

# Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats

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## Summary

1. Relationships were examined among photosynthetic capacity ( $A_{\text{mass}}$  and  $A_{\text{area}}$ ), foliar dark respiration rate ( $R_{\text{d-mass}}$  and  $R_{\text{d-area}}$ ), stomatal conductance to water ( $G_s$ ), specific leaf area (SLA), and leaf nitrogen (N) and phosphorus (P) across 79 perennial species occurring at four sites with contrasting rainfall levels and soil nutrients in eastern Australia. We hypothesized that the slope of log–log ‘scaling’ relationships between these traits would be positive and would not differ between sites, although slope elevations might shift between habitat types.
2.  $A_{\text{mass}}$ ,  $R_{\text{d-mass}}$ , SLA,  $N_{\text{mass}}$  and  $P_{\text{mass}}$  were positively associated in common slopes fitted across sites or rainfall zones, although rather weakly within individual sites in some cases. The relationships between  $A_{\text{mass}}$  (and  $R_{\text{d-mass}}$ ) with each of  $N_{\text{mass}}$  and SLA were partially independent of each other, with  $A_{\text{mass}}$  (or  $R_{\text{d-mass}}$ ) increasing with SLA at a given  $N_{\text{mass}}$ , or with  $N_{\text{mass}}$  at a given SLA (only weakly in the case of  $A_{\text{mass}}$ ). These results improve the quantification and extend the generalization of reported patterns to floras largely unlike those studied previously, with the additional contribution of including phosphorus data.
3. Species from drier sites differed in several important respects. They had (i) higher leaf N and P (per dry mass or area); (ii) lower photosynthetic capacity at a given leaf N or P; (iii) higher  $R_{\text{d-mass}}$  at a given SLA or  $A_{\text{mass}}$ ; and (iv) lower  $G_s$  at a given  $A_{\text{area}}$  (implying lower internal CO<sub>2</sub> concentration).
4. These trends can be interpreted as part of a previously undocumented water conservation strategy in species from dry habitats. By investing heavily in photosynthetic enzymes, a larger drawdown of internal CO<sub>2</sub> concentration is achieved, and a given photosynthetic rate is possible at a lower stomatal conductance. Transpirational water use is similar, however, due to the lower-humidity air in dry sites. The benefit of the strategy is that dry-site species reduce water loss at a given  $A_{\text{area}}$ , down to levels similar to wet-site species, despite occurring in lower-humidity environments. The cost of high leaf N is reflected in higher dark respiration rates and, presumably, additional costs incurred by N acquisition and increased herbivory risk.

**Key-words:** Carbon gain, nitrogen use, plant strategies, water use

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## Introduction

Although there is great diversity among plant species in growth form, leaf size, leaf shape and canopy arrangement, there are also some general relationships, occurring across a wide range of species, in leaf traits central to the carbon fixation ‘strategy’ of plants. For example, in between-species comparisons of outer canopy leaves, specific leaf area (SLA, leaf area per mass) tends to be

correlated with leaf nitrogen per unit dry mass ( $N_{\text{mass}}$ ), photosynthetic ( $A_{\text{mass}}$ ) and foliar dark respiration rates ( $R_{\text{d-mass}}$ ), but negatively correlated with leaf lifespan (various combinations of these relationships have been reported by Bolstad, Mitchell & Vose 1999; Diemer 1998; Eamus *et al.* 1999; Field & Mooney 1986; Medina 1984; Mulkey, Kitajima & Wright 1995; Niinemets 1999; Reich *et al.* 1998; Reich *et al.* 1999). Consequently, much variation between plant species can be understood as a single spectrum of correlated traits.

Reich *et al.* (1997, 1999) found that the proportionality of these trait relationships (slopes on log–log axes) did

not differ between sites from tropics to tundra, while slope elevations (intercepts) did vary. However, as many environmental factors are confounded in comparisons between widely divergent habitats, we do not know how predictably the relationships vary between different habitat types. Here we address that question by comparing leaf traits of species from sites of contrasting soil nutrient status and rainfall in eastern Australia. Australia is a continent with overwhelmingly ancient, weathered, nutrient-poor soils, on which vegetation types are largely determined by rainfall and soil phosphorus (Beadle 1962; Webb 1968). Thus we also set out to extend the generality of knowledge on leaf trait relationships into a flora largely unlike those studied previously.

We measured leaf traits on a total of 79 perennial species from four sites (nutrient-rich and nutrient-poor sites in each of two rainfall zones), focusing on the proportionality or 'scaling relationships' among SLA, leaf N and P concentration, photosynthetic capacity and dark respiration rate, and stomatal conductance to water ( $G_s$ ). Previously, leaf P has rarely been considered in conjunction with these other traits (Reich, Ellsworth & Uhl 1995). Leaf lifespan is being determined as part of a complementary, longer study. Specific expectations were as follows.

1. Average leaf traits would differ with site nutrient status, species from nutrient-rich soils having higher mean SLA,  $N_{\text{mass}}$  (Chapin 1980; Cunningham, Summerhayes & Westoby 1999),  $P_{\text{mass}}$ ,  $A_{\text{mass}}$  and  $R_{d\text{-mass}}$  than species from nutrient-poor soils.
2. Average leaf traits would differ with rainfall, species from drier sites having lower mean SLA (Schulze *et al.* 1998; Specht & Specht 1989) and higher mean  $N_{\text{area}}$  (perhaps due to the lower SLA or as a response to the stronger average irradiance in arid habitats; Cunningham *et al.* 1999; Mooney, Ferrar & Slatyer 1978).
3. SLA,  $N_{\text{mass}}$ ,  $P_{\text{mass}}$ ,  $A_{\text{mass}}$  and  $R_{d\text{-mass}}$  would scale positively with one another at each site and also across all species, with scaling slopes not differing from site to site (Reich *et al.* 1998; Reich *et al.* 1999).

4. However, slope elevations might differ between site types (Reich *et al.* 1999).

5. Both  $A_{\text{mass}}$  and  $R_{d\text{-mass}}$  would scale positively with  $N_{\text{mass}}$  at a given SLA, and with SLA at a given  $N_{\text{mass}}$ , indicating that both leaf structure and nutrient content independently affect carbon fixation and use (Reich, Ellsworth & Walters 1998a; Peterson *et al.* 1999).
6. Leaf P would have significance beyond leaf N in predicting  $A_{\text{mass}}$ , as Australian soils tend to be particularly P-deficient compared to soils from other continents (Atwell, Kriedemann & Turnbull 1999).

## Materials and methods

### SITE AND SPECIES SELECTION

In each of two rainfall zones (coastal New South Wales: rainfall 1220 mm per year; western NSW: 387 mm per year) two vegetation types were chosen on the basis of contrasting soil nutrient status, so that attributes of the vegetation could be compared as rainfall contrasts and nutrient contrasts. As far as possible, sites were matched for other climatic attributes such as seasonality of rainfall (relatively aseasonal at each pair of sites), mean annual temperature, and slope (sites were flat to gently sloping). Climate 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.

Five to ten random soil samples were taken per site (core ≈5 cm diameter, 15 cm deep), air-dried and analysed for total soil P (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 (combustion/mass spectrometry), and cation-exchange capacity (extraction with 0.1 M BaCl<sub>2</sub> + NH<sub>4</sub>Cl, analysed by atomic absorption). Nutrient analyses were carried out at CSIRO Plant Industry, Canberra. All indices confirmed that nutrient-rich and nutrient-poor

**Table 1.** Description of the four study sites

Parameter	Wetter, high P	Wetter, low P	Drier, high P	Drier, 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) (max, min)	22.0, 13.0	22.0, 13.0	24.1, 11.1	24.1, 11.1
Mean relative humidity (0900 h) (%)	68	68	49	49
Soil type (parent material)	Red-brown clay (weathered volcanic dyke)	Yellow-grey sand (Hawkesbury sandstone)	Light red clay (residual deposits overlying Mt Hope volcanics)	Loamy red sand (Quaternary dune systems)
Total P (μg g <sup>-1</sup> )	442 (232)	93.6 (27.9)	250 (33.5)	132 (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 <sup>-1</sup> )	55.6 (21.7)	9.0 (1.6)	65.8 (23.7)	38.7 (9.4)

Wetter sites were located in Kuringai Chase National Park (Sydney), drier sites in Round Hill Nature Reserve (western NSW). The standard deviation for soil analyses is given in parentheses after the mean;  $n = 5$  for wetter sites, 10 for drier sites. Soil description for drier sites follows Cohn (1995).

soils had been chosen within each rainfall zone, 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. Rainfall contrasts across all species or between nutrient-rich and nutrient-poor sites were valid in the sense that the large difference in rainfall was probably the main contrasting site property.

Between 17 and 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 wetter, nutrient-poor site. Elsewhere, all available species were used provided 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 kilometres apart were sampled for each site type. Initially the study design was limited to dicots only, but this criterion was relaxed where any particularly abundant non-dicot species were encountered so that site representability was maintained (one conifer, one cycad and one grass were included, each at different sites). Five species occurred at more than one site (at both nutrient-rich and nutrient-poor sites at low rainfall in all cases); these were not combined in analyses as the aim was to compare traits of representative vegetation at each site. The 79 study species ('species' is used here in the loose sense to include subspecies and, in two cases, currently unrecognized varieties) were taxonomically diverse, representing 24 families, and included trees, shrubs, subshrubs and one perennial grass, N<sub>2</sub>-fixers and non N<sub>2</sub>-fixers, mostly C<sub>3</sub> but two C<sub>4</sub> species, and species with broad leaves, needle leaves and no leaves (but photosynthetic stems). The full species list and raw data are available on request.

#### MEASUREMENT OF LEAF TRAITS

Standard methods were followed for measuring leaf traits (Bassow & Bazzaz 1997; Eamus *et al.* 1999; Reich *et al.* 1998; Reich *et al.* 1999). All leaf traits were measured on young to medium-aged, fully expanded, outer-canopy leaves. Measurements of photosynthetic capacity ( $A_{\text{mass}}$  and  $A_{\text{area}}$ ), dark respiration rate ( $R_d$ ) and stomatal conductance to water ( $G_s$ ) were made using two portable photosynthesis systems equipped for automatic temperature, CO<sub>2</sub> and water vapour control (CIRAS-1, PP Systems, Hitchin, UK) and operated in the differential mode. We used standard cuvettes (broadleaf PLC-B and narrowleaf PLC-N). Leaves were collected from mid- to late morning (0800–1200 h), still attached to branches (Dang *et al.* 1997; Mitchell, Bolstad & Vose 1999; Reich *et al.* 1998), and measurements of  $A$  and  $G_s$  were made immediately. For the larger-leaved species, only the portion fitting in the cuvette was used for measurements; for small-leaved species gas exchange was measured on multiple leaves

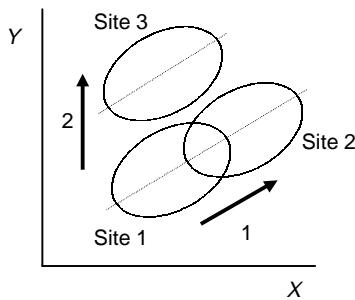
simultaneously. Photosynthesis and  $G_s$  measurements were made at saturating or near-saturating light conditions (infrequently, artificial light sources were used when clouds obscured the sun), and at semi-controlled temperatures (mean PAR 1429 μmol m<sup>-2</sup> s<sup>-1</sup>, SE 11.9, n = 487; mean temperature 25.5 °C, SE 0.9 °C), with an average of 6.2 samples taken per species, all from different individuals (except *Exocarpos aphyllus*). Branches used for  $R_d$  measurements were kept moist and stored in the dark at cool temperatures (≈5 °C, to minimize any decline in carbohydrate status prior to measurement) for 1–3 h before being warmed up and dark respiration measured (mean temperature = 25.0 °C, SE 0.04 °C, n = 472; average sample size 6.5 per species). As stem material was present in the cuvette for  $R_d$  measurements for 16 species, this was also dried and weighed, and an adjusted foliar dark-respiration index calculated by assuming that the rate of stem respiration per unit mass was on average 0.68 times that of the rate for leaf material. We used this ratio based on an analysis of measured rates for stems and associated leaves for 13 species from three different studies (Walters, Kruger & Reich 1993; Walters & Reich, 2000; J.L. Machado and P.B.R., unpublished results), for which the mean ratio of stem  $R_d$ /leaf  $R_d$  was 0.68 (±0.06 SE among species). An analogous index was calculated for  $R_d$  on an area basis.  $R_d$  measurements reported here are for these adjusted indices. The mean difference between adjusted and unadjusted measures was 10%. Overall, the two indices were strongly correlated ( $r = 0.992$ ) and the choice of one or the other would not have changed the results in a qualitative sense.

Projected leaf area was determined with a flat-bed scanner and image analysis software (DELTA-T, Cambridge, UK). Leaves were oven-dried for a minimum of 48 h at 65 °C, weighed, finely ground, and analysed for Kjeldahl N and P.

#### DATA ANALYSIS

Individual measurements were averaged for each species-site combination, as we were primarily interested in cross-species trait relationships and differences in these relationships among sites. Variance components analysis (ANOVA, type I sums of squares) revealed that between-species variation in leaf traits was generally greater than or equal to that within species, in line with previous findings (Bassow & Bazzaz 1997; Reich *et al.* 1999); the proportion of variance explained by species was  $A_{\text{mass}}$  72%,  $A_{\text{area}}$  46%,  $G_s$  50%, SLA 89%,  $R_d$ -mass 77%,  $R_d$ -area 70%. All variables showed approximately log-normal distributions, but were deemed normal following log transformation (Kolmogorov-Smirnov test,  $\alpha = 0.05$ ).

Standardized major axis (SMA) slope-fitting techniques were considered most appropriate for describing bivariate relationships as X as well as Y variables had variation associated with them due to both measurement error and species sampling, hence it was inappropriate



**Fig. 1.** Hypothetical shifts between sites in species-trait combinations for two traits  $X$  and  $Y$  (same SMA slopes assumed). Shift 1: correlated upward shifts in  $X$  and  $Y$  result in same SMA elevation for sites 1 and 2. Shift 2: an upward shift in  $Y$  combined with no change in  $X$  results in a higher SMA elevation for site 3 than for site 1.

to minimize sums of squares in the  $y$  dimension only (Sokal & Rohlf 1995). These ‘scaling’ slopes, calculated on log-transformed variables, give the proportional relationship between variables. SMA slopes are generally steeper than the corresponding model 1 slopes, with the SMA slope equal to the model 1 slope divided by the correlation coefficient between  $\log Y$  and  $\log X$ .

An SMA slope can be thought of as the first principal (or major) axis of the roughly elliptical cloud of points obtained when two normally distributed variables are plotted against each other (Fig. 1). In comparing the clouds of points from two sites, a number of results are possible. First, the slope of the principal axes may differ between sites. If the slopes do not differ (expectation 3), the two clouds may (i) overlap in both dimensions (no difference in SMA elevation); (ii) be shifted along the axis relative to each other (no difference in slope or elevation – however, shifts in site means will be correlated; Fig. 1, shift 1); (iii) be shifted in one dimension only (resulting in a difference in slope elevation, and a shift in site means in one dimension only; Fig. 1, shift 2).

SMA slopes were fitted for each site individually, with confidence intervals (95%) calculated following Pitman (1939). Tests for homogeneity of slopes and calculation of common slopes followed Warton & Weber (2001), using a likelihood ratio method. Where a common slope could be fitted (test for homogeneity,  $P > 0.05$ ), differences in elevation (intercept) of slopes were tested by  $t$ -test or ANOVA (and *post hoc* Tukey’s HSD test where appropriate) of group mean  $Y'$ , where  $Y'$  is  $Y$  transformed as  $Y - bX$  for each group and  $b$  is the common slope (slopes transformed so slope = 0 and group means compared). These analyses used an SMA analogue of standard ANCOVA. Model 1 multiple regressions were used for examining trait relationships involving two independent variables as there is no straightforward analogous procedure using SMA slopes. Comparisons of site means for individual traits were made with  $t$ -tests or ANOVA. All statistical tests were significance tested at  $\alpha = 0.05$ . Marginally significant

results ( $0.05 < P < 0.10$ ) are reported as such; significance levels for clearly non-significant results ( $P > 0.10$ ) are not listed in every case, for brevity.

## Results

### COMPARISON OF TRAIT MEANS BY SOIL NUTRIENTS AND RAINFALL

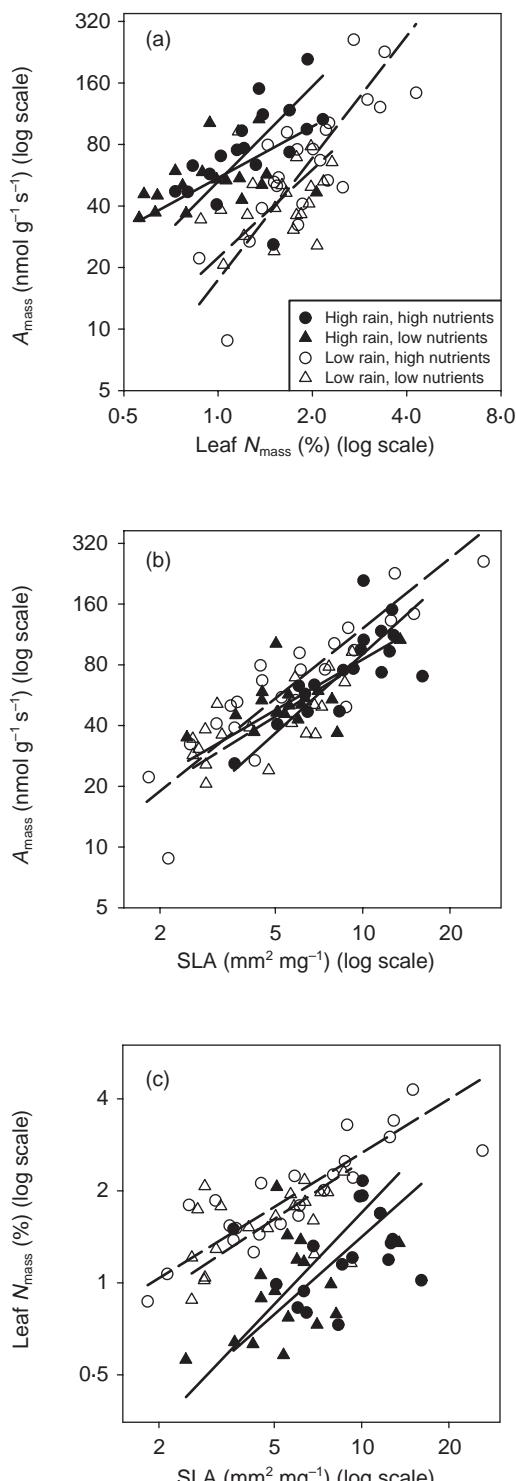
As predicted (expectation 1), species from nutrient-rich soils had higher mean leaf  $N_{\text{mass}}$ ,  $P_{\text{mass}}$  and  $A_{\text{mass}}$  than species from nutrient-poor soils, whether comparing species from nutrient-rich and nutrient-poor sites within each rainfall zone separately, or with all species pooled (all  $P < 0.05$ ). Comparing all species or wetter sites only, mean SLA was higher on nutrient-rich soils ( $P < 0.010$ ), yet no difference in mean SLA was found with soil nutrients for drier sites.  $R_{\text{d-mass}}$  was marginally higher ( $0.05 < P < 0.10$ ) at nutrient-rich sites in comparisons between dry-site species and across all species, but no difference was found between the wetter sites. No consistent trends with site nutrient status were found for other leaf traits.

On average, species from drier sites had higher leaf N and P per dry mass or area, and higher  $R_{\text{d-area}}$ , whether comparing the pairs of nutrient-rich and nutrient-poor sites separately or with all species pooled (all  $P < 0.001$ ). Mean SLA was lower and  $R_{\text{d-mass}}$  higher at dry sites in comparisons across all species or between the two nutrient-rich sites, but not when comparing the two nutrient-poor sites. In summary, expectation 2 was broadly supported by the data, and trends in dark respiration rates tended to follow those in leaf N.

### PHOTOSYNTHETIC ASSIMILATION ( $A$ ) VERSUS LEAF NITROGEN AND SLA

$A_{\text{mass}}$  and  $N_{\text{mass}}$  were positively associated at all sites, with a stronger relationship (higher  $r$ ) at the nutrient-rich site within each rainfall zone (Fig. 2a; Table 2). Individual slopes were heterogeneous ( $P = 0.026$ ), but neither slopes nor elevations differed between sites within either rainfall zone (although slopes were marginally heterogeneous at high rainfall;  $P = 0.06$ ). Fitting common slopes within each rainfall zone,  $A_{\text{mass}}$  increased faster than proportionately with  $N_{\text{mass}}$  (1.8 at dry sites, 1.2 at wetter sites), although these slopes had overlapping confidence intervals and only the dry-site slope was significantly steeper than 1. At dry sites  $A_{\text{mass}}$  was lower at a given  $N_{\text{mass}}$  than at wetter sites.

Photosynthesis–N relationships tended to be weaker when the axes were rescaled via SLA to an area basis (Table 2). Individual slopes were non-heterogeneous ( $P = 0.958$ ), with a common slope of 0.84 (95% CI, 0.72–0.99). Again, there were clear differences in slope elevation, with lower  $A_{\text{area}}$  at a given  $N_{\text{area}}$  for dry-site species (pairwise rainfall contrasts, all  $P < 0.002$ ), and no difference between sites within either rainfall zone.



**Fig. 2.** Standardized major axis (SMA) relationships between  $A_{\text{mass}}$ ,  $N_{\text{mass}}$  and SLA. In all analyses, where SMA slopes did not differ significantly in slope or elevation, common slopes were fitted firstly within rainfall zones or secondly, across all species. Dashed lines indicate SMA slopes for low-rainfall sites, solid lines indicate slopes for high-rainfall sites. Slope and  $r^2$  values are given in Table 2. (a)  $A_{\text{mass}}$  on  $N_{\text{mass}}$ . Common slopes fitted within each rainfall zone: low rain 1.82 (95% CI 1.45, 2.29); high rain 1.19 (0.87, 1.63). (b)  $A_{\text{mass}}$  on SLA. Individual slopes did not differ ( $P = 0.221$ ), with a common slope of 1.09 (0.95, 1.24). (c)  $N_{\text{mass}}$  on SLA. Individual slopes did not differ ( $P = 0.176$ ), with common slope of 0.67 (0.52, 0.86), but higher  $N_{\text{mass}}$  at a given SLA at low rainfall (pairwise contrasts on rainfall, all  $P < 1 \times 10^{-5}$ ).

$A_{\text{mass}}$  and SLA were positively related at all sites (Fig. 2b), with individual slopes not differing significantly from one another. The common slope of 1.09 indicated close-to-proportional scaling between the two traits. There were no differences in slope elevation with soil nutrient status within either rainfall zone, or between rainfall zones themselves.

$N_{\text{mass}}$  and SLA were positively associated at all sites (Fig. 2c), with individual slopes non-heterogeneous, and a common slope of 0.67. Clear differences between dry-site and wet-site species emerged, with 1.7 times higher  $N_{\text{mass}}$  at a given SLA at dry sites. Higher  $N_{\text{mass}}$  at a given SLA indicates higher  $N_{\text{area}}$  also. No differences were found in slope elevation between nutrient-rich and nutrient-poor sites within either rainfall zone.

Multiple regressions of  $A_{\text{mass}}$  on  $N_{\text{mass}}$  and SLA were used to explore further the interplay between these traits (expectation 5). With species pooled by rainfall (given the distinction by rainfall in Fig. 2a,c), partial regression coefficients indicated that  $A_{\text{mass}}$  increased with SLA at a given  $N_{\text{mass}}$ , yet increased only weakly (and marginally significantly at high rainfall only) with  $N_{\text{mass}}$  at a given SLA (Table 3). Similar results were obtained with sites considered individually (results not shown). The magnitude and significance of these coefficients cannot be directly compared with those from the bivariate analyses (SMA analogues would be steeper than model 1 coefficients).

#### LEAF PHOSPHORUS

$P_{\text{mass}}$  and  $N_{\text{mass}}$  were strongly associated at the two dry sites, yet only weakly associated at the wetter sites (Fig. 3a; Table 2). Individual slopes were non-heterogeneous ( $P = 0.392$ ). Species from drier sites had higher  $P_{\text{mass}}$  at a given  $N_{\text{mass}}$  in comparisons of the pairs of nutrient-rich and -poor sites. At low rainfall, individual slopes did not differ in elevation, while at high rainfall, the elevation was higher at the nutrient-rich site.

$A_{\text{mass}}$  and SLA showed similar relationships to  $P_{\text{mass}}$  as to  $N_{\text{mass}}$  (Fig. 3b).  $A_{\text{mass}}$  and  $P_{\text{mass}}$  were positively associated at all sites, although the relationship was weak at the Sydney high-nutrient site. Still, slopes did not differ between sites. Species from drier sites had lower  $A_{\text{mass}}$  at a given  $P_{\text{mass}}$ . At low rainfall, individual slopes did not differ in elevation, while at high rainfall, the elevation was higher at the nutrient-poor site.

SLA and  $P_{\text{mass}}$  were positively associated at all sites (Fig. 3c), although again the relationship was weakest at the wetter, nutrient-rich site. Slopes were non-heterogeneous, with tests for elevation differences indicating higher  $P_{\text{mass}}$  at a given SLA at dry sites (therefore they also had higher  $P_{\text{area}}$ ), and higher  $P_{\text{mass}}$  at a given SLA at the nutrient-rich site within each rainfall zone.

We suggested that leaf P would have additional significance after leaf N in predicting  $A_{\text{mass}}$  (expectation 6). In fact, this turned out to be supported only at nutrient-poor sites (and then rather weakly), where

**Table 2.** SMA slopes (95% confidence intervals in parentheses), and correlation  $r$  and  $P$  values\* for individual sites

$Y$	$X$	Wetter, high P	Wetter, low P	Drier, high P	Drier, low P
$A_{\text{mass}}$	$N_{\text{mass}}$	1.55 (1.01, 2.37), 0.56, 0.016	0.83 (0.51, 1.36), 0.37, 0.146	1.98 (1.52, 2.59), 0.80, <0.001	1.43 (0.92, 2.23), 0.29, 0.207
$A_{\text{area}}$	$N_{\text{area}}$	0.78 (0.49, 1.24), 0.41, 0.095	0.85 (0.54, 1.36), 0.49, 0.048	0.92 (0.59, 1.36), 0.06, 0.803	0.81 (0.52, 1.26), 0.34, 0.133
$A_{\text{mass}}$	SLA	1.30 (0.93, 1.84), 0.75, <0.001	0.83 (0.53, 1.31), 0.52, 0.034	1.16 (0.94, 1.43), 0.89, <0.001	0.89 (0.64, 1.24), 0.72, <0.001
$N_{\text{mass}}$	SLA	0.84 (0.52, 1.37), 0.31, 0.208	1.00 (0.62, 1.62), 0.43, 0.086	0.59 (0.46, 0.74), 0.85, <0.001	0.62 (0.41, 0.94), 0.48, 0.029
$P_{\text{mass}}$	$N_{\text{mass}}$	0.82 (0.50, 1.35), 0.25, 0.318	0.68 (0.40, 1.15), 0.003, 0.992	1.06 (0.77, 1.45), 0.71, <0.001	1.09 (0.77, 1.53), 0.69, 0.001
$A_{\text{mass}}$	$P_{\text{mass}}$	1.88 (1.13, 3.13), 0.02, 0.953	1.23 (0.75, 2.00), 0.39, 0.124	1.87 (1.36, 2.57), 0.70, <0.001	1.32 (0.90, 1.93), 0.57, 0.007
$P_{\text{mass}}$	SLA	0.69 (0.42, 1.15), 0.03, 0.906	0.67 (0.42, 1.09), 0.44, 0.076	0.62 (0.50, 0.77), 0.88, <0.001	0.68 (0.48, 0.96), 0.67, 0.001
$R_{\text{d-mass}}$	$N_{\text{mass}}$	1.31 (0.86, 2.00), 0.58, 0.011	1.28 (0.83, 1.99), 0.57, 0.016	1.95 (1.45, 2.62), 0.75, <0.001	1.53 (1.01, 2.30), 0.48, 0.027
$R_{\text{d-area}}$	$N_{\text{area}}$	0.91 (0.62, 1.33), 0.68, 0.002	0.74 (0.45, 1.24), 0.27, 0.303	1.44 (0.96, 2.16), 0.40, 0.058	0.91 (0.61, 1.36), 0.51, 0.019
$R_{\text{d-mass}}$	SLA	1.11 (0.71, 1.72), 0.50, 0.034	1.28 (0.90, 1.83), 0.75, 0.001	1.14 (0.83, 1.56), 0.71, <0.001	0.95 (0.67, 1.36), 0.66, 0.001
$R_{\text{d-mass}}$	$A_{\text{mass}}$	0.85 (0.57, 1.26), 0.64, 0.004	1.54 (0.94, 2.51), 0.38, 0.136	0.98 (0.70, 1.39), 0.63, 0.001	1.07 (0.73, 1.56), 0.58, 0.006
$A_{\text{area}}$	$G_s$	0.98 (0.66, 1.45), 0.66, 0.003	1.28 (0.87, 1.87), 0.71, 0.002	0.95 (0.65, 1.38), 0.54, 0.007	0.64† (0.46, 0.89), 0.72, <0.001

\* $P$  values refer to the null hypothesis that the traits would have a correlation of 0, although this is not strictly correct as we expected all leaf traits to be positively associated based on reports in the literature (see Introduction).

†With the outlier *Eutaxia microphylla* removed (see text) the slope was 0.77 (0.57, 1.02),  $r = 0.80$ ,  $P < 0.001$ .

$P_{\text{mass}}$  added 15% (high rain) to 27% (low rain) explanatory power after  $N_{\text{mass}}$  to multiple regression models predicting  $A_{\text{mass}}$  with the regression coefficients for  $P_{\text{mass}}$  higher than those for  $N_{\text{mass}}$  (Table 3). In contrast, adding  $P_{\text{mass}}$  made little difference at nutrient-rich sites (2–3% extra explanatory power), with the regression coefficients for  $N_{\text{mass}}$  higher than for  $P_{\text{mass}}$  in these cases.

#### LEAF DARK RESPIRATION ( $R_{\text{d-mass}}$ AND $R_{\text{d-area}}$ )

$R_{\text{d-mass}}$  was positively related to  $N_{\text{mass}}$  at all sites (Fig. 4a). Individual slopes did not differ between sites, with a common slope of 1.6 indicating that  $R_{\text{d-mass}}$  scaled greater than proportionally with leaf N. At a given  $N_{\text{mass}}$ ,  $R_{\text{d-mass}}$  was higher at the high-rain, nutrient-poor site than at either dry site, and marginally higher than at the high-rain, nutrient-rich site ( $P = 0.068$ ).  $R_{\text{d-area}}$  was positively related to  $N_{\text{area}}$  at each site (Table 2), with no differences between slopes ( $P = 0.173$ ) or elevations ( $P = 0.191$ ), and a common slope of 0.98.

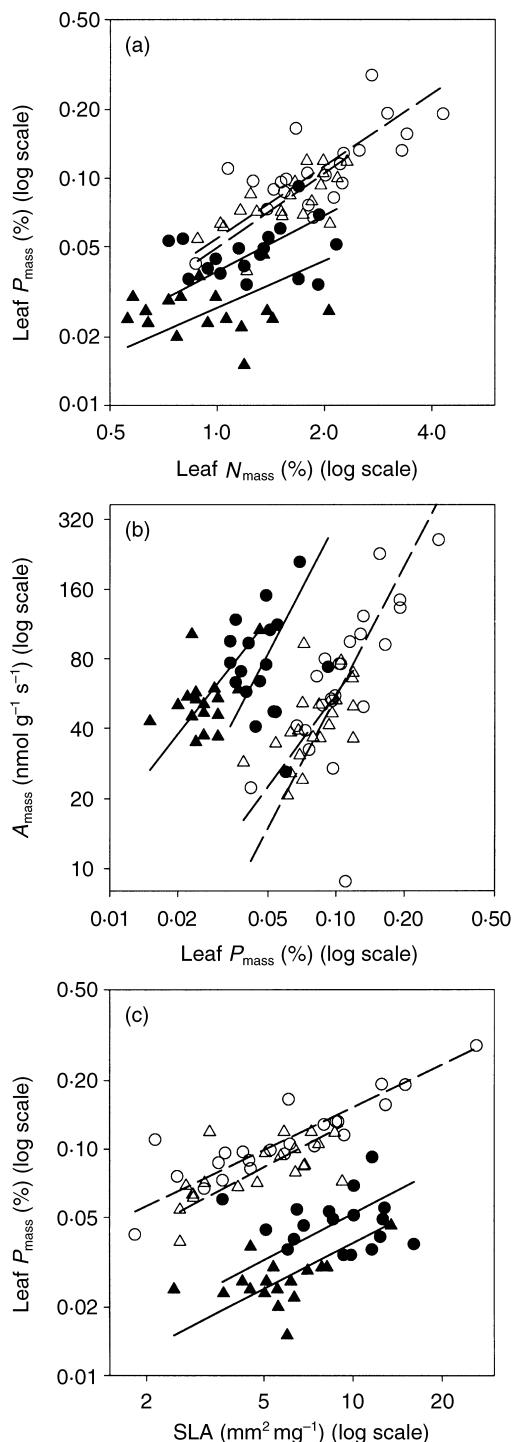
$R_{\text{d-mass}}$  was positively related to SLA at all sites (Fig. 4b), with non-heterogeneous individual slopes (common slope 1.1).  $R_{\text{d-mass}}$  was clearly higher at dry sites at a given SLA, following the elevation differences between  $N_{\text{mass}}$ –SLA slopes. In addition, slope elevation was higher at low nutrients when comparing the two wetter sites. Multiple regressions of  $R_{\text{d-mass}}$  on SLA and  $N_{\text{mass}}$  (expectation 5) indicated that the  $R_{\text{d-mass}}$ –SLA and  $R_{\text{d-mass}}$ – $N_{\text{mass}}$  relationships were somewhat independent of each other. For example, with species pooled by rainfall,  $R_{\text{d-mass}}$  increased with  $N_{\text{mass}}$  at a given SLA and increased with SLA at a given  $N_{\text{mass}}$  (Table 3). Similar results were obtained in regressions run for each site individually, although with wider confidence intervals (and reduced statistical power) the regression coefficients were significantly  $>0$  in few cases (results not shown).

$R_{\text{d-mass}}$  scaled positively with  $A_{\text{mass}}$ , with clear differences in slope elevation but not in slope indicating that dry-site species had  $\approx 1.8$ -fold higher  $R_{\text{d-mass}}$  at a given  $A_{\text{mass}}$  (Fig. 4c). The common fitted slope of 1.04

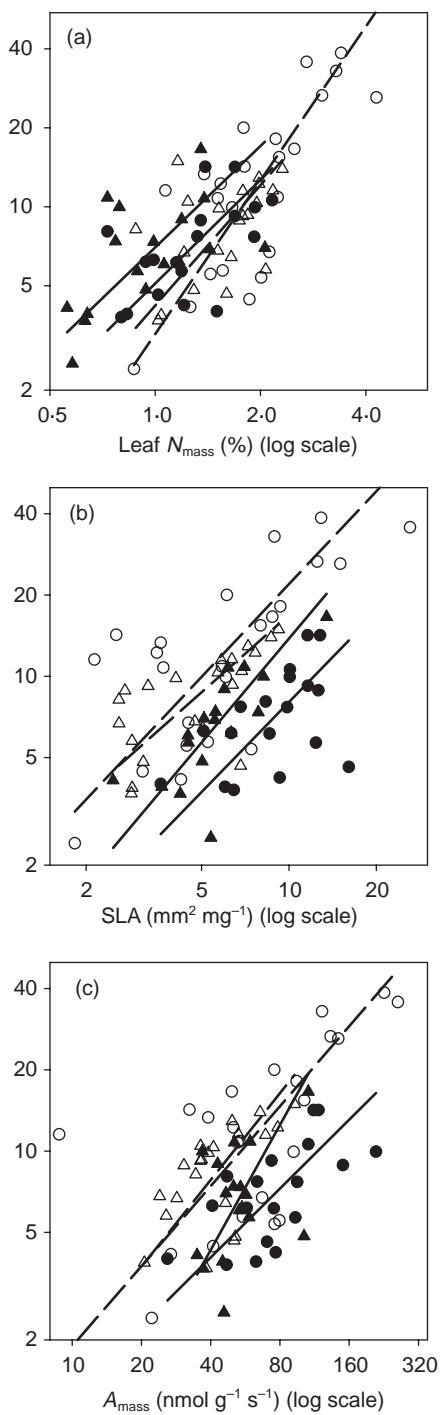
**Table 3.** Model 1 multiple regressions (species pooled by rainfall) of  $A_{\text{mass}}$  against  $N_{\text{mass}}$  and SLA, and  $R_{\text{d-mass}}$  against  $N_{\text{mass}}$  and SLA

	Variables		Wet sites			Dry sites		
	Dependent	Independent	$r^2$ , $F$	$\beta$	$P$	$r^2$ , $F$	$\beta$	$P$
$\log A_{\text{mass}}$	$\log N_{\text{mass}}$		0.57, 21.1	0.31 (−0.02, 0.64)	0.068	0.72, 53.4	0.31 (−0.14, 0.77)	0.173
	SLA			0.62 (0.34, 0.90)	<0.001		0.81 (0.53, 1.09)	<0.001
	Intercept			1.27 (1.03, 1.50)	<0.001		1.06 (0.91, 1.21)	<0.001
$\log R_{\text{d-mass}}$	$\log N_{\text{mass}}$		0.42, 11.6	0.44 (0.06, 0.81)	0.025	0.58, 27.7	0.72 (0.17, 1.28)	0.012
	SLA			0.39 (0.07, 0.71)	0.019		0.46 (0.12, 0.81)	0.010
	Intercept			0.48 (0.21, 0.75)	0.001		0.49 (0.31, 0.67)	<0.001
High P	$\log A_{\text{mass}}$	$\log N_{\text{mass}}$	0.33, 3.66	0.92 (0.19, 1.64)	0.016	0.68, 21.3	1.21 (0.47, 1.96)	0.003
	$\log P_{\text{mass}}$			−0.25 (−1.13, 0.63)	0.553		0.50 (−0.20, 1.20)	0.154
	Intercept			1.45 (0.26, 2.64)	0.020		1.94 (1.10, 2.79)	<0.001
Low P	$\log A_{\text{mass}}$	$\log N_{\text{mass}}$	0.29, 2.79	0.31 (−0.10, 0.71)	0.126	0.35, 4.78	−0.29 (−1.07, 0.50)	0.455
	$\log P_{\text{mass}}$			0.47 (−0.12, 1.07)	0.109		0.93 (0.21, 1.66)	0.015
	Intercept			2.48 (1.53, 3.43)	<0.001		2.70 (1.79, 3.61)	<0.001

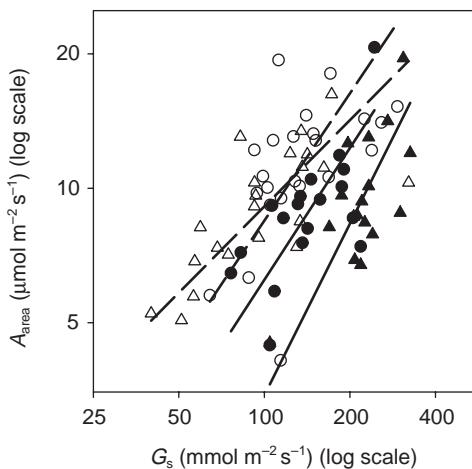
95% confidence intervals for partial regression coefficients are given in parentheses.



**Fig. 3.**  $P_{\text{mass}}$  versus other traits, symbols as for Fig. 2. (a)  $P_{\text{mass}}$  on  $N_{\text{mass}}$ . Individual slopes did not differ ( $P = 0.392$ ), common slope of 0.97 (0.75, 1.22).  $P_{\text{mass}}$  was higher at a given  $N_{\text{mass}}$  for species from drier sites (pairwise rainfall contrasts, all  $P < 0.001$ ), and for species at the nutrient-rich site within the high-rainfall zone ( $P = 0.021$ ). (b)  $A_{\text{mass}}$  on  $P_{\text{mass}}$ . Individual slopes did not differ ( $P = 0.308$ ), common slope of 1.58 (1.36, 1.86).  $A_{\text{mass}}$  was higher at a given  $P_{\text{mass}}$  for species from wetter sites (pairwise rainfall contrasts, all  $P < 1 \times 10^{-9}$ ), and for species at the nutrient-poor site within the high-rainfall zone ( $P = 0.003$ ). (c)  $P_{\text{mass}}$  on SLA. Individual slopes did not differ ( $P = 0.951$ ), common slope of 0.65 (0.41, 0.95).  $P_{\text{mass}}$  was higher at a given SLA for species at drier sites (pairwise rainfall contrasts, all  $P < 1 \times 10^{-10}$ ), and for species at the nutrient-rich sites within each rainfall zone (pairwise nutrient contrasts, all  $P < 0.02$ ).



**Fig. 4.** Foliar dark respiration versus other traits. Symbols as for Fig. 2. (a)  $R_{\text{d-mass}}$  on  $N_{\text{mass}}$ . Individual slopes did not differ ( $P = 0.292$ ), common slope of 1.57 (1.36, 1.82). At a given  $N_{\text{mass}}$ ,  $R_{\text{d-mass}}$  was higher at the high-rainfall, nutrient-poor site than at either dry site ( $P = 0.003$ ), and marginally higher than at the high-rainfall, nutrient-poor site ( $P = 0.068$ ). No difference in slope elevation was found between the two dry sites. (b)  $R_{\text{d-mass}}$  on SLA. Individual slopes did not differ ( $P = 0.698$ ), common slope of 1.12 (0.92, 1.36).  $R_{\text{d-mass}}$  was higher at a given SLA at dry sites (pairwise rainfall contrasts, all  $P < 1 \times 10^{-5}$ ), and higher on nutrient-poor soil when comparing the two wetter sites ( $P = 0.019$ ). No difference in elevation was found between dry sites. (c)  $R_{\text{d-mass}}$  on  $A_{\text{mass}}$ . Slopes did not differ ( $P = 0.296$ ), common slope of 1.04 (0.86, 1.27).  $R_{\text{d-mass}}$  was higher at a given  $A_{\text{mass}}$  for dry-site species (pairwise rainfall contrasts, all  $P < 0.002$ ), no difference within either rainfall zone.



**Fig. 5.**  $A_{\text{area}}$  on  $G_s$ , symbols as for Fig. 2. Assuming a common slope fitted across all sites of 0.94 (0.81, 1.11; see text), dry-site species had higher  $A_{\text{area}}$  at a given  $G_s$  (pairwise rainfall contrasts, all  $P < 0.007$ ), with an additional difference between nutrient-rich and nutrient-poor sites at high rainfall only ( $P = 0.002$ ).

indicated that  $R_{\text{d-mass}}$  and  $A_{\text{mass}}$  scaled proportionally with one another.

#### STOMATAL CONDUCTANCE TO WATER

$A_{\text{area}}$  increased with stomatal conductance ( $G_s$ ) within each site (Fig. 5). Slopes were weakly heterogeneous ( $P = 0.054$ ), with this effect driven strongly by one species at the drier, nutrient-poor site (*Eutaxia microphylla*). Slopes were non-heterogeneous with this species removed ( $P = 0.204$ , common slope 0.94), with higher  $A_{\text{area}}$  at a given  $G_s$  (i) at dry sites (highly significant in all pairwise contrasts; 1.3- to 2.1-fold higher), and (ii) at high versus low soil nutrients, comparing the two wetter sites (1.4-fold higher). Site mean  $G_s$  was similar, but  $A_{\text{area}}$  was higher for the dry than for the wet site when comparing species on nutrient-rich soils ( $P = 0.580$ ,  $P = 0.036$ , respectively), but  $G_s$  was lower at the dry site and  $A_{\text{area}}$  was similar when comparing species on nutrient-poor soils ( $P = 2 \times 10^{-7}$ ,  $P = 0.635$ ).

#### Discussion

##### BROAD TRENDS: SHIFTS IN TRAIT MEANS BETWEEN HABITAT TYPES

As predicted (expectation 1), species from nutrient-poor soils had generally lower leaf N and P concentrations and photosynthetic capacities than those from nutrient-rich soils, as well as deploying less leaf surface per unit leaf mass (SLA). Species with low SLA (generally thicker and/or higher density leaves; Niinemets 1999) tend to have long-lived leaves, at least partly because structural reinforcement renders them less susceptible to herbivory and other physical hazards (Chabot & Hicks 1982; Reich *et al.* 1997; Wright & Cannon 2001). Long leaf lifespan in resource-poor environments is generally thought to enhance nutrient

conservation, and to provide a longer time for the amortization of leaf construction costs in species with low rates of carbon gain (Aerts & van der Peijl 1993; Chabot & Hicks 1982; Chapin 1980; Kikuzawa 1991).

Species from drier habitats had generally higher leaf N per area than those from wetter sites, as predicted (expectation 2), as well as higher  $N_{\text{mass}}$ ,  $P_{\text{mass}}$  and  $P_{\text{area}}$ . The expected inverse trend in SLA (lower at drier sites) was partially supported by the data. Anatomically, higher  $N_{\text{mass}}$  could reflect a larger volume fraction of mesophyll cells within the leaf (Roderick *et al.* 1999). Dry-site species also tended to have higher dark respiration rates.

Despite these broad differences in leaf traits between habitats, it is important to recognize that trait variation within any one habitat tended to be larger than the mean difference between any two habitats. For this reason, it tends to be more informative to look at trait relationships rather than trends in leaf traits one at a time.

#### SCALING RELATIONSHIPS BETWEEN LEAF TRAITS

Some unifying results emerged using the conservative approach of calculating common slopes where individual SMA slopes did not differ in slope or elevation. As expected (expectation 3), photosynthetic capacity, dark respiration rate, leaf nutrients and SLA were positively associated in common slopes fitted across sites or rainfall zones, if only weakly within some individual sites. Reich *et al.* (1999) suggested that the similarity of co-ordinated relationships among leaf traits in disparate habitats provides strong evidence of convergent evolution. The 79 species studied here were taxonomically diverse and included a range of growth forms and leaf types, extending the generality of the relationships reported by Reich *et al.* (1997) and Reich *et al.* (1999) to another continent and to floras largely unlike those studied previously.

$A_{\text{mass}}$  and  $R_{\text{d-mass}}$  increased more steeply with  $N_{\text{mass}}$  than when axes were re-scaled (via SLA) to area-based rather than mass-based expressions.  $A_{\text{mass}}$  and  $R_{\text{d-mass}}$  increased close to 1 : 1 with SLA and with each other. SLA and  $N_{\text{mass}}$  were themselves positively associated, but less than proportionally, such that a doubling in SLA was associated with a 1.6-fold increase in  $N_{\text{mass}}$ . From multiple regressions it was apparent that leaf N and SLA have partially independent effects on dark respiration rate, as predicted (expectation 5), although less so on photosynthetic capacity. That is, at a given N concentration  $A_{\text{mass}}$  and  $R_{\text{d-mass}}$  increased with SLA, while at a given SLA  $R_{\text{d-mass}}$  and (perhaps)  $A_{\text{mass}}$  increased with increasing  $N_{\text{mass}}$ . Therefore the steep bivariate relationships between  $N_{\text{mass}}$  and each of  $R_{\text{d-mass}}$  and  $A_{\text{mass}}$  appeared to be composites of the less steep  $N_{\text{mass}}$ -SLA,  $A_{\text{mass}}$ -N and  $R_{\text{d-mass}}$ -N relationships.

Presumably photosynthetic capacity and leaf N are correlated because the bulk of leaf N is found in the photosynthetic complex (Field & Mooney 1986;

Lambers, Chapin & Pons 1998). Higher-SLA leaves tend to have less structural material relative to metabolic components, less internal shading and shorter gas diffusion paths (Parkhurst 1994; Terashima & Hikosaka 1995), presumably contributing to the association between  $A_{\text{mass}}$  and SLA at a given leaf N. Probably dark respiration rate increases with leaf N (at a given SLA) because, to a large extent,  $R_{\text{d-mass}}$  reflects protein turnover (Penning de Vries 1975; Ryan 1995), but also because phloem loading of photosynthates contributes to  $R_{\text{d-mass}}$  (Amthor 2000; Cannell & Thornley 2000), and high-N species had higher photosynthetic capacity. Similarly, the increase in  $R_{\text{d-mass}}$  with SLA (at a given leaf N) may have reflected increased phloem-loading associated with the higher  $A_{\text{mass}}$  of high-SLA species at a given leaf N.

#### ELEVATION DIFFERENCES IN SCALING RELATIONSHIPS

Although there were few significant differences in the slope of trait relationships between habitat types, differences in elevation were identified in many cases (expectation 4; shift type 2 in Fig. 1). Elevation differences with soil nutrient status occurred only at wetter sites, with species at the nutrient-rich site having (i) higher  $P_{\text{mass}}$  at a given  $N_{\text{mass}}$  or SLA; (ii) lower  $R_{\text{d-mass}}$  at a given  $N_{\text{mass}}$  or SLA; and (iii) lower  $A_{\text{area}}$  at a given  $G_s$ .

More notably, there were a number of elevation differences associated with rainfall. On average, dry-site species had (i) lower photosynthetic capacity at a given leaf N or P (per mass or per area); (ii) higher  $N_{\text{mass}}$  or  $P_{\text{mass}}$  at a given SLA (implying that they had higher  $N_{\text{area}}$  and  $P_{\text{area}}$ ); (iii) higher  $P_{\text{mass}}$  at a given  $N_{\text{mass}}$ ; (iv) higher  $R_{\text{d-mass}}$  at a given SLA or  $A_{\text{mass}}$  (generally following trends in N, although they also had somewhat higher  $R_{\text{d-mass}}$  at a given  $N_{\text{mass}}$ ); (v) lower  $A_{\text{area}}$  at a given  $G_s$ . These trends appear to be part of a previously undocumented difference in leaf trait syndromes of high- and low-rainfall species.

#### LEAF TRAIT SYNDROMES OF HIGH- VERSUS LOW-RAINFALL SPECIES

Low-rainfall species appeared to be engaging in a strategy that reduces water loss during photosynthesis, but incurs higher relative respiratory costs than for high-rainfall species. Water loss (transpiration) is largely a function of stomatal and boundary-layer conductance to water and the vapour pressure difference (VPD) between the interior and exterior of a leaf (Lambers *et al.* 1998). Assuming near-saturation of intercellular air spaces within a leaf, the size of this VPD is largely determined by the relative humidity of the external air and leaf temperature (Jones 1983). Thus at a given temperature, species at a low-humidity site would have higher leaf-to-air VPDs than species from a wetter site, and higher transpiration rates at a given  $G_s$ . For example, leaf-to-air VPDs were estimated to be 1·8-fold greater

at the drier sites in this study (based on average site temperature and relative humidity), indicating that dry-site species had higher average transpiration rates than wet-site species when comparing the nutrient-rich sites ( $P = 3 \times 10^{-5}$ ; where  $G_s$  did not differ between sites but  $A_{\text{area}}$  was higher at the dry site), but similar transpiration rates when comparing nutrient-poor sites ( $P = 0.098$ ; where  $G_s$  was lower at the dry site, but  $A_{\text{area}}$  did not differ). Thus species from dry sites achieved rates of carbon gain similar to (or higher than) wet-site species, with similar (or higher) transpiration rates also. Note, however, that these trends apply during active photosynthesis and do not imply that dry-site species fix as much carbon or use as much water as wet-site species over the course of a year.

Photosynthesis can be described using Fick's Law for the diffusion of gases, such that  $A_{\text{area}} = G_c(C_a - C_i)$ , where  $G_c$  is stomatal conductance to  $\text{CO}_2$ , and  $C_a$  and  $C_i$  are ambient and leaf internal  $\text{CO}_2$  concentrations, respectively (Lambers *et al.* 1998). As  $G_s$  is related to  $G_c$  by the molar diffusion ratio between  $\text{CO}_2$  and water, the result that dry-site species had lower  $A_{\text{area}}$  at a given  $G_s$  indicates that they also had lower  $C_i$  at a given  $G_s$  (or  $G_c$ ). The key question is how these species reduce  $C_i$  to these low concentrations, yet maintain net photosynthetic rates similar to, or somewhat higher than, species from more humid sites. It is likely that this was achieved via higher photosynthetic enzyme content (higher leaf N per mass or area). The benefit of higher leaf N in dry-site species appeared to be the ability to achieve a given  $A_{\text{area}}$  at a lower  $G_s$ , thus not losing more water than wet-site species. The cost of this water-conserving strategy was apparent in their lower photosynthetic capacity at a given leaf N and their higher dark respiration rates (absolutely, or at a given photosynthetic rate), although presumably additional (unmeasured) costs would be associated with the need for increased N acquisition and increased herbivory risk to high N leaves.

#### HOW GENERALLY DO LOW RAINFALL SPECIES HAVE HIGH $N_{\text{AREA}}$ ?

$N_{\text{area}}$  is the quotient of  $N_{\text{mass}}$  over SLA. Here, dry-site species had higher average  $N_{\text{mass}}$  and lower SLA than wet-site species, and hence considerably higher  $N_{\text{area}}$ . Higher  $N_{\text{mass}}$  has been suggested as a general property of arid-zone plants (Skujins 1981; West 1981). By contrast, taking a cost–benefit approach, Mooney & Gulmon (1979) argued that optimal leaf  $N_{\text{mass}}$  in arid-zone plants should be lower than that of species from more humid habitats, as photosynthetic rate would asymptote at a lower leaf enzyme content in plants subject to water stress (due to stomatal closure), while costs associated with higher enzyme concentrations would still increase linearly with greater leaf N. Considering data from many different studies, it now appears that there is no general relationship between  $N_{\text{mass}}$  and aridity (Killingbeck & Whitford 1996). However, it is likely that  $N_{\text{area}}$  is generally greater in

perennial plants of drier regions, based on their generally lower SLA (Cunningham *et al.* 1999; Maximov 1929; Mooney *et al.* 1978; Roderick, Berry & Noble 2000; Schulze *et al.* 1998; Specht & Specht 1989) and similar  $N_{\text{mass}}$ . Lower SLA is thought to confer an enhanced ability to withstand dry conditions without wilting to a point of permanent damage (Maximov 1929). We are aware of only a few reports on the relationship between  $N_{\text{area}}$  and site aridity – Killingbeck & Whitford (1996) reported results on a mass basis only – but the proposition of higher  $N_{\text{area}}$  at drier sites is supported by data from Cunningham *et al.* (1999); Mooney *et al.* (1978); and Reich *et al.* (1999).

Here we suggest that higher  $N_{\text{area}}$  in arid-zone species is associated with water conservation. Previously it has been related to the higher average irradiances experienced in the arid zone, such that leaves with high  $N_{\text{area}}$  achieve saturation of photosynthetic systems, whereas this would be unlikely in more mesic regions at the same  $N_{\text{area}}$  (Cunningham *et al.* 1999; Mooney *et al.* 1978). Here the shift in  $N_{\text{area}}$  between wet- and dry-site species was far larger than that in  $A_{\text{area}}$  (where any). While high  $N_{\text{area}}$  may indeed be partially related to high PAR levels, it appears that enhanced water conservation may be a more crucial outcome of a high- $N_{\text{area}}$  strategy. If these differences between species of arid and mesic habitats were found to be general across other continents, this may have wide implications for global carbon and nitrogen processes, and possibly for linking remote-sensed and spectral images to carbon-budget modelling, as well as for ecophysiology in general.

#### LEAF PHOSPHORUS

Common fitted slopes indicated that leaf P and N concentrations scaled positively with one another, although the relationships were loose at the wetter sites when considered individually, especially at the nutrient-poor site where there was little variation in  $P_{\text{mass}}$  between species. Still,  $P_{\text{mass}}$  showed a similar relationship to  $A_{\text{mass}}$ , as did  $N_{\text{mass}}$ , scaling together more steeply than proportionally. Presumably, photosynthetic capacity and leaf P are related because bioenergetic molecules such as ATP and NADPH play an integral part in metabolic processes such as photosynthesis and respiration (Atwell *et al.* 1999). In multiple regressions predicting  $A_{\text{mass}}$ ,  $P_{\text{mass}}$  added relatively little explanatory power after  $N_{\text{mass}}$  at nutrient-rich sites, but substantially more at nutrient-poor sites (partial support for expectation 6). Perhaps related to this trend,  $A_{\text{mass}} - N_{\text{mass}}$  slopes tended to be flatter and weaker at nutrient-poor sites, that is, photosynthesis at these sites may be relatively more P-limited than on nutrient-rich soils.

#### CONCLUSIONS: CONVERGENT EVOLUTION AND STRATEGY SHIFTS BETWEEN HABITATS

SMA (and related) analyses have been used for several decades in describing trait relationships where both  $Y$

and  $X$  variables have sampling error, and model 1 techniques are inappropriate (Sokal & Rohlf 1995). However, until now no method has been available for the multiple comparison of SMA slopes and the calculation of common slopes where non-heterogeneity can be demonstrated. Combined with the question form we used in this study (ellipse shifts; see Fig. 1), we believe significant progress can be made in describing and understanding to what extent cross-species trait relationships are similar – or have converged – in different habitat types. The idea of convergent evolution is generally taken to mean convergence towards some specified value for a trait of interest. However, for any habitat there is no apparent single ‘best solution’ for the type of traits under study here. Rather, there appears to be a spectrum of viable solutions. The leaf traits are correlated across species, and observed combinations of these co-ordinated traits fall within envelopes whose principal axes can be described by simple scaling relationships.

The data presented here have the effect of improving the quantification of these patterns, of extending generalizations between continents, and of including P data in combination with photosynthesis, dark respiration, stomatal conductance and leaf N data. However, the main new contribution of this work is organized comparisons between habitats differing in rainfall and soil nutrients, permitting us to investigate whether species differences between these habitat types consisted of shifts along a common scaling relationship, or rather of shifts in elevation of the scaling relationship (Fig. 1). Shifts in species strategies between high- and low-rainfall species mostly took the form of relatively large shifts between principal axes (shift type 2; Fig. 1) and were found in comparisons at either level of soil nutrients. By contrast, shifts in strategies between nutrient-rich and nutrient-poor soils were most pronounced for the high-rainfall sites, taking the form of shifts along the principal axis of a spectrum of variation in some cases (shift type 1; Fig. 1), and of relatively small shifts between principal axes in other cases. Thus while the basic relationship between pairs of traits differed relatively little, the boundaries of these solution envelopes varied with site aridity more than with site nutrient status, and often consisted of a different type of shift.

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