

Comparison of Trunk and Branch Sap Flow with Canopy Transpiration in Pecan

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ABSTRACT

Trunk and branch sap flow were compared with canopy transpiration in a 5-year-old pecan tree (*Carya illinoensis* 'Wichita'). Total trunk sap flow, measured by a heat balance trunk flow gauge, was 122.8 kg over a 24 h period, corresponding closely to the 113.4 kg of canopy transpiration measured by a large precision weighing lysimeter. Branches, less than half the diameter of the main trunk, had a total sap flow an order of magnitude less than the total flow in the trunk. Sap flow in a branch with a northern exposure was 41% less than that with a southern exposure. When sap flow was normalized per unit tree or branch leaf area, peak sap flow in the south branch matched that in the main trunk. Tree transpiration and the sap flow in trunk and branches began concurrently, indicating little dynamic water storage in the trunk above the gauge. The hydraulic conductance of the entire tree was 8 to $14 \times 10^{-14} \text{ m s}^{-1} \text{ Pa}^{-1}$, similar to values found for a number of woody and herbaceous species.

Key words: Sap flow, *Carya illinoensis*, transpiration, lysimeter, trunk flow gauge.

INTRODUCTION

The efficiency of the water transport system and of the regulatory mechanisms for water loss have been cited by Camacho, Hall, and Kaufman (1979) as the most important adaptive characteristics of plants with respect to water relations. Pecan has been attributed with an efficient water transport system, (Anderson and Brodbeck, 1988; Wolstenholme, 1979), yet it is unclear what its characteristics are.

The evolutionary history of pecan has endowed it with an inherently high water requirement (Wolstenholme, 1979). Indigenous to the river bottoms and flood plains of the south central USA, pecan thrives in deep, well-drained alluvial soils. Wolstenholme (1979) also speculates that the dominant tap root of pecan confers a competitive advantage in drawing upon the water table, allowing survival in areas with low annual rainfall (51–64 cm).

Two studies describe the leaf water relations aspect of water transport in pecan. Under non-limiting soil moisture conditions, Anderson and Brodbeck (1988) found little evidence of stomatal closure during conditions of high evaporative demand and midday leaf water potential depression to -1.9 MPa . Pecan leaf conductance was

high compared to most woody species, and similar to that found in C_3 herbaceous plants. They also observed a capability for rapid short-term growth in response to favourable soil moisture conditions. After watering stressed pecan seedlings, Rieger and Daniell (1988) attributed the rapid recovery of leaf water potential to a large potential gradient and low plant capacitance.

Studies of whole-tree water use have often relied on empirical equations involving environmental variables, crop coefficients, or pan evaporation data to estimate tree water use (Miyamoto, 1983). Although satisfactory for irrigation scheduling, these methods have little value for detailed studies of tree water relations. Measurement of changes in tree dimension and in tissue water content have been used to characterize water storage in large trees (Running, 1980a; Waring and Running, 1978). However, such data does not quantify tree water use, nor the flow rates in the tree system.

The recent development of trunk flow gauges, using the heat balance principle (Steinberg, Van Bavel, and McFarland, 1989) allows direct measurement of trunk or branch sap flow. When combined with water loss data from

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precision lysimetry and from leaf transpiration rates obtained by porometry, a simultaneous record of water flow through the trunk, branches and canopy can be procured. We obtained such a record to quantify water fluxes through a pecan tree under non-limiting soil moisture conditions, with the purpose of characterizing the water transport system.

MATERIALS AND METHODS

The study was carried out at an outdoor weighing lysimeter facility at the Texas Agricultural Research and Extension Center, Stephenville (32°12' N, 98°13' W), 17–20 August, 1988. Each of two lysimeters was 2.44 m in diameter and 1.52 m in depth. The weighing mechanism consisted of three strain gauge load cells, with a sensitivity of 1.0 mm of water over the surface area of the lysimeter, or 4.5 kg (McFarland, Worthington, and Newman, 1983). Data collected from the load cells were processed at 15 min intervals by a 21X datalogger (Campbell Scientific, Logan, UT., USA).

Each lysimeter contained a 5-year-old pecan tree (*Carya illinoensis* 'Wichita'), planted in the upper layer of a Windthorst fine sandy loam. The lysimeter facility was sited east–west and the tree in the east lysimeter was used as the test tree. It had an average trunk diameter of 79 mm, a height of 3.9 m, and a canopy diameter of 2.6 m. During the experimental period, the lysimeter was covered with plastic so that weight changes could be attributed solely to transpiration by the tree. The tree was watered each night to maintain well-watered conditions. Soil moisture potential never exceeded -0.03 MPa as measured by tensiometers placed to a depth of 46 cm in the lysimeter can.

Sap flow in the main trunk and in two 35 mm branches was measured with trunk flow gauges (Steinberg *et al.*, 1989). An insulated length of the trunk or a branch was heated externally at a constant rate. Temperature sensors in the gauge measured vertical temperature gradients in the trunk above and below the heater, the temperature gradient across the heater, and the temperature gradient in the insulation. Vertical and radial heat conduction and the heat carried by the moving sap were obtained from these measurements and used to calculate sap mass flow. The general methodology has been described in detail by Sakuratani (1981), Baker and Van Bavel (1987) and Steinberg *et al.* (1989).

The thermal conductivity of fresh wood from small branches of the test tree, as determined in a manner similar to that described by Steinberg *et al.* (1989), was $0.47 \text{ W m}^{-1} \text{ }^\circ\text{K}$. Previously, a value of $0.42 \text{ W m}^{-1} \text{ }^\circ\text{K}$ was obtained for *Ficus* trunk wood (Steinberg *et al.*, 1989). Because the two values were similar, and the pecan wood samples were from small branches rather than the main trunk, the value of 0.42 was used in the calculations. The lysimeter record gave no evidence of water loss from pecan trees at night. Therefore, the sheath conductance of the gauge could be obtained *in situ* using predawn gauge signals and assuming zero sap flow (Steinberg *et al.*, 1989).

The design of the gauge installed on the 79 mm trunk was based on that by Steinberg *et al.* (1989), but adapted to fit the dimensions of the trunk. Both of the two smaller gauges installed on branches were commercially available models (Model SG35A, Dynamax Inc., Houston, TX). The gauge dimensions for both gauge types are listed in Table 1. A 21X datalogger and an AM32 multiplexer (Campbell Scientific, Logan, UT.) were used to log and process gauge signals. Signals were logged every 15 s and averaged over 5 min, prior to the calculation of the sap flow rate. Sap flux measurements were also calculated per unit trunk or branch leaf area.

TABLE 1. Gauge dimensions for pecan sap flow measurements

	Trunk	Branch
Diameter (mm)	80.0	35.0
Heater length (mm)	159.0	20.0
Heater power (W)	1.2	0.4
Temperature sensor to heater distance (centre to centre) (mm)	154.5	35.0
Insulation thickness (mm)	25.0	10.0
Total length of insulation (mm)	650.0	300.0

All three gauges were installed during the late afternoon of 17 August (Calendar Day Number (CDN) 230) after the trunk and branches were lightly sanded with sandpaper to remove any loose or rough bark. Silicon grease was applied sparingly to the thermojunctions of each gauge to improve sensor–wood contact. The larger gauge was attached to the main trunk between 60 and 470 mm above the ground; the trunk was then insulated from the ground to the point of lateral branching. The smaller gauges were placed on two branches, one with a northern and the other with a southern exposure. Leaves on the former were in shade or in partial shade throughout the day, while the majority of leaves from the latter were fully sunlit from 12.00 h until 18.00 h. Average midday temperatures ranged from 35 to 40 °C during the test period, which was a sequence of mostly clear days without rainfall.

The pecan tree contained ten 35 mm branches, from which it was initially estimated that each test branch would carry approximately 9% of the total tree leaf area. At the termination of the test the total number and location of secondary branches and the total leaf number were counted on each test branch. The fresh and dry weight of all leaves from the test branches and a representative sample of the leaf area per unit fresh and dry weight were obtained in October, 1988. The leaf area of the branches, obtained from the leaf area–weight relation, was 3.7 m² for the north branch and 4.2 m² for the south branch. The leaf area of the entire tree was estimated as eleven times the average leaf area of the branches, or 43 m².

Periodically throughout both test days, leaf transpiration and conductance was measured with a LI-COR LI1600 steady state porometer (Licor, Lincoln, NB) and leaf water potential (ψ_L) was measured with a pressure chamber (Scholander, Hammel, Bradstreet, and Hemmingsen, 1966). Measurements were made on the terminal leaflet of the compound pecan leaf from locations in both the sunlit ($n \geq 5$) and shaded ($n \geq 5$) outer canopy. The crown of this pecan tree was relatively open, and at no time during the day was any portion of the canopy in dense shade. Canopy transpiration was extrapolated from an average value of the porometer measurements which weighted the sunlit and shaded canopy equally, and the estimate of the leaf area of the tree.

RESULTS

The lysimeter data showed that the daily water use of the pecan tree ranged from 100 to 150 kg per day over a 12 d period, CDN 228 to CDN 240 (Fig. 1). On CDN 232 the tree water use was 113.4 kg. During that same 24 h period the trunk flow gauge showed the total sap flow to be 122.8 kg, a difference of 8% (Fig. 2). Young pecan trees are commonly grown at 86 trees per hectare (McEachern, 1984), so that recorded water use would be equivalent to 1.037 mm over the orchard area, or 5.66 mm over the projected crown surface area.

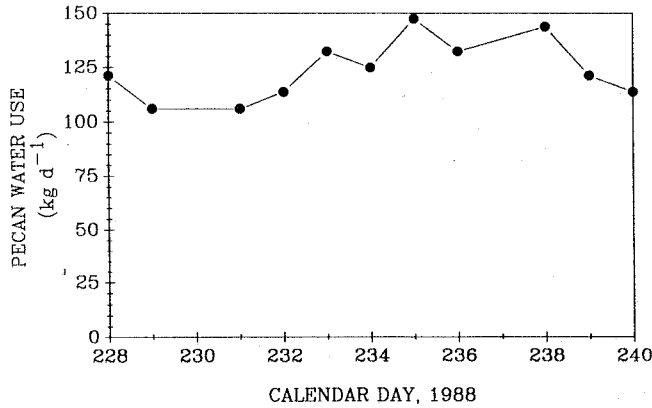


FIG. 1. Daily water use of a 5-year-old pecan tree growing in a large weighing lysimeter during August, 1988.

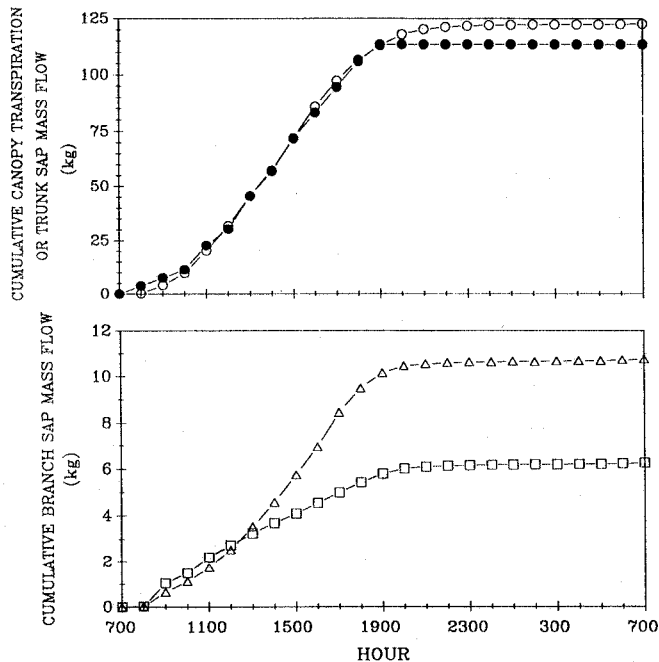


FIG. 2. Cumulative water use of pecan for CDN 232, 1988. The upper graph shows canopy transpiration (●) measured by a lysimeter and trunk sap flow (○) measured by a trunk flow gauge; the lower graph shows the south branch (△) and north branch (□) sap flow, also measured by trunk flow gauges.

The total sap flux in the south branch was 10.8 kg, an order of magnitude less than that in the main trunk, but the shape of the accumulative curves of each were similar (Fig. 2). In contrast, the water loss pattern in the north branch was markedly different. It resulted in a 24 h total of 6.3 kg, or 41% less than that of the south branch. Figures 1 and 2 also show that canopy transpiration and sap flux in the trunk and in the branches proceed in a concordant manner.

The sap flux rate per unit trunk or branch leaf area, is shown in Fig. 3. Trunk sap flux peaked near $370 \text{ g h}^{-1} \text{ m}^{-2}$ at 15.00 h. A comparison of the two branches shows

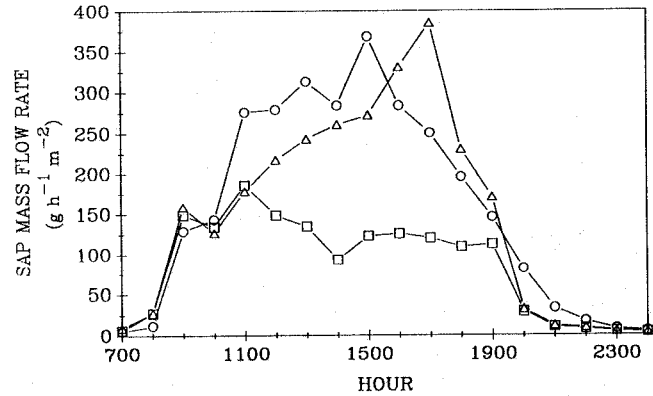


FIG. 3. Sap flow rate per unit trunk or branch leaf area for CDN 232, 1988. Trunk = ○, south branch = △ and north branch = □.

that the highest sap flow rates in the south branch, $384 \text{ g h}^{-1} \text{ m}^{-2}$, occurred near 17.00 h, while that in the north branch remained near a steady value of $150 \text{ g h}^{-1} \text{ m}^{-2}$ from 11.00 h to 19.00 h. Nevertheless, the normalized rates are of the same order of magnitude, for trunk and branches alike.

Hourly rates of trunk sap flux and of canopy transpiration measured by lysimetry and calculated by porometry are compared in Fig. 4. The diurnal course of water use was typical for a summer day, beginning about 08.00 h, increasing during the morning hours to a peak at midday, and decreasing in the afternoon. No pronounced lag can be seen between trunk sap flow and canopy transpiration, as measured by either of the two methods (Figs 4, 5). However, canopy transpiration ceased rapidly after sundown, while sap flow proceeded at a decreasing rate until early morning. Also, between 07.00 h and 09.00 h approximately 4.0 kg of water was transpired before the onset of sap flow. This amount corresponded to 3% of the total daily sap flow. The minor initial lag between canopy transpiration and sap flow was followed by a rapid

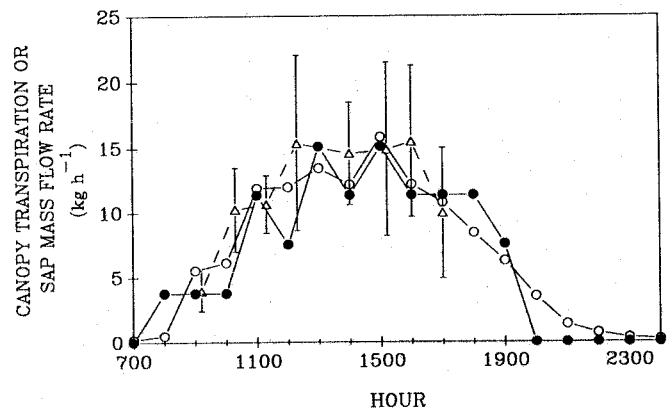


FIG. 4. Measured (●) and calculated (△) canopy transpiration and trunk sap flow (○) for CDN 232, 1988. Calculated transpiration is the mean of 4 or more porometer measurements ± 1 s.d.

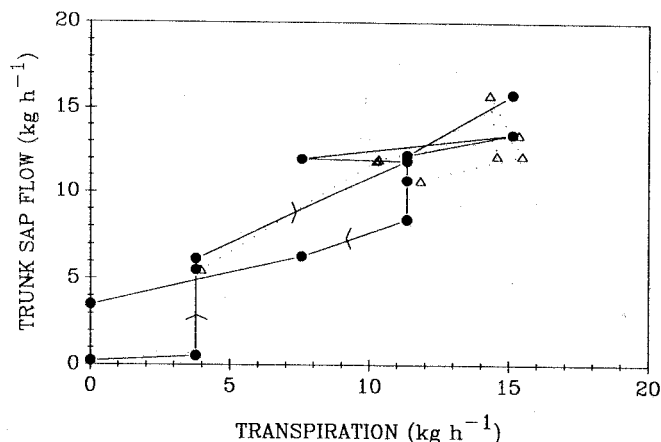


FIG. 5. The relation between trunk sap flow and measured (●) or calculated (△) canopy transpiration in pecan.

increase of the latter, followed by parallel increases in the value of both to about 15 kg h^{-1} (Fig. 5).

The diurnal course of leaf water potential, given in Fig. 6, can be seen to depend on the exposure of the leaves. Water potential of both sunlit and shaded leaves declined in a similar fashion until 12.00 h to 13.00 h. Thereafter, the ψ_L of sunlit leaves declined to approximately -2.0 MPa , while that of shaded leaves remained constant near -1.3 MPa . The average minimum ψ_L of all leaves sampled was -1.53 MPa at 14.00 h. At this time, cumulative tree water loss (56.7 kg) equalled cumulative sap flux (57.3 kg). The leaf conductance to water vapour of sunlit and shaded leaves was not significantly different throughout the day, although that of sunlit leaves tended to be higher in the afternoon.

The relationship between the increase in transpiration or in sap flux and the decrease in water potential has been used to calculate the conductance of the liquid flow pathway in trees (Landsberg, Blanchard, and Warrit, 1976). Our data, given in Fig. 7, show that the leaf water potential decreased with increasing flow rates in a linear fashion, even though greater variability is evident in the data during periods of high demand (flow rates greater than $80 \text{ mg m}^{-2} \text{ s}^{-1}$) (Fig. 7). From the data a linear regression gives the conductance of the liquid flow pathway in pecan as $8 \text{ to } 14 \times 10^{-14} \text{ m s}^{-1} \text{ Pa}^{-1}$ (equivalent to $0.8 \text{ to } 1.4 \times 10^{-9} \text{ s}^{-1}$, taking a 1.0 m water column to be equivalent to 10^5 Pa).

DISCUSSION

In this study the flow rate of sap was measured in the trunk, in the branches and in the leaves of a 5-year-old, well-watered pecan tree. Concurrent measurement of trunk sap flow by a trunk flow gauge and whole tree water loss by a precision weighing lysimeter showed sap flux to be within 8% of actual water loss, a close measure of the tree water use on a 24 h basis. This agreement was obtained in the field under conditions of a high evapora-

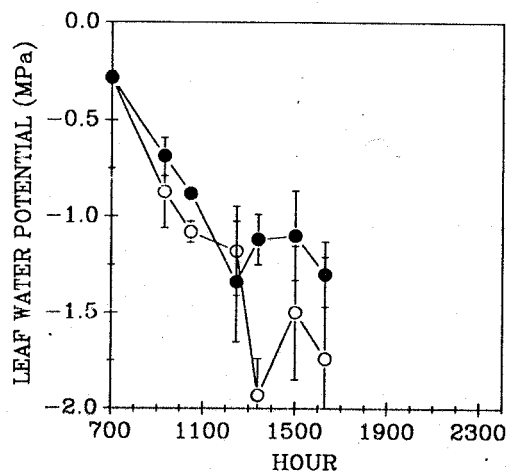
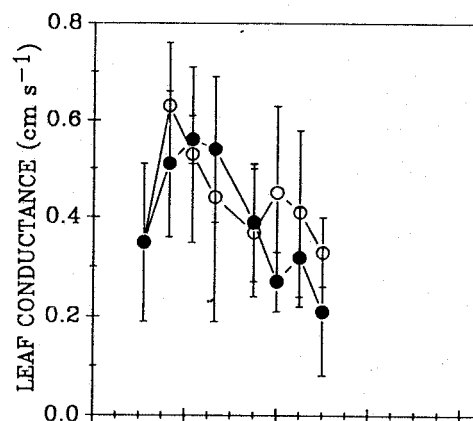


FIG. 6. Diurnal course of leaf diffusive resistance and water potential for the sunlit (○) or shaded (●) canopy on CDN 232, 1988. Data points and error bars equal to the mean ± 1 s.d.

tive demand. The peak sap flow rates of 15 kg h^{-1} were an order of magnitude higher than any recorded earlier with a gauge of similar design (Baker and Van Bavel, 1987; Steinberg *et al.*, 1989).

Branches slightly less than half the diameter of the main trunk had a total sap flow rate an order of magnitude lower than that in the trunk. But, when trunk and branch flow were normalized on a per unit leaf area basis, the sap flow in the branches was similar to that in the trunk. Others have compared sap flow rates in branches or whole trees of different sizes, and different species, normalized on projected crown area, xylem water conducting trunk cross-section area, leaf dry weight, or unit trunk volume (Čermák, Úlehla, Kučera, and Penka, 1982; Čermák, Jeník, Kučera, and Židek, 1984). We believe that normalizing trunk or branch data by the leaf area is superior to other methods, as long as it is done within a single species.

Sap flux in the southern branch was 41% higher than in the northern branch of the same diameter, caused by the difference in exposure to radiation. Examples of different

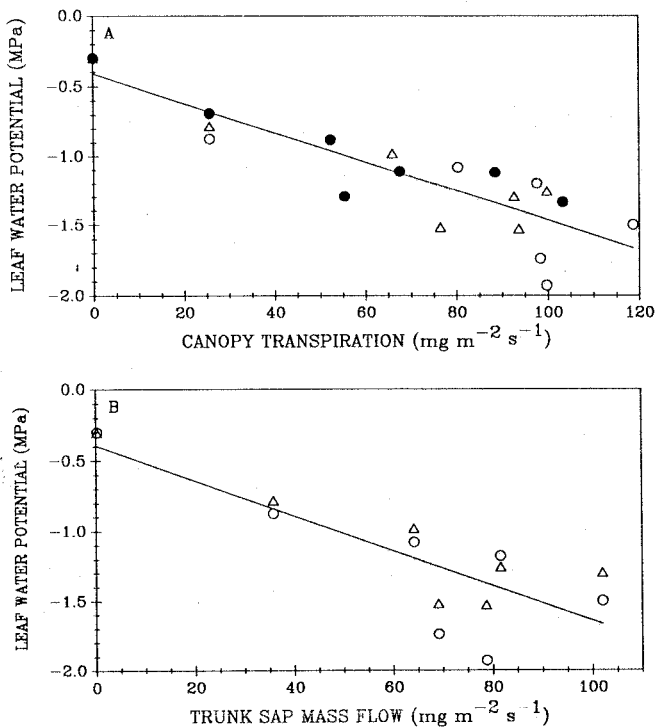


FIG. 7. The relation between (A) sun canopy (○) shade canopy (●) or average (△) leaf water potential and transpiration (porometer), and (B) average (△) or sunlit canopy (○) leaf water potential and trunk sap flow.

water use rates between irradiated and shaded branches within a tree canopy have been documented elsewhere. Čermák *et al.* (1984) reported sap flow in shaded willow branches was 79% of that in sunlit branches, while Daum (1967) cited a case where sap flow direction was actually reversed in a shaded branch, to supply the irradiated crown. Hinkley and Ritchie (1970) provided evidence of high rates of water redistribution within a tree crown, and believed that ψ_L , transpiration and diffusive resistance at any location were a function of the local microclimate and transpiration activity in other sections of the crown. We found that ψ_L was consistently lower in the sunlit canopy, despite a similarity in leaf conductance between irradiated and shaded leaves. Furthermore, the cumulative sap flow pattern in the trunk resembled that in the sunlit branch. These findings demonstrate that the xylem flux rate in the main trunk was driven primarily by the steepest potential gradient between soil and leaf.

The sap flow rate in a branch, obtained with a gauge, could be used to estimate whole tree water use if a trunk gauge or another method cannot be used. In such a case, care must be taken to ensure an adequate number of gauges and their proper placement within the canopy so that the average of the flow rates is representative of the entire tree canopy, and the respective leaf areas must be known.

Early in the morning a relatively small amount of

water, 4.0 kg, was transpired before xylem sap flow began. Schultze *et al.* (1985) noted a higher availability of stored water for transpiration in the crown as compared with the main trunk in both *Larix* and *Picea*. Therefore, the small early morning lag between pecan sap flow and canopy transpiration may represent water immediately available in the leaves, petioles or small branches. We observed no lag between the onset of sap flow in the branches and the main trunk. Schultze *et al.* (1985) also noted little lag between upper and lower trunk flow in *Larix*. We recorded a time difference between peak trunk and branch sap flux rates in pecan, but do not attribute it to any lag in the tree system, but rather to the local microclimate differences in the canopy.

On the whole transpiration and sap flow tracked closely together, indicating little capacitance in the trunk or crown. At 14.00 h, when the average tree water potential depression had reached the daily minimum, there was no difference between the accumulated canopy transpiration and trunk sap flux. Landsberg *et al.* (1976) has theorized that the water flux for transpiration is supplied both from stored water in the tree and from the soil via the roots. In pecan, it is possible that stored water is recharged almost immediately upon depletion, but a more likely scenario is that the entire transpiration stream comes directly from the soil. Our data suggests the capacitance of pecan to be similar to that of *Salix* (Čermák *et al.*, 1984), but much less than that given for *Larix* and *Picea* (Schultze *et al.*, 1985) where the lag between the onset of sap flow and transpiration was several hours.

The conductance of the pecan tree remained steady throughout the day, similar to what was found by Cohen, Fuchs, and Cohen (1983) for citrus. We again attribute this result, which implies a linear relation between driving potential and flow rate, to the low water capacitance of the pecan tree. In other species, such as Douglas-fir (Waring and Running, 1978), quite different results have been observed. The value for the conductance obtained was higher than for most woody species, but similar to values recorded for herbaceous plants as shown in Table 2 and by Helkvist, Richards, and Jarvis (1974; Table 4).

Use of the trunk flow gauge makes it possible to measure the liquid conductance of trees easily. Changes in conductance have been used as an indicator of tree water stress (Elfving, Kaufman, and Hall, 1972) or infestation by pathogens that invade the root or the xylem and damage the water absorption and transport system (Zimmermann, 1983). Hence the measurement can have direct diagnostic value.

We concluded that water transport in pecan trees is relatively efficient. Pecan is capable of withstanding a depression of the leaf water potential to -2.0 MPa without a reduction in the transpiration rate. Also, the hydraulic conductance of pecan was high compared to values for other woody plants. Finally, the lack of a

TABLE 2. Liquid flow conductance in some woody and herbaceous species

Species		Conductance per unit leaf area ($\times 10^{-14} \text{ m s}^{-1} \text{ Pa}^{-1}$)
Larch	<i>Larix</i> (Schultze et al., 1985)	0.809
Spruce	<i>Picea</i> (Schultze et al., 1985)	0.647
Lodgepole Pine	<i>Pinus contorta</i> (Running, 1980b)	0.1–1.0
Apple	<i>Malus pumila</i> (Landsberg et al., 1975)	2.7–3.1
Juniper	<i>Juniperus virginiana</i> (Ginter-Whitehouse et al., 1983)	2.13
Soybean	<i>Glycine max</i> (Boyer, 1971)	7.14
Oak	<i>Quercus alba</i> (Ginter-Whitehouse et al., 1983)	11.8
Sunflower	<i>Helianthus annuus</i> (Boyer, 1971)	16.0
Black Walnut	<i>Juglans nigra</i> (Ginter-Whitehouse et al., 1983)	25.6

significant lag between water flow in the trunk, the branches and the canopy suggests that the transpiration stream proceeds directly from the roots. These three findings explain the effective water transport system of the pecan tree.

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