

# Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients

IAN J. WRIGHT and MARK WESTOBY

*School of Biological Sciences, Macquarie University, Sydney 2109, Australia*

## Summary

**1** Species-pairs from woody dicot lineages were chosen as phylogenetically independent contrasts (PICs) to represent evolutionary divergences along gradients of rainfall and nutrient stress, and within particular habitat types, in New South Wales, Australia. Seedlings were grown under controlled, favourable conditions and measurements were made for various growth, morphological and allocation traits.

**2** Trait correlations across all species were identified, particularly with respect to seedling relative growth rate (RGR) and specific leaf area (SLA), a fundamental measure of allocation strategy that reflects the light-capture area deployed per unit of photosynthate invested in leaves.

**3** Across all species, SLA, specific root length (SRL) and seed reserve mass were the strongest predictors of seedling RGR. That is, a syndrome of leaf and root surface maximization and low seed mass was typical of high RGR plants. This may be a high-risk strategy for individual seedlings, but one presumably mitigated by a larger number of seedlings being produced, increasing the chance that at least one will find itself in a favourable situation.

**4** Syndromes of repeated attribute divergence were identified in the two sets of gradient PICs. Species from lower resource habitats generally had lower SLA. Thus, in this important respect the two gradients appeared to be variants of a more general 'stress' gradient.

**5** However, trends in biomass allocation, tissue density, root morphology and seed reserve mass differed between gradients. While SLA and RGR tended to shift together along gradients and in within-habitat PICs, no single attribute emerged as the common, primary factor driving RGR divergences within contrasts. Within-habitat attribute shifts were of similar magnitude to those along gradients.

*Keywords:* phylogenetically independent contrasts, relative growth rate, specific leaf area, specific root length, stress

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## Introduction

On average, seedlings of species characteristic of favourable habitats have a higher potential relative growth rate (RGR) than those from unfavourable habitats. In other words, when grown under controlled, favourable conditions their RGR is greater (Lambers & Poorter 1992). However, in the field there must be trade-offs between growth and other plant functions as high RGR species do not pre-

dominate in unproductive environments. Furthermore, a spread of potential RGR is apparent among species from any habitat type.

Relative growth rate can be split into three components such that:

$$\text{RGR} = \text{NAR} * \text{LMR} * \text{SLA}$$

that is, the product of the net assimilation rate (NAR; rate of dry mass increase per unit leaf area), leaf mass ratio (LMR; ratio of leaf to total mass) and specific leaf area (SLA; leaf area per unit leaf mass). In a number of studies, most of the between-species variation in RGR has been accounted for by variation in

SLA (Lambers & Poorter 1992). SLA is determined both by leaf lamina thickness and by tissue density (Witkowski & Lamont 1991), and is negatively related to leaf life span (Reich *et al.* 1992; Reich 1993). It is therefore not just an indicator or correlate of RGR and other plant traits, but a fundamental measure of allocation strategy that reflects the light-capture area deployed per unit of photosynthate invested into leaves. It is like the expected rate of return on an investment, and high SLA carries with it a high risk that the leaf tissue produced may have a short income-returning life. Other characteristics associated with between-species variation in seedling RGR include seed mass, specific root length (SRL; the root length achieved per unit root dry mass) and plant tissue density (Boot & Mensink 1990; Marañón & Grubb 1993; Ryser & Lambers 1995; Ryser 1996). These results derive mostly from experiments involving European grasses and herbaceous species although, more recently, a literature dealing with woody floras has begun to develop (Huante *et al.* 1995; Cornelissen *et al.* 1996; Swanborough & Westoby 1996; Hunt & Cornelissen 1997).

In this study, seedlings of 33 evergreen woody species from New South Wales (temperate eastern Australia) were grown under controlled, favourable conditions and measurements were made of seedling RGR and a number of morphological attributes. Species were selected to form sets of phylogenetically independent contrasts (PICs; Burt 1989) along gradients of decreasing soil nutrients ('nutrient PICs'), decreasing rainfall ('rainfall PICs') and within particular habitats ('within-habitat PICs'). The aims of the study were twofold. First, we wanted to identify trait correlations across all species with particular reference to RGR, SLA and SRL. Secondly, we were interested in the extent to which shortages of soil nutrients and rainfall can usefully be pooled together under the one general heading of 'stress', as advocated for example by Grime (1977) and Chapin (1980) but as disapproved of by Grubb (1985). If the overall nature of the stresses in low nutrient and low rainfall habitats are similar (e.g. if any type of stress is associated with low RGR, or because low soil water leads *de facto* to low nutrient availability), we would expect to find common trait shifts in nutrient and rainfall PIC when seedlings are grown under standard conditions. Alternatively, if successful resource acquisition in the two habitat types requires very different strategies, we would expect different trait shifts to occur.

This study represents an advance on previous studies in a number of ways. First, we assess the generality of previous findings across a reasonably large Australian woody flora. Secondly, we deliberately contrast species in relation to environment (specifically comparing two growth-slowing factors). Thirdly, we provide replication of contrasts across a number of lineages. We were interested in a number of specific predictions arising mostly from previous findings in

the literature. We expected that, across all species, (i) variation in RGR would primarily be driven by differences in SLA, rather than by variation in LMR or NAR; (ii) high RGR plants would have both high SLA and high SRL, i.e. a general strategy of maximizing absorptive surfaces; (iii) a negative relationship between RGR and seed reserve mass would be evident; and (iv) high RGR species would exhibit lower tissue density than low RGR species. A fifth prediction was that along gradients SLA and thus RGR would decrease from high to low nutrients and high to low rainfall unless a counteracting trend was apparent in either LMR or NAR.

## Materials and methods

### SPECIES SELECTION

Rainfall PICs compared species typical of low-medium nutrient soils in the coastal region (annual rainfall typically 1000–1250 mm; heath/dry sclerophyll vegetation) with those typical of low-medium nutrient soils in western New South Wales (annual rainfall typically 200–400 mm; open shrubland). Nutrient PICs considered only the coastal region and compared species typical of low nutrient Hawkesbury sandstone soils (mostly heath species; total soil P typically 40 p.p.m.) with species from higher nutrient basalt or shale soils (dry/wet sclerophyll vegetation; total soil P typically 300–1000 p.p.m.). Total phosphorus was chosen as the index of soil nutrient status because it is commonly the most limiting nutrient in Australian soils (Beadle 1967), it is derived from the parent rock at a site and is relatively insoluble. Consequently, it is a better indicator of site properties from the point of view of which plant strategies can sustain populations there than, say, soil nitrogen. Within-habitat contrasts were constructed within low rainfall, low nutrient and high nutrient habitats.

Species contrasts were constructed using woody perennial dicot species whose distributions satisfied the above criteria (following Jacobs & Pickard 1981 and Harden 1990), and for which field-collected seed was available from native seed supply companies and from collections held at Macquarie University. Contrasts were formed at a variety of taxonomic levels, following Harden (1990; in which Caesalpinaceae, Fabaceae and Mimosaceae are given family rank within Fabales). Climbers, prostrate and succulent species were excluded. For several species the seeds obtained were found to be non-viable and a replacement species was then sought for the contrast, although in three cases this was not possible. Constraints imposed by the design meant that the species used were largely drawn from Myrtaceae, Proteaceae and Fabales. As a consequence, the three sets of PICs were not phylogenetically independent from each other. All possible PICs satisfying the constraints were used, resulting in five contrasts in each of the

three categories (nutrient, rainfall and within-habitat PICs; Table 1). Some contrasts were between growth forms (tree vs. shrub, particularly along the nutrient gradient), although this was avoided where possible. Species used and their adult characteristics can be found in the *Journal of Ecology* archive on the World Wide Web (<http://www.open.ac.uk/OU/Academic/Biology/JEcol/JEarchiv/JEarcmen.htm>).

#### GROWTH CONDITIONS

Seeds were germinated on filter paper moistened with de-ionized water, in Petri dishes kept in the growth chambers where the seedlings were subsequently grown. Where necessary, pregermination treatments were applied, e.g. scarification or immersion in boiling water (Fabales); removal of outer seed membrane (some Proteaceae); sterilization of seed coat in 2.5% chlorine bleach solution (*Pittosporum*). On the day following radicle emergence, seedlings were planted out individually in pots containing coarse river sand (pasteurized for 2.5 h at 70 °C) topped with *c.* 1.5 cm horticultural vermiculite. Pot dimensions were 7 × 7 × 23 cm, volume *c.* 1100 cm<sup>3</sup> (unused cardboard milk cartons). The extremely small-seeded *Melaleuca* and *Callistemon* spp. were germinated in ster-

ilized fine sand and planted out when the root was *c.* 1 cm long. Day/night temperatures in the growth chambers were maintained at 22°/16 °C; photoperiod was 16 h at 160 ± 10 μmol m<sup>-2</sup> s<sup>-1</sup>. Integrated daily photosynthetically active radiation (PAR) flux was therefore *c.* 9.2 mol m<sup>-2</sup> day<sup>-1</sup>. Pots were thoroughly flushed with a modified Hoagland's solution every second day and top-watered with a small amount of de-ionized water on intervening days. As well as containing all appropriate micronutrients, the nutrient solution (pH = 5.6) contained macronutrients in the following concentrations: NO<sub>3</sub><sup>-</sup> 3.38 mM, NH<sub>4</sub><sup>+</sup> 0.125 mM, H<sub>2</sub>PO<sub>4</sub><sup>-</sup> 0.375 mM, K<sup>+</sup> 1.75 mM, Ca<sup>2+</sup> 1.25 mM, Mg<sup>2+</sup> 0.250 mM, SO<sub>4</sub><sup>2-</sup> 0.563 mM.

Neither water nor nutrients should have been limiting: in general, as long as the nitrogen concentration in the soil solution remains above 0.2–0.3 mM, the uptake system for mineral nitrogen of most species is saturated (Garnier & Freijisen 1994). In contrast, it is unlikely that the species' photosynthetic systems were saturated at a PAR of 9.2 mol m<sup>-2</sup> day<sup>-1</sup>. While this is certainly a lower flux than canopy conditions in the field, it is none the less comparable with other similar studies (Grime & Hunt 1975; Garnier & Freijisen 1994; Cornelissen *et al.* 1996; Hunt & Cornelissen 1997). Importantly, rather than creating 'ideal' or 'optimum'

**Table 1** Species-pairs (PICs) contrasted along nutrient and rainfall gradients, and within habitats. In gradient contrasts high nutrient and high rainfall species are listed first

Species	Family	Order	Contrast label
<b>Nutrient contrasts</b>			
<i>Eucalyptus saligna</i> – <i>E. sieberi</i>	Myrtaceae	Myrtales	Eucalyptus
<i>Acacia binervata</i> – <i>A. jonesii</i>	Mimosaceae	Fabales	Acacia
<i>Stenocarpus sinuatus</i> – <i>Banksia oblongifolia</i>	Proteaceae	'Proteales'	Proteaceae
<i>Lophostemon confertus</i> – <i>Leptospermum leavigatum</i>	Myrtaceae	Myrtales	Myrtaceae
<i>Senna barclayana</i> – <i>Gompholobium latifolium</i>	Caesalpinaceae Fabaceae	Fabales	Fabales
<b>Rainfall contrasts</b>			
<i>Eucalyptus amplifolia</i> – <i>E. largiflorens</i>	Myrtaceae	Myrtales	Eucalyptus
<i>Acacia cognata</i> – <i>A. burkitii</i>	Mimosaceae	Fabales	Acacia
<i>Melaleuca linariifolia</i> – <i>Callistemon brachyandrus</i>	Myrtaceae	Myrtales	Myrtaceae
<i>Hakea dactyloides</i> – <i>Grevillea striata</i>	Proteaceae	'Proteales'	Proteaceae
<i>Pultenaea daphnoides</i> – <i>Senna artemisioides</i> ssp. <i>sturtii</i>	Fabaceae Caesalpinaceae	Fabales	Fabales
<b>Within-habitat contrasts</b>			
<b>Low nutrient</b>			
<i>Eucalyptus apiculata</i> – <i>E. burgessiana</i>	Myrtaceae	Myrtales	Eucalyptus
<i>Angophora floribunda</i> – <i>E. grandis</i>	Myrtaceae	Myrtales	Myrtaceae
<i>Banksia ericifolia</i> – <i>Hakea gibbosa</i>	Proteaceae	'Proteales'	Proteaceae
<b>High nutrient</b>			
<i>Hovea acutifolia</i> – <i>Pittosporum undulatum</i>	Fabaceae Pittosporaceae	Fabales Apiales	Eudicot
<b>Low rainfall</b>			
<i>Bossiaea walkeri</i> – <i>Dodonaea peduncularis</i>	Fabaceae Sapindaceae	Fabales Sapindales	Rosidae

conditions for all species studied, the aim of such studies is to create standard conditions favourable enough for all species to achieve exponential growth. Under such a regime, the measurement of seedling growth parameters should be considered a bioassay allowing a fair ranking of species with respect to one another.

Pot positions were randomized at least twice weekly. For each species, unhealthy plants were discarded and those remaining assigned randomly to one of three harvests. Since root morphology was of interest, we sought to ensure that pot space did not hinder root growth. Thus, the three harvests for each species were spaced as far apart as possible (to improve resolution in estimating RGR; Poorter & Garnier 1996) but subject to the restriction that the last harvest occurred before pot space became limiting. Seedlings were divided into root, cotyledon, leaf and stem components. Saturated (fresh) weights were obtained from material stored overnight between moist paper towels at 4 °C, dry weights from material oven-dried at 75 °C for 48 h. Whole-plant tissue density and density of individual organs were estimated by the ratio of dry mass to saturated (fresh) mass (Garnier & Laurent 1994; Ryser & Lambers 1995). Mean sample size for whole-plant dry weight (and estimation of RGR) was 26.4 seedlings per species, while smaller sample sizes were used for other attributes for most species (details available in the *Journal of Ecology* archive on the WWW).

Root systems were kept intact during harvesting and spread out on a glass plate after staining in 2.5% aqueous methyl violet solution. Root, cotyledon and leaf images were created by scanning fresh material on a flatbed scanner at 400 d.p.i. Projected leaf and cotyledon area, root length and mean root diameter were measured using Delta-T Scan<sup>®</sup> (Kirchhof & Pendar 1993). Average root diameter was calculated over the entire root system using the 'length sin  $\theta$ ' procedure (Kirchhof & Pendar 1993), by which a weighted mean value is calculated from a length–diameter distribution. Seed reserve mass was determined from a minimum of 20 oven-dried seeds (75 °C for 48 h) per species after the removal of the testa and any dispersal structures (e.g. the elaiosomes of *Acacia* species).

#### ESTIMATION OF RGR AND OTHER PARAMETERS

In 25 of 33 species, true leaves were not present at the time of first harvest (7–14 days, depending on species) or leaves were still relatively unexpanded and leaf area was less than *c.* 5% of total deployed photosynthetic area, in which case leaf mass was counted as part of stem mass along with the petiole. Most species had, however, entered a phase of exponential growth by this first harvest, as indicated by a formal statistical test for non-linearity of the slope of a linear regression of  $\ln$  dry mass against time (Zar 1984). Of the seven

'non-linear' exceptions (WWW), four were accelerating and three decelerating. No causes were identified that might have resulted in this behaviour: there was no correlation between accelerating RGR and lack of true leaves at first harvest, nor were decelerating species running out of pot space. Therefore, we thought it best to use the RGR value calculated over the entire growth period for all species.

Mean values were calculated for all parameters over both harvest intervals but the results and discussion presented concern only the second interval as the proportion of expanded to newly formed leaf was greater at this time, resulting in more representative values for parameters such as SLA, NAR, LMR, etc. (i.e. less between-individual variability). Leaf attributes were calculated separately for cotyledons, leaves and leaves plus cotyledons ('effective' specific leaf area; see Table 2 for list of attribute abbreviations). Results presented are for effective leaf area as cotyledons were green and persistent for all species except *Acacia elata* and *A. jonesii* (shed by second harvest), no noticeable increase in growth rate accompanied the transition from a photosynthetic surface comprising cotyledons only to one which was mostly leaf, and parameters calculated on the basis of leaf only were extremely tightly correlated with leaf + cotyledon.

Data analysis mostly took the form of linear regression and correlation: when we had reason to test a predictive relationship, linear regression was used; for assessing non-directional relationships Pearson correlation coefficients were calculated. Differences in group means for species categorized by taxonomic group and adult growth form were tested with ANOVA followed by Tukey's HSD *post hoc* test. All statistical analyses were carried out with SPSS for Windows vs. 6. The interpretation of PIC patterns was approached in a qualitative manner rather than through formal significance testing as the hypotheses explored required replication at the level of PICs and we were able to construct only five contrasts in each category (although more species were studied in total than is usual for growth analysis). Although building up replicates within a species gives more confidence in the given mean value ascribed to each species and can be used to test for a difference between two particular species in a contrast, it is irrelevant (pseudo-replicated) with regard to the question of generalizing across lineages (Westoby *et al.* 1998), which was our aim. Similarly, replication in the number of species used at each end of a PIC would give confidence in the generalization across species in that divergence, but is irrelevant with regard to generalizing across lineages. Consequently, only 'majority trends' in each set of PICs (4/5 or 5/5) were considered indicative of a consistent relationship.

Although species were selected according to a PIC design, trait relationships across the full 33 species are described first because they are of interest in themselves and trends across PICs can be better under-

**Table 2** List of abbreviations used in the text

Abbreviation	Definition	Unit
RGR	Relative growth rate: instantaneous rate of dry mass increase per unit dry mass already present. Calculated from linear regression of ln dry mass against time; equivalent to SLA * LMR * NAR	mg mg <sup>-1</sup> day <sup>-1</sup>
LAR	Leaf area ratio: leaf + cotyledon area per unit plant dry mass (= LMR * SLA)	mm <sup>2</sup> mg <sup>-1</sup>
SLA	Specific leaf area: total area of leaves + cotyledons per unit dry mass of leaves + cotyledons	mm <sup>2</sup> mg <sup>-1</sup>
LMR, SMR, RMR	Leaf, stem or root mass ratio: ratio of leaf + cotyledon, stem or root dry mass to plant dry mass	–
NAR	Net assimilation rate: instantaneous rate of dry mass increase per unit leaf + cotyledon area per day	mg mm <sup>-2</sup> day <sup>-1</sup>
SRL	Specific root length: root length per unit root dry mass	mm mg <sup>-1</sup>
dm/sm	Tissue 'density': ratio of dry mass to saturated (fresh) mass	–

stood and interpreted with the across-species results in mind.

## Results

### TRENDS IN RGR AND OTHER ATTRIBUTES ACROSS ALL SPECIES

Across all 33 species, RGR ranged from *c.* 0.03 to 0.13 mg mg<sup>-1</sup> day<sup>-1</sup>. It showed a stronger relationship with leaf area ration (LAR) ( $R^2 = 0.65$ ,  $P < 0.001$ ; Fig. 1a) than with NAR ( $R^2 = 0.01$ ,  $P = 0.515$ ; Fig. 1b). The dependence of RGR on LAR was almost entirely due to SLA (SLA as predictor of RGR:  $R^2 = 0.58$ ,  $P < 0.001$ ; Fig. 1c) rather than LMR (LMR as predictor of RGR:  $R^2 = 0.03$ ,  $P = 0.321$ ; Fig. 1d). Other biomass-allocation parameters were also related to relative growth rate. A strong positive relationship was apparent between root mass ratio (RMR) and RGR (correlation  $r = 0.66$ ,  $P < 0.001$ ; Fig. 2a), while stem mass ratio (SMR) and RGR ( $r = -0.55$ ,  $P = 0.001$ ; Fig. 2b) and cotyledon mass ratio and RGR ( $r = -0.44$ ,  $P = 0.014$ ) were negatively related. The various measures of tissue dm/sm (ratio dry mass/saturated mass) mostly showed little relationship with RGR, with the exception of cotyledon dm/sm ( $r = 0.53$ ,  $P = 0.002$ ).

SRL spanned a large range (*c.* 10–350 mm mg<sup>-1</sup>) and was positively related to RGR ( $r = 0.75$ , Fig. 2c). Variation in SRL was mostly due to variation in mean root diameter ( $r = -0.73$ ,  $P < 0.001$ ) rather than in root tissue dm/sm ( $r = 0.14$ ,  $P = 0.439$ ). SRL was also highly correlated with SLA ( $r = 0.73$ ,  $P < 0.001$ ), that is, maximization of leaf area per unit leaf mass was strongly associated with maximization of root length per unit root mass. This was achieved by building thin roots (measured) or thin leaves (inferred) rather than with watery (low dm/sm) tissue.

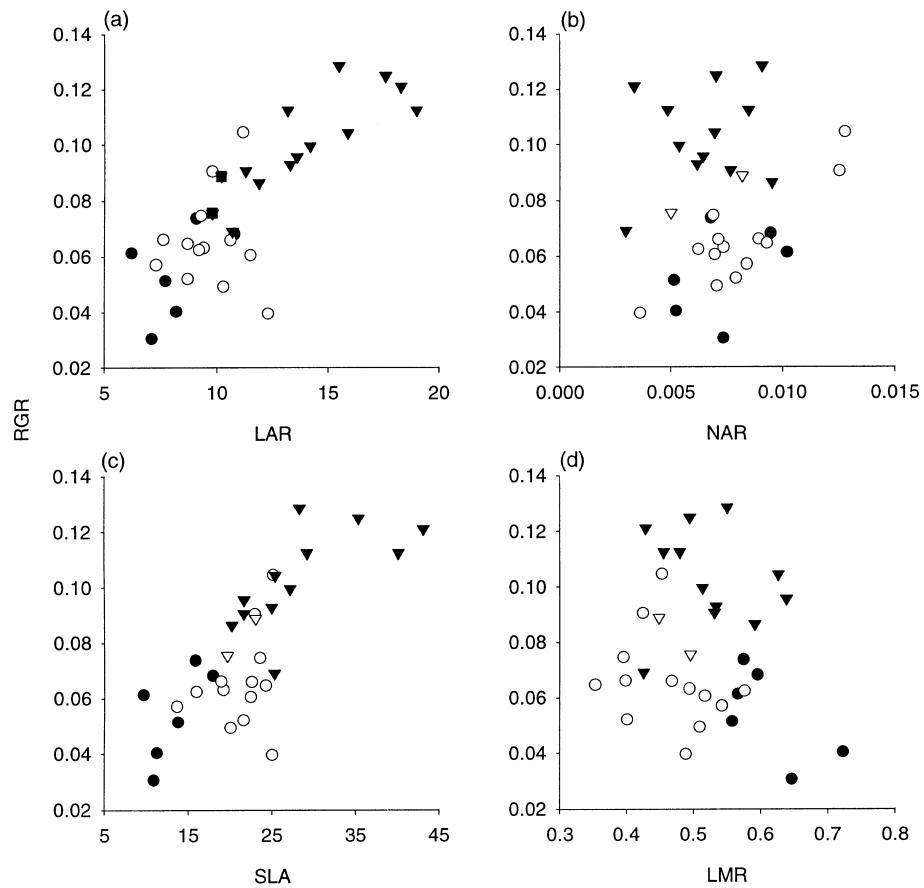
Seed reserve mass, spanning nearly three orders of magnitude, had a strong negative relationship with

RGR (ln seed mass against RGR:  $r = 0.81$ ; Fig. 2d), at least up to masses of *c.* 12 mg (ln mass = *c.* 2.5), where a spread of RGR values occurred. Small-seeded species characteristically developed high SLA cotyledons (ln seed mass vs. SLA of cotyledons:  $r = -0.84$ ,  $P < 0.001$ ) and allocated a relatively large proportion of mass to roots (ln seed mass vs. RMR:  $r = -0.66$ ,  $P < 0.001$ ), with the roots themselves having high SRL (ln seed mass vs. SRL:  $r = -0.84$ ,  $P < 0.001$ ). SLA of cotyledons only was itself a strong predictor of SLA of leaves only ( $R^2 = 0.77$ ,  $P < 0.001$ ).

### COMPARISONS BETWEEN TAXA AND GROWTH FORM

Multivariate ordination (semi-strong hybrid multi-dimensional scaling; Belbin 1993) was used to identify whether the scored attributes would cause species to sort according to habitat, taxonomic group or otherwise. While no pattern was evident with respect to habitat, broad sorting of species by taxonomic affiliation occurred such that three main groups were evident (not shown): Proteaceae, Myrtaceae and Fabales (Caesalpinaceae, Fabaceae and Mimosaceae). The three taxa differed substantially in average values for many attributes (ANOVA followed by Tukey HSD test). Myrtaceae had higher mean RGR, SLA, SRL, RMR and cotyledon dm/sm, but lower mean seed mass and SMR, than Fabales or Proteaceae. Fabales had lower plant dm/sm than Myrtaceae, and lower root dm/sm than either Myrtaceae or Proteaceae. Proteaceae had higher cotyledon mass ratio and LMR than either Myrtaceae or Fabales, and higher SLA and RMR than Fabales.

As nine of 13 tree species were Myrtaceae and 10 of 13 shrubs were Fabales, comparisons between growth forms yielded similar results to comparisons between taxonomic groups. Independent of whether the tall shrubs/small trees were included in shrub or



**Fig. 1** Relationship between RGR and component attributes across the 33 study species. RGR vs. (a) LAR, (b) NAR, (c) SLA, (d) LMR. Key: (▼) Myrtaceae; (●) Proteaceae; (○) Fabales; (▽) other. Units: RGR,  $\text{mg mg}^{-1} \text{day}^{-1}$ ; LAR,  $\text{mm}^2 \text{mg}^{-1}$ ; NAR,  $\text{mg mg}^{-1} \text{mm}^{-2}$ ; SLA,  $\text{mm}^2 \text{mg}^{-1}$ ; LMR, unitless ratio.

tree categories, comparison of mean attribute values across growth forms (two-tail *t*-test,  $\alpha = 0.05$ ) showed higher SRL, cotyledon  $\text{dm}/\text{sm}$  and plant  $\text{dm}/\text{sm}$ , and lower SMR in trees than shrubs.

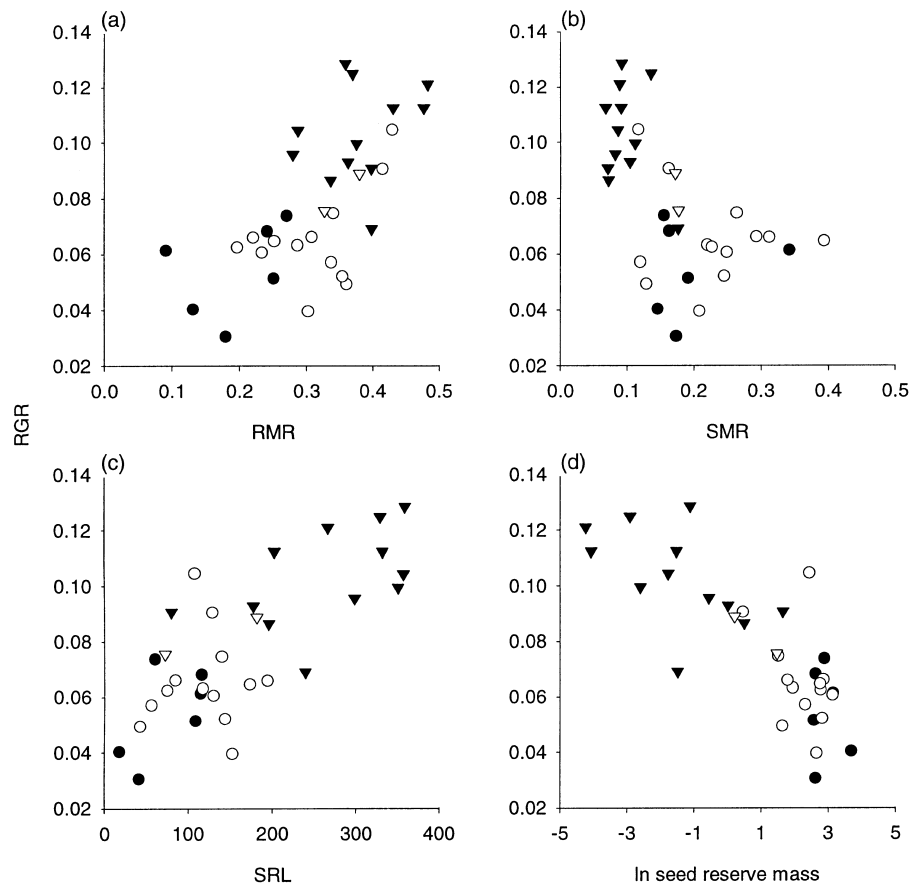
#### ATTRIBUTE RELATIONSHIPS ALONG THE RAINFALL GRADIENT

For rainfall and nutrient PICs, shifts in RGR and its components down the gradients are illustrated in 'correlated change' graphs (Fig. 3). Plotted values were calculated by subtracting the attribute value for the high rainfall (or nutrient) species from that of the low rainfall (or nutrient species) within each PIC. A negative shift in, say, SLA can be viewed on its own (point falls in either left-hand quadrant) or in relation to another attribute (negative shift in both SLA and RGR: point falls in lower left quadrant). Positively correlated change in both attributes, without regard to the gradient, would cause a point to fall in either lower left or upper right quadrants; similarly, negatively correlated change (without regard to gradient) would cause a point to fall in either upper left or lower right quadrants. Note that our a priori hypothesis

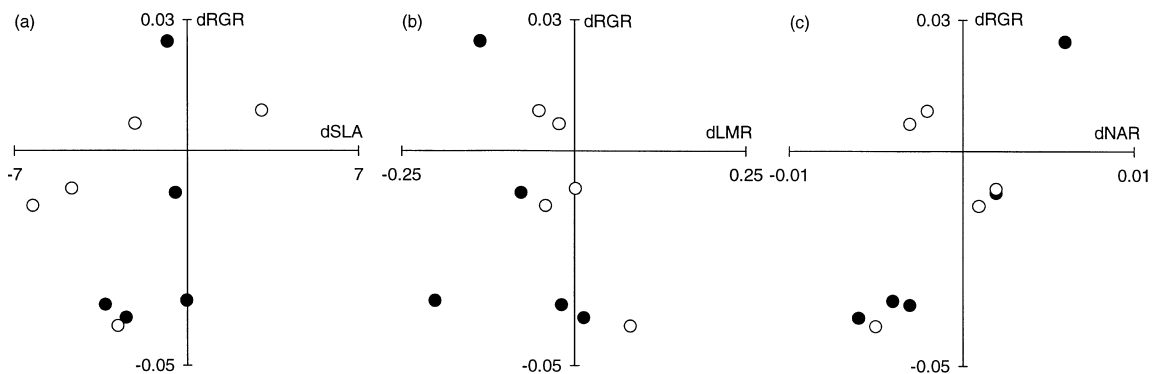
was that SLA would exhibit negative shifts down both gradients, and in doing so would cause negative shifts in RGR unless strong counteracting trends were found in LMR, NAR or both.

Within rainfall PICs, LAR shifted negatively down the gradient in four of five contrasts, mostly due to negative shifts in SLA (4/5) rather than in LMR (no trend). NAR shifted negatively down the gradient in three of five contrasts. Overall, however, the opposing trends in LAR and NAR resulted in three negative and two positive RGR shifts down the gradient. Comparison of relative shift size between RGR and its components revealed that SLA was the primary factor behind RGR divergence (irrespective of direction) in three of five contrasts.

Root  $\text{dm}/\text{sm}$  was generally lower (4/5), and mean root diameter higher (5/5), in the low rainfall species of each PIC. Since the trend in root thickness was much stronger than that in root tissue  $\text{dm}/\text{sm}$ , SRL was still clearly lower in all five low rainfall species (Fig. 4a). Negative shifts down the gradient also occurred in plant  $\text{dm}/\text{sm}$ , while seed reserve mass showed a positive shift in four of five contrasts. A weak decreasing trend was evident in stem mass



**Fig. 2** Relationship between RGR and selected attributes across the 33 study species. RGR vs. (a) RMR, (b) SMR, (c) SRL, (d) seed reserve mass. Key: (▼) Myrtaceae; (●) Proteaceae; (○) Fabales; (▽) other. Units: RGR,  $\text{mg mg}^{-1} \text{day}^{-1}$ ; RMR and SMR, unitless ratios; SRL,  $\text{mm mg}^{-1}$ ; seed reserve mass,  $\log_e \text{mg}$ .



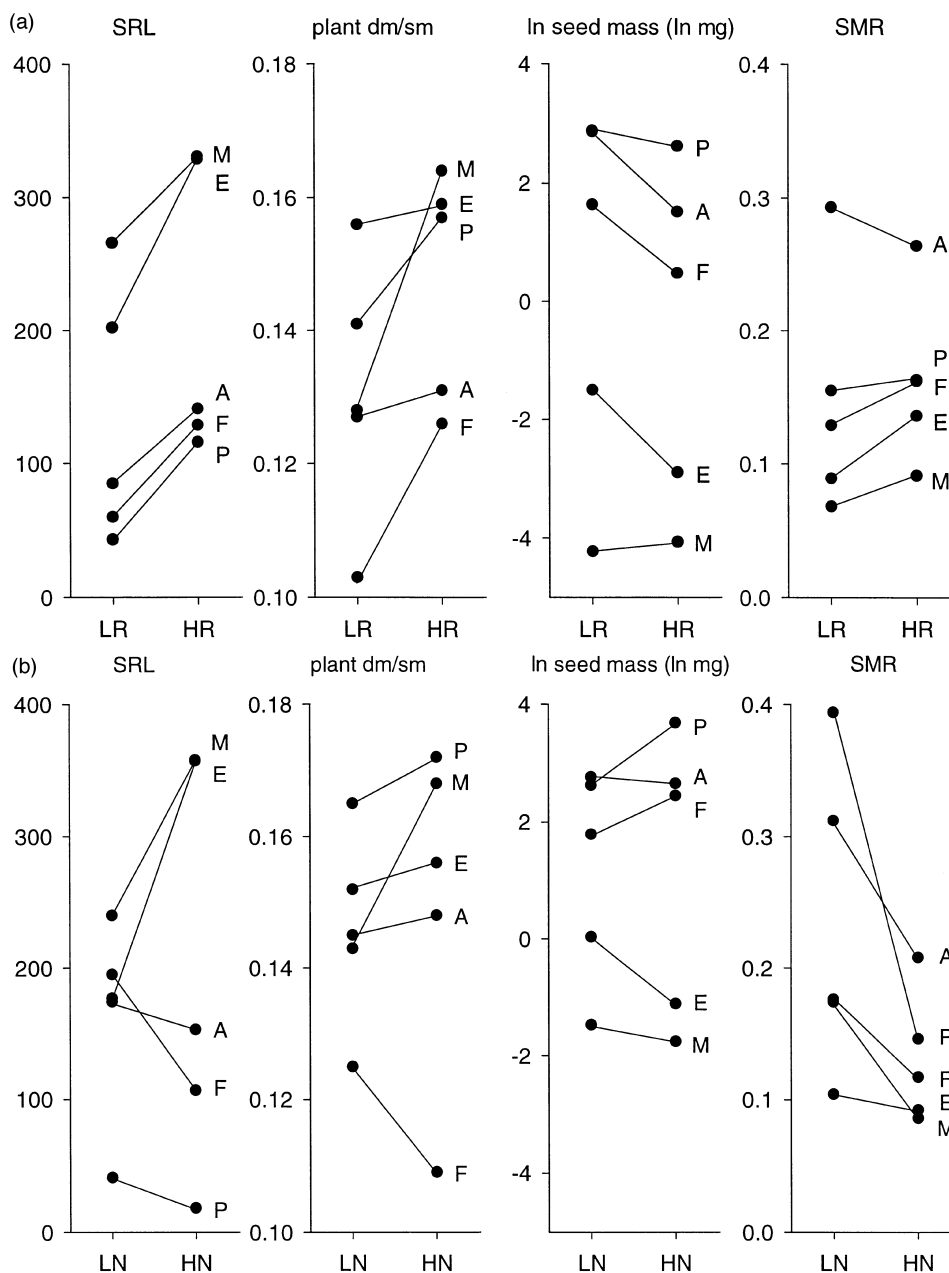
**Fig. 3** Correlated-change graphs portraying divergences in selected attributes with respect to divergences in RGR down the rainfall and nutrient gradients. Divergences in (a) SLA (dSLA), (b) LMR (dLMR) and (c) NAR (dNAR) are shown against divergences in RGR. Key: (●) nutrient PICs; (○) rainfall PICs. Units: RGR,  $\text{mg mg}^{-1} \text{day}^{-1}$ ; SLA,  $\text{mm}^2 \text{mg}^{-1}$ ; NAR,  $\text{mg mg}^{-1} \text{mm}^{-2}$ ; LMR, unitless ratio.

ratio. Clear trends were not apparent in the other attributes.

ATTRIBUTE RELATIONSHIPS ALONG THE NUTRIENT GRADIENT

Within nutrient PICs, majority trends (4/5) of lower SLA and lower LMR in low nutrient species (Fig. 3) resulted in consistent negative shifts (5/5) in LAR down

the gradient. NAR shifted negatively down the gradient in three of five contrasts and increased in two. The positive NAR shift in the *Acacia* contrast was of sufficient size to negate the negative shift in LAR; hence, negative shifts in RGR were observed in only four of five contrasts. Despite the similar direction of trends in SLA and RGR, the primary factor driving divergence in RGR within individual PICs (irrespective of direction) was NAR in four of five contrasts and LMR in the other.



**Fig. 4** Divergences in SRL ( $\text{mm mg}^{-1}$ ), plant dry mass/saturated mass, ln seed reserve mass (ln mg) and stem mass ratio along (a) rainfall and (b) nutrient gradients. Species pairs in each PIC are joined by a line. Key: A, *Acacia*; E, *Eucalyptus*; F, Fabales; M, Myrtaceae; P, Proteaceae; LR, low rainfall; HR, high rainfall; LN, low nutrients; HN, high nutrients.

No consistent trends were found along the nutrient gradient in RMR, root thickness or SRL (Fig. 4b). A weak decreasing trend was apparent in whole plant tissue dm/sm, but not for individual organs. Seed reserve mass showed no trend. Proportional mass allocation to stem (SMR) was consistently higher in the low nutrient species of each PIC.

#### GRADIENT VERSUS WITHIN-HABITAT CONTRASTS

The intention behind including within-habitat contrasts was to see whether within-habitat divergences in RGR were driven by the same RGR components

as in gradient contrasts, and to compare the absolute size of attribute shifts along gradients to those occurring within habitats.

Considering individual within-habitat PICs, shifts in RGR were primarily driven by SLA in three cases and by NAR and LMR in one contrast apiece. None the less, RGR and SLA diverged in the same direction in four of five PICs. Thus, as in between-habitat contrasts, SLA and RGR tended to shift together but divergences in RGR were not consistently and primarily driven by SLA. The average absolute size of attribute shifts was compared between gradient and within-habitat PICs (Table 3). Since two of the within-habitat contrasts were formed at higher levels than



**Table 3** Gradient vs. within-habitat contrasts: mean within-PIC shifts for selected attributes (interval 2). Units: RGR, mg mg<sup>-1</sup> day<sup>-1</sup>; SLA, mm<sup>2</sup> mg<sup>-1</sup>; NAR, mg mg<sup>-1</sup> mm<sup>-2</sup>; SRL, mm mg<sup>-1</sup>; seed mass, mg

Contrast		RGR	LMR	SLA	NAR	SRL	Plant dm/sm	Seed mass	SMR
Nutrients (n = 5)	Mean	0.029	0.089	1.399	0.0041	85.9	0.011	6.85	0.102
	SD	0.012	0.080	1.414	0.0016	67.5	0.009	11.03	0.085
Rainfall (n = 5)	Mean	0.015	0.039	3.775	0.0026	78.2	0.017	4.15	0.028
	SD	0.015	0.030	1.673	0.0017	29.9	0.014	5.30	0.026
Within-habitat (n = 5)	Mean	0.013	0.040	3.687	0.0025	89.3	0.020	6.81	0.060
	SD	0.007	0.028	1.494	0.0017	109.5	0.006	4.27	0.054

those used in gradient PICs, the comparisons were made both including and excluding these two: in fact, inclusion of the higher-level PICs had no systematic effect on shift size and they are therefore included in Table 3. The absolute values of the shifts were highly variable, and for several attributes this led to means and standard deviations of similar magnitude for all contrast types. Shifts in attribute values along gradients (when averaged over gradient types) were not consistently greater than in within-habitat contrasts. In fact, shifts in within-habitat contrasts tended to be similar in magnitude to those in rainfall contrasts, and may have been higher (SLA) or lower RGR, LMR, (SMR) than in nutrient contrasts.

## Discussion

### SEEDLING RGR AND ITS COMPONENTS

Across all species the tight positive relationship between RGR and LAR was driven almost entirely by SLA, rather than by the proportion of mass allocated to leaves (LMR). This central role of SLA in determining seedling potential RGR is thus general across European grasses, herbs and woody perennials (Poorter & Remkes 1990; Garnier 1992; Cornelissen *et al.* 1996; Hunt & Cornelissen 1997), Central and South American trees (Huante *et al.* 1995; Lusk *et al.* 1997) and Australian herbs, shrubs and trees (Saverimuttu & Westoby 1996; present study). In contrast, little generality has emerged for the relationships between RGR and LMR or NAR (Lambers & Poorter 1992; above references).

Broadly speaking, species characteristic of habitats with lower nutrient levels are not capable of high RGR (Chapin 1980), even when seedlings are compared under favourable conditions (Grime & Hunt 1975; Poorter & Remkes 1990). This appears to be the result of selection in resource-poor environments favouring attributes such as those that enhance leaf longevity and, hence, conservation of nutrients, rather than selection acting on RGR itself (Aerts & van der Peijl 1993; Reich 1993; van der Werf *et al.* 1993).

In eight of 10 gradient PICs, SLA (and LAR) was lower in the species from the more resource-poor habitat (4/5 along each gradient). These results from

seedlings accord with recent results for field-grown adult plants contrasted along similar nutrient and rainfall gradients in New South Wales (Cunningham *et al.*, in press). In that study, 16 out of 19 PICs showed downward shifts in SLA from high to low rainfall or nutrients, with anatomical modifications such as the reinforcement of vasculature or epidermis (which potentially enhance leaf longevity by decreasing herbivory or susceptibility to wilting) contributing to lower SLA within PICs. Cross-species analyses have also found generally lower SLA in habitats with low nutrients (Poorter & Remkes 1990; Lusk *et al.* 1997) or low rainfall (Mooney *et al.* 1978; Specht & Specht 1989; Schulze *et al.* 1998). Thus, this trend appears to be general across lineages and between adults and seedlings.

As predicted, RGR tended to decrease down both gradients (7/10 PIC), and six of the negative shifts were correlated with a negative shift in SLA. However, only two were primarily driven by shifts in SLA, with four due to NAR and one to LMR. Thus, while RGR tended to shift in the expected direction overall (albeit more strongly on the nutrient gradient than on the rainfall gradient), as did SLA, the causal link between the two appeared less strongly than we expected.

### SPECIFIC ROOT LENGTH

As an indicator of root architecture, specific root length is in many ways analogous to SLA for leaves, being influenced by both root diameter and tissue density, and it too reflects the potential for resource acquisition per unit mass. Beyond this, the analogy breaks down, thick roots having additional advantages such as potentially enhanced anchorage and water flow functions. For woody perennials, calculation of the SRL of an entire root system is most meaningful in the early stages of growth, before significant amounts of secondary thickening occur.

Across all species SRL and RGR were positively related, with variation in SRL mostly due to variation in mean root diameter rather than in root tissue dm/sm. Previous results concerning the relationship between RGR and SRL defy generalization. For grasses, Ryser & Lambers (1995) and Ryser (1996)

reported a positive association, with high SRL mostly a result of low tissue density, while Boot (1989) found a negative relationship, suggesting that fast growing species may have a greater proportion of thicker roots (and thus lower SRL), reflecting the need for a more efficient transport system. No correlation between SRL and RGR was found among 24 monocots and dicots by Poorter & Remkes (1990). Similarly, no clear relationship has previously emerged between SRL and habitat favourability. For example, grasses from nutrient-poor habitats were shown to have higher SRL and relatively more fine roots (Berendse & Elberse 1989; Boot 1989), while no correlation was found between SRL and site fertility for five perennial grasses by Boot & Mensink (1990).

Here, no clear trends in SRL, root diameter or root dm/sm were evident along the nutrient gradient. In contrast, SRL consistently decreased down the rainfall gradient due to increasing root diameter. This could indicate selection for increased efficiency of water uptake during seedling establishment in low rainfall habitat or, alternatively, greater diameter might confer an enhanced ability to penetrate dry soil. This trend was strong enough to counteract the opposing effect on SRL of decreasing root tissue dm/sm, which implies increased root longevity.

#### DIVERSITY OF STRATEGIES WITHIN HABITATS

In general, attribute shifts in within-habitat PICs were of at least the same magnitude as those in gradient PICs. Two factors come into play here. First, use of a gradient PIC design constrained species selection to species-pairs from clades in which both low and high rainfall (or nutrient) species were represented. In the New South Wales flora, this immediately ruled out the majority of species for which seeds were available, and the average size of attribute shifts within the lineages studied is therefore likely to be smaller than the shift between means for all species occurring within habitats at the poles of a resource gradient (Westoby *et al.* 1998). Secondly, and perhaps more importantly, a range of SLA (and other) strategies is observed within any one habitat. This itself is, at first, difficult to account for: if an SLA strategy with a particular expected light capture per unit leaf mass invested is viable, then how could a strategy with, say, 10 times lower expected light capture per unit leaf mass also be competitive within the same vegetation? However, some specific mechanisms are known through which this might happen, such as shade species having higher SLA (Pons 1977; Björkman 1981) and later-successional species having longer leaf retention times (Aerts & van der Peijl 1993), at least in successions driven by nitrogen cycling. A more general reason might be that low SLA leaves have greater longevity (Reich 1993). This means that low SLA species, while having low expected instantaneous light capture rates, nevertheless may have expected

total light capture over the leaf's lifetime per gram dry mass invested that is at least as great as that of a high SLA leaf. In summary, it may be that different SLA strategies are not as dramatically different when their effect is considered over the course of a leaf's lifetime as they appear initially. Still, the exact basis for coexistence of a wide range of SLA strategies remains to be elucidated.

#### TISSUE DENSITY AND BIOMASS ALLOCATION

High RGR herbaceous species often have lower density leaf tissue, contributing to their generally higher SLA and shorter leaf longevity (Garnier & Laurent 1994; van Arendonk & Poorter 1994; Ryser & Lambers 1995; Ryser 1996). In woody species, the positive relationship between tissue 'wateriness' and RGR has been most apparent across growth forms and leaf habits (deciduous/evergreen), similar to the relationship between LMR and RGR (Cornelissen *et al.* 1996). In the present study all measures of tissue dm/sm were unrelated to RGR except for cotyledon dm/sm, which showed the opposite (i.e. positive) trend to that expected. SLA was neither associated with leaf dm/sm across all species nor along gradients. Our results for woody species, then, conflict with previous findings for herbaceous species.

Across all species a positive relationship was found between RMR and RGR, while no trend was found in RMR along the nutrient or rainfall gradients. Chapin (1980) and Lambers & Poorter (1992) reported that at optimal nutrient supply both high RGR and high nutrient plants have lower RMR than low RGR and low nutrient species, but Boot & Mensink (1990), Garnier (1991) and Huante *et al.* (1995) have reported exceptions to this prospective rule. Results reported here reinforce the impression that any relationship between RMR and either RGR or site favourability is equivocal.

The negative relationship found between SMR and RGR across all species indicated a higher proportion of mass invested in structural compared to non-structural tissue (i.e. roots and leaves) in low RGR species. This trend was also connected with differences between taxonomic groups and growth form, such that low SMR was typical of Myrtaceae and trees. However, within PICs SMR increased down the nutrient gradient in all five contrasts and no correlation with growth form was apparent. High SMR could decrease the impact of herbivory if associated with increased stem density, but stem dm/sm was not significantly correlated with SMR across all species, nor did it shift with SMR along the nutrient gradient. Thus it unclear what advantage increased SMR might confer in low nutrient habitats.

#### SEED MASS AND COTYLEDON FUNCTION

Seed (reserve) mass showed an approximately log-normal distribution. In seed mass was negatively cor-

related with RGR, a pattern demonstrated a number of times previously (Grime & Hunt 1975; Shipley & Peters 1990; Jurado & Westoby 1992; Marañón & Grubb 1993). Small-seeded species had high SLA cotyledons (also found by Hladik & Miquel 1990; Garwood 1995; Kitajima 1995), as well as high SLA leaves and high SRL – this was apparent both across all species and along the rainfall gradient, where seed mass shifted positively down the gradient in four of five contrasts. Thus, species with few storage reserves at the time of germination appeared to be maximizing both above- and below-ground functions simultaneously, a high-risk strategy for individual seedlings, but one presumably mitigated by a larger number of seedlings being produced, increasing the chance that at least one will find itself in a favourable situation.

An interesting question is why species with large seeds and low SLA cotyledons also produce low SLA leaves. Large seededness generally indicates large storage reserves (and low cotyledonary photosynthetic rates; Kitajima 1992, 1995), facilitating enhanced survival in the face of hazards such as deep shade and physical damage (Westoby *et al.* 1996) or summer drought (Milberg *et al.* 1998). In contrast, low leaf SLA results from factors such as thicker leaves, proportionally more cell wall, more structural defences, etc. (Dijkstra 1989), all apparently adaptations to enhance leaf longevity. That is, while the relationship between SLA of cotyledons and leaves is predictable, the basis for it is not understood, especially since a general relationship between seed size and habitat favourability is not yet clear (Westoby *et al.* 1996).

### Conclusions

Across 33 New South Wales species spanning a range of habitats, both SRL and SLA (of leaves, cotyledons, or both) emerged as strong predictors of seedling RGR. As predicted, a general strategy of leaf and root surface maximization was typical of high RGR plants. The expected negative relationship between RGR and seed reserve mass was also confirmed, while that between RGR and tissue density received no support from the data.

Within both sets of gradient PICs, SLA generally decreased with decreasing site favourability. Specific leaf area is an attribute that we believe to reflect fundamental aspects of plant strategy. Thus, in this important respect, gradients of decreasing nutrients or rainfall appear to be variants of a more general 'stress' gradient. RGR also generally decreased down each gradient, but the trend was somewhat stronger on the nutrient than rainfall gradient.

In several respects, attribute shifts associated with the two gradients differed. Consistent shifts in SMR occurred along the nutrient gradient while rainfall PICs diverged with respect to plant tissue dm/sm,

SRL and seed reserve mass. Two further results were of particular note. First, RGR shifts in all three sets of PICs, irrespective of direction, were correlated with shifts in SLA in 12/15 cases but were not driven consistently by any one factor. Secondly, the magnitude of attribute shifts in within-habitat PICs were of much the same size as those along gradients. Together with other recent work comparing variation in plant attributes within and between habitat types, these results emphasize that strategy variation in many attributes is at least as great, if not greater, within communities as between them.

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