Water Transport in the Liana *Bauhinia fassoglossensis* (Fabaceae)$^1$

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ABSTRACT

To determine the efficiency of xylem conductance in the liana (woody vine) *Bauhinia fassoglossensis* Kotschy ex Schweinf., we measured hydraulic conductance per unit stem length (measured $K_s$), leaf-specific conductivity (LSC = $K_b$/distal leaf area), transpiration rate ($E$), xylem water potential ($\Psi$), vessel number, and vessel diameter. The measured $K_s$ was 49% ($SE = 7\%$) of the predicted $K_s$ from Poiseuille’s law. The mean LSC for unbranched stem segments was $1.10 \times 10^{-4}$ square meters per megapascal per second ($SE = 0.07$). LSCs were much lower (about 0.2) at branch junctions. At midday, with $E$ at $7 \times 10^{-4}$ meters per second, the measured drop in $\Psi$ was about 0.08 megapascal per meter along the stems and branches and about 0.27 megapascal in going from stem to leaf. In addition, there was a drop of about 0.20 megapascal at branch junctions as predicted by $E$/LSC. In diurnal measurements leaf $\Psi$ never dropped below about −1.2 megapascal. For long (e.g. 16 meters) stems, the predicted midday drop in $\Psi$ through the xylem transport system might be great enough to have substantial physiological impact.

The long and slender stems of lianas (woody vines) are commonly thought to be extremely efficient in water transport due to their long and wide vessels (5, 6, 8, 15–17, 29, 30). However, although there is much evidence that liana vessels are wider than in closely related trees (5, 8, 10), there are few published data to indicate whether liana stems are particularly efficient at supplying their leaves with water.

Xylem transport efficiency is often expressed as the measured hydraulic conductance per unit stem length (measured $K_s$), which is defined as the xylem flow rate divided by the pressure gradient ($dp/dx$). When such measurements are made on intact plants, they are valid only when taken along unbranched portions of the plant axis that do not bear leaves. On branched systems and/or systems with different transport distances to each leaf, a single $K_s$ measurement can be meaningless (18, 26). Our approach to modeling the various hydraulic pathways is to measure $K_s$ in isolated stem segments from throughout the shoot systems (8, 11, 12, 27, 28).

Poiseuille’s law for ideal capillaries can be used to relate vessel number and diameter to $K_b$ by the following formula:

$$predicted\; K_b = \pi \sum \frac{d_i^4}{128 \eta}$$

with $K_b$ in m$^4$ MPa$^{-1}$ s$^{-1}$, $\eta$ = dynamic viscosity of the fluid (MPa s), and the summation is over all conducting elements (diameter $d_i$) for the ith capillary in m.

To determine how effective a stem is at supplying its leaves, we need to consider not only measured $K_s$ and predicted $K_b$, but also the leaf area that the stem segment supplies and the $E$ of the leaves (27). LSC is equal to measured $K_s$ divided by the leaf area distal to the stem segment. LSCs have the advantage that they allow a theoretical basis for relating measured $K_s$ to $dp/dx$ in shoot systems with long and complex transport pathways (19, 26–28):

$$dp/dx = E/LSC$$

with $dp/dx$ in MPa m$^{-2}$, $E$ in m$^2$ water s$^{-1}$ m$^{-2}$ leaf area (= m s$^{-1}$), and LSC in m$^2$ water s$^{-1}$ MPa$^{-1}$ m$^{-1}$ (= m$^2$ MPa$^{-1}$ s$^{-1}$). LSCs have been reported for conifers (11, 12, 27) and dicotyledonous trees (28), but there are few published LSC data for lianas.

In the present report, we test the usefulness of Equation 1 in predicting $K_s$ in *Bauhinia fassoglossensis*. More importantly, we examine the influence of stem xylem conductance on the $\Psi$ in this species. This report is the first of a series on water transport in *Bauhinia*, which is an interesting genus because it contains trees, shrubs, and liana species, which differ considerably in their xylem anatomy as well as life form.

MATERIALS AND METHODS

Plant Material

A single clone of *Bauhinia fassoglossensis* Kotschy ex Schweinf. was used. The shoots were mostly horizontally oriented and grown in full sun at Fairchild Tropical Garden in Miami, FL. All field measurements were made between June 1986 and September 1987.

Measurements of Leaf $\Psi$

Leaf $\Psi$ measurements were made with a pressure chamber. In some cases the leaves were covered with a sheet of plastic
wrap, cut from the plant, and immediately placed in the pressure chamber. In cases where simultaneous collections were made, it was necessary to store cut leaves in a shaded, aluminum foil-covered, zip-lock bag containing a damp paper towel for periods of up to 2 h before making the \( \Psi \) readings. In tests of our methods, we found no statistically significant change over time in measured \( \Psi \) among leaves that were stored for these periods. The pressure in the chamber was raised slowly (about 6 kPa s\(^{-1}\)) until the end point was reached. The pressure was then partially released, and the end point was remeasured. When the second reading differed from the first by more than 20 kPa, which was unusual, the pressure was again partially released and a third reading made. The balance pressure for a particular leaf was taken as the mean of the two readings, or, when a third measurement was necessary, the mean of the second and third readings.

**Diurnal Studies of \( E, g_s \), and leaf \( \Psi \)**

These were performed on a sunny day following a period of heavy rains. In the previous evening, on nine stems we marked the leaves that were 10 to 19 nodes behind the stem apex. Node 6 represented the first firm (normal) leaf. We loosely covered 10 randomly selected marked leaves with newspaper to eliminate dew formation in the early morning. The sampled leaves were from stems and branches that ranged from about 3 to 7 m in length from apex to root base. Starting at 0630 h, shortly before sunrise (0640 h), we removed the newspaper and then made measurements of \( E \) and \( g_s \) with a Li-Cor 1600m steady state porometer. We repeated the measurements on the same 10 leaves at intervals of about 2 h until 2044 h, which was after sunset (2015 h). For each porometer reading, we waited until the readout was stable, which usually took less than 3 min. At each interval, at least six randomly selected marked leaves, each from a different marked stem, were enclosed within a plastic bag and cut from the plant for measurements of leaf \( \Psi \) with a pressure chamber as described above.

**Measurements of LSCs**

LSCs were measured on five shoot systems on 4 different days. The longest shoot system we used was over 15 m in length. All leaves were marked by their position and cut from the plant in the early morning. Leaf areas were measured with a Li-Cor leaf area meter equipped with a conveyor belt. Stems were cut under water and taken to the laboratory, where stem segments were recut under water to lengths of 0.5 m, or, in one stem system, 0.3 m. This was much longer than the average vessel length we found in this material [mean vessel length = 0.18 m, median length about 0.06 m, using the methods described in reference (9)]. The ends of the stem segments were shaved smooth with a fresh razor blade, the distal end was fitted with vinyl tubing, and the remaining stumps of the leaf petioles were covered with fingernail polish to eliminate leakage. Stem segments were then vacuum-infiltrated at ~87 kPa for 5 min to remove any surface embolisms. Stems were perfused with a freshly prepared and filtered solution of 0.05% formalin in 10 mM KCl to minimize any artifacts from pit membrane swelling (28) or microbial growth (24). The measured \( K_s \), defined as the measured flow rate divided by the applied \( dp/dx \), was determined via gravity feed with a pipet and stopwatch (28). LSCs were calculated as measured \( K_s \) divided by the leaf area distal to that stem segment. In cases where the stem segments directly bore leaves, 50% of the leaf area within the stem segment was included in the LSC calculation. This assumes that 50% of the segment-born leaves were distal and 50% were proximal of the midpoint of a segment, which was the point used for the \( dp/dx \) calculations.

**Predicted \( K_s \)**

In many cases, following \( K_s \) measurements we perfused the same stem segments with 0.5% (w/v) aqueous safranin to mark the conductive pathway. The length of dye perfusion time (about 12 min) was equal to 4 times the time it took for the stem segment with the lowest \( K_s \) to pass some of the dye through its entire length. Dye perfusion was followed by perfusion with clear tap water to remove excess dye and thus minimize lateral diffusion. The stem segments were transversely sectioned in the median portion with a sliding microtome, immediately dehydrated to minimize spread of the dye, and mounted in Permount. A Nikon photostereoscope with transmitted light capabilities was used to prepare Kodachrome slides of stem sections. The slides were projected onto large sheets of white paper upon which each vessel was marked off as its inner diameter was measured with a ruler. This allowed us to measure easily every vessel in the stem section \( (n = 99-659) \) without measuring a particular vessel twice. The measurement errors due to spherical aberration of the projection lens were less than 1%. When a vessel was not circular in transverse view, the maximum and minimum diameters were averaged for use in Equation 1. To test whether we had overestimated the predicted \( K_s \) by not properly correcting for the elliptic shapes of vessels, we recalculated this value for all the vessels in three stem segments using the formulas provided by Calkin et al. (4). These calculations indicated that our measurements of predicted \( K_s \) are inflated by about 4%. The projected slides were also used to determine xylem transverse area and sapwood area, which was defined as the xylem area containing safranin-stained vessels.

**Measured versus Predicted \( dp/dx \)**

The bagged leaf method (14) was employed to measure the stem \( \Psi \) at different points along the stem. In *B. fausolensis* leaves persist on stems for up to 55 nodes after they mature, which represents a distance of 4 m. A set of adjacent distal and a set of adjacent proximal leaves were bagged to eliminate their transpiration and thus allow them to equilibrate with their insertion point on the stem. Less than 10% of the leaves on a shoot were bagged. To determine the drop in \( \Psi \) from the stem to a leaf, comparisons were made between the \( \Psi \) of bagged leaves and of adjacent unbagged leaves on the same stem. The stem \( dp/dx \) was calculated as the difference in \( \Psi \) between the two sets of bagged leaves, divided by the distance between sets. Since there were several adjacent leaves in each
set, the midpoint of each group was used to determine the distance.

Leaves were bagged as follows. In the late afternoon, leaves were tightly covered with a thin plastic wrap and enclosed in double plastic bags containing a damp paper towel. The distal and proximal groups of bagged leaves were then covered with plastic wrap and finally wrapped in aluminum foil. The following morning (predawn) or the following midday, the bagged leaves and, in some of the experiments, adjacent unbagged control leaves, were collected and the $\Psi$ of each leaf was measured with a pressure chamber. Mean $\Psi$ was determined for each group of bagged leaves.

To determine predicted $dp/dx$ on the same stems, $E$ and $g_s$ were measured on unbagged marked leaves at 1 h intervals until the bagged leaves were collected. For accurate determinations of whole shoot $E$, the marked leaves were spaced at regular intervals (e.g. every sixth node) along the entire shoot to minimize bias for sun versus shade leaves or young versus old leaves. At least 10 leaves were measured at each time interval. In some experiments, both abaxial and abaxial $E$ and $g_s$ measurements were made, whereas in other cases only abaxial measurements were recorded, with adaxial $E$ calculated as a percentage of the abaxial rate.

On the following day, measurements of LSC were made on the same shoots as used for the measurements of $E$, $g_s$, and $dp/dx$. LSCs were calculated both with and without inclusion of the bagged leaves for the leaf area measurement so we could distinguish between ‘normal’ and LSCs. Predicted pressure differentials were calculated by adding the pressure differential predicted by Equation 1 to pressure differentials due to differences in height, which was about 1 m maximum since the shoots were mostly horizontal. For calculations of predicted $dp/dx$, $E$ in Equation 1 was averaged for the 2.5 h period prior to sampling, which represented the ‘midday peak’ in $E$.

RESULTS

Diurnal Studies

Based upon measurements between 0920 and 1246 h, $E$ and $g_s$ from the adaxial (upper) leaf surface were, respectively, 19.5% ($SE = 2.6\%$) and 16.8% ($SE = 2.2\%$) that of the abaxial (lower) leaf surface ($n = 64$).

$E$ and $g_s$ were measured as zero after dusk and before dawn (Figs. 1 and 2). Maximum $E$ during the mostly sunny summer days when stem $dp/dx$s were measured was about $7 \times 10^{-8}$ m s$^{-1}$, with $g_s$ dropping sharply during the period from about 10 AM until $dp/dx$s were measured at midday (Fig. 2). On the day of the complete diurnal study, which was a sunny day following a period of frequent rains, $E$ was higher (a maximum of $11.1 \times 10^{-8}$ m s$^{-1}$) than on the other days and $g_s$ dropped rather gradually throughout the afternoon (Fig. 1).

On any particular day, the leaf $\Psi$ would be similar immediately after dusk and before dawn (Fig. 1). On three different dates, predawn and postdusk leaf $\Psi$ ranged from $-0.02$ MPa ($SE = 0.008$) to $-0.24$ MPa ($SE = 0.016$). On or before midday, leaf $\Psi$ dropped to about $-0.95$ MPa. The lowest individual leaf $\Psi$ we found from 118 control leaves samples for this study was $-1.15$ MPa.

Figure 1. Diurnal study of transpiration ($E$ for abaxial only), stomatal conductance ($g_s$ for abaxial only), and leaf water potential ($\Psi$). Bars indicate standard errors. This study was done on a completely sunny day following several days with afternoon rains. Arrows at top indicate dawn and dusk.

LSCs

Based upon data from six stem systems there was a statistically significant linear relationship between measured $K_s$ and the leaf area distal to the stem segments (Fig. 3; Table I). The ratio was measured $K_s$ to distal leaf area is equal to LSC. Since the junctions (Fig. 4) leading into lateral branches had particularly low LSCs (Figs. 3 and 4), junction values were omitted from the regression line calculation for Figure 3 and the $'r'$ value for $K_s$ versus leaf area in Table I. The mean LSC for all the sampled stem segments, excluding junctions, was $11.0 \times 10^{-7}$ m$^2$ MPa$^{-1}$ s$^{-1}$ ($SE = 0.7$).

LSCs are shown for the most extensive shoot system that we examined (Fig. 4). Other than particularly low LSCs leading into branch junctions, LSCs in branches were similar to those of the main stem. There was no consistent increase or decrease in LSC in going from the distal to proximal portions of the plant axis. The predicted stem $\Psi$s at various places along this shoot system are shown in Figure 5. This assumes $E$ values similar to those in Figure 2. The predicted $dp/dx$s along the branches were similar to those along the main stem. However, under periods of high $E$, the predicted $dp/dx$ is much steeper at the junction going into the branches than it is along the unbranched portions of the axes. The predicted additional $\Psi$ drop caused by a branch junction at a
junctions, which in Standard ductance \((g, \text{at})\) than the size of the symbols. stem the to\(\text{seems}\) a Figure 3. Measured hydraulic conductance \((G_s)\) of \(0.27 \text{ MPa}\) in going from the stem to the leaf xylem (Table II).

**Measured and Predicted Stem \(dp/dx\)**

These were measured and calculated for individual stems with the mean results shown in Table III. At predawn, the \(dp/dx\) was close to zero, but at midday the measured and predicted \(dp/dx\) were, respectively, 0.083 and 0.076 MPa \(\text{m}^{-2}\). Although averaged measured results from these experiments showed a close correspondence to predicted \(dp/dx\) both at predawn and at midday, the measured results in individual experiments ranged widely from the predicted (Table III).

**Correlations with Measured \(K_s\)**

As shown in Table I, measured \(K_s\) was significantly correlated with the number of vessels in the stem segment, mean vessel diameter, maximum vessel diameter, and with the predicted \(K_s\) from Equation 1. The strongest correlation was with predicted \(K_s\) \((r = 0.88; \text{see Fig. 6})\), and the weakest with vessel number \((r = 0.43)\) and stem xylem diameter \((r = 0.42)\). The measured \(K_s\) was, on the average, 49\% of the predicted \(K_s\) \((\text{se} = 7, n = 22)\). There was no statistically significant correlation between stem xylem diameter and LSC \((r = 0.11; \text{Table I})\).

**DISCUSSION**

Based upon LSCs, stems of *Bauhinia fassoglensis* do not appear to be any more efficient in supplying their leaves with water than are stems of other large woody plants. The LSCs of *B. fassoglensis* are greater than have been reported in trunks of coniferous trees \((8, 11, 12, 27)\), but within the range of values reported for dicotyledonous trees \((8, 28)\).

The relative decrease in LSCs at branch junctions (i.e. hydraulic constrictions), appears to be similar to that reported for trees \((11, 12, 27, 28)\). Within *B. fassoglensis*, LSCs were similar for the lateral branches and the main stem, and, at least in the mature stem portions, there was no consistent change in LSCs along the length of the shoot. This is in sharp contrast to published results for coniferous and dicotyledonous trees \((11, 12, 27, 28)\), in which LSCs were many times greater in the main stem as in the lateral branches. This is also in contrast to results by Salleso *et al.* \((19)\), who found much higher LSCs near the base than the tip of stems of the liana *Vitis vinifera*. However, we did not measure LSCs on very young stem segments bearing the youngest leaves, as did Salleso *et al.* \((19)\).

Salleo *et al.* measured \(E\) indoors with a potometer and used Equation 2 to predict \(dp/dx\) in *Vitis vinifera*: from 0.01 MPa \(\text{m}^{-2}\) near the base of 1-year-old stems to 6.5 MPa \(\text{m}^{-2}\) near the apical nodes \((19)\). The \(dp/dx\) we found for stems of *B. fassoglensis*, of about 0.08 MPa \(\text{m}^{-2}\), were much less steep than has been reported for small herbaceous plants \((3, 14)\), but similar to those found in coniferous trees \((14)\).

The stems of *B. fassoglensis* are efficient in the sense that

**Figure 2.** Transpiration \((E = \text{abaxial + adaxial})\) and stomatal conductance \((g_s, \text{for abaxial only})\) on the four shoots used for bagged leaf experiments. Standard error bars are shown when they were greater than the size of the symbols. \(E\) was integrated over the 1.5 h period prior to measuring water potential in the bagged leaves. The arrow at the top indicates dawn.

**Figure 3.** Measured hydraulic conductance per unit length \((\text{measured } K_s)\) in isolated stem segments versus the leaf area that was distal to the stem segments. Results are from four shoots. Each point represents a single stem segment. The solid points represent branch junctions, which were excluded from calculations of the regression line. See Table I.

**typical midday \(E\) value \((7 \times 10^{-8} \text{ m}^2 \text{s}^{-1})\) was about 0.2 MPa (Fig. 5).**

**Measured \(\Psi\) Drop from Stem to Leaf**

At predawn (about 0630 h), there was no statistically significant difference in the mean \(\Psi\) of bagged leaves and adjacent unbagged controls (Table II). This indicates no detectable \(\Psi\) drop from the stem to the leaf.

In contrast, at midday the unbagged (transpiring) leaves had \(\Psi\)s that were significantly lower \((P = 0.001)\) than the adjacent bagged leaves. This indicated a drop in \(\Psi\) of about 0.27 MPa in going from the stem to the leaf xylem (Table II).
Table I. Summary of Regression Analysis for Several Parameters

<table>
<thead>
<tr>
<th>X</th>
<th>Y</th>
<th>Y-intercept</th>
<th>Slope</th>
<th>n</th>
<th>r</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf area</td>
<td>Measured Kn</td>
<td>1.13</td>
<td>1.13</td>
<td>33</td>
<td>0.96</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Measured Kn</td>
<td>Predicted Kn</td>
<td>0.750</td>
<td>1.58</td>
<td>22</td>
<td>0.88</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Measured Kx</td>
<td>Max vessel diameter</td>
<td>238</td>
<td>27.3</td>
<td>22</td>
<td>0.79</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Measured Kx</td>
<td>Mean vessel diameter</td>
<td>46.5</td>
<td>4.53</td>
<td>22</td>
<td>0.72</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Measured Kx</td>
<td>No. of vessels</td>
<td>293</td>
<td>29.2</td>
<td>22</td>
<td>0.43</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Stem xylem diameter</td>
<td>Measured Kx</td>
<td>-2.38</td>
<td>0.91</td>
<td>23</td>
<td>0.42</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Stem xylem diameter</td>
<td>LSC</td>
<td>13.3</td>
<td>-0.49</td>
<td>23</td>
<td>-0.11</td>
<td>NS*</td>
</tr>
</tbody>
</table>

*Not significant at the 0.05 level of probability.

Figure 4. Leaf-specific conductivity (LSC in $10^{-7}$ m$^2$ MPa$^{-1}$ s$^{-1}$) for a shoot of *B. fassoglensis*. Leaves were abscised from all but the distal parts of the shoot system. Note low LSCs at branch junctions (arrows). See predicted pressure gradients for this shoot in Figure 5.

the relatively narrow stem segments we sampled, from 3 to 6 mm in xylem diameter ($\bar{x} = 4.6$ mm, se = 0.88), had nearly identical midday dp/dxs as 30 to 50 mm diameter stems of *Thuja occidentalis*, which are reported to have measured and theoretical dp/dxs of about 0.07 MPa m$^{-1}$ (27). Using the data of Tyree et al. (27), 4.6 mm diameter stems of *T. occidentalis* would have midday dp/dxs that were 4.3 times steeper than the *B. fassoglensis* stems (0.34 MPa m$^{-1}$ versus 0.08 MPa m$^{-1}$). We assume that this is due to the fact that the tracheids of *Thuja* are much narrower and have greater resistance than do the vessels of *B. fassoglensis*.

There is surprisingly little information on stem dp/dxs in dicotyledonous trees, mostly due to the difficulty of making these measurements. Zimmerman (28) reported a theoretical dp/dx of about 0.02 MPa m$^{-1}$ in the trunks of many dicotyledonous trees, but much greater values in lateral branches.
Table III. Measured and Predicted Stem Xylem Pressure Gradients

Measured gradients were determined from the bagged leaf method, predicted gradients were calculated from transpiration rate/leaf-specific conductivity. Results were averaged for three predawn and four midday experiments each on an unbranched stem. At predawn, negative numbers could occur due to the 0.01 MPa m⁻¹ gravity gradient since proximal leaves were in some cases slightly elevated above the distal ones.

<table>
<thead>
<tr>
<th></th>
<th>Predawn</th>
<th>Midday</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R ± SE</td>
<td>(range)</td>
</tr>
<tr>
<td>Measured</td>
<td>0.006 ± 0.004</td>
<td>0.004–0.008</td>
</tr>
<tr>
<td>Predicted</td>
<td>0.0003 ± 0.002</td>
<td>–0.001–0.004</td>
</tr>
</tbody>
</table>

Figure 6. Predicted versus measured hydraulic conductance per unit length ($K_h$). Predicted $K_h$ is based upon Poiseuille's law for ideal capillaries. Each point represents one stem segment, the solid symbols are for branch junctions. The dotted line shows when predicted $K_h = \text{measured } K_h$. See Table I.

Scholander et al. (20) reported $dp/dx$s in stems of the temperate liana Vitis labrusca, but his monometer method gave accurate results only at positive stem $\Psi$s, such as occurred often at night and in the spring before the new leaves matured. Under these nontranspiring circumstances, they found a $dp/dx$ equal to that of the gravity gradient, that is, 0.01 MPa m⁻¹. They reported maximum positive stem $\Psi$s of 0.48 MPa at the base of the stems in April before leaf expansion. Similarly, Sperry et al. (25) reported positive stem $\Psi$ measurements of up to 0.1 MPa in this species. For B. fassoglensis we have found predawn maximum positive stem $\Psi$s of 0.005 MPa, but this was only after periods of heavy rains (FW Ewers, JB Fisher, unpublished data).

The results of the present report suggest that for B. fassoglensis, the resistance to water flow by the xylem transport system is an important, potentially limiting factor in the water relations. At midday, the drop in $\Psi$ appears to be about 0.08 MPa m⁻¹ along stems and branches, about 0.20 MPa at branch junctions, and about 0.27 MPa in going from the stem to the leaf xylem. The resistance to water flow may become particularly important in long stems, such as the one modeled in Figures 4 and 5.

The values for $E$, $g_s$, and leaf $\Psi$ for B. fassoglensis were within the range of results previously reported for temperate (1, 23) and tropical vines (10). The maximum $E$ values in Figure 1 were much greater than in Figure 2. Neither old (yellow) nor shade leaves were used in the diurnal measurements. In the bagged leaf experiments (Fig. 2), greater efforts were made to ensure that representative leaves (young, old, sun, shade) were sampled for $E$ throughout the entire shoot system. In addition, the sampled stems in the complete diurnal study were shorter and were exposed to more recent precipitation than those for the bagged leaf experiment. The short stems should have reduced the dynamic water stress, and the recent precipitation could have minimized the static water stress and maximized water storage, leading to high $E$ in the complete diurnal study (Fig. 1). With these high $E$ values, the predicted stem $dp/dx$s would be almost twice as steep as any shown in Figure 5.

The major deficiency of Equation 2 is that it does not take into account water moving into and out of storage along the shoot. This may be one reason that in some cases the measured $dp/dx$ was greater than, and, in other cases, less than the predicted $dp/dx$ (Table III). In addition, Equation 2 would not account for situations, such as occurs in Vitis vinifera, where $K_h$ changes on a diurnal basis (22).

There are at least three limitations to the bagged leaf method for measuring stem $dp/dx$s. First, the method is destructive; a particular leaf can be used only once. Second, the $\Psi$ can be determined only at those points along the stem that bear leaves. Third, the bagged leaves themselves have a certain capacitance and resistance; they will never behave as perfect monometers, but will instead lag behind the changing stem $\Psi$. The stem hygrometer method (7) may prove to be better for measuring stem $dp/dx$s, but this method is difficult to apply in the field.

Beger (2) reported that vessels of the lianas Atragene alpina, Vitis vinifera, and Aristolochia sipho were 100% efficient in the sense that the measured $K_h$ was 100% of the predicted $K_s$. Berger's studies have never been corroborated, but it has been suggested that since liana vessels are extremely long, they behave more like ideal capillaries than do vessels of other growth forms (29, 30). However, we found nothing unusual about vessels of B. fassoglensis in terms of conformity to Poiseuille's law for ideal capillaries. The measured $K_h$ was, on
average, 49% of the value predicted from Poiseuille's law. This is similar to ratios found in many other vascular plants (4, 13, 21, 30).

A number of factors could result in the measured $K_a$ being less than the predicted $K_a$. Since vessels are of finite length, water must pass through pits to move from one vessel to the next. In addition, various factors, such as irregularities in the vessel wall, tapering of vessels, and perforation plates could result in localized turbulent flow, decreasing transport efficiency. A vessel does not always move in a straight line down a stem, thus the actual length of the transport pathway may be greater than the stem length. Finally, some of the vessels we recorded as conductive may have been stained from lateral spread of the safranin.

To summarize, stems of the liana *B. fassoglensis* are similar in conductive efficiency to stems of other large woody plants, and the xylem vessels conform to Poiseuille's law in a manner similar to most vascular plants where this has been tested. As in other large woody plants, the efficiency of the xylem transport system could be an important factor limiting growth and development. The liana stems are unusual in the sense that even very narrow stems of this species are similarly efficient as much wider stems of trees. This is probably due to the wide vessels in the liana.

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LITERATURE CITED