Short communication:

Leaf trait relationships in Australian plant species

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Abstract. Leaf trait data were compiled for 258 Australian plant species from several habitat types dominated by woody perennials. Specific leaf area (SLA), photosynthetic capacity, dark respiration rate and leaf nitrogen (N) and phosphorus (P) concentrations were positively correlated with one another and negatively correlated with average leaf lifespan. These trait relationships were consistent with previous results from global datasets. Together, these traits form a spectrum of variation running from species with cheap but frequently replaced leaves to those with strategies more attuned to a nutrient-conserving lifestyle. Australian species tended to have SLAs at the lower end of the spectrum, as expected in a dataset dominated by sclerophyllous species from low fertility or low rainfall sites. The existence of broad-scale, 'global' relationships does not imply that the same trait relationships will always be observed in small datasets. In particular, the probability of observing concordant patterns depends on the range of trait variation in a dataset, which, itself, may vary with sample size or species-sampling properties such as the range of growth forms, plant functional 'types', or taxa included in a particular study. The considerable scatter seen in these broad-scale trait relationships may be associated with climate, physiology and phylogeny.

Keywords: dark respiration, leaf lifespan, photosynthesis, plant strategies, specific leaf area.

Introduction

Quantifying leaf trait relationships across multiple species and habitats can provide information about major dimensions of variation among plant species, and about the broad evolution of traits, trait relationships, and the shaping of these by climate, soil nutrients or other factors (e.g. Field and Mooney 1986; Schulze *et al.* 1994; Reich *et al.* 1997, 1999; Wright *et al.* 2001; Lamont *et al.* 2002; Westoby *et al.* 2002). This information provides a context for interpreting more detailed studies of leaf (eco)physiology as well as providing input for modelling changes in vegetation, fluxes of carbon (C) and N with land-use and climate change (Moorcroft *et al.* 2001; Berry and Roderick 2002; Bonan *et al.* 2002).

At the global scale, leaf traits such as specific leaf area (SLA), leaf lifespan (LL), leaf N concentration (N_{mass}), photosynthetic capacity per unit leaf mass (A_{mass}) and dark

respiration rate (Rd_{mass}) are correlated with one another (Schulze *et al.* 1994; Reich *et al.* 1997). In this paper we have brought together published and unpublished data for Australian plants for these traits and assess whether the previously reported 'global' relationships are also seen in Australia. We also quantified the relationships of leaf P concentration (P_{mass}) to the other leaf traits. This is of particular interest given the generally low levels of P in Australian soils, and since leaf P was not considered in the previous data compilations. This study also differs from most previous compilations in that, rather than being dominated by species from the northern hemisphere, it almost entirely concerns sclerophyllous species from fire-prone habitats. These are general characteristics of much of Australian vegetation (Atwell *et al.* 1999). Focussing on phylogenetic patterning of A_{mass}–N_{mass}–SLA relationships, we also describe factors that contribute to the scatter in

broad, cross-species relationships. Finally, concentrating on the relationship between SLA and N_{mass}, we examined the extent to which the global or across-many-site relationship is also seen among sets of co-occurring species, and assess the extent to which the strength of observed relationships in data subsets relates to sample size and the extent of trait variation.

Materials and methods

Data were compiled from published sources (Specht and Rundel 1990; Schulze *et al.* 1998; Wright *et al.* 2001; Lamont *et al.* 2002; Wright and Westoby 2002; Prior *et al.* 2003) and from E. Veneklaas, P. Poot and P.B. Reich (unpublished data). Habitats sampled included shrublands, woodlands and forests, and ranged from 12.0 to 27.5°C in mean annual temperature and 300–1750 mm average annual rainfall (data from nearest weather stations). In these studies leaf traits were measured for species growing in their natural habitats. Trait values used here were species means for each species at a site. Traits were generally measured on young- to medium-aged but always fully expanded, outer-canopy leaves (see source papers for more detail on sampling protocols). The leaf traits measured in these studies are generally thought to represent traits of leaves when they are near their peak physiological potential, before any significant age-related decline in photosynthetic capacity occurs, or before nutrients are translocated to new leaves in developing and better lit parts of the canopy. We use the term photosynthetic 'capacity' to refer to maximum photosynthetic rates measured at near-saturating light conditions, ambient CO_2 concentration, and under relatively well watered conditions. Species-sampling protocols varied from study to study. Only trees were sampled by Schulze *et al.* (1998) and Prior *et al.* (2003), only species of *Hakea* (Proteaceae) were sampled by Lamont *et al.* (2002), while mixtures of growth forms and taxa were included in the other studies. The dataset comprised 300 records, for 258 species in 42 families. Shrubs were the most represented growth form (194 records), followed by trees (92 records), herbs (6), grasses (7) and vines (1). The dataset was 'site-based', that is, made up of data for (28) sets of co-occurring species. Three to thirty species were sampled per site (mean 10.7).

In multi-species datasets, leaf traits tend to be strongly log-normally distributed (Reich *et al.* 1997; Niinemets 2001). This was also the case here. Consequently, the data were log_{10}-transformed in order to satisfy the basic assumptions for regression and correlation that data should be normally distributed, and variance in one variable should be homogeneous across the range of the other. Correlation coefficients for trait relationships across species within individual sites were assessed for homogeneity by the standard procedure, whereby the weighted sums of squares of the Z-values corresponding to the correlation coefficients are χ^2 tested (Sokal and Rohlf 1995). Other statistical tests used SPSS for Windows v 11.0.1 (SPSS Inc., Chicago, IL).

Results and discussion

Specific leaf area, A_{mass}, Rd_{mass}, and N_{mass} concentrations were positively correlated among species, while average leaf lifespan was negatively correlated with these other leaf traits (Table 1). These relationships were consistent with those seen in previous data compilations (Field and Mooney 1986; Schulze *et al.* 1994; Reich *et al.* 1997, 1999). Comparing the Australian data within the global dataset of Reich *et al.* (1997) indicated that the datasets overlap over most of their range (Fig. 1). There was some tendency for Australian species to occur towards the lower N_{mass} or lower SLA regions of graph-space, as expected given that the dataset was dominated by woody species from low nutrient soils. Still, for the LL–A_{mass} and A_{mass}–SLA relationships (Fig. 1*c*, *f*) the Australian species were more or less in the middle of the observed trait-range, with several coniferous trees having lower A_{mass}/lower SLA/longer LL trait combinations on the one hand, and grasses, herbs and pioneer species having higher A_{mass}/higher SLA/shorter LL trait combinations on the other.

Leaf phosphorous (P_{mass}) varied between 0.01 and 0.28% and was log-normally distributed (220 species; back-transformed log-mean of 0.04%). These concentrations were very clearly towards the lower end of the known range for evergreen species (Aerts and Chapin 2000). Similar to N_{mass} but generally more weakly, P_{mass} was correlated with the other leaf traits (Table 1). N_{mass} and P_{mass} were themselves tightly correlated (r=0.85, n = 220, P<0.0001).

The independent effects of traits on one another were explored with 3-way relationships. For example, both SLA and leaf N independently influenced photosynthetic capacity and dark respiration rate (Fig. 2*a*, *b*). Presumably A_{mass} and N_{mass} are correlated because the bulk of leaf N is found in the photosynthetic complex (Field and Mooney 1986; Lambers *et al.* 1998). The independent SLA effect is most likely due to leaves with low area per mass having longer diffusion paths from stomata to chloroplasts, limiting the photosynthetic capacity possible for a given leaf protein content, or from lower proportional N investment to photosynthetic *v.* non-photosynthetic leaf components in low SLA species (Hikosaka *et al.* 1998; Poorter and Evans 1998). Most likely, Rd_{mass} increases with N_{mass} because to a large extent Rd_{mass} reflects protein turnover but also because

Table 1.   Pearson correlation values and sample sizes (in parentheses) for the leaf trait relationships
All relationships were highly significant, *P*<0.0001. Leaf traits were log_{10}-transformed before analysis

| Trait	A_{mass}	Rd_{mass}	N_{mass}	P_{mass}	Leaf lifespan
SLA	0.79 (135)	0.56 (103)	0.73 (299)	0.64 (219)	−0.72 (128)
A_{mass}	–	0.57 (103)	0.56 (135)	0.44 (103)	−0.71 (126)
Rd_{mass}	–	–	0.69 (103)	0.59 (78)	−0.68 (97)
N_{mass}	–	–	–	0.85 (220)	−0.54 (128)
P_{mass}	–	–	–	–	−0.54 (98)

phloem-loading of photosynthates contributes to Rd_{mass} (Amthor 2000), and high N_{mass} species had higher A_{mass}. The physiological basis for the independent SLA effect on dark respiration rate is less clear than for photosynthetic capacity (Reich *et al*. 1998). However, it is possible that this at least partially reflects increased phloem-loading associated with the higher A_{mass} of high-SLA species at a given leaf N.

Correlations between traits such as photosynthetic capacity, leaf nutrient concentrations and leaf lifespan probably reflect trait co-ordination rather than largely causal relationships. Here, both A_{mass} and leaf P were independently correlated with leaf lifespan (Fig. 2c), as were A_{mass} and N_{mass} (not shown; two-dimensional LL–N_{mass} relationship shown in Fig. 1d). By contrast, P_{mass} had no extra predictive power for either A_{mass} or Rd_{mass} after N_{mass} in multiple regression models (partial regression coefficients for P_{mass} were clearly non-significant, $P>0.4$). This was especially interesting given that Australian vegetation is generally thought to be limited more by low P availability than by low N availability.

Taken together, these leaf traits can be considered as forming a 'spectrum' of variation among plant species (whether Australian or from elsewhere), running from those with short-lived leaves but high leaf area per mass, high nutrient concentrations, high dark respiration rates and high potential for carbon assimilation, to species with long-lived leaves and low nutrient concentrations and lower maximum physiological rates. The spectrum can be characterised as running from species that invest in cheap but frequently replaced leaves to those more adapted to a nutrient-conserving 'lifestyle' (Reich *et al*. 1997). Obvious outliers are almost completely absent in either the bivariate or three-dimensional graphs, suggesting a high degree of generality for the trait relationships.

Still, a second notable feature of these relationships is that there is substantial variation in any one trait at a given value of another. For example, taking the bivariate relationship between A_{mass} and N_{mass}, 5-fold or more variation in A_{mass} is seen at any given N_{mass} (Fig. 1a). Several factors may contribute to the vertical scatter in this and the other relationships. First, there may be covariation associated with third, fourth or fifth variables that affects the relationship between the two variables portrayed. For example, adding SLA to a regression of A_{mass} on N_{mass} took the r^2 of the relationship from 0.32 to 0.63 for these Australian species. Second, there also may be variation associated with climate, whereby separate parallel relationships occur for species occurring in different climate zones, leading to more scatter
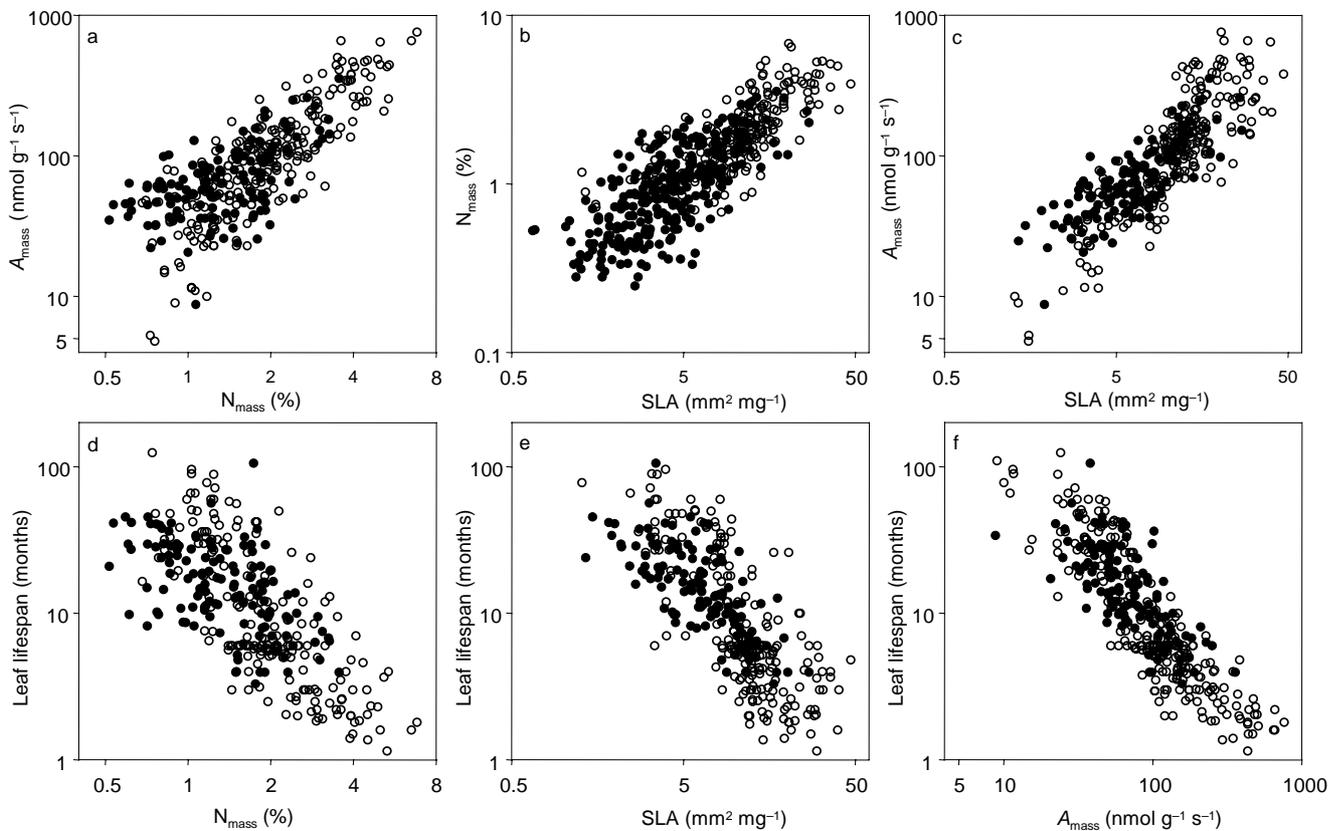
Fig. 1. Leaf trait relationships for Australian species (filled circles) and from the global dataset of Reich *et al*. (1997) (open circles). Data for selected Australian genera from panels *a–c* are shown in Fig. 3. Correlation statistics for Australian species are given in Table 1.
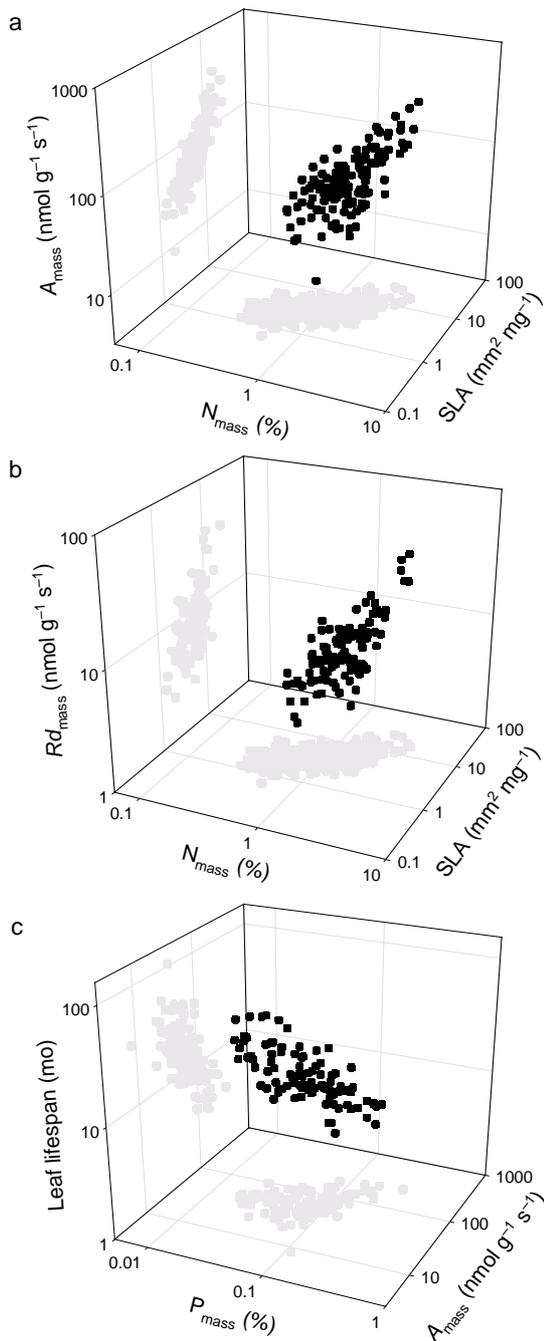
Fig. 2. Relationships among leaf traits for Australian plant species. The direction of the data cloud in three dimensional space can be ascertained from the two-dimensional shadows projected downwards and sideways. (*a*) Photosynthetic capacity (A_{mass}) *v.* N_{mass} and SLA. Both N_{mass} and SLA had significant main effects in the associated multiple regression model (SLA: $P<0.0001$; N_{mass}: $P=0.020$), model $r^2=0.63$, $n = 135$. (*b*) Dark respiration rate (Rd_{mass}) *v.* N_{mass} and SLA. Both N_{mass} and SLA had highly significant main effects in the associated multiple regression model (SLA: $P=0.0006$; N_{mass}: $P<0.0001$), model $r^2=0.53$, $n = 102$. (*c*) Leaf lifespan (LL) *v.* A_{mass} and P_{mass}. Both A_{mass} and P_{mass} had highly significant main effects in the associated multiple regression model (both A_{mass}: $P<0.0001$; P_{mass}: $P=0.0004$), model $r^2=0.62$, $n =96$.

when all the data are pooled. For example, in perennial species from eastern Australia, LL–SLA relationships have been shown to be vertically offset, such that low-rainfall species have shorter LL at a given SLA (Wright *et al.* 2002), while A_{area}–stomatal conductance (g_s) relationships were offset such that low-rainfall species had higher photosynthetic capacity per unit leaf area (A_{area}) at a given g_s (Wright *et al.* 2001). Third, there may be variation associated with phylogeny, or with different life histories or physiologies. For example, in this Australian dataset, A_{mass}–N_{mass} and N_{mass}–SLA relationships for *Eucalyptus* and *Acacia* species were clearly offset, whereby the potentially N_2-fixing species had higher N_{mass} for a given A_{mass} and higher N_{mass} at a given SLA (Fig. 3*a*, *b*). *Hakea* species were typified by having low N_{mass}, and amongst these species N_{mass} and SLA were only very weakly related ($r=0.21$, $n = 97$, $P=0.036$). Despite these differences, there was no apparent difference between the taxa when A_{mass}–SLA relationships were considered (Fig. 3*c*). Fourth, there may be variation related to using easy-to-measure but physiologically imprecise measures such as total leaf N, since species can vary in the partitioning of N between photosynthetic and non-photosynthetic components, as well as among different components within each of these two broad categories (Lambers *et al.* 1998). Finally, there must also be some sampling error contributing to the scatter.

It is unknown to what extent the differences between A_{mass}–N_{mass} and N_{mass}–SLA relationships among the *Hakea*, *Eucalyptus* and *Acacia* genera were driven by other plant traits, but some pertinent points can be made. It is worth noting that these taxa differ in their emphasis on type of nitrogen-uptake mechanisms or in root structure. *Hakea* species tend to have proteoid (cluster) roots, a specialisation enhancing P uptake. *Eucalyptus* species tend to have symbioses with ectomycorrhizal fungi, which enhances both NH_4^+ and P uptake. Most *Acacia* species fix N_2 via symbioses with bacteria in their root nodules, at least under moist conditions, and many are also known to be mycorrhizal (Sprent 1994).

Obtaining nitrogen by N_2-fixation is thought to be relatively expensive compared with obtaining N from other sources (Gutschick 1981; McKey 1994). Consequently, the clear trend of high leaf N_{mass}, but low A_{mass} at a given N_{mass}, of *Acacia* merits further investigation. One prospective explanation for this trend is that *Acacia* species have a lower proportion of leaf N in their photosynthetic complex than *Eucalyptus* and *Hakea*, and a higher proportion of N devoted to other functions such as defence against herbivory. However, we are unaware of any study in which N-partitioning has been systematically studied for these genera. Another possibility is that there are higher intercellular or mesophyll–cell wall resistances to diffusion of CO_2 in *Acacia*, though this seems unlikely; if anything, one would predict that *Hakea* species, with their generally dense
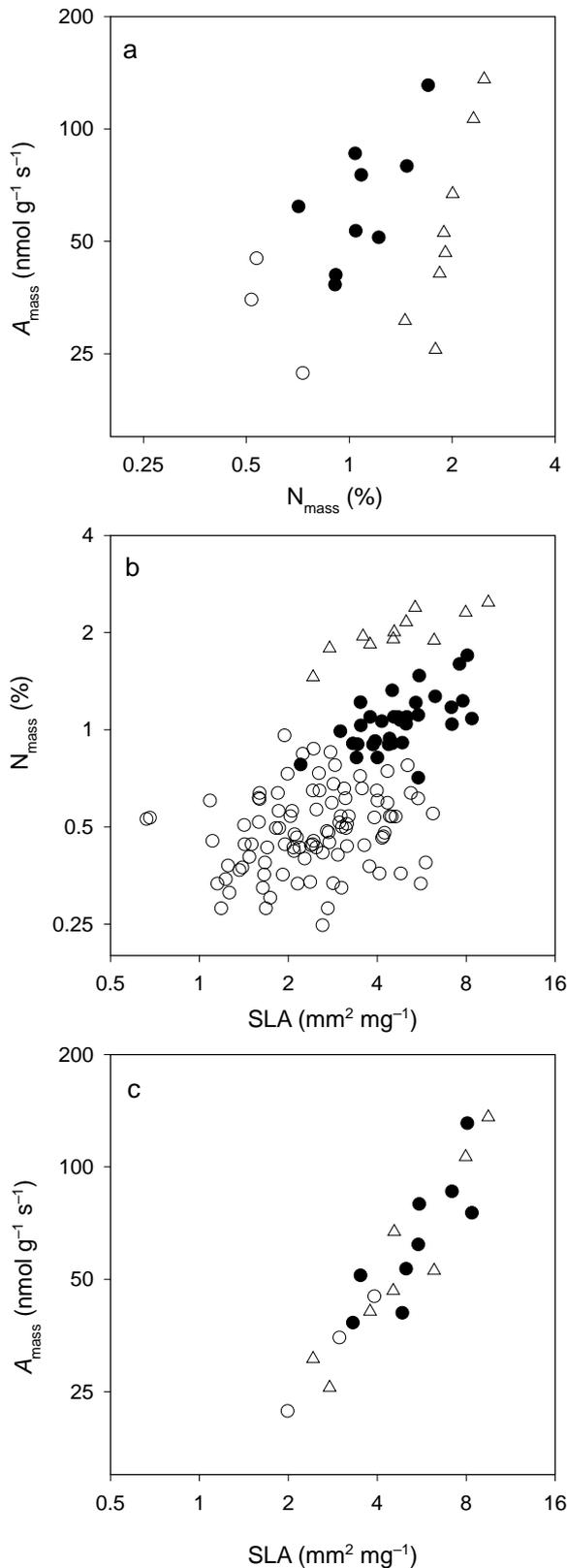
Fig. 3. A_{mass}–N_{mass}–SLA relationships for Australian *Eucalyptus* (filled circles), *Acacia* (triangles) and *Hakea* species (open circles). All axes are log-scaled.

leaf tissue (data not shown), to have higher internal resistances if any of the three genera did. A third and more promising possibility is that the high leaf N in *Acacia* is part of a water conservation strategy that contributes to their success, particularly in low rainfall habitats. In previous work concerning several dozen sclerophyllous species from eastern Australia we found that higher leaf N allowed greater draw-down of CO_2 during photosynthesis, reducing the transpirational cost of carbon fixation but, in doing so, incurring several additional costs, one of which was reduced photosynthetic rates at a given leaf N concentration, at least considered on a leaf-area basis (Wright *et al*. 2001; Farquhar *et al*. 2002; Wright and Westoby 2002; Wright *et al*. 2003).

Patterning of trait relationships with sample size and trait variance

Considered across hundreds of species from around the world these trait relationships seem to be quite general, with the same basic patterns found in different biomes, plant functional types and growth forms (Reich *et al*. 1997, 1998, 1999). However, individual sets of species may not necessarily show the same pattern of trait correlations. Below we discuss how this may relate to the number of species sampled or to the range of variation in the traits under study, as well as to differences in trait relationships among different sets of species.

   Imagine a relationship seen across hundreds of species between two traits X and Y, as in Fig. 4. Now imagine taking six species ranging in trait X from a to b, and then assigning random Y values to them from within the range of Y observed between points a and b. Across these six species, it would be difficult not to have a relationship between X and
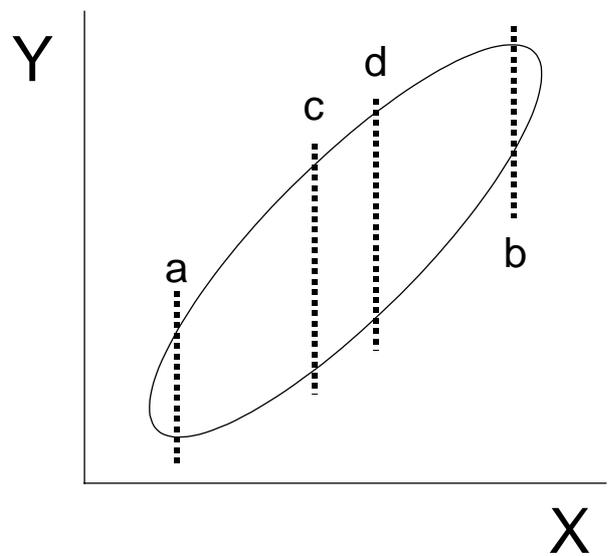
Fig. 4. Hypothetical relationship between two traits Y and X, and the effect that the extent of variation in the species under study may have on the strength of the observed relationship (see text for explanation).

Y that was consistent with the broad relationship seen across the hundreds of species. Now imagine repeating this exercise for six species ranging in trait X between points c and d. Among this second set of species virtually any relationship could be observed between traits Y and X. That is, at the most simple level the chance of observing
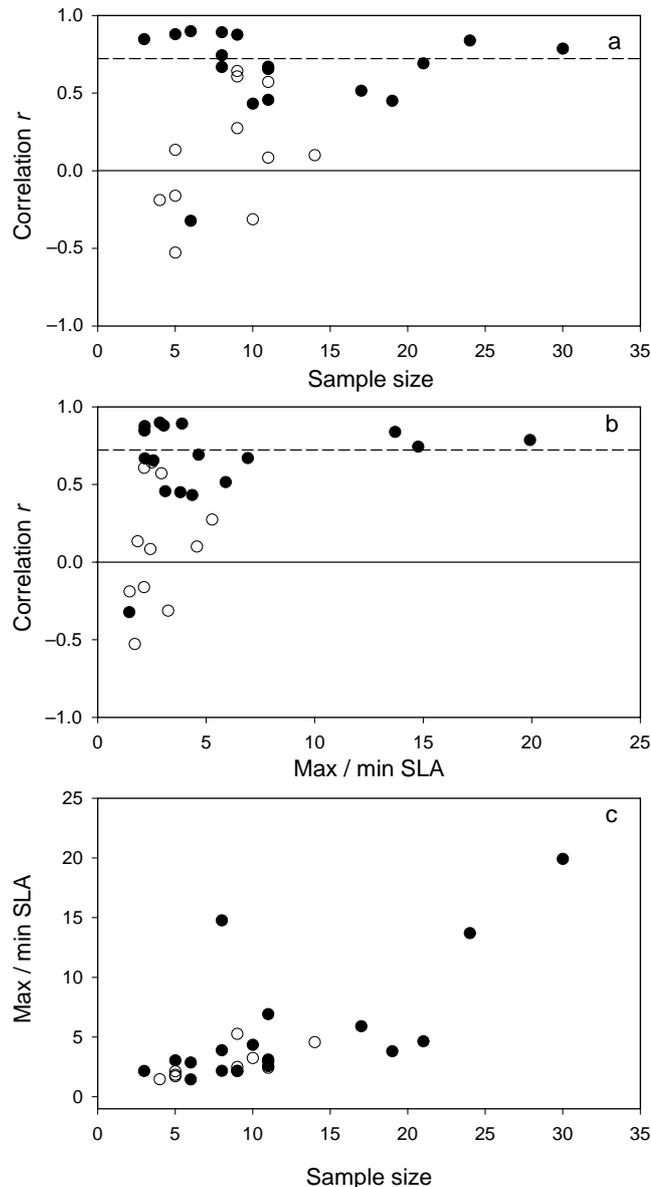
Fig. 5. Effect of sample size and variation in SLA on N_{mass}–SLA relationships fitted within individual sites. Sites where only *Hakea* species were sampled are indicated with open symbols. (*a*) Funnel plot of correlation *r* values for the trait relationship for each site *v.* sample size. The correlation seen across all species is shown as a dashed line. (*b*) Funnel plot of correlation *r* values for the trait relationship for each site *v.* the range of variation in SLA (maximum SLA/minimum SLA for each site). The correlation coefficient (*r*) across all species is shown as a dashed line. (c) Relationship between the range of variation in SLA and sample size for each site.

patterning in subsets of a global relationship should depend on the spread of trait-values along the axes for the subset.

Indeed, this is what we observed when we examined variation in N_{mass}–SLA relationships between different sets of co-occurring species (Fig. 5). In larger datasets, or datasets with greater variation in SLA, a positive relationship was observed between the traits that had similar strength (in terms of correlation *r*) as seen across the total dataset (dashed line in Fig. 5*a*, *b*). In smaller datasets, or datasets with less than 6-fold variation in SLA, there was considerable scatter in the strength of observed correlations. This distinct funnelling or convergence of correlation *r* values with increasing sample size is known from meta-analyses across experimental studies, leading to these types of graphs being known as 'funnel plots' (Egger *et al.* 1997).

Larger datasets tended to have more variation in SLA among species (Fig. 5*c*). The funnel plots suggested that to detect broad trait relationships among species the range of variation in the traits must be large (e.g. at least one order of magnitude) compared with the scatter in one trait at a given value of another trait. A small range of trait variation in a set of species may relate to small sample size, or to limiting sampling to within a narrow taxonomic group or perhaps to within a limited climatic range. Our argument is not that reports of a lack of a cross-species relationship between two traits for which a broad relationship is known are necessarily incorrect. Rather, we present a cautionary story about making conclusions about generality based on small data-sets, echoing the sentiments of Reich (1993). In particular, it can be difficult to differentiate the possibility that different trait relationships really do occur among particular sets of species (e.g. Niinemets and Kull 2003) from the possibility that observed relationship heterogeneity is an artefact from taking many variously-sized samples from an, in fact, homogeneous population. For the Australian N_{mass} and SLA data, a test for heterogeneity among the correlation coefficients fitted to individual sites was indeed significant ($P=0.018$). That is, this test suggested that the N_{mass}–SLA relationships do differ between sites. However, had the *P*-value from the test been >0.05, we would have concluded that the heterogeneity was indistinguishable from that expected by chance alone. Indeed, if all the *Hakea*-only data (Lamont *et al.* 2002) were removed from the analyses (for which N_{mass} and SLA correlations were generally non-significant within individual sites), the test for heterogeneity was clearly non-significant ($P=0.296$). The *Hakea* data represent an interesting case since even across all 98 data points there was quite a range of SLA, yet still N_{mass} and SLA were only very weakly related ($r^2=0.05$, $P=0.034$). Again, it is unclear what lay behind this (lack of a) trend. The traits were not correlated among either the 68 broad-leaved *Hakeas* nor among the 30 needle-leaved *Hakea* species, so broad differences in leaf type did not provide any explanation.

Conclusions

Ecophysiologists face the challenge of drawing together data and theory from different scales — of scaling between leaves, canopies, plant stands and ecosystems, and determining to what extent information gathered at one level applies at other levels and to other taxa. Gathering together data at the species level, as we have done here, provides insight into the evolution of plant strategies and provides a context for a more detailed understanding of the ecology and physiology of plants. Broad relationships exist between traits such as SLA, leaf lifespan, A_{mass}, Rd_{mass}, leaf N and P, not only across Australian species, but also across species from around the world. However, the existence of a broad (global/continental) relationship cannot necessarily be translated to comparisons across species varying 5-fold or less in traits such as SLA, just as extreme caution should be exercised in attempting to identify very general patterns from small samples. Determining the extent to which conflicting results reflect sampling artefacts compared with situations where different trait relationships are 'real' (e.g. for particular habitat types, taxa or growth forms) presents an interesting challenge for the future.

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