



Effect of drought stress on the physiology and early growth of seven *Senegalia (Acacia) Senegal* (L.) Britton provenances

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Abstract

Decline of *Senegalia senegal* (*Acacia senegal*) in its natural range has been observed and attributed mainly to harsh environmental conditions such as frequent drought occurrences. The objective of this study is to assess the effect of water stress on growth, biomass allocation and photosynthetic capacity in *Senegalia senegal* seedlings. Seeds were collected from seven provenances in Senegal and grown under greenhouse conditions in a randomized complete block design with 5 replications. Seedlings were subjected to three cyclic droughts by watering them when average soil moisture content dropped to 4.7%, 2.7%, and 2.1% during the first, second, and third dry down cycles, respectively. With the exception of net photosynthetic rate, stomatal conductance and transpiration at the second and third dry down cycles, no drought by provenance interaction was found for any trait measured. Ngane provenance had a lower root/shoot ratio and allometric analysis revealed that Ngane allocated less biomass to roots than shoots. Ngane developed superior growth traits and biomass production, despite similar net photosynthetic rate with other provenances before treatments started. Overall, drought stress significantly reduced biomass, stem height, diameter and leaf gas exchange. Total biomass was reduced by 28.5%, whereas root/shoot ratio was increased by 25% compared to control. Significant interaction on leaf gas exchanges at the second and third dry down cycles reveals different sensitivity levels to drought among provenances with the Ranerou provenance exhibiting no decline in leaf gas exchange. No significant difference of stomatal limitation among genotypes was found, which is indicative of the complex process of photosynthesis and the need for extended times scales for measurements to better depict physiological sensitivity of *Senegalia senegal* to drought.

Keywords *Senegalia senegal* · Provenance · Drought · Leaf gas exchanges

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Introduction

Senegalia senegal (L.) Britton, mostly known as *Acacia senegal*, is a multipurpose tree and the main gum arabic producing species distributed throughout the arid and semi-arid lands in Africa. It is reported to be adapted to a wide range of soils types, soil pH and climate (Von Maydell 1986) and is known for its high tolerance to water stress (Gaafar et al. 2006). However, water stress can result in heavy mortality such as during severe droughts in the 1970s when 80% of gum forests in West Africa were lost (Wate 1979). Loss of this species is further exacerbated by low natural regeneration due to a high mortality rate following seed germination (Seif el Din 1969). In addition, a prolonged dry period after a short growing season (July–September) limits artificial regeneration under field conditions in semi-arid areas such as Senegal. Therefore, plant establishment and growth are critical in the early developmental stage of such species.

In response to water limitations, plants are able through physiological regulations, morphological adjustments, and changes in allocation to adjust their growth and often become more drought tolerant. Often, drought tolerant species allocate more resources to root growth than shoot growth for their survival in dry environments (Aroca 2012). Root to shoot ratio is crucial and may confer adaptability to plants in water-limited habitats. However, the root response to drought is variable (Liu et al. 2000; Zollinger et al. 2006) and the response of *Senegalia senegal* roots to drought is unknown. Changes in allocation can result from a faster increase of root growth than shoot growth, a reduction of shoot growth without change in root growth, or a less restricted root growth (Espinoza et al. 2013; Li 1998; McMichael and Quisenberry 1991; Zollinger et al. 2006). Studies have reported that biomass partitioning to organs is controlled by mechanisms inherent to species/genotypes which influence the ability of plants to cope with changing environments (Aroca 2012; Haugen et al. 2008; Hausmann et al. 2005; Otieno et al. 2005). Allometric analyses (Ledig et al. 1970) that determine how biomass allocation patterns change in response to water stress may help in elucidating patterns of morphological plasticity in genotypes which may be related to initial survival, growth and ultimately gum arabic productivity.

In water limited ecosystems drought tolerance mechanisms are especially important to the survival, growth, and productivity of tree species (Kozlowski et al. 1991). Stomatal closing and leaf shedding are among drought avoidance strategies that limit water loss, but these reduce photosynthesis and suppress growth (Taiz et al. 2015). *Senegalia senegal* is native to dry lands; however, studies examining eco-physiological adaptation in genotypes (Diatta et al. 2022; Gaafar 2005; Gray et al. 2013; Isaac et al. 2011; Lassouane et al. 2013; Sarr et al. 2021; Siam 2011; Vassal et al. 1992) are still scarce. Siam (2011) reported that higher intrinsic water use efficiency induced by strong stomatal control would be a selective trait for more drought tolerant *Senegalia senegal* genotypes. Indeed, stomatal regulation plays an important role in photosynthesis acclimation to water stress (Xu and Zhou 2008). Physiological factors related to drought tolerance are likely to differ between genotypes and this information can be used to improve management of *Senegalia senegal* in the semi-arid lands of the sahelian area.

In the Sahelian regions, *Senegalia senegal* is considered an endangered tree species due to high mortality rate as result of consistent severe aridity (Poupon and Bille 1974). Therefore, to improve planted seedling survival and growth in these natural and harsh environments a better understanding of drought effects on physiological and morphological adaptation is

crucial and will aid in assessment of genotypes for reforestation purposes in various dryland regions of Africa. This study examines the growth and physiological response of 7 *Senegalia senegal* provenances to drought stress. Our specific objectives are to: (1) determine if *Senegalia senegal* genotypes differ in leaf gas exchange, morphological adjustments and biomass accumulation in response to cyclic drought, and (2) determine if leaf gas exchange is related to *Senegalia senegal* growth response to drought.

Materials and methods

Plant material and growth

The study was conducted in a greenhouse, at Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA, which was kept above 25 °C and ventilated with box fans when temperatures exceeded 32 °C. Ambient light was extended using sodium vapor lamps in order to maintain a 16-hour photoperiod with minimum photosynthetic photon flux density of 100 $\mu\text{mol s}^{-1}$. Seeds of seven *Senegalia senegal* provenances were obtained from National Institute for Forestry Research of Senegalese Institute for Agricultural Research in Senegal in 2014 (Table 1). Seeds were chemically scarified with concentrated sulfuric acid (98%) for 10 min and germinated into shallow flats filled with Promix BX (Premier Tech Horticulture, Quakertown, PA) after being rinsed thoroughly with water. Once emerged, young germinals were transplanted individually to tubes (SC10 super cell, 3.8 cm diameter x 21 cm deep, Stuewe and Sons, Tangent, OR) containing Promix BX and grown for 3 months. Seedlings were transplanted into 2.3 L plastic pots (Treepots, 30.5 cm height and 10.2 width, IGC Greenhouse Megastore, Danville, IL) filled with a 2:1 mix of Promix BX and washed sand. Seedlings were initially kept well-watered and fertilized with 2.5 g slow release Osmocote (14-14-14, N-P-K Scotts Miracle-Gro Marysville, Ohio) and grown for 1 more month prior to experimental treatment.

Experimental design and treatments

The experimental design was a randomized complete block with 2 water treatments (control-well watered and moderate drought stress) and 7 provenances replicated 5 times, providing a total of 70 experimental units. Because *Senegalia senegal* drops leaves during severe drought, we used a moderate level of drought stress in order to avoid leaf shedding. The moderate drought treatment was designed to mimic field conditions during the rainy season when drought often occurs and then rainfall subsequently resumes. Therefore, we adopted a dry down cycle treatment for which plants were not watered until the soil volumetric moisture content, averaging initially 28%, dropped to 4.7%, 2.7%, and 2.1%, at the first, second, and third dry down cycles, respectively. At the end of each dry down the plants were rewatered to reach the initial soil volumetric moisture content.

Measurements and harvest

Plant stem height and ground-line diameter of all plants were measured at the end of the experiment. Leaf gas exchange was measured on the newest fully mature leaf using a por-

Table 1 *Senegalia senegal* seed sources, locations, mean annual rainfall (the average between 2007–2017) and soil types of the 7 provenances (or the closest meteorological stations) used in this study. Diamenar, Diery Birane, Ngane, Ranerou and Velingara were collected in their sites of origin while Daiba and Kidira were obtained in Dahra from a provenance trial established in 1994

Provenances	Latitude (W)	Longitude (N)	Elevation (m)	Mean annual rainfall (mm)	Predominant soil types (Tappan et al. 2004)
Daiba	15° 21' 95"	13° 06' 92"	28	458	Ferruginous tropical sandy soils, slightly leached
Diamenar	15° 59' 7"	15° 52' 5"	10	346	Red-brown sandy soils, and ferruginous tropical sandy soils
Diery Birane	15° 23' 7"	15° 23' 5"	45	301	Red-brown sandy soils, and ferruginous tropical sandy soils
Kidira	14° 27' 23"	12° 13' 89"	39	651	Very shallow, loamy, gravelly, rocky, highly leached ferruginous soils over laterite and Precambrian parent material
Ngane	14° 12' 6"	16° 12' 3"	2	672	Ferruginous tropical and ferralitic soils; loamy sands over fine sandy loam at depth
Ranerou	15° 17' 4"	13° 57' 4"	35	473	Ferruginous tropical sandy soils, slightly leached
Velingara	15° 00' 8"	14° 41' 5"	25	915	Ferralitic tropical; ferruginous tropical sandy to clayey soils over laterite in the east; hydromorphic in the valleys

table infrared gas analyzer (LI-6400 Lincoln, Nebraska, USA). Environmental conditions in the leaf cuvette were set at 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD), 398 $\mu\text{mol mol}^{-1}$ reference CO_2 concentration, 25 °C block temperature, and a flow rate of 400 $\mu\text{mol sec}^{-1}$. Photosynthetic rate (A), transpiration (E), and stomata conductance (G_s) were measured immediately before treatments began, and then at the end of each dry cycle when the average soil moisture volumetric content was at a minimum prior to rewatering. Leaf area enclosed in the cuvette was determined using WinRHIZO Software (version 2005b Pro, Regent Instruments Inc, Quebec, Canada) and an EPSON Expression 1680 scanner (Epson America Inc., Long Beach, California).

Intrinsic water use efficiency (WUE_i) was estimated as the ratio between net photosynthetic rate and transpiration. Stomatal limitations were computed following the equation $L_s = (C_a - C_i)/C_i$ where C_a is CO_2 concentration in the ambient air, C_i is the internal CO_2 concentration (Jones 1985). According to this theoretical method, C_a equals C_i at no stomatal limitation (resistance). When C_i goes down, the drop in CO_2 concentration corresponds to stomatal limitation. C_i was calculated by the LI 6400 during leaf gas exchange measurements. Soil volumetric water content across a depth of 0 to 12 cm was monitored twice a week using a HydroSense soil moisture meter (Campbell Scientific, Inc, Logan UT). Two compound leaflets were selected from each plant after measurements to assess a chlorophyll

content index using a SPAD chlorophyll meter (SPAD-502 Minolta CO.LTD. Japan). As the leaflets were too small to fill the entire frame of the SPAD meter, a standardized 2 mm circular leaf disk was removed using a Disposable Biopsy Punch with PLUNGER (Miltex, Inc. York, PA) and placed on the optical screen.

At the end of the experiment (84 days after the start of treatment) all plants were harvested. We manually washed soil off the roots, separated plant parts (leaf, stem, and root) and then dried them at 65°C to constant weight. Before drying, root area and leaf area from each plant were measured by using WinRHIZO Software (version 2005b Pro, Regent Instruments Inc, Quebec, Canada) and an EPSON Expression 1680 scanner (Epson America Inc., Long Beach, California).

Data analysis

Analysis of variance was used to determine the effect of drought, provenance and their interaction on the biomass and the physiology of *Senegalia senegal*. Data were tested for normality and constant variance in order to meet assumptions of ANOVA and regression analysis. A Box-Cox transformation was used when needed to improve normality and homoscedasticity. Student's t-test and Tukey's Honestly Significant Difference test were performed to determine the significance for two means and several mean comparisons respectively at 0.05 probability level. We conducted an allometric analysis between natural log (ln) transformed growth variables and used a type II regression model to determine the slope in order to look for any allometric scaling relation between above ground and below ground biomass. Our allometric relation is expressed as a power function $Y_1 = \beta Y_2^\alpha$ (where Y_1 and Y_2 represent the two different variables, β and α are the scaling constant and exponent, respectively).

Results

Averaged across all provenances, throughout the tree dry cycles, drought stress on *Senegalia senegal* (t-test, $n=35$) significantly affected biomass ($p<0.0001$), stem height ($p<0.0001$), and diameter ($p<0.0001$) of seedlings (Table 2). Overall, biomass components were reduced by the drought treatment, ranging from a 16.3% reduction in root area ($p=0.021$) to 38.7% reduction in leaf area ($p<0.001$). Shoot and root dry weight were reduced by 35% and 19% respectively, and total biomass was reduced by 28.5% ($p<0.0001$). Root/shoot ratio was increased by 25% ($p<0.0001$).

Across all provenances, the allometric scaling coefficient for shoot to root growth was also changed significantly due to the drought treatment (0.93 versus 0.77).

There was no significant drought by provenance interaction in our biomass findings; however, there was a significant provenance main effect for biomass components (Tukey honest significant difference, $n=10$), stem height ($p<0.0001$), and diameter ($p=0.041$) (Table 3). Total dry weight per seedling averaged from 8.7 g for Diamenar and Kidira to 17.5 g for Ngane. Root/shoot ratios did not differ significantly between provenances, with the exception of Ngane which was much lower, averaging only 0.6 compared to all the others, which ranged from 1.7 to 1.4. Allometric analysis of Ngane in comparison with all other provenances suggests that the differences in root/shoot ratio is due to a shift in allocation

Table 2 The effect of the drought treatment on *Senegalia senegal* seedling growth parameters for all provenances. Values are averaged across the tree dry cycles. Student's t-test comparison is given. Means followed by the same letters on each line are not significantly different at $p < 0.05$

Treatment ^a	Control	Drought
Root area (cm ²)	463 ± 26 a	388 ± 23 b
Leaf area (cm ²)	257 ± 17 a	157 ± 15 b
Root weight (g)	5.7 ± 0.4 a	4.6 ± 0.3 a
Leaf weight (g)	1.8 ± 0.1 a	1.1 ± 0.1 b
Stem weight (g)	3.7 ± 0.4 a	2.4 ± 0.3 b
Shoot weight (g)	5.5 ± 0.5 a	3.6 ± 0.4 b
Total weight (g)	13.0 ± 0.9 a	9.3 ± 0.7 b
Root/shoot	1.2 ± 0.1 b	1.5 ± 0.1 a
SLA (m ² /kg)	15.7 ± 1.3 a	14.7 ± 0.3 a
Chlorophyll content	2.1 ± 0.1 a	1.9 ± 0.1 a
Diameter (mm)	9.1 ± 0.2 a	7.5 ± 0.2 b

^aThe drought treatment was a total of 3 dry cycles where plants were not rewatered until soil moisture content reached 4.7%, 2.7%, and 2.1%, at the end of the three successive dry cycles respectively

from roots to the shoot in Ngane (allometric scaling coefficient is 0.65 for Ngane versus 0.87 for other provenances). Stem height, diameter, leaf area, leaf weight, stem weight, shoot weight, and total weight were significantly higher in Ngane provenance. Daiba displayed the highest root area (539.9 cm²) and root weight (6.7 g).

There was a significant drought, provenance and drought by provenance interaction on net photosynthetic rate (A), stomatal conductance (G_s), transpiration (E), and intrinsic water use efficiency (WUEi) (Table 4). Before the induction of drought stress, no significant differences in leaf gas exchange was found between provenances (Table 4; Fig. 1). However, at the second and third dry down periods, there was a significant drought by provenance interaction for A, G_s , and E (Table 4).

In general, with the exception of Ranerou, all provenances had lower leaf gas exchanges during the second and third dry down cycle (Fig. 2a and b). In the second drought cycle, Daiba, Diamenar, Diery Birane, and Ngane had significantly lower net photosynthetic rates and Daiba, Diery Birane, and Ngane had lower stomatal conductance and transpiration (Fig. 2a). At the third dry down cycle, when drought stressed, Daiba and Velingara had significantly lower A, G_s , and E (Fig. 2b). For stomatal limitation, no main effects or interaction were significant.

Discussion

Biomass components of *Senegalia senegal* seedlings were considerably reduced by drought stress. Similar to our results, Merine et al. (2015) reported a significant effect of water stress on *Senegalia senegal* seedling growth and total dry weight. However, in their experiment fertilizer remedied drought effect on growth similar to what was reported by Sarr et al. (2017) where *Senegalia senegal* seedling biomass was increased by fertilizer application under drought stress. In our study there was no drought by provenance interaction on biomass, hence no particular provenance is more or less tolerant to drought. The higher root/shoot ratio we found in the drought treatment (1.50 versus 1.19) is likely due to shifts in

Table 3 Provenance effect on stem height, diameter and biomass on *Senegalia senegal* seedlings. LS Means Tukey honest significant difference (HSD) is given. Means followed by the same letters on each line are not significantly different at $p < 0.05$

Source	Daiba	Diamenar	Kidira	Ngane	Diery Birane	Ranerou	Velingara
Root area(cm ²)	539±68 a	403±36 abc	358±31abc	525±39 ab	353±37 bc	461±41 abc	339±31 c
Leaf area(cm ²)	216±31 b	156±17 b	196±36 b	330±36 a	147±24 b	235±25 ab	168±32 b
Root weight (g)	6.7±1.0 a	4.2±0.5 b	4.5±0.5ab	5.3±0.5 ab	5.3±0.5 ab	5.4±0.4 ab	4.7±0.6 ab
Leaf weight (g)	1.5±0.3 b	1.1±0.2 b	1.1±0.2 b	2.6±0.3 a	1.1±0.1 b	1.5±0.2 b	1.2±0.2 b
Stem weight (g)	3.6±0.7 b	2.2±0.2 bc	2.0±0.3c	6.6±0.7 a	2.3±0.3 bc	2.7±0.2 bc	2.3±0.4 bc
Shoot weight (g)	5.1±0.9 b	3.3±0.4 b	3.1±0.4b	9.3±1.0 a	3.4±0.4 b	4.2±0.3 b	3.4±0.6 b
Total weight (g)	13.4±2.0 ab	8.7±0.9 b	8.7±1.1b	17.5±1.7 a	9.8±1.0 b	11.1±0.6 b	9.3±1.4 b
Root/shoot	1.4±0.2 a	1.4±0.1 a	1.5±0.1 a	0.6±0.1 b	1.7±0.1 a	1.4±0.2 a	1.5±0.1 a
Stem height (cm)	40.6±2.4 ab	31.6±1.5 bc	29.3±2.2 c	49.4±3.2 a	32.8±2.4 bc	40.4±1.8 ab	37.7±3.9 bc
Diameter (mm)	8.4±1.6 ab	8.0±1.8 b	8.3±1.4 ab	9.8±1.5 a	8.0±1.3 b	8.2±1.5 b	7.6±0.9 b

allocation to the root systems (Chapin 1991; Chiatante et al. 2015; Espinoza et al. 2013, 2014; Harris 1992). An increased root/shoot ratio in response to drought will likely favor water uptake and has been observed frequently in many drought tolerant species (Lei et al. 2006; Liu et al. 2011). Ngane which accumulated a higher total biomass than the other provenances presented a lower root/shoot ratio that is likely due to a faster increase in top growth than in root growth. This finding corroborates an early study on *Senegalia senegal* (Mustafa et al. 1996) which found that drought tolerance among different provenances was positively associated with both higher dry matter accumulation and low root/shoot ratio. Niklas (2005) stated that plant size may have a great influence on resource allocation as larger plants will have to invest a larger fraction of their biomass in corresponding tissues. Also, Coleman et al. (1994) argued that plant size is the primary cause of changes in resource allocation. However, the theory of size dependency on resource allocation does not seem to be applicable to our finding, especially the allocation between above and below ground biomass for Ngane. Based on our allometric analysis, biomass allocations to root and shoot were statistically different ($P < 0.0001$) between Ngane (0.65) and the other provenances (0.87). This indicates that the drought treatment caused a shift in allocation from shoots to roots, and that the change in root/shoot ratio is not just a size dependent shift in allocation. Our results corroborate Coyne and Bradford (1985) that there is evidence of genetic variation in morphological adjustment to drought.

The Ngane provenance, displaying the highest growth does not exhibit the highest net photosynthetic rate (A). Our research and that of many others (Chmura and Tjoelker 2008; McGarvey et al. 2004) clearly shows that the relationship between growth and physiological process is more complex than using CO_2 assimilation rate to predict growth. In this study, growth was not directly related to photosynthetic rate and in fact was not consistent with growth traits between provenances. It is evident that photosynthetic capacity has a positive association with a biomass production, but there are studies that showed no or little association of photosynthetic capacity with growth in many species (Chmura and Tjoelker 2008; King et al. 2008; McGarvey et al. 2004; Pinheiro et al. 2008; Rodney et al. 2001). Plant growth also involves phyto-hormones regulation and phases of cell division, enlargement and differentiation (Aroca 2012) that were not investigated in this study.

The differences in drought response in leaf gas exchange between provenances revealed potential genotypic variabilities between the tested provenances. Photosynthesis as affected by water status depended on not only genotypes, but also drought severity (Chaves et al. 2003). In our study, significant drought by provenance interaction occurred when soil volumetric moisture content dropped to 2.7% and 2.1% at the second and third dry down cycles, respectively. Aroca (2012) reported that a reduced soil moisture content may induce stomatal closure in order to minimize water loss while reducing net photosynthetic rate. It appears likely for these seed sources that under drought stress stomatal conductance regulates water loss through transpiration thereby affecting net photosynthetic rate (Farquhar and Sharkey 1982). The greater drop of leaf gas exchanges between control and drought treatments noticed on Ngane at the second dry down cycle may be explained by its specific stomatal size and density compared to other *Senegalia senegal* provenances (Sarr et al. 2017; Bertolino et al. 2019). However, few studies exist on the link between stomatal morphology and tree response to drought.

The physiology of Kidira and Ranerou seedlings was influenced to a lesser extent by the drought treatment and suggests these sources may be less susceptible to drought stress. Dif-

Table 4 Effects of block, drought, provenance, and drought-provenance interaction on net photosynthetic rate (A), stomatal conductance (Gs), transpiration (E), intrinsic water use efficiency (WUEi) and stomatal resistance (L_s) of *Senegalia senegal* seedlings

Initial stage	Variable	Block	Drought	Provenances	Drought*Provenances
	A	*	ns	ns	ns
	Gs	**	ns	ns	ns
	E	**	ns	ns	ns
	WUEi	ns	ns	ns	ns
	L _s	***	ns	ns	ns
Dry Down Cycles					
First	A	ns	**	ns	ns
	Gs	ns	**	ns	ns
	E	ns	**	ns	ns
	WUEi	***	ns	ns	ns
	L _s	***	ns	ns	ns
Second	A	**	***	ns	**
	Gs	**	***	ns	*
	E	**	***	ns	*
	WUEi	ns	**	ns	ns
	L _s	ns	**	ns	ns
Third	A	ns	***	ns	**
	Gs	*	**	**	**
	E	**	**	**	**
	WUEi	**	ns	ns	ns
	L _s	*	ns	ns	ns

*P<0.05, ** p<0.01, ***p<0.0001, ns (not significant)

^aDry down cycles correspond to the last day of each drying cycle before plants were rewatered

ferences in relative stomatal limitation did not explain this result as it did not differ significantly between provenances. At the second and third dry down cycles Kidra and Ranerou had on average a percent stomatal limitation of 38.6% and 42.5% while the other sources averaged 44.4% and 41.8%, respectively.

Chlorophyll concentration does not appear to be a factor in our gas exchange or growth responses as it was not affected by water stress or provenances (Tables 2 and 3). This result was consistent with the finding of Lassouane et al. (2013) who revealed no significant difference of chlorophyll content between controlled and drought stressed *Senegalia arabica*.

Conclusion

Drought treatment significantly reduced growth, biomass allocations, and photosynthetic performance of *Senegalia senegal* seedlings. However, there was no drought by provenance interaction on any growth variables. Mainly drought stress resulted in more biomass allocated to roots. This study shows that under moderate drought stress, no provenance displayed intrinsic features on WUEi, stomatal resistance, and growth traits. With leaf gas exchange, there was a drought by treatment interaction during the second and third dry down cycle. Both Kidira and Ranerou were able to maintain their gas exchange rate during drought while Diamenar, Diery Birane, and Ngane had reduced gas exchange. This suggests that Kidira and Ranerou may be more drought tolerant and possibly growth differences would appear with more time. Hence, drought intensity, time and length of preconditioning have to be tested on these provenances to depict adaptation strategies in the long term.

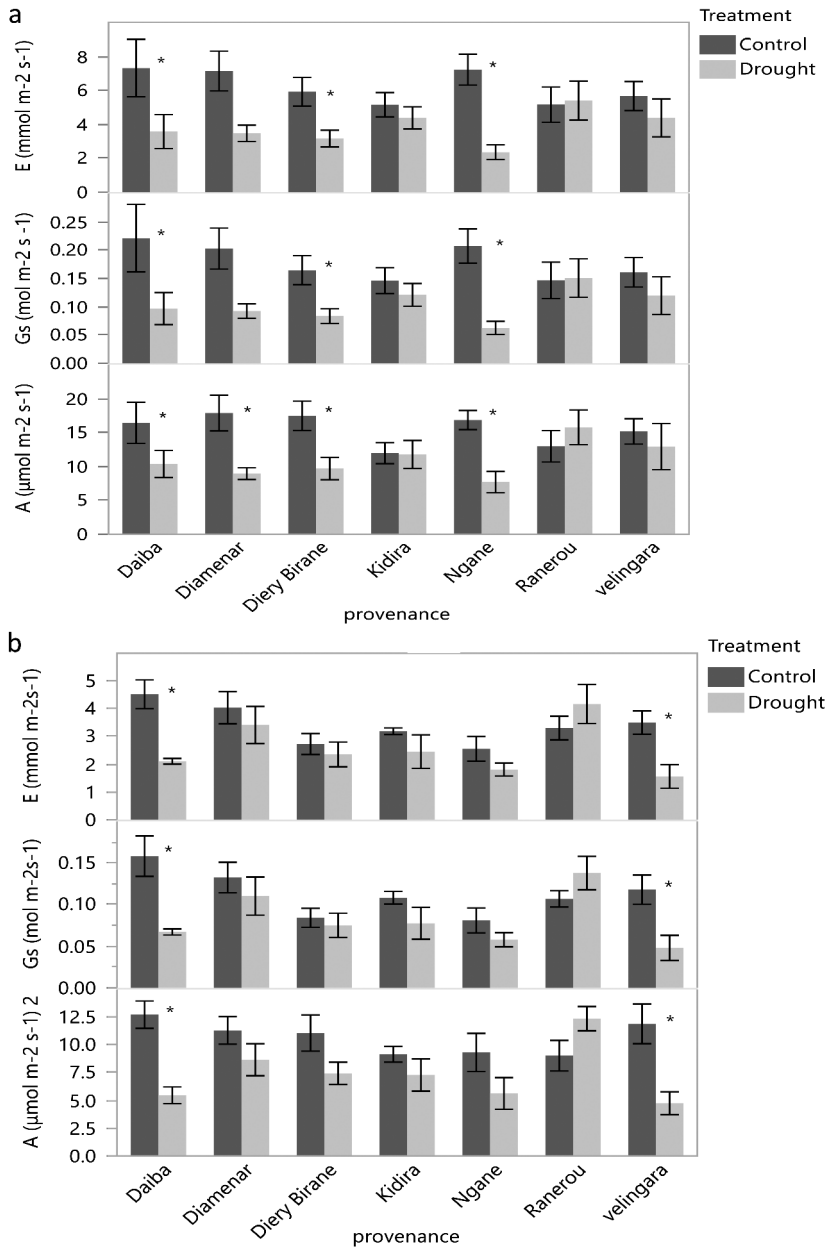


Fig. 2 Photosynthetic rate (A), stomatal conductance (Gs), and transpiration (E) as affected by provenance and drought treatment at the second (a) and third (b) dry down cycles. Bars show treatment means. Error bars are standard errors (\pm SE). * indicate significant differences between treatments at $P < 0.05$ after Tukey HSD test

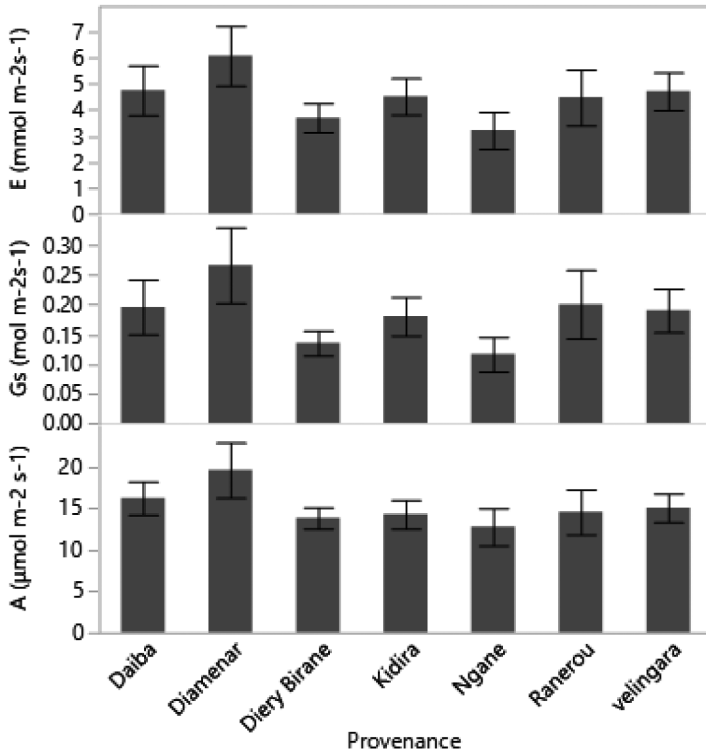


Fig. 1 Average net photosynthetic rate (A), stomatal conductance (Gs), and transpiration (E) of *Senegalia senegal* provenances prior to the start of the drought treatment. Error bars are standard errors (\pm SE)

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Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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