# Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests

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## ABSTRACT

**A strong relationship between hydraulic supply of water to leaves and maximum photosynthetic capacity was found in a group of seven conifers and 16 angiosperm species, including two vessel-less taxa, from similar rainforest communities in New Caledonia and Tasmania (Australia). Stem hydraulic supply was expressed as the hydraulic conductivity of branches in terms of leaf area supplied ($K_L$) and leaf photosynthetic capacity was measured as the mean quantum yield of PSII ($Ø_{PSII}$) in leaves exposed to full sun, as determined by chlorophyll fluorescence analysis. A single, highly significant linear regression ($r^2 = 0.74$) described the relationship between hydraulic conductivity and quantum yield in all species. This suggests that the maximum photosynthetic rate of leaves is constrained by their vascular supply. In both rainforest locations, the $K_L$ of conifer wood overlapped broadly with that of associated vessel-bearing and vessel-less angiosperms indicating a degree of hydraulic convergence in these forests.**

*Key-words*: angiosperm; conifers; fluorescence; hydraulic conductivity; leaf-specific; quantum yield; vessel-less.

## INTRODUCTION

Xylem hydraulic characteristics have, in recent years, been shown to exert a strong influence over many aspects of the form and function of plants. Transpiration rates of plants ranging in size from small herbs to forest trees appear to be limited by hydraulic constraints of the vascular tissue (Andrade *et al*. 1998; Meinzer *et al*. 1999; Mencuccini & Comstock 1999), and recently vascular systems have also been implicated as the major force controlling allometric scaling in the size, form and even population density of woody plants (West, Brown & Enquist 1999). This control comes about because water flow through higher plants generally obeys the Ohm's law analogue (Van den Honert 1948) and hence the hydraulic properties of the vascular system determine the relationship between transpiration flux and leaf water potential ($\Psi_L$) by dictating the conduc-

tivity of the hydraulic pathway between the leaf and soil (Tyree & Ewers 1991). Probably the most intensively studied part of the plant vascular system is the stem, perhaps because the physics of sap flow through stems is relatively simple, approximated by treating the stem as a collection of tubes (Shinozaki *et al*. 1964) or tapered tubes (West *et al*. 1999). Plant stems not only carry the water supply for transpiration but also provide physical support for the foliage, and hence the size of a stem or branch determines the leaf area it can support. Traditionally, the amount of leaf area attached to a branch was considered to be a function of the mechanical properties of the branch and the mass of the foliage (Niklas 1994), although more recently the concept of leaf area being linked to the hydraulic conductivity of the associated vascular tissue has been supported (Zimmermann 1978; 1983; Tyree *et al*. 1991; Pataki, Oren & Phillips 1998).

Because the hydraulic conductivity of the pathway from soil to leaves determines how much $\Psi_L$ falls below the soil water potential during evapotranspiration, it follows that there should be a link between the hydraulic conductivity of a plant and the transpirational demand of its foliage. Such links have been demonstrated by differences in the vascular supply of water to sun and shade foliage of both individual species (Maherali, DeLucia & Sipe 1997; Schultz & Matthews 1993; 1997), and single trees (Cochard *et al*. 1997), suggesting that factors such as light exposure and evaporative demand interact with the stem hydraulic conductivity per unit leaf area ($K_L$) (Bond & Kavanagh 1999). This interaction has also been implicated in the broad trends of stomatal response to vapour pressure deficit (VPD) across the range of vascular plants (Franks & Farquhar 1999). If the transpirational demand and hydraulic supply of leaves correlate, then the photosynthetic rate should also be reflected in the hydraulic supply, as evaporative water loss and $CO_2$ uptake follow the same pathway.

Given the importance of xylem hydraulic conductivity to plant function, it is interesting that within the seed plants there is a significant functional and morphological distinction between the wood structure of angiosperms and gymnosperms. In angiosperms, axial water flow in the xylem mostly occurs through long, large diameter conduits called vessels. The conduits in conifer xylem are much smaller in

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length and diameter making the specific hydraulic conductivity ($K_{sp}$; conductivity per sapwood area) of conifer wood much lower than that of angiosperms (Tyree & Ewers 1991; 1996; Becker, Tyree & Tsuda 1999). The expected result of this is that angiosperms should either be able to operate with reduced xylem investment per unit leaf area (i.e. with a lower sapwood to leaf area ratio; Huber value) or sustain higher rates of transpiration than conifers with equivalent Huber values and water potential gradients. It has also been suggested that the higher conductivity of angiosperm xylem gives them a competitive advantage during regeneration, thus accounting for the relative success of angiosperms compared with conifers in productive environments (Bond 1989). These hypotheses remain largely untested, although some hydraulic conductivity measurements have found the $K_L$ of conifers to be within the range of associated angiosperm taxa (Becker *et al.* 1999).

In this study, we examine the relationship between $K_L$, quantum yield of PSII electron transport ($\emptyset_{PSII}$), and leaf-water potential ($\Psi_L$) in branches of angiosperm and conifer species from tropical and sub-alpine rainforest communities in order to test for a correlation between foliar demand and vascular supply of water. Although the conductivity of individual stems is much higher than the conductivity of whole plants, studies have shown a broad correlation between the two (Tyree, Velez & Dalling 1998; Becker *et al.* 1999; Brodribb & Hill 2000), and hence we assume $K_L$ reflects whole-plant conductivity. A correlation between $\emptyset_{PSII}$ and $K_L$ therefore would not only indicate co-ordination between leaf demand for water and hydraulic supply, but also provide a link between whole-plant, and stem hydraulic conductivity, thus enabling stem hydraulics to be used as a proxy for maximum transpiration and photosynthesis.

Quantification of the photosynthetic capacity of the leaf area on a branch is extremely difficult, time consuming and potentially inaccurate using conventional gas-exchange (IRGA) equipment in the field, and for this reason chlorophyll fluorescence was employed to determine photosynthetic potential. The use of fluorescence as a tool for probing photosynthetic electron transport and carbon assimilation in the light has been relatively limited in $C_3$ plants due to uncertainty in the relationship between linear electron transport and $CO_2$ uptake (Genty, Briantais & Baker 1989; Bilger, Schreiber & Buck 1996). This is mainly because chlorophyll fluorescence provides information about the reduction state of PSII and hence does not allow discrimination between electrons used for carboxylation as opposed to oxygenation of Ribulose 1,6 bi-phosphate, the Mehler reaction, and non-assimilatory electron transport routes (Edwards & Baker 1993; Cheeseman *et al.* 1997; Fryer *et al.* 1998; Flexas *et al.* 1999). Despite this, good correlations between $CO_2$ assimilation measured by infra-red gas analysis (IRGA) and that calculated by $\emptyset_{PSII}$ have been shown under a range of light, temperature and humidity conditions in $C_3$ species (He & Edwards 1996). Here we have used chlorophyll fluorescence to provide relative information about the $\emptyset_{PSII}$ in species measured under very

similar, non-limiting conditions of light, temperature, water availability and $CO_2$ concentration. Under these conditions, it is likely that differences in photorespiration would be small, and a previous study of a diverse group of conifers using a similar fluorescence protocol showed a very good correlation between maximum photosynthetic electron transport rate and maximum $CO_2$ assimilation (Brodribb & Hill 1997). Relative quantum yields should also be closely related to stomatal conductances and transpiration rates, considering that the relationship between $CO_2$ uptake and stomatal conductance in $C_3$ plants is effectively conserved (Körner, Farquhar & Wong 1991). The two main advantages of using fluorescence as a measure of photosynthesis are, first, that the period required for individual leaf measurements is very small, allowing a large number of measurements to be made on each branch, and second that the equipment is highly portable, enabling measurement of plants which are effectively inaccessible to IRGA equipment.

The rainforest communities investigated were evergreen mixed conifer-angiosperm forests in New Caledonia and Tasmania (Australia). These sites were selected because the coexistence of conifers and angiosperms at both locations allowed us to test whether consistent differences were evident between vessel-bearing angiosperms and vessel-less conifers in the hydraulic supply of water to the leaf, $\Psi_L$, and photosynthetic capacity. At least one species from the vessel-less angiosperm family Winteraceae was present at each location, enabling a comparison of the effect of vessels both within the angiosperms and between angiosperms and conifers.

## MATERIALS AND METHODS

### Study sites

Fieldwork was carried out in August 1999 in New Caledonia and January 2000 in Tasmania. The New Caledonian site was located on Mt. Dzumac (22°02′ S latitude, 166°28′ E longitude) in mature mixed conifer-angiosperm rainforest growing at an altitude of approximately 900 m on ultramafic soil. This mountain experiences a high rainfall, the majority of which falls in summer months, although winter rainfall is also substantial. Climate data are limited for this site with 2 years of annual rainfall totalling 1816 mm and 2742 mm, approximately half of this falling from December–March (Enright & Goldblum 1998). Mean monthly temperatures fall in the range 14–22 °C (unpublished results IRD). Twelve evergreen woody tree species were measured including eight angiosperms: *Ascarina rubicaulis* (Solms)*, Carpolepis laurophylla, Cunonia pterophylla* (Schlecte)*, Nemuaron vieillardii* (Baillon) Baillon, *Nothofagus codonandra* (Baill.) Van Steenis, *Loxodiscus coriaceus* (Hook.f)*, Styphelia* spp. *and* the vessel-less *Zygogynum baillonii* Van Tieghem, and four conifer species: *Acmopyle pancheri* (Brogn. & Gris) Pilger, *Agathis lanceolata* Warburg, *Falcatifolium taxoides* (Brogn. & Gris) de Laubenfels, and *Retrophyllum comptonii* C.N.Page.

The Tasmanian part of this study was carried out at Mt. Field (42°41′ S, 146°35′ E) in a dwarf sub-alpine mixed conifer forest, growing at 1200 m in a humic soil. Rainfall at Mt. Field is approximately 2200 mm, with no appreciable dry season, and mean monthly maximum temperatures ranging from 14·5 °C in summer to 2·5 °C in winter. Nine evergreen woody tree and shrub species were selected including three conifers; *Diselma archeri* (Hook.f.), *Podocarpus lawrencei* (Hook.f.) and *Phyllocladus aspleni-ifolius* (Labill.) Rich ex Hook.f., and six angiosperms; *Nothofagus cunninghamii* (Hook.) Oersted, *Atherosperma moschatum* Labill., *Richea scoparium* Hook.f., *Eucalyptus coccifera* Hook.f., *Leptospermum rupestre* Hook.f., and the vessel-less *Tasmannia lanceolata* (Poiret) A.C.Smith.

In order to maximize the range of $K_L$ and $Ø_{PSII}$, we also included two fast-growing pioneer species known to have high $K_L$ (Brodribb & Hill, 2000). These were *Eucalyptus regnans* F. Muell. and *Toona australis* (F. Muell.) Harms. Five plants of each of these two species were grown in a glasshouse under optimal conditions of light, temperature and nutrition.

## Stem hydraulic conductivity

Maximum vessel lengths in all species were measured by cutting branches approximately 1 m from the most distal apex and applying a small air pressure to the cut end of the branch. The distal end of the branch was then trimmed back until air bubbles were seen emerging from vessel ends. All stems for hydraulic conductivity measurements were cut to approximately the same length (0·2–0·3 m), which was 10% larger than the largest vessel length measured. This ensured no open vessels were present, and that variation in branch length between species was small.

Sun-exposed branches were collected from four individual trees of each species and measured in the field. Lateral branches were always used as these are more conservative in their $K_L$ than leaders (Zimmermann 1983). Segments cut from these laterals were chosen such that there were no major branches along their length. Stem hydraulic conductivity ($K_H$) was defined as the mass flow rate of water through an excised stem segment per unit pressure gradient (kg s$^{-1}$ MPa$^{-1}$ m). We used a low-pressure steady-state flow meter (SSFM) method, which uses the drop in pressure across a tube of known conductance to measure the flow rate into the stem segment, together with the pressure at the stem fitting, to calculate $K_H$; (Zwieniecki *et al.* 2000; Feild & Holbrook, in press). This method was chosen over traditional methods for measuring stem $K_H$ using an analytical balance because of the remoteness of the field sites. Briefly, an elevated reservoir was used to drive water through a 1·25 m long piece of capillary tubing (PEEK, Upchurch Scientific, WA, USA) and the stem segment, arranged in series. The reservoir water was filtered through a 0·1 $\mu$m filter before reaching the stem. Two pressure transducers (PX236, Omega Engineering Inc., Stamford, CT, USA) were used to measure the pressure at each end of the capillary tube, allowing both the pressure drop across

the capillary tube and the delivery pressure to the stem segment to be determined. The capillary tube could be easily interchanged with PEEK capillary tubes of different inner diameters (and lengths) to make it so that the conductance of the tube was approximately equal to that of the stem (Zwieniecki *et al.* 2000). The conductance of each tube was determined in the laboratory by comparing the pressure drop across the tube at a known temperature to the outflow rate measured by an analytic balance (± 0·01 mg). Four delivery pressures (0·0008, 0·0015, 0·0025, 0·0035 and 0·050 MPa) were used and a linear calibration equation determined for each capillary tube (Zwieniecki *et al.* 2000). Capillary tubes were calibrated before travel to the field and then immediately upon return to check for drift. After correcting for temperature, a 2% change was observed in the calibration value over a 2 month period. Stems were measured under delivery pressures ranging from 0·003 to 0·01 MPa. In this range, mass flux is linearly related to applied pressure for stems (Sperry *et al.* 1988). Data were recorded when steady-state pressure readings were achieved (typically 10 min) after connection to flowmeter apparatus. During all measurements, stem temperature was measured with a copper-constantan thermocouple (30 American wire gauge, Omega Engineering) so that the effect of temperature on viscosity of water flux could be removed by normalizing all measurements to 20 °C (Sperry *et al.* 1988).

Branches were sampled at times when losses of hydraulic conductivity due to embolisms were probably at a minimum [i.e. early morning (0800–0930 h) on wet, cloudy days]. Sampled branches were cut in the field, triple bagged in plastic and transported immediately to a laboratory in a tent. Both ends of the stem segment were shaved with a fresh razor blade before attachment to the SSFM. Sapwood-area specific conductivity ($K_{sp}$; kg MPa$^{-1}$ m$^{-1}$ s$^{-1}$) was determined by dividing stem $K_H$ by the sapwood cross-section area. Sapwood cross-section was measured with a micrometer along the major and minor axes of the distal stem end and the surface area contributed by the pith was subtracted (Sperry *et al.* 1988). Leaf specific conductivity ($K_L$; kg MPa$^{-1}$ m$^{-1}$ s$^{-1}$) was determined by dividing $K_H$ by the total leaf area supported (i.e. distally) by that branch. After determination of $K_H$, sapwood area of the distal part of the stem was measured as was the leaf area distal to the stem segment. In New Caledonia leaf, outlines were traced onto paper and leaf area measured in the laboratory using a digital camera (EDC-1000, Electrim Corp. Princeton, USA), while in Tasmania leaves were transported back to the laboratory in plastic bags prior to leaf area determination.

## Water potential

Leaf water potentials were measured only on New Caledonian species. An average $\Psi_L$ was determined for each species from four individuals measured during midday on a single cloudless day. Leaves were cut from fully exposed branches and immediately transferred to dark humid bags. All leaf samples were collected within a 30 min period and

measured over the following 30 min. Measurements of $\Psi_L$ were carried out using a Scholander pressure bomb attached to a high-pressure bicycle pump.

## Chlorophyll fluorescence

The quantum yield of PSII electron transport ($\varnothing_{PSII}$) was determined in the light using a PAM-2000 portable fluorometer (Waltz, Effeltrich, Germany) operated in the field according to Bilger *et al.* (1996). Preliminary measurements made throughout the day indicated that $\varnothing_{PSII}$ determined at a PPFD of 1000 μmol m$^{-2}$ s$^{-1}$ peaked at around midday, and there was no evidence of midday depression of $\varnothing_{PSII}$ (T. J. Brodribb, unpublished results). Therefore all measurements were made within 60 min of midday on a single cloudless day at both Mt Dzumac and Mt Field. Five measurements of $\varnothing_{PSII}$ were made on each of five representatives of each species. We selected fully expanded leaves from exposed, undamaged branches and $\varnothing_{PSII}$ 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 full sun. Saturation pulses were applied for 0·8 s at an intensity of 3500 μmol m$^{-2}$ s$^{-1}$. In full sun, the PPFD on Mt. Dzumac was 1700 μmol m$^{-2}$ s$^{-1}$ while on Mt. Field it was 1900 μmol m$^{-2}$ s$^{-1}$. Mean leaf temperatures in New Caledonia and Tasmania were similar and ranged between 23·2 °C and 20·1 °C respectively.

## RESULTS

A large range of leaf-specific hydraulic conductivities was found in both New Caledonian and Tasmanian species, extending from a maximum of 2·94 × 10$^{-4}$ kg s$^{-1}$. MPa$^{-1}$ m$^{-1}$ in *C. pterophylla* to a minimum of 0·308 × 10$^{-4}$ kg s$^{-1}$ MPa$^{-1}$ m$^{-1}$ in *P. aspleniifolius*. The mean $K_L$ for New Caledonian taxa (1·72 × 10$^{-4}$ kg s$^{-1}$ MPa$^{-1}$ m$^{-1}$) was slightly higher than for Tasmanian taxa (1·57 × 10$^{-4}$ kg s$^{-1}$ MPa$^{-1}$ m$^{-1}$), although differences were not significant. A correspondingly large range in $\varnothing_{PSII}$ was observed, extending from 0·29 in *C. pterophylla* to an extremely low mean of 0·04 in *P. aspleniifolius*. Full sun conditions decrease the sensitivity of the fluorometer and this, combined with the natural variability to produce standard errors of up to a maximum of 25% of the mean (Fig. 1).

A strong linear correlation was observed between $K_L$ and $\varnothing_{PSII}$ (Fig. 2). The intercept of the regression was not significantly different from zero indicating the relationship between $\varnothing_{PSII}$ and $K_L$ was probably proportional. Independent (type II) regression analysis of Tasmanian and New Caledonian data showed no significant differences in the slopes or intercepts, and hence data from both sites were pooled together. It is clear from Fig. 2 that conifers produced lower $K_L$ and $\varnothing_{PSII}$ than the associated angiosperms at both sites, and this was confirmed by a *T*-test which was significant at the $P < 0.001$ level. A much weaker but still significant correlation ($r = 0.492$; $0.01 < P < 0.02$) was observed between $K_{sp}$ and $\varnothing_{PSII}$ con-
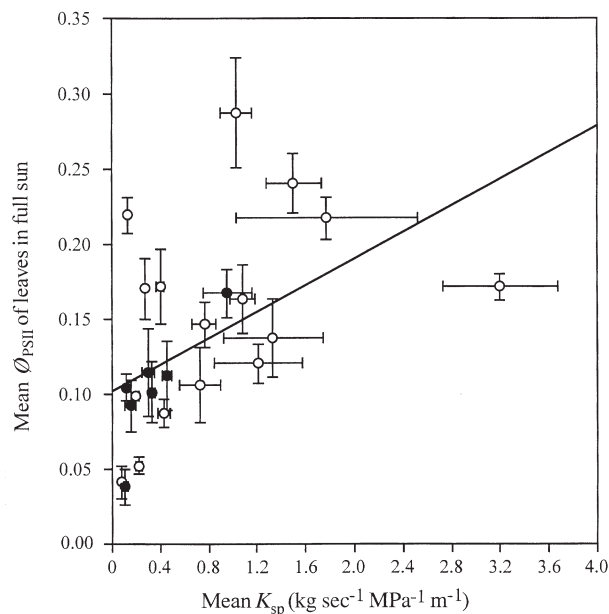


**Figure 1.** Illustrates a weak linear correlation ($r^2 = 0.49$) between mean specific conductivity ($K_{SP}$) of stem wood ($n = 4$) from seven conifers (●) and 16 angiosperms (○) and mean $\varnothing_{PSII}$ ($n = 5$) measured in full sun. Standard error bars are shown for both $K_{SP}$ and $\varnothing_{PSII}$.

firming the expected result that $\varnothing_{PSII}$ was better correlated with conductivity per unit leaf area (Fig. 1).

Amongst the angiosperms from both New Caledonia and Tasmania, the vessel-less taxa *Z. baillonii* and *T. lanceolata* produced the lowest values of $K_L$, with *A. moschatum* the only other angiosperm producing comparably low $K_L$ and $\varnothing_{PSII}$.

Simultaneous readings of $\Psi_L$ made on New Caledonian taxa illustrated that conifers produced lower water potentials than associated angiosperms at midday under conditions of full sun and high soil moisture (Fig. 3). The range of mean $\Psi_L$ exhibited by angiosperm taxa was − 0·67 to − 0·30 MPa while conifers fell in the range − 0·99 to − 0·69 MPa. There was a weak but significant correlation between $\Psi_L$ and $K_L$ ($P < 0.05$) although this correlation was not significant if conifers were removed from the data.

Huber values (sapwood area per leaf area) showed more variation between sites than within, with no significant difference between conifers and angiosperms either at Mt. Dzumac or Mt. Field (Table 1; *t*-test).

## DISCUSSION

The highly significant relationship between $\varnothing_{PSII}$ in full sun and $K_L$ shown here for a group of rainforest conifers and angiosperms suggests a close link between the photosynthetic capacity (and hence evapo-transpirational demand) of foliage, and the hydraulic supply of water to the leaves. Several studies have indicated that leaves respond to vascular limitations during drought (Bond & Kavanagh 1999;
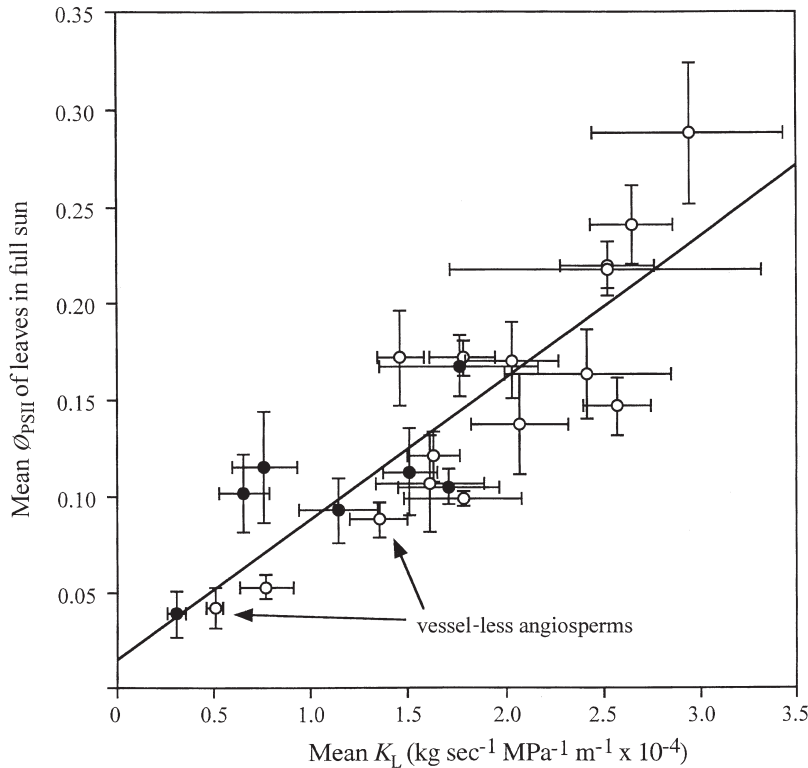
**Figure 2.** A strong correlation ($r^2 = 0.74$) is shown between mean leaf-area specific conductivity ($K_L$) of stems ($n = 4$) from seven conifers (●) and 16 angiosperms (○) and mean $\varnothing_{PSII}$ ($n = 5$) measured in full sun. The x-intercept of the regression is not significantly different from zero suggesting a proportional relationship. Two vessel-less species from the family Winteraceae are arrowed.

Brodribb & Hill 1999; Kolb & Sperry 1999) primarily to avoid cavitation of the xylem tissue. Figure 2, however, illustrates that the photosynthetic capacity of leaves under optimal conditions is related to the hydraulic conductance of the supporting xylem tissue. This relationship appears to apply to all taxa investigated including conifers and both vessel-less and vessel-bearing taxa from New Caledonia and Tasmania. The correlation between hydraulic and leaf photosynthetic data provides a connection between the suite of traits linked by allometry, such as leaf length, surface area, internode length and stem cross-sectional area (Ackerly & Donoghue 1998; Brouat *et al*. 1998) and leaf traits linked by physiology, such as leaf photosynthetic rate, leaf nitrogen, specific leaf area and leaf life span (Ackerly & Reich 1999). Currently these two constellations of characters are considered to evolve independently, although the data here suggest an interaction through $K_L$.

By focussing on optimal conditions, the data here indicate the potential to infer maximum leaf photosynthetic rates from hydraulic data. Because $\varnothing_{PSII}$ is effectively a proxy for assimilation rate under uniform conditions of light intensity and intercellular $CO_2$ concentration ($c_i$) (He & Edwards 1996; Brodribb & Hill 1997 ), it is related to the rate of evapo-transpiration by the leaf-to-air vapour-pressure deficit. The importance of $c_i$ is that it dictates the fraction of electrons from PSII being used for oxygenation of RuBP as opposed to carboxylation (Muraoka *et al*. 2000). Thus, it would be expected that a single model of $\varnothing_{PSII}$ from $K_L$ would only describe plants from conditions of similar vapour-pressure deficit and $c_i$ (e.g. full sun exposure, unlim-

ited water supply, and similar altitude). The effects of VPD are potentially very significant because the water-use efficiency of carbon assimilation is inversely proportional to the VPD. Species growing under conditions of high VPD
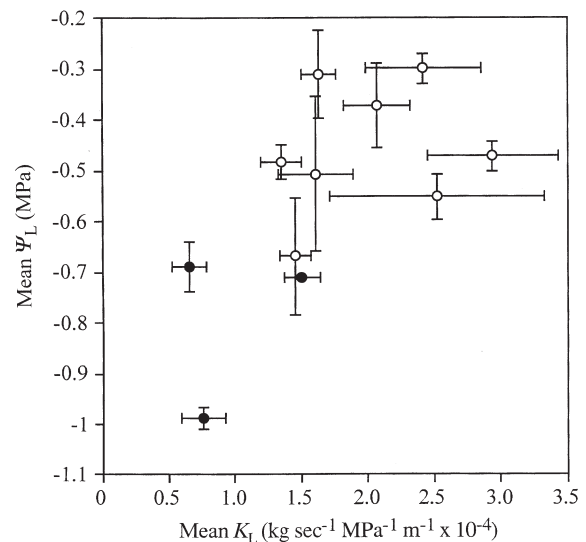


**Figure 3.** A plot of mean leaf water potential ($n = 4$) versus mean $K_L$ ($n = 4$) for three conifers (●) and eight angiosperms (○) from New Caledonia. Although mean $\Psi_L$ of the three conifers was lower than the mean for angiosperms (*t*-test) was no significant correlation between $K_L$ and $\Psi_L$ either within groups or in the pooled data.

**Table 1.** Mean ± SE ($n = 4$) leaf and sap-wood area specific stem hydraulic conductivity (kg s$^{-1}$ MPa$^{-1}$ m$^{-1}$), PSII quantum yield at midday ($n = 5$) and Huber value (sapwood area per unit leaf area; $n = 4$) for branches of 21 conifer and angiosperm species from New Caledonia and Tasmania, as well as two glasshouse grown angiosperm species from mainland Australia

| Species (Family) | $K_{sp}$ | $K_L \times 10^4$ | $\emptyset_{PSII}$ | Hv $\times 10^4$ |
|---|---|---|---|---|
| **Mt. Dzumac (New Caledonia)** | | | | |
| *Acmopyle pancheri* (Podocarpaceae) | 0·33 ± 0·02 | 0·66 ± 0·13 | 0·102 ± 0·02 | 2·02 ± 0·20 |
| *Agathis lanceolata* (Araucariaceae) | 0·95 ± 0·20 | 1·76 ± 0·41 | 0·168 ± 0·02 | 2·60 ± 0·52 |
| *Falcatifolium taxoides* (Podocarpaceae) | 0·30 ± 0·05 | 0·76 ± 0·17 | 0·115 ± 0·03 | 2·70 ± 0·54 |
| *Retrophyllum comptonii* (Podocarpaceae) | 0·45 ± 0·04 | 1·51 ± 0·14 | 0·113 ± 0·02 | 3·50 ± 0·39 |
| *Ascarina rubicaulis* (Chloroanthaceae) | 1·08 ± 0·10 | 2·42 ± 0·43 | 0·164 ± 0·02 | 2·20 ± 0·20 |
| *Carpolepis laurophylla* (Myrtaceae) | 1·77 ± 0·75 | 2·52 ± 0·80 | 0·218 ± 0·01 | 0·62 ± 0·10 |
| *Cunonia pterophylla* (Cunoniaceae) | 1·03 ± 0·13 | 2·94 ± 0·49 | 0·288 ± 0·04 | 2·80 ± 0·19 |
| *Loxodiscus coreaceus* (Sapindaceae) | 0·40 ± 0·03 | 1·46 ± 0·12 | 0·172 ± 0·03 | 3·80 ± 0·46 |
| *Nemuaron vieillardii* (Atherospermataceae) | 1·21 ± 0·36 | 1·63 ± 0·13 | 0·121 ± 0·01 | 2·00 ± 0·27 |
| *Nothofagus codonandra* (Nothofagaceae) | 1·33 ± 0·41 | 2·07 ± 0·25 | 0·138 ± 0·03 | 2·10 ± 0·29 |
| *Styphelia* sp. (Epacridaceae) | 0·73 ± 0·17 | 1·61 ± 0·28 | 0·107 ± 0·03 | 2·30 ± 0·17 |
| *Zygogynum baillonii* (Winteraceae) | 0·43 ± 0·05 | 1·35 ± 0·15 | 0·088 ± 0·01 | 3·20 ± 0·44 |
| **Mt. Field (Tasmania)** | | | | |
| *Diselma archeri* (Cupressaceae) | 0·12 ± 0·01 | 1·71 ± 0·26 | 0·105 ± 0·01 | 13·80 ± 1·61 |
| *Phyllocladus aspleniifolius* (Podocarpaceae) | 0·11 ± 0·02 | 0·31 ± 0·05 | 0·039 ± 0·01 | 2·99 ± 0·99 |
| *Podocarpus lawrencei* (Podocarpaceae) | 0·15 ± 0·04 | 1·14 ± 0·20 | 0·093 ± 0·02 | 9·27 ± 2·42 |
| *Atherosperma moschatum* (Atherospermataceae) | 0·22 ± 0·03 | 0·77 ± 0·14 | 0·053 ± 0·01 | 3·47 ± 0·25 |
| *Eucalyptus coccifera* (Myrtaceae) | 0·76 ± 0·10 | 2·57 ± 0·17 | 0·147 ± 0·02 | 2·87 ± 0·33 |
| *Leptospermum rupestre* (Myrtaceae) | 0·19 ± 0·03 | 1·78 ± 0·30 | 0·099 ± 0·01 | 9·60 ± 0·84 |
| *Nothofagus cunninghamii* (Nothofagaceae) | 0·27 ± 0·02 | 2·03 ± 0·24 | 0·171 ± 0·02 | 7·53 ± 0·56 |
| *Richea scoparium* (Epacridaceae) | 0·13 ± 0·01 | 2·52 ± 0·24 | 0·220 ± 0·01 | 21·00 ± 2·37 |
| *Tasmannia lanceolata* (Winteraceae) | 0·08 ± 0·01 | 0·50 ± 0·04 | 0·042 ± 0·01 | 6·70 ± 0·71 |
| **Glasshouse** | | | | |
| *Eucalyptus regnans* (Myrtaceae) | 3·20 ± 0·47 | 2·65 ± 0·21 | 0·241 ± 0·02 | 0·65 ± 0·09 |
| *Toona australis* (Meliaceae) | 1·50 ± 0·23 | 1·78 ± 0·17 | 0·172 ± 0·01 | 0·87 ± 0·11 |

will therefore require more water to maintain similar rates of $CO_2$ uptake (and $\emptyset_{PSII}$) and may thus be expected to develop higher values of $K_L$ than species growing at low VPD. The other parameter likely to influence the $\emptyset_{PSII}$ versus $K_L$ function is temperature, through its effect on fluid viscosity. A plant growing at 10 °C will have approximately 25% lower hydraulic conductance, and thus 25% lower stomatal conductance than the same plant growing at 20 °C all else being equal. Assuming good correlation between stomatal conductance, photosynthetic rate and $\emptyset_{PSII}$ this should result in $\emptyset_{PSII}$ being approximately 25% lower at the lower temperature. Hence the slope of the $\emptyset_{PSII}$ versus $K_L$ function should be temperature dependent, responding to the temperature of the whole hydraulic pathway during measurement. Possibly this temperature effect would be removed by measuring the rate of $CO_2$ uptake rather than $\emptyset_{PSII}$. This is because higher temperatures increase photorespiration by reducing $CO_2$ specificity of RubisCo (Brooks & Farquhar 1985) and changing the solubility ratio of $CO_2$ to $O_2$ (Ku & Edwards 1977). Interestingly, for a temperature increase of 10 °C to 20 °C the relative magnitudes of the viscosity and photorespiratory effects are similar (Brooks & Farquhar 1985; Ghashghaie & Cornic 1994), but because they act in opposite directions the relationship between $CO_2$ uptake and $K_L$ may be temperature independent.

The mean temperature difference between the field sites at Mt. Field and Mt. Dzumac is approximately 10 °C, however, mean leaf temperatures during $\emptyset_{PSII}$ determinations were similar at both locations. This explains the very similar slopes of $K_L$ versus $\emptyset_{PSII}$ for plants from Mt. Field compared with Mt. Dzumac (Fig. 2). The data here do suggest that Mt. Field plants on average produced slightly lower $\emptyset_{PSII}$ than those from Mt. Dzumac with equivalent $K_L$, however, these differences were not significant due to the considerable scatter in the data. A possible reason for this slight difference could be that root temperatures at Mt. Field were lower than at Mt. Dzumac, decreasing root conductivity by viscosity effects. The fact that species from both New Caledonia and Tasmania produced mean $K_L$ and $\emptyset_{PSII}$ which were related by very similar regressions, indicates that other factors potentially affecting the relationship, such as moisture availability in the soil, and the leaf to air VPD, must be similar at both sites. This is supported by the limited climatic data for these two mountains indicating high rainfall and low VPD. Strong similarities are also evident in the structure of plant communities (Gibson *et al.* 1995; Jaffré 1995) at both locations, suggesting that despite their geographic separation these two locations provide similar environments.

The linkage between hydraulic and photosynthetic capacity demonstrated here under optimal conditions pre-

sumably occurs by coupling through $\Psi_L$. Essentially, a greater hydraulic supply to leaves allows the leaf to realize a higher stomatal conductance (for both water and carbon dioxide) while maintaining $\Psi_L$ roughly constant. It is probable, however, that measurements made under stressful conditions may not show such a correlation. The reason for this is that the dynamics of changing photosynthetic yield, hydraulic conductivity and $\Psi_L$ during stress (particularly water stress) will be species dependent (e.g. Brodribb 1996). As a result there may be a large range in the ratio of photosynthetic yield to hydraulic conductivity in a single community during stressful conditions such as drought. The phenomenon of feed-forward stomatal response to atomospheric and soil drought (Cowan 1977; Thomas & Eamus 1999) is an example of a condition where the co-ordination of hydraulic conductivity, $\Psi_L$ and photosynthesis breaks down, and under these circumstances $\emptyset_{PSII}$ would not correlate with $K_L$. Another problem with measuring under stressful conditions is that the relationship between $\emptyset_{PSII}$ and $CO_2$ assimilation deteriorates under conditions such as low temperature (Fryer *et al*. 1998) and drought stress (Krall & Edwards 1992) due to increased electron flow to photorespiration and the Mehler reaction. Under such conditions $\emptyset_{PSII}$ will be poorly correlated with stomatal conductance, and thus, probably, $K_L$.

Although our measurements indicate that conifers and vessel-less angiosperms produce lower mean $K_{SP}$ (Fig. 1) and $K_L$ (Fig. 2) than associated angiosperms (as well as lower $\Psi_L$ in conifers; Fig. 3), the data also highlight the functional overlap between these groups (Tyree & Ewers 1991; Becker *et al*. 1999; Brodribb & Hill 2000). Evidence for this functional overlap is seen in the significant convergence of wood physiological characters in all plant groups including conifers, vessel-less and vessel-bearing taxa investigated at both Mt. Field and Mt. Dzumac. This is illustrated by the fact that $K_{SP}$ in all plant groups were significantly lower at Mt. Field than Mt. Dzumac (0·22 compared with 0·83 kg $s^{-1}$ $MPa^{-1}$ $m^{-1}$; Table 1) while $K_L$ values from both sites fell into similar ranges. Morphological convergence has also been shown between leaves of conifers investigated here and broad-leaved angiosperms (Brodribb & Hill 1997) suggesting that neither the presence nor absence of vessels is strongly selected under the conditions present at Mt. Field and Mt. Dzumac. It appears that under the stable, wet conditions provided by both Mt. Field and Mt. Dzumac, convergence over long periods has allowed coexistence of diverse and ancient plant lineages.

Our results show a good correlation between relative maximum demand for leaf water measured by $\emptyset_{PSII}$ and hydraulic supply of water to leaves (Fig. 1) in a diverse range of plants from two similar rainforest communities. This relationship illustrates an important link between leaf photosynthetic physiology and the characteristics of hydraulic supply through the xylem, though further work is needed to investigate the effects of water availability and VPD on this hydraulic-photosynthetic correlation. We have also shown that although the stem hydraulic conductivities of conifers and vessel-less angiosperms are, on average, lower than that of associated vessel-bearing angiosperms, considerable overlap exists, illustrating a degree of convergence in wood conductivity between the associated species at each site.

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