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Seasonal impacts on leaf attributes of several tree species growing in three diverse ecosystems of SE Australia

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Abstract

Patterns of leaf attributes were examined for 6 woody species growing in a eucalypt woodland, a mangrove, or a heathland in coastal New South Wales, Australia during winter and summer. It was found that the rate of assimilation per unit leaf dry mass (A_{mass}) of the mangrove species was largest, woodland species exhibited an intermediate rate, and heathland species had the smallest values of A_{mass} . Mean habitat A_{mass} did not change from winter to summer in the woodland nor mangrove species but increased significantly in the heathland. SLA was largest for the mangrove species, and smallest for the heathland species, with woodland species showing intermediate values. Average specific leaf area (SLA) of all species within a habitat did not change from winter to summer. Mean foliar N of the mangrove species was highest, intermediate for woodland species and lowest for heathland. N_{mass} was significantly related to A_{mass} in both summer and winter and the individual slopes for this relationship in summer and winter differed. In contrast, a common slope was fitted to the relationship between SLA and A_{mass} for the two seasons. A common slope between seasons was also shown for the relationship between SLA and N_{mass} . There was no significant difference in slope elevation between summer and winter for the SLA– N_{mass} relationship. Trends within relationships among leaf attributes were the same as those found for a wide range of plant species worldwide, but the absolute values were lower than those found elsewhere. Therefore the “global relationships” in terms of trends (positive or negative) that have been determined overseas apply in Australia but the elevation of the slope and the magnitude of the slope are reduced (A_{mass} versus N_{mass}) or increased (A_{mass} versus SLA and N_{mass} versus SLA) compared to global trends.

Introduction

Plants grow in a wide variety of environmental conditions and are subject to a range of stresses and limitations to growth. A plant must respond to local conditions to be competitive and exploit the resources available in its environment (Lambers and Poorter 1992; Cunningham *et al.* 1999; Dyer *et al.* 2001). One suite of adaptations are changes to leaf-scale attributes that occur to increase survival and productivity in a given habitat (Berendse and Aerts 1987). In particular, rates of light saturated assimilation (A_{\max}), specific leaf area (SLA) and foliar nitrogen (N) content can differ by an order of magnitude or more in different species or at different sites (Reich *et al.* 1997).

Plants growing in nutrient-rich environments tend to have higher photosynthetic rates than plants growing in nutrient-poor environments (Field and Mooney 1986). Photosynthetic carbon gain is an important factor in determining plant growth and, on a larger scale, ecosystem primary production (Pereira 1994; Eamus 2003). Therefore, adaptations in photosynthetic rate are of fundamental significance to plants in the natural environment.

Generally, leaves with low specific leaf area (SLA, ratio of leaf area to leaf dry mass) are long-lived evergreen leaves with large amounts of structural and defensive compounds to enable survival in harsh environments (Niinemets 2001).

Nitrogen (N) availability is often the primary factor limiting growth in many environments (Berendse and Aerts 1987; Pereira 1994) and is required in large amounts for photosynthesis. In nutrient poor environments, a plant can reduce N loss by increasing leaf life span through the development of tougher, thicker leaves (lower SLA) and accumulation of defensive compounds to reduce herbivory (Berendse and Aerts 1987; Lambers and Poorter 1992). Thus, evergreen species tend to occur in nutrient poor environments (Aerts 1995).

The study of leaf attributes and their inter-relationships may reveal the adaptive strategies adopted by plants in different habitats. Several studies have determined relationships among leaf attributes that are considered global because they are observed in a wide range of species, habitats and environments. Thus photosynthesis, foliar nitrogen and SLA are all positively correlated with each other and inversely correlated with leaf lifespan (Reich *et al.* 1995; Reich *et al.* 1997; Reich *et al.* 1998; Niinemets 1999; Reich *et al.* 1999). Although these studies have included boreal, alpine and montane forests, sub-tropical and tropical forests, rainforests, savannas, desert shrub and

heathland, they have rarely included Australian habitats. Recent work by Wright and coworkers is beginning to fill this gap (Wright and Cannon 2001; Wright *et al.* 2001).

Most of the habitats used in the meta-analyses of leaf attributes (Reich *et al.* 1999; Niinemets 2001) are cooler, with more fertile soils and a lower aridity index (*sensu* Eamus *et al.* 1999) than many habitats of Australia. Therefore, we cannot assume that relationships among leaf attributes determined in vegetation in the northern hemisphere will apply to all Australian vegetation. Whilst there have been a few tests of these relationships within Australia (Warren *et al.* 2000; Wright *et al.* 2001; Prior *et al.* 2003), further detailed studies are required to provide a more representative sample for Australian vegetation and extend the global database to include vegetation that to-date has largely not been included.

The aim of this study was first, to quantify leaf attributes for selected species over two seasons (winter and summer) in three vegetation types, thereby allowing determination of relationships among leaf attributes and to establish whether seasonality has any impact on these relationships; and second, to compare slopes of relationships for Australian vegetation with that of the “global” relationships discussed by Reich and co-workers.

Methods

Study sites, species and climate

Three habitats were selected to represent three common coastal vegetation types of South Eastern Australia. These were a coastal heathland, an open Eucalypt woodland located on a sandstone ridge and a mangrove.

The heathland was located in the Royal National Park, 36 km south of Sydney approximately 1 km from the ocean. Soils are shallow and low in fertility. Maximum vegetation height was 1.5 m and dominated by woody shrubs. The ridge-top woodland site was located in the Berowra Valley Regional Park 20 km north-west of Sydney. Soil is derived from Hawkesbury sandstone with rocky outcrops. The height of the upper tree layer was 10-15 m and dominated by *Eucalyptus haemastoma*, *E. gummifera* and *Banksia serrata*. The mangrove site was located along Berowra Creek in the Berowra Valley Regional Park. The soils consist of the sandstone-derived soils from the slopes around the creek as well as silt build-up from tidal inundation. Two species of mangrove, *Avicennia marina* and *Aegiceras corniculatum* were present at this site. The approximate height of vegetation was 5 m.

Each site had a sampling area of approximately 1 ha and this was divided into two replicate plots to test for within-site variability. Plants were selected randomly throughout these two plots.

Six species that were dominant in at least one habitat were selected. *Angophora hispida* (Smith) Blaxell (Myrtaceae) was sampled in both the woodland and heathland. *Banksia oblongifolia* Cavanilles (Proteaceae) was also sampled in both the woodland and heathland. *Persoonia lanceolata* Andrews ssp. *lanceolata* (Proteaceae) was sampled in the heathland only. *Eucalyptus haemastoma* Smith (Myrtaceae) was sampled in the woodland only. *Avicennia marina* (Forsk.) Vierhapper var. *australasica* (Walpers) Moldenke (Avicenniaceae) and *Aegiceras corniculatum* (Linnaeus) Blanco (Myrsinaceae) were sampled at the mangrove site.

Mean annual rainfall for all three sites is approximately 1100 mm with slightly more rain occurring in summer than winter. Mean maximum and minimum temperatures range 17 °C to 27 °C and from 5 °C to 17 °C respectively.

Photosynthesis and foliar nitrogen content

Light saturated photosynthesis (A_{\max}) was measured with an HCM-1000 portable infra red gas analyser (IRGA; Walz, Germany) operated in differential mode. Measurements of intact, fully expanded leaves were taken in the morning (between 0930 h and 1130 h local time) between May and August (winter) 2001 and in February and March (summer) 2002. Leaves were in full sunlight at the time of sampling and light-saturating conditions ($\text{PAR} > 1000 \mu\text{mol m}^{-2}\text{s}^{-1}$) used throughout the study. Ambient levels of atmospheric CO_2 , humidity and temperatures were maintained in the leaf chamber at the start of each measurement period. Three leaves, on each of three plants, in each of two plots, for each species, were sampled.

All leaves measured for photosynthesis were collected for subsequent analysis for foliar N content. If individual leaves provided insufficient material for N analysis, the three closest leaves of the same age were also collected and used. Leaves were oven-dried at 70 °C. Petioles and midribs were removed and the laminae ground to a fine powder.

Each leaf was analysed for foliar N content following the Total Kjeldahl Nitrogen (TKN) procedure (Lachat Method 13-107-06-2-D), using 0.2 g dry mass of leaf material digested in concentrated sulfuric acid. Samples were digested on a block digester with heat ramping from 160 °C to 390 °C,

at which temperature samples remained for a period of two hours. Samples were then prepared for analysis with spectrophotometry to determine the amount of total N in the leaf. Blanks and reference samples were used to quantify accuracy.

Specific leaf area and photosynthetic nitrogen use efficiency

Specific leaf area (SLA) was calculated as the ratio of leaf area to leaf dry mass, using leaf discs taken from two leaves from each of five plants in each plot.

Photosynthetic nitrogen use efficiency (PNUE) was calculated for each leaf as the ratio of photosynthesis (A_{mass} ; $\text{nmol g}^{-1} \text{s}^{-1}$) to foliar N content (mg N g^{-1}).

Statistical analyses

Analysis of variance (ANOVA) was employed in comparisons of each attribute, first within each species at a site, then between species at a single site, and then between sites. ANOVAs were also performed to detect differences in leaf attributes between seasons. Additionally, ANOVAs were performed for *A. hispida* and *B. oblongifolia* between the woodland and heathland for direct comparison between two vegetation types.

Model II regression analysis was used to examine relationships between attributes, because variation was associated with both the *X* and *Y* variables due to measurement error and species sampling (Sokal and Rohlf 1995). Calculated on log-transformed variables, standardised Major Axis (SMA) slopes were fitted to each season separately to determine whether relationships differed between summer and winter (Falster et al. 2003). If slopes were found to be homogeneous (test for homogeneity, $P > 0.05$), a common slope was calculated using a likelihood ratio method, where the test statistic closely approximates a chi-squared distribution with Bartlett correction (Warton and Weber 2002). Subsequently, a test for differences in elevation (i.e. intercept) between summer and winter was performed, similar to standard analysis of covariance (ANCOVA) (Wright et al. 2002). Relationships were examined among species within a site and also across sites.

Results

For each species at each site, data were analysed for significant variation between the two plots. Because no significance differences between plots were found, data were pooled and species averages used in all subsequent analyses.

Photosynthesis and specific leaf area

During summer and winter, mean A_{area} and A_{mass} for each site (species combined) differed significantly from each other (Table 1). However, the ranking of these sites differed for A_{area} and A_{mass} . Woodland species maintained the largest A_{area} , the mangrove species were intermediate and heathland had the smallest A_{area} in both seasons. In contrast, A_{mass} of the mangrove species was largest, woodland species exhibited an intermediate rate, and heathland species had the smallest values of A_{mass} (Table 1).

For both *A. hispida* and *B. oblongifolia* A_{area} and A_{mass} were usually higher for plants growing in the woodland than in coastal heathland, in agreement with the ranking for habitat means (Table 1).

A_{area} and A_{mass} did not change from winter to summer in the woodland and mangrove habitat means but increased significantly in summer in the heathland (Table 1). For individual species A_{area} and A_{mass} did not change seasonally within the mangrove; in the woodland there was an increase only in *B. oblongifolia*. All heathland species had higher A_{area} and A_{mass} in summer than winter (Table 1).

In winter and summer, differences in specific leaf area (SLA) between habitats (thus, comparing habitat averages of all species) were significant in some but not all comparisons. SLA was largest for the mangrove species, and smallest for the heathland species (Table 1). This pattern was repeated when comparing values of SLA for a single species growing in two sites; *A. hispida* and *B. oblongifolia* had significantly larger SLA in the woodland than the heathland. Several significant differences in SLA among species within habitats were also observed (Table 1). Average SLA of all species within a habitat did not change from winter to summer for woodland and heathland but increased significantly for the mangrove (Table 1).

Foliar nitrogen content and photosynthetic nitrogen use efficiency

During winter, differences in foliar N between habitats were significant. Mangrove mean foliar N was highest, and foliar N lowest for heathland (Table 1). *A. hispida* had a significantly lower foliar N in the heathland than the woodland. In contrast, *B. oblongifolia* did not show a significant difference in foliar N between sites in winter (Table 1).

During summer, foliar N content among sites showed significant differences, with the ranking the same as in winter (Table 1). Mean foliar N content for each habitat was significantly higher in summer than winter in all three habitats and most species showed this trend (Table 2).

Woodland species had the highest instantaneous PNUE ($A_{\text{mass}} / N_{\text{mass}}$) of all sites in both summer and winter, with species at the heathland site exhibiting the lowest PNUE in winter and the mangroves the lowest PNUE in summer (Table 2). This ranking was maintained when comparing the common species between the heath and woodland sites.

Relationships amongst photosynthesis, nitrogen and specific leaf area

Note that in Figure 1, all values are log values.

As N_{mass} increased, A_{mass} increased significantly in summer (slope = 0.46; 95% CI = 0.27, 0.77; intercept = 1.41; $r^2 = 0.71$, $P = 0.009$) but only marginally significantly in winter (slope = 1.19; 95% CI = 0.60, 2.37; intercept = 0.67; $r^2 = 0.44$, $P = 0.07$) (Fig. 1a). Individual slopes for the $N_{\text{mass}}-A_{\text{mass}}$ relationship in summer and winter were heterogeneous (test for heterogeneity of slopes = 4.96, $P = 0.03$), precluding the possibility of fitting a common slope to winter and summer data. When the winter relationship was considered without the heathland data, the slope of the $N_{\text{mass}}-A_{\text{mass}}$ relationship was not significantly different from the slope of the summer relationship (test for heterogeneity of slopes = 0.17, $P = 0.67$).

As SLA increased, A_{mass} increased significantly in winter (slope = 2.14; 95% CI = 1.18, 3.90; intercept = -1.97; $r^2 = 0.60$, $P = 0.02$) but not in summer (slope = 1.12; 95% CI = 0.55, 2.26; intercept = -0.07; $r^2 = 0.41$, $P = 0.09$). A common slope (slope = 1.65, 95% CI = 1.04, 2.57) could be fitted to the winter and summer data the relationship between SLA and A_{mass} as the individual slopes were homogeneous (test for heterogeneity of slopes = 2.21, $P = 0.16$) (Fig. 1b). Marginally, there was no significant difference in slope elevation between summer and winter for the SLA- A_{mass} relationship ($F_{1, 14} = 3.84$, $P = 0.07$).

As SLA increased, N_{mass} increased significantly in both summer (slope = 2.43; 95% CI = 1.50, 3.93; intercept = -3.20; $r^2 = 0.75$, $P = 0.06$) and winter (slope = 1.80; 95% CI = 1.12, 2.89; intercept = -2.22; $r^2 = 0.76$, $P = 0.005$) (Fig. 1c). The slopes of the SLA- N_{mass} relationship were homogeneous (test for heterogeneity of slopes = 0.95, $P = 0.32$), and a common slope could be

applied (slope = 2.08, 95% CI = 1.55, 2.81) (Fig. 1c). There was no significant difference in slope elevation between summer and winter for the SLA– N_{mass} relationship ($F_{1,14} = 4.29$, $P = 0.06$).

To facilitate direct comparisons of bivariate trait relationships in our dataset with patterns emerging in datasets from other continents (e.g. Reich et al. 1997), we pooled summer and winter data and performed simple (Model I) linear regressions. A_{mass} was positively related to N_{mass} ($F_{1,14} = 12.18$, $r^2 = 0.47$, $P = 0.004$), with the regression relationship: $\log(A_{\text{mass}}) = 1.22 + 0.62\log(N_{\text{mass}})$. A_{mass} was positively related to SLA ($F_{1,14} = 10.96$, $r^2 = 0.44$, $P = 0.005$), with the regression relationship: $\log(A_{\text{mass}}) = -0.42 + 1.29\log(\text{SLA})$. N_{mass} was positively related to SLA ($F_{1,14} = 29.13$, $r^2 = 0.68$, $P < 0.0001$), with the regression relationship: $\log(N_{\text{mass}}) = -2.08 + 1.75\log(\text{SLA})$.

Discussion

Specific leaf area

The range of SLA measured in the present study (40 – 80 cm² g⁻¹) was low in comparison with other species worldwide (30 – 500 cm² g⁻¹; Turner and Tan 1991; Reich et al. 1995; Reich et al. 1998, Meziane and Shipley 1999; Poorter and De Jong 1999). Other Australian studies found SLA to be lower than values found elsewhere (Fordyce et al. 1995; Atkin et al. 1998; Cunningham et al. 1999; Eamus et al. 1999). Low SLA in Australian plants reflects their sclerophylly, a dominance of evergreen species and is an adaptation to nutrient poor soils (Wright et al 2002). Thicker leaves have more structural tissue and defensive secondary compounds and therefore are more resistant to drought and herbivory (Lambers and Poorter 1992; Bell and Williams 1997). Leaf longevity also increases in response to low nutrient soils (Chabot and Hicks 1982; Witkowski et al. 1992; Cunningham et al. 1999).

SLA was largest at the mangrove site, probably because of the high water content of mangrove leaves (Ball 1988), and the higher (relative to the other two sites) nutrient availability of mangroves. The higher nutrient availability of the mangrove site is reflected in the larger foliar N content of the two mangrove species compared to all other species in the present study.

The heathland had the lowest SLA of all three habitats. The heathland environment has lower soil fertility, shallower soils and less water storage capacity (Specht and Specht 1999; Howell and Benson 2000) than the woodland and receive significant levels of sea-spray. Reduced nutrient availability in the heathland site is reflected in the lower foliar N content of heathland species compared to other species. Similarly, both *A. hispida* and *B. oblongifolia* had significantly lower

SLA (and mean foliar N contents) in the heathland compared to the woodland. *B. oblongifolia* had the lowest SLA of all species in the study at both sites in both seasons, suggesting that it may invest more energy into longevity, rather than growth, as revealed in its reduced height compared with any other species, and very long lived leaves, longer than many other species (Witkowski *et al.* 1992).

Photosynthesis: species, habitat and seasonal comparisons

In the present study, A_{area} ranged from 7-15 $\mu\text{mol m}^{-2} \text{s}^{-1}$, similar to most broad-leaved woody shrubs and trees around the world (Niinemets 1999) and other Australian studies (Witkowski *et al.* 1992; Bell and Williams 1997; Eamus and Cole 1997; Eamus *et al.* 1999; Warren *et al.* 2000; Wright *et al.* 2001). In contrast, A_{mass} of the species in the present study were much lower (30 to 100 $\text{nmol g}^{-1} \text{s}^{-1}$) than most plants in most habitats worldwide (15 to 300 $\text{nmol g}^{-1} \text{s}^{-1}$). The difference in comparisons for A_{area} and A_{mass} arise due to the lower SLA of our study species.

During winter, all three sites had significantly different mean habitat A_{mass} . The mangrove species had the largest A_{mass} and this was associated with the largest foliar N content. Mangroves are located in nutrient rich silt (compared to woodland and heathland soils) and therefore may be expected to exhibit a high A_{mass} , in response to this enhanced availability of N.

Heathland species had the lowest A_{mass} . Water and nutrient availability is lowest at this site, and this is reflected in the smaller standing biomass in the heathland than in the woodland or mangrove and the lowest foliar N content. Additionally, coastal heathlands experience high levels of exposure to wind and salt spray, which further exacerbate water stress and thereby inhibit assimilation. The importance of habitat as a determinant of assimilation rate is further shown by comparing annual average A_{mass} and foliar N in *A. hispidula* and *B. oblongifolia* in the two different habitats. Both of these parameters were lower for both species in the heathland compared to the woodland.

For most comparisons at a species level, A_{mass} did not vary between winter and summer. This was despite a significant increase in foliar N content occurring in most species in the summer compared to winter (Table 1). The lack of an apparent response of A_{mass} to increased foliar N content could be due to two factors. First assimilation could have been N saturated in winter, an unlikely possibility given the depauperate soil of our sites. In addition, the positive relationship observed in the present study between foliar N content and A_{mass} is evidence that assimilation was not N saturated. Second, the significant increase in leaf temperature observed in the summer may have taken leaf

temperature to supra-optimal levels, with a concomitant decline in assimilation rate, despite enhanced foliar N levels.

Foliar nitrogen content, photosynthesis and photosynthetic nitrogen use efficiency

The range of foliar N observed in the present study (5 – 15 mg N g⁻¹) is at the low end of the range observed overseas (10 – 70 mg N g⁻¹; Diemer *et al.* 1992; Reich *et al.* 1995; Middleton *et al.* 1997; Damesin *et al.* 1998; Reich *et al.* 1998; Reich *et al.* 1999) and are consistent with other Australian and South African studies (Witkowski *et al.* 1992; Fordyce *et al.* 1995; Midgley *et al.* 1995; Bell and Williams 1997; Eamus *et al.* 1999; Warren *et al.* 2000).

A_{mass} was positively and significantly correlated with foliar N across sites in this study, consistent with studies worldwide (Niinemets 1999; Reich *et al.* 1998; Eamus *et al.* 1999; Eamus and Cole 1997; Witkowski *et al.* 1992, Wong and Dunin 1987; Wright *et al.* 2001). Comparison of the slopes in the present study and global relationships is discussed below.

At moderate levels of N availability, instantaneous photosynthetic nitrogen use efficiency (PNUE) increases with decreasing nitrogen availability (Berendse and Aerts 1987; Pastor and Bridgham 1999). Thus, if a plant does not have a high level of nitrogen, it will tend to use what is available very efficiently to maximise its effects on photosynthesis. This relationship was not observed in the present study. The woodland had the highest PNUE for both seasons, but it did not have the lowest foliar N in either season. Similarly, the heathland did not have the highest PNUE in either season despite having the lowest foliar N. The mangrove species had the highest foliar N but only had the lowest PNUE in summer. Furthermore, values of PNUE were not higher than observed worldwide, where foliar N levels are generally higher.

Plants growing in especially low nutrient soils will have a reduced PNUE rather than an increased PNUE observed in soil of moderate or higher N availability. This is because partitioning of nitrogen in leaves of plants growing on low nutrient soils is not the same as N partitioning in leaves of plants growing in moderate or high nutrient soils (Berendse and Aerts 1987). Plants in especially infertile soils retain their leaves for longer to minimise nutrient loss. In order to do this, they invest more carbon and nitrogen in structural and chemical defenses against mechanical or herbivore damage (Berendse and Aerts 1987; Lerdaun 1992). Consequently, there is less nitrogen devoted to photosynthetic enzymes and more devoted to leaf longevity. Consequently PNUE is reduced. This can be inferred from a comparison of *B. oblongifolia* in the woodland and heathland. Despite the

same level of foliar N for plants at both sites, A_{mass} was much lower at the heathland site. A better index of NUE might be the total C gained over the life of the leaf, rather than the instantaneous measure used here.

The relationship between photosynthesis and specific leaf area

The significant and positive relationship between SLA and A_{mass} across all three habitats in this study is similar to that observed elsewhere (Gulmon and Chu 1981; Reich *et al.* 1998; Niinemets 1999; Poorter and De Jong 1999; Reich *et al.* 1999; Eamus *et al.* 1999; Wright *et al.* 2001). SLA is positively related to A_{mass} because it represents an increase in area for light capture per unit of leaf. Decreased SLA is correlated with a greater allocation of biomass to structural rather than metabolic processes (Reich *et al.* 1998). A_{mass} declines with decreased SLA because of increased internal shading of cells (Reich *et al.* 1998) and the diffusion path for CO₂ from stomata to chloroplasts is longer (Reich *et al.* 1998).

The relationship between foliar nitrogen content and specific leaf area

Foliar N was positively correlated to SLA across all three sites in this study. This relationship has been observed over a wide range of species in many different habitats (Gulmon and Chu 1981; Lambers and Poorter 1992; Midgley *et al.* 1995; Reich *et al.* 1995; Reich *et al.* 1998; Meziane and Shipley 1999; Poorter and De Jong 1999; Reich *et al.* 1999; Dyer *et al.* 2001; Witkowski *et al.* 1992; Cunningham *et al.* 1999; Eamus *et al.* 1999; Wright *et al.* 2001).

SLA is an indication of sclerophylly in leaves (Cunningham *et al.* 1999). The lower the SLA, the more sclerophyllous the leaves. Sclerophylly is an adaptation to low resource availability, such as nutrients or water, and confers increasing protection against damage with increasing leaf longevity (Edwards *et al.* 2000). A low foliar N suggests that nitrogen in the soil is limiting. Therefore, low foliar N should be associated with a low SLA, as was consistently observed.

Global comparisons

From the type I regressions presented in Reich *et al.* 1997 (Figure 1 of Reich *et al.* 1997), and the type I regressions of the present data, it is clear that the Australian species, contrary to *a priori* expectations, appear to be less efficient users of nitrogen than observed in global relationships. The slope of the A_{mass} versus N_{mass} relationship is significantly lower than that presented by Reich *et al.*

(1997) (0.62 compared to 1.42) indicating that for the same amount of N invested in leaves, a lower rate of A_{mass} was achieved. Similarly the slope of the N_{mass} versus SLA relationship is larger in the present study compared to that of Reich *et al.* (1997) (1.75 compared to 0.53). Thus, for a given value of SLA, more N is contained in the leaves of the species in the present study than the global slopes of Reich *et al.* (1997). Finally, consistent with these two results, for the present study, the slope of the relationship between A_{mass} and SLA is larger than that obtained by Reich *et al.* (1997) (1.29 compared to 1.08). Generally the range of A_{mass} , N_{mass} and SLA observed in the present study is at the lower end of the range of values observed globally (Reich *et al.* 1997) and it is now apparent that the return (in terms of carbon fixed) on the investment of N in the leaf is also lower. We suggest that this may be a function of the high degree of sclerophylly observed in Australian terrestrial plants compared to those species studied overseas. Sclerophylly is associated with a high structural mass per unit leaf mass and a consequent dilution of the N content expressed per unit leaf dry weight.

Conclusion

In Australia, plants have lower values for specific leaf area, A_{mass} and foliar nitrogen content than the majority of species studied worldwide. This is a result of differences in soil fertility, aridity and the preponderance of sclerophylly, compared to most other habitats throughout the world.

Relationships among leaf attributes within a single species at a site or among species at a site could not be readily detected, especially in these environments of low soil fertility because the range of values for leaf attributes were small and hence slopes of relationships were slight. Leaf attributes were thus best examined by comparing across sites and amongst species. Trends within relationships among leaf attributes were the same as those found for a wide range of plant species worldwide, but the slopes differed from those found elsewhere. Therefore the “global relationships” in terms of trends (positive or negative slopes) that have been determined overseas apply in Australia but the elevation of the slope and the magnitude of the slope are reduced (A_{mass} versus N_{mass}) or increased (A_{mass} versus SLA and N_{mass} versus SLA) compared to global trends.

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Table 1 Mean summer and winter values for assimilation rate (expressed on an area and mass basis) and specific leaf area (SLA) and foliar nitrogen content for 6 species growing in 3 habitats. Standard errors are presented in parentheses and means followed by a different letter within a column are significantly different from each other.

Site	Species	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
		A_{area} $\mu\text{mol m}^{-2} \text{s}^{-1}$	A_{area} $\mu\text{mol m}^{-2} \text{s}^{-1}$	A_{mass} $\text{nmol g}^{-1} \text{s}^{-1}$	A_{mass} $\text{nmol g}^{-1} \text{s}^{-1}$	SLA $\text{cm}^2 \text{g}^{-1}$	SLA $\text{cm}^2 \text{g}^{-1}$	N mg/g	N mg/g
Woodland	<i>Angophora hispidata</i>	11.88a (1.38)	12.37a (0.52)	64.13 a (8.52)	66.9a (3.0)	53.61a (1.31)	54.33a (0.88)	7.902a (0.15)	8.2a (0.32)
Woodland	<i>Banksia oblongifolia</i>	18.15b (1.10)	15.31a (0.53)	87.39b (5.21)	70.3b (2.0)	48.39b (1.74)	46.12b (0.71)	8.722a (0.34)	6.28b (0.18)
Woodland	<i>Eucalyptus haemastoma</i>	15.85b (1.68)	15.81a (0.68)	78.31b (7.21)	86.9b (4.0)	50.46a,b (1.96)	55.95a (1.69)	10.81b (0.53)	8.08a (0.35)
Average		15.29b (0.99)	14.50a,b (1.07)	76.61b (4.50)	74.70a,b (6.20)	50.82a,b (1.05)	52.13a (3.04)	9.02c (0.37)	7.52a,b (6.2)
Heathland	<i>Angophora hispidata</i>	13.29a (1.19)	8.43c (0.40)	75.09a (9.64)	41.5c (2.0)	55.56a (2.49)	49.71a,c (1.16)	9.25c (0.38)	5.85c (0.16)
Heathland	<i>Banksia oblongifolia</i>	14.59a,b (0.59)	6.94d (0.82)	60.39a,b (2.58)	29.0d (3.0)	41.51d (1.38)	42.12d (0.76)	7.56a (0.55)	6.59b (0.14)
Heathland	<i>Persoonia lanceolata</i>	10.67c (0.88)	6.41d (0.52)	56.14c (4.89)	30.40d (2.0)	52.80a (2.97)	47.98b,c (1.21)	6.54d (0.29)	6.23bc (0.12)
Average		12.85a,d (0.64)	7.26d (0.60)	63.87a,d (4.0)	33.6d (4.0)	49.99b (1.96)	46.60b (2.30)	7.73a,e (0.35)	6.23b,c (0.21)
Mangrove	<i>Aegiceras corniculatum</i>	11.64a (1.27)	12.46e (0.60)	92.59a (11.05)	97.5e (5.0)	67.95e (5.80)	79.67d (2.33)	17.44f (0.63)	11.42d (0.23)
Mangrove	<i>Avicennia marina</i>	13.10a (0.67)	12.23e (0.46)	94.19a (7.12)	90.4e (3.0)	72.01e (3.56)	75.50d (2.57)	22.24g (0.68)	19.85e (0.85)
Average		12.91a (0.53)	12.35e (0.12)	93.46e (6.01)	94.0e (3.6)	72.15e (2.72)	77.59d (2.09)	19.96h (0.89)	15.64d,e (4.2)

Table 3. Mean PNUE for each species and each season, standard errors are in parentheses. Letters that differ after a mean within a column indicate significant differences. Different superscript numbers after the mean for averages indicate significant differences when comparing averages within a column.

Site	Species	Winter PNUE (nmol C (g N) ⁻¹ s ⁻¹)	Summer PNUE (nmol C (g N) ⁻¹ s ⁻¹)
Woodland	<i>A. hispida</i>	8.16 (0.52)a	8.36 (1.12)a
Woodland	<i>B. oblongifolia</i>	11.19 (0.42)b	10.25 (0.76)a
Woodland	<i>E. haemastoma</i>	10.75 (0.46)b	7.39 (0.81)b
<i>Average</i>		10.03 (0.95) ¹	8.67 (0.57) ¹
Heathland	<i>A. hispida</i>	7.09 (0.30)c	8.0 (0.75)a
Heathland	<i>B. oblongifolia</i>	4.40 (0.51)d	8.74 (0.70)a
Heathland	<i>P. lanceolata</i>	4.88 (0.40)d	8.25 (0.73)a
<i>Average</i>		5.47 (0.83) ²	8.33 (0.40) ¹
Mangrove	<i>A. corniculatum</i>	8.54 (0.42)a	5.39 (0.69)c
Mangrove	<i>A. marina</i>	4.55(0.14)d	4.24 (0.25)d
<i>Average</i>		6.55 (2.00) ²	4.76 (0.37)c,d

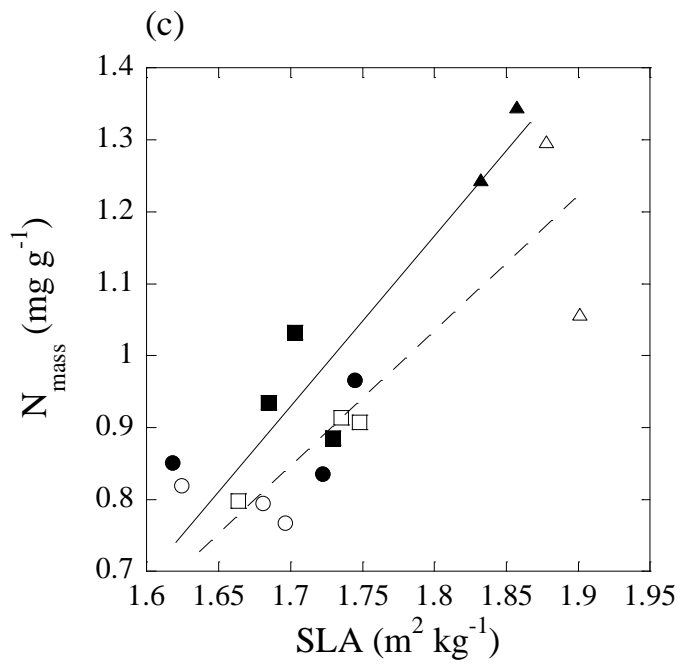
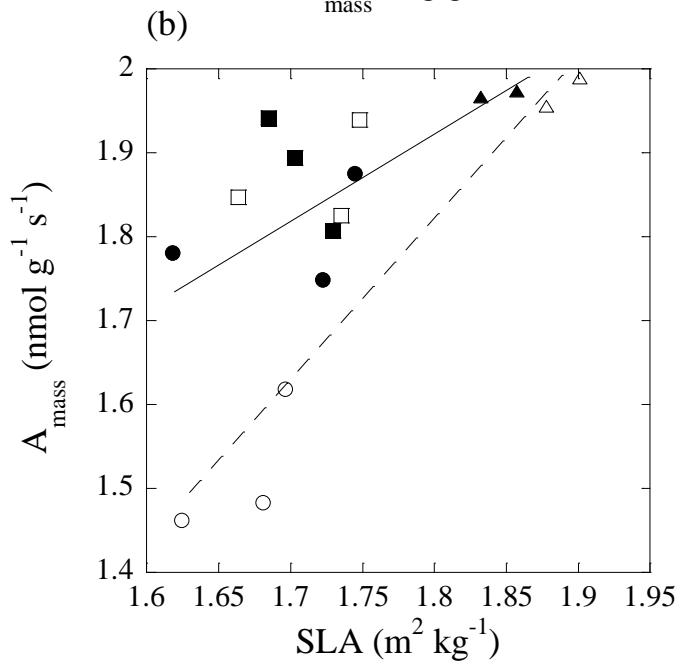
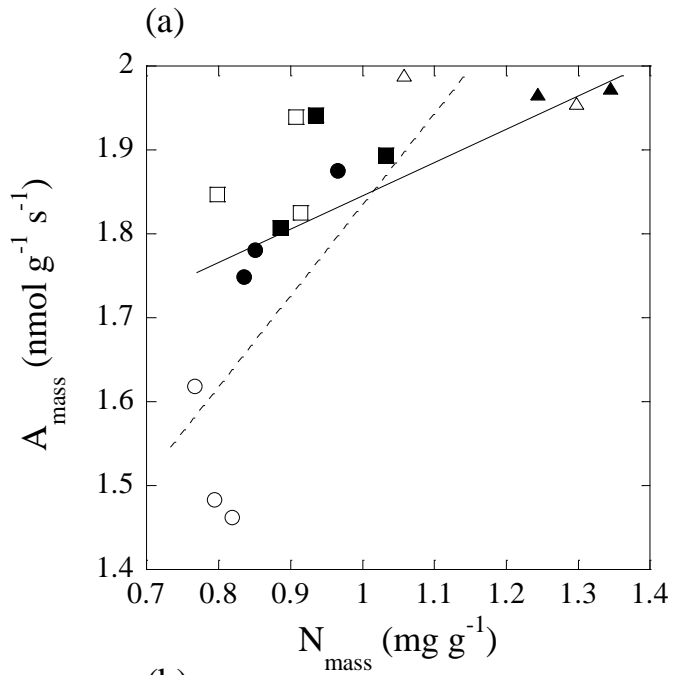


Figure Legend

Fig. 1 Relationships between (a) A_{mass} and N_{mass} , (b) A_{mass} and SLA, and (c) SLA and N_{mass} . ■ = summer woodland, ▲ = summer mangrove, ● = summer heathland, □ = winter woodland, Δ = winter mangrove, ○ = winter heathland. Model II regression lines are provided separately for summer (unbroken line) and winter (broken line).