Water relations and transpiration of honey mesquite on 2 sites in west Texas

CHANGGUI WAN AND RONALD E. SOSEBEE

Abstract

Transpiration rates and internal water relationships of honey mesquite *(Prosopis glandulosa)* were investigated weekly during May through September 1986 on sandy loam and clay loam, both upland sites in west Texas. Average transpiration rates peaked at approximately 7 mmol m^{-2} s^{-1} at 1100 hr during wet periods and reached a plateau between 4 and 5 mmol m^{-2} s^{-1} between 1200 and 1400 hr. During dry periods, the average transpiration rates reached their maximum plateau of 2 mmol m^{-2} s^{-1} at 1000 hr and declined between 1200 and 1600 hr. The transpiration rates ranged from an average of 3.28 ± 2.05 mmol m^{-2} s^{-1} for trees on a sandy loam site to an average of 3.85 ± 1.94 mmol m^{-2} s^{-1} for those on a clay loam site. Stomatal closure in midsummer caused a substantial increase in leaf temperature. Mesquite has developed other means, such as leaf orientation, wax accumulation, and reduction in canopy development, to avoid drought. Stomatal conductance of mesquite is very responsive to soil water availability and dryness of the air, and is less responsive to internal water status. This research further substantiates that mesquite behaves like a facultative phreatophyte in west Texas.

Key Words: ***Prosopis glandulosa;* leaf conductance; xylem water potential; facultative phreatophyte; water stress; drought avoidance.**

Honey mesquite has been described as an extravagant water user. Early research has shown that honey mesquite takes 1,725 kg water to produce 1 kg of phytomass (McGinnies and Arnold 1939). Nilsen et al. (1983) reported that the average transpiration ratio for honey mesquite was about 800 g water for 1 g aerial phytomass produced. Therefore, large quantities of water are required to maintain the high productivity of honey mesquite (Nilsen et al. 1983).

The aboveground net primary production of mesquite is higher than one would expect from classical relationships between precipitation and productivity (Whittaker 1978). Virginia and Jarrell (1983) suggested that enhanced productivity seems to be decoupled from limitation by surface water resources. Nilsen et al. (1983) stated that desert phreatophytes, such as honey mesquite, can have high summer productivity in the Sonoran Desert because water loss is not curtailed. Nilsen et al. (1987) also found that seasonal growth of mesquite was not influenced by precipitation or temperature. However, irrigated mesquite trees produced more foliage and had considerably higher transpirational water loss than nonirrigated trees in west Texas (Easter and Sosebee 1975).

Like desert xerophytes, mesquite can acquire soil water that is held at rather high matric forces. Haas and Dodd (1972) recorded soil water potential of -1.5 MPa to at least 150-cm depth. Mesquite can survive under soil water potential as low as -3.0 MPa, by reduction in leaf area, increase in thickness of the leaf cuticle and almost complete cessation of growth (Fisher et al. 1972). Mesquite maintains a positive net photosynthesis at water potentials less than -4.0 MPa (Strain 1970).

Nilsen et al. (1983) stated that when growing in a wash woodland of the Sonoran Desert where the water table was 4 m deep, honey mesquite avoided drought by using available groundwater. Consequently, mesquite maintained leaf conductances greater than 6.5 mm s^{-1} throughout the growing season and a considerable amount of water was lost through transpiration. In some semiarid areas of west Texas where the water table is 8 m deep, or deeper, one could ask "Do mesquite trees exhibit the same drought avoidance mechanisms as shown in the wash woodland?" This research was conducted to study transpiration rates and plant water relations of honey mesquite growing on 2 sites of a semiarid west Texas rangeland with focus on drought avoidance mechanisms.

Methods and Materials

The study was conducted on mesquite infested rangeland located on the Texas Tech University campus, Lubbock. Honey mesquite trees were selected on 2 sites, sandy loam and clay loam. The sandy loam site is characterized by an Amarillo fine sandy loam soil (fine-loamy, mixed, thermic Aridic Paleustalfs) and the clay loam site is characterized by an Olton clay loam soil (fine, mixed, thermic Aridic Paleustolls). The clay loam site has a higher water holding capacity; therefore, it is more mesic. Climate of the area is semiarid with an average annual precipitation of 450 mm. Monthly and annual precipitation vary considerably with May and June being the wettest months. The average frost-free period is 211 days, from early April to early November. Vegetation in the area has a shrub stratum of honey mesquite and a herbaceous stratum dominated by buffalograss *(Buchloe dactyloides),* blue grama *(Bouteloua gracilis),* and broom snakeweed *(Xanthocephalum sarothrae).*

Mesquite xylem water potential was measured daily at dawn and hourly to bihourly from 0800 to 1700 hours using a pressure chamber (Scholander et al. 1965). Petioles were excised from the plants and measurements were made with time lapse of less than 1 minute. Pressure was applied to the chamber at a moderate rate (0.05 MPa sec^{-1}) to avoid error. Soil water content was determined with a neutron attenuation technique at 15-cm increments in the profile of 30 to 165 cm. Soil moisture measurements were taken once a week; 3 replications were used for each measurement. A pressure membrane plate apparatus (Gardner 1965) was used to develop a soil water retention curve with water potentials as low as -1.5 MPa. Soil matric potential data were derived from soil water contents by using the water retention curve.

Stomatal conductance, transpiration, air, and leaf temperature, photon flux density, and relative humidity were measured with a Li-Cor 1600 steady-state porometer. A cylindrical chamber was installed on the porometer and used to accommodate the sample leaves. Leaves with an area of 3 to 5 cm^2 were placed in the chamber when the measurements were taken. Measurements were taken on trees growing on the 2 sites 7 to 8 times a day from 0800 until 1700 hours on both sites with a time interval of 15 minutes between measurement on trees of the 2 sites. Three replications were made for each measurement and the averages are reported. Ten mesquite trees (replications) were randomly selected on each site. Measurements were taken weekly on clear days May through September, 1986. The data were subjected to regression analyses and t-test.

The actual diffusive resistance (R1) was determined from the following equation:

$$R1 = (Rd + 0.15)(TA/LA) - Rb$$

Authors are graduate research assistant and professor, Department of Range and Wildlife, Texas Tech University, Lubbock 79409. This is a contribution of the College of Agricultural Sciences, Texas Tech University, No. T-9-531.

Manuscript accepted 19 May 1990.

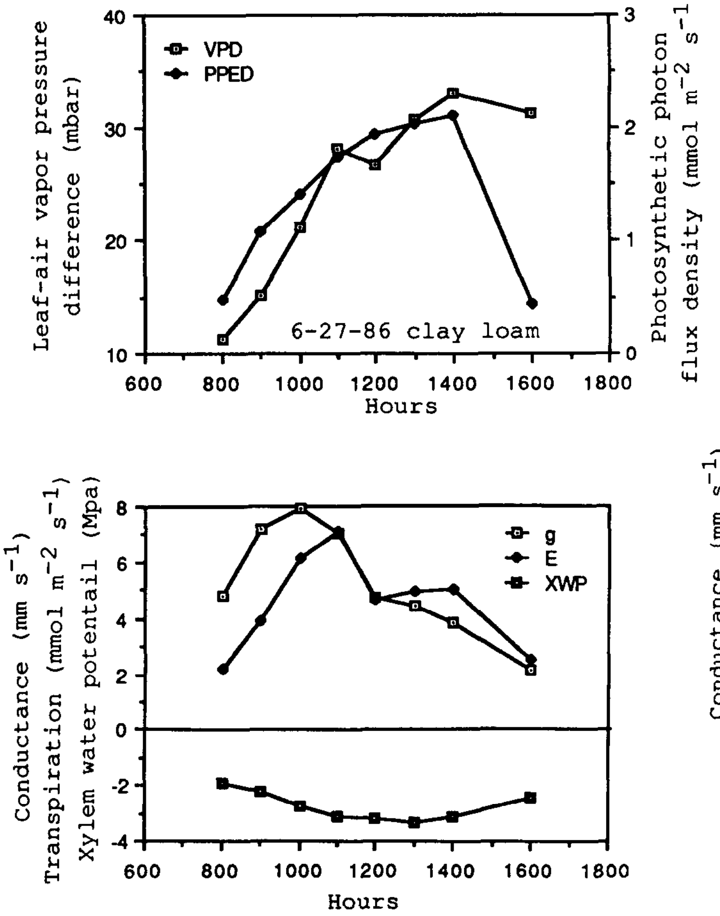

Fig. 1. Leaf-air vapor pressure difference (VPD) transpiration (E), leaf conductance (g), photosynthetic photon flux density (PPFD) and xylem water potential (XWP) in a representative mesquite tree during a wet day (27 June 1986, soil matric potential -0.03 MPa) on Texas Tech campus, Lubbock.

where:

Rd = diffusive resistance displayed by the porometer,
TA = true area of the sample leaf and,
LA = leaf area entered into the Li-Cor 1600,
Rb = boundary layer resistance. In Li-Cor 1600, a default value of Rb was set at 0.15 s cm^{-1}.

The average boundary layer resistance (Rb) of mesquite leaves was calculated to be 0.149 to 0.160 s cm^{-1}, using the equation (Cowan and Milthorpe 1968):

$$Rb = 1/[0.294(u/b)^{1/2}],$$

where:

u = wind speed, cm s^{-1} and,
b = the surface dimension of the leaf (about 0.4–0.5 cm for mesquite leaves). The calculated Rb was very close to the default value of Rb in the Li-Cor 1600 porometer. Rb was much smaller than stomatal resistance (>1 s cm^{-2}) and was not a major resistance in transpirational water loss.

The actual stomatal conductance was determined as the reciprocal of actual diffuse resistance and actual transpiration rate was the product of measured transpiration rate and LA/TA.

Results and Discussion

Leaf conductance and transpiration of mesquite declined during the drought of July as compared to a wet June (Fig. 1 and 2). Six-fold reduction in daily average leaf conductance (from 5.23 to 0.84 mm s^{-1}) in the summer was a reflection of reduced soil water availability. When soil water was less available, mesquite trees did not transpire as much as those receiving ample water (daily average transpiration 1.46 vs. 4.54 mmol m^{-2} s^{-1}), regardless of the atmospheric evaporation demand. Coupling of stomatal conductance with soil water availability was more obvious for trees growing on the different soil types. The seasonal trend of daily average transpiration rate on the 2 sites follows the same pattern as soil water potential (Fig. 3). Before mid-June, soil matric potential of the clay loam was considerably higher than that of the sandy loam; so were the transpiration rates. From 13 June to 8 July, the soil matric potentials were high (>–0.5 MPa) on both sites, and greater transpiration rates were found on the sandy loam, indicating a greater uptake from that site. A related study has shown that mesquite taps deep horizons sooner on the sandy loam as compared to the clay loam site. In July, water content in 30 to 165 cm profile was 57% of field capacity on the sandy loam, while it remained 80% on the clay loam (Wan 1987). Consequently, stomatal conductance and transpiration were over 2-fold greater for trees on the clay loam site in midsummer because the soil water content was higher (Fig. 4).

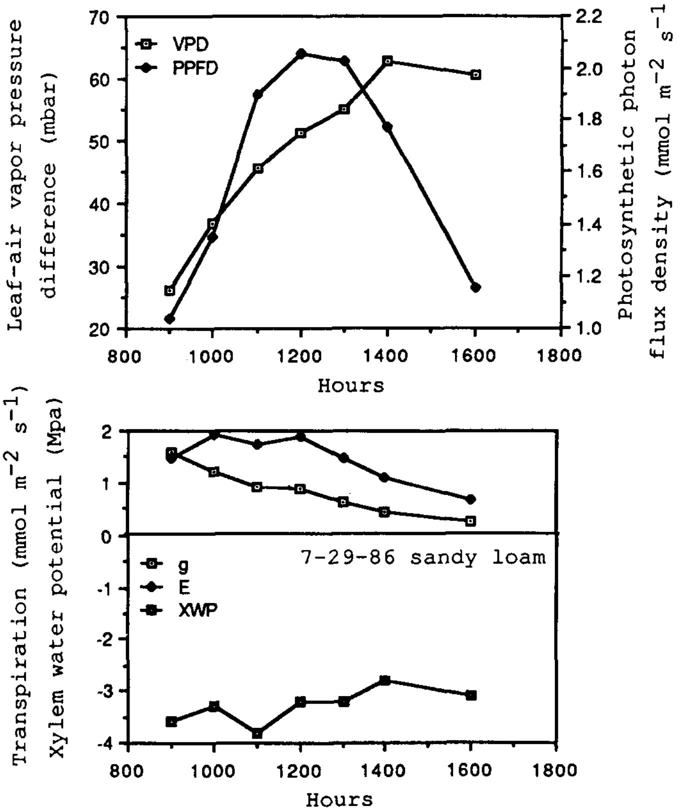

Fig. 2. Leaf-air vapor pressure difference (VPD), photosynthetic photon flux density (PPFD), transpiration (E), leaf conductance (g) and xylem water potential (XWP) in a representative mesquite tree during a drought day (29 July 1986, soil matric potential -1.5 MPa) on Texas Tech campus, Lubbock.

In late July, mesquite trees had similar xylem water potentials on both clay loam and sandy loam sites in spite of different amounts of available soil water. However, they transpired at different rates (Fig. 5). From 29 July to 6 August, trees on the clay loam transpired 59 to 125% more water than trees on the sandy loam site with similar leaf areas.

When soil water was most available, as on 6 June, the trees transpired more water (more than 2-fold) than on 31 July when soil water was limited. Yet, the xylem water potential was higher on 6

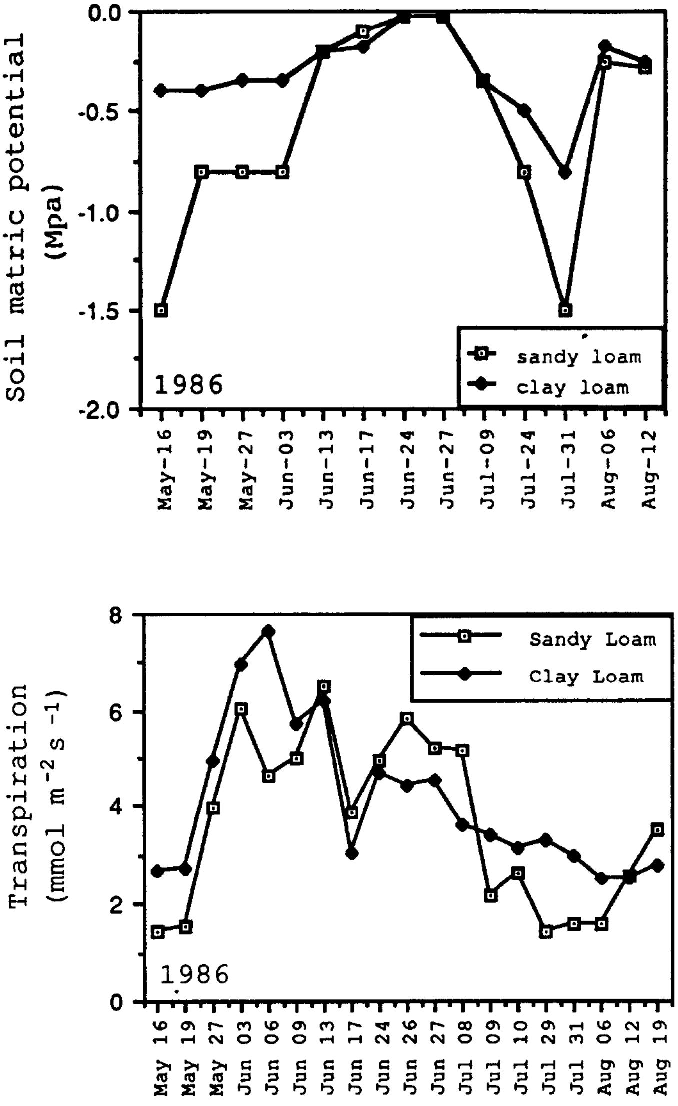

Fig. 3. Seasonal changes in soil matric potential (MPa) (upper figure) and daily average transpiration rate (lower figure) on the sandy loam and the clay loam sites. Soil matric potential was derived from soil water content at 60-cm depth based on water retention curves.

June (–3.1 MPa) than that in late July (–3.8 MPa). Through an efficient water transport system, the plant with ample water supply (6 June) can maintain higher xylem water potentials with increased transpiration rates, and thus avoid water stress (Hall and Schulze 1980). In contrast, when the soil is dry, the trees greatly restrict transpirational water loss in the afternoon through stomatal closure. Thus, water potential recovered or became less negative in the afternoon (Fig. 1 and 2) because transpirational water loss declined. Slopes of the curves in Figure 4 represent resistance to water flow which is largely dominated by soil water availability for a particular plant species (Schulze and Hall 1982). When dawn xylem water potential decreased to about –2 MPa in trees on the sandy loam soil, resistance increased and transpiration was greatly reduced.

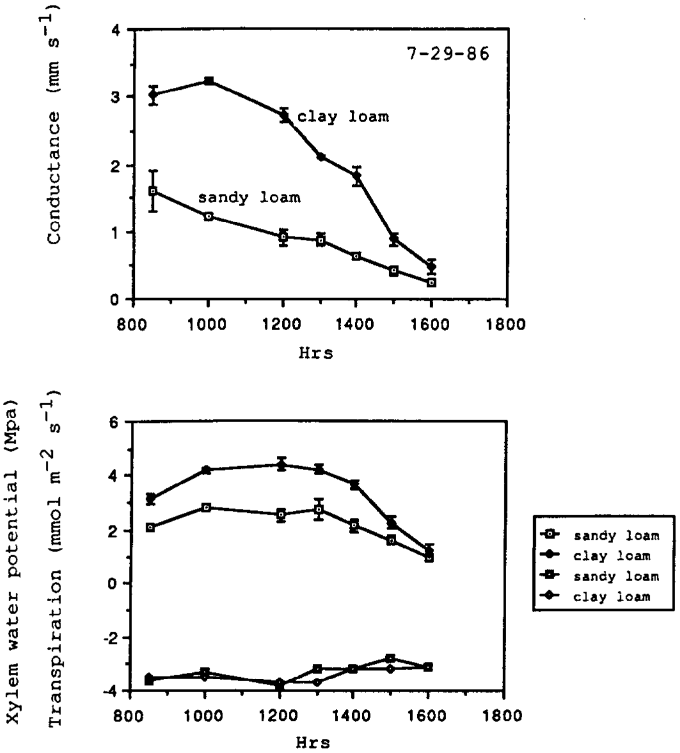

Fig. 4. Diurnal changes in leaf conductance, transpiration and xylem water potential in mesquite trees on 29 July 1986. The measurements were taken on trees growing on 2 sites on the Texas Tech campus, Lubbock. The error bars represent standard error of means. The average soil water content in 30–165 cm profile was 10.6% and 6.6% for the clay loam and sandy loam, respectively. Soil matric potential at 60-cm depth (highest matric potential in the profile) was –0.7 MPa and –1.5 MPa for the clay loam and sandy loam, respectively. Differences in conductance and transpiration between the 2 sites were significant ($P<0.01$).

Stomata respond sensitively to changes in VPD. Stomatal closure is sufficient to reduce transpiration rate even when mesquite is subjected to higher evaporation demands. On 26 June 1986, as VPD increased from 18.8 mbar at 1100 hours to 25.8 mbar at 1500 hours, the transpiration rate decreased by 38% (from 10.6 to 6.5 μg cm^{-2} s^{-1}), which otherwise would have increased by 37% if the stomatal conductance had remained the same. This response represents a feedforward control. It can prevent water potential from declining as evaporative demand increases. The plant water potential remained stable at –3.1 MPa in the afternoon as a result

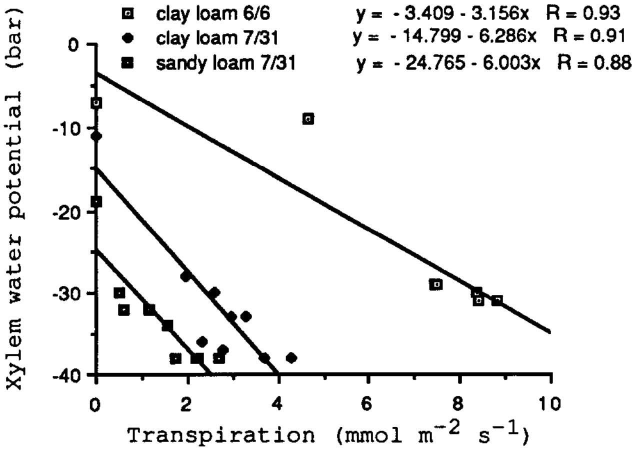

Fig. 5. Relationship between xylem water potential and transpiration in mesquite trees growing on Texas Tech campus, Lubbock, Texas May through September 1986. The intercept on Y axis is dawn xylem water potential. Soil matric potential at 60-cm depth was –0.4 MPa on 6 June and was –0.7 MPa and –1.5 MPa for the clay loam and sandy loam, respectively, on 31 July.

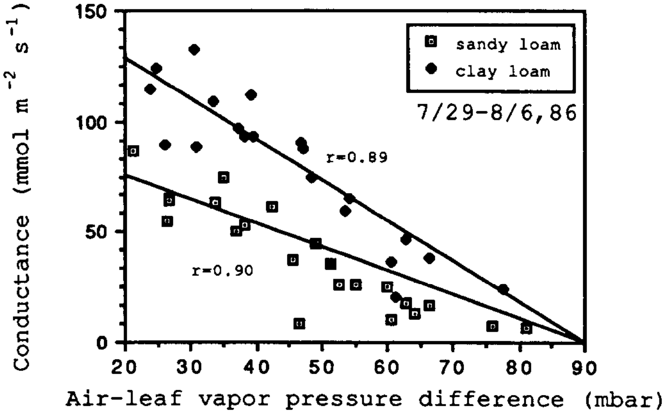

Fig. 6. Leaf conductance of mesquite on 2 sites as a function of air-leaf vapor pressure difference. The measurements were made from 3 trees on each site 29, 1 July, and 6 August 1986 on the Texas Tech campus, Lubbock. Soil matric potential at 60-cm depth was -0.7 MPa on the clay loam and <-1.5 MPa on the sandy loam.

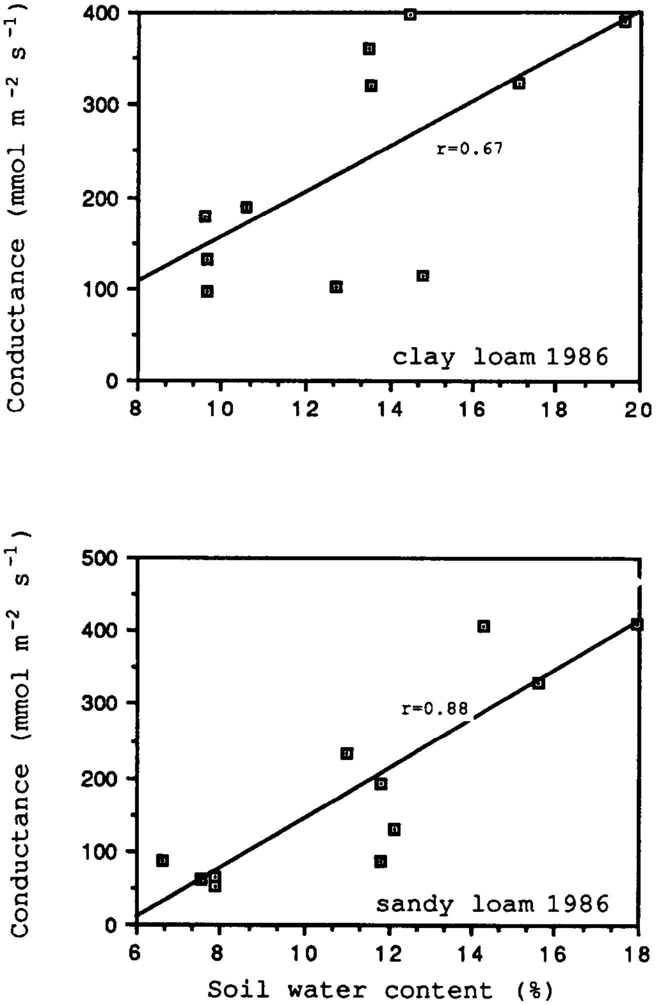

Fig. 7. Relationship between daily maximum leaf conductance and soil water content (w/w). Leaf conductance is an average of 3 measurements. Soil water content represents an average of the 30 to 60 cm profile (n = 9). P = 0.0064 for the clay loam and 0.0068 for the sandy loam soils. Soil water content declined from June to early August.

of stomatal closure. A linear response of stomata to VPD was observed during a drought period on the 2 sites (Fig. 6).

Stomatal aperture is not only affected by VPD, but also by soil water status. Previous work (Easter and Sosebee 1975) has shown that mesquite trees on a xeric site did not transpire as much as those on a more mesic site when environmental conditions (except soil water potential) were the same. Our data indicate that maximum daily stomatal conductance is linearly ($P<0.01$) correlated with soil water status on both the fine sandy loam (r = 0.88) and the clay loam soil (r = 0.67) (Fig. 7). As soil water was depleted, daily maximum stomatal conductance was greatly reduced. Hence, in June when soil water was most available, the trees had daily maximum stomatal conductances of 2.8 to 6-fold higher than in midsummer.

Stomatal conductance of mesquite is less responsive to internal water status. In midsummer, leaf conductance exhibited a continuous decline from morning until afternoon, but xylem water potential dropped to the lowest level at midday and increased in the afternoon (Fig. 4). In the wet season, however, midday stomatal closure was probably caused by lower xylem water potential (Fig. 1).

On a typical sunny day on the Texas Tech campus in the summer, total solar radiation was about 1000 W m^{-2} in the afternoon. If the soil is wet and stomata are open, mesquite can transpire 7.5 mmol m^{-2} s^{-1}. Under these conditions latent heat transfer plays a significant role in the plant's energy balance and about 33% of incident radiation can be dissipated by transpirational cooling (43.78 J mmol^{-1} × 7.5 mmol m^{-2} s^{-1}/1000 W m^{-2}). Mesquite's highest average daily rate of transpiration was only 7.64 mmol m^{-2} s^{-1}, which is much lower than cultivated pasture species such as alfalfa *(Medicago sativa)* (Sosebee 1980). Some desert species, such as *Phragmites communis* growing in a moist habitat, but under high evaporative demands, can transpire at much higher rates than mesquite trees, thus bringing leaf temperatures to 8° C lower than the ambient temperature (Pearcy et al. 1974). For our trees, leaf temperatures of 1° C lower than ambient were uncommon. In most cases, leaf temperatures were higher than ambient temperatures even when the soil water was readily available (through midday stomatal closure). This indicates that a mesquite tree is a conservative plant in consumptive water use. It maintains its leaf temperature close to the ambient, instead of several degrees below (Table 1). In the latter case, extra water has to be transpired, which represents wasted water, especially when the leaf temperature is within the optimum range for photosynthesis. This dehydration avoidance mechanism may not bring any benefit to mesquite trees, since on the native rangeland, water saved may be used by the competitive plant species or lost through evaporation. However, dehydration avoidance allows conservation of water since deep

Table 1. Diurnal change in air and leaf temperature on a typical summer day. Each number is an average of 3 measurements. Data were collected on 31 July 1986.

	Sandy loam		Clay loam	
Hour	Air	Leaf	Air	Leaf
800	27.8	27.7	27.4	26.8
1000	31.5	31.4	30.1	30.0
1100	35.4	34.7	33.4	32.9
1200	36.1	36.1	35.8	35.7
1300	38.4	38.9	37.6	37.3
1400	39.8	40.3	39.7	39.9
1500	41.5	42.1	39.9	40.2
1700	42.9	43.5	42.5	42.6
$\bar{x}$	36.7	36.8	35.8	35.7

water sources can only be exploited by deep-rooted plants such as mesquite.

In summer drought, latent heat transfer of mesquite on the sandy loam site was reduced such that only a few percent of incident solar radiation was dissipated by transpiration (daily average transpiration was 1.7 mmol m^{-2} s^{-1}; 1.7 mmol^{-2} s^{-1} × 44 mmol^{-1} ÷ 1000 W m^{-2} = 7.48%). Net photosynthesis in the late afternoon was reduced to zero at a leaf temperature of 43.5° C (Wan 1987). The corresponding transpiration was only 0.52 mmol m^{-2} s^{-1}, one-fourth of the value for trees on the clay loam site. It appeared that higher leaf temperatures and increased water stress in trees on the sandy loam site were responsible for reduced metabolic activity. Since transpirational cooling was not sufficient to dissipate the extra energy load, mesquite has developed other means to cope with water and high temperature stresses. There are some prominent features the plant employed for this adaptation:

1. Change leaf angle: In spring when soil was wet and VPD was low, changes in leaf orientation were not observed. On hot summer afternoons, the plant turned its leaves parallel to the sun rays, so energy absorption was reduced.

2. Increase in wax and pubescence as the season progresses. Scanning electromicroscope photographs of leaf surfaces exhibit sunken stomata surrounded by a wax layer and hairs. Hydrophobic wax and hairs not only prevent water escape from leaf surfaces but also reflect a considerable amount of solar radiation.

3. Increase in leaf thickness and decrease in leaf size. The specific leaf weight increased from 4 mg cm^{-2} in April to 17 mg cm^{-2} in August. By this means, the leaf surface area was reduced, and less energy was absorbed. As leaves became smaller, air turbulence was favored and more energy was dissipated through convection.

4. Reduced canopy development. Mesquite has 2 types of leaves: early leaves, which emerge at budbreak and reach full maturity around mid-May, and late leaves, which appear later in the growing season and complete their expansion after May. A mild water stress in early to mid-June exerted different influences on expansion and growth in the 2 types of mesquite leaves. More late leaves appeared on trees growing on the mesic clay loam than on the sandy loam site. In mid-June, 1986, 14% of mesquite trees on the clay loam had late leaves, whereas, only 5% of trees on the sandy loam site had late leaves. Like many plants, drought deciduous species in particular, honey mesquite also sheds some of its leaves in droughts.

On the sandy loam site, trees are shorter and the canopy is smaller compared to trees on the more mesic clay loam site. This is an important desiccation avoidance mechanism. It gives the plant a better change to survive a severe drought. Carter (1964) reported that during the severe drought from 1950 through 1956, many mesquite trees died in south Texas. However, the hardest hit stands occurred on clay soils. Most mature trees were killed, but young trees or trees with several stems resulting from pruning were largely unaffected. These observations imply that a small canopy is a mandatory modification for the plant to cope with water stress because it results in increased water supply relative to the demand, leading to an improved plant water balance.

It is difficult to make an universal estimate of water consumption for trees in different environments. In semiarid west Texas, in a wet year with annual precipitation of 530 mm, on an upland site that characteristically has limited soil water supply, the average transpiration rate was 3.85 ± 1.94 mmol m^{-2} s^{-1} for trees on the clay loam site and 3.28 ± 2.05 mmol m^{-2} s^{-1} for trees on the sandy loam site May through September. These values are based on 130 paired measurements in different periods. Trees on the clay loam site had greater stomatal conductance and transpiration rates (P<0.01) than those on the sandy loam site.

On the southern High Plains of Texas, honey mesquite avoids desiccation by stomatal closure and greatly reduced transpirational water loss in midsummer. Daily maximum leaf conductance was only 1.6 mm s^{-1} for trees on a sandy loam site and 3.2 mm s^{-1} for trees on a clay loam site. Stomatal closure creates some problems in leaf energy balance in midsummer. Leaf temperatures as high as 42–43° C were recorded on some trees, which led to complete cessation of photosynthesis. However, mesquite has developed various means to avoid high energy absorption. The very common response of mesquite trees to water stress is restricted late leaf development and reduction in canopy size. This reduction in transpiring area, together with stomatal closure, helps reduce water loss in the summer. Because the sandy loam is drier in the summer and the stomata of the trees are more tightly closed, it seems that herbicide would have to be applied earlier in the year on the sandy loam compared to the clay loam site.

Literature Cited

Carter, M.G. 1964. Effect of drought on mesquite. J. Range Manage. 17:275-276.

Cowan, I.R., and F.L. Milthorpe. 1968. Plant factors influencing the water status of plant tissues. *In:* Kozlowski, T.T. (ed.), Water deficits and plant growth. Academic Press, London, New York. 1:137-193.

Easter, S.J., and R.E. Sosebee. 1975. Influence of soil water potential on the water relationships of honey mesquite. J. Range Manage. 28:230-32.

Fisher, C.E., H.T. Wiedemann, J.P. Walter, C.H. Meadors, J.H. Brock, and B.T. Cross. 1972. Brush control research on rangeland. Texas Agr. Exp. Sta. MP-1043. p. 18.

Gardner, W.H. 1965. Water content. *In:* C.A. Black [ed.] Methods of soil analysis. Part 1. Agron. 9:82-127.

Haas, R., and J.D. Dodd. 1972. Water stress patterns in honey mesquite. Ecology 53:674-80.

Hall, A.E., and E.D. Schulze. 1980. Drought effects on transpiration and leaf water status of cowpea in controlled environments. Aust. J. Plant Physiol. 7:141-47.

McGinnies, W.G., and J.F. Arnold. 1939. Relative water requirements of Arizona range plants. Ariz. Agr. Exp. Sta. Tech. Bull. p. 80.

Nilsen, E.T., P.W. Rundel, and M.R. Sharifi. 1981. Summer water relations of the desert phreatophyte *Prosopis glandulosa* in the Sonoran desert of southern California. Oecologia 50:271-76.

Nilsen, E.T., M.R. Sharifi, P.W. Rundel, W.M. Jarrel, and R.A. Virginia. 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., M.R. Sharifi, and P.W. Rundel. 1984. Comparative water relations of phreatophytes in the Sonoran desert of California. Ecology 65:767-778.

Nilsen, E.T., M.R. Sharifi, R.A. Virginia, and P.W. Rundel. 1987. Phenology of warm desert phreatophytes: seasonal growth and herbivory in *Prosopis glandulosa* var. *torreyana* (honey mesquite). J. Arid Environ. 13:217-229.

Pearcy, R.W., J.A. Berry, and B. Bartholomew. 1974. Field photosynthetic performance and leaf temperature of *Phragmites communis* under summer conditions in Death Valley, California. Photosynthetica 8:104-108.

Scholander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. Science 148:339-346.

Schulze, E.D., and A.E. Hall. 1982. Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. P. 181-230 in Large, O.L., P.S. Nobel, S.B. Osmand, and H. Ziegler [ed.]. Encycl. Plant Physiol. 128.

Sosebee, R.E. 1980. Water—a precious commodity to everyone. Research Highlights. Texas Tech Univ. Lubbock.

Strain, B.R. 1970. Field measurements of tissue water potential and carbon exchange in the desert shrubs *Prosopis juliflora* and *Larrea diraricata.* Photosynthetica. 4:118-122.

Virginia, R.A., and W.M. Jarrell. 1983. Soil properties in a mesquite-dominated desert ecosystem. Soil Sci. Soc. 47:138-144.

Wan, C.G. 1987. Photosynthesis and water use in honey mesquite. Ph.D. Diss. Range and Wldlife. Texas Tech Univ.

Whittaker, R.H. 1974. Communities and ecosystems. McMillan Published Co., Inc. New York.