Soil and leaf water relations of differentially moisture-stressed honey mesquite (*Prosopis glandulosa* Torr)*

R. J. Ansley, P. W. Jacoby, C. H. Meadors,
& B. K. Lawrence

*Texas A&M University Agricultural Research and
Extension Center, P.O. Box 1658, Vernon, TX 76384, U.S.A.*

The objective of this study was to determine plant/soil water relations of honey mesquite (*Prosopis glandulosa* Torr.) following preconditioning to different levels of moisture stress. Moisture stress of 12 naturally occurring trees (mean height 3·2 m), located in north Texas, was manipulated through the use of drip irrigation and sub-canopy rain shelters. Pre-dawn leaf water potential and average daily stomatal conductance were greatest in irrigated trees and least in rain-sheltered trees on 27 June and 28 July 1986 after 1 and 2 months of stress preconditioning, respectively. Following a common irrigation of all trees (equivalent to 35–40 mm precipitation) on 28 June and 29 July, pre-dawn leaf water potential increased to similar levels in all trees within 1 day. Increase to maximum average daily stomatal conductance was delayed in moisture-stressed trees following the July watering, suggesting that moisture stress inhibited ability to respond to moisture availability. A positive relationship was found between soil moisture content and pre-dawn leaf water potential, and between soil moisture and average daily stomatal conductance. However, average daytime leaf water potential was unaffected by soil moisture content.

Introduction

Much of our knowledge of the water relations of honey mesquite (*Prosopis glandulosa* Torr.) has come from studies in the Sonoran Desert of southern California (Mooney *et al.*, 1977; Nilsen *et al.*, 1981, 1983, 1984; Jarrell & Virginia, 1990). In this arid environment, mesquite exist as deep-rooted phreatophytes (Phillips, 1963; Levitt, 1980; Sharifi *et al.*, 1982; Nilsen *et al.*, 1986). Comparatively little data are available concerning plant/soil water relations of mesquite in higher rainfall regions such as north central Texas, where annual precipitation is 8 to 10 times greater than the Sonoran Desert (Easter & Sosebee, 1975). On some semi-arid Texas sites, mesquite are dependent on shallow lateral roots for water—a rooting strategy associated with frequent rewetting of surface soil horizons (Heitschmidt *et al.*, 1988; Ansley *et al.*, 1990).

Studies have attempted to quantify mesquite/soil water relations in semi-arid environments over an entire growing season (Haas & Dodd, 1972; Thomas & Sosebee, 1978; Wan & Sosebee, 1990). However, seasonal changes in vapour pressure deficit interfered with an

accurate assessment of the influence of soil moisture on leaf water relations. No studies have reported the response of differentially moisture-stressed mesquite to moisture events, although Sala & Lauenroth (1982) noted the significance of small rainfall events on the physiological condition of semi-arid plants. Our goal in the present study was to quantify, under relatively constant ambient conditions, the relationships between soil moisture, leaf water potential, and stomatal activity of semi-arid mesquite. A second objective was to examine the response of differentially moisture-stressed mesquite to simulated rainfall events.

Materials and methods

Site description

The study was conducted on the W. T. Waggoner Estate located 30 km south of Vernon in the northern Rolling Plains ecological area of Texas (33°52′N, 99°17′W; elevation 368 m). Average annual precipitation is 665 mm, which occurs in a spring/fall bimodal pattern. Peak rainfall months are May (119 mm) and October (77 mm). The region supports primarily warm season grasses and forbs dominated by a moderate overstory (<30% canopy cover) of mesquite and the shrub lotebush (*Ziziphus obtusifolia*). Components of the understory include the C_4 grasses buffalograss (*Buchloe dactyloides*) and sideoats grama (*Bouteloua curtipendula*), and the C_3 grass Texas wintergrass (*Stipa leucotricha*). Soils of the study area are Udertic Paleustolls of the Deandale series and Typic Paleustalfs of the Kamay series. Both soils are clay loams developed from sandstone/shale parental material. Slopes are less than 3%.

Treatment installation

Twelve multistemmed trees were selected as experimental units from the overstory component of the study site on the basis of uniformity in canopy shape and basal stem number. Plant shapes were selected to follow that of a parabolic frustrum to facilitate construction of sub-canopy rain shelters. Trees were 3·0–3·5 m in height with canopies of 4–6 m diameter at the widest part. All woody vegetation including non-experimental mesquite occurring within 10 m of each experimental tree was removed by chain-sawing aerial portions and saturating remaining plant bases with diesel oil. Each experimental tree was containerised with a sheet metal and plastic vertical barrier to a depth of 2·5 m during January 1986 (Ansley *et al.*, 1988). The containers were open at the bottom. Four 2·5 m long × 5 cm diameter aluminum access tubes were installed within each root container at 2 m laterally from the tree centre for soil moisture measurement. All 12 trees were equipped with a trickle irrigation system via underground polyvinyl chloride (PVC) tubing connected to a 23,000 l tank and electric pump powered by a 4·5 kW generator. Water from a municipally approved drinking system was supplied via water truck to the tank.

Root containerisation, irrigation and rain shelters were used to generate surplus and reduced soil moisture levels available to three groups of four mesquite trees. 'Surplus' trees received precipitation plus periodic trickle irrigation. Reduced soil moisture levels for 'rainout' trees were created by installing a sub-canopy rain shelter. Each shelter consisted of a plastic sheet stretched over a wood frame and suspended 1 m above the soil surface and beneath the canopy foliage (Jacoby *et al.*, 1988). Trees exposed only to rainfall were selected as 'control' trees.

Rain shelters were imposed 29 May 1986, about 2 months following budbreak of mesquite. Trees were preconditioned through soil moisture manipulation for 1 month

prior to a common watering of all trees on 28 June (Table 1). Post-irrigation measurements in this trial were terminated when a 26 mm rain occurred on 2 July. Trees were preconditioned for an additional month prior to a second common watering which began on 29 July. Rain on 3 August halted further sampling in the second trial. Between the first and second common irrigations, surplus trees received 133 mm more and rainout trees received 124 mm less water than control trees, a range of 257 mm.

Response variables

Stomatal conductance of lower leaflet surfaces was measured using a LICOR LI-1600 porometer (LICOR Inc, Lincoln, NE). All leaves that were measured were located on the perimeter of the canopy and fully exposed to the sun. Two leaves were measured per tree during each sample period which occurred at 2, 5, 8 and 11 h post-sunrise.

Leaf water potential was measured using a Scholander-type pressure bomb at pre-dawn (pre-dawn leaf Ψ), and during porometer sampling (daytime leaf Ψ). Two leaves were excised from the centre of each canopy at 1·5–2 m height and water potential determined as outlined by Turner (1981).

Photosynthetic photon flux density (400–700 nm) was determined using a LICOR LI-190S-1 Quantum Sensor at each point where conductance was measured. Two readings were taken, one with the sensor oriented vertically and a second with the sensor at leaf angle facing away from the basal centre of the tree. Values reported in this study represent

Table 1. *Water additions by irrigation and precipitation in three different soil moisture treatments during spring and summer 1986*

Date	Water* type	Water amount (mm)		
		Surplus	Control	Rainout
19 May	p	28	28	28
26 May	p	22·2	22·2	22·2
29 May	RS			
31 May	p	6	6	—
04 June	p	45·0	45·0	—
10 June	s	26·5	—	—
16–17 June	p	31·9	31·9	—
19 June	s	45·9	—	—
23 June	p	5·0	5·0	—
28 June	c	38·2	38·2	38·2
01–03 July	p	19·8	19·8	—
11 July	p	6·2	6·2	—
15 July	s	31·7	—	—
21 July	p	11·2	11·2	—
22 July	s	29·1	—	—
29 July	c	34·5	34·5	34·5
Total (29 May–27 June)		160·3	87·9	0
Total (29 June–28 July)		98·0	37·2	0
Total (29 May–28 July)		296·5	163·3	38·2

* p, precipitation; s, irrigation of surplus trees only; c, common irrigation of all trees. RS, rain shelter installation.

an average of the two readings. Vapour pressure deficit was determined using a hygrother-mograph which was calibrated periodically with a sling psychrometer.

Volumetric soil moisture (θ) was measured at 30 cm increments to a depth of 210 cm using the neutron attenuation method (Greacen, 1981). Measurements were made on each day that leaf parameters were measured. Soil moisture measurements were calibrated to field samples following bulk density determination. Soil water retention curves were determined at each depth for each soil series using a pressure plate apparatus (Richards, 1965), and soil matric potential (soil Ψ_m) was calculated based on retention curve equations.

Statistical analysis

Because of a slight variation in soils across the study site, a randomized complete block design was established with four blocks (soils), three treatments (surplus, control, rainout), and four replicates (individual trees) to assess significant differences in θ, soil Ψ_m, conductance and leaf Ψ between treatments. A repeated-measures analysis of variance was used to determine differences between treatments on a particular day, and differences between dates within a treatment (Steel & Torrie, 1980). Prior to analysis, leaf variables were averaged over all sample periods within each day.

Data from all dates (pre- and post-common irrigation) were used to examine relation-ships between soil and plant variables. Plant variables were averaged over all sample periods within a treatment and date. Soil variables were averaged over certain depths within a treatment and date, as designated in the figures. Linear and curvilinear regression techniques were used to determine each relationship.

Results

Ambient conditions

Photosynthetic radiation followed similar diurnal curves on all sample days, except during the 2 h post-sunrise sample period on 29 June when a slight haze blocked the sun (Fig. 1). Vapour pressure deficit followed similar diurnal patterns on all sample days, but generally was greater during the July irrigation trial than during June. Peak vapour pressure deficit occurred on each day during mid-afternoon.
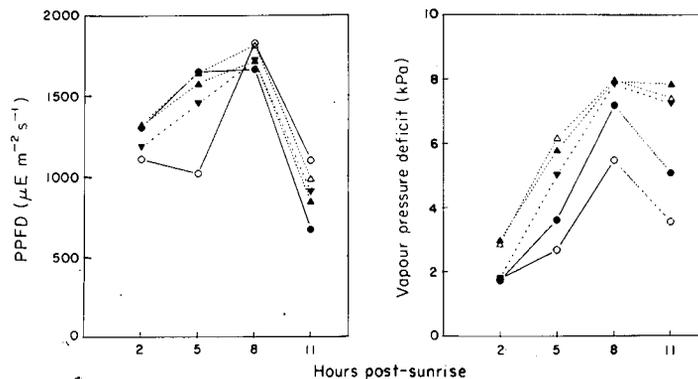

Figure 1. Diurnal photosynthetic photon flux density (PPFD) near sampled leaves, and vapour pressure deficit on each sample date. PPFD was averaged over all 12 trees. ●, 27 June; ○, 29 June; ▲, 28 July; △, 30 July; ▼, 01 August.

Response to long-term preconditioning

Volumetric soil moisture (θ) and soil matric potential (soil Ψ_m) were greatest beneath surplus trees and least beneath rainout trees on 27 June and 28 July 1986, following month-long intervals of stress preconditioning (Fig. 2). Differences in θ and soil Ψ_m between surplus and rainout trees were greatest at 30 + 60 cm depth on both dates. Soil Ψ_m was maintained near or greater than -0.5 MPa at most depths beneath surplus trees, but was near or below agronomic wilting point (-1.5 MPa) at all depths beneath rainout trees. Soil moisture beneath control trees was between that of surplus and rainout trees at most depths.

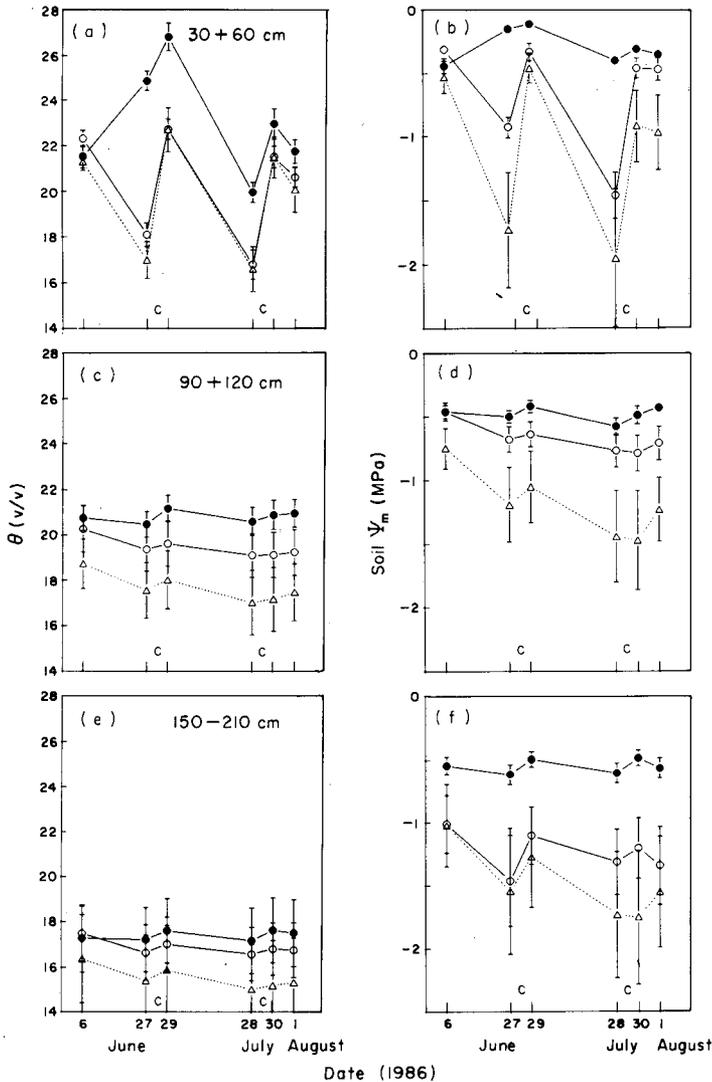Pre-dawn leaf Ψ was significantly different between the three moisture treatments on 27

Figure 2. Volumetric soil water content (θ) and soil matric potential (soil Ψ_m) at different soil depths beneath mesquite trees exposed to three moisture treatments during spring and summer 1986. Vertical bars indicate ± 1 standard error of the mean ($n = 4$). c, common irrigation of all trees. ●, Surplus; ○, control; △, rainout.
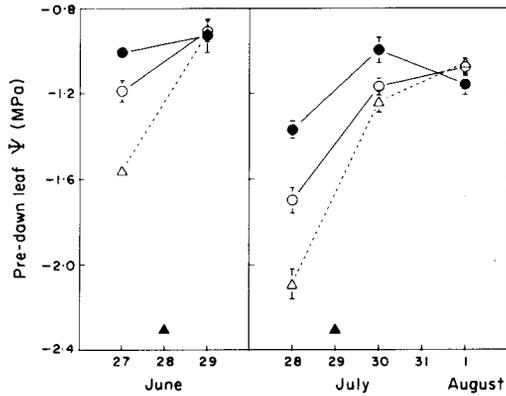
Figure 3. Pre-dawn leaf water potential (pre-dawn leaf Ψ) of mesquite exposed to three soil moisture treatments prior to and following common irrigation on two dates ($\blacktriangle$) in 1986. Vertical bars indicate $\pm$S.E. $\bullet$, Surplus; $\bigcirc$, control; $\triangle$, rainout.

June and 28 July, following month-long preconditioning prior to each of two common irrigation events (Fig. 3). Rainout trees had the lowest pre-dawn leaf Ψ on both dates. Effects of increasing environmental stress from 27 June to 28 July were evident by a decline in pre-dawn leaf Ψ in all treatments. The lowest pre-dawn leaf Ψ recorded during the study was $-2 \cdot 09$ MPa which occurred in rainout trees on 28 July.

Following sunrise, daytime leaf Ψ decreased in all treatments to below $-2 \cdot 5$ MPa, but increased after 2 h post-sunrise on both pre-irrigation dates [Fig. 4(a),(c)]. Differences in
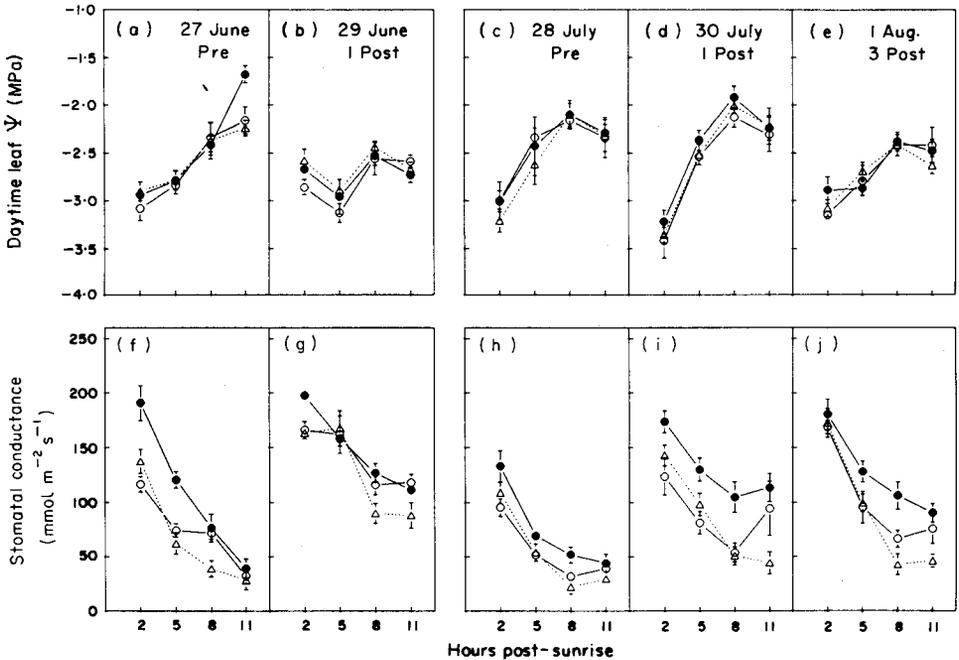

Figure 4. Daytime leaf water potential (daytime leaf Ψ) [(a)–(e)] and stomatal conductance [(f)–(j)] of trees exposed to three soil moisture treatments on several dates in 1986. Vertical bars indicate ± 1 S.E. Pre = 1 day prior to common irrigation, 1 Post = 1 day post-common irrigation. 3 Post = 3 days post-common irrigation, $\bullet$, Surplus; $\bigcirc$, control; $\triangle$, rainout.

Table 2. *Average daily stomatal conductance (mmol m^{-2} s^{-1}) of trees in each soil moisture treatment*

Date	Treatment		
	Surplus	Control	Rainout
27 June	106·8 a; y	73·7 b; y	66·8 b; z
29 June	148·5 a; w	140·7 ab; w	127·3 b; x
28 July	74·7 a; z	54.6 b; z	53·8 b; z
30 July	130·6 a; wx	88·3 b; xy	84·1 b; y
01 Aug	126·3 a; x	101·5 b; x	90·1 b; y
Average	117·4 a	91·8 b	84·4 b

Means followed by different letters (a–c) indicate a significant difference between treatments within a date. Means followed by different letters (w–z) indicate a significant difference within a treatment ($p \leq 0·05$; $n = 4$).

daytime leaf Ψ between treatments were not apparent on any date before or after common irrigation. Stomatal conductance declined each day from maximum levels at 2 h post-sunrise [Fig. 4(f)–(j)]. Seasonally, conductance declined from 27 June to 28 July in all treatments [Fig. 4(f), (h)]. Surplus trees had greater conductance than other trees on both dates, although there was less difference between treatments on 28 July than on 27 June.

Response to common irrigation

Following common irrigation on 28 June and 29 July, differences in θ and soil Ψ_m between treatments were reduced but not eliminated (Fig. 2). Equalization of soil variables between treatments was most apparent at 30+60 cm depth. Differences in pre-dawn leaf Ψ between treatments were eliminated within 1 day following each irrigation, although in the July trial pre-dawn leaf Ψ continued to increase in stressed trees (control and rainout) from 1 to 3 days post-irrigation (Fig. 3). Stomatal conductance increased in all trees within 1 day following each irrigation [Fig. 4(g),(i)]. Following the 29 July irrigation, maximum levels of average daily conductance occurred within 1 day in surplus trees but did not occur until 3 days post-irrigation in control or rainout trees (Table 2). In both irrigation trials absolute average daily conductance was greatest in surplus trees before and after irrigation (Table 2), but percentage increase in average daily conductance, as well as in pre-dawn leaf Ψ, from pre-irrigation levels was eventually greatest in either control or rainout trees (Table 3).

Table 3. *Per cent increase in pre-dawn leaf water potential and average daily stomatal conductance from pre-irrigation levels following 34–40 mm irrigation on two dates*

Date of common irrigation	Days post-irrigation	Pre-dawn water potential			Average daily conductance		
		Surplus	Control	Rainout	Surplus	Control	Rainout
28 June	1	8·9 c	23·5 b	41·0 a	39·0 b	90·9 a	90·6 a
29 July	1	27·0 b	31·2 ab	40·7 a	74·8 a	61·7 ab	56·3 b
29 July	3	15·3 c	36·5 b	49·3 a	69·0 b	85·8 a	67·4 b

Means within a row and variable followed by similar letters are not significantly different ($p \leq 0·05$; $n = 4$).
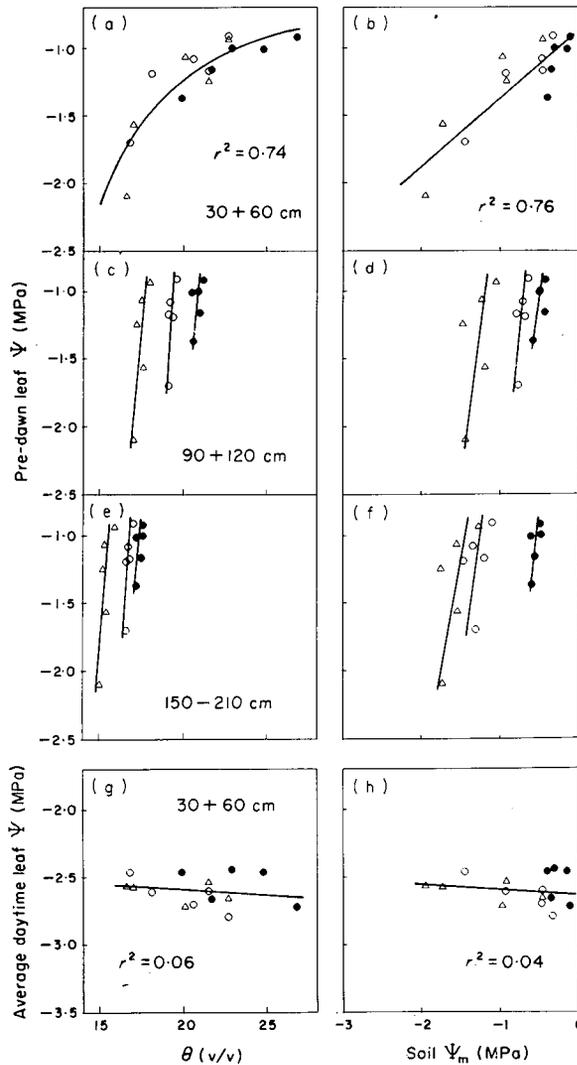
Figure 5. Relation between volumetric soil moisture or soil matric potential at different soil depths when plotted against pre-dawn leaf water potential [(a)–(f)] and average daytime leaf water potential [(g)–(h)]. Lines are fitted from regression equations and the coefficients of determination (r^2) are indicated. ●, Surplus trees; ○, control trees; △, rainout trees. Each point represents mean of four trees on a particular date. Dates used: 27 June, 29 June, 28 July, 30 July and 1 August.

Leaf/soil water relationships

Pre-dawn leaf Ψ decreased with decreasing θ and soil Ψ_m at 30+60 cm soil depths [Fig. 5(a),(b)]. Pre-dawn leaf Ψ was relatively insensitive to changes in θ until θ decreased to 22%, below which response was very steep [Fig. 5(a)]. Conversely, pre-dawn leaf Ψ was sensitive to changes across the entire range of measured soil Ψ_m [Fig. 5(b)]. Separation of response by treatment was not well expressed in the relation between pre-dawn leaf Ψ and θ or soil Ψ_m at 30+60 cm depth. Below 60 cm depth there was no clear relationship between pre-dawn leaf Ψ and θ or soil Ψ_m, other than points within each treatment were clustered vertically [Fig. 5(c)–(f)]. Treatment clusters were separated laterally due to
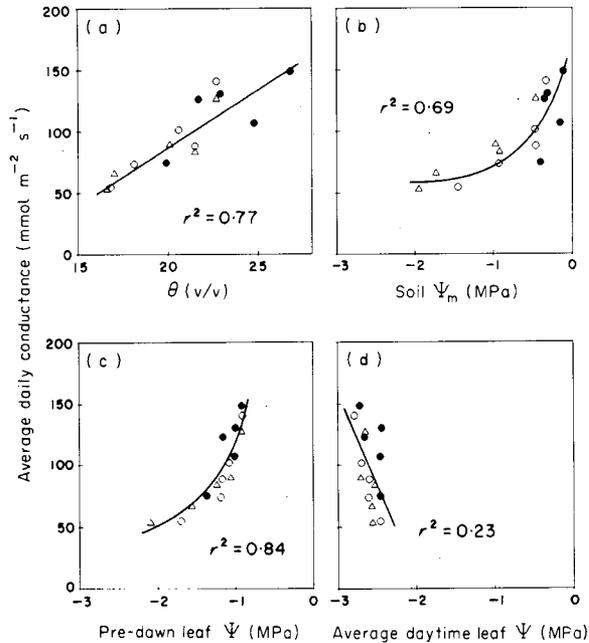
Figure 6. Average daily stomatal conductance when plotted against (a) soil moisture, (b) soil matric potential (soil variables were averaged over 30 and 60 cm depths), (c) pre-dawn leaf water potential, and (d) average daytime leaf water potential. Lines are fitted from regression equations and r^2s are indicated. ●, Surplus trees; ○, control trees; △, rainout trees. Dates used were the same as in Fig. 5.

differences in soil moisture between treatments. The vertical orientation of points within each treatment cluster indicated that the relationship between soil moisture and pre-dawn leaf Ψ was largely decoupled at these depths. These results provide evidence as to the shallow-rooted nature of mesquite at this site.

In contrast to responses of pre-dawn leaf Ψ, average daytime leaf Ψ was unaffected by changes in θ or soil Ψ_m [Fig. 5(g)–(h)]. Average daily conductance increased with increasing θ, soil Ψ_m, and pre-dawn leaf Ψ [Fig. 6(a)–(c)]. The relationship between average daily conductance and θ was linear, while curvilinear relationships were found between average daily conductance and soil Ψ_m or pre-dawn leaf Ψ. Responses of average daily conductance were independent of average daytime leaf Ψ [Fig. 6(d)].

Discussion

Leaf/soil water relations

Nocturnal rehydration of mesquite leaves (i.e., pre-dawn leaf Ψ) was a function of soil moisture content. The curvilinear relationship expressed between volumetric soil moisture (θ) at 30+60 cm depth and pre-dawn leaf Ψ in mesquite [Fig. 5(a)] was similar to that reported for *Acacia drepanolobium* in Kenya by Hesla *et al.* (1985), in that pre-dawn leaf Ψ was only slightly influenced by a decline in θ until a threshold was reached, below which pre-dawn leaf Ψ was strongly influenced.

The positive linear relationship found between θ and average daily stomatal conductance supports the hypothesis that mesquite uses more water if more is available (Biscoe, 1972; Moseley, 1983). Soil moisture levels were apparently not high enough to produce a characteristic levelling of conductance at high θ, as described for other woody species

(Schulze, 1986; Rosenthal et al., 1987). Our results in general agree with Easter & Sosebee (1975) and Thomas & Sosebee (1978), who found greater transpiration in irrigated than non-irrigated, field-grown mesquite trees. However, Wendt et al. (1968), in a glasshouse study, found little difference in transpiration of mesquite seedlings under a wide range of soil water potentials. Apparent conflicts in the literature such as this may relate to plant age and/or field vs. glasshouse conditions.

The relationships of average daily stomatal conductance to each of the two soil variables, θ and soil Ψ_m, in terms of linearity vs. curvilinearity, were opposite to those of pre-dawn leaf Ψ [Figs 5(a),(b), 6(a),(b)]. This suggests that the relationship between the two leaf variables, pre-dawn leaf Ψ and average daily conductance, was curvilinear instead of linear, and this is what was found [Fig. 6(c)]. Our results agree with findings for other woody species which indicated that conductance decreased with decreasing pre-dawn leaf Ψ (Running, 1976; Hinkley et al., 1978; Pereira et al., 1987). The relationship between these variables suggests that water loss through stomata during a particular day was primarily a function of nocturnal tissue rehydration.

Nilsen et al. (1983) reported that pre-dawn leaf Ψ in Sonoran Desert mesquite remained near $-2\cdot5$ MPa throughout the growing season. Using Nilsen's data, we calculated average daily conductance of Sonoran mesquite during a mid-July day to be near 140 mmol $m^{-2} s^{-1}$. While this conductance value is higher than expected, based on the relationship between pre-dawn Ψ and conductance developed from our study in Fig. 6(c), this difference is explained by the unique conditions which were conducive to phreatophytic behaviour of mesquite at Nilsen's study site (Jarrell & Virginia, 1990).

In contrast to the clear relationship between pre-dawn leaf Ψ and average daily conductance, we found no relationship between average daytime leaf Ψ and average daily conductance. Our findings are similar to those reported for black walnut (Juglans nigra), soybean (Glycine max), and cotton (Gossypium hirsutum), in which a wide range of conductance occurred within a narrow range of daytime leaf Ψ (Brown et al., 1976; Davies & Kozlowski, 1977; Turner et al., 1978; Schultz & Hall, 1982). These results suggest that adjustments to a baseline level of leaf Ψ were necessary prior to stomatal function on each day. Nilsen et al. (1981) found that midday leaf Ψ of mesquite in the Sonoran Desert of California was commonly lower than -4 MPa from June through November, but that stomatal activity remained uncoupled from midday leaf Ψ until $-4\cdot8$ MPa was reached. We were unable to lower midday leaf Ψ below $-3\cdot2$ MPa, even after water was eliminated from rainout trees for 2 months.

While there was no relation between average daily values of conductance and leaf Ψ, the curves shown in Fig. 4 suggest a diurnal relationship between these two variables. The decline in conductance following a diurnal peak at 2 h post-sunrise and concomitant increase in leaf Ψ indicate that stomatal closure in the afternoon stimulated tissue rehydration, which increased leaf Ψ. This finding disagrees with studies on some woody species which indicated that conductance declined with decreasing daytime leaf Ψ (Davies & Kozlowski, 1977; Szarek & Woodhouse, 1977; Schulze & Kuppers, 1979). In general, however, our findings concur with those of Nilsen et al. (1981) and others who concluded that stomatal closure was more related to soil water status than to daytime leaf Ψ (Schulze & Hall 1982; Schulze, 1986; Davies et al., 1987; Davies et al., 1990).

Influence of stress on response to watering

Responses of differentially moisture-stressed mesquite to common irrigations were evaluated according to rapidity and magnitude of response. We were unable to ascertain duration of response because of rains on 2 July and 3 August which terminated each post-irrigation trial before plant responses in any treatment had returned to pre-irrigation levels.

Rapidity of response was evaluated only during the July trial in which observations were

made 1 and 3 days after irrigation. The results suggest that moisture stress exhibited by rainout and control trees delayed rapidity of response, as measured by increases in pre-dawn leaf Ψ and average daily conductance following irrigation. Mean pre-dawn leaf Ψ in control and rainout trees 1 day prior to the 29 July irrigation were the lowest recorded during the study ($-1\cdot70$ and $-2\cdot01$ MPa, respectively). Apparently a threshold level of stress was necessary before responses to moisture availability were affected.

Magnitude of response was interpreted in two ways: (1) absolute, or (2) relative (i.e. percentage increase from pre-irrigation levels). While absolute pre-dawn leaf Ψ was not different between treatments following either the June or July irrigation, we did find that absolute average daily conductance was greatest in surplus trees following each irrigation. These results agree with Ludlow et al. (1980) and Kaufmann (1981) who indicated that stress history had a significant effect on stomatal behaviour, even though leaf water potential recovered quickly after rewatering. Our study indicated that long-term pre-conditioning with elevated soil moisture enhanced absolute magnitude of response to a simulated rainfall.

When viewed as a percentage increase from pre-existing levels, relative magnitude of response to irrigation was greater in more stressed trees and least in surplus trees. This suggests that greater physiological adjustments were required by more stressed individuals when responding to moisture events. Responses of non-stressed (i.e. surplus) trees may have been near maximum potential prior to irrigation which would limit magnitude of post-irrigation responses.

Conclusions

In summary, stomatal conductance and pre-dawn leaf Ψ of mesquite were positively related to soil moisture. This was in contrast to daytime leaf Ψ which was not well related to soil moisture. Because pre-dawn Ψ was closely related to both soil moisture and conductance, pre-dawn leaf Ψ was determined to be the best single indicator of overall moisture stress in mesquite. Pre-dawn leaf Ψ below $-1\cdot6$ MPa appeared to retard the response of mesquite to simulated rainfall.

References

Ansley, R. J., Jacoby, P. W. & Lawrence B. K. (1988). Root containerization for physiological studies of shrubs and trees on rangeland. Journal of Range Management, 41: 90–91.

Ansley, R. J., Jacoby, P. W. & Cuomo, C. J. (1990). Leaf water relations of honey mesquite following severing of lateral roots: influence of location and amount of subsurface water. Journal of Range Management 43: 436–442.

Biscoe, P. V. (1972). The diffusion resistance and water status of leaves of Beta vulgaris. Journal of Experimental Botany, 23: 930–940.

Brown, K. W., Jordan, W. R. & Thomas, J. C. (1976). Water stress induced alterations of the stomatal response to decreases in leaf water potential. Physiological Plantarum, 37: 1–5.

Davies, W. J. & Kozlowski, T. T. (1977). Variations among woody plants in stomatal conductance and photosynthesis during and after drought. Plant and Soil, 46: 435–444.

Davies, W. J., Mansfield, T. A. & Hetherington, A. M. (1990) Sensing of soil water status and the regulation of plant growth and development. Plant, cell & Environment 13: 709–719.

Davies, W. J., Metcalfe, J. C., Schurr, U., Taylor, G. & Zhang, J. (1987) Hormones as chemical signals involved in root to shoot communication of effects of changes in the soil environment. In Hood, G. B., Jackson, M. B., Lenton, J. R. & Atkin, R. (Eds.), *Hormone Action in Plant Development—A Critical Appraisal*. pp. 201–216. Butterworths: London. 315 pp.

Easter, S. J. & Sosebee, R. E. (1975). Influence of soil water potential on the water relationships of honey mesquite. *Journal of Range Management*, 28: 230–232.

Fisher, C. E., Hoffman, G. O. & Scifres, C. J. (1973). The mesquite problem. In McCully, W. G. (Ed.), *Mesquite Growth and Development, Management, Economics, Control, Uses*. Texas Agricultural Experiment Station Research Monograph No. 1. 84 pp.

Greacen, E. L. (1981). *Soil Water Assessment by the Neutron Method*. East Melbourne, Victoria, Australia 3002: CSIRO, 140 pp.

Haas, R. H. & Dodd, J. D. (1972). Water-stress patterns in honey mesquite. *Ecology*, 53: 674–680.

Heitschmidt, R. K., Ansley, R. J., Dowhower, S. L., Jacoby, P. W. & Price, D. L. (1988). Some observations from the excavation of mesquite root systems. *Journal of Range Management*, 41: 227–231.

Hesla, B. I., Tieszen, H. L. & Boutton, T. W. (1985). Seasonal water relations of savanna shrubs and grasses in Kenya, East Africa. *Journal of Arid Environments*, 8: 15–31.

Hinckley, T. M., Lassoie, J. P. & Running, S. W. (1978). Temporal and spatial variations in the water status of forest trees. *Forest Science Monograph* 20. Published by Society of American Foresters. 72 pp.

Jacoby, P. W., Ansley, R. J. & Lawrence, B. K. (1988). Design of rain shelters for studying water relations of rangeland shrubs. *Journal of Range Management*, 41: 83–85.

Jarrell, W. M. & Virginia, R. A. (1990). Soil cation accumulation in a mesquite woodland: sustained production and long-term estimates of water use and nitrogen fixation. *Journal of Arid Environments*, 18: 51–58.

Kaufmann, M. R. (1981). Water relations during drought. In Paleg L. G. & Aspinall, D. (Eds), *The Physiology and Biochemistry of Drought Resistance in Plants*. pp. 55–70. New York: Academic Press, 492 pp.

Levitt, J. (1980). *Responses of Plants to Environmental Stress. Vol. II—Water, Radiation, Salt and Other Stresses*. New York: Academic Press, 607 pp.

Ludlow, M. M., Ng, T. T. & Ford, C. W. (1980). Recovery after water stress of leaf gas exchange in *Panicum maximum* var. trichoglume. *Australian Journal of Plant Physiology*, 7: 299–313.

Mooney, H. A., Simpson, B. B. & Solbrig, O. T. (1977). Phenology, morphology, physiology. In Simpson B. B. (Ed.), *Mesquite—Its Biology in Two Desert Ecosystems*. pp. 26–41. US/IBP Synthesis Series No 4. Stroudsburg Penn: Dowden, Hutchinson and Ross, 250 pp.

Moseley, M. E. (1983). Conservation helps a dry creek flow again. *Rangelands*, 5: 255–258.

Nilsen, E. T., Sharifi, M. R. & Rundel, P. W. (1981). Summer water relations of the desert phreatophyte *Prosopis glandulosa* in the Sonoran desert of southern California. *Oecologia*, 50: 271–276.

Nilsen, E. T., Sharifi, M. R., Rundel, P. W., Jarrell, W. M. & Virginia, R. A. (1983) Diurnal and seasonal water relations of the desert phreatophyte *Prosopis glandulosa* (honey mesquite) in the Sonoran desert of California. *Ecology* 64: 1381–1393.

Nilsen, E. T., Sharifi, M. R. & Rundel, P. W. (1984). Comparative water relations of phreatophytes in the Sonoran desert of California. *Ecology*, 65: 767–778.

Nilsen, E. T., Sharifi, M. R., Rundel, P. W., Jarrell, W. M. & Virginia, R. A. (1986). Influences of microclimatic conditions and water relations on seasonal leaf dimorphism of *Prosopis glandulosa* var. *torrevana* in the Sonoran desert, California. *Oecologia*, 69: 95–100.

Pereira, J. S., Tenhunen, J. D. & Lange, O. L. (1987). Stomatal control of photosynthesis of *Eucalyptus globulus* Labill trees under field conditions in Portugal. *Journal of Experimental Botany*, 38: 1678–1688.

Phillips, W. S. (1963). Depth of roots in soil. *Ecology*, 44: 424.

Richards, L. A. (1965). Physical condition of water in soil. In *Methods of Soil Analysis*. No 9, Part 1. pp. 8–10. American Society of Agronomy.

Rosenthal, W. D., Arkin, G. F., Shouse, P. J. & Jordan, W. R. (1987). Water deficit effects on transpiration and leaf growth. *Agronomy Journal*, 79: 1019–1026.

Running, S. W. (1976). Environmental control of leaf water conductance in conifers. *Canadian Journal of Forestry Research*, 6: 104–112.

Sala, O. E. & Lauenroth, W. K. (1982). Small rainfall events: an ecological role in semiarid regions. *Oecologia*, 53: 301–304.

Schulze, E.-D. (1986) Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. *Annual Review of Plant Physiology*, **37**: 247–274.

Schulze, E.-D. & Hall, A. E. (1982). Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. In Lange, O. L. *et al.* (Eds), *Physiological Plant Ecology* II Vol 12B. pp. 181–224. *Encyclopedia of Plant Physiology*. Berlin: Springer Verlag, 747 pp.

Schulze, E.-D. & Kuppers, M. (1979). Short-term and long-term effects of plant water deficits on stomatal response to humidity in *Corylus avellana* L. *Planta*, **146**: 319–326.

Sharifi, M. R., Nilsen, E. T. & Rundel, P. W. (1982). Biomass and net primary production of *Prosopis glandulosa* (Fabaceae) in the Sonoran desert of California. *American Journal of Botany*, **69**: 760–767.

Steel, R. G. D. & Torrie, J. H. (1980). *Principles and Procedures of Statistics: a Biometrical Approach.* (2nd Edn) New York: McGraw Hill, 633 pp.

Szarek, S. R. & Woodhouse, R. M. (1977). Ecophysiological studies of Sonoran desert plants. II. Seasonal photosynthesis patterns and primary production of *Ambrosia deltoidea* and *Olnea tesota*. *Oecologia*, **28**: 365–375.

Thomas, G. W. & Sosebee, R. E. (1978). Water relations of mesquite—a facultative phreatophyte. In Hyder, D. N. (Ed.), *Proceedings of the First International Rangeland Congress*, Denver, CO, pp. 414–418.

Turner, N. C. (1981). Techniques and experimental approaches for the measurement of plant water status. *Plant and Soil*, **58**: 339–366.

Turner, N. C., Begg, J. E., Rawson, H. M., English, S. D. & Hearn, A. B. (1978). Agronomic and physiological responses of soybean and sorghum crops to water deficits. III. Components of leaf water potential, leaf conductance, $^{14}CO_2$ photosynthesis and adaptation to water deficits. *Australian Journal of Plant Physiology*, **5**: 179–194.

Wan, C. & Sosebee, R. E. (1990). Relationship of photosynthetic rate and edaphic factors to root carbohydrate trends in honey mesquite. *Journal of Range Management*, **43**: 171–176.

Wendt, C. W., Haas, R. H. & Runkles, J. R. (1968). Influence of selected environmental variables on the transpiration rate of mesquite [*Prosopis glandulosa* var. *glandulosa* (Torr) Cockr]. *Agronomy Journal*, **60**: 382–384.