Leaf-size divergence along rainfall and soil-nutrient gradients: is the method of size reduction common among clades?

P. G. M^CDONALD*†, C. R. FONSECA‡, J. McC. OVERTON§ and M. WESTOBY

Department of Biological Sciences, Macquarie University, NSW 2109, Australia

Summary

1. Ecologists have long recognized that plants occurring in areas of low rainfall or soil nutrients tend to have smaller leaves than those in more favourable regions.

2. Working with a large data set (690 species at 47 sites spread widely through southeast Australia) for which this reduction has been described previously, we investigated the morphology of leaf size reduction, asking whether any patterns observed were consistent across evolutionary lineages or between environmental gradients.

3. Leaf length, width and surface areas were measured; leaf traits such as pubescence or lobing were also scored qualitatively. There was no correlation between soil phosphorus and rainfall across sites. Further, there was no evidence that pubescence, lobing or other traits assessed served as alternatives to reduction of leaf size at the low ends of either environmental gradient.

4. Leaf size reduction occurred through many combinations of change in leaf width and length, even within lineages. Thus consistent patterns in the method of leaf size reduction were not found, although broad similarities between rainfall and soil P gradients were apparent.

Key-words: Leaf physiognomy, leaf shape, phylogeny, soil phosphorus

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Introduction

Leaf size tends to decline with: increasing elevation (Cordell *et al*. 1998; Givnish 1984; Halloy & Mark 1996); decreasing mean annual temperature (Dolph 1977; Givnish 1984; Nunez-Olivera, Martinez-Abaigar & Escudero 1996; Wolfe 1995); mean annual rainfall (Beard 1945; Cowling & Campbell 1980; Givnish 1984; Stone & Bacon 1995; Wolfe 1995); and lower soil fertility (Ashton & Hall 1992; Beadle 1954; Chapin 1980; Cunningham, Summerhayes & Westoby 1999; Dolph & Dilcher 1980; Rodriguez, Keltjens & Goudriaan 1998; Webb 1968). The present paper investigates the nature of this decline in more detail, in a situation where leaf width reduction along rainfall and soil

nutrient gradients has been described previously in relation to leaf area per mass and the potential height of plant species (Fonseca *et al*. 2000). Patterns are considered as both correlations across species and evolutionary divergences or phylogenetically independent contrasts. First, we assessed whether leaf size reduction occurred predominantly through leaves being narrower, shorter or smaller in both length and width in poorer environments. Second, we asked whether leaf traits such as pubescence or lobing act as alternatives to leaf size reduction. Third, we investigated whether responses differed among clades of plants; and fourth, whether responses differed along the soil nutrient gradient compared to the rainfall gradient.

In Australia, rainfall and total soil phosphorus are seen as the most important abiotic factors shaping vegetation structure (Beadle 1962; Beadle 1966; Cunningham *et al*. 1999). Soil P determines what kinds of species occur at a given location, as total soil P is decided by the geomorphology of the site rather than by traits of the vegetation, as might be the case for soil nitrogen or other measures of available nutrients (Cunningham *et al*. 1999; Fonseca *et al*. 2000).

It is generally thought that smaller leaf sizes are favoured at lower rainfall because larger leaves develop

†Author to whom correspondence should be addressed. E-mail: p.mcdonald@anu.edu.au
*Present address: Division of Botany and Zoology, School of Life Sciences, Australian National University, Canberra, Australia 0200.
‡Present address: Laboratório de Interação Animal–Planta, Centro 2, UNISINOS, São Leopoldo, RS, Brazil, CEP. 93022-000.
§Present address: Landcare Research, Private Bag 3127, Hamilton, New Zealand.

thicker boundary layers of still air (Givnish 1978; Givnish 1979; Givnish 1984; Givnish & Vermeij 1976; Parkhurst & Loucks 1972; Schuepp 1993; Vogel 1970). Larger leaves therefore shed heat more slowly and are heated above air temperature more than smaller leaves. This overheating will become increasingly important as rainfall declines, because transpiration is also effective in shedding heat, and because when there is less total foliage per unit ground area, more of the leaves are exposed to direct radiation. Hence, smaller leaves are favoured towards lower rainfall.

The functional basis of leaf size reduction towards lower total soil P is less clear. Some suggestions, for example that a smaller leaf size is favoured because of the slower growth of plants on infertile soils (Rodriguez *et al.* 1998), can equally be interpreted as favouring smaller investment in total leaf area, as opposed to leaf size *per se*. Despite this, smaller leaf size at low soil P is consistently observed (Cunningham *et al.* 1999; Fonseca *et al.* 2000). Consequently, these possibilities were tested along the soil P and rainfall gradients.

Other leaf traits may also reduce radiative overheating, for example, pubescence or a glossy/waxy cuticle may increase reflectance (Ehleringer 1982; Johnson 1975; Miller 1983; Sandquist & Ehleringer 1997; Smith & Nobel 1977). Similar-sided leaves are indicators of a relatively steep leaf angle, whereas leaves with horizontal orientation typically concentrate photosynthetic tissue on the upper side, and stomata on the underside. Steeper leaf angles may reduce leaf overheating and thus transpiration in dry climates. Lobed leaves have shorter airflow paths across their surfaces relative to entire leaves of the same total area. Lobed leaves should therefore be able to shed heat more rapidly by convection (Givnish 1978; Givnish 1979; Parkhurst & Loucks 1972; Schuepp 1993). Therefore steep leaf angle or lobing might function as alternatives to smaller leaf size – clades with these traits might not reduce leaf size to the extent of those without them. Conversely, it might be argued that the same environments and lifestyles that favoured pubescence or steep leaf angle would also favour smaller leaf size, producing a positive rather than a negative correlation. Thus the relationship between these leaf characters and leaf size reduction was of interest in this study.

Materials and methods

DATA COLLECTION

A total of 47 sites throughout New South Wales in south-eastern Australia were selected to span two orders of magnitude of total soil P (range 22–2063 µg g^{-1}) and one order of magnitude of mean annual rainfall (range 206–2034 mm). Soil P and rainfall were uncorrelated across the 47 sites (Pearson's correlation coefficient = −0·20, *P* = 0·43). Variation in temperature was restricted by confining sites to a latitudinal band of 30–35°S and to elevations below 800 m asl (see

Fonseca *et al.* 2000 for site details). Five soil cores were taken at each site, each 10 cm deep. These were pooled to average out within-site soil heterogeneity, then analysed by the Soil Laboratory at James Cook University, Townsville, Australia, for total soil P and N. Soil P was assessed according to the protocol outlined by Fonseca *et al.* (2000), while N was determined using the single-digestion method of Anderson & Ingram (1989), after initially grinding soil samples to 0·2 mm and digesting with sulphuric acid and hydrogen peroxide. Nitrogen was then determined colorimetrically by the salicylate–hypochlorite method of Baethgen & Alley (1989).

In all, 1190 samples of three leaves were collected from each evergreen perennial species present in plots: a total of 690 species, 109 of which occurred at more than one site. Epiphytes, parasites and annuals were excluded from analyses, as these species could not be expected to have the same relationship as evergreens with year-round environmental parameters. For brevity, 'leaf' is used here to refer to any green surface carrying out most of the plant's photosynthesis. Leaves sampled were adult, free of herbivore damage, and had recently expanded fully. Leaves were taken from as near to a full sun position, and from as many different individuals, as possible. Within-species variation was small relative to variation across species (data not presented).

In the laboratory, images of individual leaves were scanned using an HP DeskScan II Scanner (Hewlett Packard, USA) and quantified using DELTA-T SCAN image analysis software (Delta-T Devices, Burwell, UK). Attributes quantified were leaf area (mm^2), length (mm) and width (mm). Length was measured along the midrib of the leaf, rather than the linear distance between base and apex, to account for falcate leaves. Width was defined as the diameter of the largest circle that could be fitted within the leaf's margin. Individual leaflets of compound species were treated as equivalents of simple leaves.

The categorical variables of pubescence, lobing and presence of a glossy or waxy cuticle were scored as present/absent from field samples, from herbarium specimens from a nearby locality, or from descriptions in Harden (1993). Leaves were scored as different-sided if veins were prominent on one side only and the two sides were different colours. As specimens/descriptions could not be obtained for all species, analyses of leaf traits were restricted to 474 of the 690 species sampled.

DATA ANALYSES

Cross-species methods

Continuous variables were log$_{10}$-transformed to improve normality. If species occurred at multiple sites, means were used, including site properties. If categorical traits differed between sites, median scores were chosen (this was rare). Cross-species statistical

tests were assessed at α = 0·05 using spss for Windows version 8·0 (SPSS Inc., Chicago, IL).

Evolutionary divergences

Evolutionary divergences were assessed using phylogenetic regressions (Grafen 1989; Grafen 1991; Grafen 1992). In these analyses the item of evidence is the node or radiation in a phylogeny, rather than the present-day species (Grafen 1989). The working phylogeny used in assessing evolutionary divergences was constructed to family level following APG (1998) and Bremer, Bremer & Thulin (1998); lower nodes followed Wright *et al.* (2000). Families of unknown affinity at order level were placed at the most fully resolved point in the phylogeny. This method retains all data, yet adds no extra divergences and thus degrees of freedom, making it unlikely to bias regressions. Similarly, all samples not completely identified were incorporated in a polychotomy at the most fully resolved point.

Phylogenetic regressions were carried out using PHYLO8.GLM version 8 for IBM (Royal Statistical Society, London, 1997) run using GLIM 4. As the working phylogeny is incomplete with respect to the actual phylogeny (not all species within clades were sampled), we used the fully general method to determine branch lengths (Grafen 1991). The method of branch length determination did not significantly affect results.

Nodes were identified that experienced a residual divergence in either soil P or rainfall greater than 0·3 orders of magnitude, after partialling out the effect of the other factor. These two groups of nodes define evolutionary divergences along soil P and rainfall gradients, respectively. Divergences were expressed such that divergences in leaf length were positive. Only species identified at least to genus were incorporated in these analyses. Species classified to the family level or less would have biased calculations of means, as each branch in a polychotomy was given equal weighting regardless of the number of species sampled within it. Leaf shape changes at divergences of more than 0·5 orders of magnitude of length or width were then summarized into four classes. In length-only change, divergence in log length was more than twice as great as divergence in log width. In width-only change, divergences in log width were more than twice as great as divergences in log length. In isometric change, log length and log width divergences were within twofold of each other. In opposite change, log width increased while log length decreased.

Results

Across species, leaf area, length and width tended to decline towards lower soil P and lower rainfall, with considerable scatter (Fig. 1). This was expected, and was previously reported for site means of leaf width by Fonseca *et al.* (2000). More variation was explained by

Table 1. Effects of soil phosphorus and mean annual rainfall on leaf surface area, length and width as determined by phylogenetic regressions ($P < 0.001$ for all regressions)

Test gradient	Control gradient	Size attribute	$F_{1,260}$	R^2
P	Rainfall	Surface area	57·80	0·182
		Length	17·93	0·065
		Width	66·67	0·204
Rainfall	P	Surface area	41·58	0·138
		Length	21·18	0·075
		Width	53·87	0·172

rainfall than by soil P for all three leaf size attributes (Fig. 1). Multiple regressions showed that soil P and rainfall had largely additive effects. Close to the same amount of variation in these relationships was explained as the sum of simple regressions for each gradient alone (leaf area, R^2 both gradients = 0·246, soil P R^2 = 0·074, rainfall R^2 = 0·137; length, R^2 both gradients = 0·106, soil P R^2 = 0·021, rainfall R^2 = 0·072; width, R^2 both gradients = 0·25, soil P R^2 = 0·088, rainfall R^2 = 0·126; all $P < 0.0005$).

Similarly, evolutionary divergences for all three leaf size attributes were significantly correlated with divergence in soil P after controlling for divergence in rainfall and vice versa (Table 1). Leaf area, length and width all tended to be smaller on the lower P or lower rainfall side of divergences. Phylogenetic regressions generally explained more variation than cross-species analyses.

After controlling for the soil P and rainfall gradients, soil N, mean annual temperature and site elevation added little further predictive power explaining variation in leaf area in cross-species analyses (multiple regression predicting leaf area from all site properties: $R^2 = 0.253$ *vs* $R^2 = 0.246$ for soil P and rainfall alone, residuals not significantly greater; $F_{3,684} = 2.34$; $F_{\text{crit } 3,\infty} = 3.12$; $P > 0.05$). This was expected as the sampling regime minimized variation in elevation and mean annual temperature, and soil N was correlated with soil P. Similarly, evolutionary divergences in all three leaf size attributes were not explained further by divergences in mean annual temperature, elevation or soil N after controlling for divergences in soil P and rainfall (data not presented, all $P > 0.35$). Hence leaf divergence was studied in relation to soil P and rainfall only, following the original design of the sampling.

ARE OTHER LEAF TRAITS ALTERNATIVES TO LEAF SIZE REDUCTION?

For most leaf traits (such as pubescence or lobing) examined in cross-species analyses, there was no evidence of an interaction between trait presence/absence and leaf size, after controlling for main effects (Table 2). Leaf size did decline towards lower rainfall among different-sided leaves ($R^2 = 0.119$, $F_{1,179} = 55.3$, $P < 0.0005$), but not among similar-sided leaves
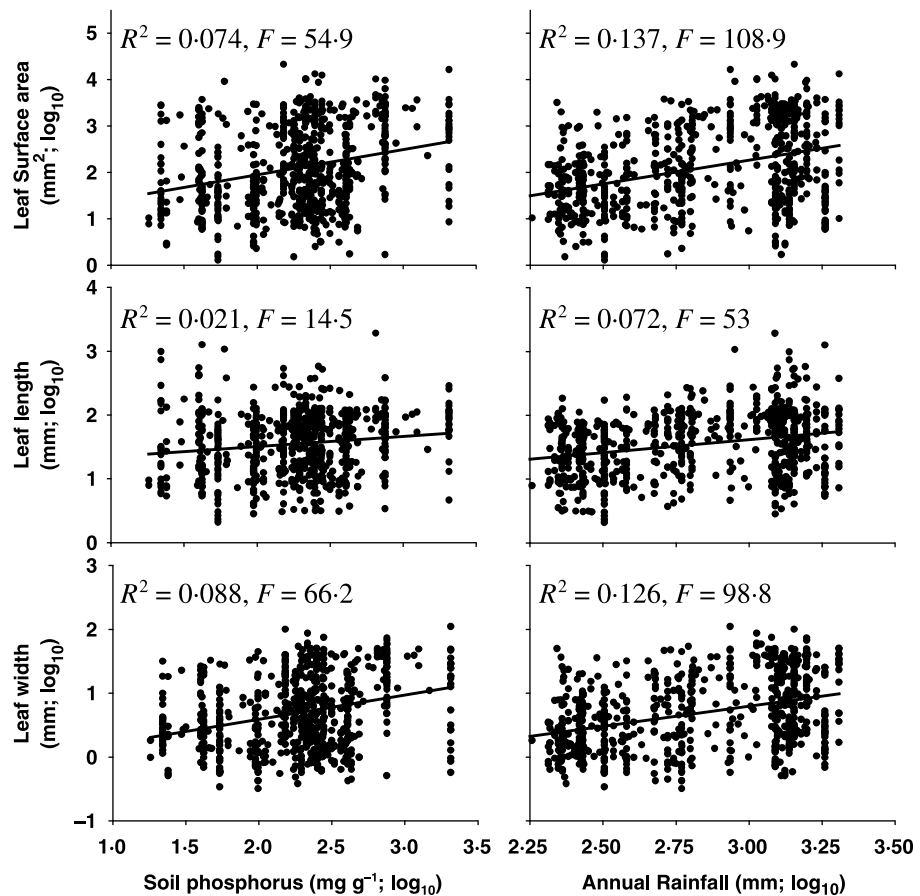
Fig. 1. Leaf surface area, length and width along soil phosphorus and mean annual rainfall gradients. Data points represent mean values for 690 species of non-parasitic perennials sampled from 47 sites throughout south-eastern Australia. *F* values have 1,688 degrees of freedom, $P < 0.0005$ for all relationships.

Table 2. Results of ANCOVAs examining the relationship between leaf surface area along the soil phosphorus and mean annual rainfall gradients and the presence/absence of the categorical leaf characteristics: pubescence, lobing, waxy/glossy cuticle and similar-sided leaves

Test gradient	Leaf character	$F_{1,471}$	P
P	Pubescence	0·001	0·98
	Lobing	0·03	0·86
	Similar-sided leaves	3·32	0·07
	Glossy/waxy cuticle	0·54	0·46
Rainfall	Pubescence	0·14	0·23
	Lobing	3·34	0·07
	Similar-sided leaves	15·11	<0·0005*
	Glossy/waxy cuticle	0·005	0·95

*Significance at $\alpha = 0.05$.

($R^2 = 0.041$, $F_{1,293} = 2.64$, $P = 0.11$; significant interaction in Table 2). However, species with different-sided leaves averaged larger leaf areas than similar-sided species across most of the rainfall range, which does not support the idea that similar-sided leaves (vertical leaf angles) function as an alternative to small leaf size.

Similarly, the presence or absence of leaf traits largely did not affect evolutionary divergences in leaf area along the soil P or rainfall gradient (Table 3). The

only significant interaction observed involved the presence/absence of lobing along the rainfall gradient. However, the direction of this interaction was again contrary to the hypothesis that increased lobing is an alternative to decreasing leaf area towards lower rainfall. Clades static with respect to the level of lobing had the smallest decrease in surface area, regardless of whether they had unlobed or lobed leaves. Further, the interaction with lobing was only marginally significant, and it should be borne in mind that 10 different tests at $\alpha = 0.05$ were carried out (Table 3). It therefore appears unlikely that lobing is an alternative to reducing leaf size at lower rainfall.

EVOLUTIONARY DIVERGENCES IN LEAF SIZE: EVIDENCE FOR CLADE-SPECIFIC RESPONSES

Given that leaf area tended to decrease towards lower rainfall and soil P, we investigated how this was accomplished in terms of changes in leaf length and width. Of 263 higher nodes in the phylogenetic tree, 122 represented divergence of more than 0·3 in log soil P after partialling out the effect of the rainfall gradient (Fig. 2a). Among these 23, 39, 42 and 18 were classified as changing shape in isometric, width-only, length-only or opposite fashion, respectively (Table 4).

Table 3. Interaction term statistics for leaf surface area with pubescence, lobing, similar-sided leaves and glossy/waxy cuticle status in a multiple phylogenetic regression along soil phosphorus and mean annual rainfall gradients

Test gradient	Interaction	F ratio	P
P	Area × pubescence	$F_{1,228} = 0.02$	>0.5
	Area × lobing	$F_{1,259} = 0.53$	>0.5
	Area × similar-sided leaves	$F_{1,228} = 2.23$	>0.2
	Area × glossy/waxy cuticle	$F_{1,228} = 0.02$	>0.5
Rainfall	Area × pubescence	$F_{1,228} = 1.03$	>0.5
	Area × lobing	$F_{1,259} = 5.41$	<0.05*
	Area × similar-sided leaves	$F_{1,228} = 0.07$	>0.5
	Area × glossy/waxy cuticle	$F_{1,228} = 1.48$	>0.2

*Significance at $\alpha = 0.05$.

There were 85 nodes representing divergence in log rainfall of more than 0·3 after controlling for the effects of soil P (Fig. 2b); among these 15, 23, 36 and 11 were classified as changing shape in isometric, width-only, length-only or opposite manner, respectively (Table 4). These distributions were significantly different from a 1 : 1 : 1 : 1 ratio (soil P $\chi^2 = 13.67$, df = 3, $P = 0.003$; rainfall $\chi^2 = 17.17$, df = 3, $P = 0.001$). However, the most striking feature of the distribution of changes was that all four were commonly observed, with no strategy dominating along either gradient (Fig. 2). Further, mixtures of leaf shape adjustments were not significantly different between soil P and rainfall divergences ($\chi^2 = 1.40$, $P = 0.71$; Table 4), with nodes tending to follow the same broad patterns along both gradients.

We could find few clear patterns among lineages in the shape adjustments to soil P or annual rainfall gradients. Asterids and caryophyllales tended to show width-only change, while rosids as a group tended to show length-only change along both gradients. However, this commonality was not representative of the data set as a whole (Table 4), with a mixture of adjustments present in most clades.

Discussion

As expected, a reduction in leaf size towards lower soil P and rainfall was observed in both cross-specific analyses and among evolutionary divergences. However, the aim of this study was to determine the manner of this reduction in leaf size. Reduction in leaf length and width (isometric change) could easily be achieved by abbreviation of leaf expansion. On this basis, isometric leaf size reduction was expected to be the most common method. However, leaf narrowing with little shortening, or shortening with little narrowing, were at least as common along both gradients.

It might be expected that developmental propensities in particular clades would favour one sort of leaf size adjustment over another. Similarly if herbivory intensity (Brown & Lawton 1991; Obeso 1997; Rivero-Lynch, Brown & Lawton 1996; Stone & Bacon 1995); architectural considerations (Ackerly & Donoghue 1998; Brouat et al. 1998; White 1983); leaf chemistry (Cunningham et al. 1999); or leaf orientation (Valladares & Pugnaire 1999) varied between clades, any of these factors might affect the fitness of particular leaf shapes in a given environment. However, we found little
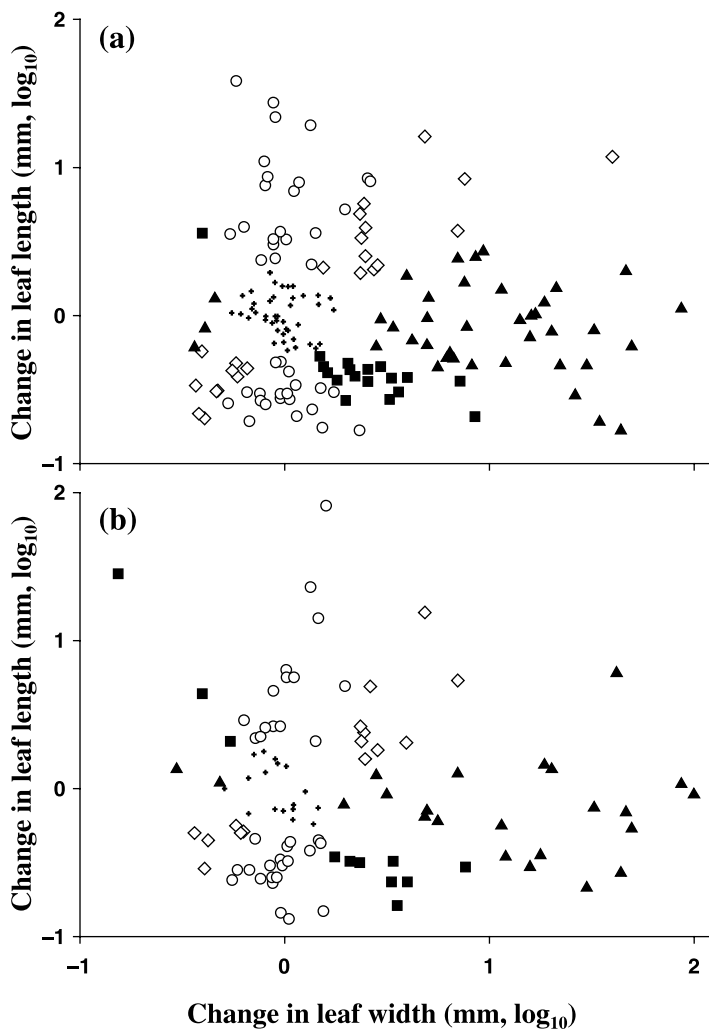

Fig. 2. Mean responses of clades in terms of changes in leaf length and width to (a) changes in soil phosphorus greater than 0·3 orders of magnitude after controlling for the effects of mean annual rainfall; and (b) changes in mean annual rainfall greater than 0·3 orders of magnitude after controlling for the effects of soil P. Individual clades are also marked (see text) according to the method of leaf size reduction: opposite (■); isometric (◇); width-only (▲); length-only (○) change; or 'static' (+), where deviations recorded were less than 0·5 orders of magnitude.

Table 4. Method of leaf size reduction utilized by higher nodes in the working phylogeny in response to changes in soil phosphorus or in mean annual rainfall greater than 0·3 orders of magnitude, after controlling for the effects of the other gradient

Clade	No. nodes	P				Rainfall			
		O	I	W	L	O	I	W	L
Total	**263**	**18**	**23**	**39**	**42**	**11**	**15**	**23**	**36**
Filicopsida	2	0	0	0	1*	0	0	0	0
Spermatopsida	**260**	**18**	**23**	**39**	**41**	**11**	**15**	**23**	**36**
Coniferopsida	1	0	0	0	0	0	0	0	0
Angiosperms	**258**	**18**	**23**	**39**	**41**	**11**	**15**	**23**	**36***
Monocots	**48**	**3**	**4**	**6**	**6**	**3**	**3**	**2**	**5**
Commelinoids	30	2	2	3	5	1	1	2*	4
Eudicots	**202**	**13**	**18***	**33**	**34**	**8**	**12**	**21**	**28**
Proteales	13	0	2	0	2	0	1	0	1
Core Eudicots	**184**	**13**	**15**	**33***	**30**	**8**	**11**	**21**	**26**
Caryophyllales	14	0	0	4	0	0	0	4	0
Rosids	**106**	**12**	**9**	**7**	**25***	**4**	**9**	**6**	**22***
Eurosids I	58	4	4	4	14	3	7	2	10
Eurosids II (A)	21	1	0	1	6	0	0	2	7*
Eurosids II (B), Myrtales	26	7	5	2	4*	1	2	2	4
Asterids	**55**	**0**	**5**	**19**	**5**	**3**	**2**	**10**	**4**
Euasterids I	20	0	2	7	1	1	1	4*	0
Euasterids II	23	0	2	6	4	2*	1	1	4

Clades were classified as using either opposite (O); isometric (I); width-only (W); or length-only (L) change, see Materials and methods for definitions).
*Response of a node at the base of an entire clade.

evidence for clade-specific patterns in the shape changes associated with leaf size reduction. While asterids and caryophyllales often adjusted leaf width alone, and rosids leaf length, these responses were universal for only four nodes sampled within the caryophyllales. Moreover, common responses among other clades were not observed.

If smaller leaf size is selected at low rainfall, and perhaps soil P, principally to decrease the likelihood of leaf overheating in the sun, other leaf traits such as pubescence, lobing and a steep leaf angle (similar-sided leaves) might be expected to interact with the evolution of smaller leaf size. Nevertheless, most such interactions were absent in this flora. The two inter-actions that were statistically significant were not consistent with substituting these traits for smaller leaf size to avoid overheating. Thus these two inter-actions should probably not be regarded as biologically meaningful.

A long-standing issue in plant ecology is to what extent different types of environmental stressors favour a common suite of traits (Chapin, Autumn & Pugnaire 1993; Grime 1977) *vs* distinct traits (Grubb 1985; Harper 1982). Some relationships among leaf traits hold true across a wide range of environments, for example, leaf area per mass (specific leaf area, SLA), leaf lifespan, potential photosynthetic rates (A_{max}) and leaf N concentrations are interrelated (Reich 1993; Reich, Walters & Ellsworth 1997; Reich *et al*. 1999). These relationships persist at lower rain-fall and humidity, but are shifted to shorter leaf lifespan and higher leaf N at a given SLA (Wright, Westoby & Reich 2002). Cunningham *et al*. (1999)

investigated chemical and structural traits of leaves in species pairs that represented independent evolutionary divergences and were contrasted in relation to either rainfall or soil P. Some trait shifts were similar at low rainfall compared to low soil P; others were different. Fonseca *et al*. (2000), reporting the field work on which the present paper also draws, examined site means for leaf width, SLA and potential canopy height. They showed not only that leaf width declined towards both lower rainfall and lower soil P, but also that it declined in the same relationship to SLA. In this sense, common leaf width–SLA combinations were found under both low rainfall and low soil P. On the other hand, leaf width declined in a different relationship to potential plant height at low soil P compared to low rainfall.

Our analyses found no evidence that leaf size reduc-tion occurred in different ways along rainfall gradients compared to soil P gradients, with a mixture of each type of shape change spread throughout all lineages. One possible interpretation of this result is that both gradients favour similar leaf-trait combinations. However, leaf size reduction occurred in many ways, at different phylogenetic divergences, along each gradient. Further, patterns of common methods of leaf size reduction were not found within lineages, nor were correlations of shape change and other leaf traits such as pubescence detected. Taken together, this suggests that many mechanisms are possible for reducing leaf size. The similarities between the soil P and rainfall gradients observed in this data set are more likely to be caused by averaging across many different reductions, and are not evidence for strong evolutionary convergence.

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References

Ackerly, D.D. & Donoghue, M.J. (1998) Leaf size, sapling allometry, and Corners Rules – phylogeny and correlated evolution in Maples (*Acer*). *American Naturalist* **152**, 767–791.

Anderson, S.E. & Ingram, J.S.I. (1989) *Tropical Soil Biology and Fertility: A Handbook of Methods*. CAB International, Wallingford, UK.

APG (1998) An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* **85**, 531–553.

Ashton, P.S. & Hall, P. (1992) Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *Journal of Ecology* **80**, 459–481.

Baethgen, W.E. & Alley, M.M. (1989) A manual colorimetric procedure for measuring ammonium nitrogen in soil and plant Kjeldahl digests. *Communications in Soil Science and Plant Analysis* **20**, 961–969.

Beadle, J.S. (1962) Soil phosphate and the delimination of plant communities in eastern Australia II. *Ecology* **43**, 281–288.

Beadle, J.S. (1966) Soil phosphate and its role in moulding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. *Ecology* **47**, 992–1007.

Beadle, N.C.W. (1954) Soil phosphate and the delimination of plant communities in eastern Australia. *Ecology* **35**, 370–375.

Beard, J.S. (1945) *The Natural Vegetation of Trinidad*, Vol. 20. Clarendon Press, Oxford, UK.

Bremer, K., Bremer, B. & Thulin, M. (1998) *Classification of Flowering Plants*, www.systbot.uu.se/classification/classification98.html. Department of Systematic Botany, Uppsala University, accessed 1999.

Brouat, C., Gibernau, M. & Amsellem, L. & McKey, D. (1998) Corners Rules revisited – ontogenetic and interspecific patterns in leaf-stem allometry. *New Phytologist* **139**, 459–470.

Brown V.K. & Lawton, J.H. (1991) Herbivory and the evolution of leaf size and shape. *Philosophical Transactions of the Royal Society of London – Series B* **333**, 265–272.

Chapin, F.S. (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**, 233–260.

Chapin, F.S., Autumn, K. & Pugnaire, F. (1993) Evolution of suites of traits in response to environmental stress. *American Naturalist* **142**, 78–92.

Cordell, S., Goldstein, G., Muellerdombois, D., Webb, D. & Vitousek, P.M. (1998) Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient – the role of phenotypic plasticity. *Oecologia* **113**, 188–196.

Cowling, R.M. & Campbell, B.M. (1980) Convergence in vegetation structure in the Mediterranean communities of California, Chile and South Africa. *Vegetatio* **43**, 191–197.

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.

Dolph, G.E. (1977) The effect of different calculational techniques on the estimation of leaf area and the construction of leaf size distributions. *Bulletin of the Torrey Botanical Club* **104**, 264–269.

Dolph, G.E. & Dilcher, D.L. (1980) Variation in leaf size with respect to climate in the tropics of the Western Hemisphere. *Bulletin of the Torrey Botanical Club* **107**, 154–162.

Ehleringer, J. (1982) The influence of water stress and temperature on leaf pubescence development in *Encelia farinosa*. *American Journal of Botany* **69**, 670– 675.

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.

Givnish, T.J. (1978) Ecological aspects of plant morphology: leaf form in relation to environment. *Theoretical Plant Morphology* (ed. R. Sattler), pp. 83–142. Leiden University Press, Leiden.

Givnish, T.J. (1979) On the adaptive significance of leaf form. *Topics in Plant Population Biology* (eds O.T. Solbrig, S. Jain, G.B. Johnson & P.H. Raven), pp. 375–407. Columbia University Press, New York.

Givnish, T.J. (1984) Leaf and canopy adaptations in tropical forests. *Physiological Ecology of Plants of the Wet Tropics* (eds E. Medina, H.A. Mooney & C. Vazquez-Yanes), pp. 51–84. Dr W. Junk, The Hague, the Netherlands.

Givnish, T.J. & Vermeij, G.J. (1976) Sizes and shapes of liane leaves. *American Naturalist* **110**, 743–778.

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

Grafen, A. (1991) A User's Guide to the Phylogenetic Regression Program, PHYLO.GLM, Version 1.03. Royal Statistical Society, London.

Grafen, A. (1992) The uniqueness of the phylogenetic regression. *Journal of Theoretical Biology* **156**, 405–423.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**, 1169–1194.

Grubb, P.J. (1985) Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization. *The Population Structure of Vegetation* (ed. J. White), pp. 595–621. Dr W. Junk, The Hague, the Netherlands.

Halloy, S.R.P. & Mark, A.F. (1996) Comparative leaf morphology spectra of plant communities in New Zealand, the Andes and the European Alps. *Journal of the Royal Society of New Zealand* **26**, 41–78.

Harden, G.J. (1993) *Flora of New South Wales*. University of NSW Press, Sydney.

Harper, J.L. (1982) After description. *The Plant Community as a Working Mechanism* (ed. E.I. Newman), pp. 11–25. Blackwell Scientific Publications, Oxford, UK.

Johnson, H.B. (1975) Plant pubescence: an ecological perspective. *Botanical Review* **41**, 233–258.

Miller, P.C. (1983) Canopy structure of Mediterranean-type shrubs in relation to heat and moisture. *Mediterranean-Type Ecosystems* (eds F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis), pp. 133–166. Springer-Verlag, Berlin.

Nunez-Olivera, E., Martinez-Abaigar, J. & Escudero, J.C. (1996) Adaptability of leaves of *Cistus ladanifer* to widely varying environmental conditions. *Functional Ecology* **10**, 636–646.

Obeso, J.R. (1997) The induction of spinescence in European holly leaves by browsing ungulates. *Plant Ecology* **129**, 149–156.

Parkhurst, D.F. & Loucks, O.L. (1972) Optimal leaf size in relation to environment. *Journal of Ecology* **60**, 505–537.

Reich, P.B. (1993) Reconciling apparent discrepancies among studies relating life span, structure and function of leaves in contrasting plant life forms and climates: 'the blind man and the elephant retold'. *Functional Ecology* **7**, 721–725.

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, USA* **94**, 13730–13734.

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.

Rivero-Lynch, A.P., Brown, V.K. & Lawton, J.H. (1996) The impact of leaf shape on the feeding preference of insect herbivores – experimental and field studies with *Gapsella and Phyllotreta*. *Philosophical Transactions of the Royal Society of London – Series B* **351**, 1671–1677.

Rodriguez, D., Keltjens, W.G. & Goudriaan, J. (1998) Plant leaf area expansion and assimilate production in wheat (*Triticum aestivum* L.) growing under low phosphorus conditions. *Plant and Soil* **200**, 227–240.

Sandquist, D.R. & Ehleringer, J.R. (1997) Intraspecific variation of leaf pubescence and drought response in *Encelia farinosa* associated with contrasting desert environments. *New Phytologist* **135**, 635–644.

Schuepp, P.H. (1993) Tansley Review 59: Leaf boundary layers. *New Phytologist* **125**, 477–507.

Smith, W.K. & Nobel, P.S. (1977) Influences of seasonal changes in leaf morphology on water-use efficiency for three desert broadleaf shrubs. *Ecology* **58**, 1033–1043.

Stone, C. & Bacon, P.E. (1995) Leaf dynamics and insect herbivory in a *Eucalyptus camaldulensis* forest under moisture stress. *Australian Journal of Ecology* **20**, 473–481.

Valladares, F. & Pugnaire, F.I. (1999) Tradeoffs between irradiance capture and avoidance in semi-arid environments assessed with a crown architecture model. *Annals of Botany* **83**, 459–469.

Vogel, S. (1970) Convective cooling at low airspeeds and the shapes of broad leaves. *Journal of Experimental Botany* **21**, 91–101.

Webb, L.J. (1968) Environment relationships of the structural types of Australian rainforest vegetation. *Ecology* **49**, 296–311.

White, P.S. (1983) Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. *Bulletin of the Torrey Botanical Club* **110**, 203–212.

Wolfe, J.A. (1995) Paleoclimatic estimates from tertiary leaf assemblages. *Annual Review of Earth and Planetary Sciences* **23**, 119–142.

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.

Wright, I.J., Clifford, H.T., Kidson, R., Reed, M.L., Rice, B.L. & Westoby, M. (2000) A survey of seed and seedling characters in 1744 Australian dicotyledon species: cross-species trait correlations and correlated trait-shifts within evolutionary lineages. *Biological Journal of the Linnean Society* **69**, 521–547.