Plant, Cell and Environment (1992) **15**, 471–477

Hydraulic architecture of sugarcane in relation to patterns of water use during plant development*

F. C. MEINZER,[1] G. GOLDSTEIN,[1,†] H. S. NEUFELD,[1,‡] D. A. GRANTZ[2,§] & G. M. CRISOSTO[1,*]

[1] *Experiment Station, Hawaiian Sugar Planters' Association, P.O. Box 1057, Aiea, and* [2] *USDA/ARS, Experiment Station, HSPA, P.O. Box 1057, Aiea, HI 96701, USA*

ABSTRACT

Hydraulic conductance was measured on leaf and stem segments excised from sugarcane plants at different stages of development. Maximum transpiration rates and leaf water potential (Ψ_L) associated with maximum transpiration were also measured in intact plants as a function of plant size. Leaf specific hydraulic conductivity (L_{sc}) and transpiration on a unit leaf area basis (E) were maximal in plants with approximately 0·2 m^2 leaf area and decreased with increasing plant size. These changes in E and L_{sc} were nearly parallel, which prevented Ψ_L in larger plants from decreasing to levels associated with substantial loss in xylem conductivity caused by embolism formation. Coordination of changes in E and leaf hydraulic properties was not mediated by declining leaf water status, since Ψ_L increased with plant size. Hydraulic constrictions were present at nodes and in the node-leaf sheath-leaf blade pathway. This pattern of constrictions is in accord with the idea of plant segmentation into regions differing in water transport efficiency and would tend to confine embolisms to the relatively expendable leaves at terminal positions in the pathway, thereby preserving water transport through the stem.

Key-words: Saccharum spp.; sugarcane; hydraulic conductivity; xylem cavitation; transpiration; stomata.

Symbols and abbreviations: A, leaf surface area; E, transpiration per unit leaf area; L, hydraulic conductance; L_{sc}, leaf specific conductivity; TVD, top visible dewlap; Ψ, water potential.

INTRODUCTION

The intrinsic or absolute efficiency of xylem water transport through a plant segment is often expressed as the hydraulic conductance (L) per unit segment length

$$L = q/(\Delta P/\Delta x) \qquad (1)$$

where q is the rate of water flow through the segment and $\Delta P/\Delta x$ is the pressure gradient driving the flow. Recently, the hydraulic architecture of a number of woody species has been characterized from the standpoint of the relative rather than the absolute efficiency of the xylem in supplying water to different parts of the plant (Tyree *et al.* 1983; Ewers & Zimmermann 1984a,b; Ewers, Fisher & Chiu 1989). A commonly used measure of this relative efficiency of water transport is the leaf specific conductivity (P_{sc}), which is defined as L divided by the leaf area (A) distal to the segment, i.e.

$$L_{sc} = L/A. \qquad (2)$$

L_{sc} can be used to determine the magnitude of the *in situ* pressure gradient generated along a segment in supplying its attached leaves with water because

$$\Delta P/\Delta x = E/L_{sc} \qquad (3)$$

where E is the prevailing transpiration rate on a unit leaf area basis. Thus, L_{sc} and E provide additional information needed to interpret the functional significance of differences in intrinsic xylem properties (e.g. L) within individual plants or among species. That is, at a given E, a segment with a larger L_{sc} value will always experience a smaller pressure gradient than a segment with a smaller L_{sc} value. This comparison cannot be made directly using only L because the pressure gradient depends on both E and the total leaf area supplied by the segment.

Studies of transpiration and xylem pressure gradients in relation to hydraulic architecture assume additional significance in the context of the vulnerability of xylem to loss in conductivity through cavitation and embolism formation (Tyree & Sperry 1989). Considerable variation among species has been reported in the magnitude of xylem tension at which substantial cavitation- and embolism-induced loss in conductivity begins to occur (Tyree & Dixon 1986; Sperry, Tyree &

---

[*] Published as Paper No. 754 in the journal series of the Experiment Station, HSPA.

[†] Present address: Botany Department, University of Hawaii, Honolulu, HI 96822, USA.

[‡] Present address: Biology Department, Appalachian State University, Boone, NC 28608, USA.

[§] Present address: University of California, Kearney Agricultural Center, Parlier, CA 93648, USA.

Correspondence: Frederick Meinzer, Hawaiian Sugar Planters' Association, P.O. Box 1057, Aiea, HI 96701, USA.

Donnelly 1988). The magnitude of xylem sap tension developed at a particular location in a plant is a function of the xylem water flux, the soil water potential and the sum of the resistances in the flow pathway to that point. It has recently been suggested that stomatal regulation of transpiration in many species results in operational levels of xylem tension just above the point of catastrophic blockage from embolism formation (Tyree & Sperry 1988). However, there is little information available concerning the possible coordination of transpiration with tissue hydraulic properties during plant development.

In growing sugarcane, we have observed that stomatal conductance and total apparent hydraulic conductance of the soil/root/leaf pathway exhibit parallel changes as plant size increases (Meinzer & Grantz 1990). In our previous study, the apparent hydraulic conductance was determined from measurements of transpiration and hydrostatic pressure differences using an Ohm's law analogy. The location and nature of the developmental changes in hydraulic conductance were not determined. Stomatal opening and closing responses following partial defoliation and root pruning, respectively, suggested that the coupling between vapour and liquid phase conductance may have been mediated by a chemical signal originating in the roots. The objectives of the present study were to characterize the developmental course of hydraulic conductances and associated changes in the hydraulic architecture of sugarcane and to determine the relationship between these hydraulic parameters and patterns of regulation of water use and leaf water status during plant development. In contrast with our previous studies, hydraulic properties were assessed by direct measurement of water flow through isolated plant segments subjected to a constant pressure difference. An additional objective was to locate possible hydraulic constrictions where the pressure gradient would abruptly become steeper at high rates of transpirational water movement.

MATERIALS AND METHODS

Plant material

Sugarcane (*Saccharum* spp. hybrid cv H65-7052) plants were grown from stem segments containing lateral buds. In the greenhouse, nodal segments containing single buds were planted in 11 dm^3 soil-filled pots and irrigated twice daily. Field-grown plants were obtained from well-irrigated commercial sugarcane fields near Waipahu, Oahu, Hawaii. The shoot architecture of sugarcane consists of a single, erect stem with alternate, widely spaced, erect leaves. Leaf blades are typically 100–200 cm long and 2–8 cm wide. Internodes may be up to 25 cm long. The reference point for enumerating node and internode position was the node at which the top visible dewlap (TVD) leaf is attached. This was designated as node zero and additional nodes were numbered consecutively down the stalk. The TVD leaf is the youngest non-elongating leaf whose blade is fully exposed and not enclosed in the sheaths of older leaves. The area of the leaf blade attached to each node was measured with an area meter (Delta-T Devices Ltd, Cambridge, UK).

Hydraulic conductance

Leaf segments for conductance measurements were obtained by excising entire TVD leaf blades from field- and greenhouse-grown plants at the junction between the blade and sheath. The remaining leaf blades were excised for measurement of total leaf area per plant. The bases of the TVD leaf blades were recut under water and the leaves were transported to the laboratory. In the laboratory, the middle portion of the leaf was submerged in a 10 mol m^{-3} oxalic acid solution while a 20-cm section was excised midway between the base and tip of the blade. Previous measurements using a compressed air technique (Ewers & Fisher 1989) indicated that 20 cm was roughly 2·5 times the average maximum xylem vessel length. A 0·75 × 7 cm segment of lamina was then excised from the midpoint of the section, midway between the midrib and leaf margin with a sharp razor blade. This leaf segment remained submerged in the oxalic acid solution while it was inserted into a slit in a rubber stopper and connected to the hydraulic conductivity apparatus. Flow induced by a 0·0125 MPa gravitational pressure difference was measured over two successive 3-min intervals. The segments were then flushed by applying a regulated pressure of 0·1 MPa for 2 min. After flushing, the segments were again subjected to the 0·0125 MPa gravitational pressure difference and the conductance was measured as before. Conductance before flushing was usually within 10% of conductance determined after flushing.

Stem segments were obtained by first removing all of the leaves from a stalk then excising the stalk near the soil surface. The leaves were saved for measurement of the total area and area associated with each node. In the laboratory, the desired internode or nodal segments were obtained by cutting the stalk under water. The length of the internode segments used was approximately 7–10 cm and was determined by the total internode length. Nodal segments were approximately 8–10 cm long and an effort was made to maintain a constant ratio of internode to node tissue in each nodal segment used. Conductance measurements were made as described for leaf segments except that rapid flow rates through stems permitted time intervals of 1 min to be used.

Hydraulic conductance (L, mmol s^{-1} m MPa^{-1}) was calculated from the flow rate (mmol s^{-1}) of a degassed, filtered 10 mol m^{-3} oxalic acid solution through leaf and stem segments, divided by the gravitational pressure gradient (MPa m^{-1}) along the segments (Eqn 1). These measurements were made with an apparatus similar to

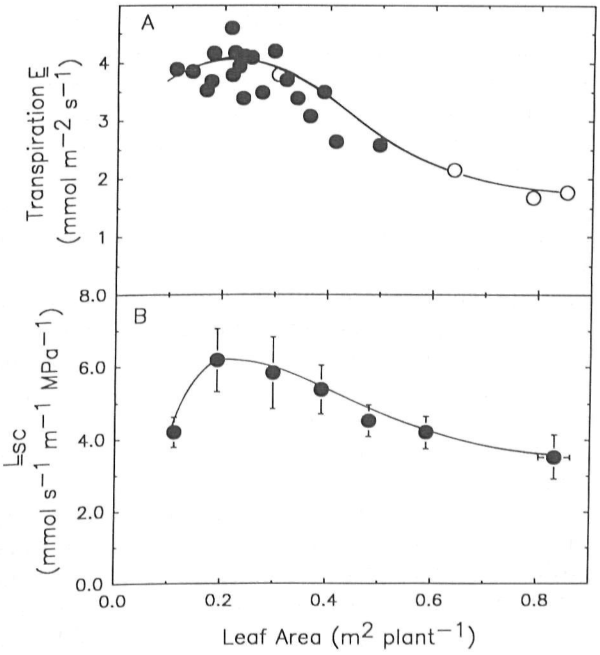

Figure 1. (A) Average transpiration rate per unit leaf area in relation to plant size for sugarcane growing in the field (○) and in the greenhouse (●). (B) L_{sc} of the uppermost fully expanded (TVD) leaf in relation to plant size. L_{sc}s and corresponding leaf areas represent averages over 0·1 m² ranges of leaf area. Vertical and horizontal bars indicate SEs (n = 5–11).

that described by Sperry, Donnelly & Tyree (1988). The apparatus was configured to accommodate six samples. Flow rates were expressed as mmol s^{-1} for comparison with conventional units used for transpiration. This facilitated calculation of *in situ* pressure gradients using leaf specific conductivity (L_{sc}) and transpiration measurements. L_{sc} of stem segments was calculated from L and the total leaf area above the segment according to Eqn 2. L_{sc} of TVD leaves was computed from L of leaf segments according to Eqn 2 in which A was the area of the leaf from which the segment was obtained, and L was multiplied by the ratio of total leaf width (excluding the midrib) to the segment width.

Determination of vulnerability of leaf xylem to cavitation and embolism formation is described in detail elsewhere (Neufeld *et al.* 1991). Briefly, leaf blades were excised at the ligule and allowed to dehydrate in the laboratory for varying periods of time. A 20-cm segment was excised approximately 30 cm from the leaf tip for determination of leaf water potential (Ψ_L) with a pressure chamber (Saliendra, Meinzer & Grantz 1990). The rest of the leaf was then submerged in the oxalic acid solution where a second 20-cm segment was cut at a distance greater than 20 cm from either cut end. Hydraulic conductivity was measured in 0·75 × 7 cm segments excised from this segment as described above. The per cent loss in conductivity corresponding to a given Ψ_L was determined from the ratio of conductivity before flushing to that after flushing for 2 min at a pressure of 0·1 MPa to remove embolisms.

Transpiration and Ψ gradients

Transpiration of greenhouse-grown plants was measured gravimetrically and scaled to a unit leaf area basis. The pots were sealed in plastic bags during measurements and weighed frequently. Weights were recorded to the nearest 0·1 g and time intervals to the nearest second. Canopy transpiration of field-grown plants was determined as evaporative heat flux with the Bowen ratio technique and was scaled to a unit leaf area basis using the leaf area index as described previously (Meinzer & Grantz 1989, 1990).

Water potential of segments of the TVD leaf blade excised approximately 1 m from the ligule was measured with a pressure chamber on clear days between 1000 and 1400 h when E was maximal. In greenhouse-grown plants, stem water potential at the soil surface was estimated from the water potential of a covered, non-transpiring leaf attached to the stem near the origin of the crown roots (Saliendra & Meinzer 1989). Since Ψ_{soil} for these well-irrigated plants was near zero, the Ψ_{stem} at this point also represents an estimate of the difference in Ψ across the entire root system.

RESULTS

E decreased with increasing plant size above approximately 0·2 m² total leaf area (Fig. 1A). Therefore, transpiration on an entire plant basis did not increase linearly with increasing leaf area; it tended to saturate above about 0·3 m² leaf area per plant after exhibiting an initial rapid increase (data not shown). This pattern was not caused by self shading because transpiration behaved similarly in field-grown plants and in isolated, well-illuminated greenhouse-grown plants. Furthermore, the shoot architecture of sugarcane would minimize self-shading.

The L_{sc} of the uppermost fully expanded leaf exhibited a plant size dependence similar to that of E and was maximal in plants with approximately 0·2 m² leaf area (Fig. 1B). The magnitudes of L_{sc} and E given in Fig. 1 suggested that substantial gradients in Ψ should develop along sugarcane leaves at maximal transpiration rates. The predicted gradient (E/L_{sc}, Eqn 3) varied from 0·67 MPa m^{-1} in plants with 0·2 m² leaf area to 0·47 MPa m^{-1} in plants with 0·83 m² leaf area (Fig. 2A; solid symbols). This gradient would have remained constant with increasing plant size if L_{sc} and E had varied with plant size in a precisely parallel fashion (Fig. 1). If stomatal regulation were such that E remained constant at its maximum value of 4 mmol m^{-2} s^{-1} with increasing plant size, while L_{sc} continued to exhibit the pattern shown in Fig. 1, the predicted gradient in Ψ along the TVD leaf would have increased to 1·2 MPa m^{-1} in plants with 0·83 m² leaf area (Fig. 2A; open symbols).

Actual measurements of Ψ_L at maximum transpiration rates in TVD leaves of greenhouse- and field-grown plants indicated a tendency for Ψ_L to increase

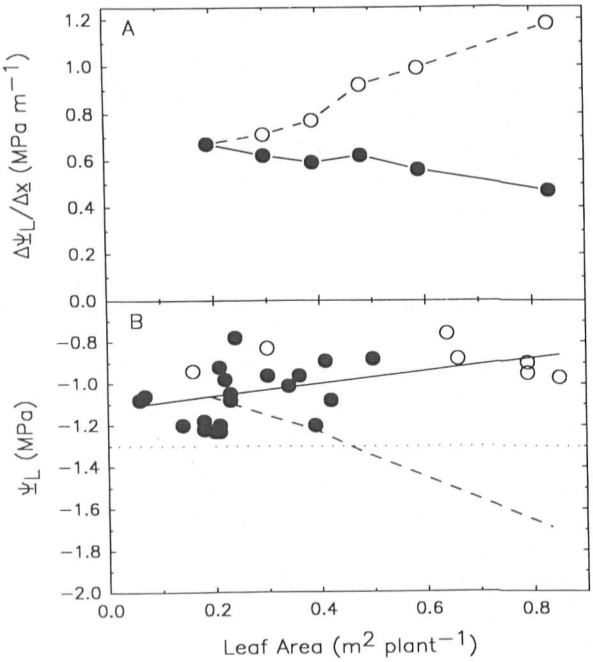

Figure 2. (A) Relationship between plant size and predicted gradient in water potential ($\Delta\Psi_l/\Delta x$) along the TVD leaf at maximum transpiration rate. Water potential gradients were calculated from data presented in Fig. 1 using either the observed relationship between leaf area, L_{sc} and transpiration (●), or assuming that transpiration remained constant at its maximum value (4 mmol m^{-2} s^{-1}) with increasing leaf area (○). (B) Average minimum leaf water potential of well-irrigated, greenhouse- (●) and field-grown (○) sugarcane in relation to plant size. The dashed line represents the predicted minimum water potential if maximum transpiration remained constant instead of decreasing with plant size as shown in Fig. 1. The dotted line indicates the water potential corresponding to 50% loss in hydraulic conductance from cavitation and embolism formation.

with increasing plant size (Fig. 2B, solid line). This was in agreement with the predicted decrease in the Ψ gradient along these leaves with increasing plant size (cf. Fig. 2A; solid symbols). If E had remained constant while L_{sc} decreased (cf. Fig. 2A; open symbols), Ψ_L would have decreased with increasing plant size (Fig. 2B, dashed line). Under these conditions, Ψ_L in plants with approximately 0·45 m^2 leaf area would have dropped below the −1·3 MPa threshold corresponding to 50% loss in hydraulic conductivity from cavitation and embolism formation (Fig. 2B; dotted line).

Analysis of the trend in L_{sc} along the flow pathway within the stem and from the stem to the leaf blade revealed hydraulic constrictions at nodes and in the leaf sheath and blade (Fig. 3). L_{sc} of internode segments was approximately an order of magnitude higher than that of adjacent nodal segments. L_{sc} dropped by an additional order of magnitude along the leaf sheath and blade. Thus, L_{sc} lower in more distal portions of the hydraulic pathway of individual leaves.

L of younger internodes near the top of the plant was higher than that of older internodes near the soil surface (Fig. 4A). L of nodal segments was considerably lower than that of internodes, and in contrast to internodes, tended to decrease with increasing distance from the soil surface. When hydraulic properties were expressed on the basis of leaf area supplied (L_{sc}), internode conductivity increased even more with height above the ground, while nodal conductivity remained constant or increased slightly. These patterns caused the predicted gradient in Ψ_{stem} in a rapidly transpiring sugarcane plant to decline substantially with increasing height above the ground (Fig. 5). The small magnitude of the stem Ψ gradient in comparison with the leaf Ψ gradient (Fig. 2A) was attributable to the large hydraulic capacity of the internodes (Fig. 4).

L_{sc}s of stem, node/leaf sheath, and leaf blade segments were used with maximum transpiration rates measured in intact plants to calculate Ψ at different points along the stem/leaf pathway (Fig. 6). Using a reference value of stem Ψ near the soil surface, obtained from the Ψ of a basal, covered, non-transpiring leaf, the predicted value of TVD leaf Ψ was in close agreement with measured values. Over 90% of the total drop in Ψ,

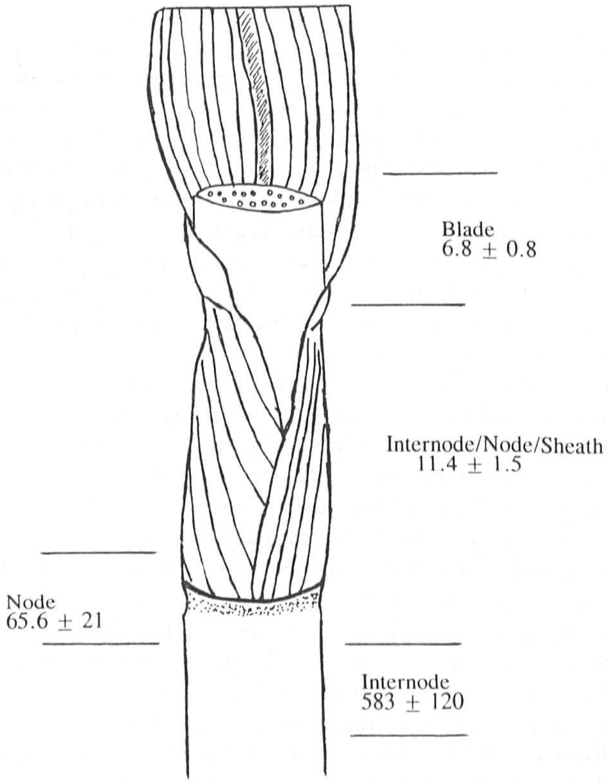

Figure 3. Diagram showing L_{sc} (±SE; n = 4) below and above the third node of a sugarcane plant. L_{sc}s for the internode and internode/node/internode are based on total leaf area above the third internode. L_{sc}s for internode/node/sheath and blade are based on the area of the leaf attached to the node. Values are in mmol s^{-1} m^{-1} MPa^{-1}.

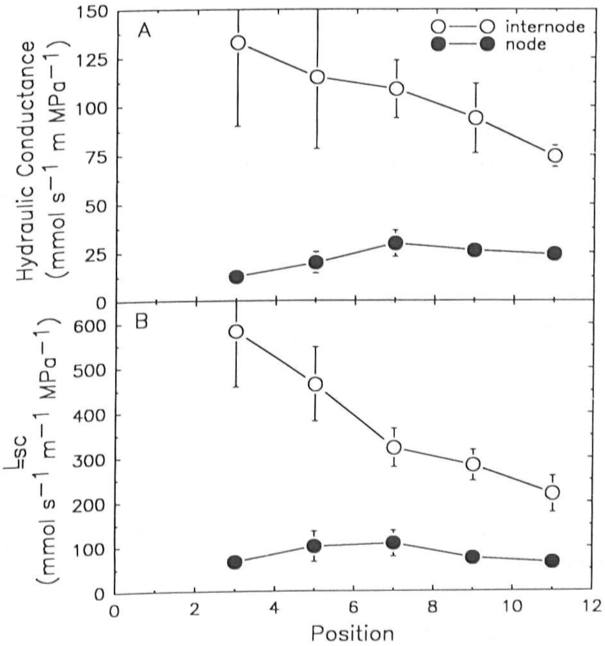

Figure 4. Hydraulic conductance and L_{sc} of node and internode segments in relation to their position along the stem. Total leaf area distal to a given node or internode was used for L_{sc} computations.

from the soil surface along a 2·4 m hydraulic pathway to a point 1 m along the TVD leaf, occurred within the leaf itself.

DISCUSSION

E and L_{sc} exhibit parallel changes with increasing leaf area in growing sugarcane. L_{sc} was measured by applying a hydrostatic pressure to excised leaf segments, and presumably represents a fixed physical property of the leaf vasculature. Transpiration, on the other hand, was measured in entire intact plants and reflects a dynamic physiological response of the stomata to changes associated with increases in plant size (Meinzer & Grantz 1990). This coordination of stomatal regulation of transpiration with leaf hydraulic properties during development prevents Ψ_L of well-irrigated plants from falling below the point at which xylem conductivity declines due to cavitation and embolism formation. Average minimum Ψ_L ranged from approximately −1·1 MPa in plants with 0·1 m^2 leaf area to −0·9 MPa in plants with 0·8 m^2 leaf area. The first detectable embolism-induced loss in *L* in the cultivar studied occurred at a Ψ_L of about −1·0 to −1·1 MPa, which increased to a 50% loss in conductivity at a Ψ_L of about −1·3 MPa, though subtantial genotypic variation in the vulnerability of sugarcane leaf xylem to cavitation exists (Neufeld *et al.* 1991).

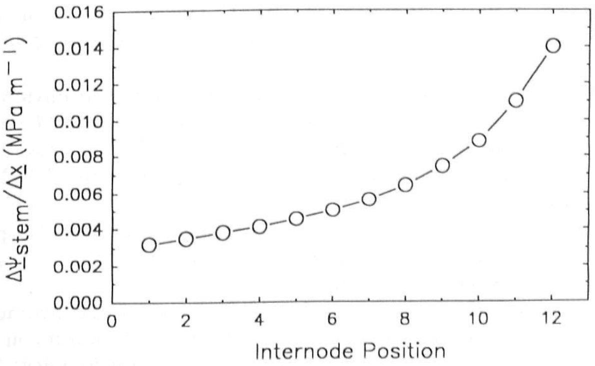

Figure 5. Predicted gradient in water potential ($\Delta\Psi_{stem}/\Delta x$) along internodes as a function of their position below the node of TVD leaf attachment. Gradients were calculated from conductivity measurements for five plants with an average leaf area of 0·68 m^2 and an average transpiration rate of 2·09 mmol m^{-2} s^{-1} (Fig. 1).

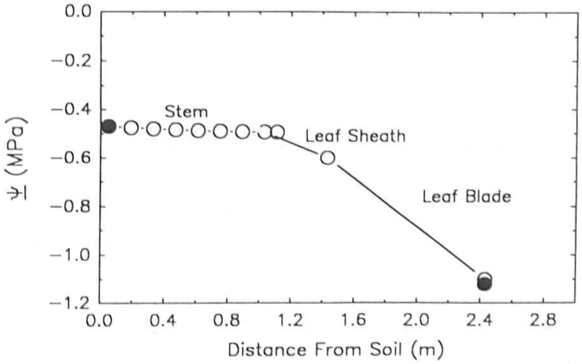

Figure 6. Predicted (○) and measured (●) water potential in greenhouse-grown sugarcane plants as a function of height above the soil surface. Average maximum transpiration rates of five plants ranging in leaf area from 0·18 to 0·23 m^2 were used with appropriate L_{sc}s of stem, node/leaf sheath and leaf blade segments to obtain predicted values of water potential.

It has been proposed that a principal consequence of stomatal limitation of transpiration in droughted plants is the avoidance of catastrophic xylem dysfunction resulting from runaway embolism formation (Tyree & Sperry 1988). Our results indicate that even in well-irrigated sugarcane plants, stomata permit Ψ_L to fall to levels slightly above those associated with substantial loss in *L* caused by embolism formation. L_{sc} and stomatal regulation of gas exchange were coordinated with changes in leaf area, root system size and the relative efficiency of the roots in supplying the leaves with water during normal development independent of soil water supply. These dynamic changes in stomatal regulation of transpiration and in leaf hydraulic properties must be taken into account in the interpretation of patterns of water use and hydraulic architecture of plants at different stages of development.

The results obtained here indicate that approximately one-half of the total hydraulic resistance of the soil/root/

leaf pathway was located in the soil and roots (Fig. 6). This is in agreement with the findings of Saliendra & Meinzer (1989), who used transpiration rates and *in situ* measurements of Ψ in plants of the same cultivar used in the present study to partition total hydraulic resistance into a shoot and a soil/root component. In a contrasting sugarcane cultivar (Saliendra & Meinzer 1989), total shoot hydraulic resistance was similar, but the soil/root resistance comprised only 28% of the total resistance.

The pattern of decreasing L_{sc} along the internode/node/leaf sheath/leaf blade pathway (Fig. 3) supports the idea of plant segmentation into regions differing in water transport efficiency and susceptibility of xylem to cavitation (Zimmermann 1983). Hydraulic constrictions at nodes and in petioles of other species (Begg & Turner 1970; Sperry 1986) result in abrupt decreases in the magnitude of the xylem pressure potential at these points. This would tend to confine cavitation and embolism formation to the relatively expendable leaves and conserve water transport through the stem which is critical for survival of meristematic zones.

The acropetal increase in L_{sc} of sugarcane stem internodes (Fig. 4) contrasts with the pattern observed in several woody species in which L_{sc} has been reported to decrease acropetally along the trunk and branches (Ewers & Zimmerman 1984a,b; Salleo, Rosso & Lo Gullo 1982). These contrasting patterns of hydraulic architecture reflect differences in shoot architecture and growth habit between sugarcane and dicotyledonous woody species. Sugarcane grows indeterminately, without branching. As stem elongation proceeds, a maximum leaf area is attained, which is maintained by a balance between leaf production and leaf shedding. Thus, as the distance between the soil and the transpiring portion of the plant increases, acropetally increasing internode conductivity would partially offset the expected decline in total stem conductivity associated with increasing stem length. This would cause the Ψ gradient along the stem to decrease with increasing distance from the soil (Fig. 5) and allow stem Ψ to remain relatively constant with increasing stem length.

The nature of the signal enabling sugarcane stomata to coordinate transpiration with changes in plant hydraulic properties is uncertain. It is unlikely that the signal is related to leaf water status or other leaf properties. Developmental patterns of stomatal conductance that regulate transpiration as shown in Fig. 1 are determined by changes in the composition of the xylem sap arriving at the leaves rather than by alterations in inherent stomatal properties at the leaf level (Meinzer, Grantz & Smit 1991). It is conceivable that xylem sap composition at sites of leaf vascular development could influence subsequent hydraulic properties of the mature leaf xylem. For example, the phytohormones auxin, cytokinin and gibberellin have been reported to influence vascular differentiation and subsequent characteristics of mature xylem elements (Aloni 1987) and are also constituents of xylem sap (Goodwin, Gollnow & Letham 1978). L_{sc} of the root system in sugarcane also exhibits developmental variation similar to that observed for stomatal conductance, transpiration and L_{sc} of the TVD leaf (Meinzer *et al.* 1991). The signals responsible for coordination of stomatal properties with root and shoot hydraulic properties during development thus appear to originate outside the leaves, probably within the roots and presumably reflect developmental variation in the relative ability of the root system to supply the shoot with water.

During moderate soil drying, Ψ_L in sugarcane remains nearly constant as a result of parallel declines in stomatal and root hydraulic conductance (Saliendra & Meinzer 1989). This may be another manifestation of a root-based signal permitting sugarcane stomata to maintain Ψ_L above levels leading to catastrophic xylem failure. This coordination of gas exchange with physical and physiological changes in hydraulic properties during development merits further study.

ACKNOWLEDGMENTS

This work was funded in part by U.S. Department of Agriculture/Agricultural Research Service cooperative agreement 58-91H-8-143 with the Hawaiian Sugar Planters' Association.

REFERENCES

Aloni R (1987) Differentiation of vascular tissues. *Annual Review of Plant Physiology* **38,** 179–204.

Begg J.E. & Turner N.C. (1970) Water potential gradients in field tobacco. *Plant Physiology* **46,** 343–346.

Ewers F.W. & Fisher J.B. (1989) Techniques for measuring vessel lengths and diameters in stems of woody plants. *American Journal of Botany* **76,** 645–656.

Ewers F.W., Fisher J.B. & Chiu S.-T. (1989) Water transport in the liana *Bauhinia fassoglensis* (fabaceae). *Plant Physiology* **91,** 1625–1631.

Ewers F.W. & Zimmermann M.H. (1984a) The hydraulic architecture of eastern hemlock (*Tsuga canadensis*). *Canadian Journal of Botany* **62,** 940–946.

Ewers F.W. & Zimmermann M.H. (1984b) The hydraulic architecture of balsam fir (*Abies balsamea*). *Physiologia Plantarum* **60,** 453–458.

Goodwin P.B., Gollnow B.I. & Letham D.S. (1978) Phytohormones and growth correlations. In *Phytohormones and Related Compounds — A Comprehensive Treatise*, Vol. II (eds D.S. Letham, P.B. Goodwin & T.J.V. Higgins), pp. 215–249. Elsevier, Amsterdam.

Meinzer F.C. & Grantz D.A. (1989) Stomatal control of transpiration from a developing sugarcane canopy. *Plant, Cell and Environment* **12,** 635–642.

Meinzer F.C. & Grantz D.A. (1990) Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant, Cell and Environment* **13,** 383–388.

Meinzer F.C., Grantz D.A. & Smit B. (1991) Root signals mediate coordination of stomatal and hydraulic conductance in growing sugarcane. *Australian Journal of Plant Physiology* **18,** 329–338.

Neufeld H.S., Grantz D.A., Meinzer F.C., Goldstein G., Crisosto G.M. & Crisosto C. (1992) Genotypic variation in vulnerability of leaf xylem to cavitation in sugarcane. *Plant Physiology*, in press.

Saliendra N.Z. & Meinzer F.C. (1989) Relationship between root/soil hydraulic properties and stomatal behavior in sugarcane. *Australian Journal of Plant Physiology* **16,** 241–250.

Saliendra N.Z., Meinzer F.C. & Grantz D.A. (1990) Water potential in sugarcane measured from leaf segments in a pressure chamber. *Agronomy Journal* **82,** 359–361.

Salleo S., Rosso R. & Lo Gullo M.A. (1982) Hydraulic architecture of *Vitis vinifera* L. and *Populus deltoides* Bartr. 1-year-old twigs: I Hydraulic conductivity (LSC) and water potential gradients. *Giornale Botanico Italiano* **116,** 15–27.

Sperry J.S. (1986) Relationship of xylem embolism to xylem pressure potential, stomatal closure, and shoot morphology in the palm *Raphis excelsa*. *Plant Physiology* **80,** 110–116.

Sperry J.S., Donnelly J.R. & Tyree M.T. (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* **11,** 35–40.

Sperry J.S., Tyree M.T. & Donnelly J.R. (1988) Vulnerability of xylem to embolism in a mangrove vs an inland species of Rhizophoraceae. *Physiologia Plantarum* **74,** 276–283.

Tyree M.T. & Dixon M.A. (1986) Water stress induced cavitation and embolism in some woody plants. *Physiologia Plantarum* **66,** 397–405.

Tyree M.T., Graham M.E.D., Cooper K.E. & Bazos L.J. (1983) The hydraulic architecture of *Thuja occidentalis*. *Canadian Journal of Botany* **61,** 2105–2111.

Tyree M.T. & Sperry J.S. (1988) Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology* **88,** 574–580.

Tyree M.T. & Sperry J.S. (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Molecular Biology* **40,** 19–38.

Zimmermann M.H. (1983) *Xylem Structure and the Ascent of Sap*. Springer-Verlag, Berlin.

Received 17 June 1991; received in revised form 6 September 1991; accepted for publication 10 December 1991