



# Stem flow and porometer measurements of transpiration from honey mesquite (*Prosopis glandulosa*)

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## Abstract

The objective of this study was to compare stem flow and porometer methods of measuring transpiration of honey mesquite (*Prosopis glandulosa*) trees on a semi-arid site. Stem flow was measured using heat balance stem flow gauges. Porometer measurements of leaf stomatal conductance ( $g_s$ ) were made within foliage layers of each stem and scaled to transpiration values for the entire stem ( $E_{\text{stem}}$ ) using stem leaf area. Simultaneous measurements using both methods were made diurnally and under artificially imposed stem shading or defoliation in June and October 1990. Stem flow and  $E_{\text{stem}}$  had similar diurnal patterns except on 2 d in June when  $E_{\text{stem}}$  increased during the afternoon while stem flow declined relative to midday values. During October,  $E_{\text{stem}}$  was greater than stem flow throughout the day. This was attributed to sampling error in which only undamaged leaves were used for porometer measurements yet, by this time in the growing season, many leaves on each stem were damaged from insects or wind and likely had lower transpiration rates. A regression coefficient between  $E_{\text{stem}}$  and stem flow of 0.79 in June and 0.91 in October suggested the two methods were comparable, but there was considerable variation between methods during peak transpiration rates. Both techniques detected that artificial shading or defoliation caused similar relative declines in transpiration. Results imply that estimates of stem transpiration can be obtained by scaling porometer measurements of leaves but accuracy declines at higher transpiration rates.

Key words: Sap flow, evapotranspiration, stomatal conductance, scaling, water relations.

## Introduction

Ecological processes in arid and semi-arid grasslands of Africa, India, Australia, and North and South America have been substantially affected by increases in woody plants during the last 50–300 years (Walker and Gillison, 1982; van Vegten, 1983). In semi-arid grasslands of the south-western United States, increased density of the arborescent legume, honey mesquite (*Prosopis glandulosa* Torr.) has had significant impact on graminoid production and landscape hydrology (Archer *et al.*, 1988; Carlson *et al.*, 1990). Accurate measurements of water use by mesquite are needed to assess hydrological implications of increased densities, and potential cost-effectiveness of efforts to reduce densities of this species.

Many plant water relations studies have involved measurement of transpiration of individual or small groups of leaves with porometers (Schulze and Hall, 1982). The advantages of porometry, especially in remote locations, are relative ease of use and capacity for measuring many individuals of a population. The method has been used widely for desert plants, including mesquite (Easter and Sosebee, 1975; Nilsen *et al.*, 1983; Ansley *et al.*, 1990; 1992).

Leaf responses, including those measured with a porometer, are often used to make assumptions regarding whole plant or community responses (Jarvis and Leverenz, 1983; Meinzer *et al.*, 1988; Givnish, 1988; Norman, 1993). However, leaf responses may not parallel whole plant responses under all conditions because of variation within the canopy (Jarvis and Catsky, 1971; Schulze *et al.*, 1985; Gold and Caldwell, 1989; Hinckley and Ceulemans, 1989). An additional concern is that porometers may not estimate transpiration accurately

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because micro-environmental conditions in the porometer leaf chamber modify wind speed and humidity (Fichtner and Schulze, 1990; McDermitt, 1990). The assumption is made that if the chamber is applied to the leaf for a short time before stomatal aperture changes, stomatal conductance can be accurately measured and transpiration calculated from conductance.

Transpiration has been measured with gauges placed on stems using heat as a tracer of sap flow (Sakuratani, 1981, 1984, 1987; Schulze *et al.*, 1985; Baker and van Bavel, 1987; Heilman and Ham, 1990; Steinberg *et al.*, 1989, 1990; Dugas, 1990; Dugas *et al.*, 1993). Mass sap flow, calculated from a heat balance, is considered equal to transpiration if the averaging period is sufficiently long and plant water capacitance can be ignored. This method provides an integrated response of all leaves on a stem and may offer greater potential than porometry for accurately estimating whole plant transpiration, although this method may have less application than porometers in remote environments.

There have been few comparisons of stem flow and porometer measurements on the same plant (Schulze *et al.*, 1985; Green *et al.*, 1989; Steinberg *et al.*, 1990; Dugas *et al.*, 1993) and none involving honey mesquite. Our objective was to compare stem flow and porometer methods of measuring mesquite transpiration, evaluate the accuracy of porometer measurements (with respect to stem flow values), and assess the potential of estimating stem or whole plant transpiration from porometer measurements.

## Materials and methods

The study was conducted in a mesquite woodland located 30 km south of Vernon, Texas, USA (33°52'N, 99°17'W; elevation, 368 m). Mean annual rainfall is 665 mm with a bimodal distribution (mean 119 mm in May and 77 mm in September). July mean maximum temperature is 36 °C. The site has an overstorey of honey mesquite (200 trees ha<sup>-1</sup>) and an understorey of buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.) and Texas wintergrass (*Stipa leucotricha* Trin. and Rupr.). Soils are fine, mixed thermic Typic Palustalfs of the Kamay series and are characterized by clay loam textures to about 1 m, underlain by calcareous sandstone/shale parent material (Koos *et al.*, 1962). Slope is less than 3%. The area was grazed by cattle until 1985 when livestock were excluded by fencing.

Above-ground growth of mesquite on the site was destroyed by anthropogenic chaining in the 1960s, resulting in coppice growth from subterranean meristem which, at the time of the current study, averaged 3.5 m in height. Six trees within 50 m of each other were used for the study. As part of another study to manipulate soil moisture and eliminate intraspecific competition, a 2 m deep vertical trench was cut around each mesquite tree and the soil wall was wrapped with plastic sheets in January 1986 (Ansley *et al.*, 1988, 1992). These barriers isolated the soil around each tree in the horizontal plane, although the bottom of each barrier was open. The barriers were not essential to the objectives of the current study. However, absolute values of

water use by these trees may differ slightly from those under natural conditions.

### Meteorological and environmental measurements

A meteorological station was positioned in the centre of the study area no more than 50 m from any study trees. Tree density and understorey vegetation were similar near the station and study trees. Wet and dry bulb sensors were at 1.5 m, and wind and global radiation sensors were at 2 m above ground, respectively. Ten minute averages of these variables were recorded during the time of stem flow measurements. Net radiation and soil heat flux were estimated as a constant fraction (0.52) of global radiation and from data of Dugas and Mayeux (1991), respectively. Potential evapotranspiration (PET) was calculated from these measurements (Pruitt and Doorenbos, 1977). Precipitation was measured on site. Four, 40 mm diameter aluminium access tubes were placed to a depth of 2 m near each tree and soil water content was measured at 0.3 m depth increments using a neutron probe. Three of the study trees were drip-irrigated on 31 May (98 mm), 13 July (17 mm), 9 August (42 mm), and 28 September (56 mm).

### Stem flow measurements

Stem flow gauges (models SGB16 and SGB19, Dynamax, Inc., Houston, TX) were used to measure transpiration from leaves on a single stem. Stem flow was calculated as a residual of a heat balance of a stem which had a known, constant heat input (Sakuratani, 1981; Baker and van Bavel, 1987).

Stem flow ( $F$ ; g<sup>-1</sup> stem h<sup>-1</sup>) was calculated from the following:

$$F = \frac{P - K_{st} \times A \times \frac{dT_b + dT_a}{dx} - K_g \times E}{C \times dT_{ba}} \quad (1)$$

where  $P$  is input power to the heater;  $K_{st}$  is stem thermal conductivity;  $A$  is stem area;  $dT_b$  and  $dT_a$  are vertical temperature gradients below and above the heater, respectively;  $dx$  is distance (m) between two thermocouple junctions both above and below the heater;  $K_g$  is gauge conductance representing radial power loss, per volt, through the gauge when  $F=0$ ;  $E$  is voltage of a thermopile mounted outside of the heater;  $C$  is xylem sap (water) heat capacity; and  $dT_{ba}$  is temperature gradient across the heater. A range of 0.3 to 0.5 W was used for  $P$  and 0.42 W m<sup>-1</sup> K<sup>-1</sup> was used for  $K_{st}$  (Steinberg *et al.*, 1989). The value of  $K_g$ , representing a 'zero set' for each stem/gauge configuration, was calculated between 04.15 and 05.30 Central Standard Time (CST) daily from Eq. (1), assuming  $F=0$  at night (Steinberg *et al.*, 1989).

Gauges were placed on 15–20 mm diameter stems which were secondary or tertiary extensions of basal support stems and occurred 1 to 2 m above the soil surface. To increase stem/gauge contact, a small amount of dielectric silicon was applied to the stem before gauge attachment. Gauges were covered with clear plastic 'cling film' for water protection and with foam insulation and aluminium foil to minimize externally-induced temperature gradients. Insulation was applied to 0.1 m long stem segments above and below the gauge.

In June, 1990, 10 min averages of  $P$  and gauge signals ( $dT_b$ ,  $dT_a$ ,  $E$ ,  $dT_{ba}$ ) were calculated from 15 s measurements made from 03.20 to 21.10 CST by a data logger (Model CR7 and 21X, Campbell Scientific, Inc., Logan, UT). In October, 15 min averages were calculated. Because stem leaf area and volume were small, plant water capacitance was ignored and stem flow was assumed to be equal to transpiration (Schulze *et al.*, 1985).

Different stems were measured in October than in June but the same trees were used throughout the study.

#### Porometer measurements

Mesquite leaves were bipinnately compound with 5 to 15 pairs of leaflets per leaf and averaged 150 to 250 mm<sup>2</sup> of one-sided surface area per leaflet. Stomatal conductance ( $g_s$ ; m s<sup>-1</sup>) was measured using two steady-state porometers (Model LI-1600, LiCor, Inc., Lincoln, NE) on 100 mm<sup>2</sup> (one surface) of the abaxial (lower) surface of individual leaflets on stems with a stem flow gauge. Duration of each porometer measurement was 20 to 40 s. Photosynthetically active radiation ( $PAR$ ; 400–700 nm) and leaf temperature ( $T_{leaf}$ ) were measured simultaneously with  $g_s$  using sensors mounted on and within the porometer leaf chamber, respectively.

Transpiration from abaxial leaf surfaces ( $E_{ab}$ ; g m<sup>-2</sup> h<sup>-1</sup>) was calculated from  $g_s$ , atmospheric humidity and boundary layer conductance (Campbell, 1977)

$$E_{ab} = (X_l - X_a) / \left( \frac{1}{g_s} + \frac{1}{g_b} \right) \quad (2)$$

where  $X_l$  is leaf absolute humidity, assuming saturation (g m<sup>-3</sup>),  $X_a$  is atmospheric absolute humidity, and  $g_b$  is boundary layer conductance (m s<sup>-1</sup>).

The  $g_b$  was calculated from the sum of the forced and free convection (Grace, 1983)

$$g_{b(\text{forced})} = \frac{0.66D^{0.67}u^{0.5}}{d^{0.5}v^{0.17}} \quad (3)$$

$$g_{b(\text{free})} = \frac{0.54D^{0.75}g^{0.25}a^{0.25}(T_s - T)^{0.25}}{d^{0.25}v^{0.25}} \quad (4)$$

where  $d$  is the characteristic dimension of the leaf (m),  $u$  is wind speed (m s<sup>-1</sup>), and  $(T_s - T)$  is the difference in temperature (K) between the leaf and the air. Physical constants at 20 °C are:  $a$ , coefficient of thermal expansion of air ( $\approx 1/293$  K<sup>-1</sup>);  $D$ , diffusion coefficient in air for water vapour ( $2.4 \times 10^{-5}$  m<sup>2</sup> s<sup>-1</sup>);  $g$ , acceleration due to gravity (9.81 m s<sup>-2</sup>);  $v$ , kinematic viscosity of dry air ( $1.5 \times 10^{-5}$  m<sup>2</sup> s<sup>-1</sup>). Meteorological station data were used to determine  $X_a$  and  $g_b$ .

Because Meyer and Meola (1978) found 40% greater stomatal density on adaxial than abaxial leaf surfaces in honey mesquite, we measured  $g_s$  on both adaxial and abaxial surfaces of 20 to 30 leaflets on 14 and 15 June and 1 October 1990. The adaxial/abaxial stomatal conductance ratio was 1.73 in both June and October. This ratio was used to adjust  $E_{ab}$  measurements to a transpiration value representative of both leaf surfaces combined ( $E_{leaf}$ ; g m<sup>-2</sup> h<sup>-1</sup>) by modifying Eq. (2) as follows

$$E_{leaf} = (X_l - X_a) / \left( \frac{1}{1.37g_s} + \frac{1}{g_b} \right) \quad (5)$$

The coefficient 1.37 was derived from adaxial/abaxial  $g_s$  ratio.

#### Diurnal experiment and scaling leaf to stem

Stem flow was measured continuously from 5 to 15 June, and on 1, 2, and 5 October 1990 on three stems on each of the six trees. Gauges were placed on south-facing stems on the canopy perimeter. One gauge malfunctioned during each of the June and October sample periods. One tree had only two stems instrumented in October. Therefore, 17 and 16 stems were used in June and October, respectively. Mean stem flow for 20 min (June) or 15 min (Oct) preceding the time of porometer measurements was compared with porometer measurements.

Total leaf area distal to each stem flow gauge was determined by removing all leaves from each stem after terminating stem flow measurements in June and October. About 10% of each stem's leaf area was measured with an area meter and total leaf area was calculated from the subsample leaf area/leaf mass ratio.

Porometer measurements were made five times per day from 09.00 through 16.00 CST on 5, 8, and 12 June, near solar noon on 10, 14, and 15 June, four times per day on 1 October, and near solar noon on 5 October 1990. Diurnal porometer measurements were limited to one day in October because of frequent storms. Each measurement period lasted about 1 h. Four leaflets were measured on each stem with a stem flow gauge (except on 10 and 14 June when only two leaflets were measured). Each leaflet was from a different leaf. Leaves measured each day were of similar age and were 2 and 6 months old in June and October, respectively.

Foliage and small branches distal to each stem gauge occupied about 0.5 m<sup>3</sup> space and were usually not shaded by foliage from other stems. However, interior leaves were shaded intermittently by perimeter leaves within each experimental stem. A stratified sampling scheme was used to account for within-stem shading effects in which half the porometer measurements were made on perimeter and half on interior leaves of each stem.

Porometer-calculated stem transpiration ( $E_{stem}$ ; g<sup>-1</sup> stem h<sup>-1</sup>) was determined by scaling  $E_{leaf}$  to a value for the entire stem by multiplying mean  $E_{leaf}$  of the 2 or 4 measurements per stem by stem leaf area.  $E_{stem}$  was compared to stem flow measurements. A comparison of leaf responses from perimeter and interior foliage layers was conducted as a substudy using data from 5, 8 and 12 June which had two  $E_{leaf}$  measurements per layer.

#### Shading experiment

To examine potential effects of within-stem shading on stem transpiration further, a portion of the total leaf area distal to the stem flow gauge was shaded by positioning a piece of plywood normal to the incident solar beam near solar noon on two stems on 15 June and five stems on 5 October 1990. Before shading was imposed,  $g_s$  was measured on five leaves that would remain in the sun and five leaves that were to be shaded on each stem. Measurements of  $g_s$  were repeated on both sets of 5 leaves about 20 min after shading was imposed. Stem flow was measured throughout the shading experiments (5 min averages in June and 1 min averages in Oct).  $E_{leaf}$  (Eq. 5) before and after shading was compared using a  $t$ -test.

Porometer stem transpiration before shading ( $E_{stem(\text{pre})}$ ) and during the shade interval ( $E_{stem(\text{shade})}$ ) was calculated from the following

$$E_{stem(\text{pre})} = (E_{leaf(\text{sun})} \times LA_{(\text{sun})}) + (E_{leaf(\text{sun} \rightarrow \text{shade})} \times LA_{(\text{sun} \rightarrow \text{shade})}) \quad (6)$$

and

$$E_{stem(\text{shade})} = (E_{leaf(\text{sun})} \times LA_{(\text{sun})}) + (E_{leaf(\text{shade})} \times LA_{(\text{shade})}) \quad (7)$$

where  $E_{leaf(\text{sun})}$ ,  $E_{leaf(\text{sun} \rightarrow \text{shade})}$ , and  $E_{leaf(\text{shade})}$  are porometer transpiration of sunlit, sunlit to be shaded, and shaded leaves, respectively, and  $LA_{\text{sun}}$ ,  $LA_{(\text{sun} \rightarrow \text{shade})}$ , and  $LA_{\text{shade}}$  are sunlit, sunlit to be shaded, and shaded portions of total leaf area distal to the stem flow gauge, respectively. Small branches distal to the stem flow gauge were marked with flagging tape to indicate whether they supported sunlit or shaded leaves. Following the shading experiment, sunlit and shaded leaves were harvested separately and  $LA_{\text{sun}}$  and  $LA_{\text{shade}}$  were determined with a leaf area meter (on all stems,  $LA_{(\text{sun} \rightarrow \text{shade})} = LA_{\text{shade}}$ ). Measurements

of  $E_{stem(pre)}$  and  $E_{stem(shade)}$  were compared with the average stem flow for 10 min before and during shading, respectively. Regression analyses were used to compare stem flow measurements to  $E_{stem(pre)}$  and  $E_{stem(shade)}$ .

#### Defoliation experiment

To compare the two methods under highly contrasting stem water fluxes, portions of leaf area were sequentially removed from six stems on 15 June and from four stems on 5 October 1990. Porometer measurements were made on four leaves per stem prior to the first defoliation.  $E_{stem}$  was calculated after each defoliation in June based on the remaining leaf area of each stem and pre-defoliation  $E_{leaf}$ . In October, porometer measurements were made prior to and following the first defoliation, and  $E_{stem}$  was calculated using the post-defoliation  $E_{leaf}$ . Stem flow was measured continuously during defoliations. Regression analysis was used to compare stem flow to  $E_{stem}$  before and after each defoliation.

Stem flow measurements were used to determine the relation between per cent of the total leaf area removed and stem transpiration. For this comparison, four additional stems were used in October and some were completely defoliated. Stem flow from non-defoliated stems was used to normalize per cent reduction in stem flow during each defoliation period.

#### Statistical analysis

Except where noted, the stem was defined as the experimental unit upon which all statistics were determined. A *t*-test was used for paired comparisons of means of  $E_{stem}$  and stem flow. Simple linear regressions were performed between  $E_{stem}$  and stem flow for the diurnal, shading, and defoliation experiments with the hypothesis that the slope ( $b_1$ ) should equal one with an intercept ( $b_0$ ) of zero. The intercept was assumed to be zero and regressions were performed using the equation  $E_{stem} = (b_1)(stem\ flow)$ .

To determine whether the slope of the  $E_{stem}$ /stem flow regression was significantly different from the hypothesized value of one, a second regression was performed using the equation,  $\Delta = (b_1)(stem\ flow)$ , in which the dependent variable,  $\Delta$ , was the difference between  $E_{stem}$  and stem flow, the independent variable was stem flow. If  $E_{stem}$  equalled stem flow,  $b_1$  in the regression  $\Delta = (b_1)(stem\ flow)$  should equal zero. A *t*-test was performed to determine if the slope of the regression,  $\Delta = (b_1)(stem\ flow)$ , was significantly different from zero ( $P \leq 0.05$ ) and this was used to determine if the slope of the regression,  $E_{stem} = (b_1)(stem\ flow)$ , was significantly different from one (SAS, 1988).

## Results

#### Meteorology and soil moisture

Wind speeds varied from 2 to 5 m s<sup>-1</sup> in June and October, while maximum temperatures were about 35 and 30 °C in June and October, respectively. Potential evapotranspiration (*PET*) reflected the generally clear skies on all sample days in June (Fig. 1). *PET* was lower and more variable in October than June due partly to cloudy skies and cooler temperatures.

Soil moisture was not limiting during either the June or October trial. Volumetric soil moisture was greater than 25% (v/v) (calculated soil matric potentials

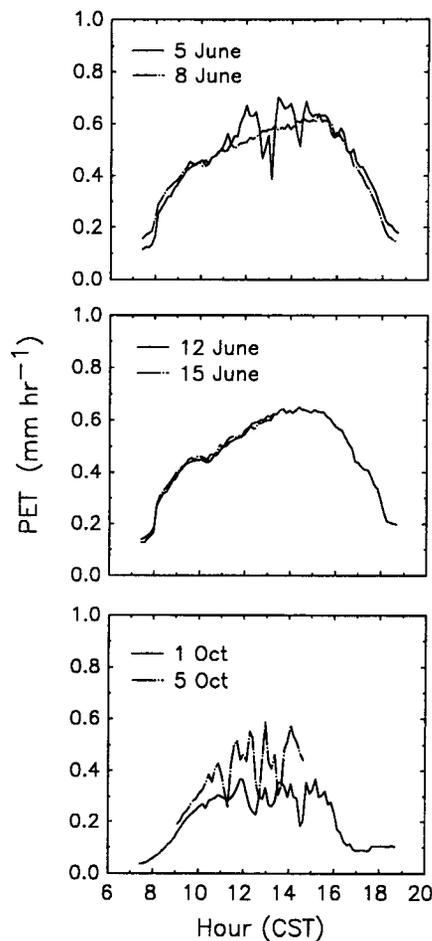


Fig. 1. Ten-minute averages of potential evapotranspiration (*PET*) on days porometer and stem flow measurements were made in June and October 1990. CST = Central Standard Time. Solar noon is at 12.37 h CST at the study site.

> -0.4 MPa) to a depth of 1.25 m during June. Precipitation from January to June, 1990, was 80% above normal and on 2 June, 3 d before the study began, it rained 74 mm. No precipitation occurred during the remainder of the month. Precipitation was 200% above average during August and the site received 42 mm from 16–22 September and 11 mm on 3 October. Soil moisture was not measured in October, but August and September precipitation suggest soil water was not limiting in October. Due to the high soil water levels, there were no significant differences in transpiration between irrigated and non-irrigated trees in June or October.

#### Diurnal experiment

Stem flow exhibited a consistent diurnal pattern with peak stem flow occurring at around 10.00–12.00 h in June and 12.00–15.00 h CST in October when stems were pooled within hourly sample periods (Fig. 2). On June dates, stem flow declined in the afternoon while *PET* peaked (Figs 1, 2). Afternoon decline in stem flow

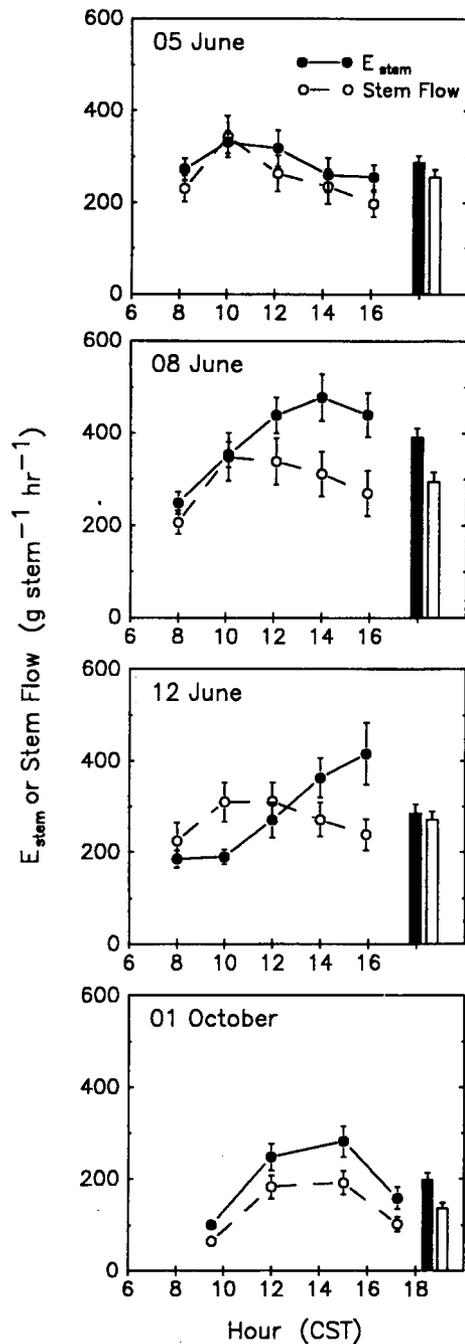


Fig. 2. Porometer transpiration ( $E_{stem}$ ) and stem flow of mesquite on four dates in 1990. Each point represents the mean of all stems measured within an hour ( $n=16$  or  $17$  stems per point). Bars represent mean value of 5 or 4 (October) points of each daily curve (solid bar =  $E_{stem}$ ; open bar = stem flow). Vertical lines around means are  $\pm 1$  s.e. of the mean. Solar noon is at 12.37 h CST at the study site.

occurred even when soil water availability was high. Stem flow did not decline as early in the day on 1 October as in June (Fig. 2), probably due to lower  $PET$  in October.

The pattern of  $E_{stem}$  was similar to that of stem flow on 5 June and 1 October. However, on 8 and 12 June,  $E_{stem}$  increased during the afternoon while stem flow

declined, relative to midday values (Fig. 2). When averaged over all stems and measurement periods,  $E_{stem}$  was 16 and 41% greater than stem flow in June (330 versus  $283 \text{ g}^{-1} \text{ stem h}^{-1}$ ;  $n=332$ ) and October (204 versus  $144 \text{ g}^{-1} \text{ stem h}^{-1}$ ;  $n=67$ ), respectively, with the difference in October significant ( $P \leq 0.05$ ). Mean  $E_{stem}$  and stem flow of all stems declined from June to October by 38% and 49%, respectively (using above values), even though mean stem leaf area declined only 20% from June ( $0.94 \text{ m}^2$ ) to October ( $0.75 \text{ m}^2$ ). Lower  $PET$  and average  $PAR$  ( $1130$  to  $670 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) in October may partially explain the difference.

The linear relationship between all paired measurements of  $E_{stem}$  and stem flow showed more variation in June ( $r^2=0.79$ ) than in October ( $r^2=0.91$ ; Fig. 3A, B). During June, slope ( $b_1$ ) of the equation,  $\Delta = (b_1)(\text{stem flow})$ , was  $-0.01$  (s.e. =  $0.03$ ,  $n=332$ ), which was not significantly different from zero. During October, slope of  $\Delta = (b_1)(\text{stem flow})$  was  $0.31$  (s.e. =  $0.05$ ,  $n=67$ ) which was significantly different from zero. From these equations it was determined that the slope of the regression between  $E_{stem}$  and stem flow was not significantly different from one in June ( $b_1=0.99$ ), but was in October ( $b_1=1.31$ ). These results suggest precision of the porometer was greater during October than June, because October regressions had higher  $r^2$  values. We interpret accuracy of the porometer to be greater during June than October, because the slope of the regression was closer to one in June. However, root mean square error of the regression was  $170.7$  in June and  $73.7$  in October. Pooling porometer and stem flow measurements for each stem over all sample periods in each month increased  $r^2$  of the  $E_{stem}$ /stem flow regression to  $0.91$  in June and  $0.94$  in October (Fig. 3C, D). Slopes of pooled regressions were similar to unpooled data.

Potential sources of variation associated with the scatter in Fig. 3A included individual stems, porometer operators, and within-stem shading. As an example of variation among stems, the  $b_1$  of the  $E_{stem}$ /stem flow regression for tree 3, stem 2 and tree 6, stem 2 was  $2.22$  ( $n=21$ ) and  $1.08$  ( $n=20$ ), respectively, on June dates ( $r^2$  was  $0.84$  and  $0.86$ , respectively). Of the two primary porometer operators during June,  $r^2$  of the  $E_{stem}$ /stem flow regression using porometer measurements was  $0.84$  ( $n=153$ ) and  $0.74$  ( $n=142$ ) for operators 1 and 2, respectively ( $b_1$  was  $0.95$  and  $1.01$ , respectively). Variation among operators may be attributed to the somewhat subjective procedure of null balancing the porometer (LiCor, 1982) to achieve leaf chamber/leaf equilibrium prior to recording data.

#### Stem foliage layer substudy

Variation in leaf transpiration ( $E_{leaf}$ ) was related to leaf position within stem foliage layers. Leaves at the foliage perimeter had greater ( $P \leq 0.05$ ) transpiration than inter-

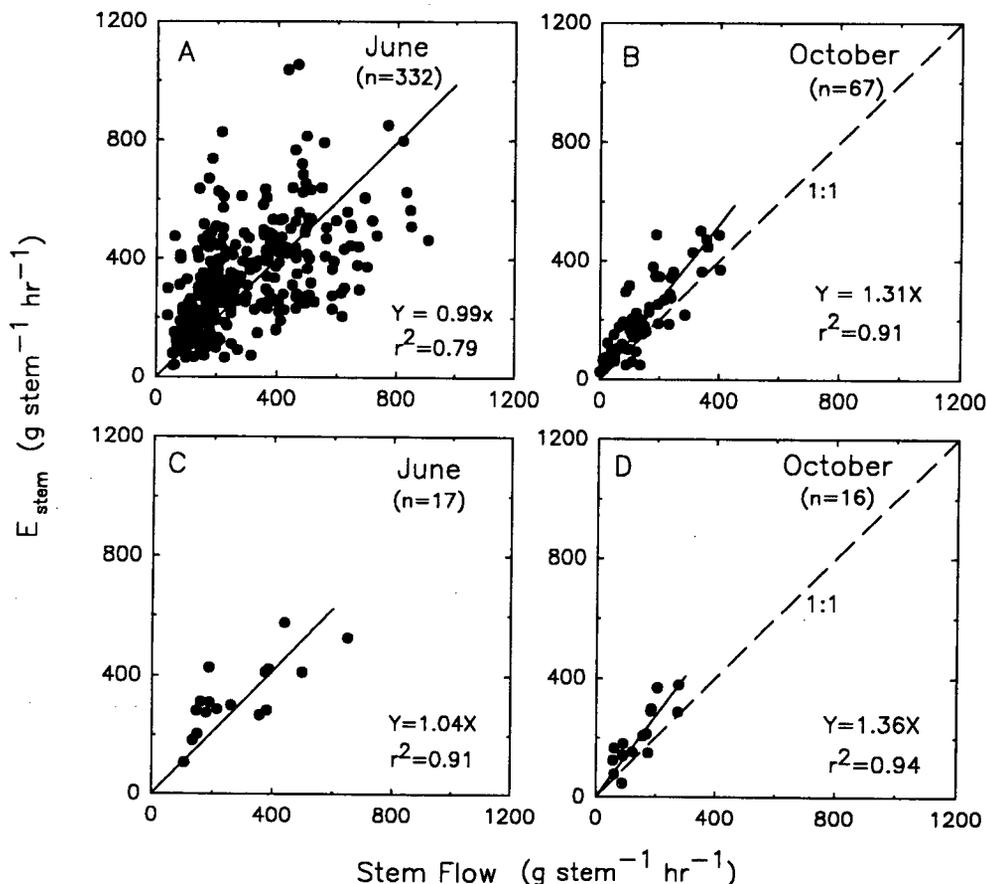


Fig. 3. Relation between stem flow and porometer transpiration ( $E_{stem}$ ) for each stem (A, B) in June (5, 8, 10, 12, 14, 15) and October (1, 5) (each  $E_{stem}$  point is the mean of 2 or 4 leaves measured with the porometer), and (C, D) when averaged for each stem over all measurement periods in June or October. Solid line is the regression (zero intercept). Dashed line is  $b_1=1$  and is shown only when regression slope is significantly different from 1.

ior leaves when data from 5, 8 and 12 June were pooled (Table 1). Differences in  $E_{leaf}$  may have related to greater PAR or leaf temperature ( $T_{leaf}$ ) at perimeter than interior positions, although porometer-measured  $T_{leaf}$  was not significantly different between positions. No  $T_{leaf}$  measurements independent of the porometer were made but  $T_{leaf}$  did not vary significantly from meteorological station air temperature.  $E_{leaf}$ , calculated using porometer  $g_s$  and meteorological station  $X_a$  and  $g_b$  (Eqs 2–5), was less than factory-calculated transpiration ( $E_{leaf-fac}$ ; LiCor, 1982) in both stem layers. Mean  $E_{stem}$ , calculated using only perimeter or interior  $E_{leaf}$  and multiplied by stem leaf area, was 352 and 297, respectively, compared to 276 g<sup>-1</sup> stem h<sup>-1</sup> stem flow. Thus, much of the deviation between porometer and stem flow measurements came from perimeter leaves.

#### Shading experiment

Mean transpiration of individual leaves ( $E_{leaf}$ ) decreased ( $P \leq 0.05$ ) by 34% (377 to 247 g m<sup>-2</sup> h<sup>-1</sup>) on 15 June when artificially shaded, while mean  $E_{leaf}$  of the continually sunlit portion of the stem foliage did not significantly

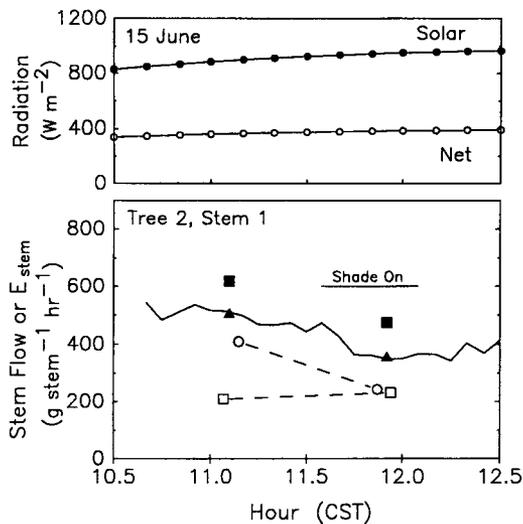
Table 1. Photosynthetically active radiation (PAR), abaxial leaf temperature ( $T_{leaf}$ ) and leaf transpiration ( $E_{leaf}$ ) within stem foliage layers;  $E_{stem}$ , calculated from  $E_{leaf}$  within each layer and for the entire stem, and stem flow (stem layer substudy: data from 5, 8 and 12 June)

Standard error is in parentheses following each mean ( $n=247$ )<sup>a</sup>. An asterisk indicates a significant difference ( $P \leq 0.05$ ) between perimeter and interior mean.

Variable (units)	Stem foliage layer		Entire-stem
	Perimeter	Interior	
PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	1525 (28)	649 (26)*	1087 (23)
$T_{leaf}$ ( $^{\circ}\text{C}$ )	34.4 (0.2)	34.1 (0.2)	34.2 (0.2)
$E_{leaf}$ (g m <sup>-2</sup> h <sup>-1</sup> )	374 (10)	311 (9)*	343 (9)
$E_{leaf-fac}$ (g m <sup>-2</sup> h <sup>-1</sup> ) <sup>b</sup>	386 (10)	324 (9)*	355 (9)
$E_{stem}$ (g <sup>-1</sup> stem h <sup>-1</sup> )	352 (12)	297 (11)*	325 (11)
Stem flow (g <sup>-1</sup> stem h <sup>-1</sup> )			276 (11)

<sup>a</sup>  $n=247$ : 3 d  $\times$  5 sample periods d<sup>-1</sup>  $\times$  6 trees  $\times$  3 stems tree<sup>-1</sup>; less 23 measurements in which either PAR (8) or stem flow (15) were not measured.

<sup>b</sup>  $E_{leaf-fac}$ : Factory-calculated transpiration (LiCor, 1982) taken directly from porometer console display and adjusted for both leaf surfaces.



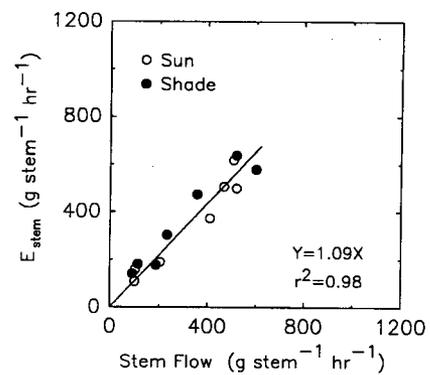
**Fig. 4.** Solar and net radiation (top) and diurnal courses of stem flow and porometer transpiration ( $E_{stem}$ ) of one stem before and after partial shading on 15 June. Solid horizontal line is duration of the shade interval. (—) Stem flow; ( $\blacktriangle$ ) mean stem flow during porometer measurements; ( $\square$ ) mean porometer transpiration of portion of stem that remained sunlit; ( $\circ$ ) mean porometer transpiration of portion of stem that was sun-to-shade and then shaded; ( $\blacksquare$ )  $E_{stem}$  of entire stem. Solar noon is at 12.37 h CST at the study site.

change (482 to 512  $\text{g m}^{-2} \text{h}^{-1}$ ). Mean  $E_{stem}$  and stem flow, which integrated shaded and sunlit portions of each stem, decreased by 22% (495 to 389  $\text{g}^{-1} \text{stem h}^{-1}$ ) and 36% (458 to 295  $\text{g}^{-1} \text{stem h}^{-1}$ ), respectively, when an average of 67% of the stem leaf area was shaded. Global radiation was essentially constant during the shade interval on 15 June. Figure 4 illustrates stem flow for a single stem during the June shading study.

Conditions were cloudier and global radiation was more variable on 5 October than 15 June. During artificial shading global radiation increased and mean  $E_{leaf}$  of the continually sunlit portion increased 37% (345 to 474  $\text{g}^{-1} \text{stem h}^{-1}$ ). Shading reduced  $E_{leaf}$  by only 9% (347 to 317  $\text{g m}^{-2} \text{h}^{-1}$ ). Mean  $E_{stem}$  increased 17% (293 to 344  $\text{g}^{-1} \text{stem h}^{-1}$ ) and mean stem flow increased 8% (279 to 302  $\text{g}^{-1} \text{stem h}^{-1}$ ) when an average of 52% of stem leaf area was shaded. Regression between  $E_{stem}$  and stem flow of the seven stems used for the shading experiment (2 in June, 5 in October) had a higher  $r^2$  (0.98; Fig. 5) than regressions from the diurnal experiments (Fig. 3). This increased precision may be attributed to a larger number of porometer measurements made per stem during the shading experiment (10) than during the diurnal experiment (4 or 2).

#### Defoliation experiment

Defoliation sequences for each stem are reported in Table 2. An average of 73% and 52% of stem leaf area remained after first and second June defoliations. Stem flow readings were discontinued before any stems in June



**Fig. 5.** Relation between stem flow and porometer transpiration ( $E_{stem}$ ) prior to and during shading. Slope of regression line is not significantly different from one.

**Table 2.** Per cent foliage remaining after defoliations during two sample dates in 1990

Date	Tree-stem	Per cent of foliage remaining		
		1st defoliation	2nd defoliation	3rd defoliation
15 June	2-2	72.7	44.5*	
	2-3	72.9	52.9*	
	3-2	61.3	35.6*	
	5-1	71.2	56.0*	
	6-1	73.7	60.7*	
	6-3	88.7	61.2*	
	<b>Mean</b>	<b>73.4</b>	<b>51.8</b>	
05 October	3-1	68.1	30.0	0
	3-3	57.6	26.6	0
	5-1	35.5	23.8	0
	5-2	47.0	17.4	0
	<b>Mean</b>	<b>52.1</b>	<b>24.5</b>	
	2-2	31.2	0	
	2-3	35.6	0	
	5-3	56.0	0	
	6-1	53.2	0	

\* Second defoliation in June was not used for stem flow/ $E_{stem}$  comparison in Fig. 6 because porometer measurements were not made on remaining leaves following defoliation.

were completely defoliated. Of the four stems in October that received two partial defoliations, similar to June, an average of 52% and 25% of stem leaf area remained after the first and second defoliations.

The  $E_{stem}$  and stem flow regression before and during defoliation indicate that June porometer measurements underestimated and the October porometer measurements overestimated transpiration when compared to stem flow (Fig. 6). Stem flow decreased with decreasing leaf area during the progressive defoliations (Fig. 7). However, about 13% of original stem flow was still measured on completely defoliated stems.

#### Leaf area and stem flow among stems

Stem flow was positively related to stem leaf area which ranged from 0.2 to 1.5  $\text{m}^2$  (including both leaf surfaces)

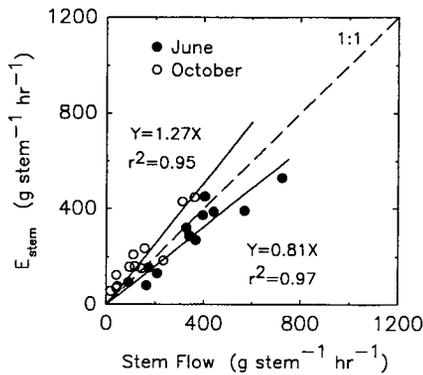


Fig. 6. Relation between stem flow and porometer transpiration ( $E_{stem}$ ) prior to and following partial defoliation of stems in June and October. Slopes of both regression lines are significantly different from one ( $P \leq 0.05$ ).

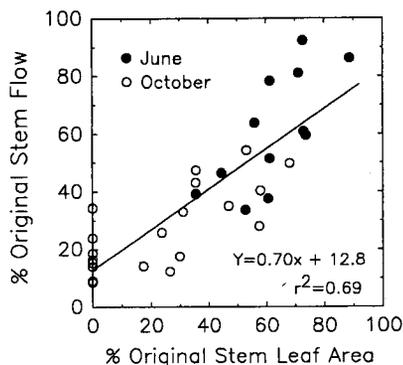


Fig. 7. Relation of per cent reduction in leaf area to per cent reduction in stem flow of mesquite stems that were progressively defoliated in June and October.

(Fig. 8). Six of the eight stems that deviated to the lower right corner of the plot in Fig. 8 (points circled) were from two irrigated trees (three stems each), suggesting that stem hydraulic conductance potential varied among trees and was to some degree independent of stem leaf

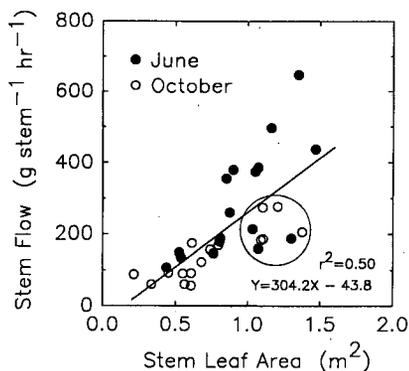


Fig. 8. Relation between stem leaf area (both leaf surfaces) and stem flow for each stem when averaged over all porometer measurement periods in June and October. Each point represents a single stem. Stem flow values are same as those used in Fig. 3, panels C and D. Circled are points deviating to the lower right corner.

area. A portion of the scatter in Fig. 8 may also be due to different stem exposures to radiation and wind, although most measured stems were on the southern aspect of the canopy.

## Discussion

Trees at our site averaged 40 stems with similar diameters as those fitted with stem flow gauges. Our data indicate stem flow averaged  $270 \text{ g h}^{-1}$  for 10 h on clear days in June (Fig. 2) which suggests daily transpiration per tree was at least  $108 \text{ kg}$ . This value is higher than the  $30$  to  $75 \text{ kg d}^{-1}$  determined by scaling leaf transpiration to whole canopies in a mesquite stand  $30 \text{ km}$  from the present study site near Throckmorton, TX in 1986 and 1987 (Ansley *et al.*, 1991). Trees in the present study had greater whole plant leaf area than those reported by Ansley *et al.* (1991).

Stem flows in this study were higher than those reported for mesquite in 1988, at a second site near Throckmorton, TX (Dugas *et al.*, 1992). This difference may relate to April through September precipitation which was  $521 \text{ mm}$  at our study site in 1990 and  $378 \text{ mm}$  at Throckmorton in 1988. Interestingly, our daily transpiration values are similar to those reported by Larcher (1975) for birch (*Betula* spp.) and by Schulze *et al.* (1985) for *Larix* and *Picea*, which were larger trees in more mesic environments. Leaf temperature and *PET* were undoubtedly lower in those studies than at our site.

In evaluating the performance of the porometers and scaling transpiration from leaf to stem, we assumed stem flow measurements were accurate. Several studies show that stem flow measurements are accurate when compared to 'ground truth' gravimetric techniques (Baker and Nieber, 1989; Heilman *et al.*, 1989; Steinberg *et al.*, 1990; Dugas and Mayeux, 1991; Dugas *et al.*, 1993, 1994). The non-zero flow after complete defoliation in our study (Fig. 8) likely represents errors in the sheath conductance. At low stem flows, a small error in sheath conductance can result in a relatively large percentage error in flow (Baker and Nieber, 1989). At moderate to high flow rates, this stem flow error (in both absolute and in percentage units) is much smaller. Water loss through petiole wounds may have contributed to the non-zero readings.

If we assume stem flow measurements were accurate, the considerable variation between methods during periods of maximum transpiration, leads us to conclude that accuracy of scaling porometer leaf measurements to the stem declined with increasing transpiration rates. Several studies agree with our findings which suggest that transpiration measured by a porometer and scaled to the stem or canopy is greater than that measured by stem flow or gravimetric techniques, especially during periods of high transpiration. Green *et al.* (1989) found good correlation between heat pulse and Penman-Monteith-

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adjusted porometer data in kiwifruit vines (*Actinidia deliciosa*), although at peak transpiration, porometer values exceeded heat-pulse values. Steinberg *et al.* (1990) found agreement between sap flow and LiCor LI-1600 porometer estimates of canopy transpiration in pecan (*Carya illinoensis*), but porometer estimates were higher than sap flow during maximum transpiration. Fichtner and Schulze (1990) found xylem flow transpiration of the vine, *Entadopsis polystachya*, to be 50% of transpiration measured on abaxial leaf surfaces with a LiCor LI-1600 porometer, although the authors did not indicate whether both leaf surfaces were used when scaling porometer values from leaf to stem. Gucci *et al.* (1990) found that porometer measurements of apricot (*Prunus armeniaca*) leaves overestimated transpiration when compared to gravimetric measurements.

Some studies have found remarkable agreement between stem flow and porometer measurements. Schulze *et al.* (1985) found that canopy transpiration in *Larix* and *Picea* trees scaled from porometer leaf measurements and total needle biomass was very close to that determined by a stem flow technique, although porometer transpiration (of needles) started about 3 h earlier each day than stem flow. We did not detect a lag time between the two methods and staggering  $E_{stem}$  and stem flow curves from Fig. 2 does not indicate a lag effect. However, our sample scheme, which took an hour to complete each sample period, may have masked any lag effects between methods. Lag time, if it existed, may explain some of the scatter in our  $E_{stem}$ /stem flow regressions.

Several sources of variation in scaling leaf measurements of transpiration to the stem were revealed in this study. Each porometer measurement of 100 mm<sup>2</sup> leaf area (one leaf surface) represented about 0.01% of total leaf area (both surfaces) distal to each stem flow gauge. The  $r^2$  between  $E_{stem}$  and stem flow in June increased from 0.79 to 0.98 when leaf measurements per stem were increased from 4 (diurnal experiment) to 10 (shading experiment).

Porometer overestimation of transpiration in afternoons, as suggested by the June data, may relate to the porometer leaf chamber warming during the afternoon. The study was at a remote site in which porometers were exposed to ambient conditions continually, although they were shaded between sample periods. In other studies of mesquite on the same site (Ansley *et al.*, 1990, 1992),  $g_s$  declined, but factory-calculated transpiration (LiCor, 1982) increased in the afternoon, similar to the present study (transpiration data from these two previous studies were not published). Ansley *et al.* (1991) found similar afternoon trends while measuring mesquite transpiration with a leaf chamber (Model LI-6000, LiCor Inc, Lincoln NE) near Throckmorton, TX.

Shading within stem foliage layers is a potential source of error when scaling from leaf to stem (Norman, 1993).

Results from our study regarding porometer measurements within foliage layers are somewhat inconclusive. While our data indicate that measuring only sunlit leaves on the foliage perimeter clearly overestimated transpiration when scaled to the stem (Table 1), results also suggest that measuring only interior leaves provided a better estimate of stem transpiration than did measuring a combination of interior and perimeter leaves. The shading study revealed a close match between stem flow and porometer methods when within-stem shading was considered, although light quality and intensity in artificially shaded regions were completely different than if shaded by foliage.

Scaling from leaf to stem must consider per cent of damaged leaves per stem, and effect of damaged leaf surface area on transpiration. We conclude that higher  $E_{stem}$  than stem flow values during October related in part to sampling procedure in which only undamaged leaves were selected for porometer measurements. Insect-damaged or partially senescent leaves probably had lower transpiration rates than undamaged leaves. It appeared that the ratio of damaged to undamaged leaves was higher in October than June.

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