Leaves at low versus high rainfall: coordination of structure, lifespan and physiology

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Summary

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• Across species, leaf lifespan (LL) tends to be correlated with leaf mass per area (LMA). Previously we found that Australian perennial species from low-rainfall sites had *c.* 40% shorter LL at a given LMA than high-rainfall species.
• Here we relate indices of leaf strength (work to shear, W_{shear}, and tissue toughness) to LL and LMA across the same suite of species. W_{shear} is the work required to cut a leaf with a blade; W_{shear} divided by leaf thickness gives tissue toughness.
• Low- and high-rainfall species did not differ in their LL at a given W_{shear}, but dry-site species had lower W_{shear} at a given LMA, leading to the observed LL – LMA shift with rainfall. These patterns were driven by 50% lower tissue toughness in dry-site species.
• The lower toughness was linked with high leaf N concentration, which is known to enhance water conservation during photosynthesis in low-rainfall species. Our results suggest that a significant cost of this strategy is reduced LL for a given investment in leaf tissue (LMA).

Key words: leaf mass per area; leaf lifespan (LL); nitrogen use; sclerophylly; toughness; water use.

Introduction

Species with high LMA leaves (high leaf mass per area) tend to have a longer average leaf lifespan (LL), both in comparisons among coexisting species, and in comparisons across species from many different habitats (Reich *et al.*, 1997, 1999; Diemer, 1998a,b; Ryser & Urbas, 2000). Understanding the basis for LL – LMA relationships is of significant interest because both traits are pivotal in the carbon-fixation 'strategy' of a species. LMA can be thought of as the investment (leaf mass) associated with a given potential rate of return (light-capture area). The LL – LMA relationship among species is thought to reflect a trade-off, with lower LMA indicating greater potential for fast growth (higher rate of return on a given investment), but longer LL indicating a longer duration of the revenue stream from that investment (Westoby, 1998). Longer LLs also enhance nutrient conservation (Escudero *et al.*, 1992; Reich *et al.*, 1992; Eckstein *et al.*, 1999; Aerts & Chapin, 2000). Reinforcing this trade-off, species with low LMA tend also to have higher photosynthetic capacity per unit leaf mass, resulting from having larger light-capture area

deployed per mass, higher leaf N concentration (Field & Mooney, 1986; Reich *et al.*, 1997; Wright *et al.*, 2001) and shorter diffusion paths from stomates to chloroplasts (Parkhurst, 1994).

Presumably, the chief reason that species with high LMA achieve long LLs is because LMA is related to leaf strength, and the more sturdy the leaves are, the more tolerant they are of physical hazards such as herbivory, wind, rain, frost, wilting and damage from the thrashing action of neighbouring branches and leaves (Chabot & Hicks, 1982; Grubb, 1986; Coley, 1988; Reich *et al.*, 1991; Wright & Cannon, 2001). Still, leaf chemistry also plays a significant role in defence, with long LL sometimes correlated with greater allocation to tannins, phenols or other defensive compounds (Coley, 1988). One general index of leaf strength is the work required to cut a leaf with a blade (Vincent, 1992; Wright & Illius, 1995; Aranwela *et al.*, 1999; Edwards *et al.*, 2000). The average work per distance along the cutting trajectory is known as the 'work to shear' (units J m^{-1}; also sometimes known as the 'force of fracture': Wright & Cannon, 2001). Dividing the average work to shear across a leaf by its thickness gives

the average toughness of the leaf tissue. That is, toughness indicates the work required to cut through a unit area of tissue ($J m^{-2}$). Leaf tissue toughness is known to be correlated with the concentration of cell wall, vascular tissue, fibre or sclerenchyma in leaves (Choong *et al.*, 1992; Wright & Illius, 1995; Lucas *et al.*, 2000). Traits such as leaf work to shear (W_{shear}), toughness and tensile strength (resistance to tearing; Hendry & Grime, 1993) have gained acceptance as being ecologically meaningful since they are related to leaf palatability, food quality, growth rate of herbivores and wear of insect mouthparts (Cherrett, 1968; Ohmart *et al.*, 1985; Southwood *et al.*, 1986; Coley, 1987; Choong, 1996; Hochuli, 1996), as well as to LL (Reich *et al.*, 1991) and litter decomposition rate (Cornelissen & Thompson, 1997; Cornelissen *et al.*, 1999).

In recent work on evergreen species from four habitats in eastern Australia (low and high rainfall sites in each of two soil nutrient classes), we found that the slopes of LL – LMA relationships were similar at all sites, yet species at drier sites had 40% shorter LL at a given LMA, or 30% higher leaf mass per area at a given LL than those at wetter sites (Wright *et al.*, 2002). A similar result – shorter LL for a given LMA at low rainfall – was also implied by data presented by Reich *et al.* (1999) from sites in the Americas. One interpretation of this result is that the generally harsher conditions at low rainfall sites result in reduced LL at a given LMA. Frequent low water potentials may irretrievably damage leaves, for example. Implicit in this argument is the idea that LMA has a similar relationship to leaf strength, irrespective of habitat. If this were the case, then we would expect LL – leaf strength relationships to be shifted similarly with site rainfall as were LL – LMA relationships (i.e. LL would be shorter at a given leaf strength at low rainfall sites). In this study we set out to test this proposition for the same set of species used by Wright *et al.* (2002), estimating leaf strength from leaf work to shear. Hence, our expectation was that LMA and W_{shear} would be similarly correlated in each of the four habitat types and, further, that LL – W_{shear} relationships would be offset with site rainfall, as were the LL – LMA relationships reported by Wright *et al.* (2002). Trait relationships were primarily examined with cross-species analyses, but 'phylogenetic' analyses were also used in order to ascertain whether within-site relationships across species were being driven by differences between higher taxonomic groups.

Materials and Methods

Site and species selection

Traits of fully expanded, outer-canopy leaves were measured on perennial species sampled from nutrient-rich and nutrient-poor sites in each of two rainfall zones in eastern Australia (site details given in Table A1, species list in Appendix). The same set of 75 species was used here for which LL and LMA were reported previously (Wright *et al.*, 2002), with the exception that leaves of *Eutaxia microphylla* (Fabaceae) were too small for work to shear to be measured. For *Exocarpos aphyllus* (Santalaceae) and *Bossiaea walkeri* (Fabaceae), both leafless stem-photosynthesisers, 'leaf' traits were actually measured on the youngest cohort of stems. For *Callitris glaucophylla* (Cupressaceae), traits were measured on terminal 'branchlets' of closely appressed leaves.

Measurement of leaf traits

Average LL for each species was estimated as the inverse of the rate of annual leaf turnover (Southwood *et al.*, 1986; Ackerly, 1996) measured over 2 years (June 1998 to June 2000). For the two leafless, stem-photosynthesising species, 'leaves' were defined as unbranched twigs, 'branches' as twigs with twigs coming off them. Both 'leaf' death and 'leaves' morphing into a 'branch' were defined as mortality; leaf longevity was then calculated as above. Note that Wright & Cannon (2001) estimated LL for species at the high rain, nutrient-poor site based on 1 year of leaf mortality censuses whereas the data presented here for that site include a second year of census data, and thus should be a more robust estimate of average LL for these species.

Table 1 Description of the four study sites. High rainfall sites were located in Kuringai Chase National Park, Sydney; low rainfall sites in Round Hill Nature Reserve, western New South Wales. Mean annual rainfall for the period June 1998 to June 2000 (the period over which LL was determined) was 1425 mm in the high rainfall area and 574 mm in the low rainfall zone. The standard deviation for soil analyses is given in parentheses after the mean; $n = 5$ for Sydney sites, $n = 10$ for low rainfall sites

	High rain, High nutrient	High rain, Low nutrient	Low rain, High nutrient	Low rain, Low nutrient
Latitude (S), longitude (E)	33°34′44″, 151°17′32″	33°41′38″, 151°08′35″	32°58′00″, 146°09′17″	32°58′35″, 146°08′45″
Vegetation type	Closed forest	Low open woodland	Open woodland	Open shrub mallee
Annual rainfall (mm)	1220	1220	387	387
Mean annual temperature °C	22.0, 13.0	22.0, 13.0	24.1, 11.1	24.1, 11.1 (max, min)
Soil type	Red-brown clay	Yellow – grey sand	Light red clay	Loamy red sand
Total P ppm	442.3 (232.0)	93.6 (27.9)	250.4 (33.5)	132.4 (14.6)
Total N percentage	0.256 (0.152)	0.030 (0.001)	0.071 (0.020)	0.031 (0.006)
Total C percentage	5.91 (3.37)	0.95 (0.09)	1.20 (0.36)	0.67 (0.15)
Cation exchange capacity meq kg^{-1}	55.6 (21.7)	9.0 (1.6)	65.8 (23.7)	38.7 (9.4)

LMA was calculated from leaf dry mass (oven-dried for 48 h at 65°C) and one-sided leaf area (flat bed scanner; needle leaves assumed to have circular cross-section and leaf area adjusted by π/2). For LMA, five leaves from each of five individuals were sampled per species for all sites except the drier, nutrient-rich site, for which one leaf from each of five individuals was sampled in December 1997 and a further 6–10 leaves collected in November 1998. Leaf tissue density (dry mass per unit volume) was calculated as LMA divided by leaf thickness.

Leaf work to shear (W_{shear}), thickness and toughness were measured for one leaf from each of three–five individuals per species (generally five), except at the high rainfall, nutrient-poor site, for which two leaves from each of 3 individuals per species were measured (Wright & Cannon, 2001), giving an overall average of 5.2 samples per species. Leaf thickness was measured at two–five points per leaf with a dial gauge micrometer. Major veins and the midrib, where present, were avoided on all but the smallest leaves; otherwise placement of the micrometer was haphazard. The cross-section of needle leaves was assumed to be circular, and average leaf thickness was adjusted accordingly in these cases (multiplied by π/4).

Leaf work to shear (W_{shear}) was determined using a custom-built machine, which was not intended to simulate any particular herbivore, but to provide a generalised measure of physical defence (Wright & Cannon, 2001). The machine measures the work required to cut a leaf at a constant cutting angle (20°) and speed, and is similar in principle to systems described by Darvell et al. (1996) and Aranwela et al. (1999). W_{shear} and tissue toughness (= average W_{shear}/thickness) measure different aspects of how robust a leaf or leaf tissue is. Both would likely be correlated with other physical properties such as leaf stiffness, tensile strength and resistance to puncture by a penetrometer (Vogel, 1988; Choong et al., 1992; Wright & Illius, 1995; Edwards et al., 2000).

One cut at right angles to the midrib was made per leaf for measurement of W_{shear}. Leaves were cut at the widest point along the lamina, or half way between the leaf base and tip if the leaf had no obviously widest point. For species with a prominent midrib, this feature could be discerned on the machine output (Wright & Cannon, 2001), and the W_{shear} and toughness of the lamina were calculated separately in addition to that integrated over the whole leaf. This was possible for 33 species (24 at high rainfall, nine at low rainfall); for the remainder it was not because the midrib was not sufficiently prominent relative to other features in the graph, or because no midrib was present (e.g. needle leaves). Whole-leaf and lamina-only measures of W_{shear} and toughness were tightly correlated (across all species, $r^2 > 0.95$, slopes not different from 1). Consequently we report whole-leaf measures only, because this makes no qualitative difference to the results, and because these measures are more analogous to other whole-leaf properties, such as LMA and density.

Leaves were sampled for determining average total nitrogen concentration over a 2.5-year period at the drier, nutrient-rich site (December 1997–June 2000) and for c. 2 years at all other sites (June 1998–August 2000). Between two and four leaf collections were made per species over that time (average 3.0). One collection consisted of leaves used for photosynthesis measurements (Wright et al., 2001). For other collections, five leaves were collected from each of five individuals for each species. Only fully expanded outer canopy leaves were sampled. Leaves were finely ground, and leaf N concentration was measured by Kjeldahl digestion followed by colorimetric analysis (undertaken at CSIRO Plant Industry, Canberra).

Data considerations

Individual leaf trait measurements were averaged for each species at a site since we were primarily interested in cross-species trait relationships, and differences in these relationships among sites. Since the pattern we were trying to understand involved a shift in trait relationships according to site rainfall, for brevity we focus just on that aspect rather than also examining shifts according to site nutrient status within rainfall zones (cf. Wright et al., 2002). Species-mean data are listed in Appendix. Variance components analyses (ANOVA, type I sums of squares, log transformed variables) indicated that > 84% of variation in leaf thickness, W_{shear}, toughness, leaf size and N concentration was associated with differences between species as opposed to within-species. Thus, treating these variables as species means in subsequent analyses was strongly supported. Species-means of all variables showed approximately log-normal distributions and were deemed normal following log transformation (Kolmogorov-Smirnov test, $\alpha = 0.05$).

Cross-species analyses

Data were analysed primarily by fitting Standardised Major Axis (SMA) slopes since each variable had variation associated with it due to both measurement error and species-sampling, hence it was inappropriate to minimise sums of squares in the Y dimension only (Sokal & Rohlf, 1995). SMA analysis is also known as Geometric Mean Regression because a SMA slope is equal to the geometric mean of the model 1 regression of Y on X, and of the reciprocal of the regression coefficient of X on Y. SMA 'scaling' slopes, calculated on log-transformed variables, give the proportional relationship between variables. Slopes were first fitted across the species within each site, with confidence intervals (95%) calculated following Pitman (1939). Tests for homogeneity of slopes and calculation of common slopes used a likelihood ratio method (Warton & Weber, 2002). The ability to calculate common slopes allows one to test for elevation (i.e. intercept) differences between individual slopes, as in standard analyses of covariance (ANCOVA). Where nonheterogeneity of slopes was

demonstrated, we tested for elevation shifts in SMAs between high and low rainfall sites at each soil nutrient level (low or high) by transforming slopes such that the common slope was 0 (Y′ = Y − βX, where β is the common slope) and then testing for differences in group mean Y′ with *t*-tests (Wright *et al.*, 2001).

Phylogenetic analyses

Key trait relationships were also explored with 'phylogenetic' analyses in order to ascertain whether cross-species relationships were being driven by differences between higher taxonomic groups. By superimposing the species-mean data onto a phylogenetic tree of the study species (Appendix Table A1), inferred evolutionary divergences in one trait can be tested for correlation with divergences in another. In these 'correlated divergence analyses' (Westoby *et al.*, 1998), each independent divergence (radiation) contributes a single item of evidence. This independence has led to these types of analyses being known as 'Phylogenetically Independent Contrast' or PIC analyses (Felsenstein, 1985; Harvey & Pagel, 1991).

A 'contrast' dataset was created for each site, in which the value assigned to each contrast was calculated as the difference between the trait values for the two nodes or species descending from the contrast-node. Node values were themselves calculated as the average of trait values for the two immediately lower nodes or species. The direction of subtraction in calculating contrasts is unimportant, providing all traits are treated in the same manner. Hence, in a graph of divergences in one trait against divergences in another, a data point indic-

ating a positive divergence in both traits would have indicated negative divergences in each trait had the subtractions been performed the other way around. Due to this symmetry, regressions of contrast data have no intercept term (they are 'forced' through the origin; Grafen, 1989; Westoby *et al.*, 1998). SMA slopes were calculated for correlated divergence analyses as the geometric mean of the model 1 regression of Y on X, and of the reciprocal of the regression coefficient of X on Y. Confidence intervals (CIs) from the regression of Y on X were used to estimate CIs for these SMA slopes (Sokal & Rohlf, 1995). Classification of species into families and higher groupings followed phylogenies published by the Angiosperm Phylogeny Group (Soltis *et al.*, 1999), while generic delineation followed (Harden, 1990) and Flora of Australia (–, 1981). Additional resolution was obtained from consensus cladistic trees utilising either molecular or morphological data, both from recent publications and from unpublished trees provided kindly by taxonomists studying the relevant groups (further details available from the authors).

Results

LL vs LMA and its components (leaf thickness and density)

Leaf lifespan (LL) varied *c.* nine-fold, and leaf mass per area (LMA) six-fold, across the 75 perennial species. LL was positively associated with LMA within each site (Fig. 1a, Table 2), as were evolutionary divergences in the two traits (Table 3). Individual cross-species SMA slopes ranged from 1.2 to 2.1 but were deemed nonheterogeneous ($P = 0.072$),
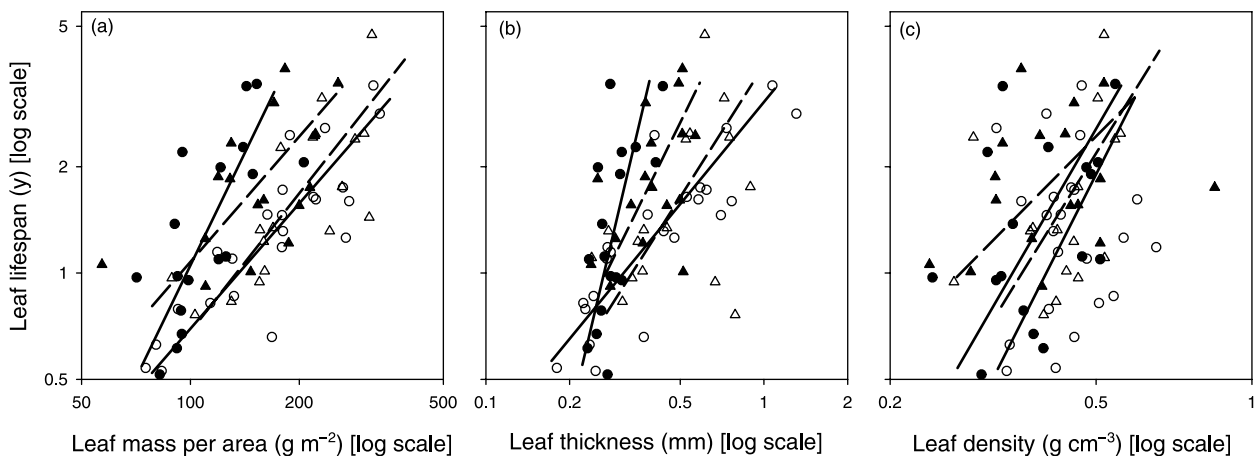
Fig. 1 Relationships between leaf lifespan (LL) and (a) leaf mass per area (LMA), (b) leaf thickness and (c) leaf tissue density. Filled symbols respresent high rainfall species, open symbols represent low rainfall species. Circles represent species at nutrient-rich sites, triangles represent species at nutrient-poor sites. Within each rainfall zone, the solid line indicates the Standardised Major Axis (SMA) slope for the nutrient-rich site, the dashed line the slope for the nutrient-poor site. Data for individual slopes given in Table 1. Tests for common slopes and elevation differences (where slopes nonheterogeneous, $P > 0.05$): (a) Slopes nonheterogeneous, $P = 0.072$, $\beta = 1.32$; Elevation: LL lower at a given LMA at low rain sites (comparisons at either soil nutrient level, $P < 0.005$). (b) Slopes heterogeneous, $P = 0.0001$; (c) Slopes nonheterogeneous, $P = 0.247$, $\beta = 2.31$; no differences in SMA elevations: all pairwise comparisons, $P > 0.09$.

Table 2 Data for cross-species Standardised Major Axis (SMA) slopes fitted within individual sites, corresponding to Figs 1–4. Data given are SMA slope (95% CI), r^2 and P-value from test for Pearson correlation between the trait pairs. Leaf lifespan: LL; leaf mass per area: LMA; W_{shear}: work to shear; N_{mass}: leaf N concentration

Traits	High rain, high soil nutrient	High rain, Low soil nutrient	Low rain, High soil nutrient	Low rain, Low soil nutrient
LL – LMA	2.1 (1.5, 3.1), 0.50, 0.001	1.2 (0.76, 1.8), 0.34, 0.014	1.2 (0.94, 1.5), 0.74, 1×10^{-7}	1.3 (0.93, 1.8), 0.59, 0.0002
LL – Thickness	3.3 (2.2, 5.1), 0.38, 0.008	1.6 (1.0, 2.5), 0.27, 0.033	0.96 (0.76, 1.2), 0.73, 2×10^{-7}	1.2 (0.84, 1.8), 0.48, 0.002
LL – Density	2.5 (1.6, 4.1), 0.14, 0.133	1.5 (0.89, 2.5), 0.06, 0.334	2.9 (1.9, 4.5), 0.003, 0.805	2.4 (1.4, 4.0), 0.01, 0.698
LL – W_{shear}	0.89 (0.59, 1.3), 0.41, 0.005	0.43 (0.28, 0.68), 0.28, 0.030	0.42 (0.31, 0.57), 0.52, 0.0001	0.51 (0.38, 0.69), 0.71, 2×10^{-5}
W_{shear} – LMA	2.4 (1.7, 3.4), 0.54, 0.001	2.7 (2.1, 3.5), 0.78, 3×10^{-6}	2.8 (2.1, 3.8), 0.53, 9×10^{-5}	2.8 (2.1, 3.8), 0.69, 4×10^{-5}
Toughness – Density	2.6 (1.7, 3.9), 0.38, 0.009	3.1 (2.2, 4.3), 0.62, 0.0002	5.1 (3.3, 7.9), 0.002, 0.848	3.8 (2.6, 5.7), 0.44, 0.004
N_{mass} – Toughness	−0.63 (−1.0, −0.39), 0.18, 0.087	−0.42 (−0.64, −0.28), 0.37, 0.010	−0.39 (−0.56, −0.26), 0.26, 0.014	−0.31 (−0.49, −0.20), 0.31, 0.020

Table 3 Data for correlated divergence analyses within individual sites. Data reported are SMA slope with no intercept term, 95% CIs, r^2 and P-values from model 1 test against a slope of 0. Note that confidence intervals are only approximate, being estimated from model 1 regression confidence intervals (Sokal & Rohlf, 1995)

Traits	High rain, high soil nutrient ($n = 14$)	High rain, Low soil nutrient ($n = 16$)	Low rain, High soil nutrient ($n = 17$)	Low rain, Low soil nutrient ($n = 14$)
LL – LMA	2.4 (1.3, 3.5), 0.38, 0.014	1.1 (0.6, 1.6), 0.29, 0.026	1.1 (0.7, 1.5), 0.58, 0.0003	1.8 (0.2, 2.4), 0.66, 0.0003
LL – thickness	2.9 (1.4, 4.5), 0.21, 0.085	1.4 (0.8, 2.1), 0.29, 0.026	1.1 (0.7, 1.5), 0.53, 0.001	1.3 (0.7, 1.8), 0.43, 0.008
LL – density	2.4 (1.0, 3.8), 0.06, 0.378	1.8 (0.8, 2.8), 0.003, 0.825	2.2 (1.1, 3.4), 0.06, 0.331	2.3 (1.0, 3.7), 0.03, 0.507
LL – W_{shear}	1.0 (0.5, 1.6), 0.26, 0.054	0.5 (0.2, 0.7), 0.23, 0.053	0.4 (0.2, 0.6), 0.29, 0.021	0.6 (0.4, 0.8), 0.62, 0.0005
W_{shear} – LMA	2.3 (1.1, 3.5), 0.25, 0.056	2.3 (1.7, 3.0), 0.75, 7×10^{-6}	2.6 (1.4, 3.7), 0.31, 0.016	3.1 (1.8, 4.4), 0.52, 0.002
Toughness – density	2.2 (1.0, 3.4), 0.19, 0.101	3.0 (1.6, 4.4), 0.26, 0.038	4.5 (2.2, 6.8), 0.05, 0.368	3.8 (2.0, 5.5), 0.38, 0.015
N_{mass} – toughness	−0.6 (−0.9, −0.3), 0.11, 0.234	0.4 (0.2, 0.6), 0.05, 0.403	−0.4 (−0.6, −0.2), 0.17, 0.105	−0.2 (−0.3, −0.1), 0.17, 0.128

with a common fitted slope of 1.3 (95% CI, 1.1–1.6). SMAs for high and low rainfall sites were clearly separated, such that LL at dry sites tended to be c. 40% shorter at a given LMA, or 30% higher LMA was seemingly required at dry sites to achieve a given LL (t-tests of Y′: nutrient-rich sites, $P = 4 \times 10^{-5}$; nutrient-poor sites, $P = 0.003$).

Of the two components of LMA, leaf thickness was more tightly correlated with LL than was tissue density. This was the case in both cross-species and correlated divergence analyses (Fig. 1b,c, Tables 2 and 3). Similarly, the elevation shifts in LL – LMA relationships between high and low-rain sites were driven more strongly by variation in leaf thickness than in density. That is, dry-site species tended to have thicker leaves at a given LL (although, since SMA slopes were heterogeneous, $P < 0.001$, shifts in elevation with rainfall could not be formally tested). There was no apparent separation of LL – density combinations according to site characteristics (Fig. 1c). On average, dry-site species had thicker leaves than high rainfall species (mean 0.45 vs 0.34 mm; t-test $P = 0.003$), but rather similar mean density (0.44 vs 0.40 g cm^{-3}; $P = 0.110$).

W$_{shear}$ vs LL and LMA

Average work to shear (W$_{shear}$) varied 87-fold between species. Within each site, leaves with higher W$_{shear}$ had higher LMA and achieved longer lifespans, both in cross-species and correlated divergence analyses (Fig. 2a,b; Tables 2 and 3). Individual LL – W$_{shear}$ slopes were heterogeneous ($P = 0.032$). However, after pooling species by rainfall zone, the slopes were nonheterogeneous ($P = 0.089$), and did not differ in elevation ($P = 0.300$). That is, the clouds of high and low rainfall points were not clearly separated in elevation as was the case for the LL – LMA or LL – leaf thickness relationships. By contrast, the SMA slopes for W$_{shear}$ vs LMA were separated by rainfall (Fig. 2b), with dry-site species having lower W$_{shear}$ at a given LMA (test for common slopes, $P = 0.888$, β = 2.7; t-tests for elevation differences within either soil nutrient class, $P < 1 \times 10^{-5}$). These key results contradicted our original assumption (see Introduction) that LMA could be considered a fair index of leaf strength, irrespective of habitat, thus the LL – W$_{shear}$ slopes would be separated by rainfall, similar to the LL – LMA slopes. The common slopes calculated across sites indicated that, within a given rainfall zone, a doubling in LMA was associated with a c. six-fold increase in leaf strength (common log-log slope of 2.7) yet only a c. 2.5-fold increase in LL (common slope of 1.3).

Toughness – density – leaf N relationships

Since leaf thickness is a component of both LMA and work to shear, the separation in LMA – W$_{shear}$ relationships according to site rainfall logically indicated a separation in density – toughness relationships between the rainfall zones (Fig. 3). Density and toughness were clearly correlated in three of four
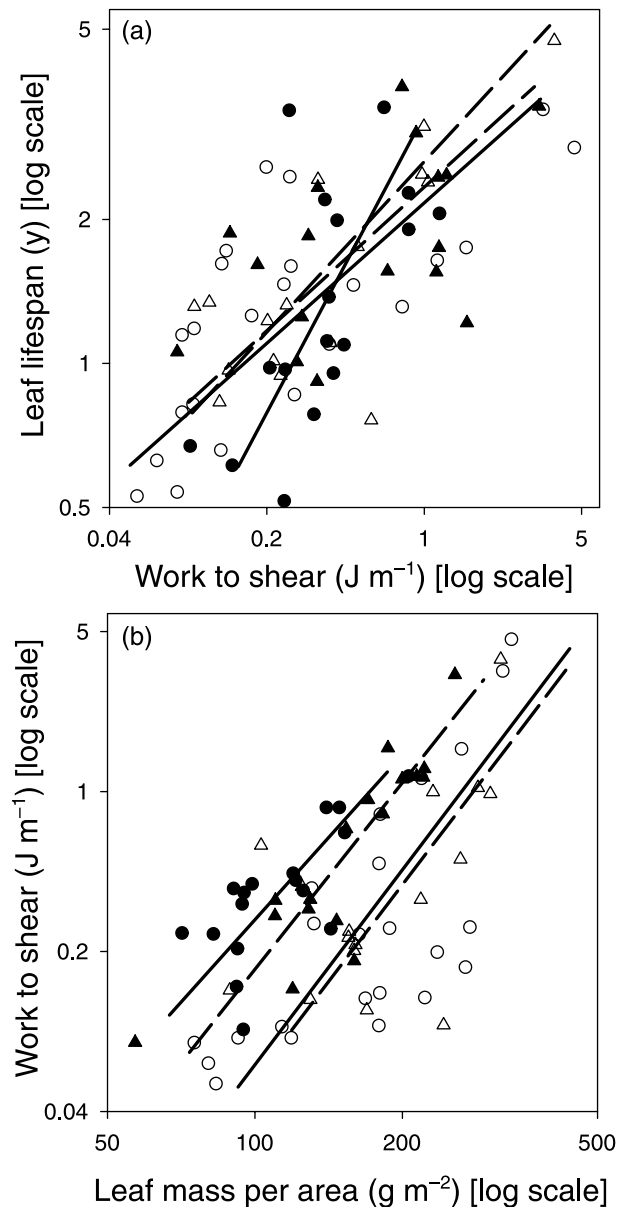
Fig. 2 Relationships between (a) leaf lifespan (LL) and work to shear (W$_{shear}$), and (b) W$_{shear}$ and leaf mass area (LMA). Filled symbols rrespresent high rainfall species, open symbols represent low rainfall species. Circles represent species at nutrient-rich sites, triangles represent species at nutrient-poor sites. Within each rainfall zone, the solid line indicates the Standardised Major Axis (SMA) slope for the nutrient-rich site, the dashed line the slope for the nutrient-poor site. Data for individual slopes given in Table 1. Tests for common slopes and elevation differences: (a) Slope heterogeneous, $P = 0.032$. Fitting common slopes within rainfall zones, slopes were non-heterogeneous ($P = 0.089$, β = 0.50), and did not differ in elevation ($P = 0.300$). (b) Slopes nonheterogeneous, $P = 0.888$, β = 2.70; Elevation: lower W$_{shear}$ at a given LMA for low rain species (comparisons at either soil nutrient level, $P < 1 \times 10^{-5}$).

sites ($r^2 = 0.38-0.62$), but not at the nutrient-rich, low rain site ($r^2 = 0.002$). Still, fitting a common SMA slope across the sites (justified on the basis of a test for slope heterogeneity, $P = 0.120$), indicated that tissue toughness was 2–3-fold

Fig. 3 Relationship between leaf toughness and density. Filled symbols represent high rainfall species, open symbols represent low rainfall species. Circles represent species at nutrient-rich sites, triangles represent species at nutrient-poor sites. Within each rainfall zone, the solid line indicates the Standardised Major Axis (SMA) slope for the nutrient-rich site, the dashed line the slope for the nutrient-poor site. Data for individual slopes given in Table 1. Slopes were nonheterogeneous, $P = 0.120$, $\beta = 3.42$. Toughness was lower at a given density for low rain species (comparisons at either soil nutrient level, $P < 0.001$).
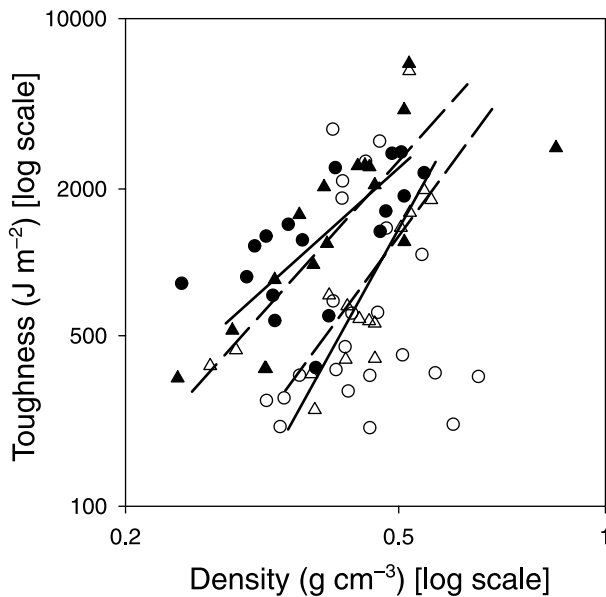
Fig. 4 Relationship between leaf N concentration (N_{mass}) and tissue toughness. Filled symbols represent high rainfall species, open symbols represent low rainfall species. Circles represent species at nutrient-rich sites, triangles represent species at nutrient-poor sites. Within each rainfall zone, the solid line indicates the Standardised Major Axis (SMA) slope for the nutrient-rich site, the dashed line the slope for the nutrient-poor site. Data for individual slopes given in Table 1. Slopes were nonheterogeneous, $P = 0.191$, $\beta = -0.41$. N_{mass} was higher at a given toughness for low rain species, comparing nutrient-poor sites only ($P = 0.024$).

greater at a given density for high rainfall species (t-tests for elevation shifts, all $P < 0.001$).

On average, leaves of low rainfall species were half as tough as those of high rainfall species (t-tests, $P < 0.05$ within either soil nutrient class), but had much higher leaf N, whether considered per unit mass (N_{mass}, 1.5-fold higher, $P < 0.01$ within either soil nutrient class) or per unit area (N_{area}, two-fold higher, $P < 0.001$ within either soil nutrient class). At all sites, leaves with higher N_{mass} were less tough (Fig. 4), as found previously by Coley (1983) and Loveless (1962), although weaker associations in correlated divergence analyses suggested that these trends were driven to some extent by differences between higher taxonomic groups (Table 3).

Discussion

Previously we found that LL – LMA relationships were shifted with site rainfall such that shorter LL was found for a given leaf mass per area at dry sites. We expected the same pattern to be seen when comparing LL with work to shear. Instead, LL – W_{shear} slopes were not separated by rainfall, yet the LMA – W_{shear} slopes were. Low rainfall species had lower W_{shear} at a given LMA, due to lower toughness at a given density. The low tissue toughness of dry-site species was associated with

their high nitrogen concentration. Below, we first discuss what may lie behind the shift in density – toughness relationships with site rainfall, and draw on supplementary data on leaf anatomy to further interpret the major patterns. Second, we discuss the apparent costs and benefits of a high LMA, high N strategy for species occurring in low rainfall zones.

Leaf tissue composition of high and low rainfall species

Many of the leaf traits common to species in dry habitats (e.g. thick, hard leaves with thick cuticles and small, thick walled cells) have been interpreted as increasing the ability of leaves to withstand high levels of desiccation without wilting, thereby avoiding the tissue and airspace compression which would slow or stop photosynthesis, or lead to leaf death (Small, 1973; Orians & Solbrig, 1977; Grubb, 1986; Turner, 1994; Cunningham *et al.*, 1999; Niinemets, 2001). Previously it has been shown that the concentration of cell wall, vascular tissue, fibre or sclerenchyma in a leaf is correlated with both tissue toughness (Choong *et al.*, 1992; Wright & Illius, 1995; Lucas *et al.*, 2000) and density (Garnier & Laurent, 1994; Roderick *et al.*, 1999). Thus, leaves of low rainfall species might be expected to be both

tougher and more dense than leaves of high rainfall species. This was not what was found for this set of species. Instead, we found that low rainfall leaves were on average about half as tough but similar in density to high rainfall leaves, and thus less tough at a given density. That a given density can result in a wide range of tissue toughness (Fig. 3) indicates that the configuration of cells and mixture of cell types can affect density and tissue toughness somewhat independently. For example, the toughness of tracheids and fibres is ten-fold greater than that expected from their cell wall concentration alone, since individual cells may be elongated with microfibrils directed uniformly at a small angle to the axis of the cell (Lucas *et al.*, 2000).

The similar mean density but lower toughness of the dry-site species under study here suggests that they had a greater proportion of low toughness tissue type(s) in their leaves. Their higher leaf N, considered on either a mass or area basis, suggests that this might predominantly have been mesophyll tissue. Some tentative support for this prospective explanation can be found from overlap with datasets in which the depths of different tissue types in leaves were estimated from transverse leaf sections (Cunningham *et al.*, 1999, D. H. Duncan & M. Westoby, unpublished results). For the 23 species in common between these datasets and ours (17 at high rain, six at low rain), low rainfall species had approximately twice as high leaf N per area (N_{area}; *t*-test, $P < 0.0001$) and twice as thick palisade mesophyll ($P = 0.036$), although the proportion of palisade was not significantly higher (59% vs 45%, $P = 0.321$).

It may be that the trends we report for species in eastern Australia are quite common differences between high and low rainfall perennial species. Although leaf strength has not been measured for large numbers of species worldwide, the tendency for leaf density, thickness and LMA to increase with site aridity is well known (Maximov, 1929; Mooney *et al.*, 1978; Specht & Specht, 1989; Schulze *et al.*, 1998; Cunningham *et al.*, 1999; Niinemets, 2001). Higher mean N_{area} with increasing aridity is also probably quite general, being reported by Cunningham *et al.* (1999), for example, and implicit in the fact that low rainfall species tend to have high LMA in combination with similar (if not higher) N_{mass} to high rainfall species (Killingbeck & Whitford, 1996). In the next section we focus on the apparent benefits of deploying high N_{area} leaves in low rainfall, low humidity habitats.

Costs and benefits of a high LMA, high leaf N strategy at low rainfall

In general, the construction cost per gram of leaf does not vary systematically with either LMA (Chapin, 1989; Poorter & De Jong, 1999) or LL (Villar & Merino, 2001). This implies that the (generally) higher LMA leaves of dry-site species are more expensive to build *per unit leaf area* than leaves of high rainfall species. Constructing leaves with high N_{area} may incur

additional costs – in terms of higher respiratory costs for protein turnover (Wright *et al.*, 2001), higher costs from N acquisition and, quite possibly, additional costs related to the increased attractiveness to herbivores of high N leaves. On the other hand, deploying high N_{area} leaves in low rainfall habitats seems to have substantial benefits. First, in terms of maximising use of the typically high irradiance in such places (Cunningham *et al.*, 1999; Roderick *et al.*, 2000; Niinemets, 2001), but – and we would argue, more importantly – high N_{area} appears to have particularly significant benefits in terms of enhancing water conservation during photosynthesis (Field *et al.*, 1983; Mooney *et al.*, 1978; Wright *et al.*, 2001). If high N_{area} is generally linked with low leaf tissue toughness, as was found for low rainfall species in this study, this implies that the economics of N and water use are intrinsically linked with the dry-mass economics of leaf construction (LMA) and LL.

The way in which adaptations of low rainfall species can be understood in terms of this argument is illustrated in Fig. 5. Both transpiration and photosynthesis approximately follow Fick's Law for the diffusion of gases through a surface: transpiration (E) = leaf-to-air vapour pressure deficit (VPD) × stomatal conductance to water (G_s); and photosynthesis (A_{area}) = $G_c(c_a - c_i)$, where G_c is stomatal conductance to CO_2, and c_a and c_i are ambient and leaf internal CO_2 concentrations, respectively (Lambers *et al.*, 1998). Low rainfall sites are characterised by low atmospheric humidity, hence high leaf-to-air vapour pressure deficits (high VPD), and thus higher transpiration rate (E) at a given stomatal conductance to water (G_s; box 2 in Fig. 5). Since G_c and G_s are related by a constant (the molar diffusion ratio between CO_2 and water), this implies higher transpirational water loss for a given G_c also. Consequently, more water would be used for a given $A_{area} : G_c$, that is *all else being equal*, the water use efficiency ($A_{area} : E$) of dry-site species would be lower (Fig. 5, box 3).

On the other hand, we have found that low rainfall species have *c.* two-fold higher N_{area} than high rainfall species (Fig. 5, box 4), and substantially higher A_{area} at a given G_c (but not higher average A_{area}; Wright *et al.*, 2001). Higher $A_{area} : G_c$ indicates a larger drawdown of internal CO_2 (Fig. 5, boxes 5, 6) which, presumably, was possible via higher photosynthetic enzyme content, as indicated by high N_{area}. *All else being equal*, this would confer higher water use efficiency (Fig. 5, box 7). Instead however, this tendency and the tendency towards lower WUE as a result of the higher leaf-to-air VPD at low rainfall (Fig. 5, box 3) appear to cancel each other out, resulting in little or no net difference in WUE between low and high rainfall species (Wright *et al.*, 2001; Fig. 5, box 8).

As described above, thicker mesophyll in leaves of dry-site species, inferred from higher leaf N, led to lower tissue toughness (Fig. 5, box 9). At a given leaf thickness, lower toughness translates into lower W_{shear} (since W_{shear} = thickness × toughness; Fig. 5, box 10), which presumably should lead to shorter LL (Fig. 5, box 11). However, dry-site
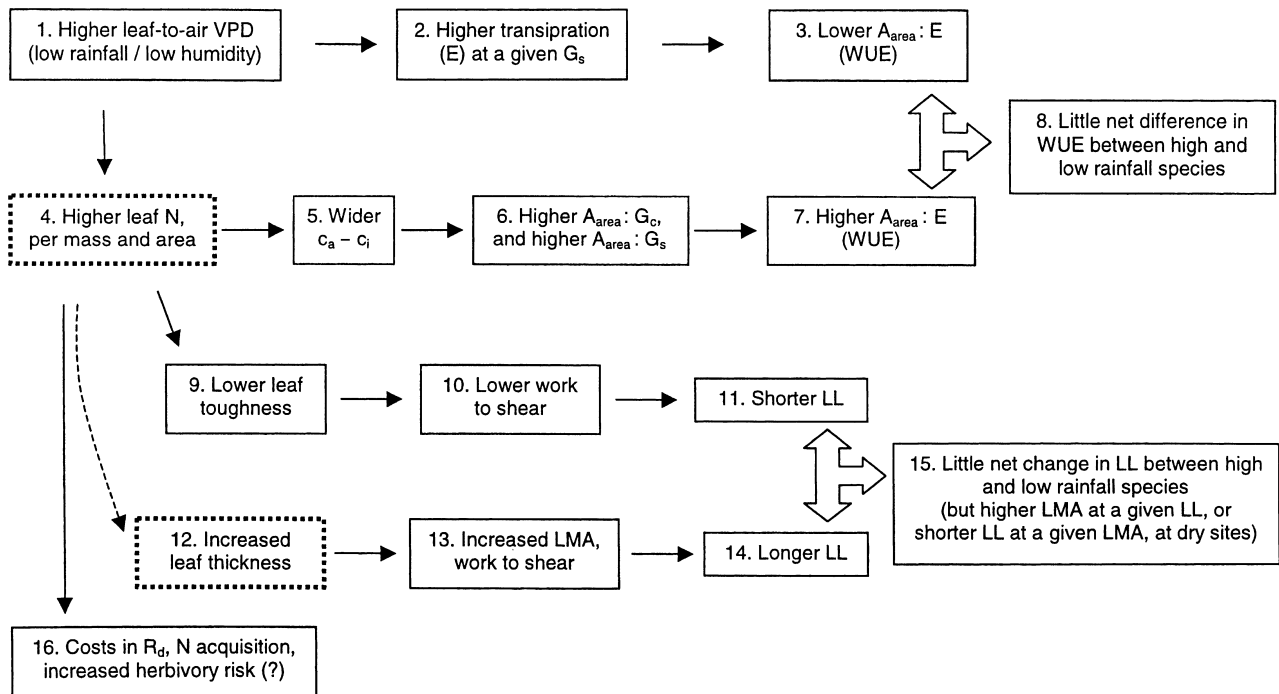
Fig. 5 Flow chart illustrating the hypothesised evolutionary adaptations of low rainfall species (higher leaf N_{mass} and N_{area}, and thicker, high LMA leaves), and the physiological/anatomical consequences of low rainfall and these adaptations. A_{area} : photosynthetic capacity per leaf area; E : transpiration; VPD : leaf-to-air vapour pressure deficit; G_c, G_s: stomatal conductance to CO_2, and to water ($G_c \propto G_s$); $c_a - c_i$: CO_2 differential between outside and inside a leaf; R_d : dark respiration.

species tended to have thicker leaves (Fig. 5, box 12). At a given tissue toughness, thicker leaves would have higher W_{shear} (Fig. 5, box 13), which would tend to increase LL (Fig. 5, box 14). These countervailing trends (increased thickness, decreased toughness) apparently buffer each other, resulting in little or no net difference in mean W_{shear} and LL, comparing high and low rainfall species. However, dry-site species tended to have higher LMA because of their thicker leaves, and thus higher LMA at a given W_{shear} or LL or, equally, lower W_{shear} and LL at a given LMA (Fig. 5, box 15).

Conclusions

At all sites, variation in LL was quite tightly associated with variation in leaf mass per area, leaf thickness and leaf strength (as estimated by W_{shear}). This was true considering the relationships across species as well as in correlated divergence analyses. Our initial assumption (see Introduction) was that harsher environmental conditions at low rainfall sites would lead to shorter LL at a given W_{shear}, just as LL was shorter at a given LMA, the chief pattern under investigation in this study. However, we found no clear separation in LL – W_{shear} relationships with rainfall, since LMA did not represent the engineering strength of a leaf equally for high and low rain species. This did appear to relate back to the harsher conditions at low rainfall sites but, instead of in the assumed manner, via the high N, water conservation strategy of low

rainfall species. The costs of this strategy are multiple (Fig. 5, box 16). Their high LMA leaves have greater construction costs per leaf area, yet a shorter revenue stream (shorter lifespan) for a given LMA. Their high N content is linked with higher rates of dark respiration and, possibly, additional costs for N acquisition and herbivory-risk (Wright *et al.*, 2001). Still, it appears that these costs trade off against the benefits of water conservation associated with high N_{area}, building an integrated picture between the physical traits of leaves, their lifespan and their physiology, and the environment in which species occur.

References

Ackerly DD. 1996. Canopy structure and dynamics: integration of growth processes in tropical pioneer trees. In: Mulkey SS, Chazdon RL, Smith AP, eds. *Tropical Forest Plant Ecophysiology.* New York, USA: Chapman & Hall, 619–658.

Aerts R, Chapin FS. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* **30**: 1–67.

Aranwela N, Sanson G, Read J. 1999. Methods of assessing leaf-fracture properties. *New Phytologist* **144**: 369–393.

Chabot BF, Hicks DJ. 1982. The ecology of leaf life spans. *Annual Review of Ecology and Systematics* **13**: 229–259.

Chapin FS. 1989. The cost of tundra plant structures: evaluation of concepts and currencies. *American Naturalist* **133**: 1–19.

Cherrett JM. 1968. A simple penetrometer for measuring leaf toughness in insect feeding studies. *Economic Entomology* **61**: 1736–1738.

Choong MF. 1996. What makes a leaf tough and how this affects the pattern of *Castanopsis fissa* leaf consumption by caterpillars. *Functional Ecology* **10**: 668–674.

Choong MF, Lucas PW, Ong JSY, Pereira B, Tan HTW, Turner IM. 1992. Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytologist* **121**: 597–610.

Coley PD. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* **53**: 209–233.

Coley PD. 1987. Interspecific variation in plant anti-herbivore properties: the role of habitat quality and rate of disturbance. *New Phytologist* **106**: 251–263.

Coley PD. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* **74**: 531–536.

Cornelissen JHC, Perez-Harguindeguy N, Diaz S, Grime JP, Marzano B, Cabido M, Vendramini F, Cerabolini B. 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist.* **143**: 191–200.

Cornelissen JHC, Thompson K. 1997. Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytologist* **135**: 109–114.

Cunningham SA, Summerhayes B, Westoby M. 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecological Monographs* **69**: 569–588.

Darvell BW, Lee PKD, Yuen TDB, Lucas PW. 1996. A portable fracture toughness tester for biological materials. *Measurement Science and Technology* **7**: 954–962.

Diemer M. 1998a. Leaf lifespans and dynamics of leaves of herbaceous perennials in high-elevation environments – news from the elephant's leg. *Functional Ecology* **12**: 413–425.

Diemer M. 1998b. LLs of high-elevation, aseasonal Andean shrub species in relation to leaf traits and leaf habit. *Global Ecology and Biogeography Letters* **7**: 457–465.

Eckstein RL, Karlsson PS, Weih M. 1999. Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytologist.* **143**: 177–189.

Edwards C, Read J, Sanson GD. 2000. Characterising sclerophylly: some mechanical properties of leaves from heath and forest. *Oecologia* **123**: 158–167.

Escudero A, del Arco JM, Sanz IC, Ayala J. 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients. *Oecologia* **90**: 80–87.

Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**: 1–15.

Field C, Merino J, Mooney HA. 1983. Compromises between water use efficiency and nitrogen use efficiency in five species of California evergreens. *Oecologia* **60**: 384–389.

Field C, Mooney HA. 1986. The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ, ed. *On the Economy of Plant Form and Function.* New York: Cambridge University Press, 25–55.

Garnier E, Laurent G. 1994. Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. *New Phytologist* **128**: 725–736.

Grafen A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London B* **326**: 119–157.

Grubb PJ. 1986. Sclerophylls, pachyphylls and pycnophylls: the nature and significance of hard leaf surfaces. In: Juniper BE, Southwood TRE, eds. *Insects and the Plant Surface.* London, UK: Edward Arnold, 137–150.

Harden GJ. 1990. *Flora of NSW.* Sydney, Australia: Royal Botanical Gardens.

Harvey PH, Pagel MD. 1991. *The Comparative Method in Evolutionary Biology.* Oxford, UK: Oxford University Press.

Hendry GAF, Grime JP. 1993. *Methods in Comparative Plant Ecology: a Laboratory Manual.* London, UK: Chapman & Hall.

Hochuli DF. 1996. The ecology of plant/insect interactions – implications of digestive strategy for feeding by phytophagous insects. *Oikos* **75**: 133–141.

Killingbeck KT, Whitford WG. 1996. High foliar nitrogen in desert shrubs: an important ecosystem trait or defective desert doctrine? *Ecology* **77**: 1728–1737.

Lambers H, Chapin FS, Pons TL. 1998. *Plant Physiological Ecology.* New York, USA: Springer-Verlag.

Loveless AR. 1962. Further evidence to support a nutritional interpretation of sclerophylly. *Annals of Botany* **26**: 551–561.

Lucas PW, Turner IM, Dominy NJ, Yamashita N. 2000. Mechanical defences to herbivory. *Annals of Botany* **86**: 913–920.

Maximov NA. 1929. *The Plant in Relation to Water. A Study of the Physiological Basis of Drought Resistance.* London, UK: Allen & Unwin.

Mooney HA, Ferrar PJ, Slatyer RO. 1978. Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus. Oecologia* **36**: 103–111.

Niinemets U. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **82**: 453–469.

Ohmart CP, Stewart LG, Thomas JR. 1985. Effects of food quality particularly nitrogen concentrations of *Eucalyptus blakelyi* foliage on the growth of *Paropsis atomaria* larvae (Coleoptera: Chrysomelidae). *Oecologia* **65**: 543–549.

Orians GH, Solbrig OT. 1977. A cost-income model of leaves and roots with special reference to arid and semiarid area. *American Naturalist* **111**: 677–690.

Parkhurst DF. 1994. Diffusion of CO_2 and other gases inside leaves. *New Phytologist* **126**: 449–479.

Pitman ETG. 1939. A note on normal correlation. *Biometrika* **31**: 9–12.

Poorter H, De Jong R. 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* **143**: 163–176.

Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology.* **80**: 1955–1969.

Reich PB, Uhl C, Walters MB, Ellsworth DS. 1991. Leaf lifespans as a determinant of leaf structure and function among 23 amazonian tree species. *Oecologia* **86**: 16–24.

Reich PB, Walters MB, Ellsworth DS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**: 365–392.

Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* **94**: 13730–13734.

Roderick ML, Berry SL, Noble IR. 2000. A framework for understanding the relationship between environment and vegetation based on the surface area to volume ratio of leaves. *Functional Ecology* **14**: 423–437.

Roderick ML, Berry SL, Noble IR, Farquhar GD. 1999. A theoretical approach to linking the composition and morphology with the function of leaves. *Functional Ecology* **13**: 683–695.

Ryser P, Urbas P. 2000. Ecological significance of leaf life span among Central European grass species. *Oikos* **91**: 41–50.

Schulze ED, Williams RJ, Farquhar GD, Schulze W, Langridge J, Miller JM, Walker BH. 1998. Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Australian Journal of Plant Physiology* **25**: 413–425.

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Phytologist

Small E. 1973. Xeromorphy in plants as a possible basis for migration between arid and nutritionally deficient environments. *Botaniska Notiser* **126**: 534–539.

Sokal RR, Rohlf FJ. 1995. *Biometry: the Principles and Practice of Statistics in Biological Research.* New York, USA: W.H. Freeman.

Soltis PS, Soltis DE, Chase MW. 1999. Angiosperm phylogeny inferred from multiple genes as a tool for comparative biology. *Nature* **402**: 402–404.

Southwood TRE, Brown VK, Reader PM. 1986. Leaf palatability, life expectancy and herbivore damage. *Oecologia* **70**: 544–548.

Specht RL, Specht A. 1989. Canopy structure in *Eucalyptus*-dominated communities in Australia along climatic gradients. *Acta Oecologica, Oecologia Plantarum* **10**: 191–213.

Turner IM. 1994. Sclerophylly: primarily protective? *Functional Ecology* **8**: 669–675.

Villar R, Merino J. 2001. Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems. *New Phytologist* **151**: 213–226.

Vincent FV. 1992. *Biomechanics-Materials: A Practical Approach.* Oxford, UK: Oxford University Press.

Vogel SV. 1988. *Life's Devices: the Physical World of Animals and Plants.* Princeton, NJ, USA: Princeton University Press.

Warton DI, Weber NC. 2002. Common slope tests for bivariate errors-in-variables models. *Biometrical Journal* **44**: 161–174.

Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**: 213–227.

Westoby M, Cunningham SA, Fonseca C, Overton J, Wright IJ. 1998. Phylogeny and variation in light capture area deployed per unit investment in leaves: designs for selecting study species with a view to generalizing. In: Lambers H, Poorter H, van Vuuren MMI, eds. *Variation in Growth Rate and Productivity of Higher Plants.* Leiden, The Netherlands: Backhuys Publishers, 539–566.

Wright IJ, Cannon K. 2001. Relationships between leaf lifespan and structural defences in a low nutrient, sclerophyll flora. *Functional Ecology* **15**: 351–359.

Wright W, Illius AW. 1995. A comparative study of the fracture properties of five grasses. *Functional Ecology* **9**: 269–278.

Wright IJ, Reich PB, Westoby M. 2001. Strategy-shifts in leaf physiology, structure and nutrient content between species of high and low rainfall, and high and low nutrient habitats. *Functional Ecology* **15**: 423–434.

Wright IJ, Westoby M, Reich PB. 2002. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf lifespan. *Journal of Ecology* **90**: 534–543.

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Appendix

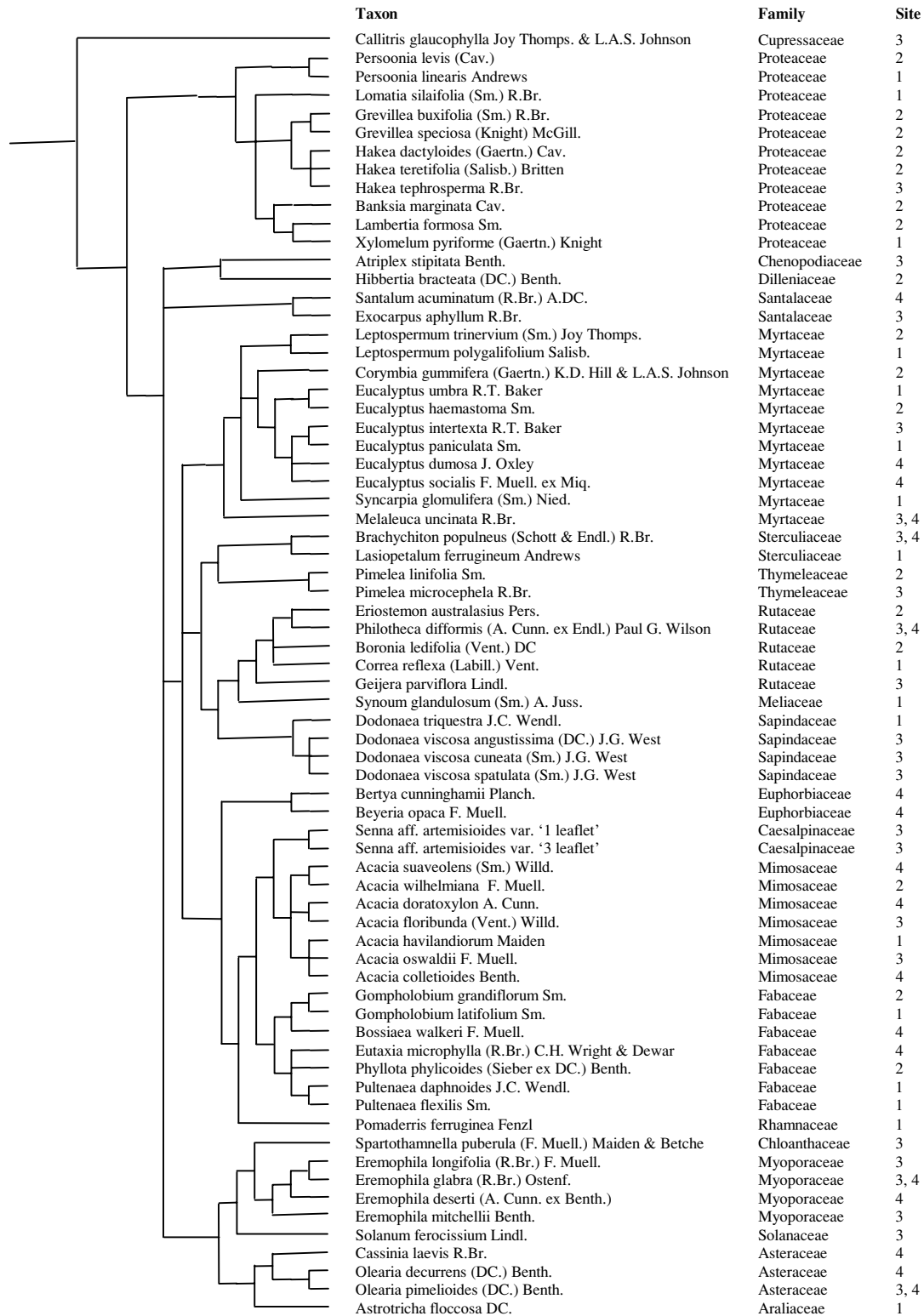| Taxon	Family	Site
Callitris glaucophylla Joy Thomps. & L.A.S. Johnson	Cupressaceae	3
Persoonia levis (Cav.)	Proteaceae	2
Persoonia linearis Andrews	Proteaceae	1
Lomatia silaifolia (Sm.) R.Br.	Proteaceae	1
Grevillea buxifolia (Sm.) R.Br.	Proteaceae	2
Grevillea speciosa (Knight) McGill.	Proteaceae	2
Hakea dactyloides (Gaertn.) Cav.	Proteaceae	2
Hakea teretifolia (Salisb.) Britten	Proteaceae	2
Hakea tephrosperma R.Br.	Proteaceae	3
Banksia marginata Cav.	Proteaceae	2
Lambertia formosa Sm.	Proteaceae	2
Xylomelum pyriforme (Gaertn.) Knight	Proteaceae	1
Atriplex stipitata Benth.	Chenopodiaceae	3
Hibbertia bracteata (DC.) Benth.	Dilleniaceae	2
Santalum acuminatum (R.Br.) A.DC.	Santalaceae	4
Exocarpus aphyllum R.Br.	Santalaceae	3
Leptospermum trinervium (Sm.) Joy Thomps.	Myrtaceae	2
Leptospermum polygalifolium Salisb.	Myrtaceae	1
Corymbia gummifera (Gaertn.) K.D. Hill & L.A.S. Johnson	Myrtaceae	2
Eucalyptus umbra R.T. Baker	Myrtaceae	1
Eucalyptus haemastoma Sm.	Myrtaceae	2
Eucalyptus intertexta R.T. Baker	Myrtaceae	3
Eucalyptus paniculata Sm.	Myrtaceae	1
Eucalyptus dumosa J. Oxley	Myrtaceae	4
Eucalyptus socialis F. Muell. ex Miq.	Myrtaceae	4
Syncarpia glomulifera (Sm.) Nied.	Myrtaceae	1
Melaleuca uncinata R.Br.	Myrtaceae	3, 4
Brachychiton populneus (Schott & Endl.) R.Br.	Sterculiaceae	3, 4
Lasiopetalum ferrugineum Andrews	Sterculiaceae	1
Pimelea linifolia Sm.	Thymeleaceae	2
Pimelea microcephela R.Br.	Thymeleaceae	3
Eriostemon australasius Pers.	Rutaceae	2
Philotheca difformis (A. Cunn. ex Endl.) Paul G. Wilson	Rutaceae	3, 4
Boronia ledifolia (Vent.) DC	Rutaceae	2
Correa reflexa (Labill.) Vent.	Rutaceae	1
Geijera parviflora Lindl.	Rutaceae	3
Synoum glandulosum (Sm.) A. Juss.	Meliaceae	1
Dodonaea triquestra J.C. Wendl.	Sapindaceae	1
Dodonaea viscosa angustissima (DC.) J.G. West	Sapindaceae	3
Dodonaea viscosa cuneata (Sm.) J.G. West	Sapindaceae	3
Dodonaea viscosa spatulata (Sm.) J.G. West	Sapindaceae	3
Bertya cunninghamii Planch.	Euphorbiaceae	4
Beyeria opaca F. Muell.	Euphorbiaceae	4
Senna aff. artemisioides var. '1 leaflet'	Caesalpinaceae	3
Senna aff. artemisioides var. '3 leaflet'	Caesalpinaceae	3
Acacia suaveolens (Sm.) Willd.	Mimosaceae	4
Acacia wilhelmiana F. Muell.	Mimosaceae	2
Acacia doratoxylon A. Cunn.	Mimosaceae	4
Acacia floribunda (Vent.) Willd.	Mimosaceae	3
Acacia havilandiorum Maiden	Mimosaceae	1
Acacia oswaldii F. Muell.	Mimosaceae	3
Acacia colletioides Benth.	Mimosaceae	4
Gompholobium grandiflorum Sm.	Fabaceae	2
Gompholobium latifolium Sm.	Fabaceae	1
Bossiaea walkeri F. Muell.	Fabaceae	4
Eutaxia microphylla (R.Br.) C.H. Wright & Dewar	Fabaceae	4
Phyllota phylicoides (Sieber ex DC.) Benth.	Fabaceae	2
Pultenaea daphnoides J.C. Wendl.	Fabaceae	1
Pultenaea flexilis Sm.	Fabaceae	1
Pomaderris ferruginea Fenzl	Rhamnaceae	1
Spartothamnella puberula (F. Muell.) Maiden & Betche	Chloanthaceae	3
Eremophila longifolia (R.Br.) F. Muell.	Myoporaceae	3
Eremophila glabra (R.Br.) Ostenf.	Myoporaceae	3, 4
Eremophila deserti (A. Cunn. ex Benth.)	Myoporaceae	4
Eremophila mitchellii Benth.	Myoporaceae	3
Solanum ferocissium Lindl.	Solanaceae	3
Cassinia laevis R.Br.	Asteraceae	4
Olearia decurrens (DC.) Benth.	Asteraceae	4
Olearia pimelioides (DC.) Benth.	Asteraceae	3, 4
Astrotricha floccosa DC.	Araliaceae	1

Fig. A1 Phylogeny of the 75 study species. Site codes: 1 High rain, high soil P; 2 High rain, low soil P; 3 Low rain, high soil P; 4 Low rain, low soil P.

Table A1 Trait values for the study species. Abbreviations: leaf lifespan (LL), leaf mass per area (LMA), work to shear (W_{shear})

Site and species	LL (y)	LMA (g m^{-2})	Density (g cm^{-3})	Thickness (mm)	W_{shear} (J m^{-1})	Toughness (J m^{-2})	Leaf N (%)
High rainfall, high soil P							
Acacia floribunda	1.11	125.5	0.47	0.27	0.37	1341	2.31
Astrotricha floccosa	0.52	82.3	0.30	0.27	0.24	873	1.59
Correa reflexa	0.97	71.0	0.24	0.29	0.24	821	1.26
Dodonaea triquetra	0.67	94.7	0.38	0.25	0.09	370	1.90
Eucalyptus paniculata	1.09	119.7	0.51	0.24	0.44	1872	1.08
Eucalyptus umbra	2.06	205.8	0.50	0.41	1.17	2837	0.91
Gompholobium latifolium	2.20	95.0	0.31	0.31	0.36	1169	1.71
Lasiopetalum ferrugineum	1.99	121.2	0.48	0.25	0.41	1626	1.16
Leptospermum polygalifolium	0.61	91.8	0.40	0.23	0.14	604	1.31
Lomatia silaifolia	2.27	139.9	0.40	0.35	0.85	2446	0.62
Persoonia linearis	3.38	142.9	0.33	0.43	0.25	578	0.77
Pomaderris ferruginea	0.96	98.7	0.32	0.31	0.39	1282	1.28
Pultenea daphnoides	0.78	94.1	0.36	0.26	0.32	1236	1.95
Pultenea flexilis	1.38	90.5	0.35	0.26	0.38	1434	2.04
Synoum glandulosum	0.98	92.1	0.33	0.28	0.21	733	1.59
Syncarpia glomulifera	1.91	148.7	0.49	0.30	0.85	2801	0.98
Xylomelum pyriforme	3.43	152.5	0.54	0.28	0.66	2332	0.87
High rainfall, low soil P							
Acacia suaveolens	2.45	220.5	0.39	0.57	1.15	2036	1.91
Banksia marginata	3.03	170.2	0.45	0.38	0.92	2459	0.85
Boronia ledifolia	1.61	159.4	0.32	0.50	0.18	366	1.19
Corymbia gummifera	1.22	186.9	0.51	0.37	1.55	4213	0.81
Eriostemon australasius	1.01	146.7	0.29	0.51	0.27	526	1.20
Eucalyptus haemostoma	1.55	199.8	0.45	0.45	1.13	2498	1.04
Gompholobium grandiflorum	2.33	129.7	0.33	0.39	0.34	848	1.23
Grevillea buxifolia	1.25	109.9	0.38	0.29	0.29	978	0.71
Grevillea speciosa	1.56	153.6	0.46	0.33	0.69	2075	0.86
Hakea dactyloides	3.45	255.8	0.52	0.49	3.24	6529	0.53
Hakea teretifolia	1.75	213.9	0.85	0.40	1.16	2946	0.52
Hibbertia bracteata	0.92	110.1	0.39	0.28	0.33	1193	1.04
Lambertia formosa	2.48	221.6	0.44	0.51	1.26	2485	0.60
Leptospermum trinervium	1.85	128.6	0.51	0.25	0.31	1213	0.85
Persoonia levis	3.79	182.4	0.36	0.51	0.80	1567	0.59
Phyllota phylicoides	1.87	119.4	0.32	0.37	0.14	366	1.24
Pimelea linifolia	1.06	56.9	0.24	0.24	0.08	335	1.48
Low rainfall, high soil P							
Acacia doratoxylon	1.64	218.8	0.41	0.53	1.14	2161	2.01
Acacia oswaldii	1.75	264.2	0.45	0.59	1.54	2601	1.84
Atriplex stipitata	0.53	83.3	0.34	0.25	0.05	212	2.90
Brachychiton populneus	1.10	130.5	0.48	0.27	0.38	1384	1.79
Callitris glaucophylla	2.58	235.6	0.32	0.73	0.20	272	1.20
Dodonaea viscosa ssp. angustissima	0.66	168.0	0.45	0.37	0.12	344	1.86
Dodonaea viscosa ssp. cuneata	0.82	113.4	0.51	0.22	0.09	418	1.98
Dodonaea viscosa ssp. spatulata	0.86	131.9	0.54	0.24	0.26	1079	1.98
Eremophila glabra	1.46	163.3	0.43	0.38	0.24	620	1.69
Eremophila longifolia	1.26	269.1	0.57	0.48	0.17	353	1.46
Eremophila mitchelli	1.18	179.1	0.65	0.27	0.10	340	1.86
Eucalyptus intertexta	1.31	180.3	0.41	0.44	0.80	1835	1.47
Exocarpos aphyllus	2.83	333.9	0.40	1.31	4.64	3522	1.07
Geijera parviflora	2.46	188.3	0.47	0.40	0.25	624	1.70
Hakea tephrosperma	3.40	320.5	0.47	1.07	3.37	3144	0.73
Melaleuca uncinata	1.46	179.1	0.40	0.70	0.49	695	1.27
Olearia pimelioides	1.15	118.7	0.42	0.28	0.08	297	2.45
Philotheca difformis	1.60	274.6	0.36	0.77	0.26	344	1.48
Pimelea microcephala	0.63	80.4	0.34	0.24	0.06	278	3.08
Senna artemisioides var 1lft	1.62	222.2	0.60	0.58	0.13	217	1.99
Senna artemisioides var 3lft	1.72	179.8	0.45	0.62	0.13	210	1.73

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Table A1 *Continued*

Site and species	LL (y)	LMA (g m^{-2})	Density (g cm^{-3})	Thickness (mm)	W$_{shear}$ (J m^{-1})	Toughness (J m^{-2})	Leaf N (%)
Solanum ferocissium	0.54	75.2	0.42	0.18	0.08	451	3.27
Spartothamnella puberula	0.79	92.4	0.41	0.23	0.08	363	2.96
Low rainfall, low soil P							
Acacia colletioides	3.13	230.8	0.50	0.72	1.00	1388	1.79
Acacia havilandii	1.75	262.7	0.46	0.89	0.51	562	1.46
Acacia wilhelmiana	1.01	160.3	0.44	0.37	0.21	586	1.89
Bertya cunninghamii	1.34	169.1	0.38	0.45	0.11	248	1.91
Beyeria opaca	1.23	159.4	0.45	0.35	0.20	574	1.72
Bossiaea walkeri	4.73	317.4	0.52	0.61	3.78	6097	1.21
Brachychiton populneus	1.10	124.7	0.52	0.24	0.38	1600	1.55
Cassinia laevis	0.83	129.8	0.42	0.31	0.12	400	1.85
Eremophila deserti	2.42	218.0	0.29	0.75	0.34	437	1.59
Eremophila glabra	1.32	155.8	0.42	0.37	0.24	661	1.83
Eucalyptus dumosa	2.49	302.3	0.56	0.54	0.98	1804	0.91
Eucalyptus socialis	2.39	285.0	0.54	0.52	1.04	1982	1.22
Eutaxia microphylla	0.97	88.8	1.89				
Melaleuca uncinata	1.32	242.7	0.55	0.69	0.55	795	1.15
Olearia decurrens	0.94	155.2	0.46	0.34	0.14	403	1.72
Olearia pimelioides	0.76	103.0	0.37	0.28	0.10	348	2.33
Philotheca difformis	2.27	177.6	0.27	0.67	0.23	376	1.37
Santalum acuminatum	**1.44**	**312.0**	**0.40**	**0.79**	**0.58**	**733**	**1.00**