Photosynthetic differences contribute to competitive advantage of evergreen angiosperm trees over evergreen conifers in productive habitats

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Summary

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• Here we explore the possible role of leaf-level gas exchange traits in determining growth rate differences and competitive interactions between evergreen angiosperms and conifers.
• We compared relationships among photosynthetic capacity (A_{max}), maximum stomatal conductance (G_s), leaf life span, nitrogen concentration (N) and specific leaf area (SLA), in sun leaves of 23 evergreen angiosperm and 20 conifer populations.
• Despite similar average leaf N_{mass}, conifer leaves lived longer on average (36 months) than angiosperms (25 months). At a standardized leaf N, A_{mass} was higher in angiosperms (56 nmol g^{-1} s^{-1}) than in conifers (36 nmol g^{-1} s^{-1}). Stepwize regression suggested that most of this difference in photosynthetic nitrogen use efficiency could be explained by G_s and SLA. Mean G_s (on an area basis) of angiosperms was higher than that of conifers (152 vs 117 mmol m^2 s^{-1}), but A_{area}–G_s relationships were similar for the two groups. At a given leaf N, conifers had lower SLA (projected area basis) than angiosperms.
• Photosynthetic differences probably contribute to the competitive advantage of angiosperm trees over conifers in productive habitats, and may be linked to the greater hydraulic capacity of vessels, enabling angiosperms to develop higher stomatal conductance and therefore sustain higher transpiration rates.

Key words: competition, growth rate, photosynthesis, leaf lifespan, specific leaf area, stomatal conductance.

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Introduction

Since their first appearance during the Cretaceous, the angiosperms have assumed increasing dominance in most terrestrial biomes, supplanting conifers and other more primitive plant groups (Bond, 1989; Enright & Hill, 1995). With a few exceptions, conifers are now only dominant at high latitudes and altitudes, and on infertile or poorly drained soils. However, the causes of this phytogeographic shift are still debated (Becker, 2000).

What traits have given angiosperms an advantage over conifers in most habitats? Early explanations based on reproductive differences (Raven, 1977; Regal, 1977) have found little support, and more recent work has explored causes and consequences of vegetative growth rate differences (Bond, 1989; Midgley & Bond, 1991). At least during the juvenile phase, maximum growth rates of conifers are usually slower than those of angiosperm associates (Enright *et al.*, 1993; Read, 1995; Cornelissen *et al.*, 1996; Reich, 1998; Lusk & Matus, 2000). This is likely to lead to suppression of conifer seedlings by angiosperm competition on productive sites (Lusk & Matus, 2000), where competitive hierarchies develop rapidly (Keddy *et al.*, 1997).

Why are many conifers slow growing? Conifers and angiosperms differ in a variety of vegetative traits that could potentially underlie growth rate differences (Bond, 1989, Becker, 2000). Paleoecologists have noted that stomatal densities of conifers have changed relatively little over geological

Table 1 Sites where leaf traits of evergreen angiosperms and conifers were measured

Site	Location	Elevation (m)	Mean temp. (°C)	Annual precip. (mm)
Concepción, Chile	36°50′ S, 73°02′ W	< 10	12.4	1300
Chillán, Chile	36°52′ S, 71°28′ W	800	14.0	2000
Puyehue, Chile	40°39′ S, 72°11′ W	350–700	8.6	3800
Southern Wisconsin, USA	43°03′ S, 89°28′ W	265	8.0	820
Coweeta, N. Carolina, USA	35°00′ S, 83°30′ W	700–850	12.5	1830
Hobcaw, S. Carolina, USA	33°20′ S, 79°13′ W	< 5	18.3	1300

time, despite fluctuating atmospheric CO_2 levels (Beerling & Woodward, 1996). Gas exchange of conifers may therefore still be constrained by conservative stomatal traits that date from the ancient origins of this lineage, during times when atmospheres were much richer in CO_2. The more recently evolved angiosperms may be better adapted to relatively low modern CO_2 concentrations, because of higher stomatal densities and more efficient stomatal control (Robinson, 1994; Becker, 2000).

However, there have been few systematic comparisons of gas exchange traits in conifers and angiosperms. Beerling & Woodward's (1996) comparison of stomatal densities and photosynthetic capacity in conifers and angiosperms was based on representatives of the two lineages that differ widely in other leaf traits apart from gas exchange. This is important because wide-ranging comparative studies have established that photosynthetic capacity and stomatal conductance scale with other leaf functional and structural traits (Reich *et al.*, 1997, 1999). Although this scaling apparently reflects universal tradeoffs determined by biophysical constraints and natural selection, precise relationships between pairs of traits (e.g. leaf nitrogen and photosynthetic capacity) can differ among taxonomic or functional groups, as well as among sites (Reich *et al.*, 1997, 1998, 1999). In order to evaluate the role of gas exchange traits in constraining conifer performance, it might be more informative to compare stomatal conductance and photosynthetic capacity of conifers and angiosperms with similar leaf lifespan and nitrogen concentration (Becker, 2000).

The main questions to be addressed in this paper are: do photosynthesis-nitrogen relationships differ in evergreen conifer and evergreen angiosperm leaves? Are any such differences linked to variation in maximum stomatal conductance? We chose to compare evergreen representatives of the two groups because of the scarcity of extant deciduous conifers.

Materials and Methods

Study sites

As relationships among photosynthetic capacity (A_{max}), maximum stomatal conductance (G_s), and leaf nitrogen concentration (N) are influenced by temperature and rainfall regimes (Reich *et al.*, 1999; Wright *et al.*, 2001), we worked only with data from temperate climates. Despite this constraint, our initial exploration indicated strong site effects in all analyses. We therefore report data only from sites where both angiosperms and conifers were present, and include site as a factor in all analyses. Data are reported from a total of six sites in the Americas: three in Chile and three in the USA (Table 1). Although total annual precipitation ranged from 800 to 3800 mm, rainfall in the driest seasonal quarter is at least 80 mm at all sites.

Species selection and measurements

We limited our study to evergreen trees and large shrubs with leaf life spans of > 12 months (Table 2). At each site, data were obtained from as many species as possible that matched this description, including exotic trees at some sites. Leaf traits were measured on at least five adult plants per species. Since some traits change with leaf age, and as leaf longevity varied widely among species, we attempted to standardize physiological (rather than chronological) leaf age. Parameters were therefore measured on young but fully expanded leaves in all species. In order to minimize the confounding effects of light environment, we selected sun leaves on plants growing in relatively open situations for all species.

For most angiosperm species, leaf life spans were estimated by monitoring leaf birth and death over a 12-month period on at least five plants per species (Reich *et al.*, 1991). For most conifers, and for those angiosperms whose leaf cohorts were distinguishable because of persistent scars of resting buds or inflorescences, retrospective methods were used to estimate leaf life spans. Average longevity was calculated by counting the number of annual cohorts with at least 50% of their leaves retained on the branch (Reich *et al.*, 1999).

Gas exchange measurement procedures and equipment differed among sites. However, in all cases measurements were made using infrared gas analysers operated in differential mode, at leaf temperatures within the range experienced in late morning on fine days during the growing season at each site. At the three South American sites, measurements were made in direct sunlight at ambient temperatures with a CIRAS-1 system (PP Systems, Hitchin, UK), and a broad leaf chamber. Because of the small size of leaves of most conifers,

Table 2 Leaf traits of evergreen angiosperms and conifers from six study sites in South and North America

Location	Species	Conifer/ Angiosperm	Leaf lifespan (months)	Leaf N (%)	SLA ($cm^2 \, g^{-1}$)	A_{area} (micromoles $m^{-2} \, s^{-1}$)	A_{mass} (nmol $g^{-1} \, s^{-1}$)	G_{area} (mmol $m^{-2} \, s^{-1}$)	G_{mass} (mmol $g^{-1} \, s^{-1}$)
Concepción	Camellia japonica	A	32	1.06	51	7.5	38	75	0.38
	Cryptocarya alba	A	31	0.85	69	10.3	71	95	0.66
	Eucryphia cordifolia	A	27	0.80	74	11.1	82	99	0.73
	Luma apiculata	A	20	1.14	61	10.2	62	143	0.87
	Nothofagus dombeyi	A	14	1.73	81	11.4	92	100	0.81
	Podocarpus saligna	C	24	0.98	60	6.2	37	68	0.41
	Sequoia sempervirens	C	46	1.18	56	6.9	38	91	0.51
	Taxus baccata	C	47	1.48	60	7.4	44	94	0.56
Chillán	Laurelia sempervirens	A	20	1.17	81	9.0	73	153	1.24
	Lomatia hirsuta	A	24	0.84	81	9.0	73	137	1.11
	Maytenus boaria	A	18	2.03	106	12.1	128	189	2.00
	Persea lingue	A	33	1.01	96	8.2	79	99	0.95
	Austrocedrus chilensis	C	29	1.09	51	7.6	39	108	0.55
	Podocarpus saligna	C	28	1.10	59	6.2	37	72	0.42
	Prumnopitys andina	C	34	0.93	68	5.6	38	51	0.35
Puyehue	Aextoxicon punctatum	A	44	0.98	74	5.6	41	73	0.54
	Dasyphyllum diacanthoides	A	16	1.21	76	9.6	73	145	1.10
	Eucryphia cordifolia	A	34	1.00	76	9.9	75	140	1.06
	Gevuina avellana	A	52	0.80	65	9.0	59	110	0.72
	Laurelia philippiana	A	27	1.45	62	6.4	40	124	0.77
	Luma apiculata	A	21	1.10	72	8.2	59	133	0.96
	Myrceugenia planipes	A	36	1.00	75	6.2	47	93	0.70
	Nothofagus dombeyi	A	20	1.29	74	11	81	164	1.21
	Podocarpus nubigena	C	78	0.75	50	7.9	40	115	0.58
	Saxegothaea conspicua	C	36	0.81	78	5.8	45	83	0.65
N. Carolina	Kalmia latifolia	A	36	1.15	95	4.8	43	172	1.63
	Rhododendron maximum	A	48	0.86	49	6.8	34	136	0.67
	Pinus rigida	C	33	1.16	49	11.3	56	317	1.55
	Tsuga canadensis	C	60	0.99	82	5.5	44	141	1.16
S. Carolina	Lyonia lucida	A	20	0.92	42	6.2	27	185	0.78
	Persea borbonia	A	18	1.64	90	6.7	62	203	1.83
	Pinus palustris	C	32	0.82	39	3.9	17	67	0.26
	Pinus serotina	C	27	0.82	36	4.1	16	94	0.34
Wisconsin	Andromeda glaucophylla	A	13	1.39	76	9.3	70	309	2.35
	Chamaedaphe calyculata	A	13	1.19	115	6.1	70	299	3.44
	Picea abies	C	72	1.78	39	10.0	39	.	
	Picea mariana	C	60	1.21	34	9.2	37	.	
	Pinus banksiana	C	27	1.24	41	9.5	39	231	0.95
	Pinus resinosa	C	36	1.17	34	6.3	24	.	
	Pinus strobus	C	21	1.70	74	8.5	63	205	1.52
	Pinus sylvestris	C	27	1.39	34	12.5	43	.	
	Thuja occidentalis	C	48	0.76	45	7.2	32	163	0.73

gas exchange was measured on several leaves enclosed simultaneously and manoeuvred to occupy most or all of the chamber window, without overlapping. In cases where leaves did not occupy the entire window, measurements were corrected after determining actual area of the enclosed sample. At the three North American sites, measurements were made under ambient conditions using an LCA-2 infrared gas analyser (ADC, Hoddeston, UK), using procedures reported in detail in Reich *et al.* (1999).

After gas exchange measurements, leaves were harvested. Their projected area was measured with a Decagon digital analysis system (North America), or with an ADC AM-100 leaf area meter (South America). Samples were then oven dried for at least 48 h at 65°C, for determination of specific leaf area (area/dry mass), and then analysed for total nitrogen by the micro-Kjeldahl method of Lang (1962).

Comparisons of area-based traits of conifer and angiosperm leaves are problematic. About half the conifer species that we studied have needle leaves, which differ from broad leaves in their ratio of projected area to surface area (Körner, 1995). There is little agreement as to the most meaningful expression of leaf area in needle-leafed conifers, but we used
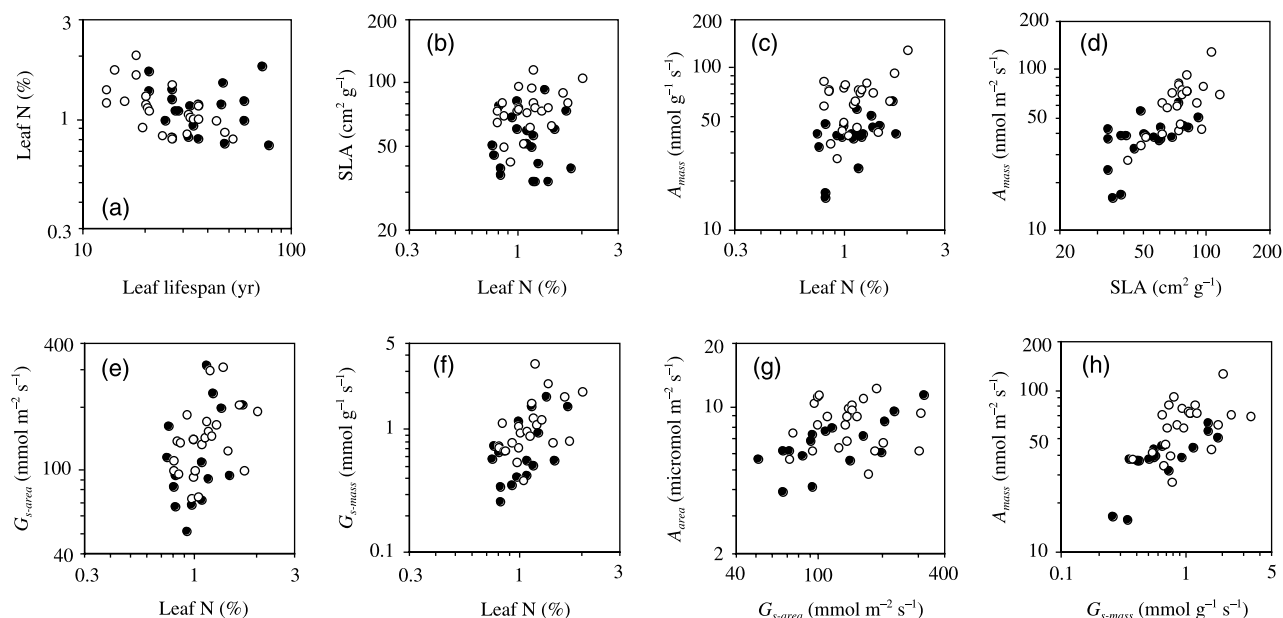
Fig. 1 Leaf trait relationships for evergreen angiosperms (open circles) and conifers (closed circles). (a) Relationship of leaf N with leaf lifespan. Correlation is highly significant for angiosperms ($r = -0.63$, $P = 0.001$) but not for conifers. (b) Relationship of specific leaf area (SLA) with leaf N. Correlation is significant for angiosperms ($r = 0.44$, $P = 0.04$) but not for conifers. (c) Relationship of photosynthesis per unit leaf mass (A_{mass}) with leaf nitrogen. Correlation is marginally significant for angiosperms ($r = 0.40$, $P = 0.06$) and significant for conifers ($r = 0.50$, $P = 0.025$). (d) Relationship of photosynthesis per unit leaf mass (A_{mass}) with SLA. Correlation is highly significant for both angiosperms ($r = 0.71$, $P < 0.0001$) and conifers ($r = 0.57$, $P < 0.008$). (e) Relationship of stomatal conductance on an area basis (G_{area}) with leaf N. Correlation is marginally significant for angiosperms ($r = 0.41$, $P = 0.05$) and not significant for conifers. (f) Relationship of stomatal conductance on a mass basis (G_{mass}) with leaf N. Correlation is significant for both angiosperms ($r = 0.51$, $P = 0.01$) and conifers ($r = 0.54$, $P = 0.03$). (g) Relationship of photosynthesis per unit leaf area (A_{area}) with stomatal conductance on an area basis (G_{area}). Correlation is not significant for angiosperms, but significant for conifers ($r = 0.68$, $P = 0.004$). (h) Relationship of photosynthesis per unit leaf mass (A_{mass}) with stomatal conductance on a mass basis (G_{mass}). Correlation is significant for both angiosperms ($r = 0.47$, $P = 0.02$) and conifers ($r = 0.75$, $P = 0.001$).

projected leaf area because of its ease of measurement. Serrano *et al.* (1997) found that light absorption by needle-leafed conifers, even in diffuse light, was slightly better correlated with projected area than with surface area. This suggests that projected area is probably the more relevant parameter to interception of the direct light that we used for most of our photosynthetic measurements. Furthermore, when we repeated our analyses using estimated leaf surface area to calculate SLA and area-based gas exchange (transforming SLA of needle-leafed species by $\pi/2$), explanatory power of most models was lower, giving additional *a posteriori* support to our choice of projected leaf area. We therefore report only results of analyses based on projected leaf area.

Statistical analyses

Analysis of covariance (ANCOVA) was used to determine if slope and elevation of trait relationships differed between conifers and angiosperms. All variables were log-transformed before analysis, to ameliorate nonnormality and heterogeneity of variance. As a result, unless otherwise stated, all mean values reported below are geometric means, obtained by back-transforming means calculated from log-transformed variables.

Although interaction terms were initially included in most analyses, they were eliminated when interaction effects were found to be clearly nonsignificant ($P > 0.15$). All analyses were carried out using JMP Statistical Discovery Software (SAS Institute, Cary, NC, USA).

Results

Relationships among leaf lifespan, nitrogen concentration and SLA

Average leaf lifespan of evergreen conifers (36 months) was longer than that of angiosperms (25 months). When leaf lifespan and site were standardized by ANCOVA, mean N_{mass} was very similar in conifers (1.09%) and in angiosperms (1.06%). Leaf N_{mass} was significantly negatively correlated with leaf lifespan in angiosperms, but not in conifers (Fig. 1a).

SLA was significantly positively correlated with N_{mass} in angiosperms, but not in conifers (Fig. 1b). When N_{mass} and site were standardized by ANCOVA, average SLA of conifers (estimated from projected leaf area) was significantly lower ($P < 0.0001$) than that of angiosperms (53 vs 71 $m^2\ g^{-1}$).

Table 3 ANCOVA showing effects of taxonomic group (angiosperms vs. conifers) and site on leaf trait relationships of evergreen trees

Dependent variable	Source of variation	F-ratio	$P < F$	Whole model R^2
(a) Leaf N	Leaf lifespan	6.2	0.018	0.31
	Site	0.9	0.48	
	Taxonomy	0.1	0.75	
(b) SLA	Leaf N	4.5	0.08	0.54
	Site	2.8	0.04	
	Taxonomy	12.9	0.0008	
(c) A_{mass}	Leaf N	11.7	0.003	0.67
	Site	4.5	0.004	
	Taxonomy	25.2	< 0.0001	
(d) A_{mass}	SLA	22.2	< 0.0001	0.74
	Site	3.4	0.014	
	Taxonomy	6.5	0.015	
(e) G_{area}	Leaf N	8.3	0.0072	0.69
	Site	10.0	< 0.0001	
	Taxonomy	7.9	0.0085	
(f) G_{mass}	Leaf N	14.6	0.0006	0.73
	Site	7.6	< 0.0001	
	Taxonomy	18.0	0.0002	
(g) A_{area}	G_{area}	39.7	< 0.0001	0.78
	Site	12.8	< 0.0001	
	Taxonomy	0.1	0.80	
	$G_{area} \times$ Taxonomy	8.3	0.007	
(h) A_{mass}	G_{mass}	87.6	< 0.0001	0.89
	Site	18.6	< 0.0001	
	Taxonomy	1.0	0.33	
	$G_{mass} \times$ Taxonomy	2.2	0.15	

A_{mass} and photosynthetic nitrogen use efficiency

A_{mass} was correlated with leaf nitrogen concentration (Fig. 1c), and the elevation but not the slope of this relationship differed significantly between the two lineages and among sites (Table 3). When N_{mass} and site were held constant by ANCOVA, mean A_{mass} of angiosperms was 55% higher than that of conifers (least squares means 56 vs 36 nmol g^{-1} s^{-1}, respectively), indicating higher photosynthetic nitrogen use efficiency (PNUE) in angiosperms.

Most of this difference in PNUE between conifers and angiosperms can be explained by variation in stomatal conductance and SLA (Table 4; Fig. 1d,e). A stepwise regression model including G_{area}, SLA, site, taxonomy (angiosperms vs conifers) and their first interactions showed that the first two variables and their interaction accounted for 44% of interspecific variation in PNUE (Table 4). Site differences contributed a further 15%. Adding taxonomic group to the model produced only a modest, marginally significant increase in explanatory power, suggesting that photosynthetic differences between conifers and angiosperms can be largely explained by the two leaf traits included in the model. G_{area} was preferred to G_{mass} for the stepwise model, as the latter is not independent of SLA.

Stomatal conductance

Although G_s on an area basis showed a positive overall relationship with leaf nitrogen (Table 3), the correlation was

Table 4 Summary of results of stepwise regression to determine how photosynthetic nitrogen use efficiency in evergreens is influenced by stomatal conductance (G_s), leaf structure (SLA), site, taxonomy (angiosperms vs conifers) and interactions of these variables

Source of variation	$P < F$	Cumulative r^2
Step One – SLA $\times$ G_s	0.0001	0.44
Step Two – Site	0.003	0.59
Step Three – Taxonomy	0.06	0.64

All effects significant at $P < 0.05$ are shown below, plus the marginally significant effect of taxonomy – implying that differences in G_s and SLA are the most important functional distinctions between conifer and angiosperm leaves in this context.

only marginally significant for conifers, and not significant among the 23 angiosperms (Fig. 1e). When N_{mass} and site were controlled by ANCOVA, mean G_{area} was significantly higher in angiosperms than in conifers (152 vs 117 mmol m^{-2} s^{-1}). G_s on a mass basis (G_{mass}) showed a tighter relationship with leaf N (Fig. 1f; Table 3), and the difference between angiosperms and conifers was more pronounced (means 1.09 vs 0.66 μmoles m^{-2} s^{-1}).

Both mass- and area-based analyses showed photosynthetic capacity to be correlated with G_s (Table 3; Fig. 1g–h). However, this relationship was more consistent on a mass basis: whereas A_{area} of angiosperms was not significantly correlated with G_{area}, both angiosperms and conifers showing strong

correlations of A_{mass} with G_{mass} (Fig. 1h). Despite the significant influence of taxonomy on the slope of the A_{area}–G_{area} relationship (Table 3), mean A_{area} was almost identical in angiosperms and conifers (7.2 vs 7.1 μmol m^{-2} s^{-1}) when site and G_{area} were controlled by ANCOVA. Angiosperms and conifers did not differ significantly in either elevation or slope of the A_{mass}–G_{mass} relationship (Fig. 1h; Table 3).

Discussion

Lower photosynthetic capacity in conifers

Leaves of evergreen angiosperms were more productive than their coniferous counterparts. A large difference in photosynthetic capacity per unit leaf mass was found when angiosperms and conifers were compared at a common leaf nitrogen concentration, indicating that the angiosperms obtained a higher rate of photosynthetic return per unit of biomass or mole of nitrogen invested in leaf tissue (Fig. 1c). Although a review by Becker (2000) found no significant difference between mass-based photosynthetic rates of conifers and angiosperms of similar leaf lifespan, his result was based on smaller sample sizes (*c.* 10 of each taxonomic group), and did not take potential site effects into account. On the other hand, photosynthetic capacity on an area basis was similar in the two groups in the present study (Fig. 1g), the lower mass-specific rates in conifers being offset by higher leaf mass per unit area (i.e. low SLA).

The needle form of many conifer leaves may confer some benefits that enable them to offset, to some extent, the advantage of angiosperm broad leaves in instantaneous performance. Needle leaves, such as those of *Pinus* and *Picea*, are able to exploit a wider range of incident light angles than the broad leaves of most angiosperms (Jordan & Smith, 1993). They can therefore probably attain near-saturated photosynthetic rates over a wider range of diurnal and seasonal variation in sun angles than broadleaved species. For the same reason, conifers' disadvantage in performance also seems likely to be ameliorated in cloudy climates where diffuse light regimes are common.

Correlates of photosynthetic differences

Differences in photosynthetic performance of evergreen angiosperms and conifers are partly attributable to variation in stomatal conductance (Table 4; Fig. 1e), which was > 30% higher on an area basis in angiosperms. On the other hand, reviews by Schulze *et al.* (1994) and Körner (1995) reported similar mean G_{area} in needle-leaf evergreen conifers and evergreen angiosperm trees, with conifers actually showing a slightly higher mean in the former review. However, neither of those studies took scaling of leaf traits into account by comparing G_s across groups at a constant nitrogen concentration or lifespan. It is also difficult to gauge the possible influence

of site effects in the data covered in the two reviews, as conifer and angiosperm data were often obtained from different sites.

The observed difference in stomatal conductance is consistent with the suggestion that extant conifers may still be handicapped by stomatal traits evolved under higher atmospheric CO_2 levels (Beerling & Woodward, 1996). The apparent failure of evolution of conifer stomatal traits to keep pace with declined CO_2 levels could reflect constraints imposed by the nature of conifer vascular systems (Beerling & Woodward, 1996). Conifer xylem typically has a lower specific conductivity than angiosperm xylem, as a result of greater hydraulic resistance in narrow-diameter tracheids than in vessels (Tyree & Ewers, 1991; Wang *et al.*, 1992; Castro-Diez *et al.*, 1998). The low hydraulic capacity of conifer xylem could therefore limit the possibilities for increasing stomatal density under low CO_2 regimes without incurring unsustainable transpiration rates. A dissenting point of view can be found in the suggestion that conifers can offset the relatively low conductivity of tracheids to some degree by developing high whole-plant ratios of sapwood area to leaf area (Becker *et al.* 1999). However, Brodribb & Field (2000) found that hydraulic supply rates per unit leaf area of Tasmanian and New Caledonian evergreen angiosperms were about 60% higher on average than those of their coniferous associates, associated with a *c.* 40% difference in mean photosynthetic capacity. Evergreen conifers and angiosperms therefore do appear to show co-ordinated differences in photosynthetic, stomatal and vascular traits.

Brodribb & Hill (1997) showed that the maximum stomatal conductance of many Southern Hemisphere members of the Podocarpaceae and Cupressaceae is depressed by partial occlusion of stomatal pores by wax plugs. Their calculations indicated that G_s in these taxa would be a startling 80–400% higher without plugs. However, it seems improbable that the selective advantage of stomatal plugs is reduction of transpiration, as the largest concentrations of stomatal wax are actually found in rainforest conifers, whereas some species from arid environments have no stomatal wax. They concluded that wax plugs are more likely to be an adaptation to humid conditions: by repelling water from the stomatal pore, wax may facilitate photosynthesis in wet environments. Additionally, wax plugs may reduce the risk of fungal invasion of stomatal pores, which may pose a special threat to conifer leaves because of their long retention times (Brodribb & Hill, 1997).

Differences in SLA also appeared to underlie the differences in photosynthetic performance of evergreen conifers and angiosperms (Table 4; Fig. 1d). SLA (calculated from projected leaf area) of angiosperms was about 34% higher on average than that of conifers of comparable leaf nitrogen content. The comparison of evergreen angiosperms and conifers therefore appears to constitute a specific case of a general pattern of modulation of photosynthesis-nitrogen relationships by SLA (Reich *et al.*, 1998). Although both components of

SLA (leaf thickness and density: Witkowski & Lamont, 1991) potentially contribute to the correlation of SLA to PNUE, Niinemets (1999) showed that conifer and angiosperm leaves differ more consistently in thickness than in density. Leaf thickness is likely to limit realization of biochemical potential mainly through its influence on light attenuation in photosynthetic tissues (Terashima & Hikosaka, 1995).

Conclusions

Results suggest that differences in the biochemical efficiency of photosynthesis may be involved in the competitive advantage of evergreen angiosperms over conifers on most productive sites (cf. Becker, 2000). Although photosynthetic differences can be partly explained by differences in leaf thickness, they may also be linked to the greater hydraulic capacity of vessels, enabling angiosperms to develop higher stomatal conductance and sustain higher transpiration rates. On the other hand, conifers' apparent ability to construct longer-lived leaves than angiosperms (Fig. 1) presumably underlies their persistence on poor sites, facilitating amortization of leaf construction costs and eventual accumulation of a large leaf area in environments that sustain only low rates of biomass production (Chabot & Hicks, 1982). Although the gas exchange data presented here correlate with evidence of lower maximum growth rates in conifers, leaf-level traits evidently cannot be translated into whole-plant carbon gain differences without information on biomass distribution and architecture at different ontogenetic stages (Bond, 1989; Lusk, 2002; Niinemets & Lukjanova, 2003). Studies of whole-plant resource use (e.g. Naumburg, Ellsworth & Pearcy, 2002) may thus be useful in understanding conifer–angiosperm interactions in relation to resource availability.

Acknowledgements

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