Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span

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Summary

1 Leaf life span (LL) and leaf mass per area (LMA) are fundamental traits in the carbon economy of plants, representing the investment required per unit leaf area (LMA) and the duration of the resulting benefit (LL). Species on dry and infertile soils converge towards higher LMA. It has been generally assumed that this allows species from low-resource habitats to achieve longer average leaf life spans, as LMA and LL are often correlated.

2 Leaf life span and LMA were measured for 75 perennial species from eastern Australia. Species were sampled from nutrient-rich and nutrient-poor sites within high and low rainfall regions. LL and LMA were positively correlated across species within each site. In addition, evolutionary divergences in LL and LMA were correlated within each site, indicating that cross-species relationships were not simply driven by differences between higher taxonomic groups.

3 Within a rainfall zone, LL–LMA combinations shifted as expected along common axes of variation such that species on poorer soils had higher LMA and longer LL, but significantly so only at high rainfall.

4 Low rainfall species were expected to have shorter LL at a given LMA or, equally, require higher LMA to achieve a given LL, i.e. shift to a parallel axis of variation, and this was observed on both nutrient-rich and nutrient-poor soils. On average, 30% higher LMA was seemingly required at dry sites to achieve a given LL. Thus, convergence towards higher LMA has different consequences for leaf life span in dry and nutrient-poor habitats.

5 The broad shifts in LL–LMA combinations between site types were also seen when comparing closely related species-pairs (phylogenetically independent contrasts) occurring on nutrient-rich and nutrient-poor soils (within each rainfall zone), and at high- and low-rainfall sites (at each soil nutrient level).

Key-words: adaptation, leaf life span, phylogenetic analysis, sclerophylly, specific leaf area

Journal of Ecology (2002) **90**, 534–543

Introduction

On average, perennial species in dry and nutrient-poor habitats have thicker or tougher (more sclerophyllous) leaves than those occurring in more resource-rich habitats (Beadle 1966; Chapin 1980; Fonseca *et al.* 2000). A widely used descriptor of this convergence in leaf form is leaf mass per area (LMA, the inverse of specific leaf area, SLA), which is itself the product of leaf thickness and dry matter concentration, DMC (Witkowski & Lamont 1991). High LMA species have been shown

to achieve greater average leaf life spans (LL) in a variety of habitats (Reich *et al.* 1997; Diemer 1998; Ryser & Urbas 2000). It is thought that structural reinforcement confers longer leaf life span by rendering leaves more tolerant of physical hazards and herbivory (Chabot & Hicks 1982; Grubb 1986; Wright & Cannon 2001). However, leaf chemistry also plays a role in defence, with long leaf life span sometimes correlated with greater allocation to tannins, phenols or other defensive compounds (Coley 1988).

LMA and leaf life span are pivotal traits 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

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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 leaf life span indicating a longer duration of the revenue stream from that investment (Westoby 1998), and enhanced nutrient conservation (Escudero *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).

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 adaptations to water stress (Maximov 1929; Cunningham *et al.* 1999; Niinemets 2001); these traits, which generally confer higher LMA, also increase resistance to wilting. However, the general occurrence of the same leaf traits in species growing on nutrient-poor soils has led others to propose that high LMA is an adaptation to increase leaf life span in habitats where rapid growth is not possible and slow tissue turnover is therefore favoured (Grime 1977; Grubb 1986; Chapin *et al.* 1993; Turner 1994). Although dominant species in nutrient-poor environments tend to have both high LMA and long LL (Monk 1966; Chapin 1980), the extent to which this is true of low rainfall perennials is poorly known. Recently, Reich *et al.* (1999) found that species at the driest of six sites in the Americas (New Mexico) had a similar range of leaf life span to those from other sites, but shorter LL at a given LMA. This result is contrary to the general expectation that *both* LMA and LL would be higher for species at low rainfall but, as many environmental factors are (naturally) confounded in comparisons between widely divergent habitats, it may not be generalizable.

We therefore measured leaf life span and LMA for 75 perennial species from nutrient-rich and nutrient-poor sites in each of two rainfall zones in eastern Australia. Australia is a continent characterized by deeply weathered, nutrient-poor soils, on which vegetation types are largely determined by rainfall and soil phosphorus (Beadle 1966). The first aim was to test for the expected correlation between LL and LMA across all the study species, and among species within each site, in a flora largely unlike those studied previously. The second aim was to determine whether shifts towards higher LMA in dry and nutrient-poor habitats (if observed) were associated with concomitant shifts in leaf life span. Sets of species form roughly elliptical clouds of points when LL is plotted against LMA (or if any two normally distributed traits are plotted against each other). Consequently, the ellipses from habitats differing in rainfall and soil nutrients can be compared in terms of the slope and elevation of their principal axes, i.e. their position in LL–LMA space (Fig. 1).
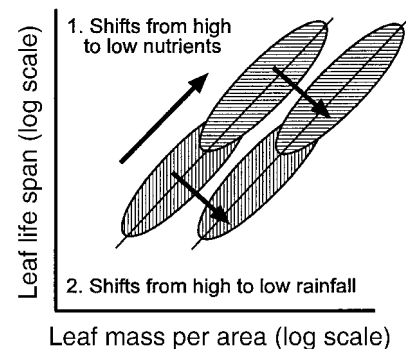
Fig. 1 Expected shifts in leaf life span (LL) and leaf mass per area (LMA) between habitats differing in soil nutrients and rainfall. Ellipses represent observed LL–LMA combinations of species at a site, with their standardized major axes (SMAs) shown. Vertical stripes indicate nutrient-rich and horizontal stripes nutrient-poor sites. Higher LMA and longer LL at nutrient-poor sites within each rainfall zone should cause a shift along a common SMA (no difference in SMA elevation; shift type 1). Higher LMA at dry sites was not expected to result in longer leaf life span, resulting in different SMA elevations; shift type 2.

Our hypotheses were:
• Higher LMA would confer increased leaf life span within each site, with the slope of the relationship invariant between habitats (Reich *et al.* 1999).
• Comparing nutrient-poor with nutrient-rich sites, selection towards increased leaf life span would be associated with a shift towards higher LMA (Grime 1977; Chapin *et al.* 1993; Turner 1994) (Fig. 1, shift type 1 along the same principal axis).
• Comparing low-rain with high-rain sites, greater LMA would be required to counteract the damaging effect of frequent low water potential on leaf life span at dry sites, such that the principal axis at low rainfall would be parallel but at lower elevation than that describing high rainfall species. That is, dry-site species would have higher LMA at a given leaf life span or, equally, shorter LL at a given LMA (Fig. 1, shift type 2).
• These results, describing patterns among present-day species, would be supported in phylogenetic analyses comparing evolutionary divergences in LL and LMA, both within individual sites and between site types.

Materials and methods

SITE AND SPECIES SELECTION

Two vegetation types were chosen in each of two rainfall zones (high rainfall, coastal New South Wales and semiarid, western New South Wales; Table 1). Five to 10 random soil samples were taken per site (core *c.* 5 cm in diameter and 15 cm deep), air dried, and total soil P was determined by solid fusion/XRF crystallography. While total soil P was used as the main index of soil nutrient status, additional indices of soil nutrient status were measured for comparison: total N, total C

Table 1 Description of the four study sites. High rain sites were located in Kuringai Chase National Park, Sydney; low rain sites in Round Hill Nature Reserve, western New South Wales. For soil analyses, the standard deviation is given in parentheses after the mean; $n = 5$ for Sydney sites, 10 for low rainfall sites

	High rain, high P	High rain, low P	Low rain, high P	Low rain, low P
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 p.p.m.	442.3 (232.0)	93.6 (27.9)	250.4 (33.5)	132.4 (14.6)
Total N (%)	0.256 (0.152)	0.030 (0.001)	0.071 (0.020)	0.031 (0.006)
Total C (%)	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)

(combustion/mass spectrometry) and cation exchange capacity (extraction with 0.1 M $BaCl_2$ + NH_4Cl, analysed by atomic absorption). Nutrient analyses were carried out at CSIRO Plant Industry, Canberra. All indices confirmed the nutrient-rich and nutrient-poor status of the selected sites, facilitating nutrient contrasts at two rainfall levels. The nutrient-poor soils were clearly more similar to each other than to the nutrient-rich soils, while the two nutrient-rich sites differed somewhat in total P. Nevertheless, the large difference in rainfall was probably the most consistent contrast between pairs of nutrient-rich and nutrient-poor sites. As much as possible, sites were matched for other attributes: all experience relatively aseasonal rainfall, have mean annual temperature of 17.5 °C and were flat to gently sloping. Precipitation data (Table 1) were taken from > 100 years records from the nearest weather station (< 30 km distant and at an equivalent altitude). All sites were located within National Park reserves.

Seventeen to 23 taxa were studied at each site, chosen from among perennial, non-climbing/twining plants. Species were chosen randomly from a previously compiled species list at the speciose high rainfall, nutrient-poor site. Elsewhere, all available species were used provided that at least five individuals could be found (except *Exocarpos aphyllus*, three individuals only). In order to obtain sufficient species at the species-poor drier sites, two subsites located several km apart were sampled for each vegetation type. Total site size varied between c. 0.2 and 0.7 ha at high rainfall, and 0.8 and 1.5 ha at low rainfall. Initially the study design was limited to dicots only, but this criterion was relaxed to maintain site representativeness given the abundance of a conifer species at the low rain, high soil P. Five species occurred at both nutrient-rich and nutrient-poor sites at low rainfall; these were not combined in analyses as the aim was to compare traits of representative vegetation at each site. The 75 study species ('species' is used in the loose sense to include subspecies and, in two cases, currently unrecognized varieties) were taxonomically diverse, representing 21 families, and included trees, shrubs and subshrubs, N-fixers and non-N-fixers, mostly C3 but one C4 species, and species with broad leaves, needle leaves and no leaves (but photosynthetic stems). The full species list and raw data are given in Appendices 1 and 3.

MEASUREMENT OF LEAF TRAITS

LMA of fully expanded, outer-canopy leaves 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 $\pi/2$). Five leaves from each of five individuals were sampled per species for all sites except the dry, nutrient-rich site, for which one leaf from each of five individuals was sampled in December 1997 and a further six to ten leaves collected in November 1998.

Fifteen 'sun' twigs were randomly chosen across several individuals of each species in mid-1998. For each twig, a leaf 'sequence' was defined from the youngest leaf (> 25% expanded) backwards along the twig to the oldest primary leaf found, whether on the same twig or, more commonly, on a branch one or more branching-orders back from the twig. The number of primary leaves in the sequence was counted. Five to six months later the number of leaves remaining in each sequence was counted and new sequences were marked, using the same branches as previously (where possible) or by tagging new branches where necessary (e.g. if the branch or plant had been damaged). Plants were re-censused using the same methods three further times, giving a sample period of 22.5–24.5 months, depending on the site. Over this period, leaves were censused on a total of 1893 branches, from 345 plants.

Average leaf life span for each species was calculated as the inverse of the rate of leaf mortality (Southwood *et al.* 1986; Ackerly 1996); that is, for a population of leaves of size N, the average leaf life span equals N divided by the rate of leaf death (or births, if one assumes births and deaths are more or less in equilibrium). Average annual mortality was calculated by pooling mortality and population size for all branches for each species within each census period, calculating a time-weighted average of turnover from the two censuses occurring in each year of the study, and taking the average across the 2 years. For the two leafless,

stem-photosynthesizing species, 'leaves' were defined as unbranched twigs, and '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. LMA was calculated for the unbranched 'leaves' (adjusted by $\pi/2$ as circular in cross-section).

CROSS-SPECIES ANALYSES

Species-mean values for LMA and LL formed the raw data for the analyses as we were primarily interested in cross-species trait relationships, and differences in these relationships among sites. Although LL was calculated from pooled data, the total variance in mortality rate for each census period was decomposed into its components in order to satisfy ourselves that leaf life span could appropriately be compared between species. The contribution of each level of variance was similar during each census period, averaging 54% for species, 11% for individual-within-species, and 35% for branch-within-individual (nested ANOVA type I variance components analysis). Similarly, between-species variation in LMA tends to be far greater than that within-species (89% vs. 11%: Wright *et al.* 2001; see also Shipley 1995; Bassow & Bazzaz 1997).

Standardized major axes (SMA) were used to describe the LL–LMA relationship as each variable had variation associated with it due to both measurement error and species-sampling, hence it was inappropriate to minimize sums of squares in the Y dimension only. SMA analysis is also known as geometric mean regression (Sokal & Rohlf 1995) 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 slopes are closely related to major axis (principal components) slopes, the former being calculated on standardized (correlation) data, the latter on unstandardized (covariance) data. Thus, these SMA 'scaling' slopes, calculated on log-transformed variables, give the proportional relationship between variables. Species-mean LMA and LL showed approximately log-normal distributions and were deemed normal following log transformation (Kolmogorov-Smirnov test, $\alpha = 0.05$). Confidence intervals (95%) were calculated for SMAs (Pitman 1939).

Tests for homogeneity of slopes and calculation of common slopes used a likelihood ratio method, with the test statistic closely approximating a chi-squared distribution with Bartlett correction (Warton & Weber 2002). The ability to calculate common slopes allows one to test for elevation (i.e. intercept) differences between groups, as in standard analyses of covariance (ANCOVA). Group shifts along a common SMA can also be tested for. Differences in elevation of SMA slopes were tested by *t*-test of group mean Y′, where Y′ is Y transformed as Y–βX for each group and β is the common slope (slopes transformed so slope = 0 and group means compared). Group-shifts along a com-

mon SMA were tested by *t*-test of group mean X′, where X′ is calculated by vector rotation (such that the common slope = 0), i.e. X′ = X cosθ – Y sinθ, where θ = −arctanβ. Differences in SMA slope and elevation, and group-shifts along common SMAs, were significance tested at $\alpha = 0.05$.

As group-shifts between or along common SMAs can be thought of as shifts in roughly elliptical clouds of points, bivariate-normal confidence-interval ellipses were calculated for illustrative purposes (as in Fig. 2b). These ellipses indicate the region in which 68% of observations would be expected to fall, i.e. they are the bivariate analogue of the univariate mean ± 1SD confidence interval for a normally distributed trait. Confidence-interval ellipses for SMAs can be calculated using a procedure analogous to that described by Sokal & Rohlf (1995) for calculating CI ellipses around principal components axes.

PHYLOGENETIC ANALYSES

For cross-species regressions, each species contributes a single data point. For correlated divergence analyses each independent *divergence* or radiation contributes a single item of evidence (sometimes known as 'phylogenetically independent contrasts' or PICs; Harvey & Pagel 1991). Two types of phylogenetic analyses were used. First, evolutionary divergences in LL and LMA were tested for correlation within each site. Secondly, divergences in LL and LMA were described for species-pairs chosen as rainfall and soil nutrient PICs. Both types of analyses relied upon a phylogenetic tree that described the most likely relationships between the study species (Appendix 1). 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 utilizing 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).

For the within-site phylogenetic analyses, a 'contrast data set' 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 indicating 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;
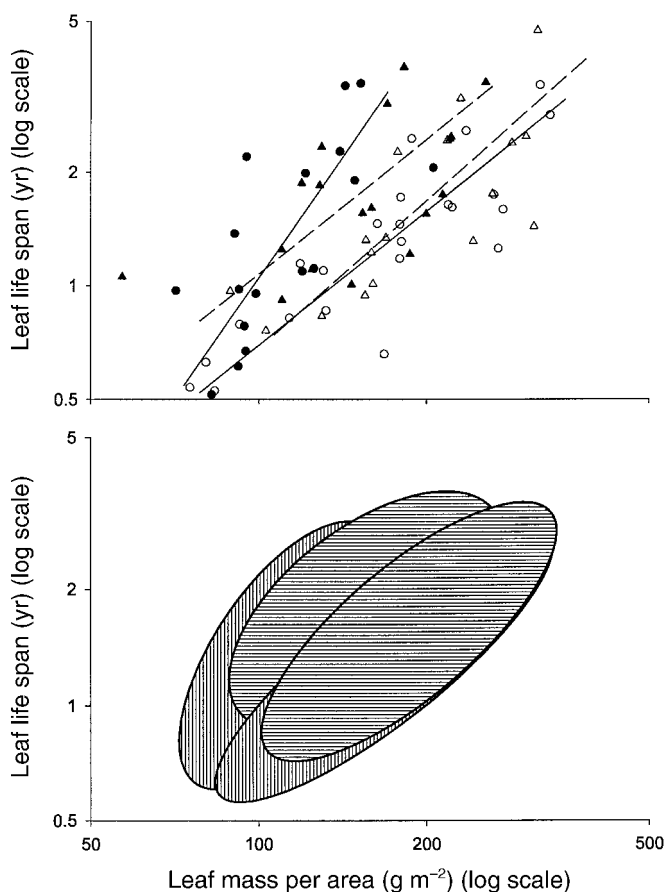
Fig. 2 (a) Relationship between leaf life span and LMA in four communities in eastern Australia. Filled symbols: high rainfall species; open symbols: low rainfall species. Circles: species at nutrient-rich sites; triangles: species at nutrient-poor sites. Within each rainfall zone, the solid line indicates the SMA slope for the nutrient-rich site, the dashed line the slope for the nutrient-poor site. Slope and r^2 values are given in Table 2. (b) Confidence-interval ellipses (see text) for the SMA slopes above (shading as in Fig. 1).

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 from the regression of Y on X were used to estimate CIs for these SMA slopes (Sokal & Rohlf 1995).

Sets of rainfall PICs were chosen to compare species within each soil class (nutrient-rich and nutrient-poor). Similarly, soil nutrient PICs were chosen to compare species within each rainfall zone. In choosing PICs, priority was given to more closely related species-pairs. That is, within-genus contrasts were chosen first, followed by contrasts comparing genera within families, then families within orders (Appendix 2). While it would have been possible to construct additional higher-level PICs (e.g. between orders within the asterids), this was not done because of the increasing uncertainty at higher levels of the representativeness of a contrast. Members of a set of contrasts are said to be phylogenetically 'independent' as no divergence (node on the phylogenetic tree) is included more than once in that set. In cases where more than one species could have been chosen as the species at one end of a contrast, priority was given according to alphabetical order

(e.g. when choosing which low rainfall subspecies of *Dodonaea viscosa* to compare with the high rainfall *D. triquetra*, *D. viscosa angustissima* was chosen rather than subspecies *cuneata* or *spatulata*). Rainfall and nutrient PICs are indicated on graphs of LL vs. LMA. A qualitative approach was adopted to describe 'majority trends' in the data (Cunningham *et al*. 1999; Wright & Westoby 1999), wherein the number of contrasts are reported for which LMA (or LL) increased or decreased when comparing the species from the resource-rich site with that from the resource-poor site. The main point of these analyses was to test for consistency across clades in the pattern observed across all species.

Results

CROSS-SPECIES ANALYSES

Leaf life span varied approximately ninefold across the 75 perennial species (0.5–4.7 years) and four- to seven-fold within any habitat. LMA varied sixfold across all species (57–334 g/m²), and approximately three- to five-fold within any habitat. As expected, LL and LMA were positively associated within each site (Fig. 2, Table 2). Individual SMA slopes ranged from 1.2 to 2.1 but were

Table 2 Within-site relationships between leaf life span (LL) and leaf mass per area (LMA). Cross-species and correlated divergence relationships were described with standardized major axis analyses. Note that confidence intervals are only approximate and symmetrical in the case of correlated divergence analyses (estimated from 95% CI from model 1 regression). For cross-species analyses, *P*-values are from Pearson correlation tests. For correlated divergence analyses, fitted slopes are 'forced' though the origin (have no intercept term); their *P*-values are from model 1 regressions, testing against a slope of 0

| Site	Cross-species analyses				Correlated divergence analyses			
	Slope (95% CI)	r^2	n	P	Slope (95% CI)	r^2	n	P
High rain, low P	2.1 (1.5, 3.1)	0.50	17	0.001	2.4 (1.3, 3.5)	0.38	14	0.014
High rain, low P	1.2 (0.76, 1.8)	0.34	17	0.014	1.1 (0.60, 1.6)	0.29	16	0.026
Low rain, high P	1.2 (0.94, 1.5)	0.74	23	10^{-7}	1.1 (0.74, 1.5)	0.58	17	0.0003
Low rain, low P	1.3 (0.93, 1.8)	0.59	18	0.0002	1.4 (0.99, 1.9)	0.70	15	0.0003

deemed non-heterogeneous (test statistic = 7.0, d.f. = 3, *P* = 0.072), with a common fitted slope of 1.3 (95% CI, 1.1–1.6).

On average, LMA was 27% higher at drier sites, yet mean leaf life span was 10% shorter (percentages calculated from means of log transformed variables). There was a clear elevation shift in LL–LMA ellipses between high- and low-rain sites, as predicted under hypothesis 3, and represented as shift type 2 in Fig. 1 (*t*-tests of Y′: nutrient-rich sites, *t* = 4.85, d.f. = 38, *P* = 4 × 10⁻⁵; nutrient-poor sites, *t* = 3.15, d.f. = 33, *P* = 0.003). Leaf life span 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 leaf life span. Still, there was apparent convergence of high and low rainfall LL–LMA combinations for the species with shortest leaf life spans (0.5–0.7 yr), these species all occurring on the nutrient-rich site within their respective rainfall zone.

At the high rainfall, nutrient-poor site, mean LMA was 28% higher and LL 35% longer than at the nutrient-rich site within that rainfall zone. Mean shifts were smaller between the two dry sites, both LMA and LL being on average 20% higher at the nutrient-poor site. Comparing species at the two high rainfall sites, the ellipses of LL–LMA combinations were significantly shifted along the common slope towards higher LMA and longer LL on nutrient-poor soil (shift type 1 in Fig. 1; *t*-test of X′, *t* = 2.31, d.f. = 32, *P* = 0.028), in line with hypothesis 2. The shift was not significant for dry-site species (*t* = 1.07, d.f. = 39, *P* = 0.291), although the three or four species with shortest leaf life span within each rainfall zone were found on nutrient-rich soils. In general, Proteaceae (mostly occurring at high rainfall sites) had longer LL than other families, while Sapindaceae and Asteraceae (mostly occurring at drier sites) had shorter LL than other families.

CORRELATED DIVERGENCE ANALYSES

Evolutionary divergences in LMA and LL were correlated within each site (Fig. 3; Table 2), indicating that the correlations observed across species (Fig. 2) were not simply driven by differences between higher taxonomic groups, and that correlated divergences in
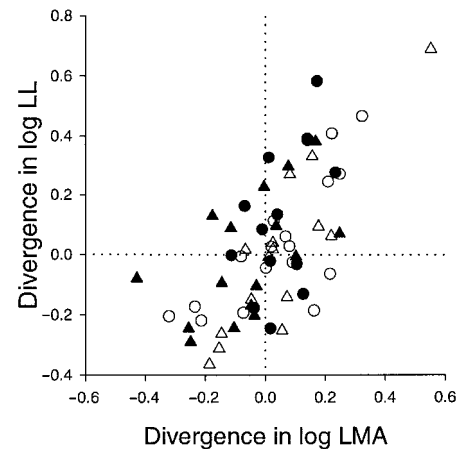

Fig. 3 Evolutionary divergences in leaf life span (LL) and leaf mass per area (LMA) in the four study sites. Fitted slopes are 'forced' through the origin (have no intercept term). Data for individual slopes given in Table 2. Site codes as in Fig. 2.

LMA and LL have occurred repeatedly in all groups and at all taxonomic levels.

In 14 of 16 rainfall contrasts (PICs), LMA was higher for the dry-site species of the species-pair (9/9 contrasts on nutrient-rich soils, 5/7 contrasts on nutrient-poor soils), whereas leaf life span was longer for the dry-site species in 10 of 16 nutrient contrasts (5/9 and 5/7 contrasts on nutrient-rich and nutrient-poor soils, respectively; Fig. 4). On nutrient-rich soils (Fig. 4a), shifts in LMA tended to be larger than the associated shifts in LL, in line with cross-species analyses (that a higher LMA was associated with a given LL at drier sites), but this was less apparent on nutrient-poor soils (Fig. 4b). In each set of rainfall contrasts there were two cases where LL was *c.* 25% to 50% shorter for the dry-site species, while the shift in LMA was around half this size, whether positive (high-nutrient species) or negative (low-nutrient species). Again, this is consistent with the cross-species result that, at a similar LMA, LL was shorter at drier sites.

LMA was higher for species on nutrient-poor soils in 12 of 19 soil nutrient contrasts (8/10 and 4/9 at high and low rainfall, respectively), and their LL was longer in 10 of 19 contrasts (6/10 high, 4/9 low rainfall; Fig. 5). In one contrast LL and LMA were approximately
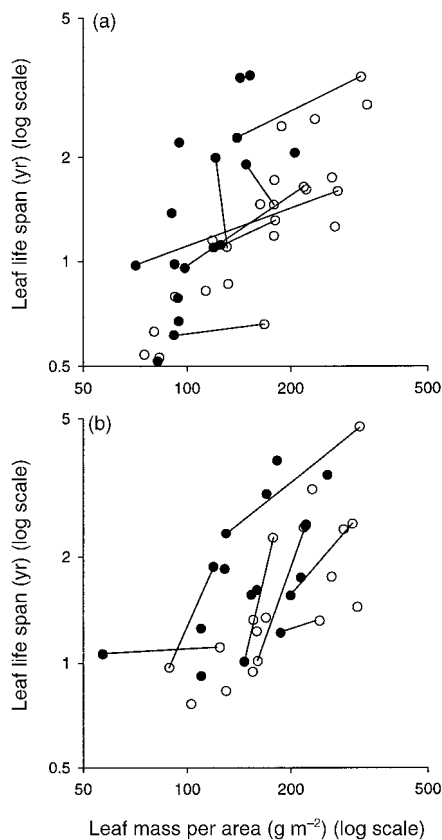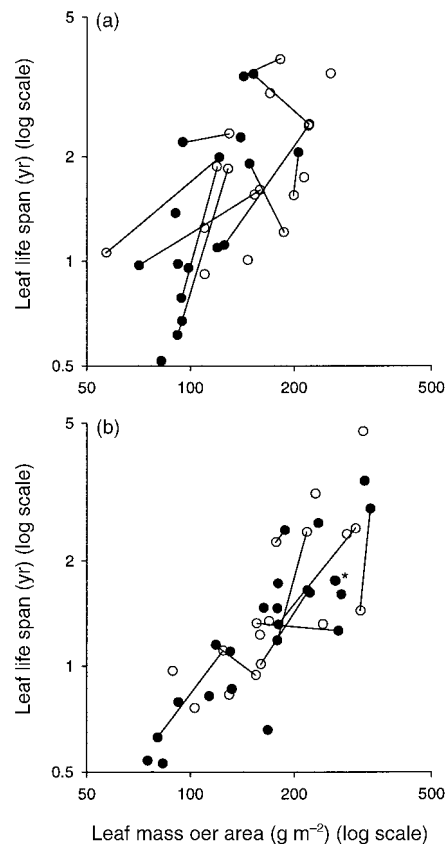
Fig. 4 Rainfall contrasts (PICs) between species on (a) high and (b) low nutrient soils. Filled symbols: high rainfall species; open symbols: low rainfall species. All species are shown, with those involved in PICs connected by solid lines. Species involved in each contrast are listed in Appendix 2.

Fig. 5 Nutrient contrasts (PICs) between species from (a) high and (b) low rainfall sites. Filled symbols: species at nutrient-rich sites; open symbols: species at nutrient-poor sites; asterisk: a contrast in which LL and LMA were approximately equal for the two species.

equal for the two species being compared (asterisk in Fig. 5b). In three contrasts shifts in LL and LMA went in opposite directions, while in 14 of 19 cases the sign of the shifts in LL and LMA were the same (both LMA and LL increased or decreased). That is, although just over half showed the expected shifts towards larger LMA and longer LL on nutrient-poor soils, the two traits generally shifted together, as would be expected within a given rainfall zone.

Discussion

LL–LMA RELATIONSHIPS AMONG COEXISTING SPECIES

As expected, leaf life span and LMA were correlated across the species within each site. Further, the slope of the relationship was not significantly different between sites. These results are consistent with the proposal that general leaf trait relationships exist across species from diverse taxonomic groups and biomes (Reich *et al.* 1999). Similar to previous reports (Reich *et al.* 1997; Diemer 1998; reanalysed as SMA slopes), the common LL–LMA slope was steeper than 1, indicating that a doubling in LMA was associated with a more-than-doubling of leaf life span. This implies that the 'light

capture area-months' (leaf area × duration) per gram leaf of high LMA species was greater than for low LMA species. If this translated directly into a fitness benefit, it might lead to runaway selection for ever-increasing LMA and LL. However, the spread of LL or LMA within any one site actually covered most of the total range of variation seen across the 75 study species. Indeed, the fact that a spectrum of LL–LMA combinations are seen in coexisting species suggests that there are relative advantages enjoyed by species right along the spectrum. This is consistent with the idea that the spectrum is underpinned by a trade-off between high short-term productivity per leaf mass and slower turnover of plant parts.

Low LMA, high photosynthetic capacity and generally faster turnover of plant parts permits a more flexible response to the spatial patchiness of light and soil resources (Grime 1994), giving low LMA species short-term advantages over high LMA species. Further, higher short-term productivity has added value because of a compound interest effect, whereby carbon fixed earlier can be reinvested in new leaves sooner (Chabot & Hicks 1982; Harper 1989; Westoby *et al.* 2000). On the other hand, the long mean residence time of nutrients made possible by long leaf life span permits a progressively larger share of nitrogen pools in a habitat to be sequestered

(Aerts & van der Peijl 1993), giving advantage to species with a high LMA–long LL strategy. In addition, over time high LMA–long LL species may accumulate a greater total leaf mass and leaf area than low LMA species, leading to similar or sometimes higher rates of above-ground net primary production (Matyssek 1986; Bond 1989; Reich *et al*. 1992; Gower *et al*. 1993).

SHIFTS IN MEAN LMA AND LL BETWEEN HABITATS

Long leaf life spans have been suggested to be advantageous in nutrient-poor habitats because nutrient retention times are extended (Schlesinger & Chabot 1977; Aerts & van der Peijl 1993), and the construction cost of low-productivity leaves can be amortized over a longer period (Chabot & Hicks 1982; Kikuzawa 1991). An upwards shift in mean LMA from nutrient-rich to nutrient-poor habitats apparently confers these advantageous longer leaf life spans, just as higher LMA confers longer LL within a given habitat. Consequently, the general pattern of higher LMA and longer LL in infertile habitats can be thought of as an extension of the relationship that occurs between coexisting species: both types of shift occur along a common spectrum of variation.

By contrast, our results show that a shift to higher mean LMA at dry sites does not necessarily confer extended LL, as previously predicted (Grime 1977; Chapin *et al*. 1993; Turner 1994). Rather, dry-site species were shifted onto a parallel spectrum of LL–LMA combinations, where an average of 30% more dry mass per leaf area was associated with the same LL as for a species at a high rainfall site. One explanation could be that greater structural reinforcement of leaves decreases the propensity to wilt to the point of leaf death under very dry conditions (Maximov 1929; Niinemets 2001), thus stronger leaves are required to achieve a given LL in dry habitat species. This explanation is being explored further by considering LMA–LL relationships along with other physical leaf traits.

Interestingly, the opposite pattern is known from comparisons of shade species with those from better-lit environments, whereby shade species have lower LMA but longer leaf life span (King 1994; Lusk & Contreras 1999; Valladares *et al*. 2000). Longer LL in shady habitats has been interpreted as being necessary to amortise leaf construction costs where only low rates of photosynthesis are possible (Williams *et al*. 1989; Kikuzawa 1995). However, it is the concomitant shift towards lower LMA that is puzzling. One possible explanation is that the physical constraint whereby an increased LL demands an increased LMA is relaxed in dense shade, i.e. the low wind, high humidity and reduced risk of wilting that characterize dense shade environments make it possible to achieve longer LL with a given level of physical reinforcement. If so, this is in fact the flip-side to the argument that greater structural reinforcement (higher LMA) is required to achieve a given LL in dry habitats.

Other explanations for high LMA in dry-site species have also been suggested. For example, thicker leaves may be advantageous in high irradiance habitats (such as arid zones) because more mesophyll can be stacked up without internal self-shading (Mooney *et al*. 1978; Smith *et al*. 1998). Similarly, under low light, internal self-shading may be avoided by constructing thin, low LMA leaves. While this line of argument may be sound, and certainly consistent with what is generally observed, it does not directly involve leaf life span, and does not easily explain the shifting boundaries of LL–LMA relationships between habitat types. The point remains that the 'envelope' of successful LMA–LL combinations in dry habitats is shifted to lower LMA at any given LL for some reason.

The results from this work show that leaf life span and LMA are correlated in a variety of habitats in eastern Australia, just as in many other environments. Further, evolutionary divergences in LMA and LL appear to have been correlated throughout history, lending further support to the adaptive interpretation of these relationships (Ackerly & Reich 1999). Considering the two traits together, the long-recognized convergence of higher average LMA in dry and nutrient-poor habitats had different implications for average leaf life span according to resource type. Returning to the investment/return analogy of leaf construction, we found that the investment (leaf mass) required to deploy a given light-capture area was greater in the dry sites, on average, for a given duration of the revenue stream from that investment. These results were most clear in the cross-species analyses, but consistent with those from the sets of PICs constructed across the two rainfall zones and two soil nutrient classes. Together these findings, gained from structured comparisons and generalized over a large number of species, help to clarify our understanding of both leaf morphology and carbon-fixation strategies across and within different habitat types.

Acknowledgements

Supplementary material

The following material is available from http://www.blackwell-science.com/products/journals/suppmat/JEC/JEC690/JEC690sm.htm

Appendix 1 Phylogeny of the 75 study species.

Appendix 2 The four sets of phylogenetic independent contrasts.

Appendix 3 Trait values for the 75 study species.

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