

Cross-species relationships between seedling relative growth rate, nitrogen productivity and root vs leaf function in 28 Australian woody species

I. J. WRIGHT and M. WESTOBY

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

Summary

1. Seedling relative growth rate (RGR) is often decomposed into the product of specific leaf area (leaf area per leaf mass, SLA), net assimilation rate (rate of mass increase per unit leaf area per unit time, NARa) and leaf mass ratio (ratio of leaf to total dry mass, LMR). Commonly, most cross-species variation in RGR is accounted for by variation in SLA, while no general relationships occur between RGR and either NARa or LMR. NARa can be factored into the product of leaf nitrogen productivity (rate of mass increase per unit leaf nitrogen per unit time, LNP) and leaf nitrogen concentration (area basis, LNCa). In this way the influence on RGR of leaf nitrogen – how it is displayed, and how it is utilized – can be investigated.

2. Seedlings of 28 Australian woody dicot species were grown under controlled, favourable conditions. Variation in SLA, LNP, LNCa and LMR explained *c.* 44%, 22%, 19% and 15% of variation in RGR, respectively. SLA and LNP were positively associated with RGR, while LNCa was negatively associated with RGR. LNP and LNCa were negatively correlated, the counteracting trends between RGR and each of these attributes resulting in no relationship between RGR and NARa. It is argued that this phenomenon may be widespread and may contribute to the inconsistency of reported relationships between NARa and RGR.

3. The functional balance between leaves and roots can be described in terms of mass allocation and morphology (static ratios or allometric coefficients) or, alternatively, in terms of leaf ‘activity’ (NAR) and root ‘activity’ (nitrogen uptake rate, NUR). At any given time most species allocated greater mass to leaves than to roots, but species with low RGR tended to be partitioning a greater ongoing proportion of new biomass to the roots rather than to the leaves, resulting in a proportionally greater increase in root surface compared with leaf surface over time. Nitrogen uptake rate was correlated with leaf and whole-plant nitrogen concentration, but not with other attributes. While it is clear that root and leaf functions must be coordinated (and thus in balance) for growth to occur, there is little evidence that this balance varies systematically with RGR across all species.

Key-words: Functional balance, net assimilation rate, specific leaf area

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Introduction

A plant's relative growth rate (RGR; rate of dry mass increase per unit dry mass present) can be decomposed as:

$$\text{RGR} = \text{NARa} \times \text{SLA} \times \text{LMR}$$

or

$$\left[\frac{dM_T}{M_T dt} \right] = \left[\frac{dM_T}{A_L dt} \right] \left[\frac{A_L}{M_L} \right] \left[\frac{M_L}{M_T} \right] \quad \text{eqn 1}$$

that is, as the product of the net assimilation rate

(rate of dry mass increase per unit leaf area per time), specific leaf area (leaf area per unit leaf mass) and leaf mass ratio (ratio of leaf to total mass; abbreviations are listed in Table 1). SLA has fairly consistently proved to be a strong correlate of between-species variation in seedling RGR under near-optimal laboratory conditions, in studies spanning a wide range of growth forms originating from many habitats (recently reviewed by Poorter & van der Werf 1998; see also Reich, Tjoelker *et al.* 1998; Wright & Westoby 1999). By contrast, little generality has emerged for the relationships

Table 1. List of abbreviations used in the text. For the majority of species leaves were pooled with cotyledons to form the 'effective leaf surface'. Cotyledons were not included for Proteaceae (N-rich storage cotyledons), *Acacia elata* or *Acacia jonesii* (Fabaceae with non-photosynthetic cotyledons)

Abbreviation	Definition	Unit
RGR	Relative growth rate: rate of dry mass increase per unit mass per unit time. Calculated from linear regression of ln dry mass against time; mathematically equivalent to $SLA \times NAR \times LMR$ or $SLA \times LNP \times LNCa \times LMR$	$mg\ mg^{-1}\ day^{-1}$
SLA	Specific leaf area: leaf area per unit leaf mass	$mm^2\ mg^{-1}$
LNP	Leaf nitrogen productivity: rate of dry mass increase per unit leaf nitrogen per unit time	$g\ g^{-1}\ day^{-1}$
LNCm	Leaf nitrogen concentration (mass basis)	%
LNCa	Leaf nitrogen concentration (area basis); equivalent to $LNCm/SLA$	$g\ m^{-2}$
NARa	Net assimilation rate: rate of dry mass increase per unit leaf area per unit time	$mg\ mm^{-2}\ day^{-1}$
LMR	Leaf mass ratio: ratio of leaf mass to plant dry mass	–
$k(M_L:M_R)$	Allometric coefficient describing ongoing partitioning of mass to leaves vs roots. Calculated as slope of reduced major axis regression of ln(leaf mass) against ln (root mass)	–
$k(A_L:L_R)$	Allometric coefficient describing formation of new leaf area compared to new root length. Calculated as slope of reduced major axis regression of ln(leaf area) against ln(root length)	–
NURm	Nitrogen uptake rate per unit root mass per unit time	$mg\ g^{-1}\ day^{-1}$
NURl	Nitrogen uptake rate per unit root length per unit time	$mg\ m^{-1}\ day^{-1}$

between RGR and LMR or between RGR and NARa (Poorter & van der Werf 1998).

Although NARa is a complex function of photosynthesis, respiration and partitioning of biomass to photosynthetic and non-photosynthetic components (Lambers *et al.* 1989), the lack of a general positive relationship between NARa and RGR seems surprising because the proportion of daily carbon gain lost in respiration is lower in high RGR species than in low RGR species (Poorter, Remkes & Lambers 1990; Reich, Walters *et al.* 1998). One possible explanation is that the processes which contribute to NARa exhibit countervailing trends with RGR, and thus become obscured when combined. Another is that these processes, and NARa itself, are relatively invariant (particularly when calculated on an area basis) and thus contribute little to variation in RGR. Further possibilities have been explored by Konings (1989), Poorter & van der Werf (1998), Veneklaas & Poorter (1998) and McKenna & Shipley (1999).

A second way of decomposing RGR, taking leaf nitrogen into account, is as follows:

$$RGR = LNP \times LNCm \times LMR$$

or

$$\left[\frac{dM_T}{M_T dt} \right] = \left[\frac{dM_T}{N_L dt} \right] \left[\frac{N_L}{M_T} \right] \left[\frac{M_L}{M_T} \right] \quad \text{eqn 2}$$

where LNP is leaf nitrogen productivity (rate of mass gain per unit leaf N per time) and LNCm is leaf nitrogen concentration (mass basis). Leaf nitrogen productivity in grass and herbaceous dicot seedlings is correlated with the rate of net photosynthesis per unit leaf N (Garnier, Gobin & Poorter 1995). Like NARa, LNP and net photosynthesis per unit leaf N are also functions of photosynthesis, respiration and biomass allocation (Pons, van der Werf & Lambers

1994; Poorter & Farquhar 1994; Garnier *et al.* 1995; Poorter & Evans 1998). Cross-species variation in leaf nitrogen concentration has been positively linked with variation in maximum net photosynthetic rate, leaf dark respiration rate and SLA in adult plants and seedlings (e.g. Mooney, Ferrar & Slatyer 1978; Field & Mooney 1986; Reich, Walters & Ellsworth 1997; Reich, Walters *et al.* 1998). In some studies LNCm has been positively associated with seedling RGR (e.g. van Arendonk & Poorter 1994; Cornelissen *et al.* 1997), in others there has been no relationship (e.g. Huante, Rincón & Acosta 1995) or even a negative association (e.g. Pons *et al.* 1994). It would seem useful then to tease apart LNCm into its two constituent components, LNCa (leaf nitrogen concentration on an area basis) and SLA; that is, to look at not only the concentration of leaf N but also how it is displayed:

$$RGR = LNP \times LNCa \times SLA \times LMR$$

or

$$\left[\frac{dM_T}{M_T dt} \right] = \left[\frac{dM_T}{N_L dt} \right] \left[\frac{N_L}{A_L} \right] \left[\frac{A_L}{M_L} \right] \left[\frac{M_L}{M_T} \right] \quad \text{eqn 3}$$

The relationship between equations 1 and 3 is simply that $NARa = LNP \times LNCa$; that is, the rate of mass increase per unit leaf area per time can be split into the rate of mass increase per unit leaf nitrogen per time and the concentration of nitrogen per unit leaf area. In this paper it will be argued that the formulation given in equation 3 is a useful approach in studying variation in RGR because (1) the dependence of plant growth on leaf nitrogen is unequivocally accepted and (2) there is no *a priori* reason why LNP and LNCa should be related. Thus if these attributes exhibit counteracting trends with RGR then this may go towards explaining the lack of relationship between NARa and RGR.

Many seedling growth analyses are primarily concerned with leaf-based physiological processes and morphology (equation 3, above, is a good example of such an approach). A complementary approach is to study the relationship between RGR and the 'functional equilibrium' between leaves and roots (e.g. Brouwer 1983; Garnier 1991; McKenna & Shipley 1999); that is, to explicitly consider growth as a balanced outcome between the leaf and root systems in terms of both mass allocation and physiological 'activity' (e.g. LNP, and nitrogen uptake rate NUR). Mass allocation can itself be considered in terms of the ongoing partitioning of new biomass to either system (allometric approach) or by comparing the result of this partitioning over time as expressed by the ratio of leaf to root mass or surface at any given time (static approach).

In a recent seedling growth analysis of 33 Australian woody perennial species, NARa accounted for only 1% of variation in RGR (Wright & Westoby 1999). In the present study, cross-species relationships between RGR, leaf nitrogen concentration, nitrogen productivity and the functional balance between leaves and roots (activities, allometric and static ratios) were examined in 28 of the 33 species used in that study.

Materials and methods

SPECIES SELECTION AND GROWTH CONDITIONS

Data were collected for laboratory-grown seedlings of 28 woody dicot species found naturally in a range of habitats in New South Wales, Australia. All but five of the species were drawn from two particularly speciose and widespread taxonomic groups in the Australian flora: Fabaceae *s.l.* (i.e. Caesalpinaceae, Fabaceae *s.s.* and Mimosaceae) and Myrtaceae. Species were initially chosen as phylogenetically independent contrasts (PICs) in order to identify attribute trends along rainfall and soil nutrient gradients, as well as cross-species trends (Wright & Westoby 1999). However, there was insufficient material for nitrogen concentration to be determined for all plant parts at each harvest for all species used in that study. Consequently, this report concentrates on cross-species trends only and does not present PIC analyses.

Seeds were germinated on filter paper moistened with deionized water. On the day following radicle emergence, seedlings were planted out individually in pots containing pasteurized coarse river sand topped with *c.* 1.5 cm horticultural vermiculite. Pot dimensions were 7 cm × 7 cm × 23 cm tall, volume *c.* 1100 cm³. Day/night temperatures in the growth chambers were maintained at 22°/16 °C, photoperiod was 16 h at 160 ± 10 μmol m⁻² sec⁻¹. Integrated daily PAR flux was therefore *c.* 9.2 mol m⁻² day⁻¹. Pots were thoroughly flushed with a modified Hoagland's solution every second day and top-watered with a small amount of deionized water on intervening days. As well as con-

taining all appropriate micronutrients, the nutrient solution (pH = 6.0) contained macronutrients in the following concentrations: NO₃⁻ 3.38 mM, NH₄⁺ 0.125 mM, H₂PO₄⁻ 0.375 mM, K⁺ 1.75 mM, Ca²⁺ 1.25 mM, Mg²⁺ 0.250 mM, SO₄²⁻ 0.563 mM. Full details of species selection criteria and growth conditions were described by Wright & Westoby (1999).

The nutrient and water regime was designed so that neither resource should have been seriously 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 & Freijesen 1994). In contrast, it is unlikely that the species' photosynthetic systems were saturated at a PAR of 9.2 mol m⁻² day⁻¹. While this is probably a lower flux than seedlings of many of these species would experience in the field, it is comparable with many similar studies (e.g. Grime & Hunt 1975; Cornelissen, Castro Diez & Hunt 1996; Hunt & Cornelissen 1997) although certainly lower than some (see Garnier & Freijesen 1994).

It is important to note that our aim was to create standard conditions favourable enough for all species to achieve exponential growth, rather than creating 'ideal' or 'optimum' conditions for all species studied. 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, despite many seedling attributes varying within any given species. Recent studies by Reich, Tjoelker *et al.* (1998) and Reich, Walters *et al.* (1998) (high vs low light), and Poorter & van der Werf (1998; meta-analysis of 57 experiments) support this claim. On the other hand, Meziane & Shipley (1999) varied experimental light and nutrient levels and found that the rank ordering of 22 herbaceous species changed considerably for RGR, somewhat for NARa and not for SLA or LMR. However, the slopes relating RGR to each of its component attributes did not change and nor did the relationships among these components.

Pot positions were randomized at least twice weekly. For each species, unhealthy plants were discarded and the remaining assigned randomly to one of three harvests. Because 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. Dry mass was determined from material dried at 70 °C for 48 h. Mean sample size for whole-plant dry mass (and estimation of RGR) was 26.4 seedlings per species, while smaller sample sizes were used for other attributes for most species. Root system, cotyledon and leaf images were created by scanning fresh material on a flatbed scanner at 400 dpi. Projected leaf area, cotyledon area and root length

were measured using Delta-T Scan[®] (Kirchhof & Pendar 1995). Material was pooled for each species from each harvest for determination of whole-plant and leaf nitrogen and carbon concentrations (Fisons elemental analyser, NA 1500-R/AS 200, Fisons Instruments Inc., Beverly, MA).

Allometric relationships between the partitioning of biomass to leaves *vs* roots, and the formation of leaf *vs* root surface, were calculated as the slope of the Model II (Reduced Major Axis) regression of the pairs of log-transformed relevant attributes (Farrar & Gunn 1998). For example, if we assume the relationship between leaf mass (M_L) and root mass (M_R)

$$M_L = b M_R^k,$$

where k is the allometric constant and b a constant, then

$$\ln M_L = \ln b + k \ln M_R.$$

Because there is no accepted method of calculating confidence intervals for Model II regression slopes, approximations were made by calculating symmetrical 95% confidence intervals from standard errors of Model I slopes (Sokal & Rohlf 1981). RGR and allometric coefficients were calculated over the entire growth period for all species, while morphological attributes, leaf nitrogen productivity and nitrogen uptake rate (rate of N uptake per unit time and unit root mass or root length) were calculated over the second harvest interval (harvests 2–3) using the appropriate formulae (Hunt 1978).

There was insufficient material for analysis of leaf N for every species for both of harvests 2 and 3. For 22 species, leaf nitrogen productivity was calculated directly and compared with LNP as inferred from NARa/LNCa (the two measures are equivalent if leaf N is constant between harvests). The two measures of LNP were tightly related ($R^2 = 0.98$, $\beta = 1.02$, $SE = 0.04$). LNP was then inferred from NARa and LNCa for the remaining six species, given (1) the tight relationship between the two measures of LNP for the other 22 species, (2) the fact that there was no systematic increase or decrease in leaf N between harvests for the species where this could be compared and (3) the theoretical prediction that internal N concentration should remain constant in seedlings undergoing exponential growth (Garnier 1991).

Data analysis mostly took the form of linear regression and correlation. When we had reason to test a predictive relationship, linear regression was used and R^2 values are reported. For assessing non-directional relationships Pearson correlation coefficients were calculated. Several of the variables exhibited highly skewed distributions and were deemed non-normal using the Shapiro–Wilks test for normality. In all cases, \log_{10} transformation rectified this problem. T -tests were used to test for differences in group means between the two major taxa (Fabaceae, 13 species, and Myrtaceae, 10 species). All statistical

analyses were carried out with SPSS for Windows version 8.0.

INVESTIGATION OF THE EFFECT OF POOLING LEAF AND COTYLEDON N

A spectrum of cotyledon types was seen in the study species, from the thin and leaf-like cotyledons of the 10 Myrtaceae species and *Pittosporum undulatum* (Pittosporaceae), to the thicker, green cotyledons of Proteaceae and most Fabaceae. Two Fabaceae, *Acacia elata* and *Acacia jonesii*, shed their (non-green, presumably non-photosynthetic) cotyledons by the time of second harvest. Because morphological parameters calculated on leaf + cotyledon and true-leaf only bases were very highly correlated, Wright & Westoby (1999) pooled leaves and cotyledons together (forming the 'effective leaf area'). The tight relationship between true-leaf and effective-leaf measures occurred partly because cotyledon area generally made up less of the photosynthetic surface by the time the attributes were measured, but also because cotyledon and leaf attributes were themselves tightly correlated (e.g. correlation of cotyledon SLA with true-leaf SLA: $r = 0.88$, $P < 0.0005$). The same approach was generally adopted here, although true-leaf and cotyledon nitrogen concentrations were measured separately for six of the larger seeded/thicker cotyledon species; that is, species for which the greatest difference between contributions of cotyledon and leaf N to overall plant growth could be expected. While cotyledon and leaf nitrogen concentrations (LNC) were very similar in the Myrtaceae and Fabaceae species, noticeably higher LNC was found in the cotyledons than in leaves of the Proteaceae (mass or area basis, *c.* 2–3 times as much), probably indicative of a storage role (e.g. Witkowski & Lamont 1996). Consequently, effective-leaf attribute values were used for all species except Proteaceae (and the two Acacias with non-photosynthetic cotyledons), for which true-leaf values were used (three Proteaceae species for which all data referred to pooled leaves plus cotyledons were removed from the data set). Results were compared with those from a second data set using true-leaf values for all species, however, the conclusions were qualitatively the same with either and so results from only the first are presented.

Results

RELATIONSHIP BETWEEN NITROGEN CONTENT, RGR AND COMPONENT ATTRIBUTES

Across all species, a 3.3-fold range in RGR (0.040–0.129 mg mg⁻¹ day⁻¹; Table 2) was associated with *c.* 6-fold variation in leaf nitrogen productivity (LNP), 5-fold variation in leaf N per unit area (LNCa), 2.8-fold variation in specific leaf area (SLA) and 2.3-fold

Table 2. Selected attributes for the 28 species. Units and abbreviations as in Table 1 Taxon: F Fabaceae, M Myrtaceae, P Proteaceae, Pi Pittosporaceae, S Sapindaceae

Species	Taxon	RGR	SLA	LNP	LNCm	LNCa	NARa	LMR	$k(M_L:M_R)$	$k(A_L:L_R)$	NURm	NURI
<i>Acacia binervata</i>	F	0.0395	25.0	3.1	2.9	1.14	0.0036	0.49	0.79	0.59	4.4	0.029
<i>A. burkittii</i>	F	0.0662	19.0	3.6	4.8	2.53	0.0089	0.40	0.91	0.56	8.2	0.101
<i>A. cognata</i>	F	0.0747	23.6	6.7	2.4	1.03	0.0069	0.40	0.88	0.90	3.0	0.021
<i>A. elata</i>	F	0.0606	22.5	2.3	6.7	3.04	0.0070	0.52	1.06	0.65	7.5	0.056
<i>A. jonesii</i>	F	0.0646	24.3	3.8	5.7	2.43	0.0093	0.35	0.59	0.23	9.2	0.053
<i>A. suaveolens</i>	F	0.0522	21.6	4.6	3.7	1.69	0.0079	0.40	0.60	0.59	1.9	0.013
<i>Angophora floribunda</i>	M	0.0908	21.6	9.3	1.8	0.83	0.0077	0.53	0.90	0.52	1.9	0.024
<i>Banksia ericifolia</i>	P	0.0514	18.2	4.8	3.0	1.64	0.0080	0.28	0.60	0.41		
<i>Bossiaea walkeri</i>	F	0.0631	19.2	5.9	2.2	1.25	0.0074	0.49	0.97	0.79	7.4	0.063
<i>Dodonaea peduncularis</i>	S	0.0888	23.0	6.7	2.6	1.22	0.0082	0.45	1.36	0.73		
<i>Eucalyptus amplifolia</i>	M	0.1250	35.3	6.0	4.8	1.35	0.0070	0.50	1.16	1.02		
<i>E. apiculata</i>	M	0.0957	21.6	4.2	2.9	1.51	0.0064	0.64	1.03	0.60		
<i>E. burgessiana</i>	M	0.0865	20.2	8.9	2.2	1.10	0.0095	0.59	0.72	0.47		
<i>E. grandis</i>	M	0.0997	27.1	5.2	3.1	1.11	0.0054	0.51	1.07	0.78		
<i>E. largiflorens</i>	M	0.1125	29.1	7.3	3.4	1.15	0.0085	0.46	1.15	0.89		
<i>E. saligna</i>	M	0.1286	28.2	9.4	2.7	0.97	0.0091	0.55	1.05	0.87		
<i>E. sieberi</i>	M	0.0930	24.9	7.4	2.1	0.83	0.0062	0.53	0.84	0.52	5.9	0.033
<i>Gompholobium latifolium</i>	F	0.0660	22.6	4.1	4.1	1.78	0.0071	0.47	0.73	0.75		
<i>Hakea dactyloides</i>	P	0.0681	24.5	8.7	3.5	1.45	0.0128	0.34	0.94	0.56	1.4	0.013
<i>H. gibbosa</i>	P	0.0613	12.7	8.4	3.0	2.39	0.0176	0.28	1.42	0.90		
<i>Hovea acutifolia</i>	F	0.0624	16.0	4.7	2.1	1.32	0.0062	0.58	0.53	0.76	0.3	0.004
<i>Leptospermum laevigatum</i>	M	0.0692	25.3	3.1	2.5	0.98	0.0030	0.43	0.87	0.73		
<i>Lophostemon confertus</i>	M	0.1044	25.3	6.8	2.6	1.04	0.0070	0.63	1.24	0.88		
<i>Pittosporum undulatum</i>	Pi	0.0756	19.7	8.1	1.2	0.62	0.0050	0.50	0.87	0.55	0.7	0.009
<i>Pultenaea daphnoides</i>	F	0.0906	22.9	13.6	2.1	0.92	0.0125	0.43	0.81	0.77	4.2	0.033
<i>Senna aciphylla</i>	F	0.0570	13.7	8.6	1.5	1.21	0.0084	0.54	0.61	0.22	0.6	0.010
<i>S. artemisioides</i> ssp. <i>sturtii</i>	F	0.0493	20.1	4.6	3.1	1.54	0.0071	0.51	0.44	0.26	4.9	0.122
<i>S. barclayana</i>	F	0.1045	25.1	13.0	2.5	0.99	0.0128	0.45	0.78	0.53	3.4	0.031

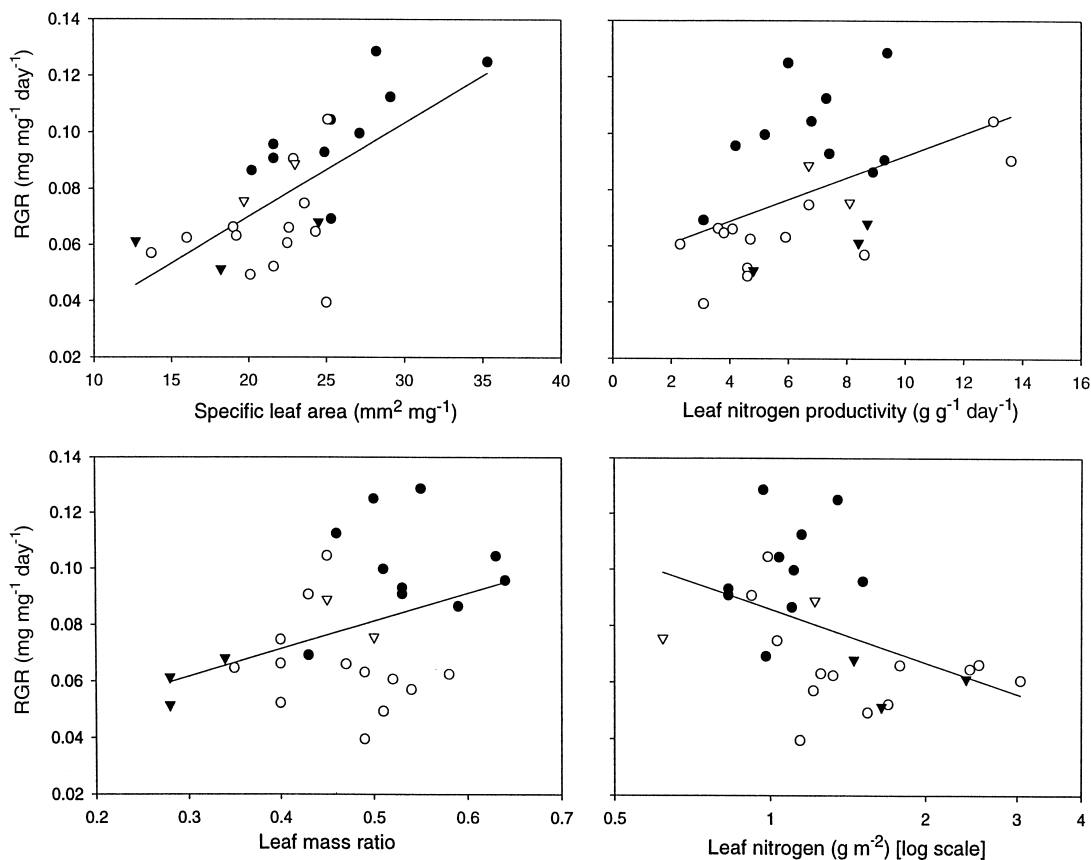


Fig. 1. Relationship between relative growth rate RGR and component attributes: (a) specific leaf area SLA, $R^2 = 0.44$; (b) leaf nitrogen productivity LNP, $R^2 = 0.22$; (c) leaf mass ratio LMR, $R^2 = 0.15$; (d) leaf nitrogen concentration, area basis LNCa, $R^2 = 0.19$; ● Myrtaceae; ○ Fabaceae s.l.; ▲ Proteaceae; △ other.

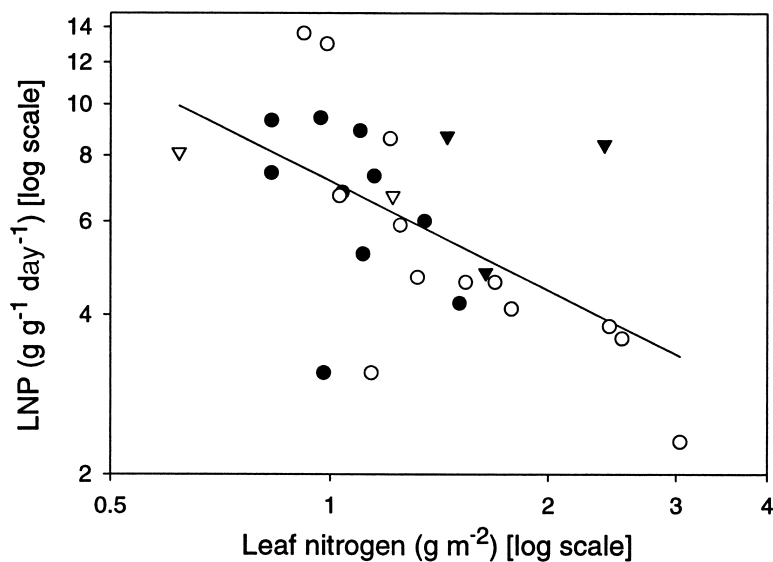


Fig. 2. Scaling relationship between leaf nitrogen productivity LNP vs leaf nitrogen per leaf area. Slope = -0.69 (95% CI -1.08 to -0.31), $r^2 = 0.34$. Symbols as for Fig. 1.

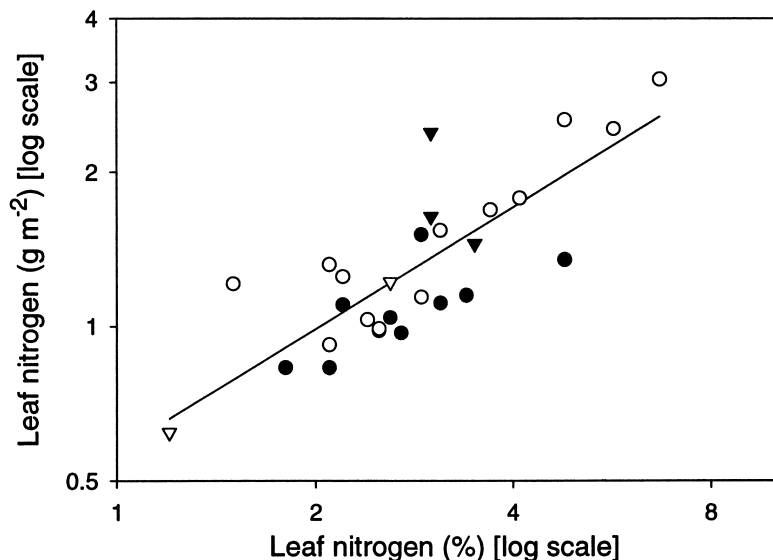


Fig. 3. Scaling relationship between leaf nitrogen per leaf area vs leaf nitrogen per leaf mass. Slope = 0.81 (95% CI 0.58 – 1.04), $r^2 = 0.66$. Symbols as for Fig. 1.

variation in leaf mass ratio (LMR). Specific leaf area exhibited a strong positive relationship with RGR ($R^2 = 0.44$, $P = 0.0001$; Fig. 1a), while leaf nitrogen productivity ($R^2 = 0.22$, $P = 0.011$; Fig. 1b) and leaf mass ratio ($R^2 = 0.15$, $P = 0.042$, Fig. 1c) both exhibited weaker positive relationships with relative growth rate. Leaf N per unit area was negatively associated with RGR ($\log \text{LNCa}$ vs RGR: $R^2 = 0.19$, $P = 0.020$, Fig. 1d).

Leaf nitrogen productivity and leaf N per unit area were negatively associated ($r = -0.54$, $P = 0.003$). The relationship between the two attributes on a log–log scale was approximately linear (Fig. 2) with a slope of -0.69 (SE 0.19). Thus, across these species a *c.* 3-fold

increase in nitrogen per unit leaf area was associated with a halving in the rate of mass increase per unit leaf N per unit time.

Leaf nitrogen per unit area is the product of nitrogen per unit leaf mass (LNCm) and leaf mass per unit area ($1/\text{SLA}$). Conversely, LNCm is the product of LNCa and leaf area per mass (SLA). Of the three possible pairwise relationships between these traits, only the two measures of leaf N concentration were tightly correlated ($r = 0.82$, $P < 0.0001$; Fig. 3), with a scaling slope of 0.81 (95% C.I. 0.58 – 1.04). SLA and leaf N per mass were only marginally associated ($r = 0.34$, $P = 0.076$), while the relationship between leaf mass per area and leaf N per area was weaker still ($\log 1/\text{SLA}$, $\log \text{LNCa}$: $r = 0.27$, $P = 0.160$). That is, ‘dilution’ of mass-based leaf N by variation in SLA was relatively small because variation in LNCm was double that in SLA (5.6 vs 2.8 , respectively). There was no relationship between RGR and LNCm ($r = -0.07$, $P = 0.726$), while LNP and LNCm were negatively associated ($r = -0.53$, $P = 0.003$).

FUNCTIONAL BALANCES BETWEEN LEAVES AND ROOTS

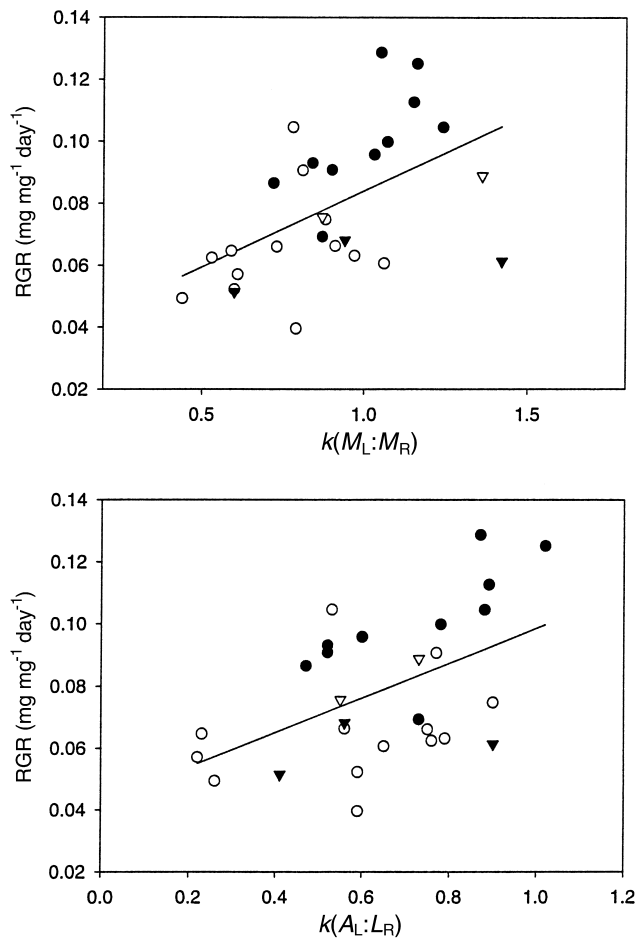
Across all species the ratio of root to leaf mass ranged from 0.34 to 1.04 . Faster-growing species generally allocated less biomass to stems than lower RGR species (correlation between RGR and stem mass ratio, $r = -0.60$, $P = 0.001$), but no more to roots than leaves (RGR vs root:leaf mass, $r = 0.15$, $P = 0.443$). However, RGR was correlated with the static ratio of root length to leaf area ($r = 0.57$, $P = 0.001$). That is, while high RGR species had both high root length per mass ($r = 0.68$, $P < 0.0001$) and leaf area per mass (SLA; Table 3), there was a greater range in the former (8.3-fold) than the latter (2.8-fold).

Two allometric coefficients were calculated: a coefficient describing ongoing allocation to leaf mass compared to root mass, $k(M_L:M_R)$ and a coefficient describing formation of new leaf area compared to new root length, $k(A_L:L_R)$. Both indices were positively associated with RGR (correlations of *c.* 0.5 ; Fig. 4). For 19 of 28 species $k(M_L:M_R)$ was significantly different from one: for 14 species it was less than one (indicating that root mass was increasing faster than leaf mass) and for five species $k(M_L:M_R)$ was greater than one (leaf mass increasing faster than root mass). In 24 of 28 species $k(A_L:L_R)$ was significantly less than one (indicating that root length was increasing proportionally faster than leaf area). The species for which this was most apparent were those with low RGR (which also tended to be species for which root mass was increasing fastest compared to leaf mass). In the remaining four species, $k(A_L:L_R)$ was not significantly different from one.

A complementary approach is to examine the relationship between growth rate and leaf and root ‘activities’. Leaf nitrogen productivity is one index of

Table 3. Bivariate Pearson correlations. Significance (two-tailed): $P < 0.001$ ***, $0.001 < P < 0.01$ **, $0.01 < P < 0.05$ *. Abbreviations as in Table 1. $n = 28$ for all cells except those involving NURm or NURI ($n = 16$)

	RGR	SLA	LNP	logLNCm	logLNCA	NARa	LMR	$k(M_L:M_R)$	$k(A_L:L_R)$	logNURm
SLA	0.66***									
LNP	0.47*	0.01								
logLNCm	-0.07	0.34	-0.53**							
logLNCA	-0.44*	-0.25	-0.54**	0.81***						
NARa	0.08	-0.27	0.60***	0.10	0.29					
LMR	0.39*	0.15	0.00	-0.30	-0.38*	-0.47*				
$k(M_L:M_R)$	0.52**	0.29	0.12	0.12	0.00	0.23	0.02			
$k(A_L:L_R)$	0.50**	0.42*	0.08	0.09	-0.13	0.04	0.05	0.69***		
logNURm	0.04	0.57*	-0.23	0.61*	0.42	0.11	-0.36	0.31	-0.01	
logNURI	-0.04	0.32	-0.23	0.52*	0.43	0.09	-0.21	0.18	-0.19	0.92***

**Fig. 4.** Relationships between relative growth rate and allometric allocation to (a) leaf mass vs root mass $k(M_L:M_R)$ and (b) leaf area vs root length $k(A_L:L_R)$. Symbols as for Fig. 1.

leaf activity; another is NAR (e.g. Garnier 1991). For roots, the rate of nutrient uptake per unit root surface per unit time can be thought of as an index of activity. Nitrogen uptake rate was calculated on root mass (NURm) and root length bases (NURI) for 16 species for which whole plant N was measured over successive harvests (giving the rate of nitrogen uptake per day

per unit root mass or root length, respectively). No relationship was found with RGR for either measure although both were positively correlated with mass-based leaf nitrogen concentration (Table 3) and whole-plant nitrogen concentration (data not shown). Nitrogen uptake rate was not correlated with any of the morphological indices of root vs leaf function, nor with LNP or NARa, but NURm was positively correlated with SLA.

TRENDS WITHIN AND BETWEEN TAXA FOR THE MEASURED ATTRIBUTES

The majority of significant cross-species relationships were also significant within one (but only one) of the two major taxa (Fabaceae, 13 species; Myrtaceae, 10 species). For example, significant correlations were found in Myrtaceae, but not in Fabaceae, between RGR and SLA ($r = 0.70$, $P = 0.025$), RGR and $k(M_L:M_R)$ ($r = 0.68$, $P = 0.032$), and RGR and $k(A_L:L_R)$ ($r = 0.70$, $P = 0.025$). By contrast, in Fabaceae and across all species, but not in Myrtaceae, RGR and LNP were correlated ($r = 0.80$, $P = 0.001$), as were LNP and logLNCA ($r = -0.72$, $P = 0.006$). The strong relationship between mass- and area-based leaf nitrogen concentration seen across all species was evident also in both groups, while those between RGR and LMR, and RGR and logLNCA, were not found in either taxon. Finally, SLA and LNCm were associated within Myrtaceae ($r = 0.84$, $P = 0.002$) but not in Fabaceae or across all species. Note that all but three of the Fabaceae species would be nitrogen-fixers if growing in the field (it is probable that the caesalpinoid *Senna* species do not fix nitrogen: Sprent 1994).

Inspection of Figs 1, 2, 3 and 4 suggests that these Myrtaceae and Fabaceae species differ across a range of seedling attributes. Two-tailed *T*-tests comparing group means support this conclusion, with significant differences (all $P < 0.02$) between the taxa found for attributes including RGR, SLA, LMR (all greater in Myrtaceae) and logLNCA (greater in Fabaceae). In summary, the cross-species trends were variously influenced by differences between the taxa and by strong

trends within one or another taxon for certain attribute-pairs, but they were rarely a result of coincident trends in both major groups. Still, there were no cases where statistically significant, opposite trends between two variables were found in the different taxonomic groups.

Discussion

RELATIONSHIP BETWEEN RGR AND COMPONENT ATTRIBUTES

Here, as in many other studies, the greatest proportion of variation in RGR was explained by variation in the light-capture area deployed per unit leaf mass, or SLA (e.g. Poorter & Remkes 1990; Garnier 1992; Huante *et al.* 1995; Cornelissen *et al.* 1996; Saverimuttu & Westoby 1996; Hunt & Cornelissen 1997; Lusk, Contreras & Figueroa 1997; Reich, Tjoelker *et al.* 1998; van der Werf *et al.* 1998). While there was no trend between RGR and mass-based leaf N, higher SLA in higher RGR species resulted in a negative relationship between RGR and area-based leaf nitrogen concentration. This 'dilution' of leaf nitrogen when calculated on an area basis can also be seen in the data of van Arendonk & Poorter (1994) and Cornelissen *et al.* (1997), in which positive relationships between RGR and LNC_m were found but not between RGR and LNC_a, because SLA and RGR were positively correlated. The degree to which LNC_m and LNC_a are themselves correlated thus depends on the variation in SLA relative to that in leaf nitrogen concentration in a data set, as does the degree to which relationships between leaf nitrogen content on area and mass bases exhibit similar relationships to other attributes such as RGR. Here, LNC_m and LNC_a were tightly associated across all species because variation in LNC_m was greater than that in SLA.

Chapin (1980, 1988) and Tateno & Chapin (1997) suggested that a negative relationship exists between seedling RGR and tissue nitrogen concentration at high nutrient supply because rapidly growing species dilute their internal N over a large biomass while slow growing species exhibit high 'luxury consumption' of essential nutrients (i.e. storage for later use). By contrast, Lambers & Poorter (1992) suggested that a positive relationship between mass-based leaf N and seedling RGR was general. Subsequent studies have found either a negative relationship between the attributes (Pons *et al.* 1994, four monocot species), no relationship (Huante *et al.* 1995, for 34 woody species; present study) or a positive relationship (e.g. van Arendonk & Poorter 1994 and Garnier & Vancaeyzeele 1994, for grasses and herbs; Cornelissen *et al.* 1997, for 82 woody species; Reich, Walters *et al.* 1998, for nine boreal tree species). Given the unquestionable relationship between growth and nitrogen-mediated carbon acquisition, the lack of a general relationship between RGR and leaf nitrogen

seems surprising. However, another factor which must be considered is variation in how 'efficiently' leaf nitrogen is used in the growth process.

NITROGEN PRODUCTIVITY

The positive relationship found here between leaf nitrogen productivity LNP and RGR is in agreement with the pattern found previously in 14 grass species by Garnier & Vancaeyzeele (1994). Leaf nitrogen productivity is an index reflecting three factors in particular: (1) the rate of photosynthesis per unit leaf N minus (2) the rate of respiration per leaf N and (3) the partitioning of leaf nitrogen between metabolic and structural components (but also between the various components of the photosynthetic machinery, e.g. Poorter & Evans 1998). At least in grasses and herbs LNP largely reflects the rate of photosynthesis per unit leaf N (Garnier *et al.* 1995), implying that it is not as strongly influenced by the other two factors. A positive relationship between seedling RGR and photosynthesis per unit leaf N may also be general across species (Poorter *et al.* 1990; Garnier *et al.* 1995), owing to a positive relationship between RGR and mass-based maximum net photosynthetic rate (e.g. Poorter *et al.* 1990; Walters, Kruger & Reich 1993; Kitajima 1994; Reich, Walters *et al.* 1998) and despite a general positive relationship between RGR and root and shoot respiration (Lambers & Poorter 1992; Reich, Walters *et al.* 1998), and a sometimes positive RGR–LNC relationship. Still, to what extent low RGR (or low LNP) species allocate relatively less leaf nitrogen to their photosynthetic apparatus than high RGR species (and more to protein-rich cell walls or nitrogen-compounds associated with stress metabolism or defence: Pons *et al.* 1994) is essentially unknown (Lambers & Poorter 1992). Certainly, at a given leaf N concentration per area, the greater the proportion of nitrogen in non-photosynthetic components the lower the apparent LNP would be (all else being equal). This might contribute towards a lack of relationship between LNP and LNC_a but it is unlikely to result in a negative relationship on its own.

It is probable that the relationship between leaf nitrogen productivity and nitrogen concentration is affected by the light conditions under which seedlings are grown. Under irradiances where realized photosynthetic rates are lower than the maximum possible, the degree of limitation may be correlated with the concentration of leaf N per area and will be reflected in a lower LNP. This line of reasoning suggests that the negative relationship between LNP and LNC_a would be strongest under low light, and that the RGR–NAR relationship may be weakest under such conditions. However, Poorter & van der Werf (1998) tested the latter proposition and found no support for it across 57 studies. Two additional points should be borne in mind: first, growing seedlings under high irradiances requires an even higher irradiance to fully

saturate their photosynthetic systems (thus there is always some degree of light 'limitation' which is not just an experimental artefact); second, that differences in species' photosynthesis per unit N is not only owing to differing nitrogen per unit leaf area, but also the result of variation in nitrogen allocation to electron transport *vs* light harvesting components, and variation in specific Rubisco activity (Poorter & Evans 1998).

So, it may often be the case that a positive relationship exists between RGR and LNP, RGR and area-based leaf N are negatively related or show no relationship (e.g. owing to the 'dilution' of mass-based leaf N by higher SLA in high RGR species), and LNP and area-based leaf N are negatively correlated, as was found here. Few data are available to test this proposition, although a negative relationship between photosynthesis per unit N and LNCA was reported by Pons *et al.* (1994) for four monocot species and by Poorter & Evans (1999) for 10 species of differing growth forms. Certainly, in data sets where LNP and LNCA trend in opposite directions with RGR the extent of the relationship between RGR and NARA will be set by the relative strength of relationships between LNCA and RGR, and LNP and RGR, all else being equal. Thus, the NARA–RGR relationship in a set of species may depend substantially on the interaction between mass-based leaf nitrogen concentration and SLA, because these attributes together determine the relationship between RGR and LNCA. Indeed, the countervailing trends in LNP and LNCA with RGR reported here appear to explain the lack of relationship between NARA and RGR reported by Wright & Westoby (1999) and offer a further prospective explanation for the lack of a general relationship between RGR and NARA.

A 'FUNCTIONAL BALANCE' BETWEEN LEAVES AND ROOTS?

Approximately 25–30% of variation in RGR was explained by variation in the ratio of root to leaf surface, or by either allometric ratio describing ongoing partitioning of mass to leaves *vs* roots, or of formation of new leaf surface compared to root surface. For the majority of species the allometric ratios were significantly different from one, indicating that the ratio of leaf to root mass or leaf to root surface was changing in a predictable fashion with time. Most previously published allometric relationships between RGR and mass allocation under constant growth conditions have been concerned with root:shoot partitioning (rather than root:leaf), suggesting that higher RGR is (rather weakly) linked with greater ongoing partitioning to the roots than to above-ground plant parts (Hunt, Nicholls & Fathy 1987; Shipley & Peters 1990; Hunt & Cornelissen 1997). Here, the opposite was true: RGR was positively correlated with k (shoot mass:root mass): $r = 0.67$, $P = 0.0001$ (data not shown).

As for the other allometric indices most species' values were less than one, meaning that it was not so much that faster-growing species were allocating more new mass to shoots than roots but that low RGR species were allocating far less new mass to their above-ground than to their below-ground systems.

No general relationships have emerged between RGR and static ratios describing allocation to roots *vs* leaves at a particular point in time. Here, no relationship was found between RGR and root:leaf mass, while RGR was positively correlated with the root length: leaf area ratio. By contrast, Garnier (1991) found that RGR was negatively correlated with the ratio of root to leaf mass in dicots but not in grasses, while Boot & Mensink (1990) and Ryser & Lambers (1995) reported no relationship between RGR and root length: leaf area for grasses and Poorter & Remkes (1990) found a negative relationship in herbaceous dicots and grasses.

There has been broader agreement about the relationship between RGR and nitrogen uptake rate, at least on a root-mass basis: Poorter *et al.* (1991), Garnier (1991), Garnier & Vancaeyzeele (1994) and Reich, Walters *et al.* (1998) have all reported a positive relationship between these attributes, although none was found here. It has been suggested that the nitrate uptake system is saturated under high-nutrient conditions such that demand for nitrogen drives uptake; thus RGR and NUR should be correlated (Lambers & Poorter 1992). However, this requires that RGR and leaf nitrogen concentration are tightly related (which is often the case, but not in all studies) and clearly conflicts with the idea of luxury consumption of essential nutrients such as nitrogen. The negative relationships found here between leaf nitrogen concentration (mass or area basis) and LNP, and between RGR and LNCA, together with the lack of a relationship between the rate of nitrogen uptake and other attributes (except for leaf and whole plant N concentration), indicate that nitrogen acquisition, display and utilization for carbon gain were not tightly coupled in this group of species. This conclusion was not simply a consequence of differing relationships within the Myrtaceae from the largely N-fixing Fabaceae, nor could it be explained by the rather low light levels at which the experiment was conducted although this may have been a contributing factor.

Conclusions

In a decomposition of seedling RGR into specific leaf area, leaf nitrogen productivity, leaf nitrogen concentration (area basis) and leaf mass ratio, *c.* 44%, 22%, 19% and 15% of variation in RGR was explained by each attribute, respectively. The product of leaf nitrogen productivity and leaf nitrogen content (area basis) is the net assimilation rate (NARA, the rate of mass increase per unit leaf area per unit time).

LNP and LNCa were negatively associated, with a scaling slope of $c. 2/3$. Given this fact, the lack of relationship between RGR and NARa (Wright & Westoby 1999) was unsurprising. Indeed, it may be that counter-vailing trends in LNP and LNCa are common, contributing to the lack of a general relationship between NARa and RGR.

Most species allocated greater mass to leaves than roots but species with low RGR tended to be allocating a greater ongoing proportion of new biomass to the roots rather than the leaves, which resulted in a proportionally greater increase in root surface compared with leaf surface over time. Nitrogen uptake rate was associated with whole-plant and mass-based leaf N concentration but not with allocation (static or allometric) to leaves vs roots, nor with indices of leaf physiological 'activity'. While it is clear that root and leaf functions must be co-ordinated (and thus in balance) for growth to occur, consideration of these results together with those published previously leads to the conclusion that there is little evidence that this balance varies systematically with RGR across species.

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