Leaf hydraulic capacity in ferns, conifers and angiosperms: impacts on photosynthetic maxima

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Summary

• The hydraulic plumbing of vascular plant leaves varies considerably between major plant groups both in the spatial organization of veins, as well as their anatomical structure.

• Five conifers, three ferns and 12 angiosperm trees were selected from tropical and temperate forests to investigate whether the profound differences in foliar morphology of these groups lead to correspondingly profound differences in leaf hydraulic efficiency.

• We found that angiosperm leaves spanned a range of leaf hydraulic conductance from 3.9 to 36 mmol m^2 s^{-1} MPa^{-1}, whereas ferns (5.9–11.4 mmol m^{-2} s^{-1} MPa^{-1}) and conifers (1.6–9.0 mmol m^{-2} s^{-1} MPa^{-1}) were uniformly less conductive to liquid water. Leaf hydraulic conductance (K_{leaf}) correlated strongly with stomatal conductance indicating an internal leaf-level regulation of liquid and vapour conductances. Photosynthetic capacity also increased with K_{leaf}, however, it became saturated at values of K_{leaf} over 20 mmol m^{-2} s^{-1} MPa^{-1}.

• The data suggest that vessels in the leaves of the angiosperms studied provide them with the flexibility to produce highly conductive leaves with correspondingly high photosynthetic capacities relative to tracheid-bearing species.

Key words: angiosperms, conifers, ferns, hydraulic conductance, leaf hydraulics, photosynthesis, stomatal coordination.

Introduction

The complicated problem of distributing water under tension to the leaf lamina has spawned diversity in the leaf hydraulic plumbing of land plants. Angiosperms typically employ a highly branched reticulate system of leaky veins, delivering water uniformly to the sites of evaporation (Zwieniecki *et al.*, 2002). Most gymnosperms by contrast possess a simple vascular network comprised of a single vein per leaf, with the role of water delivery undertaken by transfusion tissues peripheral to the xylem tracheids. Ferns as a group fall between these extremes using simply branched, occasionally reticulate vascular networks to irrigate fronds. Additional to this diversity in the spatial arrangement of veins is a diversity of xylem structure

in leaves. Angiosperm leaves commonly utilize xylem vessels in the lower vein orders whilst vessels are absent from conifers and fern laminae (although do appear in rhizomes and possibly rachides of some ferns; (Carlquist & Schneider, 2001)). How this great variation in vascular characteristics affects the performance of plants in terms of gas exchange, construction economy and growth remains unknown.

Regardless of anatomy, the resistance to water flow through leaves is high relative to the rest of the plant, with leaf hydraulic resistance estimated to be at least 25% of the whole plant resistance (Sack *et al.*, 2003) and up to 80% (Nardini, 2001). As a result, the hydraulic conductivity of leaves wields a disproportionate influence over the water relations of plants. The gas exchange behaviour of foliage must also be related to

the hydraulic characteristics of the leaf xylem due to the serial positioning of xylem and stomata in the flow path of water through the plant. Following the cohesion–tension theory, leaves draw water from the soil by a water potential gradient generated by evaporation at the leaf. The difference between soil and leaf water potential is therefore determined by the rate of water loss at the leaf, and the resistance to water flow imposed by the vasculature and non-xylem pathways radial to the vasculature. Imbalance between the supply of water through the xylem and the rate of evaporation from the stomata would lead to substantial variation in the pressure drop from soil to leaf in transpiring plants. Observation suggests that this is not the case however, and that plants tend to be somewhat conservative in the operational water potential drop from root to leaf. For this reason it is not surprising that hydraulic (xylem) and diffusive (stomatal) resistances (or conductances) have been found to be correlated in trees (Whitehead *et al.*, 1984; Meinzer, 2002).

Given the fact that the stomatal conductance of leaves correlates closely with assimilation rate both within individuals and generally across C_3 plants (Wong *et al.*, 1979), some sort of relationship between hydraulic conductance and assimilation rate is expected. However, only a handful of studies have dealt directly with the question of how xylem hydraulics relate to the photosynthetic rate. The first of these illustrated a linear relationship between stem hydraulic conductivity and photosynthetic quantum yield in a range of temperate rainforest species (Brodribb & Feild, 2000). This relationship was supported by a later study showing that artificial depression of K_{plant} led to a proportional decrease in the foliar assimilation rate of ponderosa pine seedlings (Hubbard *et al.*, 2001). Considering the large proportion of whole plant hydraulic resistance that resides in leaves, it is likely that the efficiency of water delivery to evaporating cells should correspond closely with photosynthetic rate. This was the conclusion of a recent study showing that a midday decline in leaf hydraulic conductivity of a tropical tree species was linked to midday depression of stomatal conductance and photosynthesis (Brodribb & Holbrook, 2004). We were interested to know whether a common relationship might describe the interdependence of K_{leaf} and assimilation across environmental and phylogenetic boundaries.

In the study presented here we examined how the diversity of vascular architectures in leaves from disparate phylogenetic groups is related to the efficiency of water delivery and in turn to photosynthetic performance. Species sampled included ferns, conifers and angiosperms from the climatic antipodes of Chilean cool-temperate rainforest and Costa Rican seasonally dry tropical forest. Amongst the species selected for study were leaves bearing venation patterns that ranged from reticulate to open, including conifer single vein leaves, and species with and without vessels. The morphological range of leaves studied encompassed a considerable range of leaf thickness and hardness, and hence hydraulic capacitances (equivalent to

stored water). Accordingly, leaf capacitance was also measured to determine the possible influence of this parameter on leaf water balance.

Materials and Methods

Study site and plant material

Two locations were chosen for their contrasting climate and flora. The first experimental site was a seasonally dry forest in the northwest of Costa Rica, Santa Rosa National Park (10°52′ N, 85°34′ W, 285 m above sea level). Mean annual rainfall in the park is 1528 mm, however, > 90% of this falls between the months of May and December, resulting in a pronounced dry season. Vegetation in the park is comprised of a mosaic of deciduous, evergreen and mixed forest types depending on the successional age of forest stands, with evergreen species more prominent in more mature forest patches. The second location was southern Chile where cool-temperate rainforest from two national parks was sampled. These parks, Puyehue (40°50′ S, 72°13′ W) and Conguillo (38°38′ S, 71°36′ W) are both located in the Andean cordillera and receive in excess of 3000 mm of rainfall annually, with no pronounced dry season.

In Costa Rica we sampled nine species (Table 1). Amongst these were five tree species including deciduous; *Calycophyllum candidissimum* (Rubiaceae), *Gliricidia sepium* (Fabaceae), *Rhedera trinervis* (Verbenaceae) and evergreens; *Simarouba glauca* (Simaroubaceae) and *Quercus oleoides* (Fagaceae), four fern species; *Blechnum occidentale* (Blechnaceae) and *Gleichenea bifida* (Gleicheniaceae) as well as *Selaginella pallescens* (Selaginellaceae), all of which are small stature perennial species.

In Chile we also sampled 10 tree species (Table 1), including four conifers; *Araucaria araucana* (Araucariaceae), *Austrocedrus chilensis* (Cupressaceae), *Prumnopitys andina* (Podocarpaceae) and *Saxagothea conspicua* (Podocarpaceae), as well as four evergreen angiosperms; *Drimys winteri* (Winteraceae), *Lomatia ferruginea* (Proteaceae), *Laurelia phillipiana* (Monomiaceae), *Nothofagus dombeyi* (Nothofagaceae) and two deciduous angiosperms *Nothofagus alpinus* (Nothofagaceae) and *Nothofagus obliqua* (Nothofagaceae).

All individuals sampled were on forest edges or open areas and measured leaves were always fully sunlit. Measurements were made in the field in the months of August (Costa Rica) and December (Chile) 2003.

Leaf hydraulic conductance

Three sun-exposed branches from three trees per species were collected at 09:00–10:00 h (minimizing the possibility of midday K_{leaf} depression; (Brodribb & Holbrook, 2004)), enclosed in sealed plastic bags to prevent water loss, and returned to the car/laboratory for K_{leaf} determination. K_{leaf} was measured on three leaves per branch (n = 9 per species) by

Table 1 Species, family, location, vein branching and xylem type for the 20 tree and fern species studied

ANGIOSPERMS	Country	Vein
Calycophyllum candidissimum (Rubiaceae)	CR	Reticulate/vessels
Gliricidia sepium (Fabaceae)	CR	Reticulate/vessels
Rhedera trinervis (Verbenaceae)	CR	Reticulate/vessels
Simarouba glauca (Simaroubaceae)	CR	Reticulate/vessels
Quercus oleoides (Fagaceae)	CR	Reticulate/vessels
Drimys winteri (Winteraceae)	Chile	Reticulate/tracheids
Lomatia ferruginea (Proteaceae)	Chile	Reticulate/vessels
Larelia phillipiana (Monomiaceae)	Chile	Reticulate/vessels
Nothofagus alpinus (Nothofagaceae)	Chile	Reticulate/vessels
Nothofagus dombeyi (Nothofagaceae)	Chile	Reticulate/vessels
Nothofagus obliqua (Nothofagaceae)	Chile	Reticulate/vessels
Nothofagus pumilio (Nothofagaceae)	Chile	Reticulate/vessels
FERN/FERN ALLYS		
Blechnum occidentale (Blechnaceae)	CR	Open branch/tracheids
Gleichenea bifida (Gleicheniaceae)	CR	Open branch/tracheids
Selaginella pallescens (Selaginellaceae)	CR	Single vein/tracheids
CONIFERS		
Araucaria araucana (Araucariaceae)	Chile	Open branch/tracheids
Austrocedrus chilensis (Cupressaceae)	Chile	Single vein/tracheids
Pilgerodendron uviferum (Cupressaceae)	Chile	Single vein/tracheids
Prumnopitys andina (Podocarpaceae)	Chile	Single vein/tracheids
Saxagothaea conspicua (Podocarpaceae)	Chile	Single vein/tracheids

assessing the rehydration kinetics of leaves after detachment (Brodribb & Holbrook, 2003b). Briefly, a detached sample leaf (non-evaporating) is allowed to take up water through the petiole for a fixed period of time and the change in water potential during rehydration used to calculate leaf conductance. The principle underlying this approach is that the rehydrating mesophyll behaves as a capacitor, charged through a resistor ($1/K_{leaf}$). Hence the kinetics of relaxation are described by the equation:

$$\Psi_f = \Psi_o e^{-t/RC} \qquad \text{Eqn 1}$$

(C, leaf capacitance; Ψ_o, leaf water potential prior to rehydration; Ψ_f, leaf water potential after rehydration for t seconds; and R, leaf hydraulic resistance).

K_{leaf} determination requires that the initial and final leaf water potential be measured in a sample rehydrated for a known period of time. Small branches were cut in the field and immediately bagged in the dark for a period of at least 1 h, such that stomata were closed and all leaves are at the same water potential. After measuring the initial water potential of the excised branch, a minimum of five non-senescent fully expanded sample leaves were cut underwater and allowed to absorb water for a period of between 30 and 300 s. The rehydration time was chosen to allow a relaxation of water potential to about half the initial value. For conifers with small leaves (< 20 mm) short shoots were used instead of individual leaves for rehydration following the assumption that these are functionally analogous to angiosperm compound leaves. Water potential of rehydrated leaves was then measured using an Scholander pressure chamber (PMS, Corvallis, OR,

USA) and leaf hydraulic conductance calculated from the equation:

$$K_{leaf} = C \ln[\Psi_o/\Psi_f]/t \qquad \text{Eqn 2}$$

Mean leaf capacitance (C) for each species was measured from six fully expanded leaves using the slope of the leaf pressure-volume relationship (Tyree & Hammel, 1972). Branches were cut underwater in the morning and rehydrated until Ψ_{leaf} was > −0.05 MPa, after which leaves were detached for PV determination. Leaf weight and water potential were measured periodically during slow desiccation of sample leaves in the laboratory. The initial (linear) slopes of the relative water content (RWC) vs Ψ_{leaf} curves yielded the leaf capacitance function in terms of RWC. Calculation of K_{leaf} (mmol m^{-2} s^{-1} MPa^{-1}) requires that leaf capacitance be calculated in absolute terms and normalized by leaf area. To do this, the capacitance calculated from the PV curve was multiplied by the saturated mass of water in the leaf and then divided by leaf area (Koide *et al.*, 1991; Brodribb & Holbrook, 2003b). Leaf areas were measured as projected areas with a digital camera and image analysis software (Scion Image, National Institute of Health, USA). Projected area was also measured in the conifer species as all species possessed leaves that were strongly dorsiventrally flattened.

Photosynthesis and stomatal conductance

For reasons of portability and efficiency we used chlorophyll fluorescence to measure the photosynthetic activity of leaves. The quantum yield of photosystem II electron transport (Φ_{PSII}) was determined in the light using a miniPAM portable

fluorometer (Waltz, Effeltrich, Germany) operated in the field (Bilger *et al.*, 1996). Preliminary measurements made throughout the day indicated that Φ_{PSII} determined at a PPFD of 1000 µmol m^{-2} s^{-1} peaked between 10:00 and 12:00 h, and there was no evidence of strong midday depression of Φ_{PSII} (T. J. Brodribb, unpublished data). Measurements were carried out over two cloudless days at each site with readings made between 10:00 and 14:00 h. We selected fully expanded leaves from exposed, undamaged branches and Φ_{PSII} was determined by measuring the increase in chlorophyll fluorescence during the application of a single saturating flash of light (Genty *et al.*, 1989) to leaves illuminated by the internal actinic light set to produce 1800 µmol m^{-2} s^{-1} at the leaf surface (PPFD in full sun at both sites was between 1900 µmol m^{-2} s^{-1} and 2200 µmol m^{-2} s^{-1}). Saturation pulses were applied for 0.8 s at an intensity of 3500 µmol m^{-2} s^{-1}.

At the same time as measuring chlorophyll fluorescence, maximum stomatal conductance ($g_{s\ max}$) was measured in all species between 08:00 and 11:00 h when humidity was high and irradiance was saturating. A null balance porometer (Li-1600; Licor, Lincoln, NE, USA) was nulled at ambient humidity and three healthy leaves from three individuals of each species sampled for g_s. Mean g_s from these measurements was defined as $g_{s\ max}$ for each species.

In order to determine the complete relationship between g_s and Φ_{PSII} in the tropical angiosperms it was necessary to measure leaves during the dry season as well as the rainy season because only very high stomatal conductances were recorded during the wet season. Leaves from the two evergreen tropical species (*Simarouba glauca* and *Quercus oleoides*) were sampled during the late dry season while stomatal conductances were low due to low soil water availability. On a single sunny day stomatal conductance and Φ_{PSII} were measured in a population of 40 leaves (20 leaves per species). Both parameters were measured in quick succession by moving leaves directly from the Li-1600 leaf clip into the MiniPAM leaf clip. All measurements were made at an actinic light intensity of 2000 µmol quanta m^{-2} s^{-1} at ambient temperature, which ranged between 32 and 35.9°C in all samples.

Statistical analysis

Variance in leaf hydraulic conductance data was compared by conduit type (vessel or tracheid) and plant type (angiosperm, fern, conifer) using a one-way ANOVA (JMP, SAS Institute Inc., Cary, NC). Regression analysis was undertaken using either linear or saturating curve functions from a plotting program (Sigmaplot, SPSS Inc., Chicago, Illinois).

Results

Angiosperms sampled here exhibited a very large range of K_{leaf} (Fig. 1) extending over an order of magnitude from 36 ± 5.9 mmol m^{-2} s^{-1} MPa^{-1} in the Costa Rican tree
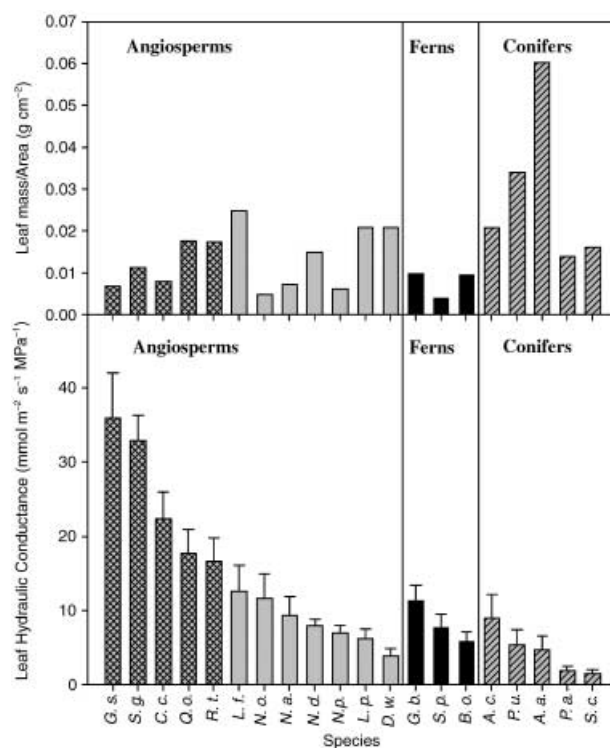

Fig. 1 Leaf dry mass per area and leaf hydraulic conductance (K_{leaf}) ($\pm$ SD; $n = 9$) for species from three broad phylogenetic groups; angiosperms from Costa Rica (cross hatched), angiosperms from Chile (grey), ferns from Costa Rica (black) and conifers from Chile (shaded). Species from each group have been ordered from largest to smallest K_{leaf}, and species names are abbreviated to single letters for generic and specific epithets.

Gliricidia sepium to 3.9 ± 0.9 mmol m^{-2} s^{-1} MPa^{-1} in the vessel-less Chilean tree *Drimys winteri*. Mean K_{leaf} in the ferns and conifers was lower than the angiosperms, however, due to the enormous variability in mean K_{leaf} among angiosperm species, differences in mean K_{leaf} between these groups were not significant. Comparison of species by conduit type indicated that the vessel bearing species produced significantly higher K_{leaf} than non-vessel bearing leaves (16.4 mmol m^{-2} MPa^{-1} compared with 5.72 mmol m^{-2} s^{-1} MPa^{-1}; $P > 0.01$). Once again the variance in the mean K_{leaf} for vessel-bearing angiosperms was approximately 10 times that for tracheid-bearing species.

K_{leaf} was linearly correlated ($r^2 = 0.87$) with stomatal conductance across all species (Fig. 2). As a group, the Costa Rican angiosperms produced the highest stomatal and hydraulic conductances whilst Chilean conifers were lowest in both parameters. Substantial overlap in the ranges of mean K_{leaf} and g_s were found in Chilean conifers and angiosperms and Costa Rican ferns, with the only significantly different group being the Costa Rican angiosperms. Although leaf hydraulic capacitance varied considerably between species, no relationship was observed between capacitance and stomatal conductance to water loss. Leaf capacitance in the conifers was
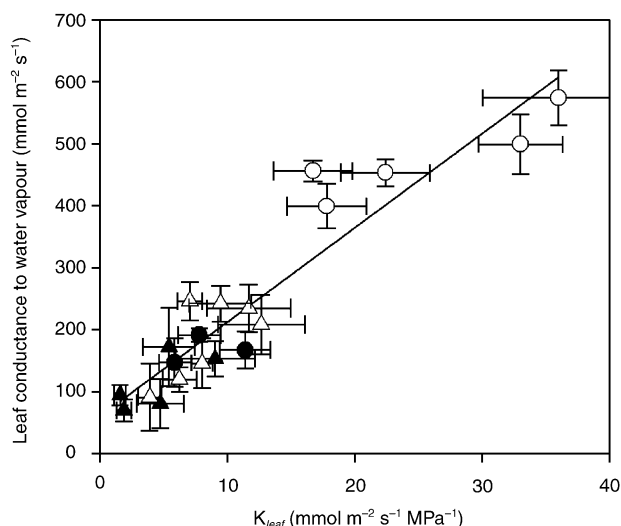
Fig. 2 A highly significant linear correlation ($r^2 = 0.87$) between mean leaf hydraulic conductance ($\pm$ SD; $n = 9$) and stomatal conductance ($\pm$ SD; $n = 9$) in a sample of tropical ($\bigcirc$) and temperate ($\triangle$) angiosperms, tropical ferns ($\bullet$), and temperate conifers ($\blacktriangle$).

Fig. 4 The relationship between mean leaf hydraulic conductance (K_{leaf}) and photosynthetic capacity (tropical ($\bigcirc$) and temperate ($\triangle$) angiosperms, tropical ferns ($\bullet$), and temperate conifers ($\blacktriangle$)), illustrating a significant saturating relationship ($r^2 = 0.86$; bold regression line) for quantum yield. The vessel-less angiosperm *Drimys winterii* is marked with a cross. Also shown are published regression curves (single point line) for the same parameters during seasonal changes of K_{leaf} in the two deciduous species *Rhedera trinervis* and *Calycophyllum candidissimum* (data from Brodribb & Holbrook, 2003a).

Fig. 3 The range of leaf capacitances amongst the species sampled (angiosperms from Costa Rica (cross hatched), angiosperms from Chile (grey), ferns from Costa Rica (black) and conifers from Chile (shaded)). Capacitance was expressed as the time for a 1 MPa drop in leaf water potential after detachment of a transpiring leaf at midday (assuming no stomatal closure). The *y*-axis is broken in order to accommodate the extremely large capacitance of the conifer *Araucaria araucana*.

significantly higher than in any other group ($P < 0.01$) whilst the tropical angiosperms exhibited lowest capacitance. Leaf capacitance was expressed in terms of the time for a 1 MPa drop in leaf water potential under maximum midday transpiration rates, assuming leaves were deprived of xylem water supply. The resultant times ranged widely from a minimum of 32 s in *Quercus oleoides* to a maximum of 108 min in the conifer *Araucaria araucana* (Fig. 3).
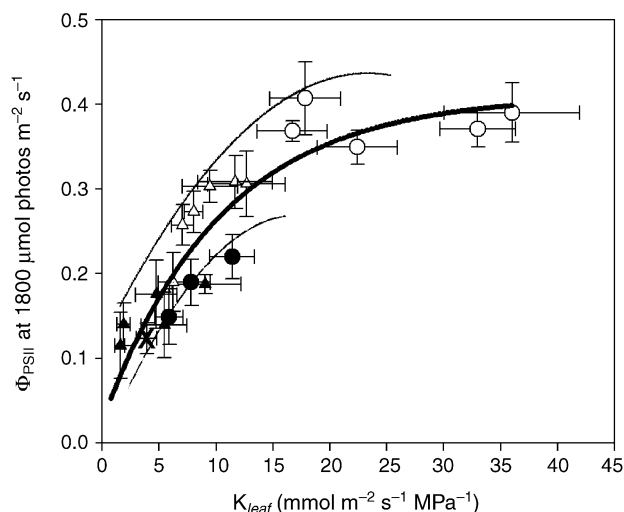
A common relationship between mean K_{leaf} and PSII quantum yield existed for all species (Fig. 4) whereby Φ_{PSII} exhibited an initially high sensitivity to K_{leaf} followed by a saturation of Φ_{PSII} at approximately 0.39. Correspondingly, the best curve fit to the pooled data was using an exponential function rising to a maximum limit of $\Phi_{PSII} = 0.40$ ($r^2 = 0.86$, $P < 0.001$). Due to the apparent saturation of Φ_{PSII} at values of $K_{leaf} > 20$ mmol m^{-2} s^{-1} MPa^{-1} the sample of tropical angiosperms here showed little influence of leaf hydraulic conductance upon Φ_{PSII}. In contrast, the temperate species and tropical ferns exhibited a profound dependence of photosynthetic rate upon the hydraulic conductance of the leaf veins and lamina. The saturating curve fitted to the pooled data (Fig. 4) was similar in shape to those previously determined for leaves of individual species from expansion to senescence (curves also shown on Fig. 4).

The contrasting relationships observed between K_{leaf} vs g_s compared with K_{leaf} vs Φ_{PSII} are reconciled by data showing that quantum yield is saturated at high stomatal conductivities (Fig. 5). Ignoring the Costa Rican angiosperms, a strong linear relationship between g_s and Φ_{PSII} could be described for the other species ($r^2 = 0.66$; $P < 0.01$). In contrast, the data from tropical angiosperms in the wet season showed virtually no dependence of Φ_{PSII} upon g_s ($r^2 = 0.03$). The best model to describe the pooled Φ_{PSII} vs g_s data was an exponential rise in Φ_{PSII} to a maximum of 0.38 ($r^2 = 0.92$). Thus, a likely source of the curvilinearity between K_{leaf} and Φ_{PSII} is saturation of Φ_{PSII} at the high stomatal conductances found in Costa
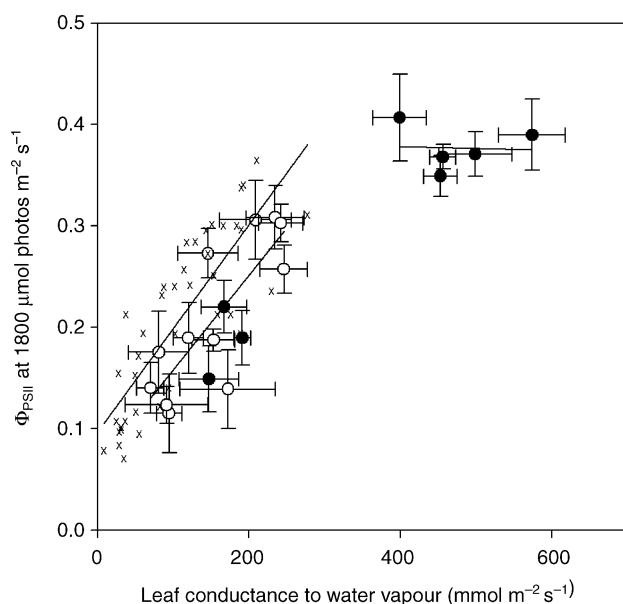
Fig. 5 The relationship between mean stomatal conductance (g_s) and the quantum yield of photosystem II electron transport (Φ_{PSII}) in the tropical (○) and temperate species (●). The apparent saturation of Φ_{PSII} in the tropical angiosperms was confirmed by remeasuring g_s and Φ_{PSII} in these five species during the early dry season once soil moisture was limiting (crosses). Under water-limiting conditions, the linear regression between g_s and Φ_{PSII} in the tropical species ($r^2 = 0.68$) was not significantly different to the linear regression ($r^2 = 0.66$) for the temperate species.

Rican species sampled during the wet season. To confirm that the tropical angiosperms were operating in the saturated part of the g_s vs Φ_{PSII} relationship during the wet season, the same species were sampled under conditions of reduced soil water (and correspondingly lower g_s) during the early dry season. These data revealed that under limiting g_s, the tropical angiosperms exhibited that same linear dependence of A on g_s as other species (Fig. 5).

Discussion

The large diversity of leaf morphologies examined here yielded a correspondingly large range in the efficiency of water conduction through leaves. Predictably, the tropical angiosperm leaves were most conductive to liquid water, with several species found to be up to 20 times more conductive than the most inefficient temperate conifers. Interestingly however, differences in K_{leaf} did not have a strong phylogenetic component, due mainly to the fact that although some angiosperms produced high hydraulic conductances, other (temperate) species fell within the K_{leaf} range of the ferns and conifers.

K_{leaf} and water loss

The presence of vessels in angiosperm leaves may be the key to enabling such diversity in hydraulic function without a

correspondingly large variation in leaf mass per unit area (Fig. 1). Xylem vessels presumably enable angiosperms to produce highly conductive veins at a minimum cost to the plant, thus enabling lightweight vascular networks to support substantial evaporative loads. Long vessels have been noted in the leaves of several of the tropical tree species investigated here with continuous vessels from the petiole to tertiary veins in both *Quercus oleoides* and *Simarouba glauca* (unpublished data). The Chilean angiosperms, in contrast to the tropical species, exhibited a narrow range of K_{leaf}, which was not significantly different to the tracheid bearing ferns and conifers. This is likely due to the fact that freezing is a regular feature of the climate at the two Chilean sites and hence the vessel diameter in leaves is likely to be small to avoid freeze thaw embolism (Feild & Brodribb, 2001). If vessel diameter is limited to a size where freeze-thaw embolism is minimal, the optimal vessel length also becomes small (Sperry & Hacke, 2004), and the vessel advantage is substantially reduced. This is particularly so when compared with tracheids of conifers which possess highly efficient pitting (torus and margo) giving them a substantially improved hydraulic efficiency per unit length (Hacke *et al.*, 2004). Such issues must go some way to explaining the coexistence of conifers and angiosperms in temperate habitats such as southern Chile.

Underlying the observed diversity in leaf hydraulics was a close link between K_{leaf} and mean maximum stomatal conductance. The existence of such a relationship is not surprising since stomatal pore characteristics have been found to be correlated with both K_{leaf} (Sack *et al.*, 2003), and vessel diameter (Aasamaa *et al.*, 2001) in a small group of temperate tree species. These data support the conclusion here that water supply and water loss capacities are internally coordinated within individual leaves. Such coordination must be driven by adaptive evolution tending to optimize investment in conductive tissues, inferring the augmentation of vascular capacity and stomatal density come at a significant cost to the plant.

The correlation between K_{leaf} and g_s illustrates several important aspects of leaf water relations. Primarily it indicates the importance of leaf hydraulic characteristics in dictating the water loss characteristics of the crown, due to strong selection for hydraulic–stomatal coordination within the leaf as well as throughout the plant as a whole. Secondly it suggests that tree species, at least those studied here, are conservative in the potential drop ($\Delta\Psi_l$) allowed to develop across leaves under normal evaporative conditions. Increasing the leaf potential drop allowed during transpiration would seem a perfectly appropriate adaptive tool for reducing the amount of xylem required to sustain transpiration. However, this type of adaptation does not appear to be important in the species here, given minimal scatter in the relationship between K_{leaf} and g_s (Fig. 2). Direct measurement of $\Delta\Psi_l$ across the range of angiosperm and conifer leaves sampled also confirmed that $\Delta\Psi_l$ remained conservative among species and across environments (mean $\Delta\Psi_l$ at midday for Chilean species was 0.51 MPa

compared with 0.49 MPa for Costa Rican species; unpublished data). This raises the question as to what costs are associated with operating at larger values of $\Delta\Psi_l$? Potential drawbacks associated with greater $\Delta\Psi_l$ (lower leaf water potential) include a requirement for increased lignin investment in both xylem (Hacke *et al.*, 2001) and leaf structure to resist collapse. It has also been suggested that minimum Ψ_l is limited by the process of phloem loading which may be unable to overcome large water potential gradients from the stem to leaf (Schulze & Zwolfer, 1994).

The dependence between K_{leaf} and g_s might be altered if water stored in the leaf represents a significant proportion of its daily water loss, as this capacitance might substitute for xylem transport capacity. As such we expected that leaf capacitance might act as a compensatory mechanism for low xylem efficiency in conifers. Indeed conifers were found to exhibit substantial leaf capacitances, with leaves able to function for long periods without a hydraulic connection to the plant (Fig. 3). However, there was no evidence for any interaction between capacitance, K_{leaf} and g_s, with all species falling on a single relationship between K_{leaf} and g_s (Fig. 2). It is possible that leaf capacitance may serve an alternative purpose of buffering leaf water potential from changes in transpiration, hence allowing a closer approach of the daily operating water potential to the cavitation limit of the xylem (Brodribb & Holbrook, 2004).

K_{leaf} and photosynthesis

It is curious that the photosynthetic capacity of leaves does not follow the same proportional relationship to hydraulic conductivity as g_s. In leaves with $K_{leaf} < 15$ mmol m^{-2} s^{-1} MPa^{-1}, photosynthetic capacity was closely correlated with hydraulic conductance. However, > 15 mmol m^{-2} s^{-1} MPa^{-1} plants appeared to earn diminishing returns for their investments in K_{leaf} and g_s, a pattern culminating with virtually no increase in Φ_{PSII} at values of $K_{leaf}> 20$ mmol m^{-2} s^{-1} MPa^{-1} (Fig. 4). The saturation of Φ_{PSII} in tropical species was confirmed from the similar saturating functions observed during seasonal changes in K_{leaf} of two of the deciduous species here (Fig. 4 and Brodribb & Holbrook, 2003a). Bearing in mind that g_s still appears equally responsive to values of $K_{leaf}> 20$ mmol m^{-2} s^{-1} MPa^{-1}, these highly conductive species will probably yield some benefit in assimilation rate due to higher carboxylation efficiency (resulting from a greater internal leaf concentration of CO_2). However, the increased photosynthetic yield resulting from increased stomatal conductance once electron transport capacity is saturated (as indicated by Φ_{PSII} saturation) is small, and does not conform to conventional ideas of gas exchange optimization (Cowan & Farquhar, 1977).

Previous studies have shown several of the most hydraulically conductive species here to be vulnerable to cavitation under relatively mild water stress (Brodribb & Holbrook,

2003b), and one species, *Simarouba glauca*, experiences diurnal cycles of midday depression of K_{leaf} during the dry season (Brodribb & Holbrook, 2004). This midday reduction in K_{leaf} was found to be associated with a profound drop in both g_s and CO_2 assimilation rate. Hence it is conceivable that in tropical species exposed to large diurnal ranges of VPD it is economical to invest proportionally more in vasculature than photosynthetic capacity such that midday depression of K_{leaf} is buffered against. These observations suggest that high maximum K_{leaf} and g_s in the Costa Rican angiosperms might be a means of optimizing the integrated daily assimilation rate rather than maximum instantaneous gas exchange.

In summary these data illustrate a strong correspondence between leaf vascular architecture and the water loss and photosynthetic characteristics of leaves. These correlated functions are linked by the common pathway for water and CO_2 exchange and a conservative range of leaf potential drops among the species here. These data emphasize the central role played by K_{leaf} in the daily function of plants, and the evolutionary competition between species.

Acknowledgements

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