

Seedling growth in conifers and angiosperms: impacts of contrasting xylem structure

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Abstract. Competitive interaction between conifers and angiosperms has moulded the structure of global vegetation since the Cretaceous. Angiosperms appear to enjoy their greatest advantage in the lowland tropics, an advantage often attributed to the presence of vessels in their xylem tissue. By monitoring the seedling growth of three members of the pan-tropical conifer family Podocarpaceae and three tropical angiosperm tree species, our aim was to determine whether these conifer and angiosperm seedlings showed distinct patterns of growth and light adaptation that might be attributed to the presence/absence of vessels. Angiosperm seedlings were consistently more efficient in terms of leaf area carried per unit stem investment, as well as more responsive to light climate than the conifer seedlings. Apparently linked to this were larger growth rate, stem hydraulic conductivity and stomatal conductance in the angiosperm sample. Stem hydraulic conductivity and maximum stomatal conductance were highly correlated among species and light treatments explaining the association between highly conductive vessel-bearing wood and high rates of gas exchange. We conclude that xylem vessels contribute to higher rates of gas exchange and more efficient production of leaf area in our sample angiosperms than in conifers. However, this advantage is limited by shade.

Introduction

The Cretaceous radiation in angiosperm diversity has been proposed as having a major influence on the subsequent decline in gymnosperm diversity (Stebbins 1974; Knoll 1986). A popular theory accounting for gymnosperm decline invokes displacement of conifers by angiosperms, putatively superior in both reproductive and vegetative potential (see Bond 1989 for review). There are good reasons to suspect that vegetative innovations in the angiosperm lineage have contributed to their success, and that these characters (namely vascular and leaf morphological traits) enable angiosperm seedlings to overwhelm conifer competitors (Bond 1989; also see review by Feild *et al.* 2004). However, it is important to bear in mind that conifer families dominate many temperate and most boreal regions, and that it is only in lowland subtropical and tropical forests that conifers tend to be absent. In order to understand which aspects of angiosperm physiology may be responsible for conifer displacement, it is most informative to compare tropical angiosperms and conifers, and to contrast their performance in an environment where angiosperm traits have proven superior.

The feature most likely to differentiate conifers and angiosperms in terms of assimilation and growth potential is the absence of vessels in conifer wood. Conifer wood is comprised solely of tracheids, generally <30 µm in lumen diameter and ~1–3 mm in length (Panshin and De Zeeuw 1980), whereas angiosperm wood typically contains large lumen cells (commonly 100–200 µm in diameter) joined in series with degraded end walls that form tubes often metres in length (Zimmermann and Jeje 1981). Because the hydraulic conductivity of tubes is proportional to the fourth power of their radius, these vessels enable angiosperms to produce wood which is many times more conductive (per cross-sectional area) to water than conifer xylem (Tyree *et al.* 1991). The benefits of highly conductive xylem are clear, given the evidence for a general correlation between xylem conductance and photosynthetic capacity (Brodribb and Feild 2000; Hubbard *et al.* 2001). However, large conduits can also become a liability under freezing conditions because of freeze–thaw embolism of xylem vessels (Sperry *et al.* 1994). This process is highly sensitive to conduit size, meaning that that most (but not all; see Pittermann and Sperry 2003) conifer tracheids are immune from freeze embolism during

winter freezing. Angiosperm xylem composed of vessels can suffer almost complete deactivation after freezing, leading to winter deciduousness in many temperate species.

The low hydraulic conductivity of conifer xylem has been suggested as a primary cause of reduced conifer competitiveness in the tropics because of the restricted distribution of water and nutrients to leaves (Bond 1989). Although this argument oversimplifies the physiological advantages of vessels over tracheids, it is appealing to imagine that the greater efficiency afforded by vesseliferous wood might enable more rapid growth of seedlings, particularly under carbon-limited (shady) conditions. The term 'efficiency' here refers to the volume of water carried per mass of carbon invested in vasculature, and it should be of great importance to plants as photosynthetic rates among species vary in proportion to the water-carrying capacity of the xylem (Brodribb and Feild 2000; Hubbard *et al.* 2001).

Given their lower xylem conductivity per cross-sectional area (K_{sp}), conifers must either (1) carry less foliage per branch, (2) produce lower rates of water loss (and photosynthesis) per leaf or (3) compensate for lower hydraulic conductivity with a larger water-potential gradient than angiosperms. First, it appears true that conifers compensate for low xylem conductivity by investing more xylem tissue per leaf, although hydraulic conductivity, when normalised to leaf area (K_l), is still generally lower in conifers than in associated angiosperms (Becker *et al.* 1999; Brodribb and Feild 2000). Second, there is some evidence that the stomatal conductance and photosynthetic rate of conifer foliage are lower than those of angiosperms, both in comparisons among neighbouring species (Brodribb and Feild 2000; Lusk *et al.* 2003) and in terms of maximum rates (Körner *et al.* 1979). Finally, there are few data to test the third hypothesis that conifer leaves operate at lower water potentials (ψ_l) than angiosperm leaves, thus enabling them to maintain similar evaporative fluxes by increasing the water-potential gradient across the plant. However, there is evidence that conifer wood is more resistant to dysfunction at low water potentials than associated angiosperms (Sperry *et al.* 1994; Tyree *et al.* 1998; Brodribb and Hill 1999), suggesting that conifer leaves may operate at lower water potentials than those of neighbouring angiosperms.

Another advantage of vessel-bearing wood is that the functions of water conduction and tree support can be differentiated. This is because a relatively small area of water-conduction tissue is required in stems (because of the presence of vessels), thus necessitating the incorporation of specialised load-bearing tissue (fibres) into the vascular bundle to support leaves. In conifers, by contrast, the tracheids perform both support and water-supply functions, with only minimal differentiation of tracheids in load-bearing parts of the plant (compression wood). This specialisation of tissues in angiosperms, one might imagine, would lead to

a greater optimisation of conductance and support functions in angiosperms. Such optimisation should become most evident in the comparison of sun and shade plants where the roles of conduction and support are likely to be the most variable.

In this study, we compare the growth rate, allometry and hydraulic properties of conifer and angiosperm seedlings from tropical and temperate climates to determine whether patterns in stem and leaf-area growth are related to K_{sp} in these species. We focus on conifer species from the most successful conifer family in the tropics, the Podocarpaceae. Podocarps are known for expressing a diversity of mechanisms for producing flattened shoots functionally analogous to angiosperm broad-leaves (Brodribb and Hill 1997), and two of the species chosen here produce rapid growth rates and broad (>5-cm-wide) leaves reminiscent of angiosperm leaves. For comparison, we used a fast-growing tropical Meliaceae, a primary tropical forest species (Rubiaceae), and a fast-growing *Eucalyptus* species. Growth of seedlings under contrasting light intensities is compared in order to test the relative flexibility of seedling allometry in these conifer and angiosperm trees.

Materials and methods

Plant material

Within the large constraints of seed availability and germinability of the tropical Podocarps we were able to find three species that served our criteria of fast-growing trees, two of which are tropical species. The three conifers chosen for this study are all rainforest taxa, two from tropical South-east Asia (*Nageia fleuryi* from tropical southern China and *Podocarpus greyii* from tropical north-eastern Australia) and one from New Zealand (*Dacrydium dacrydioides*). *Podocarpus* was chosen because it is the most diverse conifer genus in the tropics, whereas *Nageia* is a fast-growing tree with broad, multi-veined leaves. *Dacrydium* is also a highly successful tropical genus and *D. dacrydioides*, although more temperate in origin than the other conifers, is the fastest-growing conifer in New Zealand (Ebbitt and Ogden 1998). Both *N. fleuryi* and *P. greyii* regenerate in the forest understorey, whereas *D. dacrydioides* tends to regenerate in forest gaps or more commonly in open riverine environments.

The three angiosperms chosen were from tropical (*Toona australis*, Meliaceae, and *Flindersia breyleyana*, Rutaceae) and temperate (*Eucalyptus regnans*, Myrtaceae) forest. *Toona* is a common pioneer tree in north-eastern Australia from the highly successful tropical family Meliaceae. It produces large compound leaves and rapid growth (Herwitz 1993). *Flindersia* is a more shade-tolerant primary forest tree common in tropical north-eastern Australia; its contrast with the pioneer status of *Toona* was desirable to provide some control for successional status. *E. regnans* derives from a temperate south-eastern Australia and exhibits high growth rates although it is described as shade intolerant (Ashton and Kelliher 1996). All three angiosperm species were vessel bearing, with vessels >17 cm long observed in the stems of each angiosperm seedling (T. J. Brodribb, unpubl. data).

We focussed on seedling growth because this is the phase at which competition is most vigorous, and as such has been suggested as the phase during which conifers suffer competitive exclusion by fast-growing angiosperms (Bond 1989). All species were germinated in sand and six individuals of each were transferred to a high-nutrient soil mixture. Plants were grown in 5-L pots and watered daily.

Growth conditions

Two growth regimes were imposed, one high light (HL) and one low light (LL), with three replicates per species grown under each of these two light intensities. Plants in the HL treatment were in a glasshouse exposed to irradiances in the range $1300\text{--}1800\ \mu\text{mol quanta m}^{-2}\text{ s}^{-1}$ throughout the year. Low-light plants were grown under constant $30\ \mu\text{mol quanta m}^{-2}\text{ s}^{-1}$, with banks of fluorescent and incandescent bulbs providing a relatively continuous spectral distribution. Photoperiod in the LL plants was maintained at 13 h, whereas that in the HL plants ranged from 13 h to a maximum of ~ 14 h during late December. Temperatures in the LL treatment were 25°C during the day and 15°C at night, and temperatures in the HL environment ranged from a minimum of 10°C overnight in winter to a maximum of $25\text{--}35^\circ\text{C}$ during the day in summer.

Growth measurements

Measurements of both HL and LL plants were carried out approximately every 30 days for a period of 250 days. Basal-stem diameter, height of the apical bud and total leaf area were measured. Leaf area was measured by using a digital camera (EDC-1000, Electrim Corp. Princeton, USA) to photograph all branches on individuals while they were still attached to the plant and these were added together by using image analysis to give a total projected leaf area for each individual. Because of the strong bifacial flattening in the leaves of the conifer species, projected leaf area was considered the most appropriate measure. The total leaf area (cm^2) per cm^2 of basal area (LA_{stem}) was calculated from measurements of the major and minor axis of the stem at a height of 2 cm above the soil. The leaf area per leaf mass was measured on five apical leaves from each tree after the completion of growth trials.

Hydraulic conductivity

At the end of 250 days, all plants were harvested and the hydraulic conductivity of stems was measured on each individual. Sapwood specific conductivity (K_{sp}) was measured on excised segments of stem or branch (two per individual) which were longer than the longest vessel. Compressed air at 1 atm was injected into stems of sacrificial plants of each species to determine maximum vessel length. In *Eucalyptus regnans*, continuous vessels were found to extend from the base of the stem to the apex, and therefore segments were cut to include two nodes, which was sufficient to eliminate open vessels. Stem conductivity was quantified by using an electronic balance to measure the mass flow of a filtered solution of HCl (of pH 2) through the stem segment at 20°C under a head pressure of between 4 and 5 kPa as described by Sperry *et al.* (1988). Measurement of stems was carried out in the morning to ensure native embolism was minimal. Stem hydraulic conductance was calculated as the mass flow of water (kg s^{-1}) divided by the pressure gradient (MPa m^{-1}), and this was then divided by the sapwood area at the distal end of the segment to give K_{sp} . Stem conductivity was also expressed on a leaf-area basis (K_l) by dividing the conductance of the segment by the total leaf area supplied. Two stems of similar dimensions from each specimen were used to produce mean conductivities for each species ($n = 6$).

Stomatal conductance

Stomatal conductance was measured on three fully expanded leaves of each plant once seedlings were 200–220 days old, with a Li 1600 (Li-Cor, Lincoln, NE, USA) null balance porometer. Measurements were made at 1100 hours under peak diurnal irradiance to ensure maximum stomatal opening.

Statistical analysis

Linear regressions were used to summarise leaf-area growth over the period of 150–250 days (see Results). These were fitted by the least-

squares regression technique, and slopes for each individual were used to calculate mean growth over the period. Statistical comparisons between species were made by using a Students paired *t*-test, and pooled means were compared by an ANOVA (JMP, SAS Institute).

Results

Comparative growth rates

Leaf-area growth in all seedlings was characterised by a slow initial phase followed by a linear increase in leaf area after Day 150 (Fig. 1). Linear regressions fitted to leaf-area growth over time between Days 150 and 250 were highly significant in all individuals (all above $r^2 = 0.94$), and conservative within species. Leaf-area growth in HL plants over this linear phase was on average six times greater in the angiosperms than in the conifers; $54.2 \pm 12.8\ \text{cm}^2$ per day in the three angiosperms compared with $8.6 \pm 3.6\ \text{cm}^2$ per day in the conifers (Fig. 2). Under shade conditions, leaf-area growth rates were much more variable between species, in accord with their contrasting ecologies (Fig. 2). Considerable overlap existed between the range of growth rates of LL angiosperms ($25.2\text{--}5.2\ \text{cm}^2\text{ day}^{-1}$) and LL conifers ($12.5\text{--}2.0\ \text{cm}^2\text{ day}^{-1}$). Even so, the mean rate for LL angiosperms was still significantly ($P < 0.01$) greater than in the conifers.

Stem basal-diameter growth followed a similar dynamic to leaf area, allowing the growth phase after Day 150 to be summarised by the slope of a linear regression fitted to each individual. Differences in basal-diameter growth

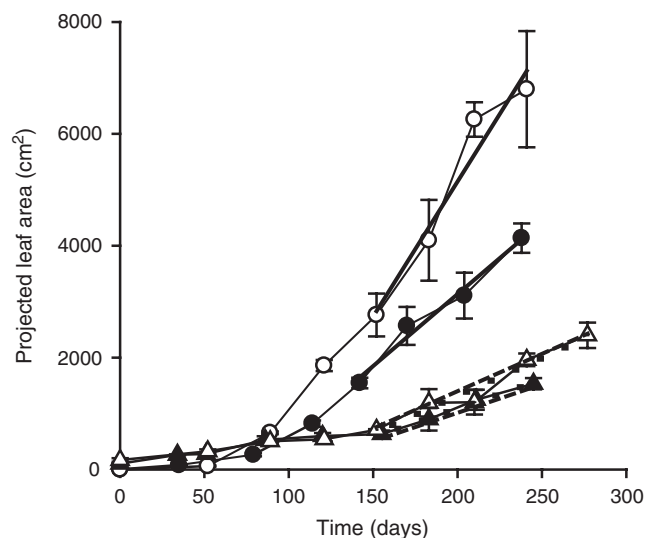


Fig. 1. The dynamics of mean leaf area growth are shown for one representative angiosperm (*Toona australis*, circles) and one conifer (*Nageia nagi*, triangles). Both low-light (filled) and high-light (open) plants showed similar patterns of growth whereby a linear increase was observed between Days 150 and 250 after germination. All species showed similar dynamics, allowing the mean leaf area growth over this period to be summarised by the slope of linear regressions (shown here as unbroken for *Toona* and broken for *Nageia*).

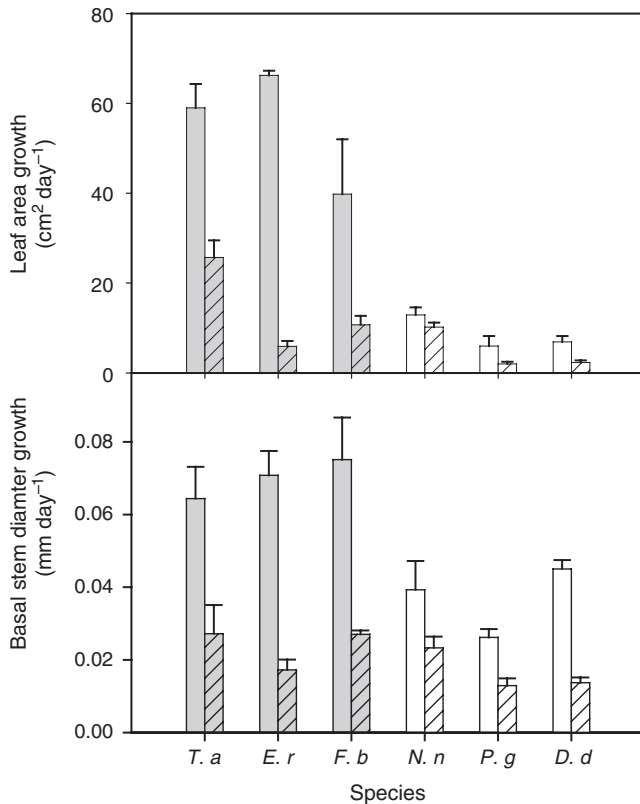


Fig. 2. Mean (\pm s.d., $n=3$) leaf-area growth rate (upper panel) and basal-stem diameter growth rate (lower panel) for the angiosperm seedlings (*Toona australis* = *T.a.*; *Eucalyptus regnans* = *E.r.*; *Flindersia breyleyana* = *F.b.*) grown in sun (grey) and shade (grey, hatched), and conifer seedlings (*Nageia nagi* = *N.n.*; *Podocarpus grayi* = *P.g.*; *Dacrycarpus dacrydioides* = *D.d.*) from sun (white) and shade (white, hatched).

rates between angiosperm and conifer seedlings were smaller than for leaf-area growth (Fig. 2). Nonetheless, all HL angiosperms yielded significantly ($P < 0.0001$) greater basal-diameter growth rates than HL conifers. In LL plants, however, considerable overlap between LL conifer and angiosperm species means led to a barely significant ($P = 0.021$) difference between these groups in the shade. Mean diameter growth in angiosperms was 66% lower in LL than in HL plants (0.024 ± 0.0007 to 0.07 ± 0.009 mm day⁻¹), whereas conifer growth was on average only 54% lower in LL plants (0.017 ± 0.0005 to 0.037 ± 0.009 mm day⁻¹).

Leaf area per basal stem area

During the 250 days of observation, the change in leaf area carried per unit basal stem area ($A_{\text{leaf}}/A_{\text{stem}}$) showed conservative patterns over time in all species. The ratio $A_{\text{leaf}}/A_{\text{stem}}$ increased rapidly after germination in all seedlings before stabilising after Days 50–100 (Fig. 3). Henceforth, the ratio $A_{\text{leaf}}/A_{\text{stem}}$ remained relatively

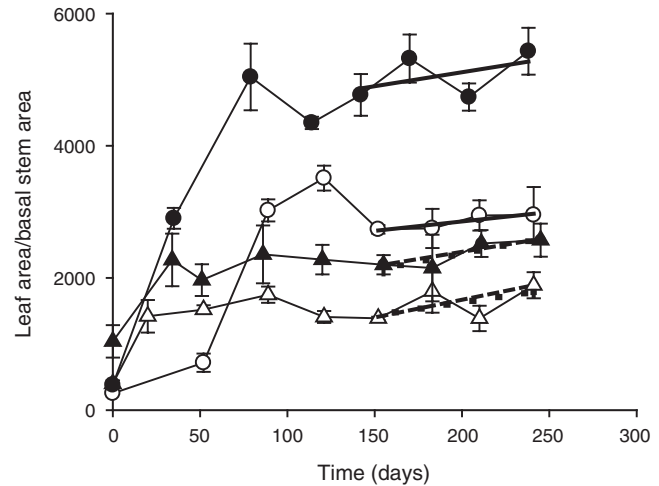


Fig. 3. Changes in the ratio of total leaf area : basal cross-sectional stem area ($A_{\text{leaf}} : A_{\text{stem}}$) in seedlings of the angiosperm (*Toona australis*, circles) and conifer (*Nageia nagi*, triangles). Seedlings grown at low light (filled) and high light (open) all behaved in a similar fashion whereby $A_{\text{leaf}} : A_{\text{stem}}$ increased rapidly, then stabilised after 150 days. Mean values for each individual were calculated over the period, Days 150–250. Error bars represent s.d. ($n=3$) for each species.

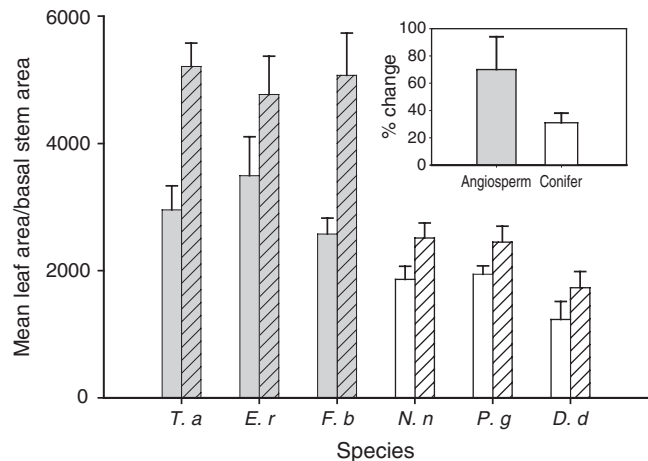


Fig. 4. Mean (\pm s.d., $n=3$) ratio of leaf area : basal stem area in the three angiosperms (grey) and conifers (white) (labelled as in Fig. 2). Angiosperm seedlings produced larger ratios of $A_{\text{leaf}} : A_{\text{stem}}$ both in the sun (open) and shade (hatched), as well as a greater difference in $A_{\text{leaf}} : A_{\text{stem}}$ between sun and shade plants (inset graph).

constant, and for each plant a mean value for $A_{\text{leaf}}/A_{\text{stem}}$ was calculated over the period from Day 150 to Day 250.

The mean ratio $A_{\text{leaf}}/A_{\text{stem}}$ amongst the angiosperm species was significantly larger than that recorded in the three conifer species under both HL and LL conditions (Fig. 4). This difference was greatest in LL plants, where the mean $A_{\text{leaf}}/A_{\text{stem}}$ in angiosperms was more than twice as high as in the conifers (5020 ± 523 v. 2232 ± 433 , respectively). Under HL conditions the difference was slightly smaller

(3009 ± 552 in angiosperms v. 1680 ± 385 in conifers) but still highly significant ($P < 0.001$).

All species were found to produce significantly larger $A_{\text{leaf}}/A_{\text{stem}}$ in shade plants than in sun plants (Student's t -test). This difference between sun and shade was most pronounced in the angiosperms, with shade individuals of *Toona* and *Flindersia* producing on average 80 and 93% more leaf area per stem than HL plants, respectively. The enhancement of $A_{\text{leaf}}/A_{\text{stem}}$ in shade, relative to sun conifers, was more modest, averaging only 34% in the three species examined (Fig. 4).

Hydraulic and stomatal conductance

The hydraulic conductivity of seedling angiosperm stems (K_{sp}) was substantially higher than that of seedling conifer stems (Fig. 5), and vessels of >17 -cm length were observed in the stems of all angiosperm seedlings (T. J. Brodribb, unpubl. data). The mean value for K_{sp} was $2.50 \pm 0.71 \times 10^{-4} \text{ kg s}^{-1} \text{ Mpa}^{-1} \text{ m}^{-1}$ in angiosperm stems, more than eight times higher than the conifer mean of $0.29 \pm 0.02 \times 10^{-4} \text{ kg s}^{-1} \text{ Mpa}^{-1} \text{ m}^{-1}$. Even when stem conductance was normalised to leaf area (K_1), all three angiosperm species were significantly ($P < 0.0001$) more conductive than the conifers in both light treatments (Fig. 5). However, in accord with the greater leaf areas carried by the angiosperm species, the values of K_1 for angiosperms and conifers were much closer than K_{sp} values. For example, mean K_1 for LL angiosperms was $1.18 \pm 0.29 \times 10^{-4} \text{ kg s}^{-1} \text{ Mpa}^{-1} \text{ m}^{-1}$, only slightly more than twice the mean for LL conifers ($0.55 \pm 0.09 \times 10^{-4} \text{ kg s}^{-1} \text{ Mpa}^{-1} \text{ m}^{-1}$). The angiosperm with the lowest K_1 , *Flindersia breyleyana*, was not

significantly different in either sun or shade to either *Nageia nagi* or *Dacrycarpus dacrydioides*.

Stomatal conductances were highest in HL angiosperms, whereas the difference between conifer and angiosperm g_s was not significant under LL conditions (Fig. 6). A link between hydraulic and stomatal conductances was found when all data were pooled, with a highly significant linear regression ($R^2 = 0.82$) suggesting a proportional relationship (Fig. 7).

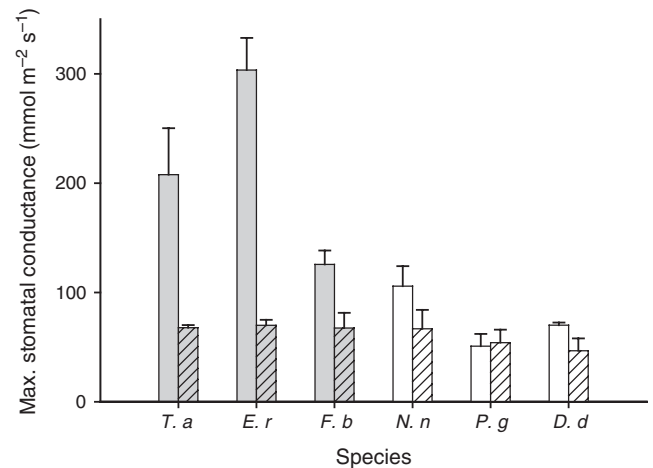


Fig. 6. Maximum stomatal conductance for leaves of angiosperm and conifer seedlings (labelled as in Fig. 2). Conifer seedlings produced lower conductances than angiosperms grown in high light, as well as less variation between sun and shade plants. However, no significant difference was found between stomatal conductance of conifer and angiosperm seedlings grown in the shade.

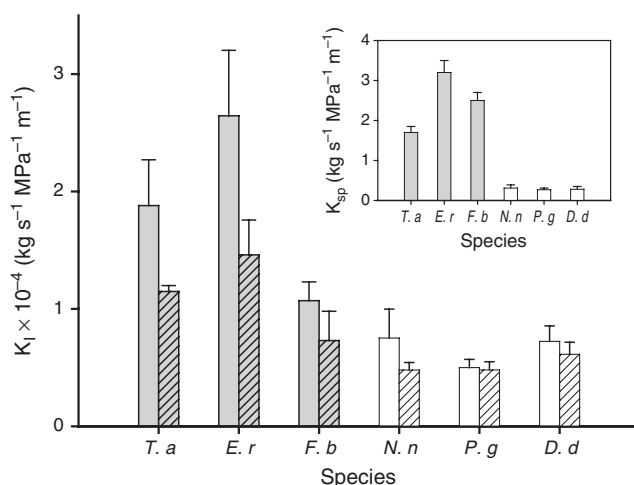


Fig. 5. Mean leaf-specific stem hydraulic conductivity (K_1) in stems of angiosperm (grey) and conifer (white) seedlings from sun (open) and shade (hatched). Angiosperms showed greater K_1 than conifers in both sun and shade, although differences were substantially less than those observed for stem-specific hydraulic conductivity (inset graph).

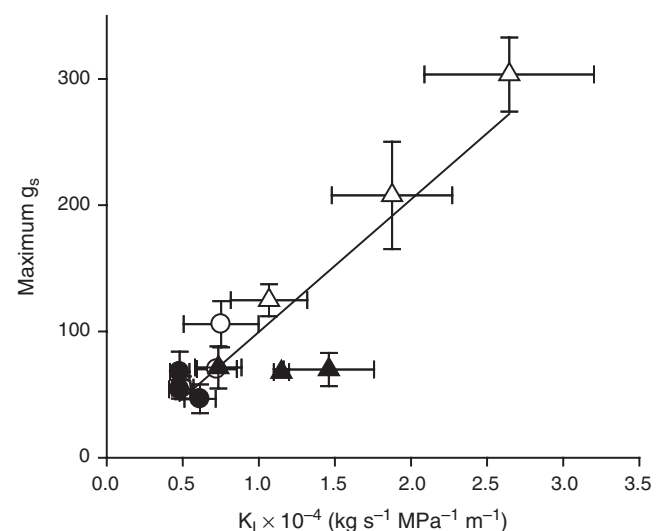


Fig. 7. Mean hydraulic and stomatal conductances are shown for conifers (triangles) and angiosperms (circles) grown at high light (open) and low light (filled). A highly significant linear regression ($R^2 = 0.82$) is illustrated, suggesting a strong dependence between these parameters.

Discussion

The data presented here provide the first detailed comparison of seedling growth, hydraulic architecture and light response between species of angiosperm and conifer trees. The aim of this comparison was to test the hypothesis that competitive outcomes between conifer and angiosperm competition are decided at the seedling stage by differences in xylem physiology. By carefully selecting conifers from the tropical Podocarpaceae, all possessing leaf characters convergent with broad-leaved angiosperms, our comparison of a few species yielded important insights into this complex question.

The conifers selected presented a range of leaf morphologies from broad flattened, to small composite leaves. However, despite this, their growth, allometric and hydraulic characteristics were generally conservative and significantly different from those of the angiosperm sample. The distinction between angiosperm and conifer representatives observed here is important, as the only systematic vegetative differences between these seedlings were the presence/absence of vessels and the presence of reticulate leaf venation in the angiosperms. For this reason, we can say with some confidence that one or both of these traits are influential in deriving the differences in growth and allometry observed here. Given the proven influence of vessels on hydraulic flow (Sperry *et al.* 1988) and ultimately photosynthetic rate (Brodribb and Feild 2000; Hubbard *et al.* 2001), the most parsimonious explanation for the patterns observed here is the absence of vessels in the conifer sample.

Xylem conductivity in the angiosperm seedlings was far greater than in the conifer seedlings (Fig. 5), owing to the presence of xylem vessels in the three angiosperm species. This would be expected to alter the amount of xylem tissue required to support downstream foliage with water, assuming similar transpiratory demands from the leaves. Indeed, it was shown that consistent differences existed between the ratio of leaf area to basal stem area in conifer and angiosperm seedlings, with angiosperms displaying significantly greater $A_{\text{leaf}}/A_{\text{stem}}$ than the conifers under both light treatments. Similar observations have been made from studies of adult trees, where the xylem area: leaf area ratio (Huber value) of conifers tended to be substantially larger than that of co-existing angiosperms (Becker *et al.* 1999). Given that $A_{\text{leaf}}/A_{\text{stem}}$ provides an index of the potential photosynthetic yield (leaf area) per unit structural allocation (stem basal area), species with large $A_{\text{leaf}}/A_{\text{stem}}$ would appear to be at an economic advantage over species with low $A_{\text{leaf}}/A_{\text{stem}}$. Hence, the observation of higher $A_{\text{leaf}}/A_{\text{stem}}$ in angiosperm seedlings is important, and suggests that these plants operate at an economic advantage. Interestingly, the ratio $A_{\text{leaf}}/A_{\text{stem}}$ was quite conservative within the angiosperms and conifers under both light treatments, despite the contrasting ecologies

represented. This suggests that, for this sample at least, the presence/absence of vessels is a more important determinant of $A_{\text{leaf}}/A_{\text{stem}}$ than other factors such as leaf specific mass (Table 1) or successional status.

High-light conditions tended to amplify the difference between conifer and angiosperm growth rates, with consistently stronger leaf-area and basal-diameter growth in HL angiosperm seedlings than in conifers. Under LL conditions, the comparison between conifer and angiosperm growth rates was more ambiguous (Fig. 2). The heterogeneity of ecologies represented by the three angiosperm species obviously contributed to the variability in LL growth performance. By contrast, the consistency of the HL advantage in the angiosperm species over the conifers suggests that this may be more of a universal feature of angiosperms *v.* conifers. Obviously, the converse is also true, that deep shade provided a more competitive environment for the Podocarps in this study, supporting the ideas of Bond (1989).

Flexibility in the ratio $A_{\text{leaf}}/A_{\text{stem}}$ was hypothesised to be an advantage conferred by the presence of vesseliferous xylem, and to some extent the data here provide support for this hypothesis. All three angiosperm species showed significantly higher $A_{\text{leaf}}/A_{\text{stem}}$ when grown in the shade than did sun-grown plants, whereas the differences between HL and LL seedlings of the conifer species were too small to be significant (Fig. 5). This flexibility in the architecture of seedling angiosperms may derive partly from the differentiation of wood into efficient conducting and support tissues (fibres). Conifers lack this specialisation and it might be envisaged that this could lead to imbalance between the demands of water supply and support. The relatively weak correlation between stem hydraulic conductivity and stomatal conductance in conifers relative to angiosperms (Fig. 7) from sun and shade indicates imperfect coordination of hydraulic supply and demand in conifers. This provides some support for the idea that these characters might be uncoupled by the competing demands of mechanical support in conifers.

It is more likely that greater flexibility in leaf area per stem area is linked to greater plasticity in leaf characters such as leaf mass per area and maximum stomatal conductance.

Table 1. Mean (\pm s.d., $n = 10$) leaf mass per area in plant seedlings grown under high light (HL) and low light (LL)

Species	Leaf mass per area $\times 10^3$ (g cm ⁻²)	
	HL	LL
<i>Eucalyptus regnans</i>	11.7 \pm 0.4	7.70 \pm 0.6
<i>Flindersia breyleyana</i>	14.7 \pm 0.33	11.3 \pm 0.51
<i>Toona australis</i>	8.43 \pm 0.81	3.42 \pm 0.34
<i>Dacrycarpus dacrydioides</i>	6.47 \pm 0.86	5.38 \pm 0.64
<i>Nageia nagi</i>	18.6 \pm 1.70	10.48 \pm 0.90
<i>Podocarpus greyi</i>	21.3 \pm 1.30	22.4 \pm 0.60

In this sample of species, the angiosperms demonstrated greater plasticity in both these characters, leading to sun plants with high maximum g_s and shade plants with low g_s and low mass per area. Perhaps relevant to this contrast are recent studies suggesting that conifer and angiosperm leaves display consistently different physiologies with respect to hydraulics and gas exchange (Cochard *et al.* 2004; Brodribb *et al.* 2005; Brodribb and Holbrook 2005). These differences, which include low hydraulic conductivity, high capacitance and tracheid collapsibility, are related to xylem anatomy and may explain the relatively mute response to sun and shade in conifer leaves.

It is curious that despite the fact that largest difference between conifer and angiosperm $A_{\text{leaf}}/A_{\text{stem}}$ was observed in shade plants, the differences in growth rates were relatively small in the shade compared with the sun. This suggests that, in our sample at least, the benefits associated with vessels, including high maximum g_s and $A_{\text{leaf}}/A_{\text{stem}}$, do not translate to enhanced growth efficiency in the shade. If this were found to be a general principle, it would have considerable bearing on recent debate surrounding early angiosperm evolution. Feild *et al.* (2004) proposed that angiosperms may have evolved in the understorey of tropical cloud forest, and it is interesting to note that many of these early angiosperms did not have vessels. If indeed the advantages of vesseliferous xylem are maximised in higher-light environments, then perhaps the evolution of vessels in angiosperms is correlated with the movement of early angiosperms out of the understorey.

Clearly, other vegetative factors such as leaf longevity, shade survival, root and leaf properties, and respiration rates must contribute to the competition between conifers and angiosperms in the tropics. Research is continuing into this important question in the hope to better comprehend the impact of vegetative traits on plant performance.

Acknowledgments

This research was funded by an Australian Research Council grant. T. J. B. is a Putnam Fellow at the Arnold Arboretum, Harvard University.

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Manuscript received 4 March 2005, accepted 4 July 2005