RESEARCH PAPER

Modulation of leaf economic traits and trait relationships by climate

Ian J. Wright[1,*], Peter B. Reich[2], Johannes H. C. Cornelissen[3], Daniel S. Falster[4], Philip K. Groom[5], Kouki Hikosaka[6], William Lee[7], Christopher H. Lusk[8], Ülo Niinemets[9], Jacek Oleksyn[2,10], Noriyuki Osada[6,11], Hendrik Poorter[12], David I. Warton[13] and Mark Westoby[1]

[1]*Department of Biological Sciences, Macquarie University, NSW 2109, Australia,* [2]*Department of Forest Resources, University of Minnesota, St Paul, Minnesota 55108, USA,* [3]*Institute of Ecological Science, Department of Systems Ecology, Vrije Universiteit, Amsterdam, The Netherlands,* [4]*Faculty of Medicine, University of Oslo, 0315 Oslo, Norway,* [5]*Department of Environmental Biology, Curtin University of Technology, Perth, WA 6845, Australia,* [6]*Graduate School of Life Sciences, Tohoku University, Aoba, Sendai 980–8578, Japan,* [7]*Landcare Research, Private Bag 1930, Dunedin, New Zealand,* [8]*Departamento de Botánica, Universidad de Concepción, Concepción, Chile,* [9]*Department of Plant Physiology, University of Tartu, Riia 23, Tartu 51011, Estonia,* [10]*Polish Academy of Sciences, Institute of Dendrology, Parkowa 5, 62–035 Kornik, Poland,* [11]*Nikko Botanical Garden, Graduate School of Science, University of Tokyo, Japan,* [12]*Plant Ecophysiology, Utrecht University, Utrecht, The Netherlands, and* [13]*Department of Statistics, School of Mathematics, University of New South Wales, NSW 2052, Australia*

Correspondence: Ian J. Wright, Department of Biological Sciences, Macquarie University, NSW 2109, Australia. E-mail: iwright@rna.bio.mq.edu.au

ABSTRACT

Aim Our aim was to quantify climatic influences on key leaf traits and relationships at the global scale. This knowledge provides insight into how plants have adapted to different environmental pressures, and will lead to better calibration of future vegetation–climate models.

Location The data set represents vegetation from 175 sites around the world.

Methods For more than 2500 vascular plant species, we compiled data on leaf mass per area (LMA), leaf life span (LL), nitrogen concentration (N_{mass}) and photosynthetic capacity (A_{mass}). Site climate was described with several standard indices. Correlation and regression analyses were used for quantifying relationships between single leaf traits and climate. Standardized major axis (SMA) analyses were used for assessing the effect of climate on bivariate relationships between leaf traits. Principal components analysis (PCA) was used to summarize multidimensional trait variation.

Results At hotter, drier and higher irradiance sites, (1) mean LMA and leaf N per area were higher; (2) average LL was shorter at a given LMA, or the increase in LL was less for a given increase in LMA (LL–LMA relationships became less positive); and (3) A_{mass} was lower at a given N_{mass}, or the increase in A_{mass} was less for a given increase in N_{mass}. Considering all traits simultaneously, 18% of variation along the principal multivariate trait axis was explained by climate.

Main conclusions Trait-shifts with climate were of sufficient magnitude to have major implications for plant dry mass and nutrient economics, and represent substantial selective pressures associated with adaptation to different climatic regimes.

Keywords

Irradiance, leaf mass per area, leaf life span, nitrogen, photosynthesis, plant strategies, rainfall, temperature.

INTRODUCTION

Plant ecologists have long been interested in quantifying how leaf morphology and physiology vary with climate. For example, plants adapted to low rainfall tend to have thick, leathery leaves (Schimper, 1903; Maximov, 1929; Turner, 1994; Fonseca *et al.*, 2000) and a high concentration of nitrogen per unit leaf area (Cunningham *et al.*, 1999; Wright *et al.*, 2001). Many plants growing in high irradiance habitats share these traits also (Niinemets, 2001). For some decades now, ecologists have also been aware that key leaf properties tend to show predictable relationships with one another. In particular, species with

high leaf mass per area (LMA) tend to have long average leaf life span (LL), low nutrient concentrations and slow maximum photosynthetic and dark respiration rates (Field & Mooney, 1986; Reich *et al.*, 1992, 1997; Turner, 1994; Enriquez *et al.*, 1996; Diemer, 1998; Niinemets, 1999). Together, these traits form a spectrum of 'leaf economics' (Wright *et al.*, 2004), running from species with potential for quick returns on investments of nutrients and dry mass in leaves (e.g. species with low LMA, such as many herbs, grasses and deciduous trees) to species with a slower potential rate of return in terms of carbon acquisition (e.g. many evergreen shrubs and trees with high LMA).

Quantifying correlations among leaf traits and how traits differ between growth forms and plant functional types (PFTs) not only gives insight into the selective pressures that have shaped the evolution of the world's vegetation, but is also crucial for reliable calibration of models designed to predict vegetation and productivity shifts with climate and land use change. Most vegetation–climate models represent the vegetation in any grid-square with a frequency distribution of PFTs. Each PFT is assigned a set of typical properties, often including leaf traits such as LMA (or its inverse, SLA), LL, leaf N concentration (N_{mass}) and photosynthetic rate. Modellers have begun using trait correlations from broad, comparative studies for assigning trait values. For example, the Lund-Potsdam-Jena Dynamic Global Vegetation Model (DGVM) (Sitch *et al.*, 2003) calculates SLA for each PFT from an assigned LL value using the SLA–LL relationship reported by Reich *et al.* (1997), whereas the Ecosystem Demography model (Moorcroft *et al.*, 2001) calculates both leaf N concentration and SLA from LL, again following Reich *et al.* (1997). Naturally, model output is considerably affected by the choice of trait values assigned to each PFT. In one of the few published sensitivity analyses that we are aware of, the relative importance of parameter variation for predicting annual net primary production (NPP) was assessed for the BIOME-BGC model (White *et al.*, 2000). All biomes were strongly affected by variation in leaf and fine root C:N ratios. In addition, woody biomes were strongly affected by leaf traits such as the percentage of leaf N in Rubisco, maximum stomatal conductance, and SLA.

One issue in assigning relevant leaf trait values to PFTs is that the magnitude of variation within PFTs may be greater than the difference in trait-means among them (Wright *et al.*, 2005). Another is that the relationships between key leaf traits may shift predictably with climate. For example, both regionally and globally, LL–LMA relationships tend to be shifted such that species from lower rainfall sites have shorter LL at a given LMA (Reich *et al.*, 1999; Wright *et al.*, 2002, 2004). And, among woody perennials from eastern Australia, species from lower rainfall sites achieve lower maximum photosynthetic rate (A_{mass}) at a given N_{mass} (Wright *et al.*, 2001). We suggest that this sort of information should be incorporated into future vegetation–climate models.

In order to understand better how site properties affect leaf traits and trait relationships at the global scale, we have drawn together trait information for more than 2500 vascular plant species from 175 sites around the world. The coverage of traits, species and sites is substantially greater than previous data compilations (Field & Mooney, 1986; Schulze *et al.*, 1994; Reich *et al.*, 1997; Diemer, 1998; Niinemets, 2001), extends to all vegetated continents and represents a wide range of vegetation types. In previous papers, we summarized broad-scale patterns from the data set such as patterning of leaf traits and trait relationships according to growth form, plant functional type and sample size (Wright *et al.*, 2005), and the patterning of LL–LMA relationships by site rainfall (Wright *et al.*, 2004). Here we present a number of more comprehensive analyses concerning the effect of climate on leaf traits and leaf trait relationships. The traits considered were LMA, LL, leaf N concentration per unit leaf mass and area (N_{mass}, N_{area}) and photosynthetic 'capacity' (measured under ambient CO_2 concentration, near-saturating light and relatively well watered conditions; A_{mass}, A_{area}). Site climate was described with standard indices: temperature, rainfall, global radiation, potential evapotranspiration and vapour pressure deficit.

We asked three types of questions:
(1) How do the leaf traits vary with climate, at the global scale? These relationships were quantified using (i) individual species at each site and (ii) site means as the unit of replication.
(2) To what extent are bivariate trait relationships modulated by climate?
(3) How much variation does climate explain along the first two principal component axes summarizing multivariate variation in LL, LMA, N_{mass} and A_{mass}?

We report the effect of climate on only a subset of all the possible pairwise leaf trait relationships: those between LL and each of LMA and A_{mass}, and those between photosynthetic capacity and each of LMA and leaf N concentration. The LL–LMA relationship is thought to reflect a trade-off, with lower LMA indicating greater potential for fast growth (more leaf area deployed for a given dry mass investment), but longer LL indicating longer duration of the revenue stream from that investment, and enhanced nutrient conservation (Escudero *et al.*, 1992; Westoby *et al.*, 1998; Eckstein *et al.*, 1999; Aerts & Chapin, 2000). The linkage between LL and A_{mass} has been emphasized in models seeking to understand the costs and benefits of different leaf phenologies, with A_{mass} being a major determinant of the time taken to pay back the construction cost of a leaf (Kikuzawa, 1991; Poorter, 1994; Kikuzawa & Ackerly, 1999; Givnish, 2002). Variations in both leaf structure and leaf N content have been shown to affect photosynthetic capacity (Field & Mooney, 1986; Reich *et al.*, 1998; Wright *et al.*, 2001). Thus, each of these relationships is important for the dry mass and nutrient economics of vegetation. We also ran a subset of analyses for evergreen species considered on their own, and (less commonly) for deciduous species, these being commonly used PFTs. These results were then compared to those seen across the whole data set.

METHODS

Leaf and climate data

Data were compiled from both published and unpublished sources. A data set was considered suitable providing that it contained data for at least two leaf traits of interest for at least four species co-occurring in the field. Only site-based data sets were used; that is, those to which we could reasonably attach climate data. The total database consists of 2548 species/site combinations from 175 sites: 2021 different species in total, with 342 species occurring at more than one site. Data sources and the data set itself are available in online Appendices associated with Wright *et al.* (2004). Site mean annual temperature (MAT) ranged from −16 °C to 27.5 °C; mean annual rainfall ranged from 133 to 5300 mm per year. This covers most of the range of MAT–rainfall space in which higher plants are found (Whittaker, 1975).

Mean annual and monthly temperature and precipitation data were compiled for each site. For a small number of sites (< 20),

Table 1 Correlations (*r* and *P* values) between climate variables assigned to each of the 175 sites. Abbreviations: MAT, mean annual temperature, VPD, vapour pressure deficit; PET, Penman–Monteith potential evapotranspiration; irradiance, daily mean global radiation

	MAT	VPD	PET	Irradiance
Rainfall	0.34 (< 0.001)	−0.05 (0.474)	0.03 (0.697)	−0.01 (0.928)
MAT		0.70 (< 0.001)	0.81 (< 0.001)	0.65 (< 0.001)
VPD			0.77 (< 0.001)	0.84 (< 0.001)
PET				0.75 (< 0.001)

climate data were available from the sites themselves. Otherwise, data were taken from the source publications from which leaf data were obtained (where given) or from the nearest weather stations, with temperature data scaled where necessary by an altitudinal lapse rate of 0.6 °C per 100 m (Körner, 1999). Climate data were also extracted from a global, interpolated $0.5 \times 0.5°$ data set containing monthly means (1961–90) for temperature, rainfall, water vapour pressure (VP) and global radiation (New *et al.*, 1999). Temperature and rainfall from the global data set were used for sites where we were unable to obtain suitable weather station data ourselves. MAT and rainfall estimates from the global data set agreed closely with site-specific or nearby-station data in most cases, giving us confidence in the VP and irradiance estimates also. Neighbouring grid-squares in the global data set were explored for better-matching data for sites where the MAT and rainfall estimates differed by > 10% (mostly mountain sites). When a close match was found, VP and radiation data were taken from that grid-square. Otherwise, VP for mountain sites was scaled using an empirical formula expressing the exponential decrease of VP with altitude (Barry, 1981). Monthly means of vapour pressure deficit (VPD) were estimated as the difference between the saturation VP of air (at the monthly mean temperature) and VP taken from the global data set. Saturation VP was calculated using the Tetens formula (Campbell & Norman, 1998). Irradiance data were not adjusted for altitude because increases in cloud cover with elevation tend to offset the increase in radiation that would be observed in clear air, though this may not always be true for high elevation sites in arid regions (Barry, 1981; Körner, 1999). Penman–Monteith potential evapotranspiration (PET) was also estimated for each site, sourced from a global $0.5 \times 0.5°$ data set calculated for the period 1987–88 (Choudhury, 1997). The albedo and surface resistance constants used for calculating PET in this data set were for actively growing, well-watered grass, so PET should be thought of as a reference value rather than as accurately describing the evapotranspiration of the vegetation at each site. PET was estimated for the problematic mountain sites from a regression equation fitted to all other sites, considering PET as a function of MAT and annual rainfall ($r^2 = 0.71$).

Climate variables were summed (rainfall) or averaged (other variables) across all months of the year, and across those months with mean temperature of ≥ 5 °C, giving an estimate of climate during the growth season. Results using yearly and growth-season climate indices were similar; hence for brevity, we only report results relating to yearly climate averages. Naturally, climate variables were cross-correlated to an extent. Across the 175 sites, VPD, PET and solar irradiance were more closely associated

with MAT than with mean annual rainfall (Table 1) although, clearly, both MAT and rainfall affect a property such as VPD.

Means of leaf traits were calculated for each species at a site where this was not already reported. Where traits were reported separately for sun leaves and shade leaves, sun–leaf data were used. If data were presented separately for recently matured and old leaves, recently matured leaves were used. That is, data for leaves closer to their 'peak' physiological stage were used where there was a choice (i.e. prior to significant age- or light-related decline in nutrient contents and photosynthetic capacity). Photosynthesis and leaf N source data were variously reported on a leaf mass or on a leaf area basis. Both formulations are of interest, and these were interconverted via LMA where this was reported as well.

Data analysis

All leaf traits were approximately log-normally distributed across the data set, as were site rainfall and VPD. Accordingly, these variables were log_{10}-transformed for all analyses. MAT, PET and global radiation were left untransformed because their distribution was approximately normal. Pearson correlation and ordinary least squares (OLS) regression were used for quantifying relationships between individual leaf traits and climate. Bivariate relationships between leaf traits were described with standardized major axis slopes (SMAs; also known as reduced major axis slopes, Sokal & Rohlf, 1995) because our primary aim was to summarize relationships between trait-pairs rather than calculating predictive regression equations (although, see below). On log–log axes, the SMA describes the best-fit 'scaling' (proportional) relationship between the traits. The effect of climate on SMA relationships was quantified by using the SMA analogue of standard analysis of covariance (ANCOVA), as follows. Species were pooled into climate bands (see Tables 3, 4 & 5) and an SMA was fitted to each band. Next, the resulting set of slopes was tested for heterogeneity. Where non-heterogeneity was demonstrated ($P > 0.05$), a common slope (*b*) was estimated. Elevation differences between individual SMAs were then tested for by comparing the species–groups for differences in mean Y', where Y' is Y transformed by the common slope (i.e. $Y' = Y − bX$). Multiple comparisons of Y' were made using the Tukey–Kramer test when variance was homogeneous among groups and the Games–Howell test when variance was heterogeneous (Day & Quinn, 1989). Both tests maintain an experimentwise significance level of 0.05, hence no posthoc correction is needed. Homogeneity of variance among groups was assessed with Levene's test. SMA routines were run using the DOS-based

computer package (S)MATR (Falster *et al.*, 2003). Further details of the statistical routines are described in the supporting documentation, available online at http://www.bio.mq.edu.au/ecology/SMATR/.

While SMA analyses are appropriate for summarizing the relationship between two variables in terms of a single slope, OLS linear regression should be used if one wants to create equations for *predicting* one trait from one or more other traits (Sokal & Rohlf, 1995; Draper & Smith, 1998). Accordingly, the effect of climate on bivariate trait relationships was also assessed using multiple regression. There was close qualitative agreement between the main trends from the SMA and regression analyses; hence, for brevity, only SMA results are reported here.

Climate variables were treated as continuous variables in regression analyses but as ordinal variables in SMA analyses. Describing climate on a continuous scale is clearly the more desirable approach, but no SMA analogue of multiple regressions has yet been well described. Instead, principal components analysis (PCA) was used to reduce multivariate variation in LL, LMA, N_{mass} and A_{mass} down to two orthogonal axes, enabling the strength of correlation between climate variables and species scores along these axes to be assessed. A significant correlation between a climate variable and species' scores along the first axis (the principal axis, 'PCA1') indicates that species shift along the axis with climate. Identifying correlated variation with scores along the second axis ('PCA2') is roughly analogous to identifying elevation shifts between SMAs in the bivariate case (strictly, it would be analogous to identifying group shifts along the standardized *minor* axis, rather than vertical 'elevation' shifts). Indeed, an SMA slope simply describes the slope of the principal axis from a PCA run on standardized bivariate data (i.e. based on the correlation rather than the covariance trait matrix; Sokal & Rohlf, 1995). Other than SMA analyses, all statistical procedures were carried out with SPSS for Windows version 11.01. For PCA

analyses, species scores along PCA1 and PCA2 were calculated using the Anderson–Runin method, giving two sets of orthogonal scores, each with mean of 0, SD of 1.

RESULTS

Patterning of leaf traits with climate

Leaf life span was positively correlated with each of MAT, rainfall, VPD, PET and irradiance (Table 2). Irradiance showed the strongest relationship, explaining 10% of variation in LL. The positive relationship between rainfall and LL was unexpected — if anything, one would expect LL to be longer in species from drier sites. However, when either MAT or irradiance was controlled in a multiple regression, the effect of rainfall on LL became non-significant ($P = 0.451$, $P = 0.196$, respectively). That is, the (weak) rainfall effect seen across all species was apparently the result of the cross-correlation of rainfall with other climate variables.

LMA increased with increasing site MAT and showed only a weak tendency to be higher at lower rainfall ($r = -0.04$, $P = 0.032$; Table 2). This was surprising because there have been many reports from smaller studies that LMA tends to be higher at drier sites. However, once variation in MAT was controlled in a multiple regression, LMA increased more strongly as rainfall decreased ($P < 0.001$), in line with previous findings. LMA was more strongly (positively) correlated with VPD, PET (both $r = 0.38$) or site irradiance ($r = 0.42$) than with either MAT or site rainfall alone.

Evergreen and deciduous species showed rather different patterns in LL and LMA with rainfall and MAT. Along a gradient of decreasing MAT, both LL and LMA increased in evergreens but decreased in deciduous species, with this difference more pronounced in LL than in LMA (Figs 1a,b). Along a gradient of

Table 2 Global correlations between leaf traits and site climate. Two sets of results are reported: (1) correlations between site climate and individual species trait values ('Species'); and (2) correlations between site climate and site mean trait values ('Sites'). Leaf traits for individual species were log_{10}-transformed before analysis, and before site means were calculated. Site rainfall and vapour pressure deficit (VPD) were also log_{10}-transformed. *n*: sample sizes for Species and Sites analyses, respectively

		MAT		Rainfall		VPD		PET		Irradiance	
		Species	Sites	Species	Sites	Species	Sites	Species	Sites	Species	Sites
LL	r	0.29	0.22	0.17	0.18	0.26	0.18	0.19	0.14	0.32	0.28
(n = 749, 55)	P	< 0.001	0.109	< 0.001	0.178	< 0.001	0.195	< 0.001	0.319	< 0.001	0.038
LMA	r	0.31	0.28	−0.04	−0.25	0.38	0.50	0.38	0.44	0.42	0.57
(n = 2370, 163)	P	< 0.001	< 0.001	0.032	0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
N_{mass}	r	−0.21	−0.22	0.01	0.14	−0.27	−0.33	−0.25	−0.29	−0.33	−0.44
(n = 2061, 145)	P	< 0.001	0.008	0.689	0.093	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
N_{area}	r	0.12	0.06	−0.21	−0.46	0.20	0.27	0.22	0.25	0.21	0.25
(n = 1975, 144)	P	< 0.001	0.449	< 0.001	< 0.001	< 0.001	0.001	< 0.001	0.002	< 0.001	0.003
A_{mass}	r	−0.18	−0.07	−0.13	−0.32	−0.17	−0.16	−0.07	0.05	−0.20	−0.18
(n = 770, 65)	P	< 0.001	0.566	< 0.001	0.009	< 0.001	0.213	0.056	0.714	< 0.001	0.143
A_{area}	r	−0.08	−0.04	−0.34	−0.52	0.09	0.10	0.12	0.20	0.03	0.07
(n = 824, 72)	P	0.020	0.744	< 0.001	< 0.001	0.010	0.398	0.001	0.100	0.453	0.575

Figure 1 Relationships between leaf life span (LL) and leaf mass per area (LMA) with each of MAT and annual rainfall for evergreen (open circles) and deciduous (filled circles) shrubs and trees. Linear regression lines are shown for illustrative purposes even when not statistically significant. (a) Log LL vs. MAT. Evergreen: $b = -0.01$, $r^2 = 0.10$, $P < 0.001$, $n = 363$. Deciduous: $b = 0.01$, $r^2 = 0.42$, $P < 0.001$, $n = 157$. (b) Log LMA vs. MAT. Evergreen: $b = -0.01$, $r^2 = 0.02$, $P < 0.001$, $n = 894$. Deciduous: $b = 0.01$, $r^2 = 0.08$, $P < 0.001$, $n = 522$. (c) Log LL vs. log rainfall. Evergreen: $b = 0.05$, $r^2 = 0.003$, $P = 0.330$, $n = 363$. Deciduous: $b = 0.22$, $r^2 = 0.08$, $P < 0.001$, $n = 157$. (d) Log LMA vs. log rainfall. Evergreen: $b = -0.41$, $r^2 = 0.22$, $P < 0.001$, $n = 894$. Deciduous: $b = 0.03$, $r^2 = 0.002$, $P = 0.322$, $n = 522$.
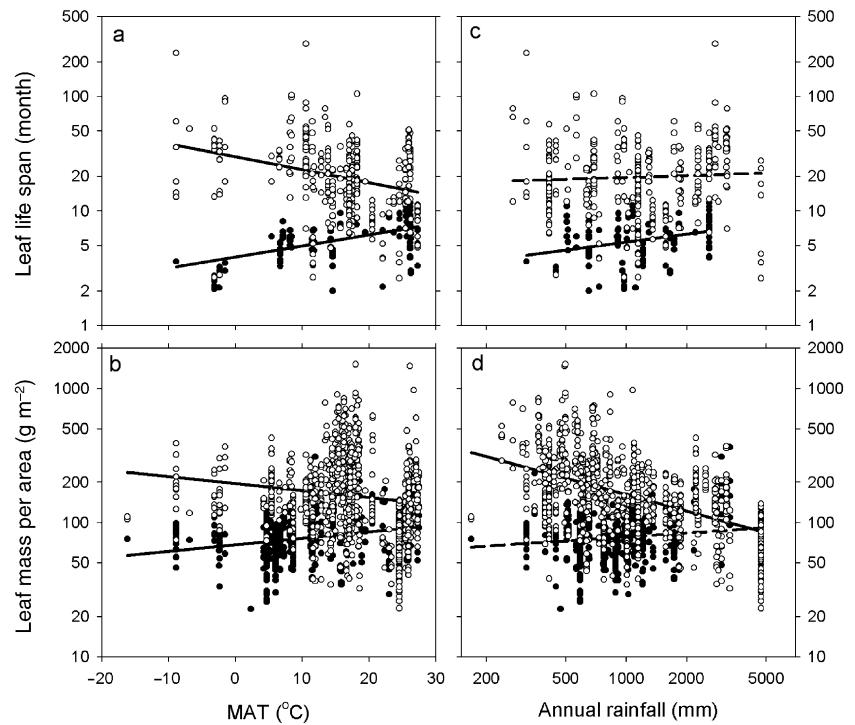
decreasing rainfall, mean LMA increased sharply in evergreens, whereas no trend was evident in LL (Figs 1c,d). Along the same gradient, both LL and LMA decreased slightly among deciduous species.

N_{mass} showed no trend with rainfall, but decreased with increasing MAT, VPD, PET or irradiance (Table 2). N_{area} tended to show the opposite pattern, being higher at higher MAT, VPD, PET or irradiance, and higher at lower rainfall. N_{area} is the product of N_{mass} and LMA. Therefore, it must have been the underlying trends in LMA rather than N_{mass} that led to higher N_{area} at hotter/drier/higher irradiance sites. N_{area} increased with irradiance with rainfall held constant, and increased with decreasing rainfall at any given level of irradiance (Fig. 2). That is, the rainfall and irradiance effects were independent of each other.

A_{mass} decreased with increasing MAT, rainfall, VPD, PET (marginally) or irradiance. Whereas A_{area} decreased with increasing MAT (weakly) and rainfall (more strongly), it was positively correlated with VPD and PET. A_{area} is the product of A_{mass} and LMA; therefore, it must have been underlying trends in LMA rather than in A_{mass} that drove the positive A_{area}–VPD and A_{area}–PET relationships.

A substantial proportion of the total variation among species in their leaf traits tends to occur between coexisting species (Poorter & De Jong, 1999; Wright *et al.*, 2004). One consequence of this is that the trait–climate relationships were in many cases stronger when site means were considered as replicates rather than individual species (Table 2). For example, rainfall explained 6% of variation in site-mean LMA vs. 0.2% at the species-level, whereas irradiance explained 33% of variation in site-mean LMA vs. 18% at the species-level. Notable exceptions were leaf life span and photosynthetic capacity, for which most trait–
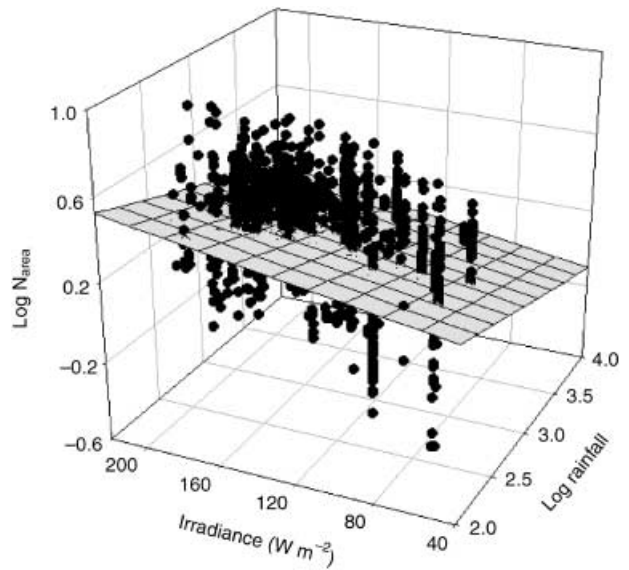

Figure 2 Leaf N per area (N_{area}; g m^{-2}) increases as a function of increasing irradiance and decreasing annual rainfall (mm year^{-1}). The best-fit plane from the following multiple regression is shown:
$$\log N_{area} = 0.0015 \text{ irradiance} - 0.182 \log \text{rainfall} + 0.563$$
(all coefficients $P < 0.001$, model $r^2 = 0.11$, $n = 1975$). Data from 144 sites.

climate correlations were of similar or weaker strength (correlation r) when considered for sites rather than species. With the much lower sample sizes for site-based analyses, relationships with similar r values were statistically non-significant (Table 2).

Modulation of leaf trait relationships by climate

Leaf life span–LMA relationships

Leaf life span and LMA were positively correlated, both across all species ($r^2 = 0.43$, $n = 678$) and within each growth form (Wright *et al.*, 2005). SMAs fitted within rainfall bands did not differ in slope (test for SMA heterogeneity, $P = 0.970$) but they did differ clearly in elevation, such that the average leaf life span achieved at a given LMA was shorter at lower rainfall (Fig. 3a). At grand mean LMA (104 g/m^2), mean LL was 8-fold higher in the wettest than in the driest rainfall class (Table 3). The slope of LL–LMA relationships became flatter with increasing MAT, VPD, PET or site irradiance, dropping from log–log slopes of 2.3 or more in the lowest MAT, VPD, PET or irradiance classes to 1.3 or

Table 3 Comparisons of LL–LMA relationships for species pooled into five rainfall classes. Classes were defined along a log-scale because rainfall was log-normally distributed. SMAs were deemed non-heterogeneous ($P = 0.970$), but clear elevation (intercept) differences were apparent, with shorter LL at a given LMA at drier sites. Multiple comparisons of SMA elevations all $P < 0.015$, except 600–1200 vs. 1200–2400 mm rainfall classes, $P = 0.181$

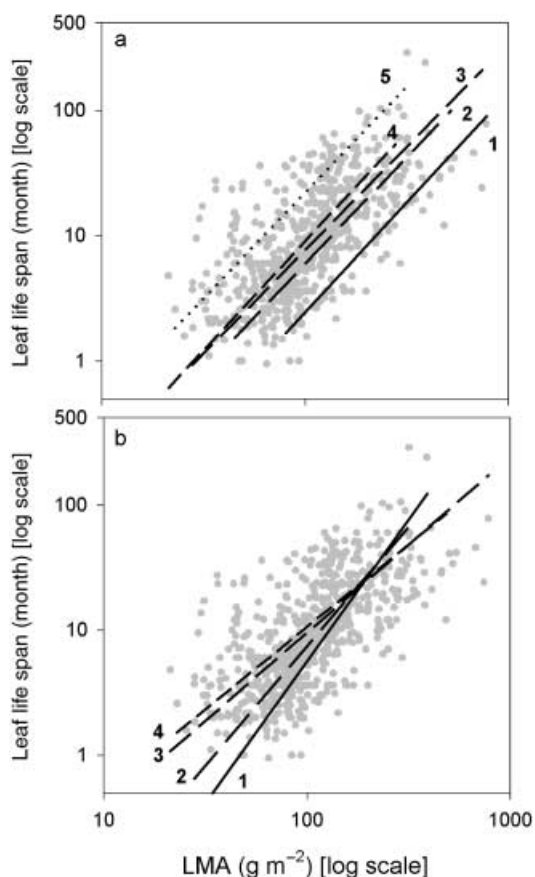| Rainfall (mm)	n	r^2	Slope (95% CIs)	LL (month) at mean LMA (104 g/m^2)
150–300	10	0.81	1.75 (1.24–2.47)	2.8
300–600	138	0.51	1.71 (1.52–1.93)	6.4
600–1200	322	0.48	1.65 (1.53–1.79)	8.2
1200–2400	146	0.38	1.74 (1.53–1.98)	9.6
2400–4800	62	0.50	1.69 (1.41–2.03)	23.6

Figure 3 Modulation of leaf life span–LMA relationships by climate. Individual standardized major axis slopes are shown for species pooled into (a) rainfall classes and (b) MAT classes. Climate classes and associated statistics are given in Tables 3 and 4.

Table 4 Trends in LL–LMA and A_{mass}–N_{mass} relationships for species grouped into climate classes. Data shown are the SMA slope and 95% confidence interval (CI), coefficient of determination (r^2) and sample size. Climate classes are log$_{10}$-classes in the case of VPD, and arithmetic classes for the other variables

		LL–LMA			A_{mass}–N_{mass}		
	Climate band	SMA (95% CIs)	r^2	n	SMA (95% CIs)	r^2	n
MAT (°C)	−10–0	2.3 (2.0, 2.6)	0.61	114	2.0 (1.7, 2.2)	0.75	65
	0–10	1.9 (1.7, 2.2)	0.49	157	2.1 (1.9, 2.4)	0.41	178
	10–20	1.4 (1.3, 1.5)	0.46	269	1.7 (1.6, 1.8)	0.60	348
	20–30	1.3 (1.1, 1.6)	0.09	138	1.3 (1.1, 1.5)	0.30	121
VPD (kPa)	0.1–0.2	2.3 (2.0, 2.6)	0.57	104	1.9 (1.7, 2.2)	0.86	40
	0.2–0.4	1.9 (1.7, 2.0)	0.64	158	1.7 (1.5, 1.8)	0.56	184
	0.4–0.8	2.0 (1.8, 2.1)	0.29	297	1.7 (1.6, 1.8)	0.50	353
	0.8–1.6	1.1 (0.92, 1.2)	0.49	119	1.6 (1.4, 1.8)	0.47	135
PET (mm y^{-1})	200–500	2.5 (2.2, 2.9)	0.56	89	2.0 (1.6, 2.5)	0.69	25
	500–800	2.0 (1.8, 2.3)	0.67	93	2.0 (1.8, 2.3)	0.60	116
	800–1100	2.3 (2.0, 2.5)	0.49	183	1.9 (1.7, 2.1)	0.52	214
	1100–1400	1.3 (1.1, 1.4)	0.45	225	1.6 (1.5, 1.8)	0.57	282
	1400–1700	0.83 (0.67, 1.0)	0.09	88	1.4 (1.1, 1.6)	0.36	75
Irradiance (W m^{-2})	60–90	2.6 (2.2, 3.0)	0.54	86	2.0 (1.6, 2.5)	0.69	25
	90–120	2.0 (1.7, 2.3)	0.62	63	2.3 (2.0, 2.7)	0.71	50
	120–150	1.9 (1.7, 2.1)	0.45	184	1.9 (1.7, 2.1)	0.45	221
	150–180	1.3 (1.2, 1.5)	0.25	267	1.7 (1.6, 1.8)	0.53	337
	180–210	1.3 (1.1, 1.5)	0.55	78	1.4 (1.2, 1.6)	0.58	79

less in the hottest/driest/highest irradiance classes (Table 4; MAT effect depicted in Fig. 3b). The same climate-related trends were seen among evergreen species as for the full data set (details not shown), indicating that the all-species trends were not being driven by differences between evergreens and other functional groups (e.g. grasses, herbs, deciduous trees and shrubs).

LL–A_{mass} relationships

Longer leaf life span was associated with lower A_{mass}, both across all species ($r^2 = 0.69$, $n = 512$) and within each major growth form (Wright *et al.*, 2005). Overall, there was relatively little effect of site climate on SMAs describing LL–A_{mass} relationships. Neither VPD, PET nor irradiance had any clear effect (details not shown). SMAs fitted within rainfall bands were non-heterogeneous ($P = 0.097$), but the only significant differences in SMA elevation were between the highest rainfall class and all other classes (all significantly lower, $P < 0.001$; all other comparisons $P > 0.1$). SMAs fitted within MAT classes did not differ in slope ($P = 0.407$) but did differ in elevation, with longer LL at a given A_{mass} in the two warmest classes than in the two coldest classes (all $P < 0.02$). However, no elevation difference was observed within each of these pairs of MAT classes (both $P > 0.095$). Comparisons made among evergreen species yielded similar results to the all-species analyses, except that there was no MAT effect on LL– LMA relationships for evergreens (details not shown).

A_{mass}–LMA relationships

A_{mass} and LMA were negatively correlated, both across all species ($r^2 = 0.50$, $n = 764$) and within each growth form (Wright *et al.*, 2005). There was no effect of site rainfall on SMA slopes ($P = 0.108$); rather, their elevation was clearly higher at drier sites, with mean A_{mass} around threefold higher at the driest sites than at the wettest, at a given LMA (Fig. 4a; Table 5). There was no clear patterning of A_{mass}–LMA relationships with respect to other climate variables: SMAs fitted within climate bands were significantly heterogeneous in all cases, but without clear trends.

Table 5 Comparisons of A_{mass}–LMA relationships for species pooled into five rainfall log-classes. SMAs were deemed non-heterogeneous ($P = 0.108$), but clear elevation (intercept) differences were apparent, with higher A_{mass} at a given LMA at drier sites. Multiple comparisons of SMA elevations all $P < 0.010$ with the following exceptions: 600–1200 mm class vs. the two lowest rainfall classes, both $P > 0.10$; comparison between the two lowest rainfall classes, $P = 0.091$; comparison between the 300–600 vs. 1200–2400 mm classes, $P = 0.058$

Rainfall (mm)	n	r^2	Slope (95% CIs)	A_{mass} (nmol g^{-1} s^{-1}) at mean LMA (103 g/m^2)
150–300	9	0.85	−1.4 (−2.0, −1.0)	169
300–600	121	0.58	−1.3 (−1.5, −1.2)	106
600–1200	339	0.58	−1.2 (−1.3, −1.1)	109
1200–2400	201	0.39	−1.5 (−1.6, −1.3)	90
2400–4800	89	0.46	−1.2 (−1.4, −1.1)	56

Photosynthesis–leaf N relationships

A_{mass} and N_{mass} were positively correlated, both across all species ($r^2 = 0.53$, $n = 712$) and within each growth form (Wright *et al.*, 2005). Clear climate-related trends were observed for this trait-pair, with SMAs becoming flatter with increasing MAT, PET or irradiance. These shifts were quite substantial, with A_{mass} increasing to the square of N_{mass} in the coldest/least arid climate bands (log–log slopes of *c.* 2), dropping down to slopes of *c.* 1.4 in the hottest/driest/highest irradiance regions (Table 4; MAT effect depicted in Fig. 4b). By contrast, there was no clear effect of VPD on either SMA slope or elevation.

Photosynthetic capacity and leaf N were more weakly related on a leaf area than on a leaf mass basis (correlations across all species, $r^2 = 0.13$ vs. 0.53; Wright *et al.*, 2005). There was no clear effect from any of the climate variables on either SMA slopes or elevations for this trait-pair (details not shown).

Assessing patterning by climate in multivariate trait space

Principal components analysis was used to reduce multivariate variation in LL, LMA, N_{mass} and A_{mass} down to two orthogonal
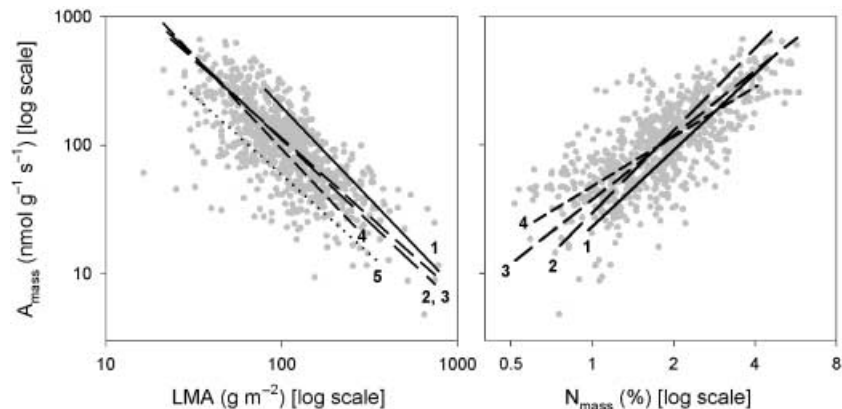

Figure 4 Modulation of A_{mass}–LMA and A_{mass}–N_{mass} relationships by climate. Climate classes and associated statistics are given in Tables 4 and 5. (a) A_{mass} vs. LMA, with individual SMA slopes shown for species pooled into rainfall classes. (b) A_{mass} vs. N_{mass}, with individual SMA slopes shown for species pooled into MAT classes.

axes, PCA1 and PCA2. All four traits were known for 492 species from 39 sites. PCA1 explained 84.4% of total trait variation among these species, PCA2 a further 10.2%. PCA1 was positively correlated with LL and LMA and negatively correlated with A_{mass} and N_{mass} (thus PCA1 represented the 'leaf economics spectrum'; Wright *et al.*, 2004). The set of species scores along PCA1 was positively correlated (all $P \leq 0.001$) with each of irradiance ($r = 0.32$), VPD ($r = 0.31$), MAT ($r = 0.23$) and PET ($r = 0.17$), and negatively correlated with rainfall ($r = -0.10$; $P = 0.028$). The only climate variable significantly correlated with PCA2 was rainfall ($r = 0.10$, $P = 0.027$). In other words, up to 10% of the spread (0.32^2) of species along the primary axis of variation was associated with individual climate variables, whereas very little of the spread along the second axis was related to climate. Together, MAT, rainfall, PET and irradiance explained 18% of variation along PCA1 (multiple regression analysis; details not shown).

Climate correlations with PCA1 were almost identical when the analysis was rerun for the same group of species but with just LMA, A_{mass} and LL (i.e. N_{mass} was excluded). In this analysis, PCA2 was strongly, positively correlated with rainfall ($r = 0.44$, $P < 0.001$) and more weakly associated with MAT ($r = 0.14$, $P = 0.003$), VPD and PET (both $r = -0.12$, $P = 0.010$). That is, once N_{mass} was added to the analysis, the amount of variation orthogonal to the primary axis that was explained by climate became much less.

Rerunning both of these analyses for evergreen species only ($n = 247$ for these four traits), climate explained a similar proportion of variation along PCA1 but substantially more variation along PCA2, particularly by site rainfall (details not shown). That is, climate-related patterning of multivariate trait relationships along PCA1 was not simply due to sorting of growth forms or PFTs across climate gradients, whereas to some degree, the scatter in the orthogonal axis PCA2 was masked by sorting of PFTs.

DISCUSSION

The geographical coverage of our data set is broad, extending to all vegetated continents. For traits such as leaf N and LMA, we now have data for almost 1% of vascular plants. For traits such as photosynthetic capacity or leaf life span, we have considerably fewer data (*c.* 750 species), and we have very few data for any leaf traits from large areas such as central and northern Africa, Russia, China and Canada. Nonetheless, the coverage of traits, species and sites is considerably greater than previous data compilations. This enabled us to (1) confirm and generalize to global scale some previously reported relationships between leaf traits and climate; and (2) report a number of novel results, especially concerning the modulation of leaf trait relationships by climate.

Relationships between individual leaf traits and climate

Ecologists have long recognized that species inhabiting arid and semiarid regions tend to have leathery, high LMA leaves (e.g. Maximov, 1929). Construction cost per unit leaf mass varies relatively little between species (Villar & Merino, 2001); hence, building high LMA leaves is more costly per unit leaf area. Leaf

traits associated with high LMA (e.g. thick leaf blade; small, thick-walled cells) have been interpreted as adaptations that allow continued leaf function under very dry conditions, or at least postpone leaf death, at least in evergreen species. However, at the global scale, we found that LMA was only very weakly related to rainfall; it was not until variation in MAT was controlled that the expected negative relationship between LMA and rainfall was observed. This appeared to reflect the fact that both LMA and MAT, and MAT and rainfall, were positively correlated. For these relationships, the trends seen among evergreen trees and shrubs differed from those seen among deciduous species: among evergreens LMA was negatively correlated with both MAT and rainfall, whereas among deciduous species LMA increased with MAT and showed no relationship to rainfall. The LMA–MAT trend in deciduous species can be best understood as relating to leaf life span: growing season length decreases with decreasing MAT, hence, on average, LL does too.

The strongest correlation between any single climate variable and either LL or LMA was with site irradiance (see also Niinemets, 2001). The LMA trend also drove a trend of increasing N_{area} with irradiance. High N_{area} in species from high irradiance sites is generally thought to allow plants to take advantage of the high light for photosynthesis, without significant internal self-shading of chloroplasts (Mooney *et al.*, 1978; Cunningham *et al.*, 1999; Farquhar *et al.*, 2002).

Many high irradiance regions are also arid. However, across the 175 sites in this study, the two variables were unrelated because there were a number of cold sites that have both low rainfall and low irradiance. Indeed, considering only the 127 sites with MAT > 10 °C, rainfall and irradiance were negatively correlated ($r^2 = 0.16$, $P < 0.001$). On average, N_{area} decreased with increasing rainfall, this effect being independent of that with irradiance. High N_{area} has previously been described as an adaptation to low rainfall: in shrubs and trees from both Australia and the USA, high N_{area} in low rainfall species has been linked to greater CO_2 drawdown during photosynthesis, leading to more economic use of water for carbon fixation (Wright *et al.*, 2001, 2003). In the eastern Australian low rainfall species, high N_{area} was also associated with generally softer leaf tissue which, in turn, was argued to lead to the observed trend of shorter leaf life span at a given LMA with decreasing rainfall (Wright & Westoby, 2002). Here we have demonstrated a similar pattern in LL–LMA relationships with rainfall, at the global scale. In addition, we found that the slope of LL–LMA relationships became flatter with increasing site MAT, VPD, PET and irradiance.

Modulation of trait relationships by site climate

The climate-related shifts in leaf trait relationships were quite substantial. While there was no difference in LL–LMA relationship slope with rainfall (with a common log–log slope of 1.7, 95% CIS, 1.6–1.8), at a given LMA mean LL was 8-fold shorter at the lowest rainfall sites than at the highest rainfall sites. A different type of trend was seen with the other climate variables: with increasing MAT, VPD, PET or irradiance, LL–LMA relationships became flatter, dropping from slopes of 2.3 or more in the lowest

MAT, VPD, PET or irradiance classes to 1.3 or less in the hottest/driest/highest irradiance classes. For a twofold increase in LMA, this translates into a *c.* 5-fold increase in LL at the coldest sites vs. a 2.5-fold increase in LL at the hottest sites. Similarly, the slope of A_{mass}–N_{mass} relationships tended to become flatter with increasing MAT, VPD, PET or irradiance, dropping from slopes of *c.* 2 down to *c.* 1.4 across the set of climate bands. Presumably, LL–LMA and A_{mass}–N_{mass} shifts of this magnitude (in either slope elevation or slope) must have important consequences for the dry mass and nutrient economics of plants, and reflect adaptation or plant responses to substantial selective pressures.

All else being equal, a logLL–logLMA slope > 1 (e.g. Table 3) 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 is translated directly into a fitness benefit, it might lead to a runaway selection for ever increasing LMA and LL. So why does this not happen? Suggested reasons favouring low LMA, short LL species sufficiently to counteract the slopes being > 1 (Westoby *et al.*, 2000), include: (1) a compound-interest effect (Harper, 1989), whereby low LMA species fix more carbon earlier, with reinvestment of this carbon in new leaves then generating more total growth; (2) reduced revenue from older leaves as a result of overshading by both surrounding vegetation and the plant itself; (3) reduced revenue from older leaves, as a result of damage from herbivores and the accumulation of algae, fungi, debris, etc. on the leaf surface; and (4) the risk that the plant will no longer be alive to benefit. But would any of these factors vary systematically with MAT, VPD, PET or irradiance, providing a prospective explanation for the trends in LL–LMA slopes that we observed? It is likely that both the pace of overshading and the accumulation of fungi and algae on leaf surfaces would be lower in drier environments, where growth is generally slower for all species. However, we are not aware of any direct measurements comparing the relative importance of these possible factors, so we are limited to conjecture at this stage.

Coordination of multiple leaf traits

All else being equal, the downwards shift in LL with decreasing rainfall (at a given LMA) would lead to lower lifetime carbon gain per unit leaf area. Yet with decreasing rainfall, we also observed a concomitant *upwards* shift in A_{mass} (again, at a given LMA) which, all else being equal, should lead to higher lifetime carbon gain per unit leaf area. Comparing species from the highest with those from the lowest rainfall classes, the 8-fold shift in LL would be likely, on the face of it, to override the 3-fold A_{mass} shift. But A_{mass} describes the photosynthetic rate achievable by relatively young leaves, under high light and well-watered conditions, rather than the average photosynthetic rate over the lifetime of a leaf. If low rainfall species have a slower age-related decline in photosynthetic rates as a result of less self-shading (via their generally more open canopies), this could at least partially offset the downwards shift in leaf life span. Further investigation of these sorts of trends would require a combination of detailed field measurements and modelling of architecture and carbon gain at the canopy-level (Naumburg *et al.*, 2001).

To develop realistic models, we need to understand better the way plants coordinate multiple leaf traits (Shipley & Lechowicz, 2000; Givnish, 2002). Were the slope shifts in LL–LMA and A_{mass}–N_{mass} relationships expressions of the same underlying factors or of pressures? What about the elevation shifts with rainfall in LL–LMA and A_{mass}–LMA relationships? Considering three or more traits at a time, we found that individual climate variables explained a similar amount of variation along the first multivariate principal component axis whether or not N_{mass} was included in the analysis. By contrast, climate explained considerably less variation along the second principal component once N_{mass} was added to the analysis after LL, LMA and A_{mass}. This observation builds on those of Reich *et al.* (1997), who found that differences in the slope or elevation of leaf trait relationships between biomes largely disappeared with the addition of additional leaf traits as covariates to the regression models used in that study. That is, shifts in one trait relationship may counteract shifts in one or more other trait-pairs, leading to little apparent effect of climate once several leaf traits are considered.

CONCLUSIONS

Here we have reported a number of very broad relationships between leaf traits and climate, and climate-related trends in the relationships among leaf traits. Of the trait relationships examined here, that between LL and A_{mass} showed the least modulation by climate, probably reflecting the fact that this trait-pair was also the most tightly correlated, considered across all species. But the climate-related trends in other trait-pairs were of sufficient size to strongly influence predictions of how vegetation and ecosystem function will be affected by climate change. Still, scaling up from leaf-level to the level of whole canopies or forests remains a significant challenge. For example, leaf trait relationships may also be modified by soil nutrients (Wright *et al.*, 2001; Niinemets & Kull, 2003), and relatively little is known about the extent to which relationships among key root or whole-plant traits are affected by site factors. Further, matching trait data with information on the relative abundance of species and with ecosystem properties such as rates of nutrient cycling through communities (Garnier *et al.*, 2004) not only represents an exciting challenge, but is also the sort of information that will greatly enhance future vegetation–climate models.

ACKNOWLEDGEMENTS

REFERENCES

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

Barry, R.G. (1981) *Mountain weather and climate*. Methuen, London, New York.

Campbell, G.S. & Norman, J.M. (1998) *An introduction to environmental biophysics*, 2nd edn. Springer, New York.

Choudhury, B.J. (1997) Global pattern of potential evaporation calculated from the Penman–Monteith equation using satellite and assimilated data. *Remote Sensing of Environment*, **61**, 64–81.

Cunningham, S.A., Summerhayes, B. & Westoby, M. (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecological Monographs*, **69**, 569–588.

Day, R.W. & Quinn, G.P. (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs*, **59**, 433–463.

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

Draper, N.R. & Smith, H. (1998) *Applied regression analysis*, 3rd edn. John Wiley & Sons, New York.

Eckstein, R.L., Karlsson, P.S. & Weih, M. (1999) Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytologist*, **143**, 177–189.

Enriquez, S., Duarte, C.M., Sandjensen, K. & Nielsen, S.L. (1996) Broad-scale comparison of photosynthetic rates across phototrophic organisms. *Oecologia*, **108**, 197–206.

Escudero, A., del Arco, J.M., Sanz, I.C. & Ayala, J. (1992) Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients. *Oecologia*, **90**, 80–87.

Falster, D.S., Warton, D.I. & Wright, I.J. (2003) (S)MATR: Version 1.0 *Standardised major axis tests and routines*. http://www.bio.mq.edu.au/ecology/SMATR/. [Accessed July 2003]

Farquhar, G.D., Buckley, T.N. & Miller, J.M. (2002) Optimal stomatal control in relation to leaf area and nitrogen content. *Silva Fennica*, **36**, 625–637.

Field, C. & Mooney, H.A. (1986) The photosynthesis–nitrogen relationship in wild plants. *On the economy of plant form and function* (ed. by T.J. Givnish), pp. 25–55. Cambridge University Press, Cambridge.

Fonseca, C.R., Overton, J.M., Collins, B. & Westoby, M. (2000) Shifts in trait combinations along rainfall and phosphorus gradients. *Journal of Ecology*, **88**, 964–977.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.-P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.

Givnish, T.J. (2002) Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica*, **36**, 703–743.

Harper, J.L. (1989) The value of a leaf. *Oecologia*, **80**, 53–58.

Kikuzawa, K. (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *American Naturalist*, **138**, 1250–1263.

Kikuzawa, K. & Ackerly, D. (1999) Significance of leaf longevity in plants. *Plant Species Biology*, **14**, 39–45.

Körner, C. (1999) *Alpine plant life: functional plant ecology of high mountain ecosystems*. Springer, Berlin.

Maximov, N.A. (1929) *The plant in relation to water. A study of the physiological basis of drought resistance*. Allen & Unwin, London.

Mooney, H.A., Ferrar, P.J. & Slatyer, R.O. (1978) Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. *Oecologia*, **36**, 103–111.

Moorcroft, P.R., Hurtt, G.C. & Pacala, S.W. (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological Monographs*, **71**, 557–585.

Naumburg, E., Ellsworth, D.S. & Pearcy, R.W. (2001) Crown carbon gain and elevated [CO_2] responses of understorey saplings with differing allometry and architecture. *Functional Ecology*, **15**, 263–273.

New, M., Hulme, M. & Jones, P. (1999) Representing twentieth-century space–time climate variability. Part I: Development of a 1961–90 mean monthly terrestrial climatology. *Journal of Climate*, **12**, 829–856.

Niinemets, U. (1999) Components of leaf dry mass per area — thickness and density — alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytologist*, **144**, 35–47.

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

Niinemets, U. & Kull, K. (2003) Leaf structure vs. nutrient relationships vary with soil conditions in temperate shrubs and trees. *Acta Oecologica*, **24**, 209–219.

Poorter, H. (1994) Construction costs and payback time of biomass: a whole plant perspective. *A whole plant perspective on carbon–nitrogen interactions* (ed. by E. Royand and E. Garnier), pp. 111–127. SPB Academic Publishing, The Hague, The Netherlands.

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, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365–392.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the USA*, **94**, 13730–13734.

Reich, P.B., Ellsworth, D.S. & Walters, M.B. (1998) Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology*, **12**, 948–958.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**, 1955–1969.

Schimper, A.F.W. (1903) *Plant-geography upon a physiological basis*. Clarendon Press, Oxford.

Schulze, E.-D., Kelliher, F.M., Körner, C., Lloyd, J. & Leuning, R. (1994) Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and

plant nitrogen nutrition: a global scaling exercise. *Annual Review of Ecology and Systematics*, **25**, 629–660.

Shipley, B. & Lechowicz, M.J. (2000) The functional co-ordination of leaf morphology, nitrogen concentration, and gas exchange in 40 wetland species. *Ecoscience*, **7**, 183–194.

Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K. & Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: the principles and practice of statistics in biological research*, 3rd edn. W.H. Freeman and Company, New York.

Turner, I.M. (1994) A quantitative analysis of leaf form in woody plants from the world's major broadleaved forest types. *Journal of Biogeography*, **21**, 413–419.

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.

Westoby, M., Cunningham, S.A., Fonseca, C., Overton, J. & Wright, I.J. (1998) Phylogeny and variation in light capture area deployed per unit investment in leaves: designs for selecting study species with a view to generalizing. *Variation in growth rate and productivity of higher plants* (ed. by H. Lambers, H. Poorterand and M.M.I. van Vuuren), pp. 539–566. Backhuys Publishers, Leiden, The Netherlands.

Westoby, M., Warton, D. & Reich, P.B. (2000) The time value of leaf area. *American Naturalist*, **155**, 649–656.

White, M.A., Thornton, P.E., Running, S.W. & Nemani, R.R. (2000) Parameterization and sensitivity analysis of the BIOME–BGC terrestrial ecosystem model: net primary production controls. *Earth Interactions*, **4**, 1–85.

Whittaker, R. (1975) *Communities and ecosystems*, 2nd edn. MacMillan Publishing Co. Inc., New York.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Garnier, E., Hikosaka, K., Lamont, B.B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D.I. & Westoby, M. (2005) Assessing the generality of global leaf trait relationships. *New Phytologist*, **166**, 485–496.

Wright, I.J., Reich, P.B. & 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, I.J., Reich, P.B. & Westoby, M. (2003) Least-cost input mixtures of water and nitrogen for photosynthesis. *American Naturalist*, **161**, 98–111.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, F.S., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The world-wide leaf economics spectrum. *Nature*, **428**, 821–827.

Wright, I.J. & Westoby, M. (2002) Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. *New Phytologist*, **155**, 403–416.

Wright, I.J., Westoby, M. & Reich, P.B. (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.

BIOSKETCHES

Ian Wright is a Research Fellow at the Department of Biological Sciences of Macquarie University. His research works towards identifying major dimensions of strategic variation among species and understanding the adaptations of plants to site factors such as climate and soil nutrients (http://www.bio.mq.edu.au/ecology/wright/wright.htm).

Peter Reich is F.B. Hubachek Senior Professor at the Department of Forest Resources of the University of Minnesota. His research aims to bridge the fields of physiological, community, ecosystem, landscape and regional ecology within the context of natural and human-induced global change (http://www.cnr.umn.edu/forestecology/reich.html).