

IMPACT OF WATER STRESS ON THE SAPWOOD ANATOMY AND FUNCTIONAL MORPHOLOGY OF *CALLIGONUM COMOSUM*

N.S. Al-Khalifah, P.R. Khan, A.M. Al-Abdulkader and T. Nasroun

King Abdulaziz City for Science and Technology, P. O. Box 6086, Riyadh 11442, Saudi Arabia

SUMMARY

This investigation reports the impact of water stress on some anatomical traits of sapwood and other functional morphological features of green assimilatory shoots of *Calligonum comosum* L'Hér. (Erta), a good source of fuel wood. The major findings of the study are that in this species drought makes for: a) narrower vessels both in earlywood and latewood, b) thicker vessel walls, c) longer vessel elements and fibers, d) a higher frequency of small latewood vessels and a lower frequency of large earlywood vessels, e) narrower growth rings, f) a lower total fraction of vessels per xylem area, g) higher wood density, h) narrower depth of conducting phloem, i) higher specific mass of green photosynthetic shoots, and j) a lower chlorophyll content. Extremely narrow vessels arranged in radial files in latewood were recognized having 40% increased volume fraction in non-irrigated plants. This adaptation is believed to play an important role in the species survival during hot summer months.

Key words: Saturated water deficit, drought, assimilatory shoots, extremely narrow vessels, wood density.

INTRODUCTION

Calligonum comosum L'Hér. (called the *Erta* plant in Arabic), a member of the Polygonaceae, is a shrubby glabrous psammophyte which may attain a height of 2 m. It is a good source of fuel wood (Chaudhary 1999). It lacks a main trunk and has rigid, lignified basal white branches and weak young branches (Migahid 1978). Leaves are highly reduced or apparently absent in this species. The plants of this species play a major role in the productivity and stability of the desert environment (Farraj 1989). C₄ physiology has been recorded in the young green shoots, which exhibit Kranz anatomy (Watson & Dallwitz 1992).

Water is the most limiting ecological resource responsible for the distribution of higher plants. The effect of water deficits on plant productivity and water use efficiency has been extensively reviewed (Furquhar *et al.* 1989; Osoria & Pereira 1994). Drought and the decreasing soil moisture content lead to a decrease in average daily sap flux in the hardwood species. Sap flux is positively correlated with tree diameter at breast height (Holscher *et al.* 2005). The degree of water stress in plants is controlled by the relative rate of water absorption and water deficit. It may be caused either by lack of

available soil moisture or too slow absorption or too rapid loss of water, or most often by a combination of all three. The decline in tissue moisture content is due to lower resistance to withdrawal of water from turgid plant tissue than to the meagre uptake through the root (Kramer & Kozlowski 1979). As described by Levitt (1972) and Kalapos (1994), species classified as water savers have a number of characteristics like, *e.g.*, less negative osmotic potential, more rigid cell walls, narrow xylem vessels capable of embolism prevention in severe drought, and strong stomatal control to minimize water loss through transpiration. To prevent a catastrophic embolism cycle, trees in xeric sites have to reduce transpiration by decreasing stomatal conductance which in turn could lead to reduced carbon assimilation (Tyree & Sperry 1988). Vessel lumen diameter and vessel frequencies per cross-sectional area of xylem are partly heritable, partly plastic traits that are extremely variable from species to species. The field of ecological wood anatomy has, to date, centered on the relationship of xylem anatomy to drought tolerance and water transport efficiency (Tyree *et al.* 1994).

Demand by the forest industry for improved productivity and plantations of indigenous species in desert areas have created a need for detailed understanding of the water relations of taxa. Keeping this in mind the present investigation was undertaken to assess the impact of water stress on the sapwood and photosynthetic organs in one of the dominant species of the sand dunes of the Saudi Arabian desert.

MATERIALS AND METHODS

Five adult plants of *Calligonum comosum* of approximately five years of age were tagged at irrigated and non-irrigated (wild) sites. Average stem diameter of irrigated stems was 2.5 cm, that of non-irrigated plants 1.68 cm. The non-irrigated site was located on the outskirts of Unaiza town in the Qassim district (latitude 26° 30' N, longitude 43° 70' E, altitude 648 m), about 366 km northwest of Riyadh, Saudi Arabia, whereas the irrigated site, a horticultural farm, was in the same area. Distance between irrigated and non-irrigated site was only 2 km. The plants at the cultivated site were irrigated by flooding twice a week. Soil at both sites was sandy with pH 7.6 (irrigated) and 7.45 (non-irrigated). Green shoots acting as chief assimilatory organs were collected for determining specific mass, chlorophyll estimation and stem blocks for the anatomical studies at 10.00 a.m. in April 2002 and 2003.

Water deficit determination

To assess the severity of drought experienced by the population of non-irrigated plants green assimilatory shoots were taken from the four sides of each plant at 10.00 a.m. in the middle of April, July and September 2002 and 2003, which were considered high stress periods. The samples collected in plastic bags were taken immediately for refrigeration before weighing. Fresh weight, turgid weight and oven-dry weight of green shoots were determined for all samples (dried at 80 °C for 48 hours in Drying oven MOV-112, Sanyo, Japan). The entire set of samples was brought to full turgor by enclosing them in a moist chamber for 12 hours. Full turgid weight was obtained by reweighing them. Later on saturated water deficit (SWD) was calculated following the method described by Kramer and Kozlowski (1979).

$$\text{SWD} = \frac{\text{Fully turgid weight} - \text{fresh weight}}{\text{Fully turgid weight} - \text{oven-dry weight}} \times 100$$

Shoot specific mass

A definite amount of green shoots was taken for the determination of specific mass. Length of all cylindrical green shoot pieces was measured before determining their fresh weight and oven-dry weight. Dry weight was divided by length to obtain dry matter present in unit length of green shoots (James & Bell 2001).

Chlorophyll estimation

The photosynthetic pigments of green assimilating shoots were extracted in N,N-dimethyl formamide (DMF) and total chlorophyll content was determined spectrophotometrically following Moran (1982).

$$\text{Ct} = 7.04 \text{ A } 664 + 20.27 \text{ A } 647$$

Block sampling, sectioning and maceration

Samples of sapwood with bark were taken from the base of all branches of selected plants of the same age from the irrigated and non-irrigated sites with the help of chisel and hammer. The collected blocks were fixed on the spot in FAA (formaldehyde acetic alcohol). The fixed blocks were cut into small pieces and preserved in an alcoglycerol solution (1 : 1 mixture of 50 % ethanol and 50 % glycerol) for softening. Thin transverse, tangential longitudinal and radial longitudinal sections were cut at 10–12 μm thickness on an AO 860 sliding microtome, NY, USA. These sections were stained with haematoxylin and Bismark brown/safranin, mounted in euperal after dehydrating in an ethanol series (Johansen 1940). For the study of fibers, wood samples were macerated following Ghouse and Yunus (1972): samples were cut into thin tangential slices; these were treated with hot 60 % HNO_3 until the tissue elements got separated from each other. All the samples were washed several times with distilled water and stained with safranin and mounted in 5 % glycerol. In each sample 100 fibers were selected at random and measured using an eyepiece micrometer. Depth of conducting phloem was measured in the stem transection. The functional phloem was recognized on the basis of living companion cells, with microscopically visible protoplasm.

Vessel volume and ring width determination

Sections were studied under a Nova vision series bright field microscope. Data were collected on the vessel dimension and vessel pore frequency mm^{-2} of sapwood. The vessels were classified based on their diameter and location in the growth ring as follows:

Wide early wood vessels: 62–162 μm

Narrow vessels: 31–61 μm

Extremely narrow vessels: 10–22 μm

The vessel volume was analyzed based on the lumen size and number of vessels mm^{-3} of sapwood. Vessel wall thickness was deducted from the vessel diameter to obtain accurate lumen size. For the measurement of ring width, stem blocks were collected from plants of the same age but having different diameters from irrigated and non-irrigated

sites. It was standardized in our previous studies showing a difference of 22.8% in stem diameter of irrigated and non-irrigated plants (Al-Khalifah *et al.* 2003). Analysis of ring width was based on the mean of five growth rings of preceding years for each branch in each plant of irrigated and non irrigated sites. The coefficient of variation of the irrigated and non-irrigated population was also checked for this parameter and then the difference between ring widths of two populations was analyzed.

Wood density

Wood density was determined according to Kocacinar and Sage (2004). Stem segments 4–5 cm long were cut out from young but mature stems of irrigated and non-irrigated plants and kept in FAA until evaluation. Samples were washed under tap water and cut longitudinally in the middle. The pith as well as the bark and cambium were removed from each sample. Fresh volume of wood was estimated by immersing the sample in a narrow graduated cylinder filled with water. Replaced water was then removed carefully from the cylinder with a pipette and weighed. Displacement weight was converted to sample volume by dividing the displacement weight (grams) by the density of water at 20 °C (0.998 g cm⁻³). The dry weight was then determined after drying at 70 °C for 48 hrs. Wood density (g cm⁻³) was calculated as dry wt/fresh volume.

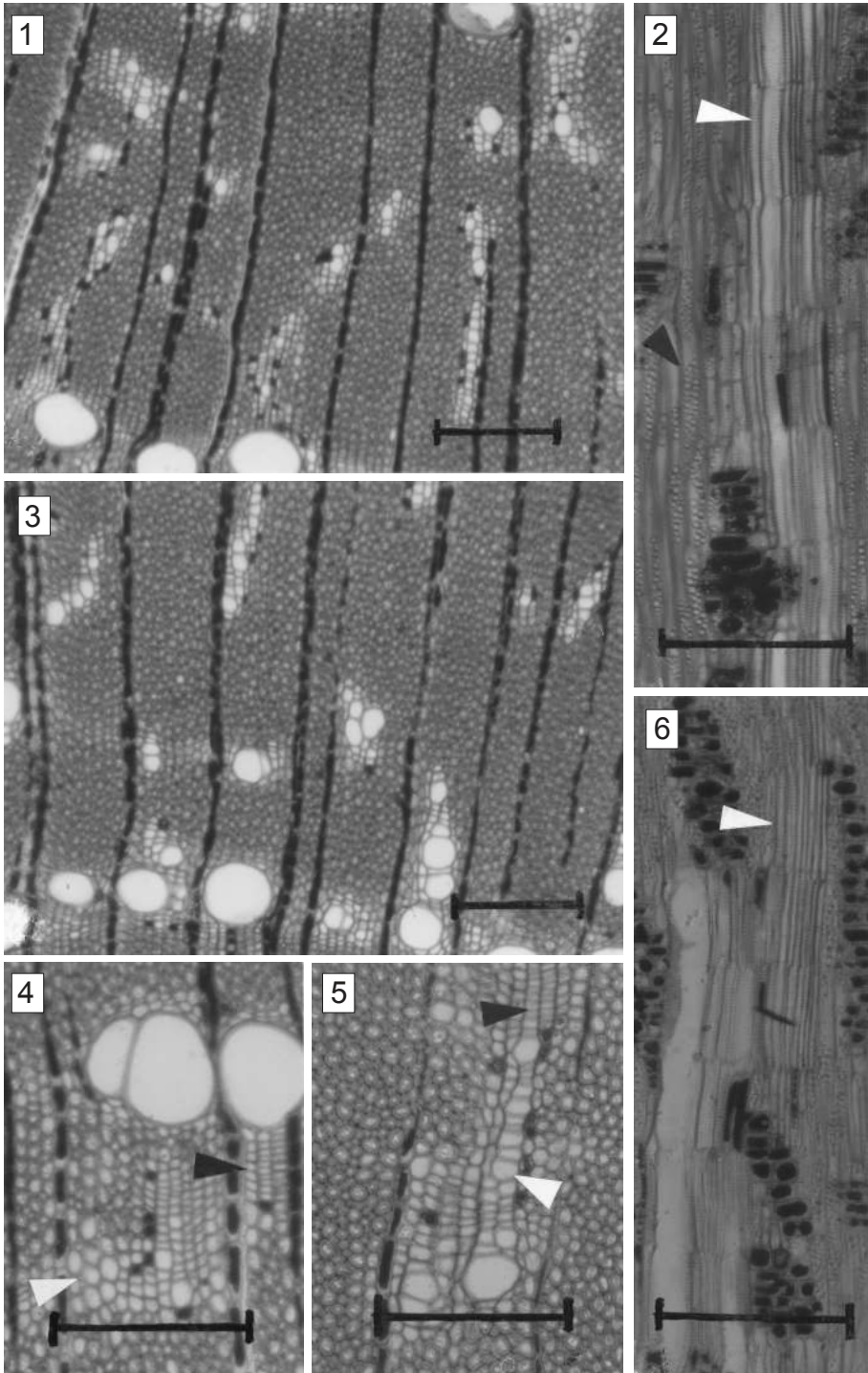
Statistical analysis

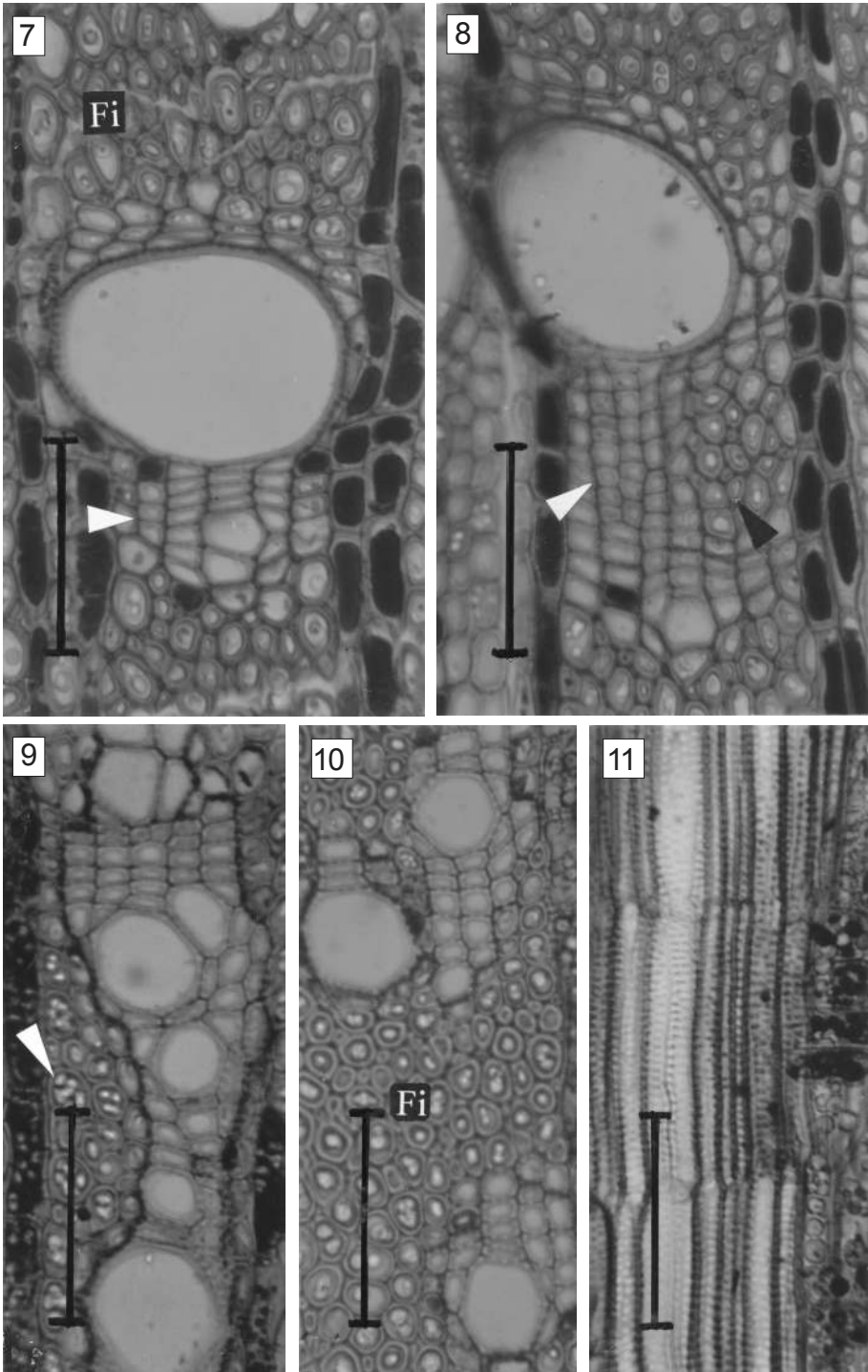
Data were analyzed statistically for standard deviation (SD), Student ‘t’ test and correlation coefficient (r) according to Snedecor and Cochran (1973). Computed mean values for all parameters of each tagged plant were used as replicate.

RESULTS

Microscopic examination of *Calligonum comosum* stem sections revealed a typical dicot structure showing a normal secondary growth pattern with ring-porous wood. Sapwood showed well demarcated growth rings. The growth rings were differentiated into earlywood and latewood that indicated the occurrence of periodic growth in this plant species. Earlywood was composed of one or two tangential rows of wide vessels, circular or oval in shape. Narrow vessels were distributed throughout the ring but their diameter was found to be decreasing towards the earlywood of the next ring (Fig. 1, 3, 5, 9 & 10). Extremely narrow vessels, arranged in radial files, were found in groups of 20–50 produced lately in latewood below the solitary wide vessels of earlywood of next year (Fig. 4, 7, 8 & 12). In general their shape was rectangular in irrigated and non-irrigated plants but sometimes squarish vessels were also recorded in non-irrigated samples

Fig. 1–6. Sapwood anatomy of *Calligonum comosum*. – 1: TS of a growth ring of non-irrigated plant showing wide vessels of earlywood in a tangential row and narrow and extremely narrow vessel groups in latewood. – 2 & 6: RLS of a non-irrigated sample showing files of narrow and extremely narrow vessels (white arrow) and fibers with starch grains (black arrow) in the latewood. – 3: TS of irrigated sample showing wide vessels. – 4 & 5: TS of non-irrigated sample showing radial files of extremely narrow vessels (black arrow), a group of axial parenchyma cells in Fig. 4 and a long chain of narrow vessels (white arrow) in Fig. 5. — Scale bars = 250 µm.





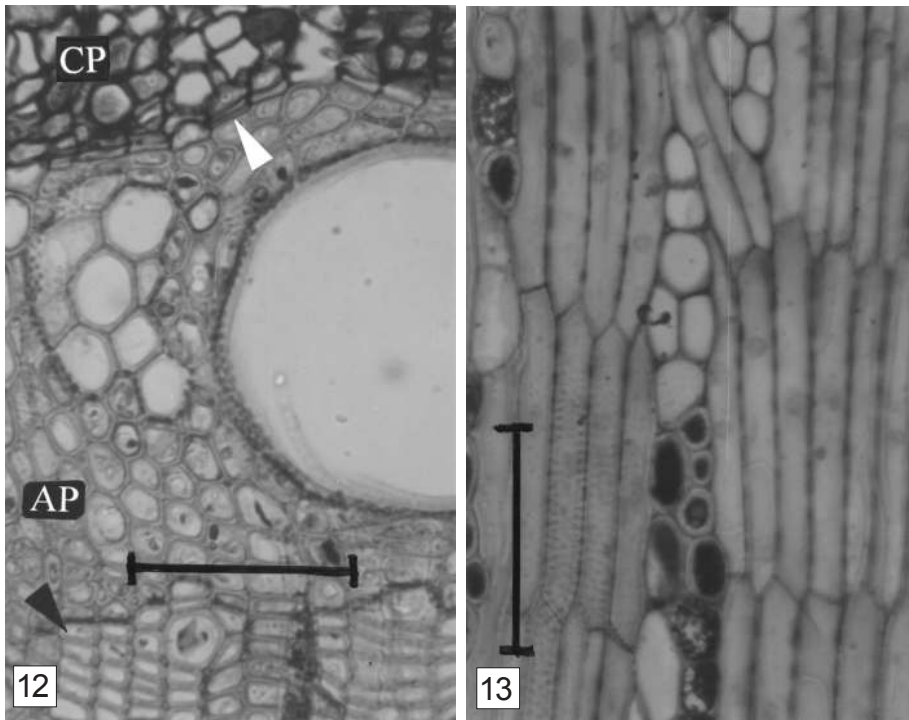


Fig. 12 & 13. Sapwood, secondary phloem, and cambium of *Calligonum comosum*. – 12: TS of non-irrigated stem showing conducting phloem (CP), cambium (white arrow), a wide vessel, a group of narrow vessels and axial parenchyma (AP), and extremely narrow vessels in radial files (black arrow). – 13: TLS of cambial zone showing storied fusiform initials. — Scale bars = 100 μm .

(Fig. 7–10). There was not much variation in the vessel element length as they were produced from a storied cambium (Fig. 2, 6, 11 & 13). The width (tangential and radial) of extremely narrow vessels was less than that of fibers and axial parenchyma (Fig. 12). The vessel elements were arranged in a stratified order in the radial longitudinal plane (Fig. 2 & 6). The wide, narrow as well as extremely narrow vessels had simple perforation plates and intervascular alternate pits. Fibers had starch grains in their lumina (Fig. 2, 6–10).

Fig. 7–11. Anatomical response to drought in *Calligonum comosum*. – 7: TS of sapwood of irrigated plant showing extremely narrow vessels in radial files (white arrow) below a wide vessel and fibers (Fi). – 8: TS of sapwood of non-irrigated plant showing a longer radial files of extremely narrow vessels (white arrow) and a group of fibers (black arrow). – 9: TS of sapwood of irrigated plant showing a group of narrow and extremely narrow vessels. Note starch grains in the lumen of fibers (white arrow). – 10: TS of sapwood of non-irrigated plant showing groups of narrow and extremely narrow vessels and fibers (Fi). – 11: Enlarged view of Fig. 2. — Scale bars = 100 μm .

Table 1. Dimensional variation due to water stress conditions in the components of sapwood.

Parameters	Non-irrigated	Irrigated	't'
Mean vessel element length (μm)	155 [± 7.8]	114 [± 5.7]	9.71**
Radial diameter of earlywood vessels (μm)	39.0 [± 2.3]	53.6 [± 3.2]	8.20**
Tangential diameter of earlywood vessels (μm)	35.9 [± 1.8]	50.7 [± 3.0]	9.33**
Mean diameter of earlywood vessels (μm)	37.5 [± 2.0]	52.1 [± 3.1]	8.77**
Wall thickness of earlywood vessels (μm)	4.0 [± 0.20]	2.3 [± 0.11]	17.02**
Radial width of extremely narrow vessels (μm)	9.1 [± 0.73]	10.5 [± 0.84]	2.77*
Tangential width of extremely narrow vessels (μm)	15.1 [± 1.20]	17.5 [± 1.40]	2.85*
Mean width of extremely narrow vessels (μm)	12.1 [± 0.96]	14.0 [± 1.11]	2.83*
Wall thickness of extremely narrow vessels (μm)	1.50 [± 0.15]	1.25 [± 0.09]	3.21*
Mean diameter of earlywood and extremely narrow vessels (μm)	31.8 [± 2.54]	38.3 [± 3.06]	3.62*
Fibre length (μm)	592 [± 62.3]	474 [± 31.2]	3.78**
Fibre width (μm)	21.9 [± 0.49]	24.7 [± 2.21]	2.72*

* Significant ($p < 0.05$); ** ($p < 0.01$).

Irrigated versus non-irrigated plants

Significantly longer but narrower vessel elements and fibers were recorded in non-irrigated samples. The diameter of wide and narrow vessels of the earlywood showed a higher value for the irrigated samples than that of the non-irrigated ones ($p < 0.01$). The same trend was followed by extremely narrow vessels of the latewood ($p < 0.05$). Wall thickness of both earlywood vessels and extremely narrow vessel pores was found to be significantly higher in non-irrigated plants (Table 1).

Table 2. Sensitivity of sapwood to drought.

Parameters	Non-irrigated	Irrigated	't'
Vessel frequency: Wide	4.2 [± 0.21]	5.0 [± 0.55]	3.15*
Narrow	24.0 [± 1.20]	15.0 [± 1.65]	9.90**
Extremely narrow	160.0 [± 12.4]	86.0 [± 4.3]	12.63**
Total	188.2 [± 12.4]	106.0 [± 8.9]	12.11**
Volume fraction of earlywood vessels (mm^3)	0.031 [$\pm 1.87 \times 10^{-3}$]	0.050 [$\pm 3.98 \times 10^{-3}$]	9.46**
Volume fraction of extremely narrow vessels (mm^{-3})	0.022 [$\pm 1.76 \times 10^{-3}$]	0.015 [$\pm 9.44 \times 10^{-4}$]	7.07**
Total volume fraction of vessels (mm^{-3})	0.053 [$\pm 3.72 \times 10^{-3}$]	0.065 [$\pm 4.58 \times 10^{-3}$]	4.64**
Ring width (μm)	1216 [± 69.6]	1982 [± 214.2]	7.60**
Depth of conducting phloem (μm)	89 [± 9.2]	147 [± 17.2]	6.66*
Wood density (g cm^{-3})	0.733 [± 0.011]	0.600 [± 0.012]	17.52**

* Significant ($p < 0.05$); ** ($p < 0.01$).

The frequency of narrow and extremely narrow vessels was significantly higher in non-irrigated samples experiencing severe drought ($P < 0.01$), *viz.*, twice as high as that in irrigated specimens (Table 2 and Fig. 7 & 8). The volume fraction of earlywood vessels was significantly lower in non-irrigated samples while the extremely narrow vessels had a significantly higher volume fraction in the same ring than the irrigated samples ($p < 0.01$). The decrease in volume fraction of earlywood vessels and increase in the extremely narrow vessels' volume fraction of non-irrigated samples was estimated to be 37% and 40% respectively as compared to the irrigated ones. The total volume fraction of earlywood vessels and extremely narrow vessels of non-irrigated plants was significantly less than that of the irrigated ones. Drought had reduced the growth of stems, as significantly narrower ring widths (39% less) with higher wood density were observed in the non-irrigated samples, presumably due to the harsh environmental conditions (Fig. 14). The depth of conducting phloem also was 40% less in non-irrigated plants (Table 2).

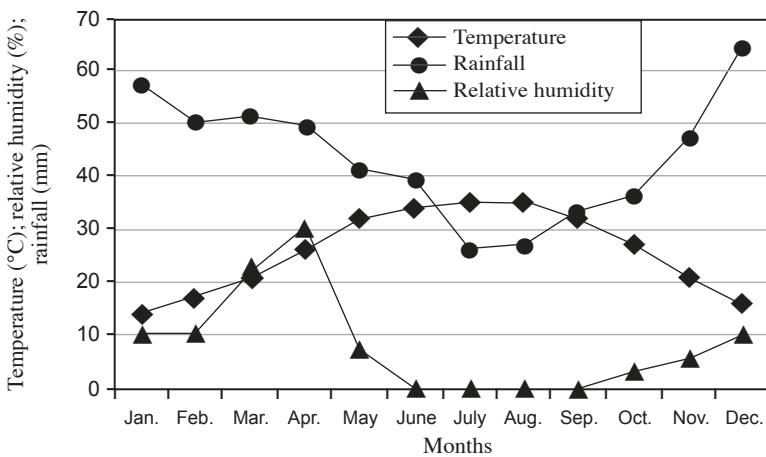


Fig. 14. Meteorological data (mean of two years) of the study area for the years 2002 and 2003.

Table 3. Correlation of saturated water deficit with the functional morphology of green assimilatory shoots and anatomical traits of sapwood.

Parameters	SMPS	CHL	RW	VV	WD
Non-irrigated SWD	0.975**	-0.369	-0.913**	-0.887**	0.963**
Irrigated SWD	0.863**	-0.121	-0.725*	-0.654*	0.735*

SWD = saturated water deficit; SMPS = specific mass of photosynthetic shoots; CHL = chlorophyll (mg)/g fresh weight of green shoots; RW = ring width; VV = vessel volume mm⁻³ of sapwood; WD = wood density.

* Significant ($p < 0.05$); ** ($p < 0.01$).

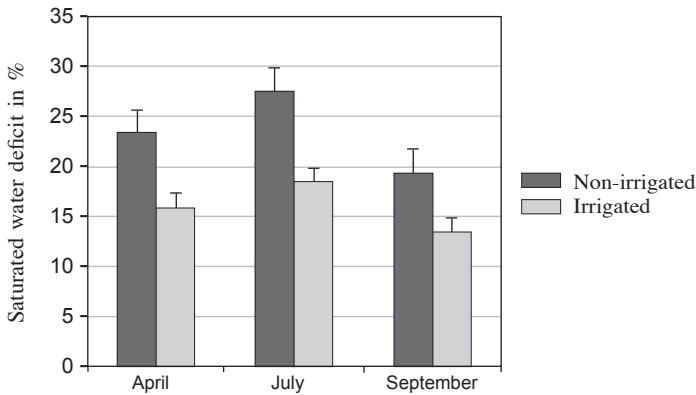


Fig. 15. Saturated water deficit with SE bar of green assimilatory shoots estimated during a high stress period (April–September).

Vessel element length, vessel diameter, wall thickness and volume fraction of early-wood vessels, frequency of extremely narrow vessels of latewood and wood density were identified as sensitive parameters to drought on the basis of their high degree of significance (having higher *t* value).

Saturated water deficit (SWD) of green assimilatory shoots was analyzed during the high stress period (April–September). SWD of non-irrigated samples was found to be highest in July (28%) when the atmospheric temperature was high followed by a decline in SWD with temperature in September (19%). A difference of 7%, 9% and 6% in SWD between non-irrigated and irrigated plants was recorded for April, July and September, respectively (Fig. 15).

Saturated water deficit showed a linear correlation with the specific mass of green shoots and wood density. SWD was negatively correlated with chlorophyll content of green assimilatory shoots, annual ring width and volume fraction of vessels of sapwood. Correlation between SWD and chlorophyll content was, however, non-significant. The degree of significance for all the pairs of parameters was higher in non-irrigated plants (Table 3).

DISCUSSION

Water deficit affects every aspect of plant growth, modifying anatomy, morphology, physiology and metabolism (Auge *et al.* 1998). Growth performance of *Calligonum comosum* was studied under the impact of water stress in the desert of Saudi Arabia. Drought significantly suppressed all the growth parameters including the stem diameter (Al-Khalifah *et al.* 2003).

The measured length of vessel elements (155 μm) and fibers (592 μm) and fiber width (21.9 μm) of non-irrigated *C. comosum* were larger than those of six different species of *Calligonum* reported for the Gansu desert of China (Ma Rui-jun *et al.* 1994). The size variation in vessel element length of six species ranged between 93 and 113 μm , fiber length between 444 and 521 μm and fiber width from 15–18 μm . However, the

vessel frequency (29–66), radial vessel diameter (56–98 μm), tangential vessel diameter (44–91 μm) and vessel wall thickness (5.1–9.3 μm) of the six *Calligonum* species from China showed much higher quantitative values than the non-irrigated *C. comosum*. *Calligonum arborescens* has the same vessel frequency (28.8) as that of *C. comosum* (28.2). Ma Rui-jun *et al.* (1994) did not report the occurrence of extremely narrow vessels in their study material. The occurrence of starch grains in the fibers of *C. comosum* has also been reported in this species from the Negev desert by Fahn *et al.* (1986).

In its natural habitat *C. comosum* is growing on sand dunes. A strong and flexible stem is required to face strong wind and sand movement. This species has presumably adapted accordingly by producing wood of higher density, with narrow, thick-walled vessels and long fibers in the narrow growth rings of stems that have a significantly smaller diameter under water stress condition, as also reported by Zahner (1968). The lower volume fraction of vessels may make the stem stronger. The same conclusion was drawn by Wagner *et al.* (1998) while working on four Chaparral shrubs of Southern California. The wood of *Eucalyptus globulus* was found to have larger vessels, occupying a greater proportion of total cross-sectional area in a collection from a site experiencing less water stress (Leal *et al.* 2003). The wood density of non-irrigated *C. comosum* observed in the present study was comparable with that of *C. turbineum* (0.71 g cm^{-3}) from Kazakhstan whereas *C. aphyllum* from another location of Kazakhstan showed a higher value of 0.82 g cm^{-3} (Kocacinar & Sage 2004).

At the whole plant level, limited soil water supply may have a strong effect on dry matter accumulation (Li 1998). A negative and significant relationship of specific mass of green shoots with its relative water content (RWC) was established in our previous study (Al-Khalifah *et al.* 2003). Specific mass of green shoots of *C. comosum* had a positive and significant correlation with SWD. The more severe the drought the thicker and more condensed the green shoots, having more dry matter per unit of length. A positive and significant correlation between leaf specific mass and leaf water content ($r = 0.67$) was reported for 21 Australian *Eucalyptus* species (Datt 1999). A significant and positive correlation has also been observed between productivity and their water content in nine desert plant species of Mediterranean coastal area (Migahid & Elhaak 2001). An increase in SWD or decrease in RWC and leaf water potential is caused by water stress (Morgan 1984).

In the present investigation no adverse effect of drought was observed on the chlorophyll content (non-significant correlation between SWD and chlorophyll contents). However, in other species water stress is reported to reduce chlorophyll synthesis (Alberte *et al.* 1975; Tyree & Jarvis 1982). Drought stress has been reported to decrease the concentration of chlorophyll a, b and carotenoids (Pukacki & Ro Zek 2005) and stomatal conductance (Fort *et al.* 1997), leading to a decrease in photosynthetic activity.

In the present study effects of drought are shown by a reduction of 39% in the ring width of non-irrigated *C. comosum*. Saturated water deficit was inversely proportional to the growth ring width, more pronounced in non-irrigated plants than in the irrigated ones. Drought has adverse effects on height and radial growth in *Quercus faginea* in the absence or low recharge precipitation during November–February at a xeric site in NE Spain. The affected oaks did not produce latewood but exhibited only wide earlywood

vessels (Corcuera *et al.* 2004). Availability of soil water has a strong bearing on the radial stem growth. Up to 90% variation in the annual ring width of arid plants can be attributed to the differences in the water stress (Zahner 1968).

Vessel element length has been considered by Baas *et al.* (1983) to be the sensitive indicator of ecological conditions of a given taxon. Narrow vessels are positively correlated with xeromorphism in any group of dicotyledons (Carlquist 1966). The area of vessels in such xeromorphic wood is invariably compensated, in part by a greater vessel number per square mm (Carlquist 1982a, b; Zimmermann 1982). In our study the frequency of narrow and extremely narrow crowded vessels with thick walls was very high in non-irrigated samples. The success of plant species in xeric conditions depends on the narrow and numerous vessels having intervascular pit resistance, which offer a high degree of safety under water stress conditions (Baas 1976; Baas *et al.* 1983; Zimmermann 1983; Carlquist 1984; Ma Rui-jun *et al.* 1994). Our results also support this view. The small diameter latewood vessels and small diameter vasicentric tracheids near the large vessels are thought to provide water transport once the earlywood and/or wider vessels have become air-filled (Carlquist 1985; Hargrave *et al.* 1994; Cochard *et al.* 1997). More or less the same hypothesis could be based on our results, but this needs yet to be tested experimentally. A significant increase in the volume fraction of extremely narrow vessels in latewood of non-irrigated plants may be an important adaptation and is believed to facilitate the necessary minimum of water conduction during periods of extreme water stress to avoid dieback. Another interesting plastic response to irrigation is the dramatic reduction of wall thickness of the wide earlywood vessels, even as their lumen diameter increased. This results in vessels build more cheaply and more efficient in transport, but also more at risk for implosion in response to water stress (Hacke *et al.* 2001).

ACKNOWLEDGMENTS

The authors are grateful to King Abdulaziz City for Science and Technology (KACST) for funding this research (Grant No. ARP-20-081).

REFERENCES

- Alberte, R.S., E.L. Fiscus & A.W. Naylor. 1975. The effect of water stress on the development of photosynthetic apparatus in greening leaves. *Plant Physiol.* 55: 317–321.
- Al-Khalifah, N.S., P.R. Khan, A.M. Al-Abdulkader, T. Nasroun & A.H. Al-Farhan. 2003. Impact of water stress on growth of two fuelwood plants of Saudi Arabia. *Ann. Arid Zone* 42: 155–163.
- Auge, R.M., D. Xiangrong, J.L. Croker, W.T. White & C.D. Green. 1998. Foliar dehydration tolerance of twelve deciduous tree species. *J. Expt. Bot.* 49: 753–759.
- Baas, P. 1976. Some functional and adaptive aspects of vessel member morphology. In: P. Baas, A.J. Bolton & D.M. Catling (eds.), *Wood structure in biological and technological research*: 157–181. *Leiden Bot. Series No. 3*. Leiden University Press, The Hague.
- Baas, P., E. Werker & A. Fahn. 1983. Some ecological trends in vessel character. *IAWA Bull.* n. s. 4: 141–159.
- Carlquist, S. 1966. Wood anatomy of Compositae: a summary with comments on factors controlling wood evolution. *Aliso* 6: 25–44.

- Carlquist, S. 1982a. Wood anatomy of Daphniphyllaceae: ecological and phylogenetic considerations, review of pittosporalean families. *Brittonia* 34: 252–266.
- Carlquist, S. 1982b. Wood anatomy of *Illicium* (Illiciaceae): phylogenetic, ecological and functional interpretations. *Am. J. Bot.* 69: 1587–1598.
- Carlquist, S. 1984. Wood anatomy and relationships of Pentaphyllaceae: significance of vessel features. *Phytomorphology* 34: 84–90.
- Carlquist, S. 1985. Vasicentric tracheid as a drought survival mechanism in the woody flora of southern California. *Aliso* 11: 37–68.
- Chaudhary, S.A. 1999. Flora of the Kingdom of Saudi Arabia. Ministry of Agriculture and Water, Riyadh.
- Cochard, H., M. Peiffer, K. Le Gall & A. Grainer. 1997. Developmental control of xylem hydraulic resistances and vulnerability to embolism in *Fraxinus excelsior* L. impacts on water relation. *J. Expt. Bot.* 48: 655–663.
- Corcuera, L., J.J. Camarero & E. Gil-Pelegrin. 2004. Effects of a severe drought on growth and wood anatomical properties of *Quercus faginea*. *IAWA J.* 25: 185–204.
- Datt, B. 1999. Remote sensing of water content in *Eucalyptus* leaves. *Aust. J. Bot.* 47: 909–923.
- Fahn, A., E. Werker & P. Baas. 1986. Wood anatomy and identification of trees and shrubs from Israel and adjacent regions [pp. 138–139]. Israel Academy of Sciences and Humanities, Jerusalem.
- Farraj, M.M. 1989. Disturbances and dangers operating on desert vegetation in Saudi Arabia. *Proc. of NCWED* 3: 164–168.
- Fort, C., M.L. Fauveau, F. Muller, P. Pabcl, A. Granier & E. Dreyer. 1997. Stomatal conductance, growth and root signalling in young oak seedling subjected to partial soil drying. *Tree Physiol.* 17: 281–289.
- Furquhar, G.D., J.R. Ehleringer & K. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* 40: 503–537.
- Ghouse, A.K.M. & M. Yunus 1972. Preparation of epidermal peels from leaves of gymnosperms by treatment with hot 60% HNO₃. *Stain Tech.* 47: 322–324.
- Hacke, U.G., J.S. Sperry, W.T. Pockman, S.D. David & K.A. McCulloh. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457–461.
- Hargrave, K.R., K.J. Kolb, F.W. Ewers & S.D. Davis. 1994. Conduit diameter and drought-induced embolism in *Salvia mellifera* Green (Labiatae). *New Phytol.* 126: 695–705.
- Holscher, D., O. Koch, S. Korn & C. Leuschner. 2005. Sap flux of five co-occurring tree species in a temperate broad-leaved forest during seasonal soil drought. *Trees-Struc. Func.* DOI: 10.1007/s 00468-005-0426-3, 1432-2285 (published online).
- James, S.A. & D.T. Bell. 2001. Leaf morphological and anatomical characteristics of heteroblastic *Eucalyptus globulus* (Myrtaceae). *Aust. J. Bot.* 49: 259–269.
- Johansen, D.A. 1940. Plant microtechnique. McGraw Hill, New York.
- Kalapos, T. 1994. Leaf water potential-leaf water deficit relationship for ten species of a semi-arid grassland community. *Plant and Soil* 160: 105–112.
- Kocacinar, F. & R.F. Sage. 2004. Photosynthetic pathway alters hydraulic structure and function in woody plants. *Oecologia* 139: 214–223.
- Kramer, P.J. & T.T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York.
- Leal, S., H. Pereira, M. Grabner & R. Wimmer. 2003. Clonal and site variation of vessels in 7-year-old *Eucalyptus globulus*. *IAWA J.* 24: 185–195.
- Levitt, J. 1972. Responses of plants to environmental stresses. Academic Press, New York.
- Li, C. 1998. Growth response of *Eucalyptus microtheca* provenances to water stress. *J. Trop. For. Sci.* 10: 379–387.

- Ma Rui-jun, Wu Shu-ming & Wang Feng-chun. 1994. Studies on anatomy and desert adaptability of stem secondary xylem in 6 species of *Calligonum*. *Acta Bot. Sinica* 36 Suppl.: 55–60.
- Migahid, A.M. 1978. Flora of Saudi Arabia. Riyadh University Publication, Riyadh.
- Migahid, M.A. & M.A. Elhaak. 2001. Ecophysiological studies on some desert plant species native to the Mediterranean area in Egypt. *J. Arid Environ.* 48: 191–203.
- Moran, R. 1982. Formulae for determination of chlorophyllous pigments extracted with N,N-dimethylformamide. *Plant Physiol.* 69: 1376–1381.
- Morgan, J.M. 1984. Osmoregulation and water stress in higher plants. *Ann. Rev. Plant Physiol.* 35: 299–319.
- Osorio, J. & J.S. Pereira. 1994. Genotypic differences in water use efficiency and C¹³ discrimination in *Eucalyptus globulus*. *Tree Physiol.* 4: 871–882.
- Pukacki, P.M. & E.K. Rozek. 2005. Effect of drought stress on chlorophyll: a fluorescence and electrical admittance of shoots in Norway spruce seedlings. *Trees-Struc. Func.* DOI: 10.1007/s00468-005-0412-9, 1432-2285 (published online).
- Snedecor, G.W. & W.G. Cochran 1973. *Statistical methods*. Ed. 6. The Iowa State University Press, Ames, Iowa.
- Tyree, M.T., S.D. Davis & H. Cochard. 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA J.* 15: 335–360.
- Tyree, M.T. & P.G. Jarvis. 1982. Water in tissues. In: O.L. Lange, P.S. Nobel., C.B. Osmond & H. Ziegler (eds.), *Water relations and carbon assimilation*: 36–71. *Physiology Plant Ecology* 11, Encyclopedia of Plant Physiology, Springer-Verlag, Berlin.
- Tyree, M.T. & J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiol.* 88: 574–580.
- Wagner, K.R., F.W. Evers & S.D. Davis. 1998. Tradeoff between hydraulic efficiency and mechanical strength in the stems of four co-occurring species of chaparral shrubs. *Oecologia* 117: 53–62.
- Watson, L. & M.J. Dallwitz. 1992. The families of flowering plants: description, illustrations, identification, and information. Retrieval version: 14th December 2000. <http://biodiversity.uno.edu/delta/>.
- Zahner, R. 1968. Water deficits and growth of trees. In: T.T. Kozlowski (ed.), *Water deficit and plant growth*. 2: 191–252. Academic Press, New York.
- Zimmermann, M.H. 1982. *Functional xylem anatomy of angiosperm trees*. Nijhoff/Junk, The Hague.
- Zimmermann, M.H. 1983. *Xylem structure and the ascent of sap*. Springer Series in Wood Science, Springer, Berlin.