

Full Length Research Paper

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

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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

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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):

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

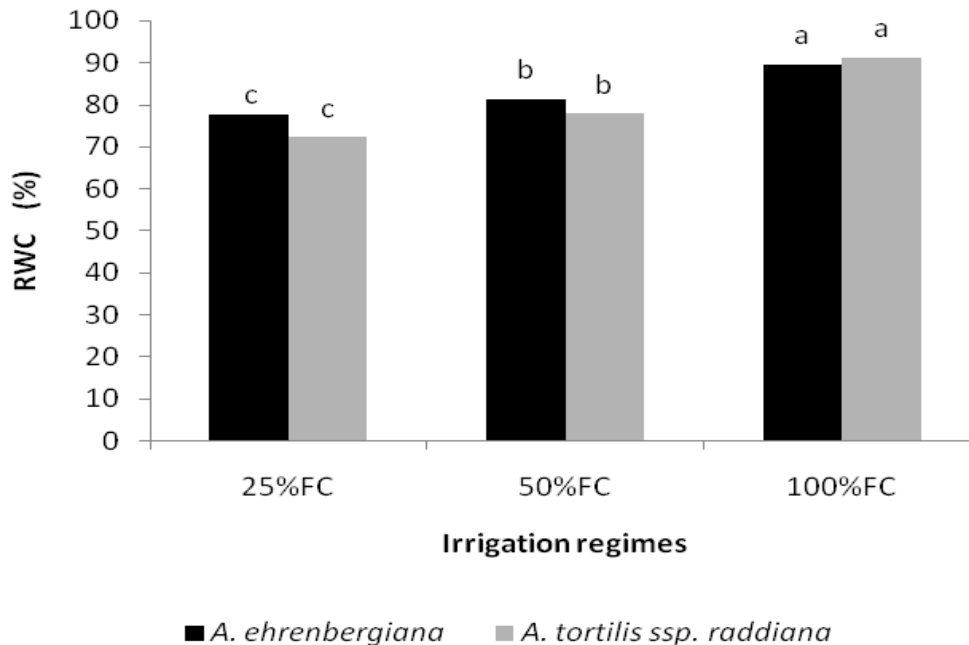


Figure 1. Effect of watering regimes on leaves RWC % (relative water content). Means followed by the same letter above a column are not significantly different at p-0.05 FC-field capacity.

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

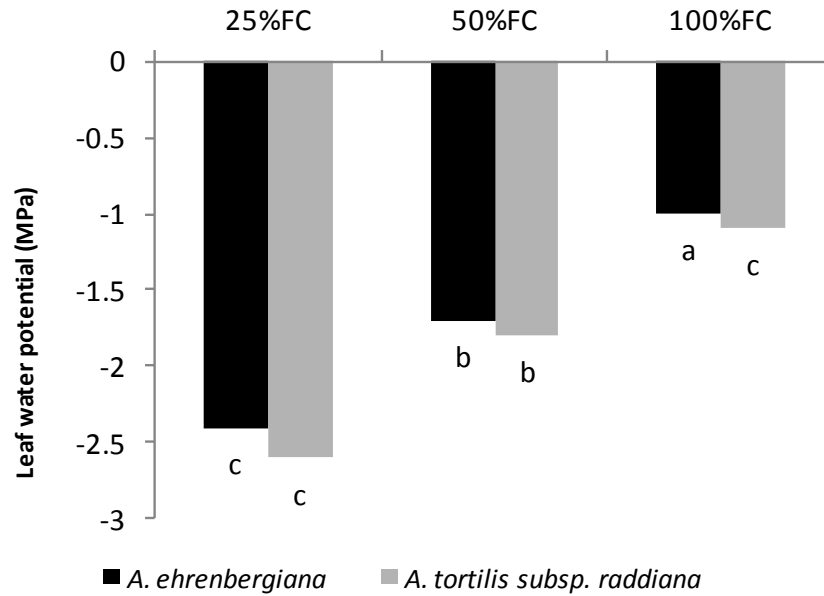


Figure 2. Effect of watering regimes on leaf water potential (MPa). Means followed by the same letter above a column are not significantly different at $p < 0.05$ FC-field capacity.

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
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	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																																																																																												
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	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																																																																																																																				
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	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																																																																																																																																
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	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																																																																																																																																																																																
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	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																																												
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	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																																																																																
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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. ehrenbergiana* and *A. tortilis ssp. raddiana*.

Species	Parameter	FC (%)			LSD ^{P=0.05}
		100	50	25	
<i>A. ehrenbergiana</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 (g plant ⁻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.

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