding observed coincides with previous results for *Acacia* shrub-trees (Aref et al. 2003; Gebrekirstos et al. 2006; Song et al. 2010) and is considered a survival mechanism for drought, when soil moisture is low (Walter 1997; Li et al. 2008; Wu et al. 2008; Song et al. 2010). In our case, we argue that greater leaf shedding of *A. seyal* with high water and high nutrient treatment may have been more related to the high air temperature (45 °C) and low air relative humidity (38 %) registered in the greenhouse in August 2010, than to substrate moisture. Though Gebrekirstos et al. (2006) reported this for adult trees, in our study this trait appears in 4-month-old plants (3rd harvest).

Finally, our results show that both species can be produced successfully in local nursery conditions; both perform well and survive with low watering. The study also shows that fast growing genotypes can be effectively isolated in local nursery conditions, which may stimulate further interesting research. We think that all issues presented point to the necessity of establishing *A. senegal* and *A. seyal* provenance trials in Ethiopia. Provenance trials are of huge interest for detecting populations with desirable characteristics for tree-breeding programs, and for the detection of differences across provenances, to know for example, which are the most appropriate for restoration of degraded lands, gum production, etc. Such provenance trials are also extremely important for studies of adaptation to climate change (see literature therein in Gray et al.

2013). For example, Gebrekirstos et al. (2008) studied the relationship between climate and the growth of *A. senegal*, *A. seyal* and *A. tortilis* in Ethiopian woodlands. They found *A. seyal* to be the most sensitive to fluctuations in the main rainy season. However, annual growth in basal diameter was much more related to precipitation in the main rainy season than to average annual precipitation in all acacias except *A. senegal*. Nicolini et al. (2010) have also shown that precipitation during the rainy season seems to be the most important climatic factor that influences ring-width growth in *A. seyal*.

Conclusions

In this study, plants of both species showed rapid growth and high quality, with no mortality during the experiment. Aboveground growth and productivity was high in both species at the expense of root system ($R{:}S = 0.3$) when nutrient and water supply were high. *A. seyal* showed the highest stem height growth potential, while *A. senegal* showed the highest basal diameter values. Water stress limited growth, biomass production and biomass partitioning considerably. Plants with low resource supply presented lower stem height, basal diameter, total dry weight, and numbers of lateral branches. In these plants, the $R{:}S$ ratio varied between 0.7 and 0.9, showing that plants allocated relatively more dry weight to the root system. Higher substrate fertility increased aboveground plant growth at the expense of root growth, even with low watering regime. Though water stress significantly limited growth under both soil conditions, substrate fertility effects were relatively higher in low than in plants with high water supply. This suggests an efficient method for producing plants suitable for afforestation in arid zones. *A. senegal* and *A. seyal* present different drought stress coping mechanisms that are independent of substrate fertility. *A. senegal* showed greater potential for allocation to roots and higher pre-dawn stem water potential. Both species can be produced successfully in local nursery conditions; both perform well and survive with low watering. The study also shows that fast growing genotypes can be effectively isolated in local nursery conditions, which may stimulate further interesting research. The study provides examples of species growth response to different water and nutrient environments.

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