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ORIGINAL ARTICLE

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

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Abstract The state of knowledge concerning the influences of tree size, xylem dysfunction, growth conditions, and within-species and between species genetics is reviewed. It is concluded that high plant hydraulic conductance is necessary for high productivity in forest trees, and this being the case, the implications for commercial forestry require further study.

Keywords Trees · Hydraulic architecture · Cohesion-tension theory

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:

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

hence

$$\Psi_L = \Psi_{soil} - R_{plant}E = \Psi_{soil} - \frac{E}{K_{plant}} \quad (2)$$

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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 will use K_{plant} and R_{plant} interchangeably in this talk. Values of K_{plant} are scaled in Eq.1 by leaf surface area, i.e., kg water flow per s per m^2 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, let me explain by some simple graph 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 external 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-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

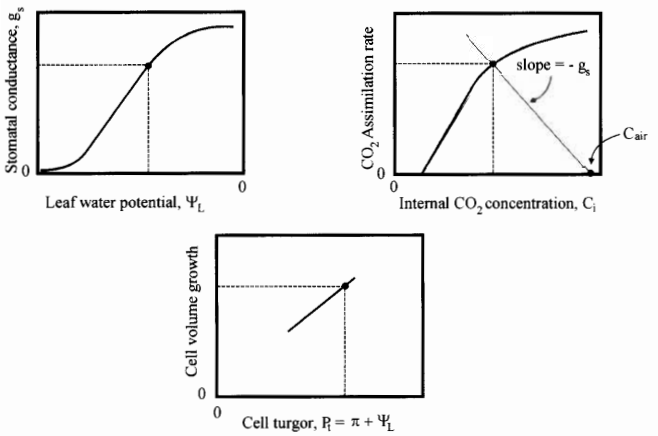

Fig. 1A–C The *dashed lines* in the graphs show the normal midday operating conditions of trees. **A** The dependence of stomatal conductance, g_s, on leaf water potential, Ψ_L, usually keeps g_s below the potential maximum value. **B** The *AC_i curve* above illustrates how CO_2 assimilation rate depends 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

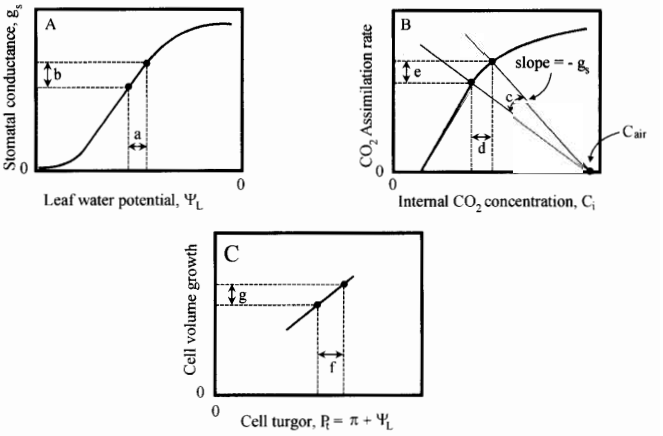

Fig. 2A–C The graphs in Fig. 1 are repeated showing how a change in hydraulic resistance causes a change in various parameters given by *double-headed arrows*. **A** An increase R_{plant} causes a decrease in Ψ_L (*a*). The decrease in Ψ_L causes a decrease in g_s (*b*). **B** A decrease in g_s causes 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 Ψ_L causes a decrease in turgor of growing cells (*f*) which causes a decrease in cell volume growth rate (*g*)

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 talk is to review the state of our 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=4,667 $D^{2.007}$ (Fig. 6). The drop in xylem pressure across the shoot, ΔP_x, should equal EA_L/k_T, hence it follows that

$$\Delta P_x = \left(7.781 \times 10^4 D^{0.605}\right)E \qquad (3)$$

Hence we have to conclude that as branches grow larger the ΔP_x grows larger too. We can actually turn Eq. 3 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,

$$\Psi_{leaf} \cong -2\left(7.781 \times 10^4 D^{0.605}\right)E \qquad (4)$$

Yang and Tyree (1993) compared predicted values of ΔP_x or Ψ_{leaf} to 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 *A. saccharum* leaves are typically –1.2 to –1.5 MPa in wet soil at the base of Mt Mansfield, Vermont, where the data for Figs. 3 and 4 were collected. So 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 (g_s) versus whole plant conductance (k_{plant}), it can easily be done. The approach you take 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. You then pick a value of g_s from Fig. 4 and look up the corresponding Ψ_{leaf}, you then find the stem diameter that yields the same Ψ_{leaf} in Eq. 1. Then you use that D value 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 you get the results in Fig. 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 Fig. 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

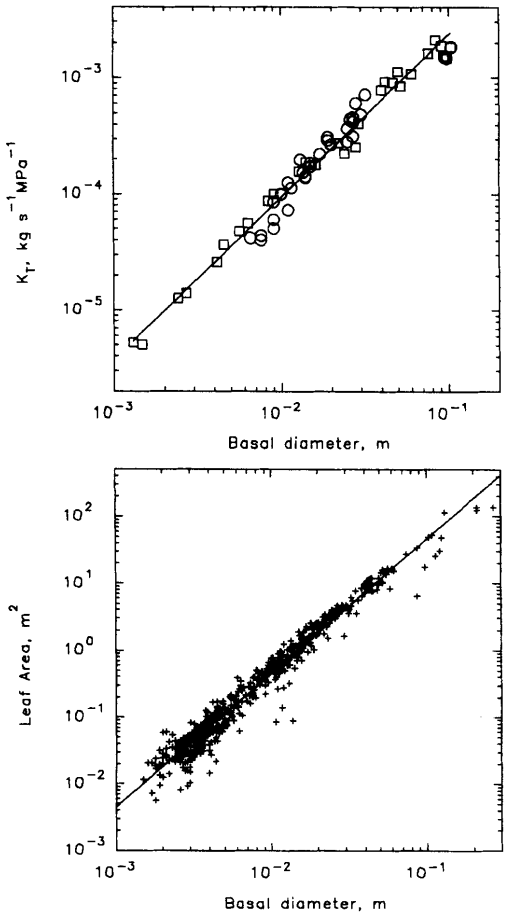

Fig. 3 *Upper*: Log k_T (whole shoot conductance) versus log D (basal diameter of the wood) of *Acer saccharum* branches. *Lower*: Log A_L (area of leaves attached to a shoot) versus log D. (From Yang and Tyree 1993)

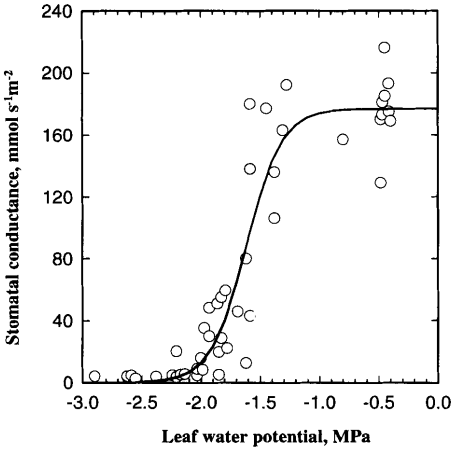

Fig. 4 Stomatal conductance of detached *Acer saccharum* leaves versus leaf water potential. The leaves were slowly dehydrated while exposed to saturating light intensity. Each point is a different leaf. The smooth curve is the data fitted to a three-parameter sigmoid curve of the form stomatal conductance $=a/\{1\text{-}\exp[b(c-\Psi)]\}$, 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)

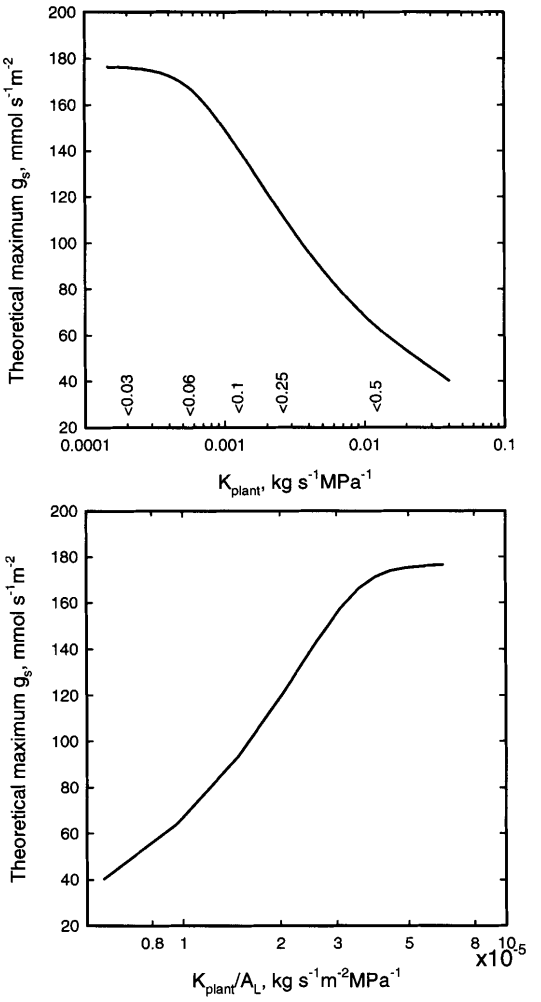

Fig. 5 *Upper*: Theoretical relationship between maximum possible stomatal conductance, g_s, and whole plant hydraulic conductance is plotted using the measured relationships for *A. saccharum* in Figs. 3 and 4. The whole plant conductance values on the x-axis correspond to basal stem diameters of 0.022–1.22 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

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

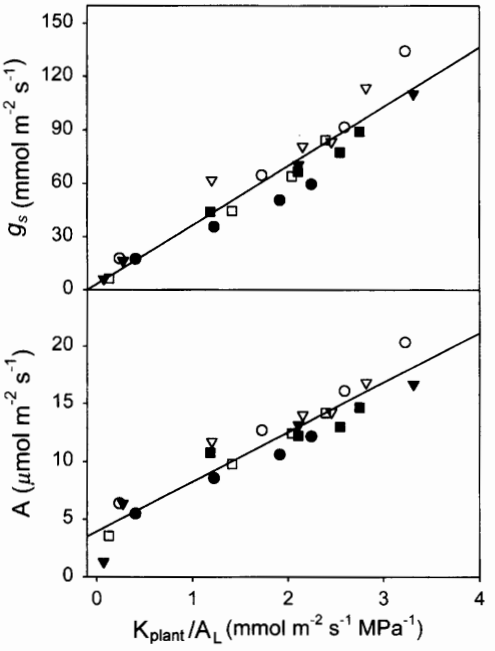

Fig. 6 Stomatal conductance (g_s) and assimilation (A) versus whole plant leaf specific conductance (k_{plant}/A_L). The leaf specific conductance of *Pinus ponderosa* seedlings was changed by air injection. Each symbol is for a different seedling (n=6) and multiple points represent multiple air injection pressures. In order to compare conductances here with others in this book note that 1 mmol s^{-1}=1.8×10^{-5} kg s^{-1} (from Hubbard et al. 2001)

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 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 summarized in Fig. 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 in Fig. 7a, b 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

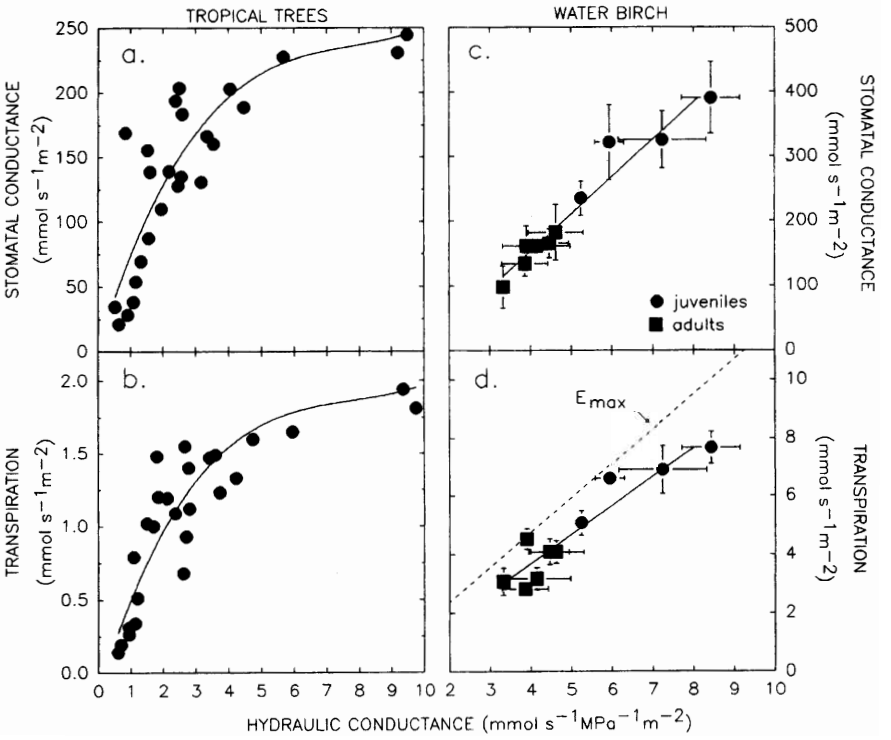

Fig. 7 Stomatal conductance (**a**, **c**) and transpiration rate (**b**, **d**) vs hydraulic conductance from bulk soil to leaf (k_{plant}/A_L). **a**, **b** Various tropical gap-species (from Meinzer et al. 1995); **c**, **d** *Betula occidentalis* juveniles and adults (from Saliendra et al. 1995)

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}. I refer you to Tyree and Zimmermann (2002) for more details, but the effects of xylem dysfunction should be much like that in Fig. 6.

So far there is evidence for a plastic response of plants to their growth environment which causes changes in k_{plant}, e.g., Fig. 7c, d. 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 tubersculata* (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 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 where correlated with difference in shoot and root conductance per unit leaf area and per unit dry-matter (Fig. 8).

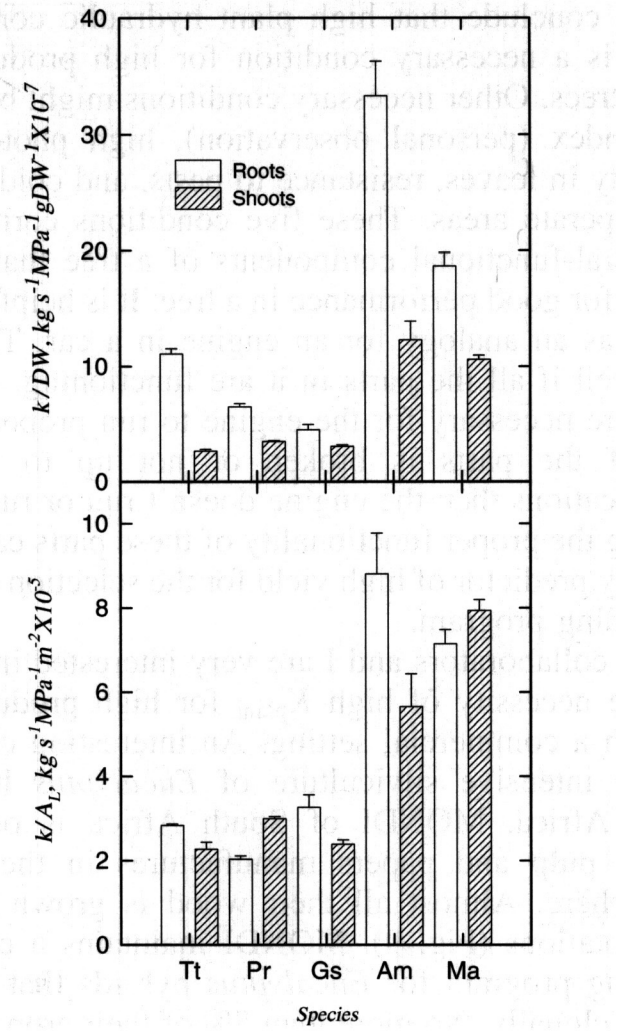

Fig. 8 Hydraulic conductances of shoots and roots scaled to dry weight or leaf-area. *Upper:* k_r per unit *TRDW* and k_{sh} per unit shoot dry weight. *Lower:* k_r and k_{sh} both scaled to leaf-area (A_L). *Error bars* are SEM, n=23–36. Data from all collection dates combined. Species abbreviations as in text. Root and shoot means for Am and Ma were significantly different from corresponding root and shoot means for *T*t, *P*r and *G*s in both A and B (Tukey test, $P \leq 0.05$). (from Tyree et al. 1998)

Fig. 9 *Photo left:* 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. *Photo right:* The equipment we use, a High Pressure Flow Meter (HPFM), is transported to the field for measurements of tree hydraulic conductance

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. All of the parts are necessary for the engine to run properly. But if one of the parts is broken or not up to tolerance-specifications then the engine doesn't run or runs poorly. Testing the proper functionality of these parts can be used an early predictor of high yield for the selection of trees in a breeding program.

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 7-year crop rotations (Fig. 9). MONDI maintains a continuous breeding program for *Eucalyptus* hybrids that are propagated clonally. No more than 5% of their crop is planted in 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 programs worldwide.

I would like to pursue possible commercial applications of what has been learned from previous studies summarized 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 labor 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. So if anyone in the audience (or reading this report) 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!

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