

Leaf size and foraging for light in a sclerophyll woodland

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Summary

1. It has been suggested that leaf size may represent a foraging scale, with smaller-leaved species exploiting and requiring higher resource concentrations that are available in smaller patches.
2. Among 26 shrub species from a sclerophyll woodland community in New South Wales, Australia, species with smaller leaves tended to occur in better light environments, after controlling for height. The dark respiration rates of small-leaved species tended to exceed those of larger-leaved species.
3. However, the higher-light environments where smaller-leaved species tended to occur had a patch scale larger than whole plants. There would not have been any foraging-scale impediment to large-leaved species occupying these higher-light patches. An alternative explanation for small-leaved species being more successful in higher-light patches, in this vegetation with moderate shading, might be that they were less prone to leaf overheating.
4. Such relationships of leaf size to light across species at a given height may be important contributors to the wide spread of leaf sizes among species within a vegetation type, along with patterns down the light profile of the canopy, and effects associated with architecture and ramification strategy.

Key-words: Foraging scale, leaf size, light, plant metabolism

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Introduction

Corner's rules (Corner 1949; Hallé, Oldeman & Tomlinson 1978) describe a positive correlation between twig cross-sectional area and the area of individual leaves supported. Here we are concerned with the relative advantages and disadvantages of occupying different points along the spectrum (White 1983a) from highly ramified species with small leaves and small twigs, to large-leaved species with less branching and large twigs (White 1983b).

Trends in leaf size have been studied in relation to temperature (Gates, Alderfer & Taylor 1968) and water relations (Taylor 1975); light (Niinemets & Kull 1994); mechanical resistance (Niklas 1996); and herbivory (Brown & Lawton 1991; but see Bogacheva 1994). Variation in leaf size has been studied at several levels: among communities across large-scale environmental (e.g. Werger & Ellenbroek 1978) or elevational (Greller & Balasubramaniam 1988) gradients; among species within communities (Smith 1978); among individuals within species (Niklas 1996); and within individuals (Vogel 1968).

Nevertheless, implications of different leaf-size strategies among species within habitats are still

poorly understood. Specifically, it is not known whether differences within habitat – including within the same vegetation layer – reflect the same environmental factors that are influential between habitats (Givnish 1987).

Ritchie & Olf (1999) modelled coexistence among species foraging at different scales, in a fractally nested world where higher resource concentrations were available only in smaller patches. This model predicted size frequency distributions of coexisting species on the basis that size reflected foraging scale. Predicted patterns were confirmed for mammalian herbivores in the Serengeti, and for plants in a Minnesota oak savanna. The model assumes that species with small foraging scales require high resource concentration, while species with broader foraging scales can tolerate lower resource concentration (Ritchie & Olf 1999).

For plants, Ritchie & Olf (1999) used leaf width as an indicator of foraging scale. It is unlikely that leaf width literally measures the foraging scale, with individual leaves finding light patches of their own size. However, because leaf size is closely correlated with twig size, leaf size might be an indicator of the scale of shoots, branch systems or even whole canopies.

In this study we set out to test the hypothesis that plant species with smaller leaves (possibly indicating a small foraging scale) occur in higher light. Our results suggested several follow-up analyses. We refined our

initial question to test whether smaller-leaved species were associated with greater light levels among plant species of similar height, at a number of different spatial scales. We also test the notion that plant species with small leaves have higher metabolic costs per unit leaf area (measured as rate of dark respiration).

Methods

STUDY AREA

This study was carried out in Ku-ring-gai Chase National Park (33°41'38" S 151°08'35" E), Sydney, Australia. The vegetation type was fire-prone, low, open sclerophyll woodland, dominated by woody shrub species, with emergent eucalypt trees up to 9 m tall. The site was last burnt in 1990. The geology of the site is Hawkesbury sandstone, weathering to low nutrient soils (total soil phosphorus 94 mg kg⁻¹, Wright, Reich & Westoby 2001). Gap fractions (see below) were mostly in the range 0.3–0.7; the shrub species were growing in dappled light rather than in dense shade with occasional sunflecks.

SAMPLING

Twenty-six abundant, woody, understorey species were selected (Fig. 1). Five random individuals of each species within a 31 400 m² area were sampled. Each measured individual was located at least 20 m from a

measured conspecific, and at least 10 m from a track passing through the site.

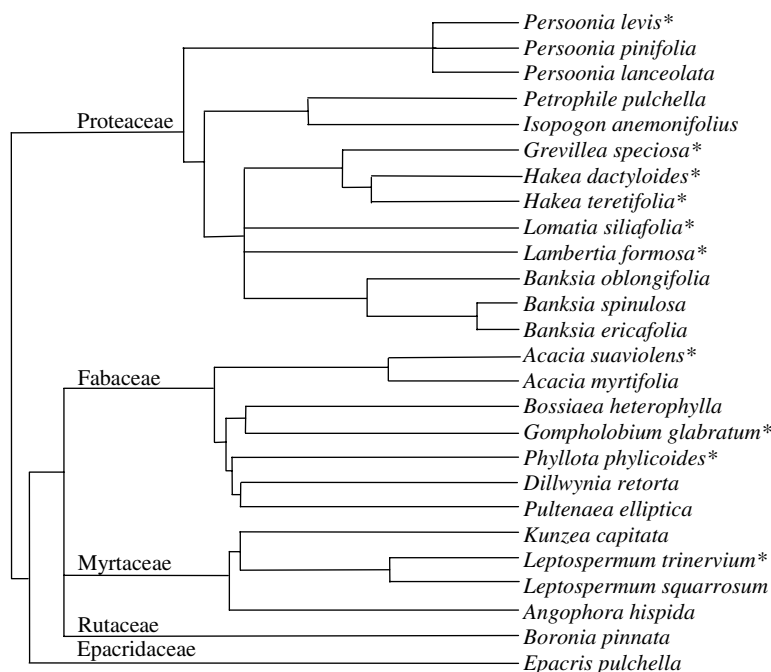
Morphometric variables and gap fraction were measured at the level of the tuft. The tuft was defined as a run of leaves from youngest to oldest, along a branching sequence, together with leaves on any side branches occurring above the oldest leaf on the main sequence. This is not the same as a 'leaf cluster' *sensu* Ackerly (1999). Three tufts were selected on each individual: the tuft with the highest leaf; the tuft with the lowest leaf; and a randomly selected tuft.

MORPHOMETRY

Morphometric variables were measured for each tuft between 1 August and 18 December 2000. The height from the ground of the highest and lowest leaf on each tuft was measured. Tuft angle to vertical was measured using a protractor with a plumb line attached. Tuft azimuth was measured using a compass. Tuft length was the sum of the lengths of all twigs and branches in a tuft, from the distal points of twigs to the oldest leaf. Tuft width and height were measured as the distance across the leaves lining individual stems of a tuft, measured in a horizontal and a vertical plane, respectively. Width and height were measured up to five times along the length of a tuft, and averaged. Tuft length, width and height were multiplied for tuft volume. The number of leaves along each tuft was counted. Where there were more than 250 leaves, the number was estimated by counting the average number per 50 mm in subsamples and multiplying by the combined length of the branches and twigs comprising the tuft. Leaf length was measured as the shortest distance from the base of the blade to the apex. For tufts with more than 10 leaves, length was measured for five, and averaged. For each species, length and area were measured for 15 or more leaves taken from plants other than those where tufts were studied. These leaves were then scanned and DELTA-T software (Cambridge, UK) used to measure their area from scanned images. For each tuft of each species, leaf areas were estimated from the leaf lengths using a second-order polynomial regression fitted to the subsample of leaves that were scanned for area.

GAP FRACTION

One to four equally spaced measurements were taken along each tuft using an LAI-2000 Canopy Analyzer (LI-COR, Lincoln, NE, USA). This instrument has a fisheye lens through which light passes onto sensors arranged in five concentric rings to receive light from different bands of zenith angles (Welles 1990). These sensors discriminate between different wavelengths of light to estimate the amount that has been scattered by foliage. Diffuse non-interrupted gap fraction (hereafter gap fraction or GF) was the reading on a study plant taken as a proportion of a reference reading



* used in analyses of dark respiration rates

Fig. 1. Phylogenetic tree for the study species. Compiled from Soltis, Soltis & Chase (1999) (among-family classification); Hoot & Douglas (1998) (within Proteaceae); and M. Crisp's classification of Mirbeliaceae and Bossiaeeae (Fabaceae; available at <http://online.anu.edu.au/BoZo/Crisp/Mirbeliaceae/phylogeny.html> as at July 2001).

taken in an open area (calculated using C2000 software, LI-COR). The GF describes the proportion of the sky not obscured by vegetation (Welles 1990). Gap fraction was calculated with the fifth ring (horizontal to 37° above horizontal) masked. Measurements had to be taken under uniform cloud cover (to ensure only diffuse light reached the sensors), with a mask restricting the view to 270° of the azimuth, to eliminate the person taking the readings from view. Gap fraction measurements on plants were taken between 8 August 2000 and 9 January 2001. The LAI-2000 provides a good estimate of the proportion of available photon flux density, integrated over a long time scale (Machado & Reich 1999).

Average light profile with height was characterized as follows. Gap fraction readings were taken at 16 systematically spaced locations within the area in which the plants were measured, between 16 January and 15 February 2001. At each location GF was measured 4, 8, 16, 32, 64, 128 and 256 cm above the ground. The expected GF at a given height, meaning the average expected gap fraction for a random position at a given height, was then estimated via logarithmic regression ($r^2 = 0.45$, $P < 0.001$, equation: $\log_{10}(\text{GF}) = 0.2544 \log_{10}(\text{height}) - 0.8552$). The $\log_{10}(\text{GF})$ observed for each tuft was then related to the expected GF at that height, to yield a height-specific gap fraction [$\log_{10}(\text{GF observed}) - \log_{10}(\text{GF expected})$].

SPATIAL SCALE OF LIGHT PATTERN

As described in the Results, we found evidence that smaller-leaved species occurred in stronger light at a given height. However, field observations did not suggest that individual tufts or leaves were locating high-light patches. Accordingly, we sought to quantify the spatial scale of light pattern. It was not possible to use the LAI-2000 for this purpose, as there were too few cloudy days within the time available. Therefore we measured the maximum height of vegetation directly above each tuft, and within radii of 0.25, 0.5, 1, 2, 4, 8 and 16 m about the highest point of each tuft. Height of vegetation was negatively associated with height-specific gap fraction (e.g. height of vegetation above tuft and height-specific gap fraction, $r^2 = 0.16$, $df = 24$, $P = 0.04$, among species).

DARK RESPIRATION

Dark respiration (per unit leaf area) data for 10 species were available from Wright *et al.* (2001).

DATA ANALYSES

Morphometric and height-specific gap fraction data for each tuft were averaged for the individual plant; individuals were averaged to give a species average. Relationships between morphological variables and gap fraction, and morphological variables and dark

respiration, were evaluated using model 1 regression analyses. Morphometric and dark respiration data were log-transformed prior to analysis, and did not differ significantly from normal (Bliss 1967) following transformation.

Height-specific gap fraction was calculated to test the notion that species with smaller foraging scales intercepted more light, at a given height. Foraging scale was positively associated with plant height, among species (e.g. mean leaf length and mean tuft height: $df = 24$, $P = 0.027$, $r^2 = 0.19$), and gap fraction decreased nearer to the ground. This probably creates a tendency for large-leaved species to be associated with larger gap fractions. We used height-specific gap fraction to test our hypothesis after controlling for this tendency. Further, it was observed that for pairs of species of similar height, the smaller-leaved species was associated with greater gap fraction in 11 out of 13 cases (see Results). Because height-specific gap fraction was calculated as the difference between two logarithmic variables, it was a ratio expressed on a log scale, and on this basis it was normally distributed.

Cross-species and phylogenetic relationships were investigated. Phylogenetic regression was performed using the program PHYLO.GLM, version 1.03 (Grafen 1989; run through GLIM), to investigate the relationships between evolutionary divergences in morphometry, gap fraction and dark respiration, based on the phylogenetic tree in Fig. 1. Because species had not been chosen for study on a phylogenetic basis, there were several polytomies in the tree, and therefore analyses of divergence were weaker (fewer degrees of freedom) than cross-species analyses. Cross-species analyses were performed using SPSS version 8.0.

Data for height of vegetation above tufts were averaged for the individual plant; individual plants were averaged to give a species average. Relationships between leaf size and height of vegetation covering tufts were quantified using logarithmic regression models on untransformed axes, for each spatial scale considered.

Results

LEAF SIZE AND LIGHT

Without correcting for height, GF was not significantly associated with leaf length ($df = 24$, $P = 0.092$, $r^2 = 0.11$); leaf area ($df = 23$, $P = 0.252$, $r^2 = 0.06$); or tuft volume ($df = 24$, $P = 0.321$, $r^2 = 0.04$). However, when pairs of species of similar height were considered, the larger-leaved species was associated with smaller gap fraction for 11 out of 13 species pairs (Fig. 2).

Considering gap fraction relative to that expected at a certain height, species with longer leaves tended to occur at smaller gap fractions, both cross-species (Fig. 3; $df = 24$, $P = 0.004$, $r^2 = 0.30$, slope = -0.144 , SE = 0.045) and as evolutionary divergences ($df = 19$,

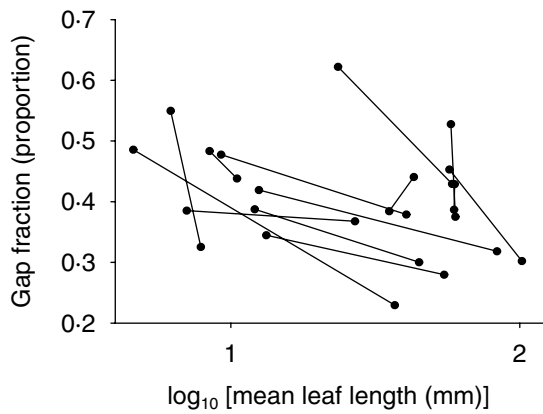


Fig. 2. Cross-species relationship between leaf length and gap fraction. Lines join pairs of species of similar height, which were selected by ranking species by mean tuft height, and selecting consecutive species.

$P = 0.026$, $r^2 = 0.23$, slope = -0.137 , SE = 0.039). The relationship for area of individual leaves was similar but weaker (cross-species $df = 23$, $P = 0.052$, $r^2 = 0.15$, slope = -0.052 , SE = 0.025 ; as evolutionary divergences $df = 18$, $P = 0.116$, slope = -0.043 , SE = 0.018). Species with greater tuft volume similarly tended to occur at smaller gap fraction at a given height (cross-species

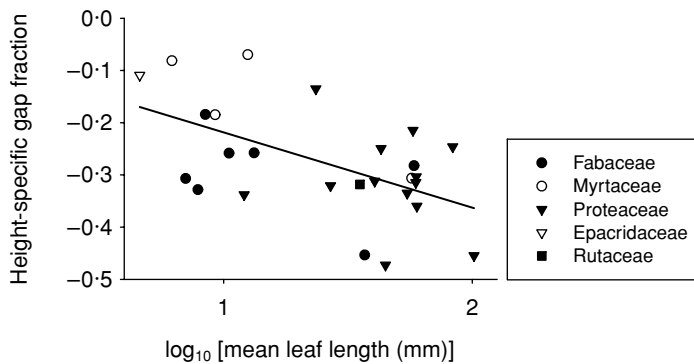


Fig. 3. Cross-species relationship between leaf length and height-specific gap fraction [$\log_{10}(\text{GF observed}) - \log_{10}(\text{GF expected})$], fitted with linear, least-squares regression.

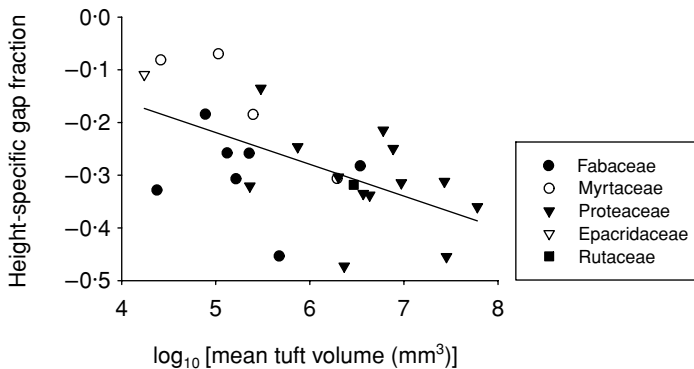


Fig. 4. Cross-species relationship between tuft volume and height-specific gap fraction [$\log_{10}(\text{GF observed}) - \log_{10}(\text{GF expected})$], fitted with linear, least-squares regression.

Fig. 4; $df = 24$, $P = 0.003$, $r^2 = 0.32$, slope = -0.060 , SE = 0.018 ; as evolutionary divergences $df = 19$, $P = 0.033$, $r^2 = 0.22$, slope = -0.057 , SE = 0.017). Gap fractions relative to height were mostly negative (Figs 3 and 4), meaning more shaded than random locations at that height. This was mainly because the gap fraction measurements were averaged down the length of each tuft, reflecting some within-tuft self-shading. However, self-shading cannot explain the patterns described. For example, cross-species, leaf length is significantly associated with gap fraction ($df = 24$; $P = 0.001$; $r^2 = 0.37$) in the absence of self-shading, when height-specific gap fraction data are restricted to the greatest value from the highest tuft on each individual plant.

Evolutionary divergence regressions had similar slopes to cross-species regressions, although significance tended to be weaker. The spread of leaf size consisted of differences between families to some extent, but relationships were usually also apparent within each family where there were enough data points (Figs 3 and 4). This indicates that the weaker significance of evolutionary divergence relationships was due mainly to fewer degrees of freedom, together with the spread within families being less than the spread between.

SPATIAL SCALE OF LIGHT CAPTURE

Species with longer leaves tended to occur under taller vegetation, where height of vegetation was measured directly above the tuft ($P = 0.008$, $r^2 = 0.26$). The same was true, though progressively less strongly, for radii of 0.25 m ($P = 0.027$, $r^2 = 0.19$), 0.5 m ($P = 0.028$, $r^2 = 0.18$), 1 m ($P = 0.023$, $r^2 = 0.20$), 2 m ($P = 0.003$, $r^2 = 0.31$), and 4 m ($P = 0.050$, $r^2 = 0.15$) around the tuft (Fig. 5). Regressions were non-significant for radii of 8 m ($P = 0.184$, $r^2 = 0.07$) and 16 m ($P = 0.585$, $r^2 = 0.01$).

LEAF SIZE AND DARK RESPIRATION

Species with longer leaves tended to have lower dark respiration rates (R_d per leaf area) cross-species, despite the few species for which R_d was known (Fig. 6; $df = 8$, $P = 0.020$, $r^2 = 0.51$, slope = -0.292 , SE = 0.100). The pattern resided substantially in the difference between Fabaceae (small leaves, high R_d) and Proteaceae (larger leaves, lower R_d) (Fig. 6), and was not significant as evolutionary divergences ($df = 6$, $P = 0.225$, slope = -0.157 , SE = 0.075). For leaf area, this relationship was found both cross-species (Fig. 7; $df = 8$, $P = 0.003$, $r^2 = 0.66$, slope = -0.165 , SE = 0.039) and as evolutionary divergences ($df = 6$, $P = 0.031$, $r^2 = 0.57$, slope = -0.118 , SE = 0.029). No relationship was found between tuft volume and dark respiration (cross-species $df = 8$, $P = 0.167$, slope = -0.078 , SE = 0.051 ; as evolutionary divergences $df = 6$, $P = 0.760$, slope = -0.016 , SE = 0.030).

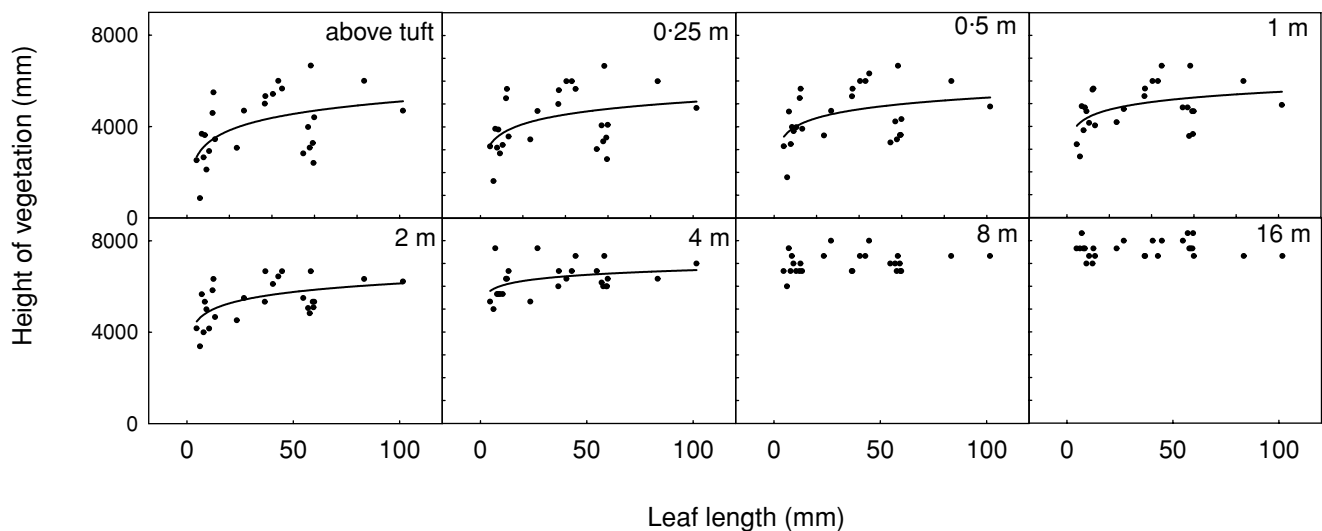


Fig. 5. Relationship between leaf length and height of vegetation for vegetation directly above tufts, and for radii of 0.25, 0.5, 1, 2, 4, 8 and 16 m around tufts. Logarithmic, least-squares regression lines are drawn where statistically significant.

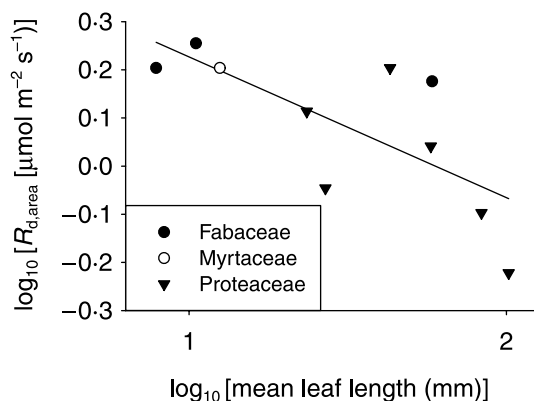


Fig. 6. Cross-species relationship between leaf length and dark respiration rate per unit leaf area ($R_{d,area}$), fitted with linear, least-squares regression.

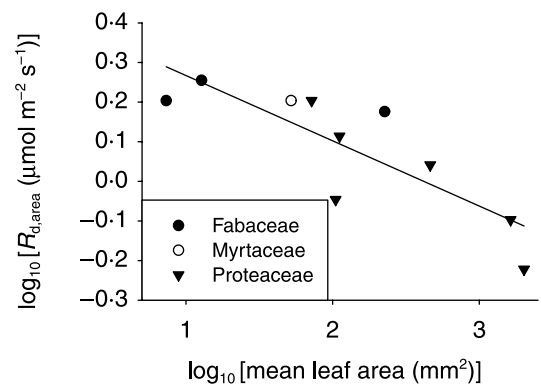


Fig. 7. Cross-species relationship between leaf area and dark respiration rate per unit leaf area ($R_{d,area}$), fitted with linear, least-squares regression.

Discussion

Plant species with smaller leaves, smaller twigs and greater ramification occurred in stronger light for a given height, while large-leaved species with less ramified branching were found in weaker light, for a given height. Among species, leaf size explained 30% of the variation in the height-specific light environment in which plants were found.

It has been widely expected that in shade, light foraging would be enhanced by long branches with long leaves (e.g. Canham 1988; Cornelissen 1993; Horn 1971; Kempf & Pickett 1981). Nevertheless, studies by White (1983b) and Ackerly & Donoghue (1998) failed to find any relationship between the Corner's rule spectrum and shade tolerance, among 48 eastern deciduous trees and 17 temperate *Acer* species, respectively. Popma, Bongers & Werger (1992) reported that seedlings and saplings of obligate gap species, occurring in stronger light, had significantly larger leaves than gap-dependent and gap-independent (shade-tolerating)

species in a tropical lowland Mexican rainforest, in contrast to the pattern in the present study.

It may be significant that a negative relationship between leaf size and light environment was detected in the present study only when light data were expressed relative to height. Irradiance decreases down through a canopy. If there is any systematic change in leaf size with height, this will complicate relationships between leaf size and light. A height correction allows variation in leaf sizes within a vegetation layer to be examined (as advocated by Givnish 1987). Few other studies have controlled for height in such a way. Niinemets & Kull (1994) reported that leaf area could be predicted by the Ellenberg *et al.* (1991) species indices for sapling light habitat (larger-leaved species distributed in weaker light) and height (larger leaves at greater height), across 85 Estonian woody species. This multiple regression model may be interpreted as describing the relationship between light and leaf size, after removing variation explained by height, making their results consistent with the present study.

Two types of mechanism have been proposed that might lead to larger-leaved species occurring in weaker light at a given height. First, there is the Ritchie & Olf (1999) view, which formed the basis for our initial hypothesis. This envisages a spectrum from species that exploit large patches but require lower resource concentration, to species that require high concentrations of resources, available only in small patches. In the case of light in an understorey, it is credible that intense light would be available only in small patches, while as patch size increases, the best light environment available would decline towards the habitat mean. The finding that small-leaved species had higher dark respiration rates was consistent with an idea that they might require higher resource supply. However, other aspects of our results were not consistent with a response to light patchiness as envisaged by Ritchie & Olf (1999). First, our results were dependent on a height correction, whereas the frequency distribution of leaf sizes presented by Ritchie & Olf (1999) as consistent with their model was not height-corrected. Second, we did not find that leaf size measured the scale at which light patchiness was exploited, either directly or as an indicator of the foraging scale of tufts or branches. Small-leaved species tended to occur under shorter vegetation (in stronger light), when measured up to a 4 m radius around each tuft, considerably greater than the scale of individual plants for these species. The scale of high light patches that small-leaved species tended to occupy was not too small to accommodate large-leaved species.

A second mechanism by which larger-leaved species might tend to occur in shaded patches is that they are more likely to be affected adversely by strong irradiance. Typically, under strong irradiance, small leaves track air temperature closely, while large leaves reach temperatures well above air temperature (Gates *et al.* 1968). Overheating is a significant risk when water for transpiration is scarce (Smith 1978). Models of leaf size (Givnish & Vermeij 1976; Parkhurst & Loucks 1972; Taylor 1975) have predicted decreasing leaf sizes with increasing temperature and decreasing water availability. These predictions have been confirmed by empirical results, across communities (Werger & Ellenbroek 1978). However, whether this process determines how patches are divided among individuals of different species within a community is unresolved (Givnish 1987). Leaf overheating seems the likeliest explanation for our results.

In summary, we found that smaller-leaved species were associated with more light in the understorey of this open woodland community. Smaller-leaved species tended to have higher rates of dark respiration, suggesting that they may have greater light demands. The spatial scale at which large-leaved plants were associated with (or sought) weaker irradiance suggests that an inability to fit into high light patches was not important. The wide spread of leaf sizes among species at a site is striking. Our results support Givnish's

(1987) idea that separating effects within a given height from effects down the light profile of the canopy can help to resolve the causes of this striking feature of vegetation.

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