Land Use and Water Resources Research

Hydraulic limits on tree performance: Transpiration, carbon gain and growth of trees*

Melvin T. Tyree

USDA Forest Service, Northeastern Experiment Station, 705 Spear Street, Burlington, Vermont USA 05402
Email: mtyree@fs.fed.us *or* meltyree@aol.com

Abstract

An overview of the relationship between plant gas exchange, the potential hydraulic gradient, the size of the plant and its hydraulic conductance is presented. Key references are used to exemplify arguments of whole-plant optimality and to explain the origin and development of the dominant paradigm for interpreting the nature of water use and growth in plants.

We have learned a great deal about hydraulic architecture of trees over the past 20 years and it is becoming increasingly evident that whole-plant hydraulic resistance or conductance can limit whole-tree performance measured in terms of the rates of transpiration, carbon gain and growth. Plant hydraulic resistance, R_{plant}, is the proportionality constant between evaporative flux density (transpiration), E, from leaves and the water potential difference between the soil, Ψ_{soil}, and leaf, Ψ_L, needed to maintain the evaporative flux density. The relationship comes from a hydraulic model called the soil-plant-atmosphere continuum model and the Cohesion-Tension theory (see Tyree and Zimmermann, 2002), which is given by:

$$\Psi_{soil} - \Psi_L = R_{plant}E = \frac{E}{K_{plant}} \qquad \text{1a)}$$

hence

$$\Psi_L = \Psi_{soil} - R_{plant}E = \Psi_{soil} - \frac{E}{K_{plant}} \qquad \text{(1b)}$$

---

*Paper presented at the 2002 Marcus Wallenberg Prize Symposium in Stockholm, Sweden, on 27 September, 2002. http://www.mwp.org/

Equation (1) can also be expressed in terms of whole plant hydraulic conductance, K_{plant}, which is equal to the inverse of R_{plant}: hence a plant with a high hydraulic conductance has a low hydraulic resistance and I use K_{plant} and R_{plant} interchangeably here. Values of K_{plant} are scaled in Eq. (1) by leaf surface area, i.e. kg water flow per second per m² of leaf surface area per MPa of change in Ψ from soil to leaf. In some cases, however, we may want to scale conductance to dry matter instead of leaf area. In that case we use k_{plant} to indicate the unscaled conductance (kg s⁻¹ MPa⁻¹) and show scaling by leaf area by k_{plant}/A_L and scaling by dry weight by k_{plant}/DW to distinguish the differences.

First of all, a simple graph explains why there should be a theoretical relationship between whole-plant hydraulic resistance and tree performance. Let us first look at some relationships of tree performance at midday (Fig. 1).

Gas exchange through leaves is rate-limited by stomatal conductance, g_s. Stomatal conductance is a function of many factors including Ψ_L; at midday g_s is often suboptimal because of typically low midday values of Ψ_L (Fig. 1A). Net assimilation rate of CO_2 is determined by the internal CO_2 concentration of leaves as determined by the so-called AC_i curve (Fig. 1B). Stomatal conductance determines the slope of the relationship between CO_2 concentration and internal CO_2 concentration, and the intersection between the CO_2 concentration line and the AC_i curve usually gives a sub-
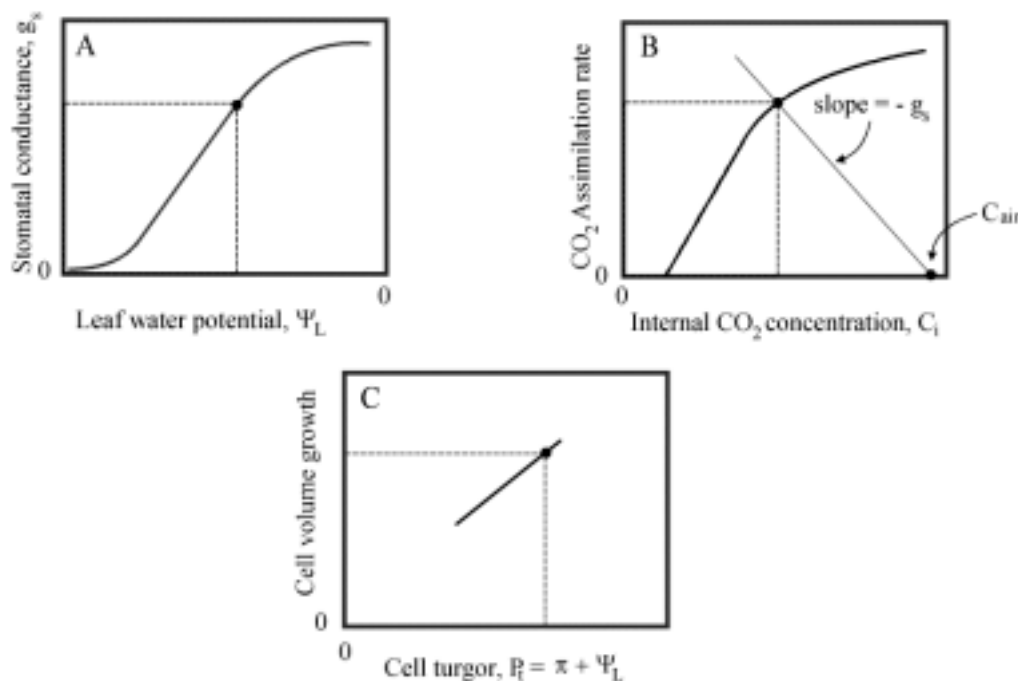
Figure 1.   The dashed lines in the graphs show the normal midday operating conditions of trees. A: The dependence of stomatal conductance, g_s, on leaf water potential, Ψ_L, usually keeps g_s below the potential maximum value. B: The AC_i curve above illustrates how CO_2 assimilation rate depends on internal CO_2 concentration. The value of g_s is slope of the straight line showing how CO_2 concentration declines from outside to inside the leaf. The intersection point with the AC_i curve gives the sub-optimal assimilation rate at midday. C: This graph shows how cell volume growth rate is influenced by cell turgor, P_t, and Ψ_L, where π is the cell osmotic pressure.

optimal value for assimilation rate. Plant growth rate is determined by the rate of carbon gain and the rate of cell volume growth. The latter is mostly due to the rate of water uptake by expanding cells, and this rate is controlled by cell turgor, P_t, which is a function of cell osmotic pressure, π, and Ψ_L as shown in Fig. 1C. Midday values of growth are also usually sub-optimal.

The parameters in Fig. 1 are sub-optimal and Ψ_L is a function of R_{plant}, hence it follows that any change in R_{plant} will also change stomatal conductance, carbon gain and growth rate at midday. Figure 2 illustrates how all the parameters of Fig. (1) will decrease following an increase in R_{plant}, i.e. a decrease in K_{plant}.

Several factors can bring about changes in whole-tree hydraulic conductance (K_{plant}) and hence influence whole-tree performance. These include:

- How tree size influences K_{Plant}
- How xylem dysfunction influences K_{plant}
- How growth conditions with little xylem dysfunction influences K_{plant}
- How genetics within species and between species influences $K_{plant.}$

The purpose of this paper is to review the state of knowledge concerning these factors. I first became aware that shoot hydraulic architecture might limit gas exchange through stomatal regulation when Yang and Tyree (1993) examined how whole shoot conductance and leaf area scaled with shoot basal diameter, D, in *Acer saccharum*. Whole shoot conductance was given by $k_T = 0.06\,D^{1.402}$ and

leaf area $A_L = 4667\,D^{2.007}$. The drop in xylem pressure across the shoot, ΔP_x, should equal EA_L/k_T, hence it follows that

$$\Delta P_x = (7.781 X 10^4\,D^{0.605})E \qquad (2)$$

Hence we have to conclude that as branches grow larger the ΔP_x grows larger too. We can actually turn Eq. (2) into an approximate predictor of leaf water potential because in a wide variety of species root and shoot conductances are approximately equal (Tyree *et al*., 1998, Becker *et al*., 1999), hence the water potential drop across the whole plant will be double that across the shoot. So if the soil is wet and the soil water potential is nearly zero, we have

$$\Psi_{leaf} \cong -2(7.781 X 10^4\,D^{0.605})E \qquad (3)$$

Yang and Tyree (1993) compared predicted values of ΔP_x or Ψ_{leaf} with the response of stomatal conductance to leaf water potential (Fig. 4) and concluded that as *A. saccharum* grows larger the change in Ψ_{leaf} should start limiting stomatal conductance.

Midday leaf water potential, Ψ_{leaf}, of *Acer saccharum* leaves are typically –1.2 to –1.5 MPa in wet soil at the base of Mt Mansfield, Vermont, where the data for Figures 3 and 4 were collected. Clearly Ψ_{leaf} is limiting stomatal conductance. Because Ψ_{leaf} decreases with increasing basal diameter — a proxy for tree size — it seems likely that stomatal conductance will be restricted increasingly as trees grow larger. Although Yang and Tyree (1993) did not go on to compute a theoretical limiting stomatal conductance
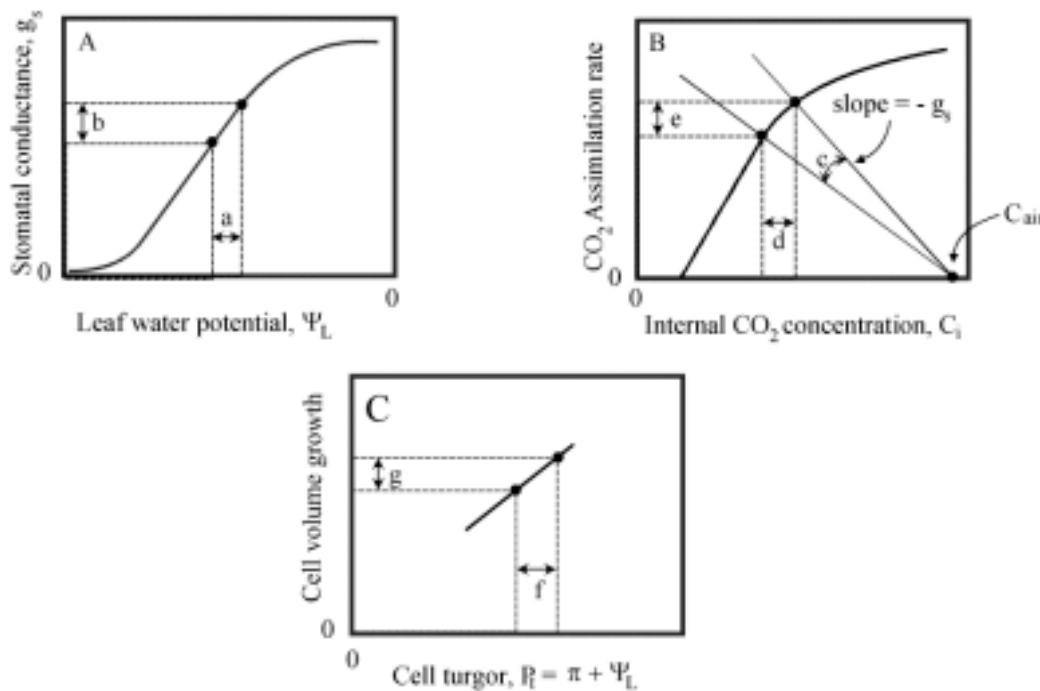
Figure 2 The graphs in Figure 1 are repeated showing how a change in hydraulic resistance causes a change in various parameters given by double-headed arrows: A: An increase R_{Plant} causes a decrease in Ψ_L (a). The decrease in Ψ_L causes a decrease in g_s (b). B: A decrease in g_s causes a decrease in the slope (c) which causes a decrease in C_i (d) and a decrease in assimilate rate (e). C: A decrease in Y_L causes a decrease in turgor of growing cells (f) which causes a decrease in cell volume growth rate (g).
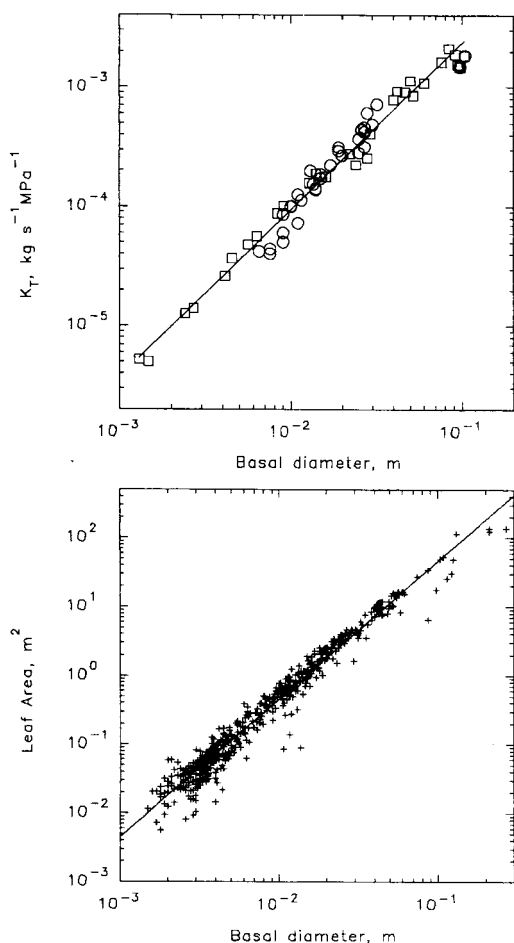

Figure 3
[left]

Upper: Log k_T (whole shoot conductance) versus log D (basal diameter of the wood) of *Acer saccharum* branches. *Lower*: Log A_L (area of leaves attached to a shoot) versus log D. (From Yang and Tyree 1993).
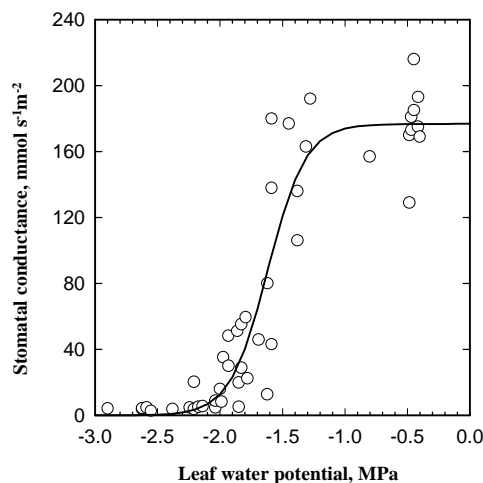

Figure 4 Stomatal conductance of detached *Acer saccharum* leaves versus leaf water potential. The leaves were slowly dehydrated while exposed to saturating light intensity. Each point is a different leaf. The smooth curve is the data fitted to a three-parameter sigmoid curve of the form stomatal conductance = a/(1-exp(b(c-Y)), where a = maximum conductance = 176.8, b = 6.66 and c = water potential at half maximum conductance = -1.616 MPa. (Adapted from Yang and Tyree 1993).

(g_s) versus whole plant conductance (k_{plant}), it can easily be done. The approach is to substitute for E in Eq. (1) the approximate value $= g_s \Delta X$ where ΔX is the appropriate driving force giving a typical midday transpiration rate. A value of g_s is then picked from Fig. 4 and the corresponding Ψ_{leaf} is looked up: you then find the stem diameter that yields the same Ψ_{leaf} in Eq. 1. This D value is then used to compute the whole plant conductance from $k_{plant} = 0.03D^{1.402} = k_T/2$. When this exercise is done for a range of g_s values it produces the results shown in Figure 5 (*upper*). A more typical way of expressing the relationship today is to plot

maximum g_s versus hydraulic conductance per unit leaf area. This relationship is shown in Figure 5 (*lower*).

What is the mechanism connecting the change in g_s and whole plant conductance? One hypothesis is rather indirect. Meinzer *et al.* (1995) suggest that as hydraulic conductance changes during plant development, associated changes in xylem sap composition and concentration are sensed in the leaf and result in corresponding changes in g_s. However, this cannot explain all instances since many people have noted very rapid changes (<15 min) in g_s in response to experimental changes in k_{plant}/A_L (Sperry *et al.* 1993; Saliendra *et al.* 1995; Fuchs and Livingston, 1996). Another explanation is that stomata respond to changes in Ψ_{leaf} caused by changes (short-term or long-term) in k_{plant}/A_L. The link to stomatal response could be a turgor mediated release of abscissic acid (Raschke, 1975).

Two different approaches have been taken to establish a relationship between whole plant hydraulic conductance per unit leaf area, k_{plant}/A_L and stomatal conductance. One way is to induce rapid changes in k_{plant} and look at immediate responses in g_s and carbon assimilation, A. This has been done in *Pinus ponderosa* seedlings, where k_{plant} was rapidly altered by injecting stems with air to induce extra embolism (Hubbard *et al.*, 2001). A strong linear relationship was found between k_{plant}/A_L and g_s and A (Fig. 6). Another way (Sperry, 2000) is to look for correlations between k_{plant}/A_L in
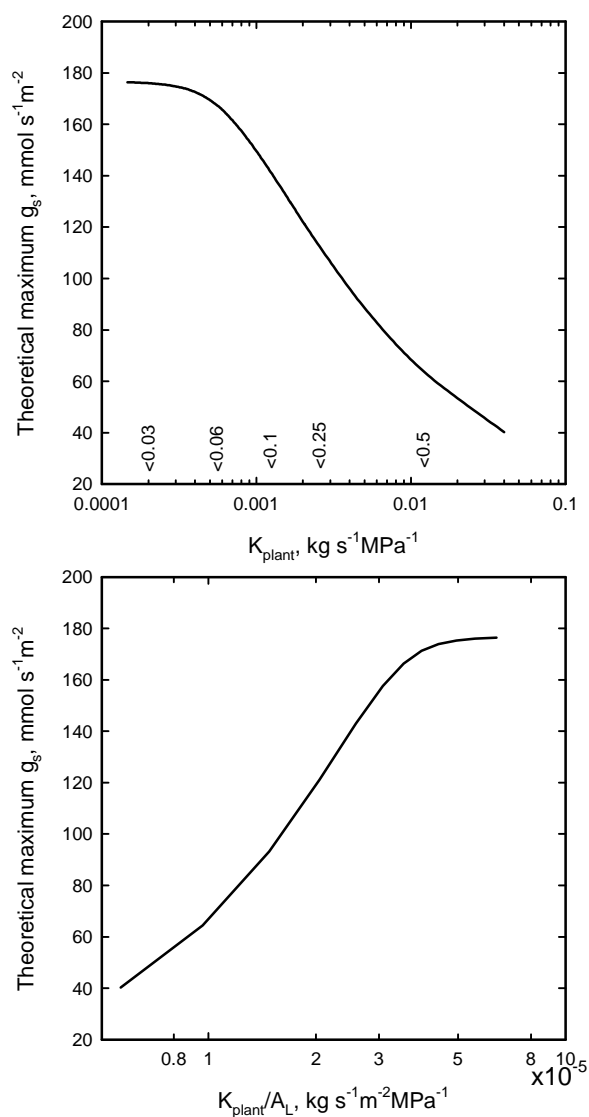

Figure 5   *Upper*: Theoretical relationship between maximum possible stomatal conductance, g_s, and whole plant hydraulic conductance is plotted using the measured relationships for *Acer saccharum* in Figs. 3 and 4. The whole plant conductance values on the x-axis correspond to basal stem diameters of 0.022 to 1.22 m and stem diameters in m corresponding to specific plant conductances are indicated on the x-axis. See text for computational details.
Lower: Theoretical relationship between g_s is plotted versus whole plant conductance per unit leaf area: k_{plant}/A_L.
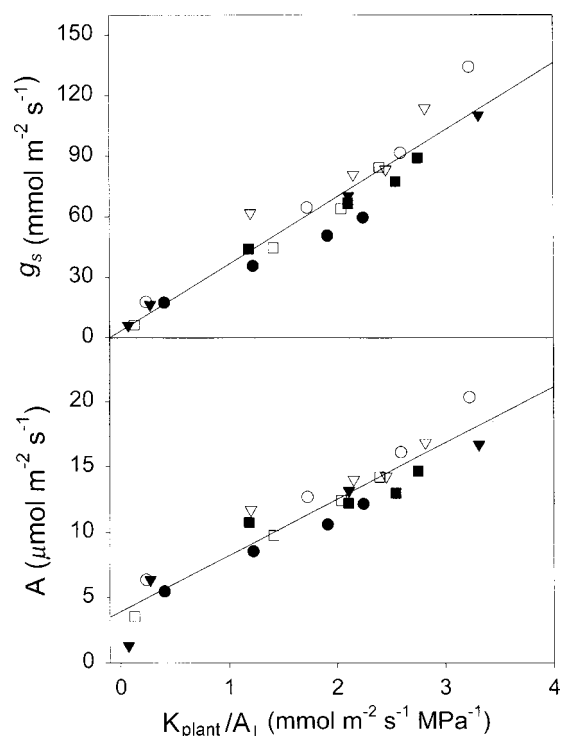
Figure 6   Stomatal conductance (g_s) and assimilation (A) versus whole plant leaf specific conductance (k_{plant}/A_L). The leaf specific conductance of *Pinus ponderosa* seedlings was changed by air injection. Each symbol is for a different seedling (n=6) and multiple points represent multiple air injection pressures. In order to compare conductances here with others in this book note that 1 mmol s^{-1} = 1.8 X 10^{-5} kg s^{-1}. (from Hubbard et al. 2001).
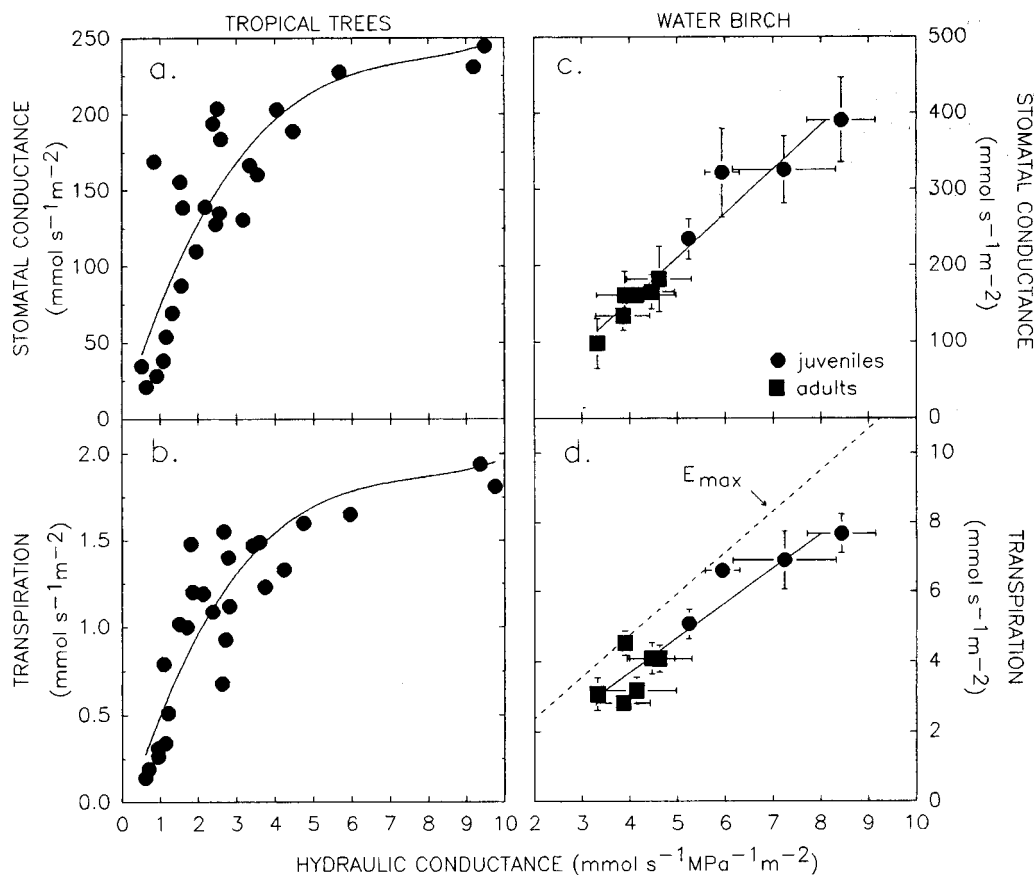
Figure 7   Stomatal conductance (a,c) and transpiration rate (b,d) vs hydraulic conductance from bulk soil to leaf (k_{plant}/A_L). (a,b) Various tropical gap-species (from Meinzer et al. 1995); (c,d) *Betula occidentalis* juveniles and adults (from Saliendra et al. 1995).

the 'native state' and g_s (Fig. 7).

Another useful approach is just to look at whole tree performance under field conditions. Such work has been done by Meinzer *et al.* (1995) and Saliendra *et al.* (1995) and is summarised in Figure 7. Meinzer estimated whole tree conductance from sap flow rates and leaf water potentials and he correlated these to leaf-level measures of stomatal conductance and assimilation rate. Each point on Figures 7a and 7b was measured on a different tree species in the neotropics. Saliendra used a similar approach on *Betula* trees of different age and growing at different distances from a river in Utah.

The quantification of the photosynthetic capacity of the total leaf area of a large branch is extremely difficult and time consuming by conventional gas exchange methods on single leaves. For this reason chlorophyll fluorescence has been employed to determine photosynthetic potential. This works because fluorescence provides information about the reduction state of photosystem II and good relationships have been found between CO_2 assimilation measured by gas exchange and the quantum yield of photosystem II. Brodribb and Field (2000) have used chlorophyll fluorescence to estimate quantum yield on 22 species of woody plants in New Caledonian and Tasmanian rainforests. They found a strong correlation between quantum yield and hydraulic conductance of whole shoots. Since leaf specific whole plant conductance increases the instantaneous gas

exchange (including net assimilation and quantum yield), we might suppose that long term growth rates might also correlate with k_{plant}/A_L and this will be the subject of the next section.

A number of other studies have shown a correlation between stem segment hydraulic conductivity and tree growth rates (Tyree *et al.* 1991; Machado and Tyree 1994), however such studies require that we assume stem segment conductivity is a proxy for whole plant conductance. A great deal has been learned about how drought and frost causes xylem dysfunction and loss of stem and root hydraulic conductivity, and hence loss of K_{plant}. Tyree and Zimmermann (2002) present further detail but the effects of xylem dysfunction should be much like that shown in Figure 6.

So far there is evidence for a plastic response of plants to their growth environment which causes changes in k_{plant}, e.g. Figures 7c and 7d. Hence it would be of interest to know if slow-growing species and fast-growing species still exhibit differences in whole-plant conductance even when all are grown in the same environment. This issue was addressed by Tyree *et al.* (1998) where five species of tropical seedlings were grown in a common environment.

Three of the species (*Trichilia tuberculata* [Tt], *Pouteria reticulata* [Pr], and *Gustavia superba* [Gs]) are shade-tolerant, slow-growing species. The other two species (*Apeiba membranacea* [Am] and *Miconia argentia* [Ma]) are light-demanding, rapidly-growing species. When all
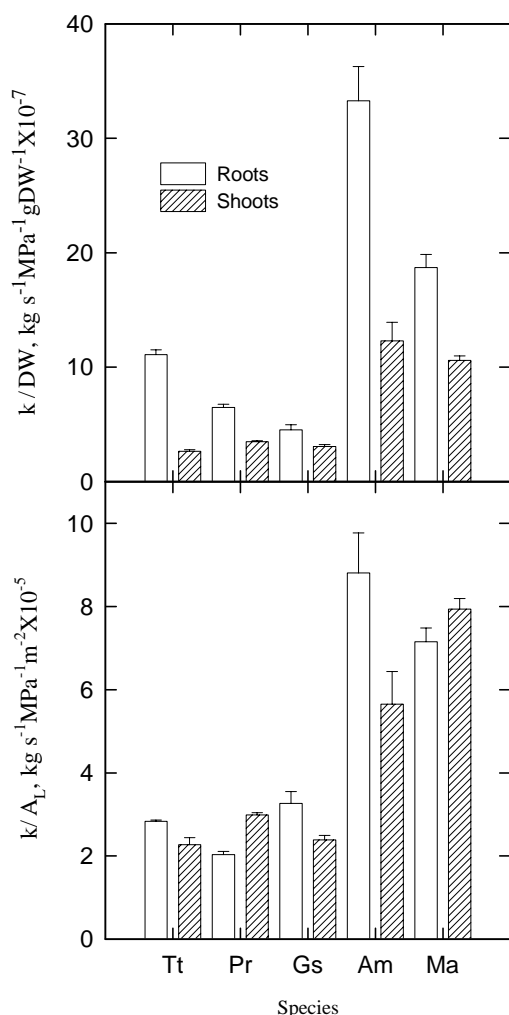
Figure 8 Hydraulic conductances of shoots and roots scaled to dry weight or leaf-area. *Upper:* k_r per unit *TRDW* and k_{sh} per unit shoot dry weight. *Lower:* k_r and k_{sh} both scaled to leaf-area (A_L). Error bars are SEM, n = 23 to 36. Data from all collection dates combined. Species abbreviations as in text. Root and shoot means for Am and Ma were significantly different from corresponding root and shoot means for Tt, Pr and Gs in both A and B (Tukey test, P ≤ 0.05). (from Tyree *et al.* 1998)

necessary for the engine to run properly. But if one of the parts is broken or not up to tolerance-specifications then the engine either does not run at all or runs poorly. Testing the proper functionality of these parts can be used as an early predictor of high yield for the selection of trees in a breeding programme.

My collaborators and I are very interested in confirming the necessity of high K_{plant} for high productivity of trees in a commercial setting. An interesting case might be the intensive silviculture of *Eucalyptus* hybrids in South Africa. MONDI of South Africa is one of the largest pulp and papers manufactures in the southern hemisphere. Almost all their wood is grown in seven-year crop rotations (Fig. 9). MONDI maintains a continuous breeding programme for *Eucalyptus* hybrids that are propagated clonally. No more than 5% of their crop is planted with any one hybrid and new hybrids are continuously introduced into plantations to avoid loss to hybrid-specific pests. This is necessary because trees with high growth rate generally have poor biochemical defenses against pests. If low hydraulic conductance is manifested at the sapling stage and if all low-conductance saplings are slow growing, then early selection of hybrids with high hydraulic conductance could save time and money in breeding or tree selection programmes worldwide.

Figure 9 *Top:* A MONDI employee cuts down a 7-year-old *Eucalyptus* hybrid while Prof. Norman Pammenter, my collaborator (far right in photo) and his graduate student watch.
Bottom: The equipment we use, a High Pressure Flow Meter (HPFM), is transported to the field for measurements of tree hydraulic conductance.

five species were grown in the same intermediate light environment the light-demanding species still grew faster than the shade-tolerant species. These differences in growth rate were correlated with difference in shoot and root conductance per unit leaf area and per unit dry-matter (Fig. 8).

We conclude that high plant hydraulic conductance, K_{plant}, is a necessary condition for high productivity in forest trees. Other necessary conditions might be low leaf area index (personal observation), high photosynthetic capacity in leaves, resistance to pests, and cold tolerance in temperate areas. These five conditions correspond to structural-functional components of a tree that are necessary for good performance in a tree. It is helpful to view a tree as an analogy for an engine in a car. The engine runs well if all the parts in it are functioning: indeed, all of the parts are

I should like to pursue possible commercial applications of what has been learned from previous studies summarised above. Unfortunately, I am at a disadvantage as an employee of the United States Forest Service because (1) large-scale silviculture is confined to countries were labour costs are low,and (2) employees of the US Forest Service are not permitted to apply for research funds from foreign sources. However, my collaborators can apply for foreign grants and I am allowed to accept foreign sources of research funds if they are offered to me independently of an application process. Therefore, if anyone reading this paper is interested in pursuing the possible commercial application of our knowledge of hydraulic architecture of trees, please feel free to contact me for referral to my collaborators!

References

Becker, P., Tyree, M.T. and Tsuda, M. 1999. Hydraulic conductances of angiosperms versus conifers: similar transport sufficiency at the whole-plant level. *Tree Physiology* **19**: 445–452.

Brodribb, T.J. and Field, T.S. 2000. Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant Cell & Environ.* **23**: 1381–1388.

Fuchs, E.E. and Livingston, N.J. 1996. Hydraulic control of stomatal conductance in Douglas-fir (*Pseudotsuga menziesii*(Mirb.) Franco) and alder (*Alnus rubra* (Bong)) seedlings. *Plant Cell & Environ.* **19**: 1091–1098.

Hubbard, R.M., Ryan, M.G., Stiller, V. and Sperry, J.S. 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant Cell & Environ.* **24**: 113–121.

Machado, J-L. and Tyree, M.T. 1994. Patterns of hydraulic architecture and water relations of two tropical canopy trees with contrasting leaf phonologies: *Ochroma pyramidale* and *Pseudobombax septenatum. Tree Physiol.* **14**: 219–240.

Meinzer, F.C., Goldstein, G., Jackson, P., Holbrook, N.M., Gutierrez, M.V. and Cavelier, J. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic conductance properties. *Oecologia* **101**: 514–522.

Raschke, K. 1975. Stomatal action. *Ann. Rev. Plant Physiol.* **226**: 309–340.

Saliendra, N.Z., Sperry, J.S. and Comstock, J.P. 1995. Influence of leaf water status on stomatal response to hydraulic conductance, atmospheric drought, and soil drought in *Betula occidentalis. Planta* **196**: 357–366.

Sperry, J.S. 2000. Hydraulic constraints on plant gas exchange. *Agric. Forest Meteorol.* **104**: 13–23.

Sperry, J.S., Adler, F.R. and Eastlack, S.E. 1993. The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. *J. Exp. Botany* **44**: 1075–1082.

Tyree, M.T., Sneidermann, D.A., Wilmot, T.R. and Machado, J.L. 1991. Water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*): Data, models and a comparison to two temperate species (*Acer saccharum* and *Thuja occidentalis*). *Plant Physiol.* **96**: 1105–1113.

Tyree, M.T., Velez, V. and Dalling, J.W. 1998. Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptations to differing light regimes. *Oecologia* **114**: 293–298.

Tyree, M.T. and Zimmermann, M.H. 2002. *Xylem Structure and the Ascent of Sap* (second edition). Springer-Verlag, New York.

Yang, S. and Tyree, M.T. 1993. Hydraulic resistance in shoots of *Acer saccharum* and its influence of leaf water potential and transpiration. *Tree Physiol.* **12**: 231–242.