

Leaf size and angle vary widely across species: what consequences for light interception?

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Summary

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- Architecture can vary widely across species. Both steeper leaf angles and increased self-shading are thought to reduce potential carbon gain by decreasing total light interception. An alternative hypothesis is that steeper leaf angles have evolved to improve day-long carbon gain by emphasising light interception from low angles.
- Here we relate variation in architectural properties (leaf angle and leaf size) to cross-species patterns of leaf display, light capture and simulated carbon gain in branching-units of 38 perennial species occurring at two sites in Australian forest. Architectural comparison was made possible by combining 3D-digitising with the architecture model YPLANT.
- Species with shallow angled leaves had greater daily light interception and potentially greater carbon gain. Self-shading, rather than leaf angle, explained most variance between species in light capture and potential carbon gain. Species average leaf size was the most important determinant of self-shading.
- Our results provide the first cross-species evidence that steeper leaf angles function to reduce exposure to excess light levels during the middle of the day, more than to maximise carbon gain.

Key words: architecture, digitising, light interception, self-shading, YPLANT.

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Introduction

Plant species coexisting in a similar light environment can vary widely in architecture, the arrangement of their components in space. Variation in several architectural traits combines to give species a distinctive visual appearance. But do these different architectures translate into different light-interception properties, or are coexisting architectures just alternative ways to achieve similar overall outcomes? Few data are presently available to assess the relative competence of alternative architectures.

If alternative shoot architectures have different consequences for light interception, the effect has to be via self-shading or leaf orientation. In this study, we set out to explore the implications of different architectures in a set of coexisting shrub species by quantifying the effect of shoot-scale leaf arrangement on leaf display, light interception and potential carbon gain. By combining several technologies that have recently become available, we have been able to quantify 3D deployment of leaves in space and its consequences for light

interception more quickly, and therefore across a wider range of species, than has previously been possible.

Leaf angle

Given a particular radiation stream, the angle of a leaf's surface to the horizontal (leaf angle) directly determines the flux of solar radiation per unit leaf area (Ehleringer & Werk, 1986; Ezcurra *et al.*, 1991). Steeper leaf angles increase light capture when the sun is at low angles in the sky (morning/afternoon and winter), whilst decreasing light captures from higher angles (midday and summer). The benefits of steeper leaf angles include a reduction in midday heat-loads, thereby increasing water use efficiency and decreasing the risk of overheating (King, 1997); a decrease in the susceptibility to mild or severe photoinhibition (Ryel *et al.*, 1993; Valladares & Pugnaire, 1999; Werner *et al.*, 2001b); and minimising water-use with respect to daily carbon gain (Cowan, 1982).

Despite substantial variation in leaf angle within individuals of a species (Baldocchi *et al.*, 1985; Russell *et al.*, 1989;

Niinemets, 1998; Kull *et al.*, 1999; Utsugi, 1999; Barclay, 2001; Werner *et al.*, 2001b), leaf angle distributions are typically unimodal, and species may differ in the mean or median of these distributions (McMillen & McClendon, 1979; Ehleringer, 1988). Leaf anatomy is co-ordinated with leaf angle, which is evidence for consistent differences in leaf angle between species (King, 1997; Smith *et al.*, 1997; Smith *et al.*, 1998). Given that species differ in leaf angle, and that there are known implications for light capture, a primary aim of the research reported here was to quantify the magnitude of inter-specific variation in light capture attributable to leaf angle.

An assumed cost of steeper leaf angles is a decrease in potential daily carbon gain through decreased light interception. Here we provide the first interspecific test of this proposition across substantial numbers of co-existing species. We contrast this with an alternative evolutionary argument for steeper leaf angles: that they have evolved to maximise daily carbon gain. A standard photosynthetic light response curve saturates at moderate light intensities (Lambers *et al.*, 1998). Consequently, species with steeper leaf angles may be able to maintain high levels of photosynthesis during periods of high radiation (sun at high angles in the sky), despite intercepting significantly less light than would a shallow-angled species. When the sun is close to the horizon, steeper leaved species may have a distinct advantage over shallower leaved species because PFD is not saturating. This could provide an overall benefit for steeper leaved species in terms of daily photosynthesis. A primary motivation for the present study was to assess whether it is possible to distinguish between steep leaf angle as favoring low-angle light interception and thereby maximising potential daily carbon gain, compared with avoiding high-angle heat load or photoinhibition, at the expense of potential carbon gain.

Self-shading

Another influence on whole-plant light capture by a species is self-shading within the individual. Self-shading decreases the net amount of leaf area exposed to diffuse and direct light. Many architectural traits reduce self-shading. Ontogenetic changes in petiole length, petiole angle and leaf size minimised self-shading in an understorey herb (Percy & Yang, 1998) and a tropical pioneer tree (Yamada *et al.*, 2000). Branching angles were close to the predicted optimum for minimising self-shading in a tropical tree species (Honda & Fisher, 1978). In simulation studies manipulating virtual plants, changes in leaf clumping (de Castro & Fetcher, 1999), branching angles (Honda & Fisher, 1978), petiole length (Takenaka, 1994), leaf area index and leaf angle (Hikosaka & Hirose, 1997; Percy & Valladares, 1999) have each been shown to alter light interception and carbon gain considerably via effects on shading. Each plant species might employ different strategies to minimise shading depending on its suite of other architectural traits (Sekimura, 1995).

Although many traits are capable in principle of influencing self-shading and leaf angle, it might still be the case that actual differences between species in these outcomes are mainly driven by one or two architectural traits. Quantifying the sources of variation between species was among our aims in the work reported here.

Three-dimensional digitising

Simulation software (Ezcurra *et al.*, 1991; Ryel *et al.*, 1993; Takenaka, 1994; Percy & Yang, 1996; Werner *et al.*, 2001a,b) and 3D digitising (Hanan & Room, 1997; Sinoquet & Rivet, 1997; Rakocevic *et al.*, 2000) make it possible to assess the importance of different architectural traits for light interception and potential photosynthesis. Three dimensional computer simulations estimate light interception and photosynthesis for individual leaves and whole plants through the day, and have been shown to correspond well with measurements (Percy & Yang, 1998; Valladares & Percy, 1998, 1999; Naumburg *et al.*, 2001). However, simulations require detailed information about the 3D layout of leaves. Generalising across large numbers of individuals or species has been limited by the time consuming nature of data collection. Together with new software specifically designed for collecting architectural information, digitising allows rapid recording of 3D point locations, greatly enhancing the speed of architectural data collection. In the current study we combine digitising technology with the three-dimensional architecture model YPLANT (Percy & Yang, 1996) to provide an architectural comparison across significant numbers of coexisting species.

Our leading question was about the relative influence of leaf angle and self-shading on interspecific differences in leaf display, light capture and potential photosynthesis. In particular we aimed to assess whether steep leaf angle could be interpreted better as functioning to avoid radiation across the middle of the day, or to improve light interception early and late in the day. Supplementary questions were: first, which architectural traits result in differences in self-shading between species? And second, what was the correlation structure amongst important architectural traits across species.

Materials and Methods

Study sites and species

Two sites were chosen within Ku-ring-gai Chase National Park, Sydney, Australia. Both were temperate forest with a high diversity of shrub species under a moderately open eucalypt canopy. The sites differed in soil fertility (94 vs 440 mg kg⁻¹ total P – Wright *et al.*, 2001) but had similar average annual rainfall (1220 mm distributed throughout the year) and temperature (22°, 13°C). The vegetation at the low nutrient site (33°41'38"S, 151°8'35"E) was fire-prone low

open sclerophyll woodland with a species rich understorey of woody shrubs, and emergent eucalypts to 15 m (Rice & Westoby, 1983). The site was last burnt in 1990. The soils are derived from Hawkesbury Sandstone parent material. The vegetation at the higher nutrient site (33°34'44"S, 151°17'32"E) is fire-sensitive closed forest, with an overstorey to 20 m dominated by *Syncarpia glomulifera*, *Eucalyptus umbra* and *Livistona australis*. Woody shrubs, climbers, ferns and cycads dominate the understorey. The soils are derived from a weathered volcanic dyke. Plant growth is continuous throughout the year, although species may exhibit a flush of new growth in spring. Further site details are provided by (Wright *et al.*, 2001). Hereafter, the sites are referred to as medium LAI (closed forest) and low LAI (open woodland) sites.

Sampling

At either site, a large number of small to moderate-sized woody perennial shrub species coexist in a similar light environment. Most species exhibit a rigid, sclerophyllous architecture, with comparatively little scope for diurnal or seasonal variation in leaf arrangement (*pers. obs.*). All species with flat or simply folded leaves, as assumed by the YPLANT software, were chosen for study. This included 26 species from the low LAI and 12 from the medium LAI site. The first three undamaged individuals of each species encountered further than 10 m away from an access track were sampled. Data were collected between 20 September 2000 and 26 November 2001.

For each individual, architectural information about the leading vertical branching unit, or 'tuft', on each plant was recorded. A tuft was defined as all leaves and side branches back to the oldest leaf along a leaf age sequence. This level of organisation represents an intermediate scale between the leaf and the whole plant, spanning the full range of leaf ages and reflecting the tendency for plants to consist of repeated architectural units. Tufts, as opposed to whole plants, were sampled for practical reasons and in an attempt to provide a size-independent unit of comparison across species. For each individual a 3D description of the tuft leaf arrangement, basal and terminal stem diameters (vernier calipers) and plant height were recorded.

Architectural information

The three-dimensional leaf arrangement of each plant was recorded using a FASTRAK® 3D-digitizer (Polhemus, Colchester, VT, USA), in conjunction with the software package FLORADIG (CSIRO Entomology, Brisbane, Australia). The digitizer includes a magnetic signal receiver and pointer, allowing the user to record the 3D spatial co-ordinates of the pointer within a hemisphere of 3 m diameter from the receiver. Individual plants are digitally reconstructed by recording a series of point co-ordinates, and the relevant

connectivity between points. Stem segments and petioles are characterized by their elevation angle, azimuth, length and diameter. Individual leaves are characterized by their length together with the azimuth and elevation angle of two vectors on the lamina surface.

YPLANT software (Pearcy & Yang, 1996) was used to estimate light interception and a potential carbon gain for different sample periods throughout a single day and integrated across entire days. The 3D description of leaf arrangement recorded for each tuft in FLORADIG was converted to the appropriate YPLANT format using a program written in C. Sampling time for individual tufts ranged from 20 min to 2.5 h, depending on the number and size of leaves. Although still time consuming, the methods presented here represent a marked acceleration of data collection in architectural studies using the YPLANT software. Full details regarding the collection of architectural information are given in Appendix S1.

Architectural model

YPLANT inputs are the geometry of leaf arrangement, a description of leaf shape, physiological parameters describing leaf photosynthetic capacity and a description of the canopy above the plant to estimate light interception and carbon assimilation rate. A solar movement submodel allows one to estimate photon flux density (PFD: $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) incident on each leaf surface at different times of day. A submodel for potential photosynthesis allows the resulting assimilation rate to be estimated, given a PFD response curve. 'Potential' photosynthesis here means the assimilation rate if PFD is limiting but other factors are not. Simulations can be conducted for any particular latitude and day of the year. Full details of the model can be found in (Pearcy & Yang, 1996), and additional verification is provided by (Pearcy & Yang, 1998; Valladares & Pearcy, 1998, 1999; Naumburg *et al.*, 2001).

Hemispherical photographs were used to describe canopy openness above the study plants. However, since we were interested in the effect of variation in architecture on light capture, all simulations were run under a single 'habitat average' canopy description. Hemispherical photographs were taken above 30 randomly selected study individuals at each site using a Nikon Coolpix 990 digital camera with a 183° fisheye attachment (Nikon Corporation, Japan). Photographs were taken on fully overcast days using standard methods for hemispherical photography (Rich, 1990; Pearcy & Yang, 1996). Photos were analyzed using the Gap Light Analyzer (GLA) software package (Frazer *et al.*, 1999). Fractional canopy openness (0–1) was calculated for 20 altitude and eight azimuth classes in each photo. Mean openness in each angle class was calculated for each photo by averaging openness across all azimuth classes, and an average openness for the habitat was calculated by averaging across all photos for each angle class. This allowed us to calculate a habitat average

Indirect Site Factor (Percy & Yang, 1996), and to estimate the average time series of direct PFD interception for any day of the year. A single average canopy profile was calculated for the summer solstice (December 21), the equinox (September 21/March 21) and the winter solstice (June 21), spanning the full range of solar trajectories experienced at the sites.

Output from YPLANT includes a quantification of leaf projection and display (the amount of leaf area facing a particular direction), which is general across locations, dates and times of day, also estimates of light capture and potential carbon assimilation rate that are specific to locations and dates and times of day. Variation in architectural traits (e.g. leaf angle) is first manifested as variation in leaf display. In turn, leaf display determines light capture and hence potential photosynthesis. We considered the effect of architectural traits on both leaf display and light interception in order to understand their consequences for potential carbon gain.

Quantifying leaf projection, display and self-shading

Leaf projection efficiency (PE) is the amount of leaf area projected towards a particular direction as a fraction of total leaf area. PE is less than 1 because most leaves are not face-on towards any particular direction. Leaf display efficiency (DE) is the proportion of the plant's total leaf area seen when looking at the plant from that direction. DE is PE as modified by leaf overlap. Logically, DE in the direction of the sun determines total tuft light capture per unit area. PE and DE were calculated for each of 160 directions (20 angle classes * eight azimuth classes), spanning the entire sky. To investigate the relative competencies of architectures at capturing light at different times of the day (i.e. when the sun is at different angles from the horizontal), PE and DE can be averaged across all azimuths for a particular elevation angle, and plotted against angle from the horizontal (Percy & Yang, 1996; Valladares & Pugnaire, 1999). Across all individuals in the study, PE and DE always changed smoothly with variation in the sun's angle in the sky, and were always highest to the horizontal and lowest to the vertical, or vice versa, or almost flat. It was never observed that PE or DE peaked at intermediate angles. Consequently patterns of leaf display and projection to different sun elevation angles can be summarized by considering only the endpoints of the graphs, that is the projection and display efficiencies to low angles in the sky (PE_H , DE_H : the proportion of the total leaf area projected, or displayed, to the horizontal) and to the vertical (PE_V , DE_V).

Two important components of tuft scale architecture can be described using these variables. Firstly, tufts can vary in PE_V and PE_H , the inherent capacity to project leaf area to high and low sun angles. The leaf projection ratio, $LPR = \log_2(PE_V : PE_H)$, provides a relative measure of the amount of leaf area projected vertically compared to that projected horizontally. Thus LPR captures the emphasis that is placed on light intercepted from high vs low angles in the sky.

Second, tufts can vary in self-shading. Self-shading is measured here as the proportional reduction in leaf projection by leaf overlap, $SS = (PE - DE) : PE$. Tuft average self-shading (SS_{AV}) was calculated for each individual by averaging SS across all 160 angle and azimuth classes. In addition, the level of self-shading to the vertical (SS_V) or the horizontal (SS_H) was calculated. To better understand determinants of average shading, the relative contribution of shading by other leaves within the tuft, and shading by either stem or petiole was calculated.

Of interest is the comparative influence of PE and SS on DE. As for leaf projection above, DE_H , DE_V and the leaf display ratio (LDR) provide measures of the relative competency of architectures at intercepting light from high and low sun angles, but incorporating the influence of self-shading.

Light interception and potential photosynthesis

Light interception for each individual was simulated in YPLANT for the summer and winter solstices and the equinox under two canopy conditions: first assuming an open canopy (no shading by neighbors), and second using habitat averaged canopy profile (average level of shading by neighbors). Light interception can be divided into its components of diffuse and direct light. For modelling we assumed low diffuse light compared to direct light (~10%) (Rich, 1990), but still diffuse light was an important contributor to incident PFD on shaded leaf area. Total light interception is the sum of diffuse and direct PFD on the lamina.

At the study sites, the maximum angle of the sun from the horizontal was 79° (solar midday on December 21), yielding a direct PFD of 2050 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on a surface normal to the solar beam. When the sun was at 15, 30, 45, 60 and 75° from the horizontal the PFD was estimated to be 63, 85, 94, 98 and 99% of this value, respectively. To assess the relative competencies of different architectures at different times of the day, instantaneous rates of light interception and assimilation were estimated when the sun was at 15, 30, 45, 60 and 75° from the horizontal on in each simulation. These solar elevations occur at different hours of the day on different days, with the sun reaching only some of the angles on solar trajectories at the equinox and winter solstice. For each angle from the horizontal, the instantaneous rate of light capture ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$) was estimated and averaged across the three days.

A 'potential carbon assimilation rate' ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was also calculated in order to assess the implications of non-linearity in the light-response curve. Because of diminishing returns in photosynthesis as light income increases, the highest light-capture levels should contribute a smaller share of total photosynthesis than of total light capture. To assess the consequences of this non-linearity, a generalized light-response curve common to all species was used to translate PFD interception into potential photosynthesis (see Appendix

S2 for details). We did not use species-specific light response curves, because our aim was to understand the consequences of particular architectures, unconfounded by any differences in light response curves. Potential carbon assimilation rates should not be interpreted as actual carbon gain for this reason, and also because they assumed no stomatal limitation of photosynthesis.

Additional variables

Aggregate descriptors of tufts were total leaf area, average leaf size, leaf number, tuft ellipsoidal area, tuft depth, main axis length (length of stem from tip to the oldest leaf), total stem length, average branch inclination (angle of stems/branches from the horizontal) and branching bifurcation angles (θ_1 , θ_2 ; see Data considerations for description; Honda & Fisher, 1978). Combinations of these yielded further variables of interest: tuft leaf area index (LAI = m^2 leaf area m^{-2} ground area) and leaf area per volume ($\text{m}^2 \text{m}^{-3}$). Aggregate tuft properties were expected to be of importance in determining self-shading. Specific Leaf Area (area : leaf dry mass) for 29 of the 38 study species was sourced from existing datasets (Wright *et al.*, 2001; Westoby & Wright, 2003).

Data considerations

Emphasis was on species means, since we were primarily interested in quantifying differences between species. Hierarchical anova was used to quantify the variation between and within species before arithmetic averaging. For leaf size, leaf number, total leaf area, tuft area and tuft volume, untransformed species means were not normally distributed, but were right skewed (Shapiro-Wilk Tests; data not shown). After log transformation these traits (and those derived from them, e.g. LAI) were normally distributed. For other traits including mean leaf angle, mean branch inclination, branching angles, leaf projection, display and self-shading traits, PFD interception and assimilation rates, untransformed species means were normally distributed.

For most architectural traits, variation between species was consistently larger than variation between tufts within a species. More than 80% of variance was between species in hierarchical anovas (data not shown) for leaf size, total leaf area, internode distance, leaf number (all \log_{10} transformed), and for mean leaf angle and all leaf projection, display and self-shading properties (untransformed). More than 50% of total variance was between species for leaf area index (LAI), leaf area per volume, tuft volume, main axis length, tuft shape and mean branch inclination (all \log_{10} transformed). These quantities could usefully be regarded as species traits, so mean values were calculated. For branching bifurcation angles (θ_1 : angle between stem orientation before and after branching point; θ_2 : angle between branch and stem section subtending branch) only 13% (θ_2) and 8% (θ_1)

of variance was between species. These quantities could not usefully be regarded as species traits, and they are not discussed further here.

All cross species analyses were performed using linear regression and correlation statistics. Evolutionary divergences (Westoby *et al.*, 1998) were not calculated since the study focussed mainly on quantifying the consequences of trait variation amongst species, rather than on the evolution of the traits themselves. However, family symbols are included in Figs 3, 4, 6, 7 to indicate the phylogeny associated with variation. When investigating scaling relationships between two variables, model II standardized major axis slopes were calculated on proportional axes (Sokal & Rohlf, 1995). To compare regression slopes among linear relationships that use common data for the x -variable, the difference in the y variables was regressed against the common predicting x variable. Where the slope of this relationship is significantly different to zero the initial slopes can be considered to differ significantly. All statistics were carried out using SPSS for Windows 8.0.2 (SPSS Inc., Chicago, IL).

Results

Variation in leaf orientation

There was a wide range of individual leaf angles in any tuft (examples in Fig. 1). Leaf angles within individuals were not significantly different from normal distributions for 90 of 114 study individuals (one sample Kolmogorov Smirnov, $P > 0.05$). Those that did differ significantly from normal had either skewed unimodal distributions (18 individuals), apparently a product of the mode being close to 0° or to 90° , or wide, even distributions (six individuals). There was no evidence for discontinuous or bimodal distributions of leaf angle. Consequently mean leaf angle (MLA) expressed differences between species satisfactorily. Most MLA variance was between species (85%, hierarchical type I Anova), rather than between individuals of the same species (15%). Species MLA varied from 32° to 78° at the low LAI site, and from 17° to 72° at the medium LAI site, with the average leaf angle at the medium LAI site significantly closer to horizontal than at the low LAI site (t -test: $t = 7.26$, $P < 0.01$).

Generally, species did not exhibit a characteristic leaf orientation azimuth. Leaf azimuths did not differ significantly from uniform distributions for 55 of 114 study individuals (one sample Kolmogorov Smirnov, $P > 0.05$). Those distributions that were nonuniform were mainly because the sampled tufts pointed in particular directions, rather than because the species as a whole pointed its leaves in particular directions. In only three out of 38 species, did all three individuals have non-uniform leaf azimuth distributions peaking in the same direction.

In summary, the mean leaf angle of species captures the main variation amongst species in leaf orientation distributions.

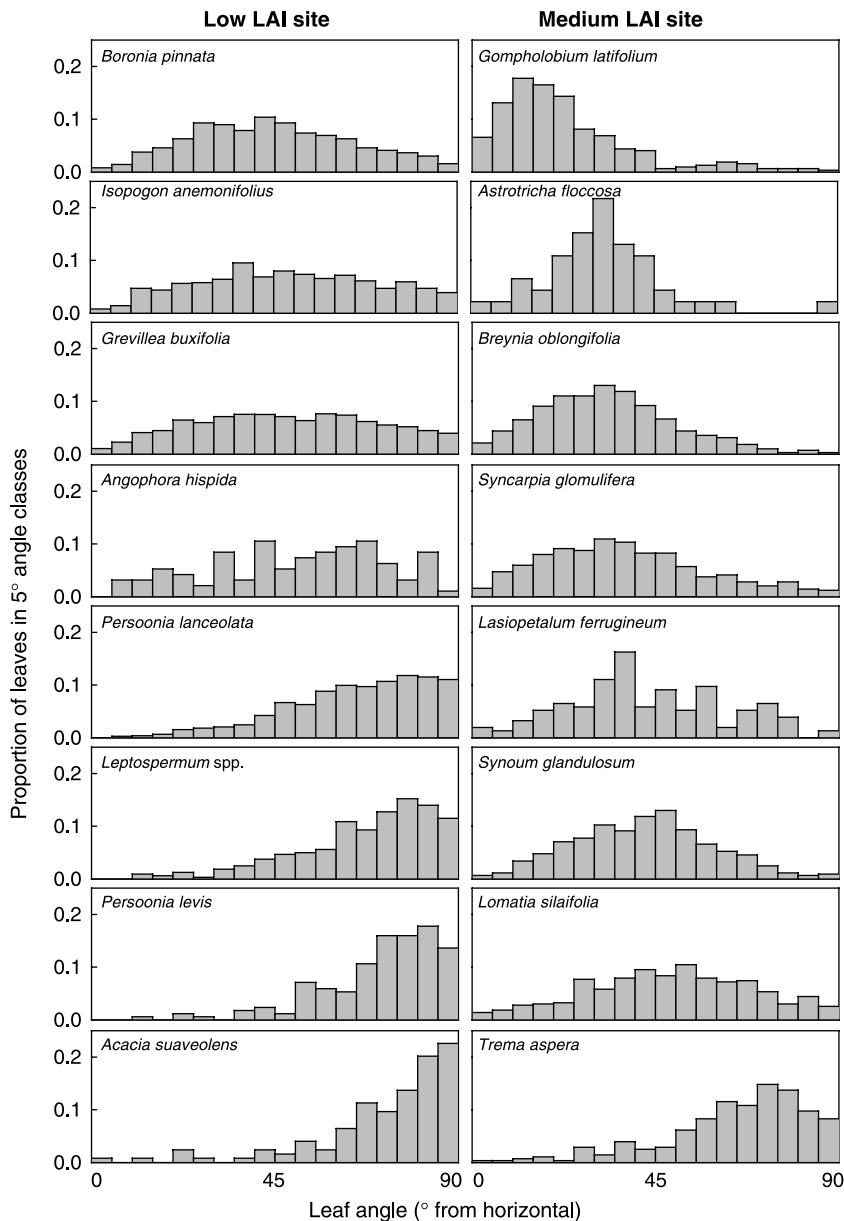


Fig. 1 Frequency distributions of leaf angle for 16 of 38 study species from the two study sites in Ku-ring-gai National Park, Australia. Data are pooled from three separate tufts per species. Leaf angle is measured as the angle from the horizontal (0 ~ flat; 90 ~ vertical/steep).

Variation in within-shoot self-shading

Self-shading decreases the net amount of leaf area available for light capture. The average proportion of leaf area that was self-shaded within the tuft (SS_{AV}) was calculated as the average level of self-shading across 160 different directions spanning the entire sky. SS_{AV} varied across species from 13 to 60% of total tuft leaf area.

The influence of leaf angle and self-shading on the projection and display of leaf area

Leaf projection efficiency to horizontal (PE_H) naturally increased with mean leaf angle, with a corresponding decrease

in leaf projection efficiency to vertical (PE_V) (Fig. 2a,2b left: open symbols). Consequently the leaf projection ratio ($LPR = \log_2(PE_V : PE_H)$) varied across species with variation in MLA (Fig. 2c). The range was from species projecting 2.18 times more leaf area to the low angles than to the vertical, to species projecting 3.36 times more leaf area to the vertical than the horizontal. All three relationships were linear across the range observed, and tight (Fig. 2; $r^2 > 0.99$).

We considered how closely species means for leaf projection traits (PE_H , PE_V , and LPR; Fig. 2 open symbols) matched with what would be expected from theoretical leaf angle distributions (Fig. 2, right). Three theoretical distributions were considered, all with random leaf azimuth orientation. First, the spherical leaf angle distribution (imagine leaf

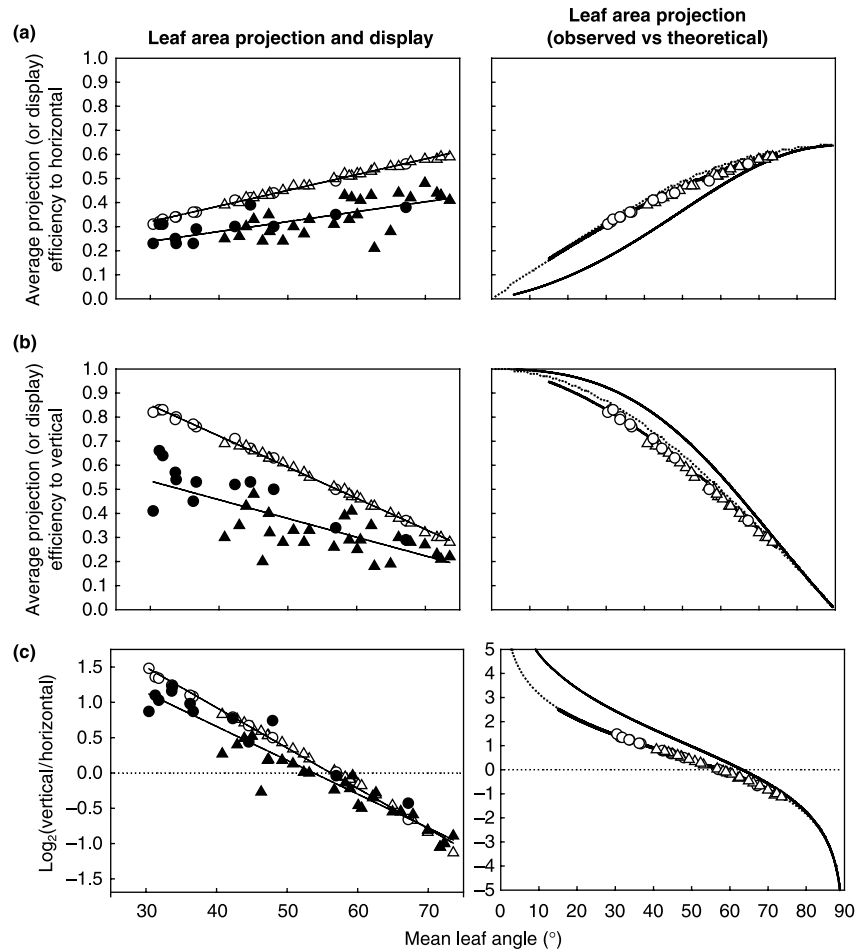


Fig. 2 Relationship between species mean leaf angle and the proportion of total leaf area projected (open symbols) or displayed (closed symbols) to (a) the horizontal (i.e. low angles in the sky) and (b) to the vertical (i.e. straight up). Also shown (c) is the ratio of leaf area projected (or displayed) to the vertical relative to low angles ($= \log_2(\text{vertical}/\text{horizontal})$). On the left, observed data are approximated by linear regression. On the right observed leaf projection data are compared with predictions from theoretical spherical (solid line), conic (dotted line) and normal (thick line) leaf angle distributions (axes re-scaled). Symbols: (triangles) low LAI site (circles) medium LAI site.

area covering the surface of a sphere) was extended to account for variation in MLA by considering the leaf angle distribution for ellipsoids of different length radii (Campbell, 1990). A spherical distribution is a special case of the ellipsoidal distribution, having radii of equal length ($\text{MLA} = 63^\circ$). Second, a constant leaf angle distribution, analogous to the situation where leaf area covers the sloped surface of a cone, was considered. Variation in MLA results from varying the height: radius dimensions of the cone. Finally, a normal leaf angle distribution was considered, where leaf angles were drawn from a normal distribution with a particular mean and standard deviation (when $\text{SD} = 0$ this is equivalent to the conic distribution), but truncated at the bounds of 0° and 90° . In all cases the area-weighted mean leaf angle was calculated.

The relationships between species averages for MLA and PE_H , PE_V or LPR corresponded tightly with the theoretical predictions from the normal distribution (with SD set at the species-average: $\text{SD} = 18.6$), less tightly with the conic distribution and only loosely with the predictions from the ellipsoidal distribution (Fig. 2a–c: right). In all three theoretical distributions, projection efficiency to horizontal (PE_H) was lower than projection efficiency to vertical (PE_V) (0.64

compared with 1.0), since compass orientation affects PE_H but not PE_V . Higher variance about MLA in the normal distribution shifted both horizontal and vertical projection efficiency downwards (relative to the conic distribution: $\sim \text{SD} = 0$), especially in the mid-range of leaf angles. This did not alter the relative leaf area projection to the horizontal and vertical (LPR), with identical predictions from the conical and normal distributions (Fig. 2c).

Leaf display efficiency to horizontal (DE_H) and vertical (DE_V) (Fig. 2a,b left: closed symbols) was less than the corresponding projection efficiency (open symbols) due to self-shading within the shoot. Display efficiencies, like projection efficiencies, were linearly related to MLA, but display efficiency was less tightly predicted from MLA than projection efficiency, due to variation in self-shading across species (DE_H : $r^2 = 0.51$, $P < 0.01$; DE_V : $r^2 = 0.64$, $P < 0.01$).

Species with shallower leaf angles had proportionately more self-shading to the vertical than to the horizontal, and the converse for species with steep leaf angles ($r^2 = 0.32$, $P < 0.001$). The effect was greater for shallow angled species, such that shading decreased the emphasis of shallow angled species on light interception from high angles more than it

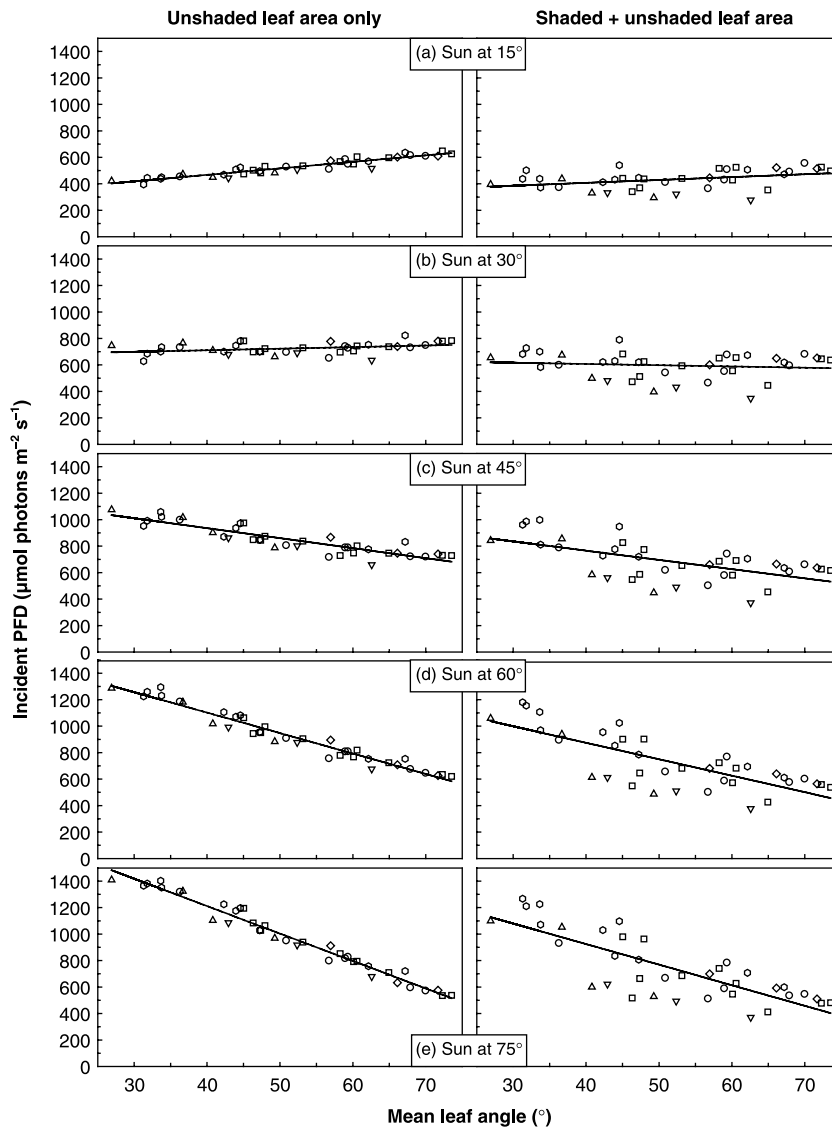


Fig. 3 Relationship between species mean leaf angle and average direct light interception by unshaded leaf area (left) and total average light interception by shaded and unshaded leaf area (right) when the sun is (a) 15° (b) 30° (c) 45° (d) 60°, and (e) 75° from the horizontal in simulations under open sky conditions. See Table 2 for correlation coefficients. Symbols: (squares) Proteaceae; (circles) Myrtaceae; (triangles) Fabaceae; (diamonds) *Acacia*; (inverted triangles) Epacridaceae; (hexagons) other families.

decreased the emphasis of steep-leaved species on light interception from low angles (Fig. 2c, slope of LDR against MLA significantly shallower than slope of LPR, d.f. = 37, $t = -3.3$, $P = 0.002$). But, MLA was not correlated with net amount of self-shading to the vertical or horizontal ($P > 0.15$). This indicates that the effect of leaf angle on self-shading is small compared to the other traits influencing average self-shading (see Architectural determinants of self-shading).

Instantaneous light interception and photosynthesis at high and low sun angles

At low sun angles (< 33°, e.g. 15°, 30° in Fig. 3 left) steeper leaved species naturally intercepted somewhat more direct sunlight, and the reverse at higher sun angles (> 33°, e.g. 45°, 60°, 75° in Fig. 3 left). Highest achievable light capture was greater at higher sun angles, as was the differentiation between

species (Fig. 3a vs Fig. 3e). This might be expected since the intensity of incoming radiation is greater at higher sun angles, but the pattern was reinforced by the difference in maximum potential projection efficiency to high and low angles (Fig. 2a,b right). Consequently, there was less difference between species of different MLA in light capture at low angles, since leaf azimuth also affects leaf projection efficiency at low angles.

Tuft average light interception includes diffuse and direct PFD incident on both the shaded and unshaded leaf area. Diffuse light interception was negatively correlated with both MLA ($r^2 = 0.55$) and SS_{AV} ($r^2 = 0.46$) at all sun angles (Table 1). The relationship between MLA and tuft-average light interception was looser than that between MLA and direct light interception, but was still significant (Fig. 3 right side; Table 1). Variation in self-shading across species increased the scatter in the relationship, with SS_{AV} significantly correlated with tuft average light capture at all sun angles (Table 1).

Table 1 Correlation coefficients between species mean leaf angle (MLA) or average self-shading (SS_{AV}) and instantaneous rates of light interception and 'potential carbon gain' for instances when the sun is at different angles from the horizontal. Potential carbon gain takes into account the diminishing returns on high rates of light interception, but should not be interpreted as field-realistic carbon gain

	Correlations with MLA					Correlations with SS_{AV}				
	15°	30°	45°	60°	75°	15°	30°	45°	60°	75°
Light interception ($\mu\text{mol m}^{-2} \text{s}^{-1}$)										
Direct light on unshaded leaf area only	0.94**	0.35*	-0.90**	-0.98**	-0.99**	n/a	n/a	n/a	n/a	n/a
Diffuse light interception	-0.73**	-0.74**	-0.73**	-0.74**	-0.74**	-0.67**	-0.68**	-0.68**	-0.68**	-0.67**
Tuft average light interception	0.38**	-0.13	-0.60**	-0.77**	-0.80**	-0.86**	-0.96**	-0.79**	-0.66**	-0.60*
Potential carbon gain ($\mu\text{mol m}^{-2} \text{s}^{-1}$)										
Assimilation rate from unshaded leaf area only	0.73**	-0.18	-0.83**	-0.95**	-0.95**	n/a	n/a	n/a	n/a	n/a
Tuft average assimilation rate	-0.05	-0.24	-0.38*	-0.48*	0.51**	-0.96**	-0.94**	-0.90**	-0.86**	-0.83**

Values are Pearson correlation coefficients, *indicates significance at $\alpha = 0.05$, ** $\alpha = 0.01$.

Relationships between MLA and total light interception (Fig. 3 right) were flatter than between MLA and direct light interception (Fig. 3 left) (significant difference in slopes, 3a: d.f. = 37, $t = -3.72$, $P < 0.001$; 3e: d.f. = 37, $t = -3.2$, $P = 0.003$), because steep-leafed species had proportionately more self-shading to low sun angles, while flat-leafed species had greater self-shading to high sun angles.

Were the patterns observed for PFD interception repeated for potential CO_2 assimilation, or did the diminishing returns on high PFD qualitatively change the conclusions? Estimated potential carbon assimilation on unshaded leaf area was significantly correlated with MLA at four of the five sun angles considered (Fig. 4 – left side; Table 1). Similar to light interception, species with steeper leaf angles had a greater rate of assimilation when the sun was at low angles, and the reverse when the sun was at high angles. However, species with steep leaf angles did not perform noticeably better in tuft-average potential carbon assimilation at low sun angles (Fig. 4a), though they did perform substantially worse at higher sun angles (Fig. 4e). This was contrary to our working hypothesis, that species with steep leaf angle would have an advantage at low sun angles. This outcome arose from the frequency distributions of light intercepted across tuft leaf area (examples in Fig. 5). At high sun angles (Fig. 4d–e), species did not differ much in the upper range of potential assimilation obtainable (Fig. 5), because light was saturating. But species with steeper MLA had more of their leaf area in the lower range of potential assimilation rates. This was partly because of the steep leaf angles themselves, but also because when leaf surfaces are not full-face towards the sun, the fact that azimuths were randomly directed rather than pointed towards the sun compass direction became more important. At low sun angles species with shallow MLA had most leaves at an angle to incoming light, but so also did species with steep MLA, because of azimuths pointing in many directions. The upshot was that MLA of species was not a substantial influence on potential carbon assimilation rate at low sun angles.

The influence of self-shading (SS_{AV}) on tuft-average potential carbon assimilation was greater than the influence of MLA (Fig. 6b, Table 1). Average assimilation rate for the entire tuft was correlated with MLA at three of the five sun angles (45°, 60° & 75°; Table 1), whilst SS_{AV} was negatively correlated with average assimilation rate at all angles (Table 1; Fig. 6b).

Whole-day light interception and photosynthesis

Average self-shading, rather than MLA, was the major determinant of whole-day light interception and potential carbon assimilation in all simulations, irrespective of time of year or of whether an overshading canopy was included (Table 2; Fig. 6).

Whole-day light interception was weakly correlated with MLA at midsummer (December 21) and at the equinoxes (September 21, March 21) but not at midwinter (June 21)

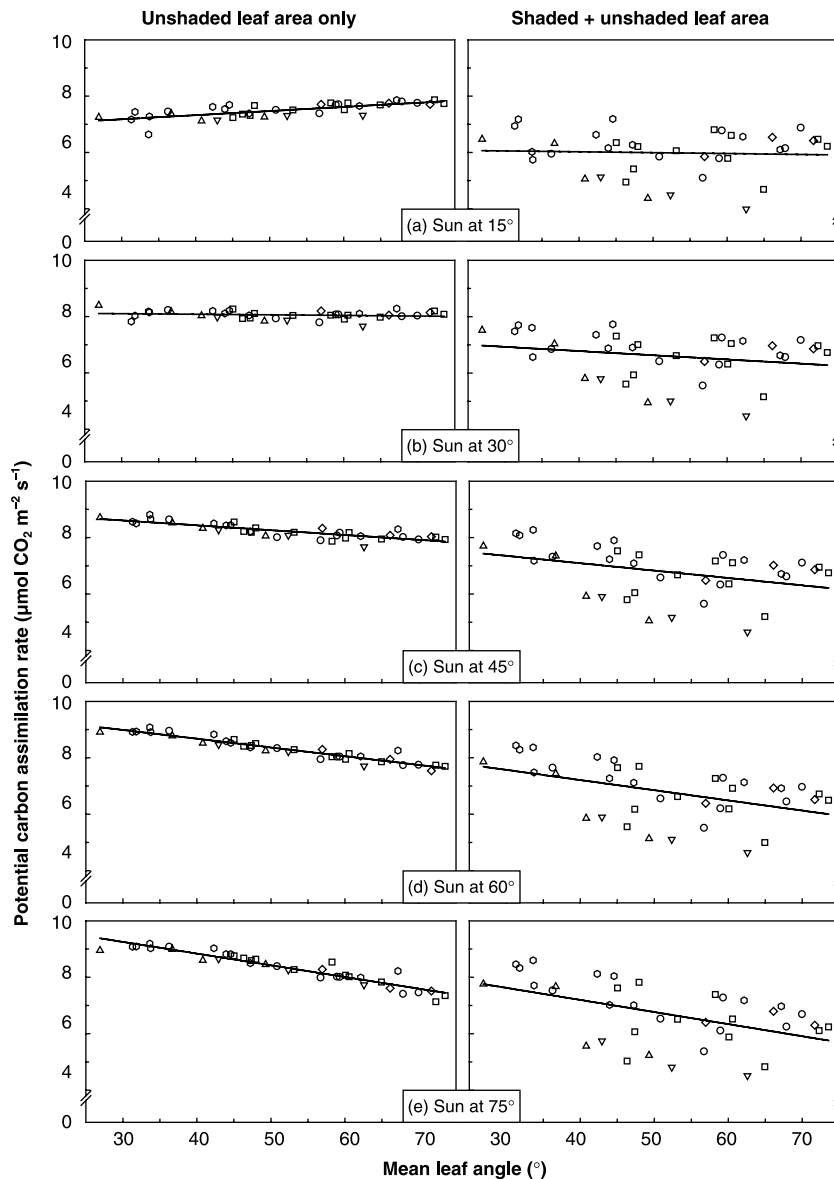


Fig. 4 Relationship between species mean leaf angle and 'potential carbon assimilation rate' from unshaded leaf area only (left) and integrated across shaded and unshaded leaf area (right) when the sun is (a) 15° (b) 30° (c) 45° (d) 60°, and (e) 75° from the horizontal in simulations under open sky conditions. Potential carbon gain takes into account the diminishing returns on high rates of light interception, but should not be interpreted as field-realistic carbon gain, as explained in the text. See Table 2 for correlation coefficients. Symbols: (squares) Proteaceae; (circles) Myrtaceae; (triangles) Fabaceae; (diamonds) *Acacia*; (inverted triangles) Epacridaceae; (hexagons) other families.

(Table 2). Such variation in daily light interception as was correlated with MLA did not translate into greater daily carbon assimilation for species with steeper leaf angles. This was contrary to our working hypothesis, that steeper leaf angles may have evolved to maximize carbon gain, but not so surprising given the minimal benefit for steep leaf angles in instantaneous light capture at low sun angles (previous section, Fig. 4). In reality potential daily carbon assimilation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) was greater for shallower leaved species in midsummer (December 21) and at the equinoxes (Sep/March 21) (closed canopy only), although the relationship was weak (Table 2).

Whole-day light interception and potential assimilation at tuft scale was strongly correlated with SS_{AV} on all days under either open or closed canopies (Table 2). Thus, at tuft scale, assimilation was more sensitive to variation in SS_{AV} than MLA.

The proportion of total daily PFD interception or potential carbon assimilation occurring while the sun was at low angles (below 33° from the horizontal) was calculated for each of the simulations (Table 3). Of interest is the range observed across species, and the relationship to MLA. The magnitudes of the proportions themselves are of less interest, since they vary depending on the particular angles chosen (below 33° in this case) and on the day of the year. In all cases except one, steeper-leaved species accomplished a significantly greater proportion of daily light interception or potential carbon assimilation while the sun was below 33° (Table 3). The widest range across species occurred on the longest day of the year (December 21) under an open canopy, when steeper-leaved species intercepted up to 14% more of their daily light budget from low angles. But this translated into only 4% difference

Fig. 5 Example frequency histograms of incident PFD on leaves of a shallow-angled (*Gompholobium latifolium*; MLA = 27°) and steep-leaved species (*Persea levis*; MLA = 74°) when the sun is at 15° and 75° from the horizontal. Data are for simulations under open sky on December 21 at -33.7° latitude. Also shown are photosynthetic light response curves for the maximum (hashed), mean (bold) and minimum (dotted) photosynthetic capacities observed across 44 species found at the two study sites. All simulations were conducted using the mean curve only.

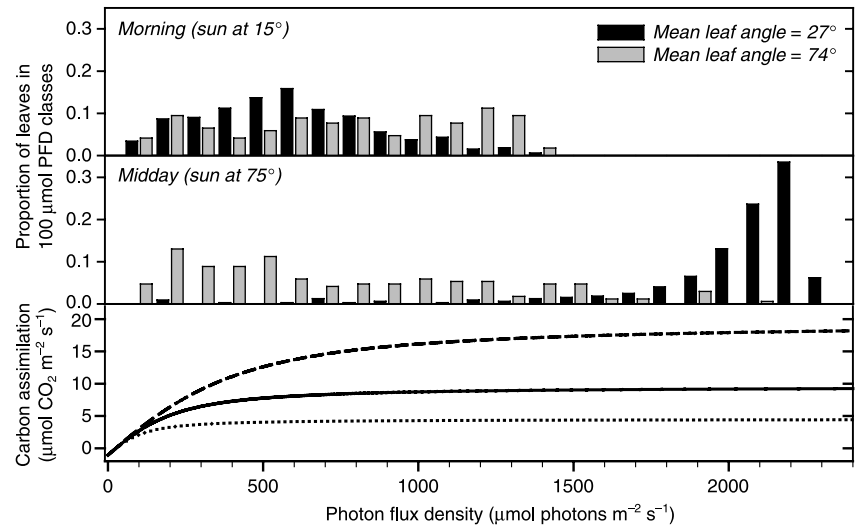
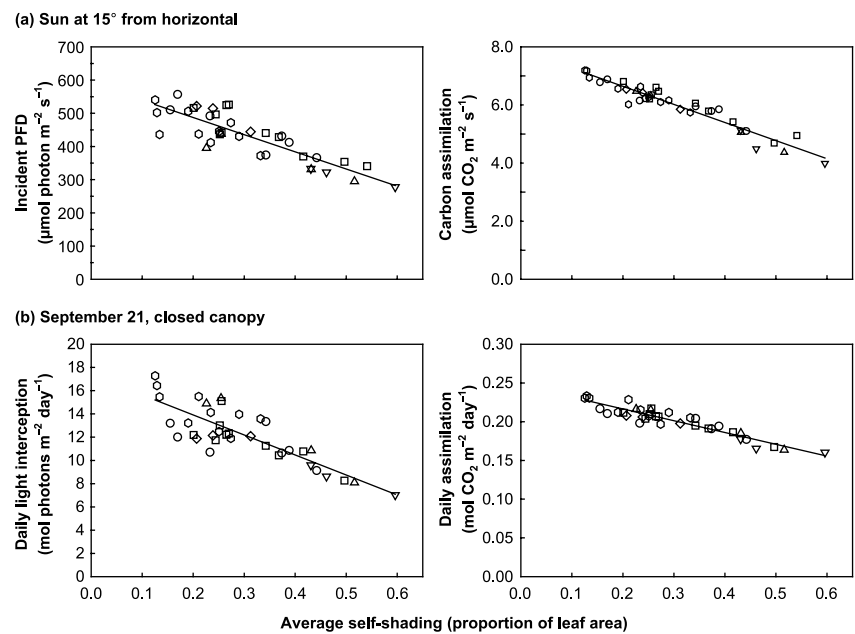


Fig. 6 Relationship between average self-shading and (a) tuft average light interception and simulated assimilation rate when the sun is 15° from the horizontal, and (b) daily integrated light interception and simulated assimilation for simulations run on September 21 at 33.7° latitude under a closed canopy. The closed canopy represents a habitat average level of shading by neighbors. See Tables 2, 3 for correlation coefficients. Symbols: (squares) Proteaceae; (circles) Myrtaceae; (triangles) Fabaceae; (diamonds) *Acacia*; (inverted triangles) Epacridaceae; (hexagons) other families.



across species in the relative contribution of potential carbon assimilation from low angles. This value was surprisingly small, given the observed differences in relative leaf display (Fig. 2c). For all species, simulations run under a canopy decreased the relative contribution from low angles compared to simulations under an open canopy, because canopies shade out low-angle light more than high-angle light.

Architectural determinants of self-shading

The chosen sampling unit was the tuft, with a view to comparing across species independently of the sizes of whole plants. However, tuft size was larger where leaves were retained longer along the main axis, by definition. Naturally,

self-shading should increase with the total leaf area sampled. Thus we were interested in the relative influence of main axis length vs other traits such as leaf size on cross species variation in aggregate tuft properties such as total leaf area, and in self-shading.

In total, the 3D positions of over 29 000 leaves across tufts of 38 species were mapped. Across species, the average number of leaves per tuft ranged from 10 to 1422 (Table 4). Total leaf area ranged from 15.6 to 4228 cm². Number of leaves was correlated positively with length of the main axis ($r^2 = 0.18$, $P < 0.01$) and negatively with leaf size ($r^2 = 0.50$, $P < 0.01$). Average leaf size ranged from 0.011 to 39.5 cm², and varied independently of main stem length ($r^2 = 0.04$, $P = 0.22$) and of SLA ($r^2 = 0.06$, $P = 0.24$). Internode length

Table 2 Correlation coefficients between species mean leaf angle (MLA) or species average self-shading (SS_{AV}) and daily integrated light interception or 'potential carbon gain' for simulations run on December 21 (D21), March/September 21 (S21) and June (J21) at -33.7° latitude under an open (-O) and closed (-C) canopy. Potential carbon gain takes into account the diminishing returns on high rates of light interception, but should not be interpreted as field-realistic carbon gain. The closed canopy represents a habitat average level of shading by neighbors

	Correlations with MLA						Correlations with SS_{AV}					
	D21-O	D21-C	S21-O	S21-C	J21-O	J21-C	D21-O	D21-C	S21-O	S21-C	J21-O	J21-C
Light interception ($\text{mol m}^{-2} \text{d}^{-1}$)												
Direct light on unshaded leaf area only	-0.70**	-0.83**	-0.49**	-0.59**	0.64**	0.49*	n/a	n/a	n/a	n/a	n/a	n/a
Diffuse light interception	-0.78**	-0.55**	-0.76**	-0.59**	-0.76**	-0.56**	-0.64**	-0.85**	-0.67**	-0.84**	-0.67**	-0.85**
Tuft average light interception	-0.65**	-0.68**	-0.48*	-0.52**	0.11	0.11	-0.78**	-0.73**	-0.85**	-0.84**	-0.86**	-0.87**
Potential carbon gain ($\text{mol m}^{-2} \text{d}^{-1}$)												
Assimilation rate from unshaded leaf area only	-0.83**	-0.95**	-0.46**	-0.72**	0.50**	0.37*	n/a	n/a	n/a	n/a	n/a	n/a
Tuft average assimilation rate	-0.35*	-0.39*	-0.28	-0.33*	-0.12	-0.16	-0.92**	-0.90**	-0.95**	-0.94**	-0.95**	-0.96**

Values are Pearson correlation coefficients, *indicates significance at $\alpha = 0.05$, ** $\alpha = 0.01$.

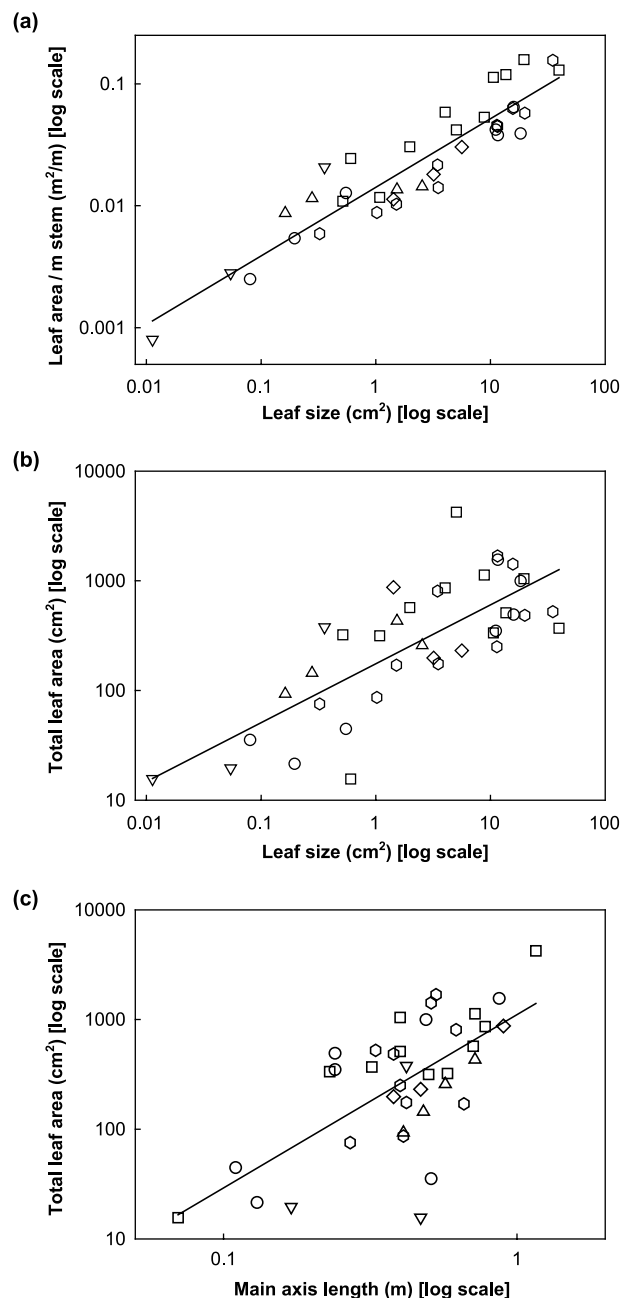


Fig. 7 Relationship between (a) individual leaf area and leaf area per meter stem ($r^2 = 0.86$, $P < 0.001$); (b) individual leaf area and total leaf area ($r^2 = 0.58$, $P < 0.001$); and (c) main axis length (distance from tip to oldest leaf) and total leaf area ($r^2 = 0.45$, $P < 0.001$) for 38 species from two sites. All axes log scaled. Symbols: (squares) Proteaceae; (circles) Myrtaceae; (triangles) Fabaceae; (diamonds) *Acacia*; (inverted triangles) Epacridaceae; (hexagons) other families.

increased with leaf size (measured by area) but not proportionally so (model II slope = 0.49; $r^2 = 0.78$, $P < 0.01$). Consequently larger-leaved species had more leaf area per meter stem (Fig. 7a; $r^2 = 0.86$, $P < 0.01$). Leaf size accounted for somewhat more of the variation in total leaf area (Fig. 7b; $r^2 = 0.58$, $P < 0.01$) than did main axis length (Fig. 7c;

Table 3 Percent daily light capture or 'potential carbon gain' occurring whilst the sun is at low angles in the sky ($< 33^\circ$ from the horizontal). The range observed across species and correlation coefficient with mean leaf angle (MLA) for simulations run on December 21, September 21 and June (J21) at -33.7° latitude under an open and closed canopy are given. Potential carbon gain takes into account the diminishing returns on high rates of light interception, but should not be interpreted as field-realistic carbon gain, as explained in the text. The closed canopy represents a habitat average level of shading by neighbors

Date	Solar time Daylength	Sun $> 33^\circ$	Canopy	Light interception		Potential carbon gain	
				Range	r (MLA)	Range	r (MLA)
December 21	5 : 00–19 : 00	7 : 45–16 : 25	Open	0.20–0.34	0.96**	0.33–0.37	0.91**
			Closed	0.11–0.20	0.95**	0.23–0.26	0.72**
Sep/March 21	6 : 07–17 : 53	8 : 50–15 : 10	Open	0.25–0.39	0.94**	0.40–0.43	0.84**
			Closed	0.17–0.26	0.92**	0.31–0.33	0.56**
June 21	7 : 10–16 : 50	11 : 30–12 : 30	Open	0.85–0.87	0.86**	0.88–0.89	0.83**
			Closed	0.70–0.74	0.80**	0.80–0.82	0.13

Values are Pearson correlation coefficients, *indicates significance at $\alpha = 0.05$, ** $\alpha = 0.01$.

$r^2 = 0.45$, $P < 0.01$). These contributions were largely independent. Partialling out leaf size or main axis length did not weaken the correlation of the other with total leaf area.

SS_{AV} varied across species from 13 to 60% of total tuft leaf area. Average shading within-tufts was partitioned into shading by adjacent leaves and shading by stems or petioles (Table 5). Shading by other leaves ranged from 10 to 47% of total leaf area, and was higher in species with more and smaller leaves per tuft, greater tuft LAI, more leaf area per volume and taller tuft shape (height/width). Shading by stems or petioles ranged from 1 to 33%, and was significantly higher in species with more and smaller leaves per tuft and taller tuft shape. Total average self-shading was most strongly correlated with the number of leaves per tuft, small leaf size and taller tuft shape (Table 5). The main contributors to variation in the number of leaves per tuft were species leaf size ($r^2 = 0.50$) and total stem length per tuft ($r^2 = 0.42$). Variation in total stem length resulted in part from our definition of a tuft. Species with longer main axes had disproportionately greater total length of stem in the tuft (model II slope = 1.67; $r^2 = 0.73$, $P < 0.01$) due to side branches. In summary, the correlation of self-shading variables with leaf number can be viewed as the combined effect of variation in leaf size and the more arbitrarily defined variation in tuft size.

Cross-correlation between architectural traits

Given the demonstrated influence of variation in key species traits in the present study (MLA, SS_{AV} , leaf size) on cross-species patterns in tuft-scale leaf display, light interception and carbon gain, we investigated the correlation with certain other traits thought to have ecological importance. In particular, specific leaf area (SLA; leaf area per leaf dry mass), maximum potential height and leaf size have been identified as important spectra of variation across species (Westoby *et al.*, 2002; Table 4). Species MLA was negatively correlated with SLA ($r^2 = 0.32$, $n = 25$, $P < 0.01$), but uncorrelated with

potential height or leaf size ($r^2 < 0.01$, $P > 0.05$). Average self-shading was negatively correlated with leaf size (see above), but uncorrelated with potential height, SLA or MLA ($r^2 < 0.05$, $P > 0.05$). Potential height was weakly correlated with leaf size ($r^2 = 0.13$, $P < 0.05$).

Discussion

In a given light microclimate, differences in light interception between alternative shoot architectures must result from differences in leaf orientation and self-shading. In the current study we quantified the effect of both leaf angle and self-shading on tuft-scale leaf display and light interception. We also assessed the consequences of nonlinear light-response curves for the photosynthetic benefit accruing from light interception. So, what was the relative influence of variation between species in leaf angle and self-shading? and which plant traits were they associated with?

Leaf angle

The current study extends previous work on the ecological significance of leaf angle variation in single or few species simulation studies (Ezcurra *et al.*, 1991; Ryel *et al.*, 1993; Percy & Valladares, 1999; Valladares & Pugnaire, 1999; Werner *et al.*, 2001b) to a large multispecies comparison. Supporting previous work, this study found that species with shallower-angled leaves intercepted substantially more light when the sun was at high angles in the sky (midday; summer; low latitudes), while species with steeper leaves intercepted a greater proportion of their daily PFD-budget from low angles in the sky (morning, afternoon; winter; high latitude).

As expected, species with shallower leaf angles had greater whole-day light interception than steeper-leaved species, except in winter. Our working hypothesis was that the diminishing returns on high PFD would qualitatively change this result for whole-day carbon gain, such that steeper-leaved

Table 4 Species mean trait values for 38 species from two sites in Ku-ring-gai National Park, Australia. Traits: Leaf Type (S = simple, C = compound, F = folded along midrib, or sm = small – leaf position simulated, see appendix S1), mean leaf angle, average self-shading, leaf area, leaf size, number of leaves per tuft, main stem length, leaf area per unit volume, leaf area index. Also included are species maximum height, specific leaf area and photosynthetic capacity per unit area sourced from existing datasets datasets (Wright *et al.*, 2001; Westoby & Wright, in press)

Species	Family	Site LAI	Leaf type	MLA (°)	Self-Sh (%)	Leaf area (cm ²)	Leaf size (cm ²)	Leaf no.	MSL (m)	LA/VOL (m ² m ⁻³)	LAI (m ² m ⁻²)	Max Ht (m)	SLA (mm ² mg ⁻¹)	Amax (µmol CO ₂ m ⁻² s ⁻¹)
<i>Acacia myrtifolia</i>	Mimosaceae	Low	S	66.1	20.7	198	3.19	60	0.38	3.13	0.47	1.65	5.5	–
<i>Acacia suaveolens</i>	Mimosaceae	Low	S	71.7	23.9	231	5.62	41	0.47	5.15	1.19	2.00	5.1	9.60
<i>Angophora hispida</i>	Myrtaceae	Low	S	50.8	38.8	492	15.9	32	0.24	12.51	1.58	3.40	4.4	–
<i>Banksia marginata</i>	Proteaceae	Low	S	53.1	34.2	570	1.98	289	0.71	1.94	0.50	4.00	5	19.50
<i>Banksia oblongifolia</i>	Proteaceae	Low	S	45.0	25.6	335	10.61	32	0.23	9.50	0.98	2.00	3.4	–
<i>Boronia pinnata</i>	Rutaceae	Low	F	43.9	29.0	170	1.51	106	0.66	1.42	0.43	1.60	5.4	–
<i>Conospermum longifolium</i>	Proteaceae	Low	S	72.3	27.0	512	13.63	38	0.4	4.96	1.22	0.85	–	–
<i>Epacris pulchella</i>	Epacridaceae	Low	Sm	42.9	43.1	20	0.05	376	0.17	6.79	0.43	2.00	10.8	–
<i>Eriostemon australasius</i>	Rutaceae	Low	S	62.1	19.0	86	1.02	86	0.41	1.82	0.32	2.00	5.5	10.10
<i>Eucalyptus gummifera</i>	Myrtaceae	Low	S	59.3	15.5	348	11.11	36	0.24	2.50	0.43	30.00	4.5	13.00
<i>Eucalyptus haemastoma</i>	Myrtaceae	Low	S	69.9	16.9	994	18.31	55	0.49	2.02	0.53	15.00	4.5	12.00
<i>Grevillea buxifolia</i>	Proteaceae	Low	Sm	47.4	41.6	322	0.52	637	0.58	2.36	0.45	2.10	7	8.60
<i>Grevillea speciosa</i>	Proteaceae	Low	S	60.1	36.8	315	1.08	286	0.5	4.80	1.08	2.35	7	8.80
<i>Hakea dactyloides</i>	Proteaceae	Low	S	60.6	26.5	1127	8.82	134	0.72	2.50	0.97	2.05	3.6	12.60
<i>Hibbertia bracteata</i>	Dilleniaceae	Low	S	47.2	25.1	75	0.32	211	0.27	2.47	0.40	1.00	7.8	6.70
<i>Isopogon anemonifolius</i>	Proteaceae	Low	S	46.3	54.1	863	4.03	213	0.78	6.83	2.06	2.00	3.4	–
<i>Kunzea capitata</i>	Myrtaceae	Low	Sm	56.7	44.2	35	0.08	442	0.51	1.19	0.25	1.80	–	–
<i>Lambertia formosa</i>	Proteaceae	Low	S	58.3	20.1	16	0.6	26	0.07	25.57	0.87	2.00	4.3	9.30
<i>Leptospermum spp.</i>	Myrtaceae	Low	S	67.9	23.3	21	0.2	107	0.13	10.84	0.54	1.60	–	–
<i>Leptospermum trinervium</i>	Myrtaceae	Low	S	58.9	37.4	45	0.55	81	0.11	26.99	1.46	5.00	8.2	4.50
<i>Leucopogon microphyllus</i>	Epacridaceae	Low	Sm	52.4	46.1	16	0.01	1422	0.47	1.01	0.18	0.90	9	–
<i>Persoonia lanceolata</i>	Proteaceae	Low	S	64.9	49.7	4228	5.04	839	1.16	2.94	1.50	2.30	–	–
<i>Persoonia levis</i>	Proteaceae	Low	S	73.5	24.4	1045	19.57	56	0.4	5.24	0.90	5.00	5.5	8.20
<i>Phyllota phyllicoides</i>	Fabaceae	Low	Sm	49.3	51.6	93	0.16	568	0.41	3.51	0.56	2.10	6.2	8.40
<i>Pultenaea elliptica</i>	Fabaceae	Low	Sm	40.8	43.1	144	0.28	545	0.48	9.64	1.66	1.50	8.6	–
<i>Pultenaea stipularis</i>	Fabaceae	Low	Sm	62.6	59.6	377	0.36	1057	0.42	10.05	1.50	2.20	–	–
<i>Acacia floribunda</i>	Mimosaceae	Medium	Sm	57.0	31.3	873	1.42	608	0.9	1.02	0.33	8.00	10.1	11.00
<i>Astrotricha floccosa</i>	Araliaceae	Medium	S	31.3	13.4	523	34.95	15	0.33	3.12	0.57	3.00	12.6	11.90
<i>Breynia oblongifolia</i>	Euphorbiaceae	Medium	C	33.7	33.2	805	3.46	236	0.62	3.35	0.66	2.00	–	–
<i>Gompholobium latifolium</i>	Fabaceae	Medium	S	26.9	22.6	257	2.54	107	0.57	1.99	0.38	2.00	–	–
<i>Lasiopetalum ferrugineum</i>	Sterculiaceae	Medium	S	44.6	12.5	175	3.5	51	0.42	1.60	0.37	3.00	9.3	8.10
<i>Lomatia siliifolia</i>	Proteaceae	Medium	F	47.9	25.2	369	39.5	10	0.32	2.26	0.33	1.50	8.3	5.90
<i>Pomaderris ferruginea</i>	Rhamnaceae	Medium	S	31.8	12.9	251	11.38	24	0.4	3.85	0.69	2.50	12.4	7.60
<i>Pultenaea daphnoides</i>	Fabaceae	Medium	S	36.7	25.5	431	1.53	282	0.72	1.08	0.34	3.00	9.9	9.60
<i>Rapanea variabilis</i>	Myrsinaceae	Medium	F	33.6	21.1	483	19.94	22	0.38	3.87	0.73	3.00	–	–
<i>Syncarpia glomulifera</i>	Myrtaceae	Medium	F	36.2	34.3	1553	11.58	137	0.87	1.59	0.61	20.00	6.3	9.20
<i>Synoum glandulosum</i>	Meliaceae	Medium	C	42.3	23.5	1683	11.53	146	0.53	3.06	0.79	4.00	11.6	6.50
<i>Trema aspera</i>	Ulmaceae	Medium	S	67.2	27.4	1419	15.66	92	0.51	3.23	0.85	1.25	–	–

Table 5 Correlation coefficients between species means for average within tuft self-shading and other architectural traits: mean leaf angle, leaf size, tuft leaf number, total leaf area, leaf area index (LAI), tuft leaf area/volume, tuft shape and average branch inclination

Proportion of leaf area shaded by plant components	MLA	Leaf size	No. leaves	Leaf area	LAI	LA/Vol	Tuft shape	Br. Incl.
Total shading by other leaves (%)	0.00	-0.27	0.53**	0.11	0.60**	0.39*	0.34*	0.07
Shading by > 2 layers of leaf only (%)	0.00	-0.43**	0.64**	0.02	0.44**	0.33*	0.44**	0.14
Shading by stems/branches (%)	0.19	-0.87**	0.79**	0.51**	-0.27	0.12	0.58**	0.00
Average Self-Shading (SS_{AV}) (%)	0.06	-0.53**	0.76**	0.05	0.29	0.16	0.49**	0.05

Values are Pearson correlation coefficients, *indicates significance at $\alpha = 0.05$, ** $\alpha = 0.01$.

species performed better overall. Consistent with this hypothesis, a proportion of leaves in steeper-leaved species did achieve higher light incomes (and hence carbon gain) at low light angles at each end of the day, together with sufficient light income for near-maximum carbon gain across the middle of the day (example in Fig. 5).

However, our hypothesis proved incorrect at the scale of whole tufts due to the strong influence of leaf azimuth on the projection of leaf area in steeper-leaved species (Fig. 2a–b). Species with steeper leaf angles had a substantial proportion of leaf area exposed to very low light intensities at all times (Fig. 5), dragging down total tuft carbon gain. Similar interspecific differences would emerge independent of the particular light response curve used (examples in Fig. 5), although quantitative differences might be greater under light-response curves having higher asymptotic photosynthetic capacity. In general, the results of this study therefore support the notion that steeper leaf angles function to reduce exposure to excess radiation during the middle of the day (Ehleringer & Werk, 1986; Ryel *et al.*, 1993; King, 1997; Percy & Valladares, 1999; Valladares & Pugnaire, 1999; Werner *et al.*, 1999; Werner, 2002), at the expense of potential daily carbon gain, more than to take photosynthetic advantage of low angle light. While this is not a new or controversial argument about steeper leaf angles, few data have previously been available to test the proposition across many species.

Costs associated with the higher light interception in shallow-angled species across the middle of the day include increased leaf temperature, higher risk of overheating, and higher risk of photoinhibition. Excess light interception increases leaf temperature. This may be a disadvantage, increasing respiration rates more than photosynthetic rates, and decreasing water use efficiency (King, 1997). Species with shallow leaf angles presumably face a greater risk of overheating when transpirational cooling is limited by water deficits.

Another cost of high light interception is the increased susceptibility to reversible (Martinez-Ferri *et al.*, 2000) or irreversible photosystem damage (Werner *et al.*, 1999). Mild photoinhibition in high light leaves, incorporated into simulations of an oak canopy (Werner *et al.*, 2001a), decreased daily carbon gain by at least 8%. Irreversible photosystem damage in horizontal leaves during drought led to subsequent

leaf abscission in a Mediterranean *Cistus* species (Werner *et al.*, 1999).

Given the costs and benefits of different leaf angles, we might expect the leaf angle of species to be co-ordinated with the average habitat. Ehleringer (1988) and Smith *et al.* (1998) investigated the patterns in leaf angle across precipitation gradients in 159 and 209 species, respectively. Mean leaf angle became progressively steeper in both herbs and shrubs with increasing aridity. Similarly, within sites steeper leaf angles may be beneficial in high light environments, such as at the top of canopies or in more open habitats. Shallow leaf angles may be particularly advantageous in light limited understories (King, 1997).

Despite this, a wide range of leaf angles is still observed within a common light environment. Studies reporting a gradient in leaf angle through a canopy often note that there is a wide range of leaf angles at any given depth or light intensity (Niinemets, 1998; Werner *et al.*, 2001b). Similarly in the present study steeper-leaved species were distributed throughout all light environments in the vegetation.

Self-shading within tufts

Variation in leaf angle explained only a small proportion of variation in instantaneous or whole-day potential carbon assimilation between species (Tables 1, 2). Up to 92% of variation was explained by the average level of self-shading within the tufts. Numerous studies have identified the importance of reducing self-shading for maximizing intraspecific carbon assimilation (Honda & Fisher, 1978; Percy & Yang, 1998), but little has been known about the levels of self-shading across species. Species studied here ranged from 13% to as much as 60% self-shading of projected leaf area within tufts (branching units). Similar levels of self-shading at the shoot level can be inferred from the low display efficiencies (0.1–0.2) of shoots of Norway Spruce (Stenberg *et al.*, 1999). This level of shading is surprisingly high, recalling also that additional within-plant shading will result from the interaction between different shoots or tufts on the whole plant.

In the present study, smaller-leaved species suffered more self-shading, despite having less total leaf area per tuft, a smaller LAI within the tuft outline and less leaf area per meter

stem. The higher self-shading was due both to crowding of leaves close to each other and to proximity of leaves to the stem. This is consistent with results from simulation studies manipulating virtual plants. Properties of smaller-leaved species, such as increased leaf-clumping (de Castro & Fetcher, 1999), decreased petiole length (Takenaka, 1994), decreased internode length (Niklas, 1988), and decreases in the relative distance of leaf area from the stem (Takenaka, 1994), have each been shown to reduce light capture and carbon gain considerably via effects on shading.

The most-discussed benefit of smaller leaves is the ability to shed heat rapidly by convection, so that small leaves do not warm above air temperature as much (Parkhurst & Loucks, 1972; Givnish & Vermeij, 1976). The higher levels of self-shading shown here would similarly benefit small leaves more in bright sun than in shade. In low light, high self-shading should be a distinct disadvantage (Givnish, 1988), favoring larger-leaved species. In the same vegetation as the present study, Bragg & Westoby (2002) found a mild tendency for larger-leaved species to occur in lower light environments within a given height class.

Correlations among architectural traits

Species differed in mean leaf angle from 24° to 74° across 38 species from two sites. Structural costs to leaf angle have been investigated by Niinemets (1998) but, to our knowledge, not across species. In the current study leaf angle was weakly related to SLA (leaf area/dry mass), with steeper-leaved species having more dry mass for a given leaf area. It seems unlikely that this association arises from structural costs. Support costs are likely to be higher for shallower-leaved species if anything, requiring both a rigid lamina and a strong petiole to hold the leaf perpendicular to gravitational forces.

Across sites towards increasing aridity, average leaf size (see Westoby *et al.*, 2002 for references) and plant height (Fonseca *et al.*, 2000) decrease, leaves become more cylindrical and thicker, and leaf angle increases (Ehleringer, 1988; Smith *et al.*, 1998). The patterns among coexisting species within sites are less well documented. In the present study there were no strong correlations among the important ecological traits of MLA, potential height, and leaf size. This suggests that within a site, each trait may be associated with different aspects of species ecological strategies.

Conclusion

The purpose of the current study was to investigate the influence of individual architectural traits on shoot-scale leaf display, and to estimate the consequences of this variation under common conditions. Species with steeper leaf angles were found to reduce exposure to midday light levels, at the expense of potential daily carbon gain. Species with smaller leaves were found to have greater within-shoot self-shading,

the effect of variation in self-shading having a larger influence on patterns across species than leaf angle. This is an important first-step in understanding the role of different architectures amongst coexisting species.

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Supplementary Material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/NPH/NPH765/NPH765sm.htm>

Appendix S1 Methods for linking the simulation software YPLANT to output from 3-D digitisers

Appendix S2 Describing a generalised photosynthetic light response curve for cross-species comparisons of potential carbon assimilation rate

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