COMMUNITY ECOLOGY

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The leaf size – twig size spectrum and its relationship to other important spectra of variation among species

Abstract There is a spectrum from species with narrow, frequently branched twigs carrying small leaves and other appendages, to species with thick twigs carrying large leaves and appendages. Here we investigate the allometry of this spectrum and its relationship to two other important spectra of ecological variation between species, the seed mass—seed output spectrum and the specific leaf area—leaf lifespan spectrum. Our main dataset covered 33 woody dicotyledonous species in sclerophyll fire-prone vegetation on low nutrient soil at 1,200 mm annual rainfall near Sydney, Australia. These were phylogenetically selected to contribute 32 evolutionary divergences. Two smaller datasets, from 390 mm annual rainfall, were also examined to assess generality of cross-species patterns. There was two to three orders of magnitude variation in twig cross-sectional area, individual leaf size and total leaf area supported on a twig across the study species. As expected, species with thicker twigs had larger leaves and branched less often than species with thin twigs. Total leaf area supported on a twig was mainly driven by leaf size rather than by the number of leaves. Total leaf area was strongly correlated with twig cross-section area, both across present-day species and across evolutionary divergences. The common log-log slope of 1.45 was significantly steeper than 1. Thus on average, species with tenfold larger leaves supported about three-fold more leaf area per twig cross-section, which must have considerable implications for other aspects of water relations. Species at the low rainfall site on loamy sand supported about half as much leaf area, at a given twig cross-section, as species at the low rainfall site on light clay, or at the high rainfall site. Within sites, leaf and twig size were positively correlated with seed mass, and negatively correlated with specific leaf area. Identifying and understanding leading spectra of ecological variation among species is an important challenge for plant

ecology. The seed mass—seed output and specific leaf area—leaf lifespan spectra are each underpinned by a single, comprehensible trade-off and their consequences are fairly well understood. The leaf-size-twig-size spectrum has obvious consequences for the texture of canopies, but we are only just beginning to understand the costs and benefits of large versus small leaf and twig size.

Introduction

Plant growth is a process where previously photosynthesized dry mass is invested in leaves, which then capture light, generate further dry mass growth and continue the process. Variation in this process of investment and reinvestment of dry mass in leaves must surely be fundamentally important in deciding which species will be competitive at which locations (which is not to say that other activities such as seed production and relations with mycorrhizae are not also important for plant fitness).

Identifying, quantifying and understanding the principal spectra of variation between species is an important aim for plant ecology. One conspicuous spectrum is variation in twig and leaf size. (For brevity, we use "leaves" here to include phyllodes or cladodes which are not morphologically leaves, but are green and are the principal light capture surface of the species.) This variation is substantial between species coexisting at a site, as well as between different habitats. Corner's Rules (Ackerly and Donoghue 1998; Brouat et al. 1998; Cornelissen 1999; Corner 1949; Halle et al. 1978; White 1983a, 1983b) state that the thicker the plant axis (stem), the larger the individual appendages (leaves, inflorescences, fruits); also the more closely spaced the ramification (branching), the thinner the ultimate axes and the smaller the appendages.

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The costs and benefits of lying at one or the other end of the twig-size—leaf-size spectrum are poorly understood. In this paper we quantify allometric (log-log) relationships between twig size, leaf size and total leaf area deployed on a twig. A log-log slope of 1 indicates that the ratio between two quantities is consistent across the measured range. A slope different from 1 may indicate an advantage at larger or at smaller leaf and twig sizes with regard to the ratio. In this way we can begin to quantify variation in this spectrum and to understand its implications.

A further aim was to ask whether the twig size-leaf size spectrum was correlated with, or alternatively orthogonal to, two other important spectra of ecological variation between species. One of these other spectra is seed mass. Species with small seeds produce more seeds from a patch of ground already occupied (Henery and Westoby 2001), whereas species with large seeds confer a greater capacity on their seedlings to survive hazards during establishment (Leishman et al. 2000; Westoby et al. 2002). The second spectrum of variation is to do with specific leaf area (SLA), the light capture area per dry mass of leaves. Low SLA leaves tend to have longer leaf lifespan, presumably because stronger leaf reinforcement is necessary to assure the longer life (Reich et al. 1997, 1999). Species with high SLA achieve better potential rate of return (light-capture area) on each milligram invested in leaf (Westoby 1998; Westoby et al. 2000); however, their revenue stream has shorter duration. Species with longer-lived leaves will accumulate more total leaf mass over time. Pines are an example that over time can achieve rapid growth rates despite low SLA, by accumulating a large leaf area per ground area (Bond 1989).

Fig. 1 Phylogenetic tree for species in the Sydney dataset. Branch lengths are not claimed to be proportional to time since evolutionary divergence

Materials and methods

The main dataset concerns perennial dicotyledonous species from low-nutrient Hawkesbury sandstone near Sydney, Australia (66 mg kg^{-1} total soil P, from five samples to 10 cm depth spaced across the site, amalgamated before analysis). The vegetation there is woody, sclerophyll, evergreen, fire-prone and species-rich. Data were collected in August 1999 as a practical exercise in Biol368 Ecology and Evolution, Macquarie University. The field site was on a broadly level plateau at latitude 33°41'38"S, longitude 151°08'35"E in Ku-Ring-Gai Chase National Park. In this vegetation seedlings establish following fire, or pre-existing individuals resprout. The previous fire occurred in 1990 at this site; consequently the individuals studied were well-established. Heights ranged from 20 cm for some low woody herbs, to 6 m for some eucalypts.

Rainfall at the site averages ca. 1,200 mm distributed through all seasons of the year. Growth slows but does not stop across the cooler months. In previous quantifications of the twig-size-leaf-size relationship (Ackerly and Donoghue 1998; Brouat et al. 1998; White 1983a, 1983b), the twig has been interpreted as a single year's growth, and twig diameters have been measured at the base of the current year's growth. In our situation most species do not show a clear demarcation between years of growth. Accordingly we defined the twig as material distal to the most distal branch-point. Thus "twigs" in our st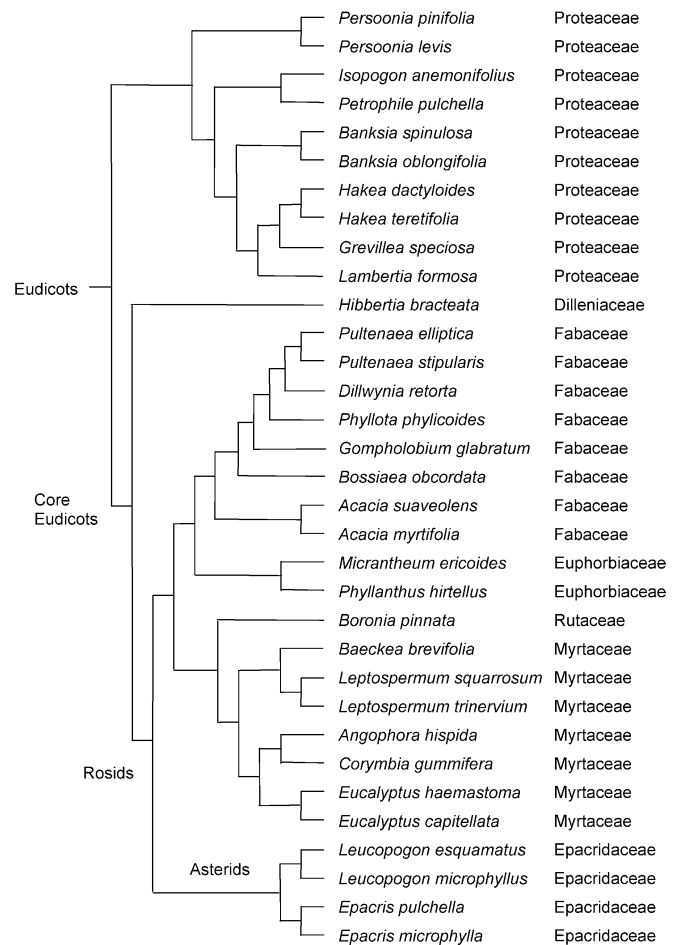udy were always unbranched, were shorter in species that branched more frequently, and did not correspond to a single year's growth.

We chose 33 woody dicotyledonous species with a view to forming a phylogenetic tree having only dichotomous branching (Fig. 1). This species-selection design produces the maximum number of radiations (nodes, branchpoints) in the tree, for a given effort in sampling species (Westoby 1999). As well as considering correlations across present-day species, we examined evolutionary divergence correlations, also known as phylogenetically independent contrasts. In these analyses each radiation contributes one item of evidence. On a graph showing divergence in trait 1 positively correlated with divergence in trait 2, the data-point for a given radiation may lie in either upper right or lower left quadrant, depending arbitrarily on the direction of subtraction across the divergence. Accordingly correlated divergence graphs are significance-tested by regressions forced through the origin.

Cross-species analysis and evolutionary divergence analysis ask different questions (Harvey et al. 1995a, 1995b; Westoby et al. 1995a, 1995b, 1995c, 1996). They are not alternative statistical techniques for the same question. Correlated divergence analysis asks whether divergence for twig diameter (for example) was consistently correlated with divergence for leaf size during the evolution of these traits, across all the radiations for which data are available. Cross-species analysis asks whether there is a consistent relationship between twig diameter and leaf size, considered across a set of species that are successfully maintaining populations today. It describes the set of trait-combinations that are ecologically

Table 1 Hierarchical variance components analysis for Sydney dataset (ANOVA type I sums of squares, converted to percentages at each level). Degrees of freedom: corrected model 98, intercept 1, species 32, individual within species 66, twig within individual within species 198; total 297 (corrected total 296)

Component	Log twig cross-section area	Log twig length	Log individual leaf area	Log leaf number	Log total leaf area	Log SLA
Species	79.7	58.6	97.9	82.9	89.5	83.4
Individual within species	4.0	8.1	0.5	1.8	0.9	3.8
Twig within individual	16.3	33.3	1.5	15.3	9.5	12.8

competent in the present day. Cross-species and evolutionary divergence correlations for a pair of traits are often similar (Ackerly and Reich 1999), but when they are not this is informative. For example, Ackerly and Reich (1999) found that leaf lifespan and leaf size were correlated across all species, but not as evolutionary divergences, since the cross-species pattern was created by the single divergence between conifers and angiosperms, deep in the phylogenetic tree. Of course, the fact that conifers are different from angiosperms in this trait-combination remains ecologically important, despite the non-significant evolutionary divergence correlation.

Three random individuals of each species were located, away from track edges. For each individual three random branches with tips at the outer surface of the plant's crown were chosen. The first branch-point back from the growing tip was located. Leaves expanded to more than 50% of typical final length were counted from the tip back to the branch point. Twig diameters were measured (vernier callipers) in the middle of the internode above the branch point. Twig cross-sectional area was calculated from the diameters. A fully expanded leaf along the twig was sampled for area and mass measurements. The sampled leaf was selected from among those that had not lost part of their area to herbivory or other damage, and to be near the median size. Projected area of the leaf was measured, laid flat on squared paper, and the leaf was dried to constant mass and weighed. Total area of leaves along a twig was estimated as number of leaves multiplied by area of the representative leaf sampled, and similarly for total mass of leaves along the twig.

For a stronger assessment of the generality of results, we include also results from two smaller datasets. These both come from lower-rainfall vegetation (mean 390 mm year^{-1}, without concentration at any particular time of year) at Round Hill Nature Reserve in inland NSW, Australia (32°58'S, 146°09'E). There are two sites differing in soil fertility, a "woodland" site on a light clay soil with 250 mg kg^{-1} total soil P in the top 10 cm, and a "mallee" site on a loamy sand with 132 mg kg^{-1}. These sites were described previously by Wright et al. (2001). Twig diameters and numbers of leaves expanded >50% were measured in June 1999 for 11 species at the woodland site and 14 species at the mallee site, including *Philotheca difformis* at both. Areas of individual fully expanded leaves (flatbed scanner) and SLA (using mass after drying for 48 h at 70°C) had been determined from 1 leaf from each of 5 individuals per species (woodland, December 1997) or from 5 leaves from each of 5 individuals (mallee, June 1998). Because these western NSW datasets included relatively few species, and were not structured with a view to maximizing the number of independent evolutionary divergences, we use them here for comparison only with the cross-species patterns from the Sydney dataset, and do not investigate evolutionary divergence correlations within them.

Data for seed reserve mass (dry mass of embryo plus endosperm if present) were drawn from previous studies in similar vegetation (Leishman et al. 1995; Westoby et al. 1990) or from unpublished datasets for western NSW.

Data considerations

Untransformed species means were not normally distributed, but were right skewed, for all traits except SLA (Shapiro-Wilks tests, not shown). After log transformation most traits were normally distributed, including SLA. Traits are quite commonly lognormally distributed across species, including SLA and seed mass (Westoby 1998).

In hierarchical ANOVA (Table 1, Sydney species only, all data log transformed), variance between species was consistently the largest component. Variance between individual plants was always less than 10%, and always smaller than variance between twigs on an individual plant. Since variance between individual plants includes environmental effects as well as genetic differences, genetic differences between individual plants are clearly a much smaller source of variation than environmental effects during development, if indeed there are significant genetic differences at all.

For analyses comparing species (which are the aim of this paper) traits were averaged arithmetically within species, then species averages (Table 2) were log$_{10}$ transformed. Model 2 regression techniques were considered appropriate for cross-species analyses since both X and Y variables included error and allometric slopes were of particular interest. Slopes were calculated as Standardised Major Axes (also known as Reduced Major Axis or Geometric Mean regressions; Sokal and Rohlf 1995). Confidence intervals for individual regression slopes were calculated following Pitman (1939). Tests for heterogeneity of regression slopes and calculation of common slopes where homogeneity of slopes was demonstrated followed Warton and Weber (2002). Differences in elevation of lines (intercept) were tested by ANOVA (and post hoc Tukey tests where appropriate) of Y', where Y' is Y transformed as $Y-bX$ for each group and b is the common slope (i.e. slopes transformed so slope =0 and group means compared). Regression of evolutionary divergence data used standard model 1 techniques.

Results

Twig size and leaf area

Cross-section area at the base of twigs was very strongly correlated with the total leaf area supported on the twig (Fig. 2a; r^2 from 0.76 at mallee site to 0.91 at Sydney site). Standardised major-axis slopes ranged from 1.38 (Sydney) to 1.86 (woodland). All were significantly steeper than 1. The SMA slope at the woodland site was not quite significantly steeper than at the Sydney site ($P=0.07$, heterogeneity of regression slopes $P=0.058$). Assuming homogeneity of slopes, the best-fit common regression slope was 1.45 (significantly steeper than 1.0), with the elevation of the relationship lower at the mallee site than at Sydney ($P=0.004$) or at the woodland site ($P=0.014$). This result indicates less leaf area supported by a given cross-section area for mallee species. At the grand mean of log twig cross-sectional area, 908 mm^2 leaf area was supported by mallee species, compared with 1,897 mm^2 for woodland species and 1,770 mm^2 for Sydney species (assuming common slope of 1.45). The relationship between twig cross-section area and total leaf

Table 2 Trait means for the 58 study species. Note that all data were log transformed prior to analyses

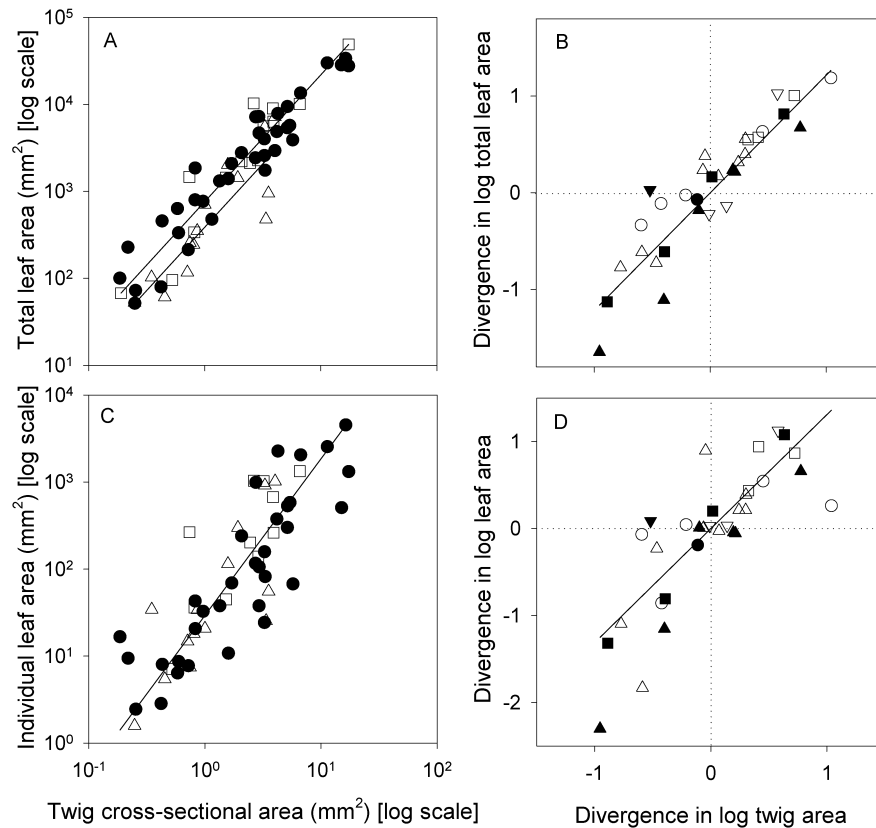| Site	Species	Family	Twig cross-sectional area (mm²)	Twig length (mm)	Number of leaves	Leaf area (mm²)	Total leaf area (mm²)	Seed reserve mass (mg)	SLA (mm²mg⁻¹)
Sydney	*Acacia myrtifolia*	Mimosaceae	5.4	174.1	9.8	582.2	5,693	8.9	5.5
	Acacia suaveolens	Mimosaceae	4.2	223.3	12.9	375.8	4,843	28.5	4.4
	Angophora hispida	Myrtaceae	6.7	141.1	6.6	2,047.9	13,425	28.5	4.4
	Baeckea brevifolia	Myrtaceae	0.4	26.1	28.0	2.8	79	0.1	7.2
	Banksia oblongifolia	Proteaceae	17.4	149.4	20.9	1,318.3	27,539	19.9	3.4
	Banksia spinulosa	Proteaceae	2.9	87.0	44.0	105.8	4,654	11.4	3.9
	Boronia pinnata	Rutaceae	2.1	121.0	11.6	239.7	2,769	1.7	5.4
	Bossiaea obcordata	Fabaceae	0.2	18.3	6.0	16.7	100	3.1	9.4
	Corymbia gummifera	Myrtaceae	4.3	131.2	3.4	2,269.6	7,817	7.3	4.6
	Dillwynia retorta	Fabaceae	0.6	117.0	98.9	6.4	632	5.5	8.3
	Epacris microphylla	Epacridaceae	0.4	118.2	56.9	8.0	455	0.0	10.9
	Epacris pulchella	Epacridaceae	0.6	71.1	38.8	8.6	334	0.1	10.8
	Eucalyptus capitellata	Myrtaceae	2.7	133.9	7.2	988.8	7,141	0.8	3.5
	Eucalyptus haemostoma	Myrtaceae	16.4	221.6	7.4	4,519.7	33,646	1.7	3.4
	Gompholobium glabratum	Fabaceae	3.3	220.0	21.3	81.8	1,745	2.7	6.9
	Grevillea speciosa	Proteaceae	2.7	163.9	20.8	116.3	2,417	27.4	5.1
	Hakea dactyloides	Proteaceae	5.2	159.8	17.7	531.4	9,389	20.0	3.3
	Hakea teretifolia	Proteaceae	5.7	424.7	57.8	67.4	3,897	14.5	1.7
	Hibbertia bracteata	Dilleniaceae	1.7	155.6	30.0	69.2	2,077	3.7	11.0
	Isopogon anemonifolius	Proteaceae	5.1	94.3	17.9	299.2	5,353	4.1	3.4
	Lambertia formosa	Proteaceae	3.3	103.7	16.3	157.8	2,577	25.1	4.3
	Leptospermum squarrosum	Myrtaceae	1.3	213.9	34.7	37.8	1,310	0.1	5.6
	Leptospermum trinervium	Myrtaceae	0.8	66.9	18.6	42.9	796	0.2	6.2
	Leucopogon esquamatus	Epacridaceae	1.0	93.8	23.6	32.6	767	6.4	10.4
	Leucopogon microphyllus	Epacridaceae	0.3	35.9	29.6	2.4	72	0.6	9.0
	Micrantheum ericoides	Euphorbiaceae	0.2	61.0	24.0	9.4	227	3.3	9.3
	Persoonia levis	Proteaceae	11.4	183.3	11.7	2,552.7	29,781	225.9	5.5
	Persoonia pinifolia	Proteaceae	2.9	201.4	191.7	37.8	7,241	174.4	7.6
	Petrophile pulchella	Proteaceae	15.0	490.0	55.9	507.8	28,379	8.0	3.9
	Phyllanthus hirtellus	Euphorbiaceae	0.7	64.7	27.6	7.7	213	1.5	7.0
	Phyllota phylicoides	Fabaceae	1.6	123.2	129.0	10.8	1,390	3.0	7.5
	Pultenaea elliptica	Fabaceae	0.8	96.7	89.4	20.7	1,849	2.2	8.6
	Pultenaea stipularis	Fabaceae	3.3	131.9	164.9	24.2	3,994	9.3	7.0
Woodland	*Acacia doratoxylon*	Mimosaceae	2.6		9.9	1,035.1	10,236	10.1	4.7
	Brachychiton populneus	Sterculiaceae	6.6		7.6	1,334.4	10,082	103.3	8.0
	Dodonaea viscosa spathulata	Sapindaceae	0.7		5.5	265.5	1,460	3.6	7.0
	Eremophila glabra	Myoporaceae	2.9		16.3	139.2	2,274	3.4	6.2
	Eremophila longifolia	Myoporaceae	3.9		24.2	261.1	6,324	95.0	3.7
	Eucalyptus intertexta	Myrtaceae	3.2		5.4	1,028.4	5,599	0.5	6.9
	Geijera parviflora	Rutaceae	3.9		13.3	671.5	8,953	23.9	5.4
	Melaleuca uncinata	Myrtaceae	0.8		9.3	36.2	338	0.1	3.4
	Philotheca difformis	Rutaceae	0.5		13.5	7.1	96	2.0	3.7
	Pimelea microcephala	Thymeleaceae	1.5		32.1	44.9	1,440	7.2	12.2
	Senna artemisioides	Caesalpinaceae	2.5		10.4	202.5	2,115	13.9	3.6
Mallee	*Acacia colletioides*	Mimosaceae	3.4		18.8	25.4	477	5.6	2.2
	Acacia havilandii	Mimosaceae	3.5		17.1	55.4	947	5.0	2.3
	Acacia wilhelmiana	Mimosaceae	0.8		13.4	18.1	243	6.0	5.0
	Bertya cunninghamii	Euphorbiaceae	0.7		7.9	14.8	117	13.3	5.2
	Beyeria opaca	Euphorbiaceae	0.3		3.0	34.3	103	8.6	5.6
	Cassinia laevis	Asteraceae	1.0		34.0	20.7	704	0.1	6.3
	Eremophila deserti	Myoporaceae	1.6		17.7	114.5	2,022	1.8	4.8
	Eucalyptus dumosa	Myrtaceae	4.0		7.0	1,019.9	7,139	0.6	2.8
	Eucalyptus socialis	Myrtaceae	3.3		6.0	918.1	5,509	0.7	3.3
	Eutaxia microphylla	Fabaceae	0.2		33.1	1.6	53	1.5	8.3
	Olearia oswaldii	Asteraceae	0.9		10.3	34.0	351	0.3	5.1
	Olearia pimelioides	Asteraceae	0.7		34.4	7.4	256	0.5	8.1
	Philotheca difformis	Rutaceae	0.5		11.2	5.4	61	2.0	4.6
	Santalum acuminatum	Santalaceae	1.9		4.8	298.5	1,426	537.3	3.3

Fig. 2a–d Relationships between leaf area and twig cross-sectional area. **a** Total leaf area versus twig area, cross-species data for the three study sites. Individual slopes were non-heterogenous; significant elevation differences were found between the Mallee SMA (*lower slope*) and each of the Sydney and Woodland SMAs, but no difference was evident between the latter two (thus, their common slope is shown). (Sydney, *filled circles*; Woodland, *open squares*; Mallee, *open triangles*). **b** Correlated change graph of evolutionary divergences in log total leaf area against log twig cross-sectional area (Sydney data only; r^2=0.84). Symbols for nodes in the phylogenetic tree: Epacridaceae, *open down triangle*; Euphorbiaceae, *filled down triangle*; Fabaceae, *open circle*; Mimosaceae, *filled circle*; Proteaceae, *open up triangle*; Myrtaceae, *filled up triangle*; higher Rosids, *filled squares*; higher eudicots, *open squares*. **c** Individual leaf area versus twig area, cross-species data for the three study sites. Individual SMAs were non-heterogeneous in slope and elevation, with a common slope of 1.80 (95% CIs 1.55–2.10). Symbols as for **a**. **d** Evolutionary divergences in log individual leaf area versus divergences in log twig area (Sydney data only; r^2=0.66). Symbols as for **b**

area was also strong when expressed as correlated evolutionary divergences (Sydney only, regression through origin, r^2=0.84, Fig. 2b).

The relationship between twig cross-section area and total leaf area was driven mainly by the size of individual leaves (Fig. 3c, d), not by the number of leaves (r^2 relating twig cross-section area to leaf number ranged from 0.003 to 0.040). No differences between sites were found for regressions of individual leaf area on twig cross-section area in either slope (P=0.460) or elevation (ANOVA P=0.107), with a common fitted slope of 1.80. The relationship between twig size and size of individual leaves is a quantification of one aspect of Corner's Rules, in vegetation different from where Corner's Rule has previously been quantified. Individual leaf area spanned about three orders of magnitude between species, at each of the three sites. Species with larger leaves deployed a greater total leaf area distal to the final branching point than smaller leaved species (Fig. 3a), with this leaf surface made up of fewer leaves per twig (Fig. 3b), even

though the twigs were longer (Fig. 3c). In this study the length of a twig was the measured distance back to the first branch point, rather than a single year's growth. Shorter twig length therefore represented greater ramification, and the relationship between leaf size and twig length is another aspect of Corner's Rules. Sydney species had more leaves per twig than species from either arid site (P=0.03 in each case), resulting in a greater total leaf area at a given individual leaf area (common slopes, but regression elevation significantly higher; Fig. 3a).

Twig and leaf size in relation to seed mass spectrum

Species with larger leaves did tend to have larger seeds (Fig. 4a, across all species r^2=0.19), as expected from Corner's Rules and as previously found by Cornelissen (1999). However, the present study did not find the triangular relationship reported by Cornelissen. As in Cornelissen's study and as might be expected, species
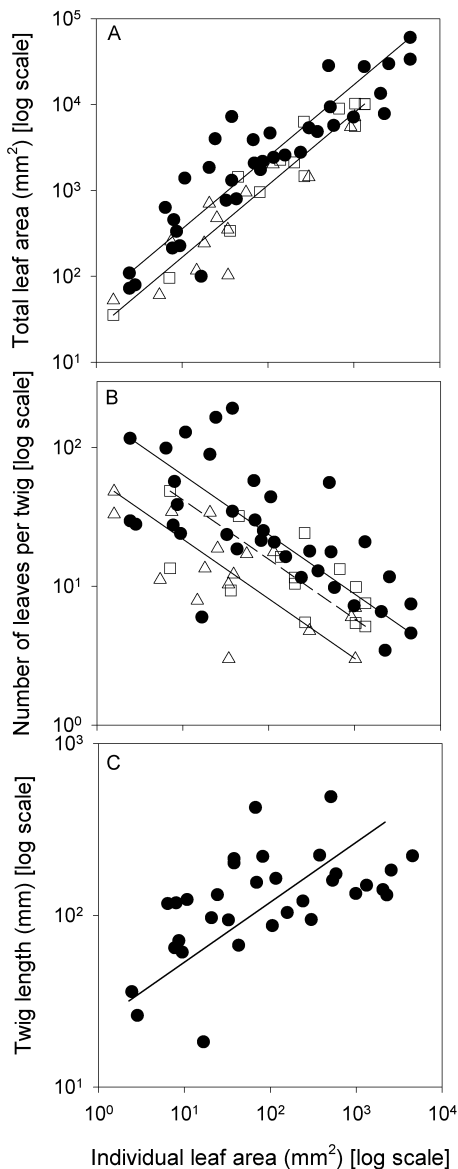
Fig. 3 Cross-species relationships between individual leaf area and **a** total leaf area, **b** number of leaves per twig, and **c** twig length. Symbols as for Fig. 2. **a** Individual SMAs were non-heterogeneous (*P*=0.678), with a common slope of 0.84 (95% CI 0.74–0.96). Significant differences were found in SMA elevations: Sydney >Woodland (*P*=0.037), Mallee (*P*=0.002), with no difference between Woodland and Mallee sites (thus, separate slopes shown for Sydney, and for pooled Mallee and Woodland data). **b** SMA slopes were non-heterogeneous (*P*=0.593), with common slope of −0.43 (95% CI −0.55 to −0.33). Significant differences were found in SMA elevations: Sydney >Mallee (*P*=0.002), with neither different in elevation from the Woodland site (*dashed line*). **c** SMA slope 0.32 (CI 0.24–0.44), *r²*=0.32 (Sydney data only)

having small leaves and twigs together with large seeds were absent (lower right region of Fig. 4a). Cornelissen did have species with large leaves and twigs together with small seeds, while we did not (upper left of Fig. 4a). For the Sydney species this relationship was of approximately equal strength both cross-species (*r²*=0.27) and considered as evolutionary divergences (*r²*=0.26; Fig. 4b). At

the other sites the relationship was weaker to varying degrees (cross-species woodland *r²*=0.20; mallee *r²*=0.02). Still, no difference with site was found between cross-species slopes (*P*=0.69). The common SMA slope of 0.91 (95% CIs 0.71–1.17) indicated that individual leaf area and individual seed mass scaled more or less in direct proportion with each other.

Twig and leaf size in relation
to SLA-leaf lifespan spectrum

In the Sydney dataset, there was a negative relationship between leaf size and SLA (Fig. 4c, *r²*=0.46). Similarly, SLA was negatively correlated with twig cross-section area (*r²*=0.56). To some extent this relationship consisted of deep phylogenetic divergences, with Epacridaceae and Dilleniaceae towards the small leaf end of the spectrum, Proteaceae and *Acacia* towards the large leaf end (Table 2). Nevertheless the relationships were consistent across most evolutionary divergences (divergence correlations *r²*=0.20 and 0.35 respectively). Similar negative correlations between leaf size and SLA, and between twig cross-section area and SLA, were found at the western NSW mallee site (*r²*=0.41, 0.73 respectively) but were absent at the woodland site (*r²*=0.06, 0.05 respectively). Still, since the confidence interval around any individual slope was fairly large, the leaf area–SLA slopes were deemed non-heterogeneous (*P*=0.872), with a common slope of −4.57 (95% CIs −5.82 to −3.59). The common slope for twig cross-section area on SLA (test for heterogeneity *P*=0.275) was −2.47 (CIs −3.11 to −1.96).

Discussion

Total leaf area should be coordinated with stem diameter for both mechanical (reviewed in Niklas 1992) and hydraulic reasons. Comparing stems of different sizes within a species at a site, leaf area supported has been shown many times to increase proportionally with sapwood cross-sectional area (Grace 1997), such that leaf area per sapwood area is a constant (the inverse of the "Huber Value"; Mencuccini and Grace 1995). However, the log-log slope of 1.45 found in this study across species at a site means that a species with tenfold higher twig cross-sectional area has approximately 30-fold higher total leaf area, on average. Larger-twigged species are operating with substantially higher leaf area per stem cross-sectional area.

The relationship between leaf area *L* and sapwood area *S* can be represented as $L=S[k(\Delta\Psi/l)c]/(Dg_s)$ (Whitehead et al. 1984a), where *k* is the average tree permeability, $\Delta\Psi/l$ is the water potential gradient through the system (difference over length), *D* is the time-averaged vapour pressure deficit of the air, and g_s is an appropriately weighted stomatal conductance. The coefficient *c* combines together some physical properties of water and air, and its variation is not important except when comparing

Fig. 4a–d Cross-species and evolutionary divergence relationships between individual leaf area and seed reserve mass (**a**, **b**), and SLA (**c**, **d**). Symbols as for Fig. 2. **a** Cross-species common SMA for the three study sites (slope of 0.91, 95% CIs 0.71–1.17). **b** Evolutionary divergences, Sydney data only; r^2=0.32. **c** Cross-species SMAs did not differ in slope (*P*=0.872), with a common slope of –4.57 (95% CI –5.82 to –3.59). SMA elevation was lower at the Mallee site than at Sydney and the Woodland (both *P*=0.004), with no difference between the latter two (thus, their common slope is shown). **d** Evolutionary divergences, Sydney data only; r^2=0.20
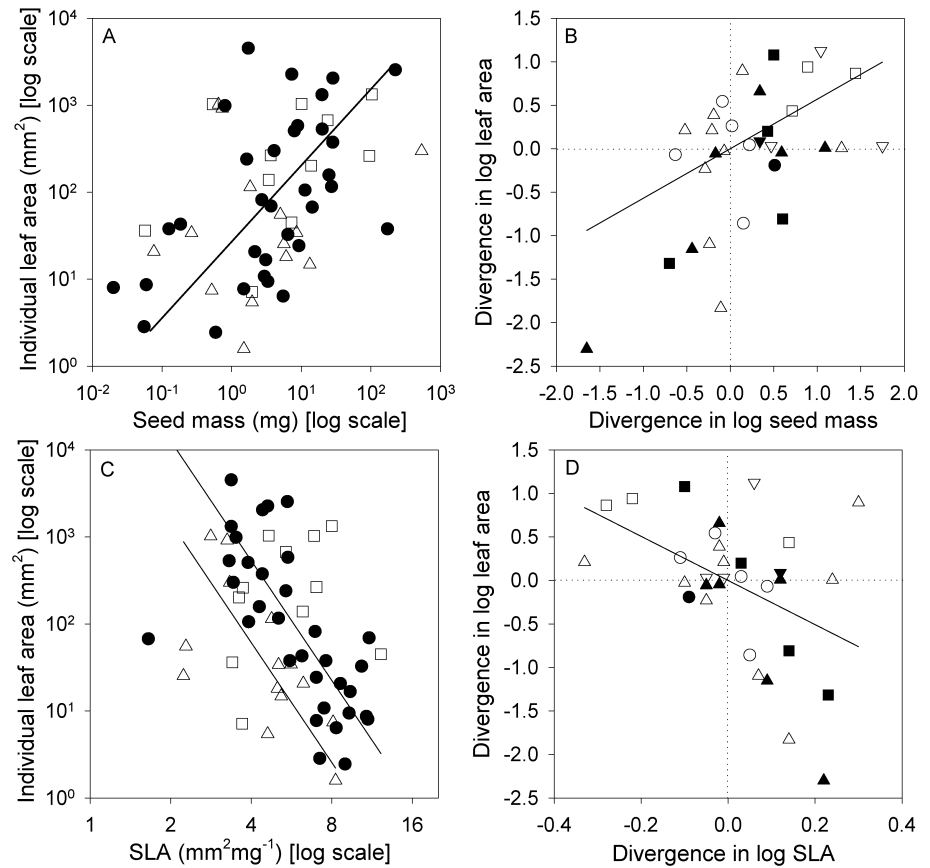
between temperatures with substantially different viscosity of water. The log-log slope of 1.45 implies that *L/S* is approximately 3-fold higher for each tenfold increase in leaf size and twig size. This means that larger-leaved species must operate with substantially higher permeability, greater water potential gradient through the plant, lower stomatal conductance, or combinations of those three. Edwards and Jarvis (1982) and Whitehead et al. (1984a, 1984b), comparing tree species growing under common climatic conditions, found that species with higher *L/S* ratio had higher permeability *k* rather than shallower water potential gradients.

Comparing sites with different vapour pressure deficit, *Pinus sylvestris* adjusted the *L/S* ratio rather than operating with a different water potential gradient (Mencuccini and Grace 1995). In the results reported here, species at the low rainfall mallee site (sandy soil) maintained on average half the leaf area of those at the other sites (low rainfall woodland on clay, high rainfall Sydney site on sand) at any given twig cross-sectional area. Thus there were differences between sites, but not a clear pattern with rainfall or vapour pressure deficit. Possibly soil moisture holding capacity was also involved.

At two of three sites, species with lower SLA tended quite strongly to have larger leaves. It begins to appear that the leaf size-SLA relationship depends strongly on the nature of the comparison across species (Westoby et al. 2002). Marañón and Grubb (1993), Shipley (1995) and

Grubb (1998) similarly found lower SLA in larger-leaved species when comparing species growing together and in similar light climate. Grubb (1998) attributed this to greater mechanical strengthening in order to support larger leaves against gravity. On the other hand comparing across a range of light climates in forests, Niinemets and Kull (1994) and Niinemets (1996) found the reverse. Across 85 and 60 Estonian woody taxa larger-leaved species tended to have higher SLA, and to occur in the more shaded lower third of the canopy. Niinemets (1998) found a similar pattern across 15 compound-leaved species. Along geographical gradients towards lower rainfall or lower soil nutrients, species typically have both smaller leaf size and lower SLA (e.g. Fonseca et al. 2000). In summary the leaf size-SLA correlation appears positive across habitats, both light-layers within forests and rainfall and nutrient gradients, but negative across species within a habitat. The upshot in large datasets will depend on the mixture of these contributions. Ackerly and Reich (1999), across 108 species from various habitats, found no correlation within angiosperms and within conifers, though angiosperms as a group had larger leaves and higher SLA than conifers. Fonseca et al. (2000) found a positive correlation across 386 species at 46 sites, variation being dominated by a wide range of rainfall and soil nutrients.

In summary we found that species with tenfold higher twig cross-sectional area averaged approximately 30-fold

higher total leaf area. This implied that larger-leaved species operate with substantially higher permeability, greater water potential gradient through the plant, lower stomatal conductance, or combinations of these trends. A challenge for the future is identifying and quantifying other potential costs and benefits along the twig-size—leaf-size spectrum. Variation in twig and leaf size was correlated with the seed mass—seed output spectrum, in line with expectations based on Corner's Rules. Relationships with the SLA—leaf lifespan spectrum were complex.

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