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MORPHOLOGICAL PLASTICITY OF *Acacia senegal* (L) WILLD. SEEDLINGS WITHIN A DROUGHT GRADIENT IN NORTH EASTERN NIGERIA

A.U. Jibo[1,2] and M.G. Barker[2]

[1]Department of Forestry and Wildlife Management, Federal University Dutse, P.M.B. 7156, Dustse, Jigawa State, Nigeria
[2]Institute of Biological and Environmental Sciences, University of Aberdeen, AB 24 3UU Aberdeen, United Kingdom

ABSTRACT

A reciprocal transplant experiment was set up (n=128) to investigate the morphological plasticity of *A. senegal* seedlings to changes in available soil moisture in Yobe State, Nigeria. Half of the *A. senegal* seedlings from each of the Nguru and Gujba populations were planted in their 'home' locations while the remaining plants swapped with seedlings from the 'away' population. Stem diameter was measured approximately every 14 days for all plants and at the end of the experiment (430 days), 50 randomly selected seedlings from each treatment were harvested to determine total dry mass partitioned into the shoot and roots. For root extraction, a trench 0.5 m x 1 m was dug with a spade to 1 m depth at about 80 cm away from the base of the seedling. Soil was carefully removed using a sharp blade from the surface downward to search for the roots. *A. senegal* seedlings from each population showed distinct growth responses to their local environment, whether 'home' or 'away'. Root: shoot ratios were related inversely to soil moisture availability. This was mainly attributed to increasing biomass allocation to roots rather than decreasing allocation to shoots. Seedlings that were transferred from a northern arid location to a more semi-arid site showed a greater plasticity than seedlings moved in the opposite direction. Results suggest that, in *A. senegal* seedlings, (a) growth and biomass allocations allowed acclimation to local soil moisture conditions, and (b) that there were differences in plasticity among seedlings from the northern and southern provenances.

Keywords: Allometry; growth responses; root-shoot ratio; root depth

INTRODUCTION

There has been a discernible shift in climate affecting the Sahelian zone of northern Nigeria (Okpara *et al.,* 2013; Ekpoh & Nsa 2011; Odjugo 2010; Olaniran 1991; 2002). During the last 30 years, at least, precipitation has both shifted southwards (60 km) and has become less intense (by 100–150 mm year^{-1}) (Nicholson 2013; Ekpoh & Nsa 2011). This is regarded by some to be part of a long-term, sustained climate change in the region (Olaniran 2002; Odjugo 2010; Federal Republic of Nigeria 1999; Nicholson *et al.,* 1998). Clearly, any overall change in soil moisture availability may have potentially important implications for ecosystems in NE Nigeria (Enete & Amusa 2010, Ehrenfeld 2005, Scholes & Archer 1997).

One species that is both ecologically and economically important in the sub-Sahel region is *Acacia senegal*, known locally as gum Arabic (*Senegalia senegal* (L) Britton) (Odee *et al.,* 2012, Bouchenak, 2010). *A. senegal* has a wide distribution (Booth & Wickens, 1988) and is particularly adapted to the hot regions of Africa especially in areas along the southern frontiers of the Saharan desert including Nigeria (NAS, 1979; Chikamai *et al.,* 1996). The gum Arabic belt is characterized by mean annual air temperature of 14–43 °C and rainfall as low as 200 mm annual, with 8–11 dry months. Mean annual rainfall ranges from 300–450 mm annual (NAS, 1979). *A. senegal* trees can also grow in areas with mean annual rainfall as high as 800 mm.

Plant species that successfully establish in dry environments often possess or develop drought adaptation. Drought adaptation properties of plants include drought avoidance or drought tolerance (Farooq *et al.,* 2009; Lopes *et al.,* 2011; Anjum *et al.,* 2012). Drought adaptations are very important for the survival and growth of plants in drought-prone environments. In desert environments, soil water deficits can often be significant, restricting the ability of some species to establish successfully (Dias-filho and Dawson, 1995).

Drought avoidance traits (Jones, 1993) are those mechanisms that minimise the occurrence of damaging water deficits, while drought tolerance properties are those physiological adaptations that enable plants to continue functioning in spite of plant water deficits (Jones, 1993). Drought avoiders possess deep root systems, leaf shedding before the onset of dry conditions, and fast growth rates in the wet season (Kramer & Boyer, 1995). Drought tolerance features of plants include having leaf properties that maintain a positive turgor by osmotic adjustment and a high bulk modulus of elasticity (Arabzadeh & Emadian, 2010).

A gradual change across the distributional range of a species with rainfall gradients supports the theoretical expectation that provenances from the drier parts of the sample region are better adapted to drought (Montes & Weber, 2009). The gradual shift *of A. Senegal* from the driest to the wettest zone may be related to climate change (Traoré *et al.,* 2012).

In *A. senegal*, large variations can occur both between and within populations, apparently in response to environmental conditions such as rainfall and soil types (Daffalla *et al.,* 2011; Josiah *et al.,* 2008; Elfeel &Warrag, 2004; Jibo *et al.,* 2018a).This suggests that there is genetic variability among the populations of the species (Brenan, 1983; Jibo *et al.,* 2018a). Despite the ecological and economic importance of this species, little is known about its response to drought and ability to acclimate to water deficits. Tree populations may exhibit continuous variation in growth, phenology, survival and other adaptive traits in regions with pronounced environmental gradients in temperature and rainfall (Jibo *et al.,* 2018b; Weber *et al.,* 2008). Vegetation in arid regions such as Northern Nigeria is dependent on rainfall, and any alteration in seasonal water availability could cause shifts in plant community structure (Weltzin & McPherson, 2000). One way in which plant phenotypic plasticity can be tested in field conditions is with reciprocal transplant experiments (Ågren, & Schemske, 2012). These can be used to evaluate the relative contributions of environmental and genetic variation to plant physiology and morphology (McGraw, 1987; Schoen *et al.,* 1986; Price & Morgan, 2006).

In this study, the focus was on morphological and growth responses in plants on a naturally occurring 120-km-long gradient of soil moisture in NE Nigeria. In particular, the potential role of differential root growth under different moisture regimes was investigated.

Drought stress strongly influences root development and root growth (Franco, 2011). Species such as *A. senegal* that are native to arid environments often have high root: shoot ratios (Aref & El- Juhany, 1999). Root growth is usually more affected by drought stress than shoot growth; resulting in a decrease in root: shoot ratio under drought-stress (Franco *et al.*, 2011), including in trees (Steinberg *et al.,* 1990). Root depth and distribution are vital components of a plant's strategy for growth and survival in water-limited ecosystems (Collins & Bra, 2007). In arid environments, or environments with a long dry season, some plant species can grow particularly deep roots (Canadell *et al.*, 1996). The hypotheses being tested in this study were that: H_1 root: shoot ratios will be related inversely to soil moisture availability and that, H_2 there will be significant variation in growth and difference in plasticity among seedlings from the northern and southern provenances.

MATERIALS AND METHODS

Study Area

Yobe State lies in the extreme corner of Northeast Nigeria. It is one of the states within the Sehelian zone. It is located between lat. 10.5° N to 13° N and long. 9.5°E to 13°E (YBSG, 1994). The climate is largely influenced by the interactions between two air masses: the tropical maritime air mass from the Atlantic Ocean and the tropical continental air mass from Sahara Desert. The climate is characterised by rapid changes in temperature and humidity. Temperatures are generally high during March-May, with the highest recorded mean monthly temperature of about 40°C in April (Ayoade, 2004). The lowest temperatures occur of December - January due to the influence of harmattan. Seasonal rainfall predictions by NIMET (2013) shows that the northern Nigeria region will have a range of mean annual rainfall that is between 300mm -1200mm. Annual rainfall lasts between three to four months (Aregheore, 2002). The relative humidity is very high during the rainy season reaching about 65 to 70%.

Soil Water Content

Soil water content at the sites was determined using a soil moisture probe Type PR2 (Delta T Devices, Cambridge UK). Access tubes were installed at 1m soil depth, at a distance of 0.3 m from the nearest seedling in the centre of the plots. Measurements were taken at 10 cm, 20 cm, 40 cm; 60 cm and 100 cm. Rainfall data obtained from Nigeria Meteorological Agency (NIMET) were used to construct mean annual rainfall isohyets for the sample region.

Plant Material

Acacia senegal (synonym *Senegalia senegal* (L.) Britton) germplasm was collected from two provenances in Yobe State, Nigeria, incorporating two principal ecological zones. Seedings from Nguru (sahelian) and Gujba the (sudanian) zones were obtained from the Rubber Research Institute of Nigeria, Gum Arabic Sub-station, Gashua, located at lat 12°46'N and Long 11°00'E alt 360m. Selection criteria were based on the provenance trial recommendations (Burley & Wood, 1978).

Seeds were soaked in water at room temperature of 27 °C for 24 h as a pre-treatment to overcome seed dormancy (Doran *et al.*, 1983). Seeds were sown in plastic pots 18 cm high and 14 cm in diameter, containing a 2:1 mixture of top soil and sand, and grown for 1 month, with regular watering in a nursery at the Rubber Research Institute of Nigeria, Gum Arabic Sub-station, Gashua.

Site Preparation and Experimental Design

Experimental sites were used to study growth rates of local compared with non-local provenances of *A. senegal* seedlings. Sites were first cleared and then deep-ploughed with a chisel plough, followed by a disc plough. At the establishment of the field trials, soil samples were taken from a pit at each site (Nguru and Gujba) at different depths (0–25 cm, 25–50 cm, 50-75 cm, 75–100 cm, 100–150 cm, 150–200 cm). Undisturbed soil sample were collected by means of metal core sampler for complete soil analysis using the cylinder soil method (Blake & Hartge 1986).

A reciprocal transplant experiment design was used, involving four equally-sized plots each at the Nguru and Gujba sites. Of these four plots, two were used for local and two for non-local populations of seedlings. *A. senegal* seedlings from Nguru and Gujba populations were planted in their 'home' locations and swapped with seedlings from the 'away' populations. Seedlings were sown at a spacing of 3 x 3m on a plot size of 25 x 25 m and have 128 seedlings each.

Growth and Biomass Measurements

Stem diameter was measured approximately every 14 days for all plants, 30 days after transplantation. Stem diameter was measured at 3 cm above ground level by an electronic vernier calliper, CD-12 Mitutoyo Corporation, Kanagawa, Japan) with a sensitivity of ± 0.01 mm. Where the stem was non-circular, two measurements were taken at right angles to one another and the average used.

At the end of the experiment (430 days), 50 randomly selected seedlings from each treatment were harvested to determine total dry mass partitioned into the shoot and roots. For root extraction, a trench 0.5 m x 1 m was dug with a spade to 1 m depth at about 80 cm away from the base of the seedling Soil was carefully removed using a sharp blade from the surface downward to search for the roots.

Once the root was spotted the soil around the root was carefully knocked loose. Root length was measured, the length was determined by laying out the washed roots on a flat surface and measurement was taken with a meter rule, before drying in 80 °C oven to obtain root dry weight. Stem and shoot dry mass and root/shoot ratios were calculated from component dry weights.

Data Analysis

A normality test was performed on all the data. All shoot and root data collected were statistically analysed by one way ANOVA performed with the aid of MINITAB ® statistical package (Release 16.12.0) & Sigma Plot ® (Release 12.0), using each variable as the response and treatment as the factor to determine possible statistically significant differences between mean the significance level applied if not otherwise stated was $P < 0.05$.

RESULTS

Soil Moisture Content

(a) Dry season (November–May 2012) (b) Rainy season (June–October 2013)

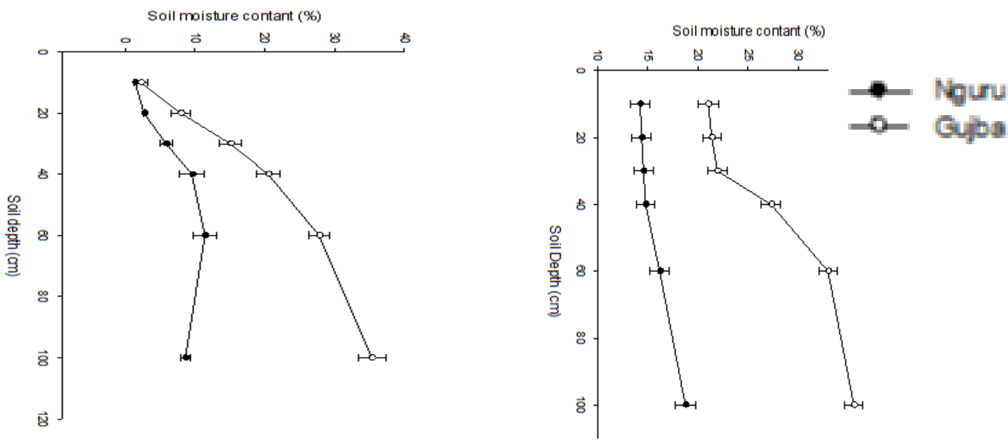

Figure 1: Mean volumetric soil moisture content (+SE) at different soil depths in Nguru (●, arid) and Gujba (O, semi-arid) at two sites during the (a) dry season (November–May 2012) and (b) the rainy season (June–October 2013).

A soil moisture probe (PR2 Delta T Devices, Cambridge UK) was used in soil water content (SMC) measurements at 10 cm, 20 cm, 40 cm; 60 cm and 100 cm. SMC was higher in the lower soil strata during the dry season at Gujba, compared with the Nguru site (Figure 1a), the topsoil dried much faster than the subsoil layers. The influence of rainfall on SMC was greater in the upper soil strata in Gujba as compared to the subsoil layers during the rainy season (June –October 2013) especially at greater depths. (Figure 1b). significant differences were evident in soil moisture at different soil depths. Soil moisture was higher at the semi-arid site, especially at greater depths.

Root Length

Analysis of variance of the root length (RL) and root: shoot ratio showed significant differences between the two provenances (Table 1). Nguru provenance had higher mean values for both variables at 220 days and at 430 days.

Biomass allocation and root morphology of *A. senegal* within the two provenances differed significantly (Table 1). Root lengths were greater in Nguru (Figure 2) and were significantly different between treatments ($F_{3, 195}$=132.19, P<0.001) and sites ($F_{1, 197}$=166.46 P<0.001). Similarly, there were significant differences in root: shoot ratio both between treatments ($F_{3, 196}$=35.80, P<0.001) and sites ($F_{1, 198}$=82.96, P<0.001). The root: shoot ratio was also higher in Nguru provenance at 220 days and 430 days.

Table 1: Analysis of variance using two-way analysis of variance

Source	DF	F value	P value	Prov.	Average
(a)Variable = root length					
Treatments	1	132.399	< 0.001	Nguru	198.95
Site	1	117.405	<0.001	Gujba	99.91
Treatments X site	1	15.705	<0.001		
Residual	76				
	79				
(b) Variable = root/shoot					
Treatments	1	27.918	< 0.001	Nguru	2.528
Site	1	7.889	0.006	Gujba	1.587
Treatments X site	1	2.681	0.106		
Residual	76				
Total	79				

(a) Variable = tap root length, (b) Variable = root/shoot. Post hoc analyses were performed using Tukey 95% simultaneous confidence intervals all pair wise comparisons among levels of provenance. DF =degrees of freedom, Prov =provenance.

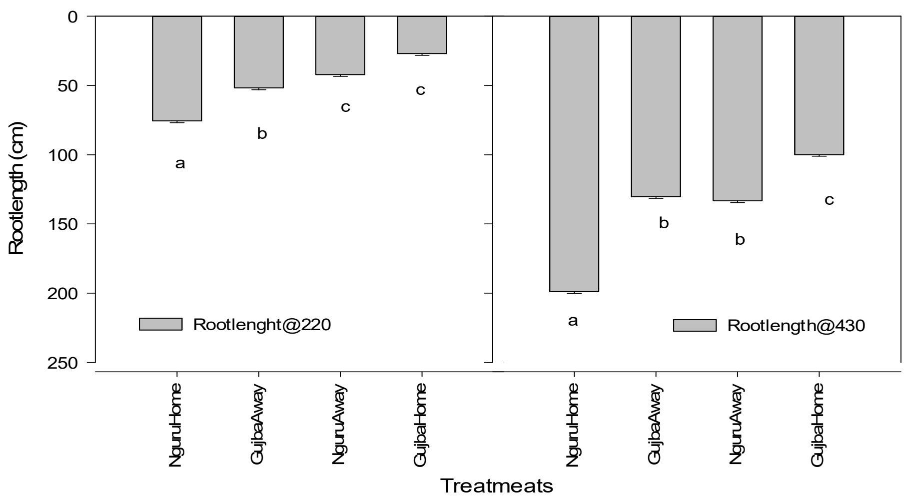

Figure 2: Mean (±SE) root length of *A. senegal* in Nguru and Gujba

Stem Diameter

The mean stem diameter in each treatment at 220 days and 430 days, are presented in Figure 3. The meanshoot diameter of *A. senegal* for the two provenances (Gujba and Nguru), shows a significant difference ($F_{3, 508}$= 34.80, P<0.001) between the treatments at 220 days and at 430 days($F_{1, 306}$= 16.33, P<0.001). There was also a statistical difference in mean shoot diameter between the two sites at 220 days ($F_{1, 306}$= 16.33, P<0.001) and 430 days ($F_{3, 304}$= 16.33, P< 0.001).

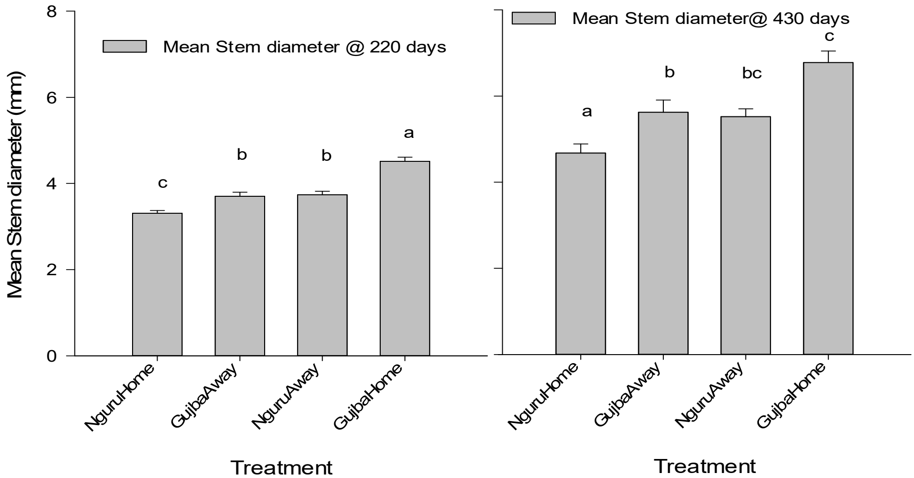

Figure 3: Mean (±SE) stem diameter of *A. senegal* in Nguru and Gujba

Stem Length

The mean shoot lengths of all plants in each treatment are presented in Figure 4, at 220 days and 430 days, The meanshoot lengths of *A. senegal* for the two provenances (Gujba and Nguru), shows a significant difference ($F_{3, 508}$= 34.80, P<0.001) between the treatments at 220 days, there was also a significant difference in mean shoot lengths between the two sites ($F_{1, 510}$= 42.23, P<0.001). However, there was no statistically significant differences among treatments at 430 days ($F_{3, 304}$= 1.01, P= 0.390).

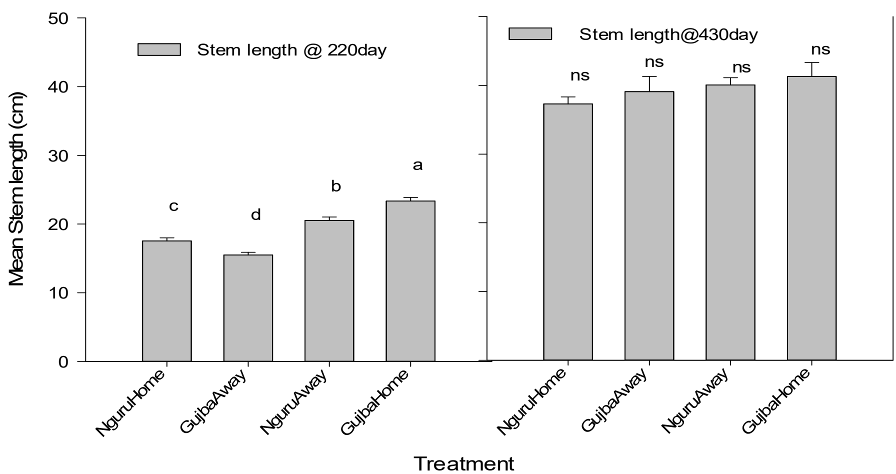

Figure 4: Mean (±SE) stem length of *A. senegal* in Nguru and Gujba

Root: Shoot Ratio

The mean root: shoot ratios in each treatment are presented in Figure 5, at 220 days and 430 days.The mean root: shoot ratio of *A. senegal* for the two provenances (Gujba and Nguru), showed a significant difference ($F_{1, 79}$= 7.889, P=0.006) between the treatments at 220 days, there was also a significant difference in mean root: shoot ratio between the two sites ($F_{1, 79}$= 42.23, P<0.001). Similarly, there were significant differences at 430 days in the root shoot ratio both between treatments ($F_{3, 196}$=35.80, P<0.001) and sites ($F_{1, 198}$=82.96, P<0.001).

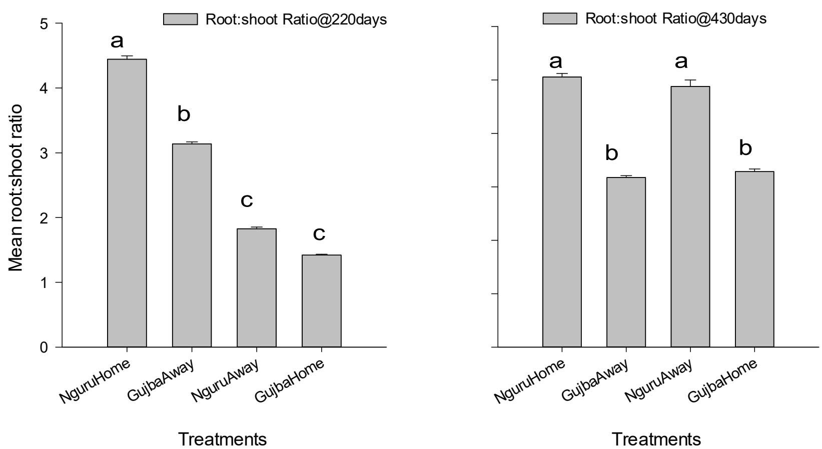

Figure 5: Mean (±SE) root/shoot ratio of *A. senegal* in Nguru and Gujba

The responses of *A. senegal* to drought acrossa moisture gradient demonstrated that there were differences in the pattern of growth between Nguru and Gujba provenances for this species. This is consistent with results in the study of *A. senegal*, the gum Arabic belt in central Sudan, and the study of *Zizipusrotundi folia* in Zimbabwe (Raddad & Luukkanen 2006; Arnt *et al.,* 2001). There was a decrement in stem diameter in the Gujba provenances in the away treatment when compared to its counterpart in Nguru provenances. This may be indicating a response to lower soil water availability. When transferred ‘away’, seedlings from both provenances did not fully acquire the stem diameter characteristics of the ‘home’ provenance. Reductions in diameter growth of acacias due to water deficit have been observed in many studies (Phillips & Riha, 1993; Barros & Barbosa, 1995; Aref & El-Juhany, 1999; Lieurance, 2007; Tomlinson *et al.,* 2013: Jibo *et al* 2018b). Plants exposed to drought stress showed different responses, according to species and severity of the drought stress. Seedlings under the limited watering regime developed deep roots (Jibo & Barker 2019), which presumably allowed seedlings to access the limited water available at greater depths in the soil.

Species of both provenances apparently adjusted their pattern of root: shoot partitioning in response to soil moisture. Root:shoot ratios were higher at the arid site. When transferred 'away', seedlings from both provenances only partially acquired root:shoot characteristics of the 'home' provenance. This suggests that change in root: shoot partitioning was required to take advantage of low-soil moisture and also to mitigate the effect of decreasing soil moisture availability (Kurpius *et al.,* 2003). However, increases in root: shoot ratios, while improving plant water status may limit carbon gain due to decreased allocation to leaf area (Munns & Sharp, 1993; Blum, 2005; Schwinning & Ehleringer, 2001).

A. senegal seeding in the clay semi-arid site seemed to utilise the water in the topsoil rather than that below, the clay soil may have retained enough water to support the plant growth in the upper soil stratum. When drought stress develops, root: shoot ratios increase. Results indicated that Nguru (arid) may establish easily in the wetter Gujba (semi- arid) without developing deeper roots because soil moisture remains above the critical threshold within the soil profile. In other words, rooting depth in *A. senegal* was positively related soil exploration and greater acquisition of water from deep soil strata (Lynch & Wojciechowski, 2015; Jibo & Barker, 2019).

Water uptake can be maximised by the allocation pattern namely increasing investment in the roots (Chaves *et al.,* 2003). The allocation of biomass to different plant organs also depends on species, ontogeny and on the environment experienced by plants (Poorter & Nagel 2000). In environments where resources are abundant, plants have little need for the plasticity of root: shoot ratio (Aikio & Markkola, 2002). However, root length may increase in a drying soil even at the expense of a reduced total shoot mass (Blum 2005, Dias-filho, 1995).

Plants in this study were considered to be locally adapted if 'home' plants perform better than 'away' plants of the same provenance in reciprocal transplantation experiments (Bowman *et al.,* 2008; Kawecki & Ebert, 2004). However, the degree to which such home-away differences are to be expected when studying pairs of populations depend on the actual environments.

Plants growing in arid and semi-arid environments appear to specialize in taking up water from specific soil layers at certain times of the year (Schwinning & Ehleringer, 2001).Species exploiting water in deeper soil layers, such as *A. senegal*, can access a more stable, longer lasting water resource that is replenished by the larger, more infrequent pulses (Dodd *et al.,* 1998). These plants take a more "slow but steady" approach to water uptake, and the characteristics of this group reflect this strategy (Weltzin & Tissue, 2003). Deep-rooted plants rely on stored inter-pulse moisture, and they must increase allocation to roots (Schwinning & Ehleringer, 2001).

CONCLUSION

The results support hypothesis tested in this study that: H_1 root: shoot ratios will be related inversely to soil moisture availability. Rooting depth may have been the major factor that influenced the physiological response of *A. Senegal* to the soil moisture; seedlings showed a growth response to soil moisture gradients within both sites.

The study also supported H_2, that there will be significant variation in growth and survival between the seedling from the northern and the southern provenances. The significant variation in morphological traits between the home and away suggests that there is variation to facilitate change to drying conditions. More biomass was allocated to the root (higher root: shoot ratio) at the more arid site. This may confer drought avoidance while reducing overall growth.

Results also supported H_2 that there will be a difference in plasticity among seedlings from the northern and southern provenances. Seedling from different provenances adjusted their biomass allocation differently when shifted within the moisture gradient. This shows that variation in soil water availability determines patterns of growth. There may be implications in the performance of *A. senegal* if there are further shifts in rainfall. *A. senegal* species may cope with changing climatic characteristics through phenotypic plasticity responses. Species with distinct adaptations may be restricted in their ability to change and evolve under a rapidly changing climate.

Species from the northern provenance should be grow in the southern provenance, as they may cope better with changing climatic characteristics and drought through phenotypic plasticity responses.

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