

# Scaling-up from leaf to canopy-aggregate properties in sclerophyll shrub species

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**Abstract:** Plant species vary widely in their average leaf lifespan (LL) and specific leaf area (SLA, leaf area per dry mass). The negative LL–SLA relationship commonly seen among species represents an important evolutionary trade-off, with higher SLA indicating greater potential for fast growth (higher rate of return on a given investment), but longer LL indicating a longer duration of the revenue stream from that investment. We investigated how these leaf-economic traits related to aggregate properties of the plant crown. Across 14 Australian sclerophyll shrub species, those with long LL accumulated more leaf mass and leaf area per unit ground area. Light attenuation through their canopies was more severe. Leaf accumulation and light attenuation were more weakly related to SLA than to LL. The greater accumulation of foliage in species with longer LL and lower SLA may counterbalance their generally lower photosynthetic rates and light-capture areas per gram of leaf.

**Key words:** leaf area index, leaf lifespan, light attenuation, plant architecture, specific leaf area.

## INTRODUCTION

Plant species vary widely in their average leaf lifespan (LL), from several weeks to several years. Specific leaf area (SLA, the ratio of photosynthetic leaf area to dry mass) varies widely also. LL and SLA have been negatively correlated in a number of local, regional and global interspecific surveys (Reich *et al.* 1997; Diemer 1998; Ryser & Urbas 2000; Wright *et al.* 2002). Low-SLA (thicker, denser) leaves are thought to achieve long LL both from being physically strong and from exhibiting high levels of secondary chemical defences (Chabot & Hicks 1982; Coley 1988; Reich *et al.* 1997). The LL–SLA relationship among species can be thought of as representing a trade-off spectrum running from species with a high potential rate of return on dry mass investment in leaves (high SLA) but short LL, to species with slower rates of return but a longer-lasting revenue stream. Species at the high-SLA end of the spectrum (e.g. many herbs, grasses and deciduous trees) tend to have high leaf N and P concentrations and fast rates of gas exchange rates (photosynthesis, dark respiration), whereas species at the low-SLA end of the spectrum (e.g. many evergreen shrubs and trees) tend to have low N and P concentrations and slow rates of gas exchange (Reich *et al.* 1997). Together, these traits capture many

important features of the dry mass and nutrient economics of carbon fixation by plants. Much variation along this ‘leaf economics spectrum’ occurs between coexisting species, although averages also shift between vegetation zones (Wright *et al.* 2004).

The work reported here investigated how this spectrum, as reflected in SLA and LL, is related to properties of the whole plant crown and its architecture. For example, one might expect longer LL to be associated with more accumulation of leaves within the plant crown. Indeed, in conifer forests long LL species are known to accumulate greater total foliage mass than species with shorter LL (Reich *et al.* 1992; Gower *et al.* 1993). In turn, species that accumulate more leaf mass might be expected to have more severe light attenuation through their canopies. At the same time, other factors might intervene. Because high-LL species tend to have low SLA, long and short LL species might differ less in total leaf area or leaf area index (LAI) (leaf area per square metre of ground) than in total leaf mass (Reich *et al.* 1992; Warren & Adams 2000). Species with long LL might have steeper leaf angles or more open branching, so that the shading power above each square metre of ground might not reflect the total leaf accumulation on the plant. Few studies have quantified the manner in which leaf traits scale up to canopy-level traits via branch architecture for more than one or two species at a time. Here, we quantified a number of these leaf and canopy-architecture traits, and the relationships between them, for 14 evergreen, sclerophyllous shrub species from eastern Australia.

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Accepted for publication August 2005.

## METHODS

### Study area and species

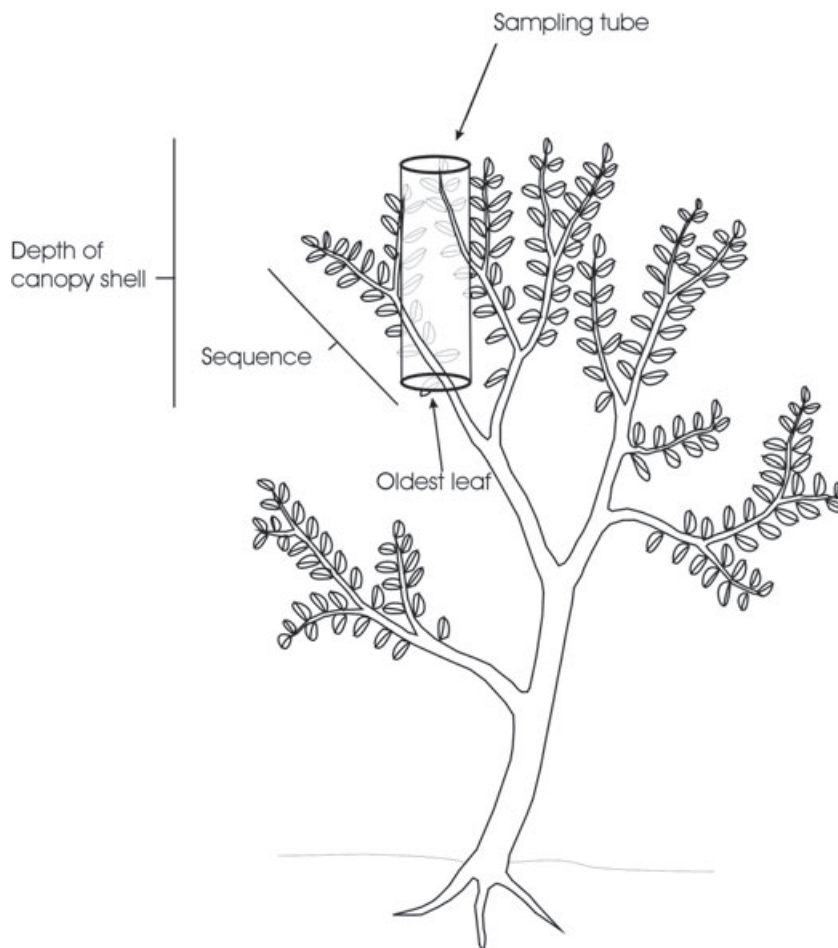
The study site was in Ku-ring-gai Chase National Park, near Sydney, Australia (33°40'53"S, 151°8'50"E). The vegetation is low-eucalypt woodland with a species-rich understorey of woody shrubs, dominated by Fabaceae, Proteaceae and Myrtaceae (Rice & Westoby 1983). The site was on a plateau surface with soils derived from the underlying Hawkesbury sandstone. Such soils tend to be very nutrient-poor: total soil  $P = 94$ , SD 28 p.p.m.; total soil  $n = 0.03$ , SD 0.001 p.p.m. (Wright *et al.* 2001). The vegetation is fire-prone, with seedlings establishing and some species resprouting vegetatively following fire. The previous fire at the site was in 1979, hence all individuals studied were well grown.

Canopy properties were measured for 14 common shrub species. Species selection was based on a parallel study in which LL and other leaf traits were being measured for 17 species at the site (Wright & Cannon

2001), with the addition of an extra species, *Banksia spinulosa*. Only species typically less than 3.5 m tall were sampled, taller canopies being harder to reach. The 14 study taxa represented six families. Sampling was between April and November 1999, and was confined within a 2-ha area to restrict effects of environmental heterogeneity. Five random plants from each species were sampled, except for *Hakea dactyloides* (only three individuals within the area). Plants were rejected if they were senescent, or subject to very high levels of herbivory, or had not reached reproductive maturity (no evidence of fruits, buds or flowers).

### Sampling canopy properties

We sampled shoots that reached the outside surface of the canopy. These would contribute more to the carbon economy of the plant and thus are of more interest than shoots potentially dormant in the shade of the canopy interior. Considering outer shoots, the canopy of a shrub can be crudely envisaged as an expanding shell (Fig. 1). We worked back from the growing tip of



**Fig. 1.** Schematic showing the positioning of a cylindrical sample volume (sample 'tube') in relation to the oldest leaf in a leaf sequence and the depth of the canopy 'shell'.

an outer shoot to the oldest leaf in the leaf age-sequence along this shoot, which constituted the inner surface of the canopy shell of foliage. Measurements were taken both along the shoot from this oldest leaf to the outside of the canopy shell, and vertically upwards from this oldest leaf to the top of the canopy shell (Fig. 1). Usually the shoot was not quite vertical, so these two directions of measurement did not coincide. Along the shoot we measured (i) average internode distance (i.e. the average distance between successive leaves); (ii) number of leaves in the chronological sequence, counting from the youngest fully expanded leaf, back to the oldest leaf on the shoot; (iii) distance between the apical tip and the oldest leaf; (iv) average distance between branches on the sequence; and (v) average branch angle along the sequence. Vertically upwards, leaves were harvested in horizontal slices within a cylindrical sample volume from the oldest leaf to the top of the plant's canopy (Fig. 1). The length of this sample volume is called depth of the canopy shell in what follows. The radius of the sample volume was 15 cm usually, but was adjusted between 5 and 20 cm as necessary depending on leaf size and texture of the canopy, to ensure the sample cylinder was wide enough to include large leaves and to avoid passing straight through a canopy gap, but small enough to avoid extending outside the canopy outline.

Dimensions of the vertical cylinder sample volume were measured on the plant using two rulers and a spirit level to ensure the central axis was vertical. The area of all leaves collected from each slice within the cylinder was measured on a flat bed scanner, giving rise to an estimate of LAI (square metre of leaf per square metre of ground) directly above the oldest leaf in the age sequence. Leaves were then oven dried at 60° for 48 h and weighed, providing average SLA for leaves within the canopy shell. We refer to the dry mass per ground area of the leaves from each sample cylinder as the leaf mass index (LMI).

### Light environment

Light attenuation down through the canopy shell was assessed with fish-eye sensors (LAI-2000 plant canopy analyser, LI-COR, Lincoln, NE, USA) that measure the per cent transmittance of diffuse light (diffuse non-interceptance, or Gap Fraction) through the foliage canopy. Measurements were taken relative to a simultaneous measure by a second sensor mounted on a tripod in a large adjacent clearing (>2 ha) and taking a measurement every 30 s. The sensors measure radiation simultaneously at five zenith angles, appropriately weighted. An optical filter restricts radiation above 490 nm to minimize contribution from light scattered by foliage. Measurements were made under

diffuse light conditions when there was continuous cloud cover. Gap Fraction is an estimate of the fraction of sky visible through the canopy and has been found to be a good predictor of growing season per cent transmittance (Comeau *et al.* 1998) and of annual light availability (Machado & Reich 1999). In this study Gap Fraction readings were taken at top and bottom of the vertical sample cylinder within each plant (Fig. 1).

### Leaf size and LL

Mean individual leaf size and LL for 13 of the 14 species were reported by Wright and Cannon (2001). Leaf size in that study referred to projected leaf area (as measured on a flat-bed scanner), which underestimates the true one-sided surface area of needle-leaved species. Here, for the needle-leaved species *Hakea teretifolia* we multiplied the reported leaf size by  $\pi/2$  to correct for this underestimation (i.e. we assumed that the needles were circular in cross-section). For *B. spinulosa* (not included in that study), leaf size was taken from leaves scanned for SLA. LL for this species could be estimated at a single visit since leaf cohorts for successive years can easily be identified. One branch per plant was randomly chosen, the oldest cohort with *c.* 50% of leaves remaining was identified, and the age of this cohort averaged over the 11 plants gave an estimate of average LL for the species (Cornelissen *et al.* 2003).

### Analysis

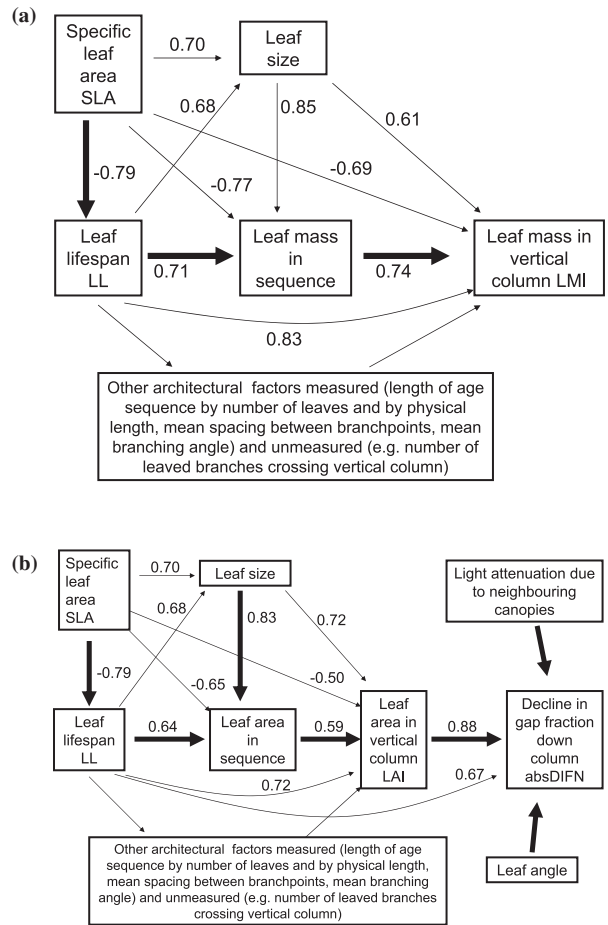
All variables except Gap Fractions were averaged across the five plants for each species and then  $\log_{10}$ -transformed to correct for strongly right-skewed distributions. Absolute decline in Gap Fraction was calculated as the difference in Gap Fraction between the top and bottom of the vertical cylindrical sample volume through the canopy shell (Fig. 1), averaged across individual plants within each species. Relative decline was calculated as the difference in  $\log$  Gap Fraction between top and bottom of the sample volume, equivalent to a ratio of the absolute Gap Fractions. Neither absolute nor relative Gap Fraction decline were further transformed since their distributions were not clearly skewed. The species-mean values for each trait are given in Table 1. Within-species variation is not examined in this paper.

The results are presented chiefly in terms of the predictive power of pairwise correlations among the measured traits (Table 2). Logically, leaf traits such as LL and SLA must scale up to canopy-aggregate properties (LMI, LAI, decline in Gap Fraction) via a number of other leaf traits and architectural properties of

**Table 1.** Species-mean traits of the 14 study species

Species	SLA	LL	n(L)	Size	Laseq	LMseq	LMI	LAI	relGFA	absGFA	SeqL	Bang	Node	Bdist
<i>Acacia suaveolens</i>	4.5	3.3	47	346	17 586	3 854	0.20	0.97	0.19	0.17	100	37.0	2.12	33.4
<i>Banksia spinulosa</i>	4.2	2.7	67	68	4 556	1 074	0.25	1.08	0.23	0.19	19	74.0	0.29	5.3
<i>Boronia ledifolia</i>	6.2	1.9	28	56	1 441	232	0.04	0.28	0.17	0.15	35	51.8	1.23	2.7
<i>Eriostemon australasius</i>	6.7	1.1	34	154	4 245	653	0.03	0.17	0.10	0.12	34	35.0	0.99	10.5
<i>Gompholobium glaberrimum</i>	6.6	3.0	29	120	2 355	365	0.14	0.93	0.27	0.23	28	39.4	0.94	3.5
<i>Grevillea buxifolia</i>	7.8	1.5	156	51	9 228	1 191	0.11	0.87	0.38	0.23	76	49.0	0.49	5.4
<i>Grevillea speciosa</i>	6.4	1.7	33	157	3 886	604	0.24	1.52	0.21	0.23	72	40.6	2.17	12.3
<i>Hakea dactyloides</i>	3.4	4.4	46	1244	24 269	7 076	1.11	3.81	0.45	0.34	77	49.7	1.72	8.6
<i>Hakea teretifolia</i>	4.7	2.6	145	217	9 779	3 345	0.63	2.85	0.25	0.25	102	49.4	0.70	8.0
<i>Hibbertia bracteata</i>	8.6	1.0	63	93	4 333	507	0.07	0.61	0.25	0.17	70	51.3	1.09	8.9
<i>Lambertia formosa</i>	4.6	3.0	34	125	5 364	1 172	0.34	1.47	0.19	0.19	27	45.0	0.79	5.7
<i>Leptospermum trimerevium</i>	9.6	1.7	26	29	1 115	120	0.16	1.43	0.26	0.23	44	45.2	1.72	2.1
<i>Persoonia levis</i>	4.5	5.6	29	3309	74 538	17 444	1.05	4.00	0.37	0.30	82	48.0	2.99	10.7
<i>Phyllota phyllicoides</i>	7.7	1.9	382	15	4 117	537	0.14	1.07	0.23	0.19	72	47.0	0.18	4.1

Data for leaf lifespan and leaf size were taken from Wright and Cannon (2001). absGFA, absolute difference in Gap Fraction; Bang, branching angle; Bdist, interbranch distance (cm); LAI, leaf area index ( $\text{mm}^2 \text{mm}^{-2}$ ); Laseq, total leaf area per sequence ( $\text{mm}^2 \text{mm}^{-2}$ ); LMseq, leaf mass index ( $\text{mm}^2 \text{mg}^{-1}$ ); LMI, leaf mass index ( $\text{mm}^2 \text{mg}^{-1}$ ); LMseq, leaf mass per sequence (mg); n(L), number of leaves per sequence; Node, internode distance (cm); relGFA, relative difference in Gap Fraction; SeqL, length of leaf sequence (cm); Size, leaf size ( $\text{mm}^2$ ); SLA, specific leaf area ( $\text{mm}^2 \text{mg}^{-1}$ ).



**Fig. 2.** Correlation coefficients among some of the principal variables. (a) Relationships involving leaf mass per ground area (leaf mass index LMI); (b) Relationships involving leaf area per ground area (leaf area index, LAI) and light attenuation.

the plant crown. Thus, we arrayed the trait correlations on diagrams that depict some possible pathways by which this scaling-up occurs (Fig. 2a,b). In these, the one-headed arrows used to connect the various leaf and architectural properties are not intended to indicate direct causal pathways, as would be the case in illustrating a formal path analysis. Rather, the diagrams are intended to provide a conceptual framework for the study and to help guide the reader through the results. Presumably, relationships between many of the measured properties reflect trait coordination just as much as strictly causal relationships.

**RESULTS**

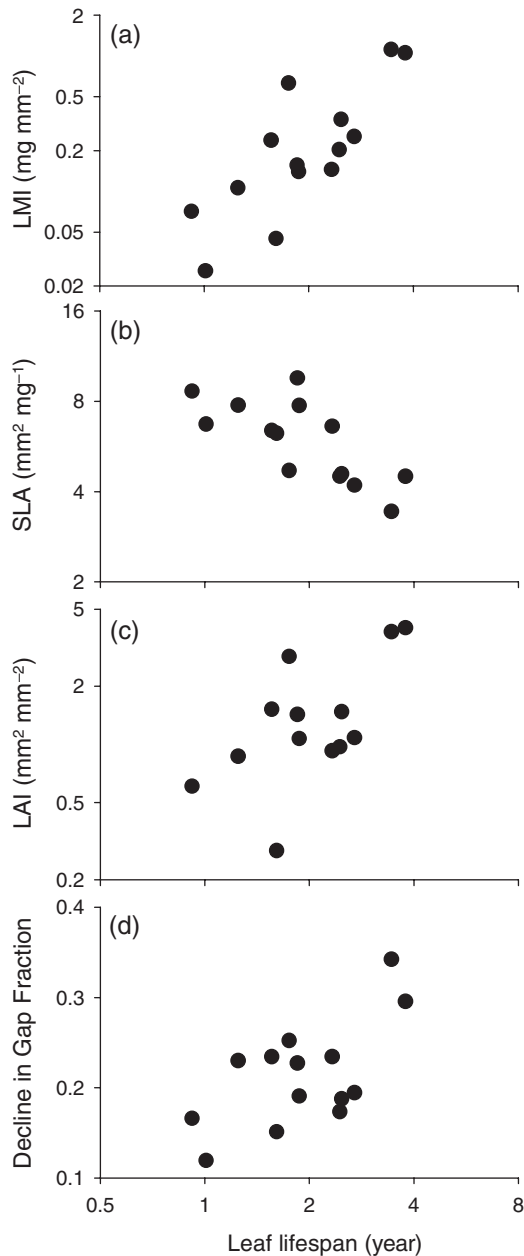
Leaf lifespan was quite a strong predictor of mean foliage dry mass per ground area through the canopy shell, hereafter called LMI ( $r = 0.83$ , Fig. 3a). SLA was negatively correlated with LL ( $r = -0.79$ , Fig. 3b),

**Table 2.** Pairwise correlation coefficients among the plant traits, across  $n = 14$  species

	SLA	LL	n(L)	Size	LAseq	LMseq	LMI	LAI	relGFA	absGFA	Bang	SeqL	Node
LL	$r$	-0.79											
	$P$	0.001											
n(L)	$r$	0.13	-0.19										
	$P$	0.649	0.518										
Size	$r$	-0.70	0.68	-0.39									
	$P$	0.005	0.007	0.162									
LAseq	$r$	-0.65	0.64	0.12	0.83								
	$P$	0.012	0.014	0.694	0.000								
LMseq	$r$	-0.77	0.71	0.09	0.85	0.98							
	$P$	0.001	0.004	0.752	0.000	0.000							
LMI	$r$	-0.69	0.83	0.03	0.64	0.67	0.74						
	$P$	0.006	0.000	0.915	0.014	0.008	0.003						
LAI	$r$	-0.50	0.72	0.11	0.51	0.59	0.62	0.97					
	$P$	0.071	0.004	0.719	0.061	0.027	0.018	0.000					
relGFA	$r$	-0.26	0.49	0.14	0.45	0.56	0.52	0.70					
	$P$	0.367	0.077	0.625	0.105	0.036	0.055	0.005					
absGFA	$r$	-0.43	0.67	0.00	0.58	0.56	0.57	0.88	0.88				
	$P$	0.120	0.009	0.995	0.031	0.039	0.033	0.000	0.000				
Bang	$r$	-0.23	0.13	0.27	-0.14	0.01	0.06	0.23	0.30	0.17			
	$P$	0.439	0.661	0.346	0.642	0.974	0.826	0.422	0.293	0.553			
SeqL	$r$	-0.02	0.10	0.39	0.35	0.56	0.50	0.43	0.40	0.40	-0.25		
	$P$	0.935	0.739	0.172	0.225	0.037	0.071	0.128	0.152	0.160	0.390		
Node	$r$	-0.17	0.28	-0.76	0.66	0.29	0.27	0.21	0.15	0.30	-0.44	0.30	
	$P$	0.563	0.333	0.002	0.010	0.312	0.351	0.473	0.601	0.299	0.117	0.295	
Bdist	$r$	-0.45	0.20	-0.02	0.60	0.67	0.65	0.14	-0.04	0.02	-0.35	0.52	0.39
	$P$	0.105	0.500	0.934	0.022	0.009	0.012	0.638	0.900	0.933	0.217	0.056	0.165

All variables were  $\log_{10}$ -transformed prior to analysis except relative and absolute Gap Fraction change. absGFA, absolute difference in Gap Fraction; Bang, branching angle; Bdist, interbranch distance (cm); LAI, leaf area index ( $\text{mm}^2 \text{mm}^{-2}$ ); LAseq, total leaf area per sequence ( $\text{mm}^2$ ); LL, leaf lifespan (year); LMI, leaf mass index ( $\text{mm}^2 \text{mg}^{-1}$ ); LMseq, leaf mass per sequence ( $\text{mg}$ ); n(L), number of leaves per sequence; Node, internode distance (cm); relGFA, relative difference in Gap Fraction; SeqL, length of leaf sequence (cm); Size, leaf size ( $\text{mm}^2$ ); SLA, specific leaf area ( $\text{mm}^2 \text{mg}^{-1}$ ).





**Fig. 3.** Predictive power of leaf lifespan for (a) leaf dry mass per ground area in a vertical cylinder above the oldest leaf along a shoot (leaf mass index – LMI); (b) leaf area per unit dry mass of leaf (specific leaf area – SLA); (c) leaf area per ground area in a vertical cylinder above the oldest leaf (leaf area index – LAI); and (d) light attenuation measured as decline in absolute Gap Fraction down the vertical cylinder. Correlation coefficients are in Table 2.

as expected. Correspondingly, SLA was also a predictor of LMI ( $r = -0.69$ ), though not quite so strongly as was LL. These relationships are shown in Fig. 2a. The complete dataset and set of correlation coefficients are provided in Tables 1 and 2.

Leaf lifespan was also a predictor of LAI ( $r = 0.72$ , Fig. 3c), though not quite so strongly as of LMI, pre-

sumably because species with long LL tended to have lower leaf area per mass (SLA). LAI, in turn, was quite a good predictor of the decline in Gap Fraction down through the canopy, whether measured absolutely ( $r = 0.88$ ) or relatively ( $r = 0.70$ ). The outcome was that LL was quite a good predictor of decline in Gap Fraction ( $r = 0.67$  for absolute Gap Fraction decline; Fig. 3d).

For more distant relationships (Fig. 2), predictive power was generally weaker. For example, SLA predicted LL, which itself predicted LMI, which predicted LAI, which itself predicted decline in Gap Fraction, but the resulting predictive power of SLA for decline in Gap Fraction was modest ( $r = -0.43$  for absolute decline, Fig. 2 and Table 2).

There was one feature of the data that we did not understand. The mechanism by which LL might be expected to influence LMI or LAI was by accumulating more leaf along age sequences on each branch. However, for both LMI and LAI the predictive power directly from LL was stronger than the predictive power through leaf mass or leaf area along the age sequence on the branch (Fig. 2). This must have been because other architectural features besides the amount of leaf along age sequences contributed to variation in LMI and LAI, and were also correlated with LL. We considered especially the potential role of leaf size, which was correlated with both LL and SLA (Fig. 2). However, leaf size did not have stronger predictive power for LMI or LAI than for leaf mass or leaf area along the sequence (Fig. 2a,b). Other architectural features that we measured similarly did not seem to have played this role. Mean spacing between branch-points, mean branching angle and length of age sequence by number of leaves and by physical length either did not have much predictive power for LAI or LMI, or were themselves weakly predicted by LL, or both (details in Table 2). Furthermore, LAI and LL were still correlated after controlling for variation in leaf size (partial regression,  $r = 0.59$ ,  $P = 0.035$ ) or when controlling for variation in the other traits one at a time (details not shown). Thus, we presume that other unmeasured architectural features must have been involved, such as the number of leaf-bearing branches crossing through the vertical cylinder sample above the oldest leaf.

## DISCUSSION

Elsewhere, LL and foliage mass accumulation have been correlated in conifer stands (Reich *et al.* 1992; Gower *et al.* 1993; Warren & Adams 2000). Similar to our study, they found leaf area accumulation more weakly related to LL than leaf mass accumulation, because lower SLA offset somewhat the higher foliage mass.

Leaf area index is an emergent property of a species that is a primary predictor of canopy light interception (Russell *et al.* 1989), and hence of whole canopy photosynthesis and productivity (Bond 1989). Light interception is often expressed as a proportional decline in light rather than as an absolute decline since photosynthetically active radiation tends to decrease exponentially downwards through a canopy (Monsi *et al.* 1973). Here, the relationship between LAI and relative decline in Gap Fraction was weaker than with absolute decline. This may have been because for a number of plants in relatively shaded positions, the proportional difference in Gap Fraction between the top and bottom of the canopy was large, even though LAI was relatively low and the corresponding absolute difference between Gap Fraction at the top and bottom of the canopy shell was small. This pattern may also lie behind the weaker relationship between LL and relative decline in Gap Fraction than with absolute Gap Fraction decline.

The primary finding from this study (of a relationship between LL and foliage accumulation within the canopy) helps us to further understand differences in plant ecological strategies associated with LL and SLA. High-SLA foliage has fast photosynthetic rates and high light-capture area per gram, but greater accumulation of foliage in long-LL-low-SLA species may counterbalance this competitive advantage of high-SLA leaves.

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