

Full Length Research Paper

Morphological and anatomical response of *Acacia ehrenbergiana* Hayne and *Acacia tortilis* (Forssk) Haynes subsp. *raddiana* seedlings to induced water stress

Hashim Ali El Atta*, Ibrahim Mohamed Aref, Abdalla Ismail Ahmed and Pervez Rasheed Khan

Department of Plant Production, College of Food and Agricultural Sciences, King Saud University, Riyadh 11451, P. O. Box 2460 Saudi Arabia.

Accepted 20 February, 2012

The response of *Acacia ehrenbergiana* Hayne and *Acacia tortilis* (Forssk) Haynes subsp. *raddiana* seedlings to 100, 50 and 25% field capacity (FC) watering regimes was studied to determine their morphological and anatomical behaviour. Both species responded morphologically as well as anatomically to water stress. Water stress caused significant ($P=0.05$) decrease in relative water content, leaf number and area and leaf water potential, chlorophyll content, and stem height and diameter. Seedlings of both species responded to water stress by the development of longer roots. Vessel segment length, radial diameter, tangential diameter, wall thickness and density were significantly ($P=0.05$) affected by water stress at 25 and 50% FC. It can be concluded that both species can adapt well under dry conditions.

Key words: Anatomical deviations, drought, morphological response, root elongation.

INTRODUCTION

Mortality of seedlings and saplings is a likely consequence of severe drought. The environmental conditions and cultivation techniques used in the nursery can produce different hardening degrees in seedlings (Van den Driessche, 1991a, b). Seedlings face serious water stress risks in arid and semi-arid areas (Siam et al., 2009). *Acacia* spp. is widely distributed in arid and semi-arid regions (Demel, 1996; Wilson and Witkowski, 1998; Aref et al., 2003). The genus *Acacia* is currently drawing great interests due to their drought stress resistance abilities (Oba et al., 2001) and multi-purpose use-values such as fodder, sources of wood and non-wood products, provision of shade and live fencing and in maintaining soil fertility through nitrogen fixation (Belsky et al., 1989; Noad and Birnie, 1989). Utilization of solar energy through photosynthesis is greatly diminished under water

deficit conditions as a result of reduced availability of CO₂ due to stomatal closure (Cornic 1994, 2001; Hamerlynck et al., 2000; Marenco et al., 2001; Flexas and Medrano, 2002). Drought and decreased soil moisture content lead to a decline in average daily sap flux in the hardwood species (Holscher et al., 2005). Under limited water supply or high evaporation, plants exhibit different strategies for survival and growth (Jones, 2004; Tambussi et al., 2007). Understanding morphological and physiological shoot, and root responses of seedlings to water deficit are critical for the production of high-quality seedlings (Franco et al., 2006). In vascular plants, water is transported through xylem under negative pressure. Xylem must overcome the mechanical stresses associated with negative pressure as well as the risk of air entering the hydraulic pathway (Bass et al., 2004). Failure may also occur when negative pressures overcome the ability of the xylem conduit walls to resist implosion which may result in cavitation (Hacke et al., 2001; Donaldson, 2002; Cochard et al., 2004; Brodribb and Holbrook, 2005). Cavitation can lead to reduced

*Corresponding author. E-mail: hmabu@ksu.edu.sa. Tel: +96614828131.

stomatal conductance (Pratt et al., 2005), reduced photosynthesis (Brodrribb and Field, 2000), and dieback of branchlets (Rood et al., 2000; Davis et al., 2002). A drought resistant plant is characterized by having rigid cell walls, low osmotic potential, narrow vessels and a reduced transpiration rate to resist embolism in conditions of severe drought (Kalapos, 1994). Decline of stomatal conductance may reduce the rate of transpiration, which may lower carbon assimilation in plants facing drought at the xeric sites (Tyree and Sperry, 1988). Emphasis has been given to the relationship between xylem anatomy and water transport efficiency and drought tolerance (Tyree et al., 1994). Water limitation is a detrimental factor for the growth of indigenous *Acacia* spp. in Saudi Arabia. Early mortality of seedlings is the major risk in successful establishments of plantations in semi-arid and arid areas. Therefore, it is extremely important to study how these seedlings adapt to water stress (Li et al., 2011).

The present study was undertaken with the objective of investigating morphological and anatomical response of *A. ehrenbergiana* and *Acacia tortilis* spp. *raddiana* seedlings to water stress and to evaluate their suitability for reforestation purposes under water deficit conditions. Experiments were carried out at the Agricultural Research Station, College of Food and Agricultural Sciences, King Saud University in Riyadh region (N 42° 24 E 46 44, Alt. 600 m a.s.l.) during the period April to December 2010.

MATERIALS AND METHODS

Seedlings production

Seeds of *A. ehrenbergiana* and *Acacia tortilis* spp. *raddiana* were collected from one tree of each species to produce uniformity and to avoid genetic diversity in the population, from the Agricultural Research Station, College of Food and Agricultural Sciences, King Saud University in Riyadh region (N 42° 24 E 46 44, Alt. 600 m a.s.l.). Seeds of each species were sown directly in plastic pots (32 × 40 cm) containing a mixture of clay and sand soil (1:2 v/v). During the first two months plants were watered every other day to maintain optimum soil moisture conditions and then as the experimental design requires. Seedlings were grown in a glass house under controlled conditions (average day / night temperature was 32°C/17 ±1°C, with 12 h day light and relative humidity 50%).

Watering regimes

Seedlings were subjected to three watering regimes, 100% field capacity (FC) (control) 50% FC (moderate watering regime) and 25% FC (severe watering regime). Eleven replicates were used for each watering regime. Another set of 20 seedlings were harvested (10 per species) to estimate initial root, stem and total plant dry weight for the calculation of relative growth rate (RGR).

Relative water content (RWC)

Relative water content (RWC) was measured every ten days after water stress onset using three leaves per plant (3rd, 4th and 5th

leaf) per replicate per treatment. Leaves were weighed immediately to obtain a fresh weight. Leaf petioles were placed in water in a beaker overnight, in the dark, so as to become fully turgid. Leaves were then re-weighed, to obtain turgid weight, and dried at 80 ± 1°C for 24 h to obtain dry weight. RWC was calculated according to Morgan (1984):

$$\text{RWC} = [(M_f - M_d)(M_t - M_d)^{-1}] \times 100$$

Where, M_f is the leaf fresh weight; M_t is the turgid weight and M_d is the dry weight.

Water potential

Relative leaf water potential of the two *Acacia* species was measured every ten days at predawn from leaves per replicate per treatment using a potential meter (WP4-T, Decagon Devices, Inc., USA).

Measurement of growth parameters

Ten seedlings per species were randomly selected and harvested after six months for measuring initial stem height and diameter, root collar diameter, shoot and root dry mass. Morphological characteristics, root and shoot length, number of leaves and leaf area were recorded. Leaf area was measured by using computer software (Area scan 2 MFC Application ver. 1001). For understanding the growth and allocation pattern, the following response parameters were assessed: Biomass determination, total relative growth rate (TRGR) and Root/shoot allocation coefficient (k).

Biomass determination

For biomass determination, plants were carefully washed in distilled water to remove adhering soil particles. Different plant parts were separated and oven dried at 80 ± 1°C until they attained a constant weight. Dry weights of different plant parts were determined for each plant.

Total relative growth rate (TRGR)

Total relative growth rate (TRGR) of the whole plant was calculated according to Hunt (1982):

$$\text{TRGR} = \frac{\ln B_2 - \ln B_1}{t_2 - t_1}$$

Where, B_1 is the initial dry weight (g); B_2 is the final dry weight (g); t_1 is the initial time (month) and t_2 is the final time (month)

Root/shoot allocation coefficient (k)

The allocation pattern was determined by calculating the root/shoot allocation coefficient (k) according to Grantz et al. (2006):

$$k = \frac{\text{RRGR}}{\text{SRGR}}$$

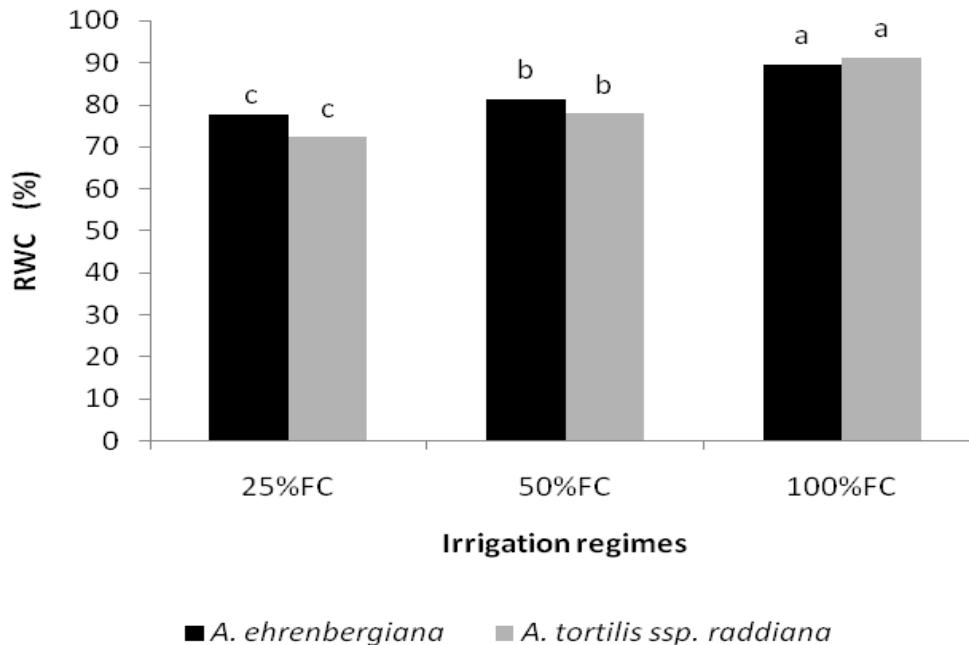


Figure 1. Effect of watering regimes on leaves RWC % (relative water content). Means followed by the same letter above a column are not significantly different at p-0.05 FC-field capacity.

Where, RRGR is the root relative growth rate; SRGR is the stem relative growth rate.

Chlorophyll content

The leaf chlorophyll concentration was analyzed at the end of the stress period (6 months) according to Porra et al. (1989). It was determined in 3 randomly selected top leaves per seedling.

Anatomical studies

For anatomical studies stem pieces were collected from third internode per replicate per treatment in the early hours of the day at final harvest and fixed on the spot in FAA (Berlyn and Miksche, 1976). After one week fixed stem pieces were preserved in alcohyl solution for softening (50% ethanol + 50% glycerol, v: v). Permanent mounts were made after cutting fine sections (8 to 10 μ m) on a sliding microtome (AO 860, American Optical Company, USA) in transverse, tangential and radial planes and stained in double combinations of Haematoxylin/Safranin, Haematoxylin/Bismark brown and Ferric chloride/Lacmoid and dehydrated in ethanol series. Anatomical wood structure was thoroughly studied and data were collected on the vessel dimension, vessel wall thickness, and vessel density from transverse (TS), tangential (TLS) and radial (RLS) sections. Two hundred vessels were measured for each replicate in each treatment using micrometer scale on Olympus CX41, Japan microscope. A scanner (Epson Expression 1680 (Scan 300 dpi, Black and White, 130 threshold) was used to analyze the area occupied by vessels.

Experimental design and statistical analysis

Experiments were conducted in a completely randomized block design with two factors (species and watering regime). The data

was analyzed by variance analysis (ANOVA) and means were separated by LSD ($P = 0.05$) using SAS statistical package (SAS, 1997).

RESULTS

Relative water content and leaf water potential

The RWC and leaf water potential showed significant ($P=0.05$) decrease with increasing water deficit in both species (Figure 1). The RWC was 89.5% (control), 81.2% (50 % FC) and 77.4% (25% FC) in *A. ehrenbergiana*. Water potential was -1.7 MPa and -2.4 MPa in the samples from 50 and 25% FC, respectively as compared to the control (-1.0 MPa) that is, exhibiting a decline of 70 and 140%, respectively (Figure 2). The RWC for *A. tortilis ssp raddiana* was 91.2% (control), 77.9% (50% FC) and 72.2% (25%. Leaf water potential was -1.1 MPa in control, -1.8 MPa in 25% FC and -2.6 MPa for 50% FC. It decreased by 63.6 and 136.3% in 50 and 25% FC, respectively (Figures 1 and 2).

Effect of watering regime on morphological parameters

The results of the analysis of the effect of watering regime on the morphological parameters of *A. ehrenbergiana* and *A.tortilis ssp raddiana* seedlings are summarized in Table 2. Growth parameters of all aerial parts (seedlings height, stem diameter, leaf area and

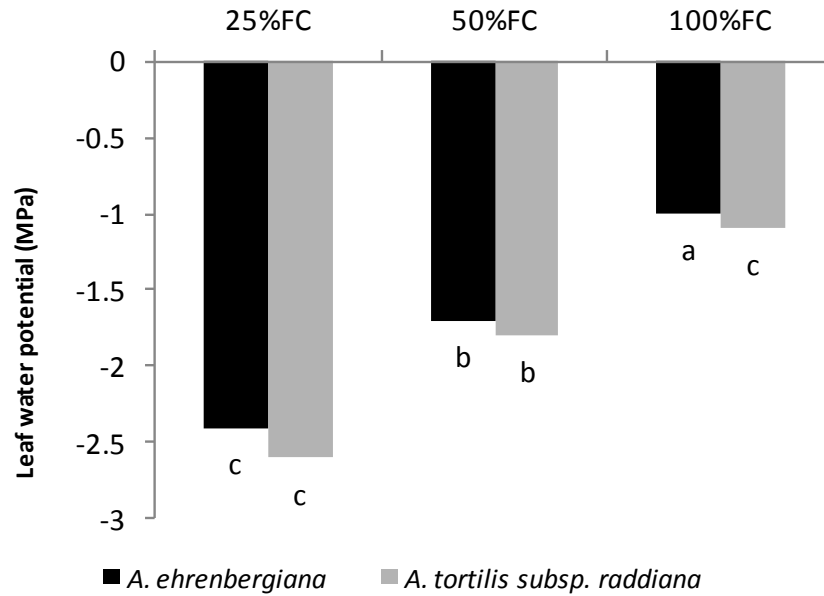


Figure 2. Effect of watering regimes on leaf water potential (MPa). Means followed by the same letter above a column are not significantly different at $p < 0.05$ FC-field capacity.

number) of both species were reduced significantly under water stress treatments (Tables 1 and 2). *A. ehrenbergiana* showed a significant reduction in seedlings height under 50 and 25% FC, respectively as compared to the control (100%FC). The response of *A. tortilis ssp. raddiana* to watering regimes was reduction in seedlings height under 50 and 25% FC, respectively as compared to the control (100%FC) (Table 3). Stem diameter of both species was reduced significantly under 50 FC and 25% FC as compared to the control. Under 50% FC, the number of leaves per seedling decreased significantly by about 11 and 23% under severe watering regime (25%FC) in both species. *A. ehrenbergiana* seedlings produced smaller leaf area under 25 and 50% FC (2.49 and 3.01 cm², respectively) as compared to 3.69 cm² under the control (Table 3). The results are similar for *A. tortilis ssp. raddiana*. Seedlings of both species have longer roots under 50%FC watering regime as compared to control (Table 3). The root length of *A. ehrenbergiana* seedlings increased by 32.8% under 25% FC and 17.6% cm under 50% FC as compared to the control. Similarly, root length of *A. tortilis ssp. raddiana* seedlings increased significantly as a result of watering regimes (Table 3).

Biomass allocation

Significant reductions were recorded in shoot dry weight and total dry weight per plant in *A. ehrenbergiana* seedlings only under 25% FC as compared to control (Table 1). Total dry weight decreased by 10% and

reduction in shoot dry weight was 22%. No significant difference was recorded in seedlings under 50% FC as compared to control. Maximum reduction of 62 and 38% was recorded in the leaf dry weight under 25 and 50% FC, respectively. Root dry weight exhibited an opposite trend and significantly increased by 22 and 29% under 50 and 25% FC, respectively compared to control (Table 3). Significant reduction was recorded in shoot and leaf dry weight and total dry weight per plant under 50 and 25% FC in *A. tortilis ssp. raddiana* seedlings as compared to control. Reduction in the total dry weight was 6 and 13%. Shoots biomass decreased by 18 and 29% and leaves biomass reduction was 39 and 62% under 25 and 50% FC, respectively. Root biomass exhibited a significant increase of 24 and 29% under 25 and 50% FC, respectively. Root to shoot ratio of both species increased significantly with increasing water deficit as compared to control (Table 3).

Growth rate

Watering regime significantly ($P = 0.05$) reduced TRGR and SRGR of *A. ehrenbergiana* seedlings but the RRGR significantly ($P = 0.001$) increased with water stress (Table 1). The TRGR of *A. ehrenbergiana* seedlings decreased significantly ($P = 0.05$) by 4.5 and 9% in 50 and 25% FC, respectively as compared to the control (Table 3). Also, the SRGR decreased significantly by 18 and 25.6% under 50 and 25% FC, respectively. Watering regime also affected the rate of root growth (RRGR) positively which increased by 18 and 29% under 50 and

Table 1. Effect of water deficit on growth parameters of *A. ehrenbergiana* (ANOVA).

Variable	Source	DF	SS	MS	F value	P	R ² (%)																																																																																																																																																																																												
SH	Model	2	223.89	111.95	52.57	0.001	83.35																																																																																																																																																																																												
	Error	21	44.71	2.13				SD	Model	2	4.52	2.26	23.67	0.001	69.27	Error	21	2.004	0.095	NL	Model	2	333.08	166.54	48.41	0.001	82.17	Error	21	72.25	3.44	LA	Model	2	5.738	2.86	262.14	0.001	96.15	Error	21	0.229	0.011	RL	Model	2	318.315	159.157	128.19	0.001	92.42	Error	21	26.073	1.241	TDW	Model	2	0.553	0.276	3.94	0.05	27.26	Error	21	1.4746	0.07	SDW	Model	2	0.54	0.268	3.78	0.05	26.48	Error	21	1.486	0.071	LDW	Model	2	0.634	0.317	553.33	0.001	98.14	Error	21	0.012	0.0006	RDW	Model	2	0.626	0.313	33.26	0.001	76.01	Error	21	0.197	0.01	RSR	Model	2	1.467	0.733	10.34	0.001	49.62	Error	21	1.49	0.0709	TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45	Error	21	0.02	0.001	SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70
SD	Model	2	4.52	2.26	23.67	0.001	69.27																																																																																																																																																																																												
	Error	21	2.004	0.095				NL	Model	2	333.08	166.54	48.41	0.001	82.17	Error	21	72.25	3.44	LA	Model	2	5.738	2.86	262.14	0.001	96.15	Error	21	0.229	0.011	RL	Model	2	318.315	159.157	128.19	0.001	92.42	Error	21	26.073	1.241	TDW	Model	2	0.553	0.276	3.94	0.05	27.26	Error	21	1.4746	0.07	SDW	Model	2	0.54	0.268	3.78	0.05	26.48	Error	21	1.486	0.071	LDW	Model	2	0.634	0.317	553.33	0.001	98.14	Error	21	0.012	0.0006	RDW	Model	2	0.626	0.313	33.26	0.001	76.01	Error	21	0.197	0.01	RSR	Model	2	1.467	0.733	10.34	0.001	49.62	Error	21	1.49	0.0709	TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45	Error	21	0.02	0.001	SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404								
NL	Model	2	333.08	166.54	48.41	0.001	82.17																																																																																																																																																																																												
	Error	21	72.25	3.44				LA	Model	2	5.738	2.86	262.14	0.001	96.15	Error	21	0.229	0.011	RL	Model	2	318.315	159.157	128.19	0.001	92.42	Error	21	26.073	1.241	TDW	Model	2	0.553	0.276	3.94	0.05	27.26	Error	21	1.4746	0.07	SDW	Model	2	0.54	0.268	3.78	0.05	26.48	Error	21	1.486	0.071	LDW	Model	2	0.634	0.317	553.33	0.001	98.14	Error	21	0.012	0.0006	RDW	Model	2	0.626	0.313	33.26	0.001	76.01	Error	21	0.197	0.01	RSR	Model	2	1.467	0.733	10.34	0.001	49.62	Error	21	1.49	0.0709	TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45	Error	21	0.02	0.001	SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																				
LA	Model	2	5.738	2.86	262.14	0.001	96.15																																																																																																																																																																																												
	Error	21	0.229	0.011				RL	Model	2	318.315	159.157	128.19	0.001	92.42	Error	21	26.073	1.241	TDW	Model	2	0.553	0.276	3.94	0.05	27.26	Error	21	1.4746	0.07	SDW	Model	2	0.54	0.268	3.78	0.05	26.48	Error	21	1.486	0.071	LDW	Model	2	0.634	0.317	553.33	0.001	98.14	Error	21	0.012	0.0006	RDW	Model	2	0.626	0.313	33.26	0.001	76.01	Error	21	0.197	0.01	RSR	Model	2	1.467	0.733	10.34	0.001	49.62	Error	21	1.49	0.0709	TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45	Error	21	0.02	0.001	SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																
RL	Model	2	318.315	159.157	128.19	0.001	92.42																																																																																																																																																																																												
	Error	21	26.073	1.241				TDW	Model	2	0.553	0.276	3.94	0.05	27.26	Error	21	1.4746	0.07	SDW	Model	2	0.54	0.268	3.78	0.05	26.48	Error	21	1.486	0.071	LDW	Model	2	0.634	0.317	553.33	0.001	98.14	Error	21	0.012	0.0006	RDW	Model	2	0.626	0.313	33.26	0.001	76.01	Error	21	0.197	0.01	RSR	Model	2	1.467	0.733	10.34	0.001	49.62	Error	21	1.49	0.0709	TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45	Error	21	0.02	0.001	SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																												
TDW	Model	2	0.553	0.276	3.94	0.05	27.26																																																																																																																																																																																												
	Error	21	1.4746	0.07				SDW	Model	2	0.54	0.268	3.78	0.05	26.48	Error	21	1.486	0.071	LDW	Model	2	0.634	0.317	553.33	0.001	98.14	Error	21	0.012	0.0006	RDW	Model	2	0.626	0.313	33.26	0.001	76.01	Error	21	0.197	0.01	RSR	Model	2	1.467	0.733	10.34	0.001	49.62	Error	21	1.49	0.0709	TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45	Error	21	0.02	0.001	SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																								
SDW	Model	2	0.54	0.268	3.78	0.05	26.48																																																																																																																																																																																												
	Error	21	1.486	0.071				LDW	Model	2	0.634	0.317	553.33	0.001	98.14	Error	21	0.012	0.0006	RDW	Model	2	0.626	0.313	33.26	0.001	76.01	Error	21	0.197	0.01	RSR	Model	2	1.467	0.733	10.34	0.001	49.62	Error	21	1.49	0.0709	TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45	Error	21	0.02	0.001	SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																																				
LDW	Model	2	0.634	0.317	553.33	0.001	98.14																																																																																																																																																																																												
	Error	21	0.012	0.0006				RDW	Model	2	0.626	0.313	33.26	0.001	76.01	Error	21	0.197	0.01	RSR	Model	2	1.467	0.733	10.34	0.001	49.62	Error	21	1.49	0.0709	TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45	Error	21	0.02	0.001	SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																																																
RDW	Model	2	0.626	0.313	33.26	0.001	76.01																																																																																																																																																																																												
	Error	21	0.197	0.01				RSR	Model	2	1.467	0.733	10.34	0.001	49.62	Error	21	1.49	0.0709	TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45	Error	21	0.02	0.001	SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																																																												
RSR	Model	2	1.467	0.733	10.34	0.001	49.62																																																																																																																																																																																												
	Error	21	1.49	0.0709				TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45	Error	21	0.02	0.001	SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																																																																								
TRGR	Model	2	0.0077	0.0038	3.97	0.05	27.45																																																																																																																																																																																												
	Error	21	0.02	0.001				SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45	Error	21	0.124	0.0059	RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																																																																																				
SRGR	Model	2	0.047	0.0234	3.97	0.05	27.45																																																																																																																																																																																												
	Error	21	0.124	0.0059				RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23	Error	21	0.0134	0.0006	k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																																																																																																
RRGR	Model	2	0.0454	0.0226	35.6	0.001	77.23																																																																																																																																																																																												
	Error	21	0.0134	0.0006				k	Model	2	2.686	1.343	7.48	0.01	41.60	Error	21	3.771	0.179	CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																																																																																																												
k	Model	2	2.686	1.343	7.48	0.01	41.60																																																																																																																																																																																												
	Error	21	3.771	0.179				CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45	Error	6	4.326	0.721	CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																																																																																																																								
CHL a	Model	2	52.971	26.486	36.73	0.0001	92.45																																																																																																																																																																																												
	Error	6	4.326	0.721				CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59	Error	6	8.182	1.364	TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																																																																																																																																				
CHL b	Model	2	9.076	4.538	3.33	0.1066	52.59																																																																																																																																																																																												
	Error	6	8.182	1.364				TCHL	Model	2	25.319	12.659	5.27	0.05	63.70	Error	6	14.426	2.404																																																																																																																																																																																
TCHL	Model	2	25.319	12.659	5.27	0.05	63.70																																																																																																																																																																																												
	Error	6	14.426	2.404																																																																																																																																																																																															

SH: Stem height (cm); SD: Stem diameter (cm) ; NL: Number of leaves; LA: Leaf area; RL: Root length; TDW: Total dry weight (g); SDW: Stem dry weight (g); RDW: Root dry weight (g); LDW: Leaves dry weight (g); RSR: Root shoot ratio; TRGR: Total relative growth rate (g/month); SRGR: Stem relative growth rate (g/month); RRGR: Root relative growth rate (g/month), k; The root/shoot allocation coefficient; CHL a: Chlorophyll a; CHL b: Chlorophyll b; TCHL: Total chlorophyll concentration. DF, Degree of freedom; SS, sum of square; MS, mean of square.

Table 2. Effect of water deficit on growth parameters of *A. tortilis* ssp. *raddiana* (ANOVA).

Variable	Source	DF	SS	MS	F value	P	R ² (%)																																																																																																																																																																																												
SH	Model	2	133.211	66.605	50.02	0.0001	82.65																																																																																																																																																																																												
	Error	21	27.962	1.332				SD	Model	2	5.987	2.994	58.48	0.0001	84.78	Error	21	1.075	0.051	NL	Model	2	358.063	179.033	47.96	0.0001	82.04	Error	21	78.39	3.732	LA	Model	2	3.931	1.965	43.18	0.0001	80.44	Error	21	0.956	0.046	RL	Model	2	210.301	105.15	35.61	0.0001	77.23	Error	21	62.013	2.953	TDW	Model	2	0.985	0.492	13.44	0.0001	56.14	Error	21	0.769	0.037	SDW	Model	2	0.956	0.479	20.84	0.0001	66.50	Error	21	0.481	0.023	LDW	Model	2	0.756	0.378	513.61	0.0001	97.99	Error	21	0.015	0.001	RDW	Model	2	0.806	0.403	21.85	0.0001	67.55	Error	21	0.387	0.018	RSR	Model	2	2.402	1.201	21.78	0.0001	67.47	Error	21	1.158	0.055	TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69	Error	21	0.009	0.001	SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17
SD	Model	2	5.987	2.994	58.48	0.0001	84.78																																																																																																																																																																																												
	Error	21	1.075	0.051				NL	Model	2	358.063	179.033	47.96	0.0001	82.04	Error	21	78.39	3.732	LA	Model	2	3.931	1.965	43.18	0.0001	80.44	Error	21	0.956	0.046	RL	Model	2	210.301	105.15	35.61	0.0001	77.23	Error	21	62.013	2.953	TDW	Model	2	0.985	0.492	13.44	0.0001	56.14	Error	21	0.769	0.037	SDW	Model	2	0.956	0.479	20.84	0.0001	66.50	Error	21	0.481	0.023	LDW	Model	2	0.756	0.378	513.61	0.0001	97.99	Error	21	0.015	0.001	RDW	Model	2	0.806	0.403	21.85	0.0001	67.55	Error	21	0.387	0.018	RSR	Model	2	2.402	1.201	21.78	0.0001	67.47	Error	21	1.158	0.055	TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69	Error	21	0.009	0.001	SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799								
NL	Model	2	358.063	179.033	47.96	0.0001	82.04																																																																																																																																																																																												
	Error	21	78.39	3.732				LA	Model	2	3.931	1.965	43.18	0.0001	80.44	Error	21	0.956	0.046	RL	Model	2	210.301	105.15	35.61	0.0001	77.23	Error	21	62.013	2.953	TDW	Model	2	0.985	0.492	13.44	0.0001	56.14	Error	21	0.769	0.037	SDW	Model	2	0.956	0.479	20.84	0.0001	66.50	Error	21	0.481	0.023	LDW	Model	2	0.756	0.378	513.61	0.0001	97.99	Error	21	0.015	0.001	RDW	Model	2	0.806	0.403	21.85	0.0001	67.55	Error	21	0.387	0.018	RSR	Model	2	2.402	1.201	21.78	0.0001	67.47	Error	21	1.158	0.055	TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69	Error	21	0.009	0.001	SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																				
LA	Model	2	3.931	1.965	43.18	0.0001	80.44																																																																																																																																																																																												
	Error	21	0.956	0.046				RL	Model	2	210.301	105.15	35.61	0.0001	77.23	Error	21	62.013	2.953	TDW	Model	2	0.985	0.492	13.44	0.0001	56.14	Error	21	0.769	0.037	SDW	Model	2	0.956	0.479	20.84	0.0001	66.50	Error	21	0.481	0.023	LDW	Model	2	0.756	0.378	513.61	0.0001	97.99	Error	21	0.015	0.001	RDW	Model	2	0.806	0.403	21.85	0.0001	67.55	Error	21	0.387	0.018	RSR	Model	2	2.402	1.201	21.78	0.0001	67.47	Error	21	1.158	0.055	TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69	Error	21	0.009	0.001	SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																
RL	Model	2	210.301	105.15	35.61	0.0001	77.23																																																																																																																																																																																												
	Error	21	62.013	2.953				TDW	Model	2	0.985	0.492	13.44	0.0001	56.14	Error	21	0.769	0.037	SDW	Model	2	0.956	0.479	20.84	0.0001	66.50	Error	21	0.481	0.023	LDW	Model	2	0.756	0.378	513.61	0.0001	97.99	Error	21	0.015	0.001	RDW	Model	2	0.806	0.403	21.85	0.0001	67.55	Error	21	0.387	0.018	RSR	Model	2	2.402	1.201	21.78	0.0001	67.47	Error	21	1.158	0.055	TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69	Error	21	0.009	0.001	SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																												
TDW	Model	2	0.985	0.492	13.44	0.0001	56.14																																																																																																																																																																																												
	Error	21	0.769	0.037				SDW	Model	2	0.956	0.479	20.84	0.0001	66.50	Error	21	0.481	0.023	LDW	Model	2	0.756	0.378	513.61	0.0001	97.99	Error	21	0.015	0.001	RDW	Model	2	0.806	0.403	21.85	0.0001	67.55	Error	21	0.387	0.018	RSR	Model	2	2.402	1.201	21.78	0.0001	67.47	Error	21	1.158	0.055	TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69	Error	21	0.009	0.001	SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																								
SDW	Model	2	0.956	0.479	20.84	0.0001	66.50																																																																																																																																																																																												
	Error	21	0.481	0.023				LDW	Model	2	0.756	0.378	513.61	0.0001	97.99	Error	21	0.015	0.001	RDW	Model	2	0.806	0.403	21.85	0.0001	67.55	Error	21	0.387	0.018	RSR	Model	2	2.402	1.201	21.78	0.0001	67.47	Error	21	1.158	0.055	TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69	Error	21	0.009	0.001	SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																																				
LDW	Model	2	0.756	0.378	513.61	0.0001	97.99																																																																																																																																																																																												
	Error	21	0.015	0.001				RDW	Model	2	0.806	0.403	21.85	0.0001	67.55	Error	21	0.387	0.018	RSR	Model	2	2.402	1.201	21.78	0.0001	67.47	Error	21	1.158	0.055	TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69	Error	21	0.009	0.001	SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																																																
RDW	Model	2	0.806	0.403	21.85	0.0001	67.55																																																																																																																																																																																												
	Error	21	0.387	0.018				RSR	Model	2	2.402	1.201	21.78	0.0001	67.47	Error	21	1.158	0.055	TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69	Error	21	0.009	0.001	SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																																																												
RSR	Model	2	2.402	1.201	21.78	0.0001	67.47																																																																																																																																																																																												
	Error	21	1.158	0.055				TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69	Error	21	0.009	0.001	SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																																																																								
TRGR	Model	2	0.014	0.007	15.55	0.0001	59.69																																																																																																																																																																																												
	Error	21	0.009	0.001				SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90	Error	21	0.052	0.002	RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																																																																																				
SRGR	Model	2	0.081	0.041	16.36	0.0001	60.90																																																																																																																																																																																												
	Error	21	0.052	0.002				RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94	Error	21	0.019	0.001	k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																																																																																																
RRGR	Model	2	0.05	0.025	26.92	0.0001	71.94																																																																																																																																																																																												
	Error	21	0.019	0.001				k	Model	2	14.064	7.032	7.15	0.0043	40.52	Error	21	20.644	0.983	CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																																																																																																												
k	Model	2	14.064	7.032	7.15	0.0043	40.52																																																																																																																																																																																												
	Error	21	20.644	0.983				CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57	Error	6	2.553	0.426	CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																																																																																																																								
CHL a	Model	2	44.482	22.241	52.27	0.0001	94.57																																																																																																																																																																																												
	Error	6	2.553	0.426				CHL b	Model	2	2.736	1.368	1	0.4229	24.94	Error	6	8.235	1.372	TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																																																																																																																																				
CHL b	Model	2	2.736	1.368	1	0.4229	24.94																																																																																																																																																																																												
	Error	6	8.235	1.372				TCHL	Model	2	49.503	24.751	30.98	0.001	91.17	Error	6	4.794	0.799																																																																																																																																																																																
TCHL	Model	2	49.503	24.751	30.98	0.001	91.17																																																																																																																																																																																												
	Error	6	4.794	0.799																																																																																																																																																																																															

SH: Stem height (cm); SD: Stem diameter (cm) ; NL: Number of leaves; LA: Leaf area; RL: Root length; TDW: Total dry weight (g); SDW: Stem dry weight (g); RDW: Root dry weight (g); LDW: Leaves dry weight (g); RSR: Root shoot ratio; TRGR: Total relative growth rate (g/month); SRGR: Stem relative growth rate (g/month); RRGR: Root relative growth rate (g/month), k, The root/shoot allocation coefficient; CHL a: CHLOROPHYLL a; CHL b: Chlorophyll b; TCHL: Total chlorophyll concentration. DF, Degree of freedom; SS, sum of square; MS, mean of square.

Table 3. Effect water stress on morphological parameters and chlorophyll of *A. ehernbergiana* and *A. tortilis ssp. raddiana*.

Species	Parameter	FC (%)			LSD ^{P=0.05}
		100	50	25	
<i>A. ehernbergiana</i>	Seedling height (cm plant ⁻¹)	40.47 ^a	36.15 ^b	33.02 ^c	1.517
	Stem diameter (mm)	4.78 ^a	4.27 ^b	3.72 ^c	0.321
	Number of leaves (plant ⁻¹)	39.87 ^a	35.37 ^b	30.75 ^c	1.929
	Leaf area (cm ²)	3.69 ^a	3.01 ^b	2.491 ^c	0.109
	Root length (cm plant ⁻¹)	27.16 ^a	31.95 ^b	36.08 ^b	1.158
	Total dry weight(g plant ⁻¹)	3.56 ^a	3.36 ^{ab}	3.19 ^b	0.275
	Shoot dry weight (g plant ⁻¹)	1.61 ^a	1.35 ^{ab}	1.25 ^b	0.277
	Root dry weight (g plant ⁻¹)	1.32 ^b	1.6 ^a	1.70 ^a	0.101
	Leaves dry weight (gplant ⁻¹)	0.63 ^a	0.39 ^b	0.23 ^c	0.025
	RSR	0.83 ^b	1.24 ^a	1.43 ^a	0.277
	TRGR (g g ⁻¹ month ⁻¹)	0.45 ^a	0.43 ^{ab}	0.41 ^b	0.032
	SRGR (g g ⁻¹ month ⁻¹)	0.39 ^a	0.32 ^{ab}	0.29 ^b	0.079
	RRGR (g g ⁻¹ month ⁻¹)	0.35 ^b	0.43 ^a	0.45 ^a	0.026
	k	0.89 ^b	1.43 ^a	1.69 ^a	0.441
	CHL a (µg ml ⁻¹)	12.42 ^a	8.70 ^b	6.55 ^c	1.696
	CHL b(µg ml ⁻¹)	1.07 ^b	3.41 ^a	2.90 ^{ab}	2.333
	TCHL (µg ml ⁻¹)	13.49 ^a	12.12 ^{ab}	9.45 ^b	3.09
<i>A. tortilis ssp. raddiana</i>	Seedling height (cm plant ⁻¹)	41.79 ^a	38.64 ^b	36.03 ^c	1.199
	Stem diameter (mm)	4.92 ^a	4.17 ^b	3.71 ^c	0.235
	Number of leaves (plant ⁻¹)	40.33 ^a	36.00 ^b	30.88 ^c	2.009
	Leaf area (cm ²)	3.70 ^a	3.22 ^b	2.71 ^c	0.222
	Root length (cm plant ⁻¹)	28.14 ^c	32.14 ^b	35.38 ^a	1.786
	Total dry weight(g plant ⁻¹)	3.79 ^a	3.57 ^b	3.29 ^c	0.199
	Shoot dry weight (g plant ⁻¹)	1.667 ^a	1.37 ^b	1.18 ^c	0.157
	Root dry weight (g plant ⁻¹)	1.43 ^b	1.78 ^a	1.85 ^a	0.141
	Leaves dry weight (plant ⁻¹)	0.69 ^a	0.42 ^b	0.26 ^c	0.028
	RSR	0.87 ^c	1.31 ^b	1.64 ^a	0.244
	TRGR (g g ⁻¹ month ⁻¹)	0.44 ^a	0.42 ^b	0.38 ^c	0.022
	SRGR (g g ⁻¹ month ⁻¹)	0.34 ^a	0.27 ^b	0.20 ^c	0.052
	RRGR (g g ⁻¹ month ⁻¹)	0.38 ^c	0.46 ^b	0.48 ^a	0.032
	K	1.09 ^b	1.74 ^b	2.94 ^a	1.031
	CHL a (µg ml ⁻¹)	11.89 ^a	9.64 ^b	6.47 ^c	1.303
	CHL b(µg ml ⁻¹)	4.51 ^a	3.23 ^a	4.24 ^a	2.341
	TCHL (µg ml ⁻¹)	16.41 ^a	12.88 ^b	10.72 ^c	1.786

FC= Field capacity %. Means followed by the same letter in a row are not significantly different at P=0.05.

25% FC, respectively (Table 3). *A. tortilis ssp. raddiana* seedlings TRGR also decreased significantly by 5 and 14% under 50 and 25% FC, respectively (Table 3). Reduction in SRGR was 20 and 40% under 50 and 25% FC, respectively. RRGR increased significantly by 21 and 27% under 50 and 25% FC, respectively. The root/shoot allocation coefficient 'k' of both species increased significantly with watering regime (Table 3).

Effect of watering regime on chlorophyll concentration

The concentration of chlorophyll a and total chlorophyll in

the leaves of both species was significantly (P=0.05) reduced under moderate and severe watering regime as compared to the control (Tables 1 and 2). Chlorophyll b concentration in the leaves of *A. tortilis ssp. raddiana* was not affected by watering regime treatment (Table 3).

Effect on anatomical features of wood

Vessel segment length significantly (P=0.05) decreased by 11.7% under 25% FC in *A. ehrenbergiana* seedlings (Table 4). However, vessel diameter increased significantly (P=0.05) at 50 and 25% FC as compared to the

Table 4. Effect of water stress on anatomical traits of wood of *A. ehrenbergiana* and *A. tortilis* ssp. *raddiana* seedlings.

Species	Parameter	FC (%)			LSD $P=0.05$
		100	50	25	
<i>A. ehrenbergiana</i>	Vessel segment length (μm)	150.39 ^a	148.78 ^a	132.75 ^b	6.789
	Vessel radial diameter (μm)	21.92 ^b	22.29 ^{ab}	22.89 ^a	0.751
	Vessel tangential diameter (μm)	21.01 ^b	22.53 ^a	21.94 ^a	0.864
	Vessel mean diameter (μm)	21.46 ^b	22.41 ^a	22.41 ^a	0.714
	Vessel wall thickness (μm)	2.52 ^b	3.84 ^a	3.87 ^a	0.165
	Vessel density (mm^{-2})	247.71 ^a	198.59 ^b	178.20 ^c	10.580
<i>A. tortilis</i> ssp. <i>raddiana</i>	Vessel segment length (μm)	135.05 ^{ab}	138.65 ^a	131.71 ^b	4.510
	Vessel radial diameter (μm)	21.67 ^a	17.66 ^c	19.95 ^b	1.020
	Vessel tangential diameter (μm)	21.82 ^a	19.78 ^b	16.97 ^c	0.997
	Vessel mean diameter (μm)	21.74 ^a	18.72 ^b	18.46 ^b	1.015
	Vessel wall thickness (μm)	2.88 ^b	4.27 ^a	4.30 ^a	0.191
	Vessel density (mm^{-2})	118.36 ^c	286.92 ^b	313.41 ^a	15.781

Means followed by the same letter in a row are not significantly different at $P=0.05$ FC= field capacity %.

control. Vessels had thicker walls developed under drought conditions. Increment in the vessel wall thickness was more in seedlings under 25% FC (53.57%) than in those under 50% FC (52.38%) as compared to the control (Table 4). Drought had a profound effect on the vessel density. Vessel number / mm^2 square of wood was found to be significantly less in 50% FC (198.59) and 25% FC (178.20) as compared to the control (247.71). The reduction was 19.82 and 28.06% in seedlings under 50 and 25% FC, respectively. Water deficit did not show distinct effect on the vessel segment length in *A. tortilis* ssp. *raddiana* seedlings (Table 4). However, vessel diameter was adversely affected by water deficit. Radial, tangential and mean diameter was reduced significantly ($P=0.05$) under 25 and 50% FC. Vessels developed quite thick walls under 50% FC (4.27 μm) and 25% FC (4.30 μm) as compared to the control (2.88 μm). Response of *A. tortilis* ssp. *raddiana* to the two watering regimes was quite profound in respect of vessel density. Vessel density was significantly ($P=0.05$) higher in seedlings under 50% FC (286.92) and 25% FC (313.41). The increase was 142 and 165%, respectively as compared to the control. The water-deficient *A. tortilis* sub species *raddiana* had a better quality of wood with long, narrow and crowded thick-walled vessel elements having higher area fraction, and a higher wood density. A negative and significant correlation between inter-treatment variation in area fraction of fibres transverse wall area (cellulose microfibril) per cross sectional area of xylem and vulnerability factor for *A. ehrenbergiana* ($r= -0.9644$) and *A. tortilis* ssp. *raddiana* ($r= -0.9303$) suggests a positive role of fibres in drought resistance.

It was employed in the present investigation to evaluate the impact of ecological conditions on the sapwood formation. Samples from 50 and 25% FC *A. tortilis* sub species *raddiana* population showed a higher degree of

xeromorphism than the control. Vf appeared to be species specific as it showed a different pattern for the two *Acacia* species.

DISCUSSION

It has been reported earlier that water stress caused a decrease in RWC and leaf water potential (Morgan, 1984; Liu et al., 2004; Merchant et al., 2007). At the whole plant level, limited soil water supply may have a strong effect on dry matter accumulation (Li, 1998). High relative light intensity coupled with drought condition has a positive effect on biomass partitioning and leaf specific mass (Lof et al., 2005). The effect of water stress on growth parameters has been well documented. For example, a reduction in leaf area in *Eucalyptus globules* (Metcalf et al., 1990) and stem elongation in young peach trees (Steinberg et al., 1990) were reported. Drought significantly reduced leaf area (Maes et al., 2009).

Seedlings subjected to moderate and severe water deficit have longer roots. This is in conformity with the results of species native to lower rainfall environments which tend to produce roots with longer links (Nicotra et al., 2002), and higher specific root length (Poot and Lambers, 2003; Tjolker et al., 2005). Drought may increase the length of root links within a species (Jupp and Newmann, 1987; Fitter and Stickland, 1992; Berntson, 1994). Many plants respond to water limitation by inhibiting lateral branching (Malamy, 2005). Rooting in deep soil horizons may be an essential component of a plant's strategy to withstand drought at the seedling stage in environments with seasonal drought (Joffre et al., 2002; Otieno et al., 2006; David et al., 2007). In the present study, the fast root growth at the early stages of development of the investigated species may represent

adaptive mechanism under water deficit conditions. The reduction recorded in *A. tortilis* spp. *raddiana* seedlings dry weight under 50 and 25% FC was mainly attributed to leaf dry weight reduction which was caused by reduction in leaf area and number under both treatments and increasing in roots dry weight did not offset that reduction but the increase in roots dry weight explained the allocation of dry matter to roots under limited watering regime. Seedlings under limited watering regime developed longer roots to uptake limited water available in the soil. The rapid development of a deep root system that can access water stored lower in the soil profile may be essential for successful seedling establishment (Joffre et al., 2002; Otieno et al., 2006). Root dry weight did not show any significant variation between 50 and 25% FC (Table 3). Drought increases the proportion of biomass allocated below ground (Taub and Goldberg, 1996; Nicotra et al., 2002; Ryser, 2006). It significantly reduced biomass and relative growth rate (Maes et al., 2009). Slow growth rate was associated with the smaller foliage area per unit foliage mass (Atkin et al., 1998). Reduction in chlorophyll has been also observed in *Haloxylon persicum* and *Acacia auriculiformis* (Liu et al., 2004). A highly significant positive correlation was found between RWC and chlorophyll content in five cultivars of date palm. In many other species, water stress was reported to reduce chlorophyll synthesis (Alberte et al., 1975; Tyree and Jarvis, 1982). Drought stress may decrease stomatal conductance (Fort et al., 1997) and concentration of chlorophyll *a* and *b* and carotenoides (Pukacki and RoZek, 2005), leading to a decrease (3 to 7 folds) in photosynthetic activity in *A. auriculiformis* (Liu et al., 2004). Low chlorophyll content and low biomass production in *A. ehrenbergiana* and *A. tortilis* sub species *raddiana* under moderate and severe drought stress might be attributed to the low photosynthetic activity in the seedlings of these two species. Stomatal conductance and leaf photosynthesis decreased with the decrease in soil water content and pre-dawn leaf water potential in *Acacia confusa* (Liang and Zhang, 1999). A lesser area occupied by vessel lumen mm^{-2} xylem results in a stronger wood (Wagner et al., 1998). The reduction in vessel area per cross-sectional area of wood in under stress plants was in part a result of a shift towards smaller diameter vessels (Thomas et al., 2004). Narrow vessels are claimed to be positively correlated to xeromorphism in dicotyledons (Carlquist, 1977). The area of vessels in such a xeromorphic wood is compensated by greater vessel number/ mm^{-2} of area of transection (Carlquist, 2001; Zimmermann, 1982). Drought had adverse effects with regard to the height and radial growth of *Quercus faginea* in the absence or with a low recharge precipitation at a xeric site in Spain (Corcuera et al., 2004). Variation in annual wood production in arid plants can be attributed up to 90% to the difference in water stress (Zahner, 1968). A correlation was found between drought resistance and xylem vulnerability to

cavitation of a number of woody species (Salleo and Lo Gullo, 1993; Cochard et al., 1996; Davis et al., 1998, 2002; Nardini et al., 2000; Vogt, 2001; Sperry and Hacke, 2002; Lo Gullo et al., 2003; Pita et al., 2003; Tyree et al., 2003; Maherali et al., 2004). This suggests that species that are capable of maintaining functional xylem conduits under extreme drought conditions have a higher chance of survival, likely because they are able to extract water from the soil and thereby prevent dehydration of their leaves and meristems. A highly significant correlation was found between xylem cavitation resistance and inter-vessel wall thickness in ten different *Prunus* species. Cavitation resistance was related to drought resistance with xerophilic species being less vulnerable to cavitation. Inter-vessel wall thickness could be used as a possible alternative to direct cavitation estimates (Cochard et al., 2008). Hacke et al. (2001) suggested that vessel wall reinforcement is required for cavitation resistance in order to prevent wall implosion when xylem pressure is highly negative. An interesting plastic response of *A. tortilis* sub species *raddiana* to 100% FC irrigation is the dramatic reduction of wall thickness of vessels, even as their lumen diameter increased. This results in vessels building more cheaply and more efficient in transport, but also more at risk for implosion in response to water stress (Hacke et al., 2001). An increase in vessel dimension occupying a greater transectional area of wood in *A. ehrenbergiana* has also been reported in *E. globulus* under low water stress condition, as compared with a higher stress site (Leal et al., 2003). Due to the large diameter, early wood vessels contribute the largest part to the water flow through the shoot (Ellmore and Ewers, 1985; Grainer et al., 1994). But the same anatomical feature renders them particularly susceptible to embolisation by frost (Ellmore and Ewers, 1986; Tyree and Cochard, 1996) or by drought stress. Increased cavitation resistance was correlated with xylem density, increased vessel wall thickness / lumen ratio of vessels, increased transverse fibre wall area and decreased fiber lumen area. A positive correlation between cavitation resistance and fibre wall area suggests a mechanical role for fibres in cavitation resistance (Jacobsen et al., 2005). Fibres play a key role in buttressing vessel walls against implosion under extreme negative pressure (Hacke et al., 2001; Jacobsen et al., 2005).

The vulnerability index is a good proxy for comparative ecological studies (Carlquist 1985). Although, embolism was correlated to vessel diameter (Carlquist, 1974, 1984, 1985, 2001), more recent studies have proposed freeze-thaw cycles as cause for embolism (Lens et al., 2003). Vulnerability in angiosperms has also been shown to be linearly related to pit-pore radius and hydrodynamic resistance was inversely proportional to the pit pore size in gymnosperms (Lancashire and Ernos, 2002). A good relationship seems to exist between sapwood specific conductivity (K_s) and maximum photosynthetic rates (Brodrribb and Field, 2000; Hubbard et al., 2001). Since

vessel diameter is a primary determinant of Ks, this must bear a relationship with the photosynthetic rate and hence with the biomass accumulation or growth of the plant. A positive and highly significant correlation between vulnerability to embolism and relative water content (RWC) of wood is reported for gymnospermic species, early wood was more vulnerable to embolism than late wood (Domec and Gartner, 2002). In angiospermic species, small diameter late-wood vessels and small diameter vasicentric tracheids near large vessels are thought to conduct water once the early wood and/or wider vessels have become air-filled (Carlquist, 1985; Hargrave et al., 1994; Cochard et al., 1997). The success of plant species in xeric condition or under severe drought depends on the narrow and numerous vessels having inter-vascular pit resistance, which offer a high degree of safety under water stress conditions (Baas, 1976; Baas et al., 1983; Zimmermann, 1983; Carlquist, 1984). Our observations support the two aforementioned views with reference to the successful growth and survival of *Acacia* seedlings under severe drought conditions.

Conclusion

We found that under watering regime treatments seedlings of both *Acacia* species characterized by shorter height, lower leaf number, smaller leaves and longer roots. Also seedlings allocated more biomass to roots in cost of lower growth rate aboveground parts and higher growth rate of underground parts (roots system). The restricted growth observed in our study can be considered as a morphological adaptation of the plant to water and environmental stresses to reduce the transpiration and induce a lower consumption of water. Nevertheless, the reduction in leaf area not only led to a reduction in transpiration but also a reduction in the photosynthetic surface area, and consequently reduced growth. Vessel diameter increased as a result of water stress. Vessels had thicker walls developed under drought conditions. Increment in the vessel wall thickness was more in seedlings under water stress as compared to the control. Drought had a profound effect on the vessel density. Vessel number / mm² square of wood was found to be significantly (P=0.05) less under water stress as compared to control. Thus, it can be concluded that both species are suitable for afforestation under dry conditions.

ACKNOWLEDGEMENT

Authors are thankful to 'King Abdul Aziz City for Science and Technology (KACST), Riyadh for granting a research project entitled "Growth activity and wood characteristics of indigenous *Acacias* of Saudi Arabia" (KACST AT 28-59) and providing financial assistance for the present work.

REFERENCES

- Alberte RS, Fiscus EL, Naylor AW (1975). The effect of water stress on the development of photosynthetic apparatus in greening leaves, *Plant Physiol.* 55: 317-321.
- Aref IM, El-Juhany LI, Hegazy SS (2003). Comparison of the growth and biomass production of six *Acacia* species in Riyadh, Saudi Arabia after 4 years of irrigated cultivation, *J. Arid Environ.* 54: 783-792.
- Atkin OK, Schortemeyer M, McFarlane N, Evans JR (1998). Variation in the components of relative growth rate in ten *Acacia* species from contrasting environments, *Plant Cell Environ.* 21: 1007-1017.
- Baas P, Werker E, Fahn A (1983). Some ecological trends in vessel character, *IAWA Bull.* 4: 141-159.
- Baas P (1976). Some functional adaptive aspects of vessel member morphology. In: Baas P, Bolton AJ and Catling DM (eds). *Wood Structure in Biological and Technological Research: Leiden Bot. Series No. 3*, Leiden University Press, The Hague. pp. 157-181.
- Baas P, Ewers FW, Davis SD, Wheeler EA (2004). Evolution of xylem physiology. In: Poole I, Hemsley A, eds, *Evolution of Plant Physiology*. Linnaean Society Symposium Series. Elsevier Acad. Press, London, pp. 273-295.
- Belsky AJ, Amundson RG, Duxbury JM, Riha SJ, Ali AR, Mwonga SM (1989). The effects of trees on their physical, chemical and biological environments in a semiarid savanna in Kenya, *J. Appl. Ecol.* 26: 1005-1024.
- Brodribb TJ, Field TS (2000). Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests, *Plant Cell Environ.* 23: 1381-1388.
- Brodribb TJ, Holbrook NM (2005). Water stress deforms tracheids peripheral to the leaf vein of a tropical conifer, *Plant Physiol.* 137: 1139-1146.
- Carlquist S (1977). Ecological factors in wood evolution: a floristic approach, *Am. J. Bot.* 64: 887-896.
- Carlquist S (1984). Wood anatomy and relationships of Pentaplyaceae: Significance of vessel features, *Phytomorphology*, 34: 84-90.
- Carlquist S (1985). Vasicentric tracheid as a drought survival mechanism, *Aliso*. 11: 37-68
- Carlquist S (2001). Comparative wood anatomy, Systematic, ecological, and evolutionary aspects of dicotyledon wood. Berlin: Springer-Verlag.
- Cochard H, Barigah ST, Kleinhents M, Eshel A (2008). Is xylem cavitation resistance a relevant criterion for screening drought resistance among *Prunus* species?, *J. Plant Physiol.* 165: 976-982.
- Cochard H, Froux F, Mayr S, Coutand C (2004). Xylem collapse in water stressed pine needles, *Plant Physiol.* 134: 401-408.
- Cochard H, Ridolfi M, Dreyer E (1996). Responses of water stress in an ABA-unresponsive hybrid poplar (*Populus koreana* x *trichocarpa* cv Peace). 2. Hydraulic properties and xylem embolism, *New Phytol.* 134: 455-461.
- Cochard H, Peiffer M, Le Gall K, Grainer A (1997). Developmental control of xylem hydraulic resistances and vulnerability to embolism in *Fraxinus excelsior* L. impacts on water relation, *J. Exp. Bot.* 48: 655-663.
- Corcuera L, Camarero JJ, Gil-Pelegrin E (2004). Effects of a severe drought on growth and wood anatomical properties of *Quercus faginea*, *IAWA J.* 25: 185-204.
- Cornic G (1994). Drought stress and high light effects on leaf photosynthesis. In: Baker N.R., Bowyer J.R. ed. *Photoinhibition of photosynthesis*. Oxford, Bios Sci. Pub. pp. 297-313.
- Cornic G (2001). Drought stress inhibits photosynthesis by decreasing stomatal aperture—not by affecting ATP synthesis, *Trends in Plant Science.* 5: 187-188.
- David TS, Henriques MO, Kurz-Besson C, Nunes J, Valente F, Vaz M, Pereira JS, Siegwolf R, Chaves MM, Gazarini LC, David JS (2007). Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought, *Tree Physiol.* 27: 793-803.
- Davis SD, Ewers FW, Portwood KA, Sperry JS, Crocker MC, Adams GC (2002). Shoot dieback during prolonged drought in *Ceanothus* (Rhamnaceae) chaparral in California: a possible case of hydraulic failure, *Am. J. Bot.* 89: 820-828.
- Davis SD, Kolb KJ, Barton KP (1998). Ecophysiological processes and

- demographic patterns in the structure of California chaparral. In: Rundel PW, Montenegro G, Jaksic F, editors. Landscape disturbance and biodiversity in Mediterranean-type ecosystems. Berlin: Springer, pp. 297-310.
- Demel T (1996). Germination ecology of twelve indigenous and eight exotic multipurpose leguminous species from Ethiopia. *For. Ecol. Manage.* 80: 209-223.
- Domec JC, Gartner BL (2002). How do water transport and water storage differ in coniferous early wood and late wood, *J. Exp. Bot.* 53: 2369-2379.
- Donaldson LA (2002). Abnormal lignin distribution in wood from severely drought stressed *Pinus radiata* trees, *IAWA J.* 23: 161-178.
- Ellmore GS, Ewers FW (1985). Hydraulic conductivity in trunk xylem of elm, *Ulmus Americana*, *IAWA Bull. n.s.* 6: 303-307.
- Ellmore GS, Ewers FW (1986). Fluid flow in the outermost xylem increment of a ring-porous tree, *Ulmus Americana*, *Am. J. Bot.* 73: 1771-1774.
- Flexas J, Medrano H (2002). Energy dissipation in C₃ plants under drought, *Funct. Plant Biol.* 29: 1209-1215.
- Fort C, Fauveau ML, Muller F, Pabel P, Granier A, Dreyer E (1997). Stomatal conductance, growth and root signaling in young oak seedling subjected to partial soil drying, *Tree Physiol.* 17: 281-289.
- Franco JA, Marti'nez-Sa'ncchez JJ, Ferna'ndez JA, Ban'õ'n S (2006). Selection and nursery production of ornamental plants for landscaping and xerogardening in semi-arid environments, *J. Hort. Sci. Biotechnol.* 81(1): 3-17.
- Grainer A, Anfodillo T, Sabatti, M, Cochard H, Dreyer E, Tomasi M, Valentini R, Breda N (1994). Axial and radial flow in the trunks of oak trees: a quantitative and qualitative analysis, *Tree Physiol.* 14: 1383-1396
- Grantz DA, Gunn S, Vu HB (2006). Ozone impacts on plant development: a meta analysis of root shoot allocation and growth, *Plant Cell Environ.* 29: 1193-1209.
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001). Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure, *Oecologia*, 126: 457-461.
- Hamerlynck EP, Huxman TE, Loik ME, Smith SD (2000). Effects of extreme high temperature, drought and elevated CO₂ on photosynthesis of the Mojave Desert evergreen shrub, *Larrea tridentate*, *Plant Ecol.* 148: 183-193.
- Hargrave KR, Kolb KJ, Ewers FW, Davis SD (1994). Conduit diameter and drought-induced embolism in *Salvia mellifera* Green (Labiatae), *New Phytol.* 126: 695-705.
- Holscher D, Koch O, Korn S, Leuschner C (2005). Sap flux of five co-occurring tree species in a temperate broad leaved forest during seasonal soil drought, *Trees-structure. Funct.* 19(6): 628-637.
- Hubbard RM, Ryan MG, Stiller V, Sperry JS (2001). Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine, *Plant Cell Environ.* 24: 113-121.
- Hunt R (1982). *Growth Curves*. Edward Arnold (Publishers) Ltd., London.
- Jacobsen AL, Ewers FW, Pratt RB, Paddock III WA, Davis SD (2005). Do xylem fibers affect vessel cavitation resistance?, *Plant Physiol.* 139: 546-556.
- Joffre R, Rambal S, Damesin C (2002). Functional attributes in Mediterranean-type ecosystems. In: Pugnaire, F., Valladares, F. (Eds.), *Handbook of Functional Plant Ecology*. Marcel Dekker, Inc., New York, pp. 348-377.
- Jones H (2004). What is water use efficiency? In: Bacon MA (Ed.), *Water Use Efficiency* Implant Biology. Blackwell Publishing, Oxford.
- Jupp AP, Newmann EI (1987). Morphological and anatomical effects of severe drought on the roots of *Lolium perenne* L. *New Phytol.* 105: 393-402.
- Kalapos T (1994). Leaf water potential-leaf water deficit relationship for ten species of a semi-arid grassland community, *Plant. Soil*, 160: 105-112.
- Lancashire JR, Ennos AR (2002). Modelling the hydrodynamic resistance of bordered pits, *J. Exp. Bot.* 53: 1485-1493.
- Leal S, Pereira H, Grabner M, Wimmer R (2003). Clonal and site variation of vessels in 7-year-old *Eucalyptus globules*, *IAWA J.* 24: 185-195
- Li C (1998). Growth response of *Eucalyptus microtheca* provenances to water stress, *J. Trop. For. Sci.* 10: 379-387.
- Li FL, Bao WK, Ning W (2011). Morphological, anatomical and physiological responses of *Campylotropis polyantha* (Franch.) Schindl. seedlings to progressive water stress, *Sci. Horticul.* 127: 436-443.
- Liang J, Zhang J (1999). The relations of stomatal closure and reopening to xylem ABA concentration and leaf water potential during soil drying and rewatering, *Plant Growth Regul.* 29: 77-86.
- Liu Li-Xia, Xu Shou-Min, Woo K. C. (2004).. Watering regime effects on photosynthesis and the xanthophyll cycle in the tropical tree species *Acacia auriculiformis* in North Australi, N. Zealand *J. Bot.* 42: 949-957.
- Lo Gullo MA, Salleo S, Rossa R, Trifilo P (2003). Drought resistance of 2-year-old saplings of Mediterranean forest trees in the field: relations between water relations, hydraulics and productivity, *Plant Soil*, 250: 259-272.
- Maes WH, Achten WMJ, Reubens B, Raes D, Samson R, Muys B (2009). Plant-water relationships and growth strategies of *Jatropha curcas* L. seedlings under different levels of drought stress, *J. Arid Environ.* 73: 877-884.
- Maherali H, Pockman WT, Jackson RB (2004). Adaptive variation in the vulnerability of woody plants to xylem cavitation, *Ecology*, 85: 2184-2199.
- Malamy JE (2005). Intrinsic and environmental response pathways that regulate root system architecture, *Plant Cell Environ.* 28: 67-77.
- Marenco RA, Goncalves JFC, Vieira G (2001). Leaf gas exchange and carbohydrates in tropical trees differing in successional status in two light environments in central Amazonia, *Tree Physiol.* 21: 1311-1318.
- Merchant A, Callister A, Arndt S, Tausz M, Adams M (2007). Contrasting physiological responses of six *Eucalyptus* species to water deficit. *Ann. Bot.* 100: 1-9.
- Metcalfe JC, Davies WJ, Pereira JS (1990). Leaf growth of *Eucalyptus globulus* seedlings under water deficit, *Tree Physiol.* 6: 221-227.
- Morgan JM (1984). Osmoregulation and water stress in higher plants, *Annu. Rev. Plant Physiol.* 35: 299-319.
- Nardini A, Salleo S, Lo Gullo MA, Pitt F (2000). Different responses to drought and freeze stress of *Quercus ilex* L. growing along a latitudinal gradient, *Plant Ecol.* 148: 139-147.
- Nicotra AB, Babicka N, Westoby M (2002). Seedling root anatomy and morphology: an examination of ecological differentiation with rainfall using phylogenetically independent contrasts, *Oecologia*, 130: 136-145.
- Noad T, Birnie A (1989). In: Noad T, Birnie A (Eds.). *Trees of Kenya*, second ed. Nairobi, p. 169.
- Oba G, Nordal I, Stenseth NC, Stave J, Bjora CS, Muthondeki JK, Bii WKA (2001). Growth performance of exotic and indigenous tree species in saline soils in Turkana, Kenya. *J. Arid Environ.* 47: 499-511.
- Otieno DO, Kurz-Besson C, Liu J, Schmidt MWT, Vale-Lobo do R, David TS, Siegwolf R, Pereira JS, Tenhunen JD (2006). Seasonal variations in soil and plant water status in a *Quercus suber* L. stand: roots as determinants of tree productivity and survival in the Mediterranean-type ecosystem, *Plant Soil*, 283: 119-135.
- Pita P, Gasco A, Pardos JA (2003). Xylem cavitation, leaf growth and leaf water potential in *Eucalyptus globulus* clones under well-watered and drought conditions, *Funct. Plant Biol.* 30: 891-899.
- Poot P, Lambers H (2003). Are trade-offs in allocation pattern and root morphology related to species abundance? A congeneric comparison between rare and common species in the south-western Australian flora, *J. Ecol.* 91: 58-67.
- Porra RJ, Thompson WA, Kriedemann PE (1989). Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochimica et Biophysica Acta*, 975(3): 384-394.
- Pratt RB, Ewers FW, Lawson MC, Jacobsen AL, Brediger M, Davis SD (2005). Mechanisms for tolerating freeze-thaw stress of two evergreen chaparral species: *Rhus ovata* and *Malosma laurina* (Anacardiaceae), *Am. J. Bot.* 92: 1102-1113.
- Pukacki PM, Rozek EK (2005). Effect of drought stress on chlorophyll a fluorescence and electrical admittance of shoots in Norway spruce

- seedlings, *Trees-structure. funct.* 19(5): 539-544.
- Rood SB, Patino S, Coombs K (2000). Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods, *Trees*, 14: 248-257.
- Ryser P (2006). The mysterious root length, *Plant Soil*, 286: 1-6.
- Salleo S, Lo Gullo MA (1993). Drought resistance strategies and vulnerability to cavitation of some Mediterranean sclerophyllous trees. In: Borghetti M, Grace J, Raschi A. editors. *Water transport in plants under climatic stress*. Cambridge: Cambridge University Press, pp. 99-113.
- SAS (1997). SAS institute INC., Cary, North Carolina.
- Siam AMJ, Radoglou KM, Basilios N, Smiris P (2009). Differences in ecophysiological responses to summer drought between seedlings of three deciduous oak species, *For. Ecol. Manage.* 258: 35-42.
- Sperry JSP, Hacke UG (2002). Desert shrub water relations with respect to soil characteristics and plant functional type, *Funct. Ecol.* 16: 367-378.
- Steinberg SL, Miller JC, McFarland MJ (1990). Dry matter partitioning and vegetative growth of young peach trees under water stress, *Aust. J. Plant Physiol.* 17: 23-36.
- Tambussi EA, Bort J, Araus JL (2007). Water use efficiency in C3 cereals under Mediterranean conditions: a review of physiological aspects, *Ann. Appl. Biol.* 150: 307-321.
- Taub DR, Goldberg D (1996). Root system topology of plants from habitats differing in soil resource availability, *Funct. Ecol.* 10: 258-264.
- Thomas DS, Montagu KD, Conroy JP, (2004). Changes in wood density of *Eucalyptus camaldulensis* due to temperature-the physiological link between water viscosity and wood anatomy, *For. Eco. Manage.* 193: 157-165.
- Tjolker MG, Craine JM, Wedin D, Reich PB, Tilman D (2005). Linking leaf and root trait syndromes among 39 grassland and savannah species, *New Phytol.* 167: 493-508.
- Tyree MT, Sperry JS (1988). Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiol.* 88: 574-580
- Tyree MT, Cochard H (1996). Summer and winter embolism in oak: impact on water relations, *Ann. Sci. For.* 53: 173-180.
- Tyree MT, Davis SD, Cochard H (1994) Biophysical perspectives of xylem evolution: is there a trade off to hydraulic efficiency for vulnerability to dysfunction?, *J. IAWA*, 15: 335-360.
- Tyree MT, Engelbrecht BM J, Vargas G, Kursar TA (2003). Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance, *Plant Physiol.* 132: 1439-1447.
- Tyree MT, Jarvis PG (1982). Water in tissues. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds). *Water Relations and Carbon Assimilation, Physiology Plant Ecology* 11, Encyclopedia of Plant Physiology, Springer-Verlag, Berlin, pp. 36-71 .
- Van den Driessche R (1991a). Influence of container nursery regimens on drought resistance of seedlings following planting. I. Survival and growth, *Can. J. For. Res.* 21: 555-565.
- Van den Driessche R (1991b). Influence of container nursery regimens on drought resistance of seedlings following planting. II. Stomatal conductance, specific leaf area and root growth capacity, *Can. J. For. Res.* 21: 566-572.
- Vogt UK (2001). Hydraulic vulnerability, vessel refilling, and seasonal courses of stem water potential of *Sorbus aucuparia* L. and *Sambucus nigra* L., *J. Exp. Bot.* 52: 1527-1536.
- Wagner KR, Evers FW, Davis SD (1998). Trade off between hydraulic efficiency and mechanical strength in the stems of four co-occurring species of chaparral shrubs, *Oecologia*, 117: 53-62
- Wilson TB, Witkowski TF (1998). Water requirements for germination and early seedling establishment in four African savanna woody plant species. *J. Arid Environ.* 38: 541-550.
- Zahner R (1968). Water deficits and growth of trees. In: Kozlowski TT (ed). *Water Deficit and Plant Growth*, Acad Press, New York, 2: 191-252.
- Zimmermann MH (1982). *Functional Xylem Anatomy of Angiosperm Trees*. Nijhoff Junk, The Hague.
- Zimmermann MH (1983). *Xylem structure and the ascent of sap*. Springer-Verlag, New York.