

## A continental-scale assessment of variability in leaf traits: within species, across sites and between seasons

Keith J. Bloomfield<sup>\*1</sup>, Lucas A. Cernusak<sup>2</sup>, Derek Eamus<sup>3</sup>, David S. Ellsworth<sup>4</sup>, I. Colin Prentice<sup>5,6</sup>, Ian J. Wright<sup>5</sup>, Matthias M. Boer<sup>4</sup>, Matt G. Bradford<sup>7</sup>, Peter Cale<sup>8</sup>, James Cleverly<sup>3</sup>, John J.G. Egerton<sup>1</sup>, Bradley J. Evans<sup>9,10</sup>, Lucy S. Hayes<sup>1</sup>, Michael F. Hutchinson<sup>11</sup>, Michael J. Liddell<sup>12,13</sup>, Craig Macfarlane<sup>14</sup>, Wayne S. Meyer<sup>15</sup>, Suzanne M. Prober<sup>14</sup>, Henrique F. Togashi<sup>5,9</sup>, Tim Wardlaw<sup>16</sup>, Lingling Zhu<sup>1,17</sup> and Owen K. Atkin<sup>1,17</sup>

<sup>1</sup>Division of Plant Sciences, Research School of Biology, Building 46, The Australian National University, Canberra, ACT 2601, Australia;

<sup>2</sup>Department of Marine and Tropical Biology, James Cook University, Cairns, Qld, Australia;

<sup>3</sup>School of Life Sciences, University of Technology Sydney, NSW 2007, Australia;

<sup>4</sup>Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2751, Australia;

<sup>5</sup>Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia;

<sup>6</sup>AXA Chair of Biosphere and Climate Impacts, Grand Challenges in Ecosystems and the Environment and Grantham Institute—Climate Change and the Environment, Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK;

<sup>7</sup>CSIRO Land and Water, Tropical Forest Research Centre, Atherton, Qld, Australia;

<sup>8</sup>Australian Landscape Trust, Renmark, SA 5341, Australia;

<sup>9</sup>Terrestrial Ecosystem Research Network, Ecosystem Modelling and Scaling Infrastructure, The University of Sydney, Sydney, NSW 2006, Australia;

<sup>10</sup>Department of Environmental Sciences, University of Sydney, Sydney, NSW 2006, Australia;

<sup>11</sup>Fenner School of Environment and Society, Australian National University, Canberra, ACT 2601, Australia;

<sup>12</sup>Centre for Tropical, Environmental, and Sustainability Sciences, College of Science and Engineering, James Cook University, Cairns, Qld, Australia;

<sup>13</sup>Terrestrial Ecosystem Research Network, Australian SuperSite Network, James Cook University, Cairns, Australia;

<sup>14</sup>CSIRO Land and Water, Private Bag 5, Wembley, WA 6913, Australia;

<sup>15</sup>Earth and Environmental Sciences, University of Adelaide, Adelaide, SA 5064, Australia;

<sup>16</sup>Forestry Tasmania, Hobart, TAS 7000, Australia;

<sup>17</sup>ARC Centre of Excellence in Plant Energy Biology, Research School of Biology, Building 134, The Australian National University, Canberra, ACT 2601, Australia.

**Running headline:** Inter- and intraspecific variation in leaf traits

## Summary

1. Plant species show considerable leaf trait variability that should be accounted for in dynamic global vegetation models (DGVMs). In particular, differences in the acclimation of leaf traits during periods more and less favourable to growth have rarely been examined.
2. We conducted a field study of leaf trait variation at seven sites spanning a range of climates and latitudes across the Australian continent. 80 native plant species were included. We measured key traits associated with leaf structure, chemistry and metabolism during the favourable and unfavourable growing seasons.
3. Leaf traits differed widely in the degree of seasonal variation displayed. Leaf mass per unit area ( $M_a$ ) showed none. At the other extreme, seasonal variation accounted for nearly a third of total variability in dark respiration ( $R_{\text{dark}}$ ).
4. At the non-tropical sites, carboxylation capacity ( $V_{\text{cmax}}$ ) at the prevailing growth temperature was typically higher in summer than in winter. When  $V_{\text{cmax}}$  was normalised to a common reference temperature (25°C), however, the opposite pattern was observed for about 30% of the species. This suggests that metabolic acclimation is possible, but far from universal.
5. Intraspecific variation – combining measurements of individual plants repeated at contrasting seasons, different leaves from the same individual, and multiple conspecific plants at a given site – dominated total variation for leaf metabolic traits  $V_{\text{cmax}}$  and  $R_{\text{dark}}$ . By contrast, site location was the major source of variation (53%) for  $M_a$ . Inter-specific trait variation ranged from only 13% of total variation for  $V_{\text{cmax}}$  up to 43% for nitrogen content per unit leaf area.
6. These findings do not support a common practice in DGVMs of assigning fixed leaf trait values to plant functional types. Trait-based models should allow for inter-specific differences, together with spatial and temporal plasticity in leaf structural, chemical and metabolic traits.

**Key-words:** aridity, dynamic global vegetation models, intraspecific variation, leaf traits, nitrogen, phosphorus, photosynthesis, respiration

## Introduction

Leaves play a vital role in the exchange of carbon between the atmosphere and land. Dynamic global vegetation models (DGVMs) therefore need to characterise leaf traits accurately if they are to fulfil the twin objectives of developing our understanding of vegetation distribution and providing parent Earth System models with a dynamic representation of carbon, water and energy budgets (Scheiter, Langan & Higgins 2013). To date, there have been two main approaches to describing leaf traits in DGVMs (Prentice & Cowling 2013). The first organises plant species into a small number of distinct groups, plant functional types (PFTs), and assigns a single coefficient or model parameter to all members of the group. The second approach uses leaf trait-trait relationships and trade-offs to predict variations in biogeochemical fluxes (e.g. Pavlick *et al.* 2013).

All healthy leaves fix carbon and under the standard biochemical model of  $C_3$  photosynthesis (Farquhar, von Caemmerer & Berry 1980), rates of carboxylation are limited by the amount of activated Ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco), which sets the maximal rate of the reaction at any given temperature ( $V_{\text{cmax}}$ ). Because of the high nitrogen (N) content of key proteins in the leaf's photosynthetic apparatus, notably Rubisco, many DGVMs treat  $V_{\text{cmax}}$  as a function of leaf N content. The relationship with N (also applied to respiration) is based on empirical observations (e.g. Kattge *et al.* 2009). Like all enzymes, Rubisco's activity is temperature-dependent and many DGVMs therefore employ the Arrhenius function to predict metabolic rates at growing temperatures above and below a reference temperature (often 25°C). This approach is based on the enzyme's observed short-term responses to temperature, but assumes that the leaf's metabolism does not acclimate to sustained changes in growth temperature; that simplifying assumption has potentially important implications for modelled fluxes (Kattge & Knorr 2007).

Thermal acclimation in plants is often studied by making comparisons between contrasting groups at a standardised measurement temperature; due to a range of processes, which might include lowered capacity or demand, acclimation can lead to warm-grown plants having a slower metabolic rate (at standard temperature) than those that experience cooler growing conditions (Atkin, Holly & Ball 2000). Acclimation may also result in changes to trait-trait relationships linking leaf metabolism with traits such as N content per unit leaf area ( $N_{\text{area}}$ ) and leaf mass per unit leaf area ( $M_a$ ) (Atkin *et al.* 2008) (see Fig. S1 in Supporting Information). Field-based evidence of seasonal thermal acclimation of leaf dark respiration ( $R_{\text{dark}}$ ) has been shown in deciduous and evergreen species growing in a variety of ecosystems (e.g. Zaragoza-

Castells *et al.* 2008; Reich *et al.* 2016). For photosynthesis ( $A$ ), however, there is less consensus on whether thermal acclimation is common, with sometimes contradictory results (Way & Yamori 2014). Importantly, the degree of photosynthetic thermal acclimation operating in natural settings, where there are often large seasonal variations in growth temperature (and other abiotic variables such as rainfall and irradiance), remains uncertain (but see Lin *et al.* 2013).

A major objection to the prevalent approach within DGVMs of assigning a single trait value to all members of a PFT is that possible sources of variation, such as climate seasonality, are ignored. Whilst plant trait initiatives such as the TRY database (Kattge *et al.* 2011) and Glopnet (Wright *et al.* 2004) have provided insights into how trait values vary among species and environmentally contrasting sites, many plant trait studies have focused on species' mean values for measurements made during a single season. The degree of intraspecific variability (ITV) is often (implicitly) assumed to be of minor importance compared to the variation among species (Violle *et al.* 2012). Although some studies have compared leaf trait values at different times of year (e.g. Misson *et al.* 2006), few have considered possible seasonal variation in trait-trait relationships. Considering traits as mean values per species, and ignoring ITV, also underestimates niche and trait overlap between species so that changes in species composition under climate change projections may be exaggerated (Jung *et al.* 2014).

Intraspecific trait variation has two potentially complementary sources: genetic differences (adaptation) and the interaction of a single genotype with altered environments (plasticity) (Albert *et al.* 2010). Total ITV can theoretically be partitioned among populations, among individuals and within individuals; but the spatial scale under consideration is important and Albert *et al.* (2011) have proposed that the extent of ITV saturates asymptotically as the scale widens to eventually encompass a species' entire environmental range. A number of recent studies strengthen the case for DGVMs to incorporate leaf trait variation: ITV has been shown to match or even exceed inter-specific variation for key traits such as  $M_a$  (e.g. Messier, McGill & Lechowicz 2010) and can be more important than species turnover in plant community responses to environmental change (Jung *et al.* 2014). In regard to trait-environment relationships, a study of specific leaf area (the inverse of  $M_a$ ) responses to light gradient across forest patches in Brazil found that the relationship between SLA and canopy openness was stronger when the analysis included both inter- and intra-specific variation (Carlucci *et al.* 2015). Most recently, a review of four state-of-the-art DGVMs, Restrepo-Coupe *et al.* (2017) found that the models performed poorly in simulating seasonal carbon fluxes in the Amazon forest. Such

difficulties are potentially greater still for ecosystems at higher latitudes where seasonal variation in climate conditions is more pronounced.

Edaphic conditions in Australia - typified over large areas by highly weathered, low-P soils - have played a major role in differentiating the flora, and plant performance is often considered more constrained by the supply of P than of N (Beadle 1962). Under such conditions, co-limitation of photosynthetic capacity by N and P may alter the form of a putative  $\mathcal{A}$ -N relationship (Kattge *et al.* 2009; Reich, Oleksyn & Wright 2009). A number of ecophysiological studies in Australia have sought to exploit the steep natural gradients in rainfall and nutrient availability across the continent. Wright *et al.* (2001) measured 79 plant species across four sites in eastern New South Wales to describe a suite of water conservation traits: higher levels of leaf N and phosphorus (P) were associated with faster rates of  $\mathcal{A}$  for a given level of stomatal conductance ( $g_s$ ), but at the cost of higher  $R_{\text{dark}}$ . In a related study, Prentice *et al.* (2014) confirmed shallower slopes for the positive  $V_{\text{cmax}}$ - $N_{\text{area}}$  relationship at drier sites, with greater N investment in photosynthetic apparatus producing faster rates of carboxylation for a given  $g_s$  (see also Schulze *et al.* 2006). Australian studies looking at seasonal variation in leaf traits have focused primarily on plant water use efficiency, but with contrasting results (Prior, Eamus & Duff 1997; Eamus *et al.* 1999).

In this study, our goal was to assess spatial and seasonal variability in leaf traits and the trait-trait relationships that underpin modern DGVMs. Such attempts face the challenge of how to contend with biodiversity linked to large environmental differences; one consequence of Australia's diverse environments and flora is that we found only four species in sufficient numbers at more than one site to permit inter-site comparisons between populations. We were interested, however, in genetic influences on trait variability at a range of scales rather than how individual species respond to environmental change. In seeking to explore sources of variation within leaf functional traits we hypothesised that:

1. For key traits related to carbon uptake and release and nutrient content ( $V_{\text{cmax}}$ ,  $R_{\text{dark}}$ ,  $N_{\text{area}}$ ), the nature of trait-trait relationships would vary with season;
2. For those sites with a pronounced seasonal shift in growth temperature, temperature-standardised metabolic rates (i.e.  $V_{\text{cmax}}$  and  $R_{\text{dark}}$  at 25°C) would be faster in the cooler season. We also considered evidence of seasonal variation in metabolic rates at those tropical sites where seasonality is characterised by rainfall rather than temperature;
3. Given the wide spatial scale within our dataset, inter-specific variation would outweigh intra-specific variation.

## Materials and methods

### Study sites and climate data

Our seven study sites are a subset of the TERN SuperSites network ([www.supersites.net.au](http://www.supersites.net.au)), which is a facility of the Terrestrial Ecosystem Research Network (TERN) (Karan *et al.* 2016). The site locations and key descriptors of dominant vegetation and soil type are presented in Table 1. The sites were chosen, from the existing network, to provide a wide range in vegetation and environmental conditions, with an emphasis on rainfall and temperature variability (Fig. S2).

Depending on the type of analysis attempted, we made use of climate data from a variety of sources. Each SuperSite is equipped with a flux tower (TERN OzFlux network) that records a common suite of meteorological data (Beringer *et al.* 2016). Our initial visits preceded the installation of the standard OzFlux system at three sites; in those instances we used the ANUClimate model (Hutchinson *et al.* 2009) and data from the Australian Bureau of Meteorology's nearest weather station. Long-term climate data for each site were obtained from interpolated values (covering the period 1970–2012) produced at 0.01° spatial resolution by the TERN eMAST facility (Ecosystem Modelling and Scaling Infrastructure; [www.emast.org.au](http://www.emast.org.au)).

We performed spatial analyses to assemble the seven sites across a matrix of bioclimatic indices that emphasised patterns of seasonality in rainfall and temperature (data not shown). The degree of similarity among the sites was interpreted using an un-rooted (phylogenetic-type) tree (Fig. S3). Based on the branching observed, we have assigned the sites to three clusters: 'Arid' comprising Alice Mulga, Calperum Mallee and Great Western Woodlands; 'Temperate' comprising Cumberland Plain and Warra; 'Tropical' comprising Daintree and Robson Creek.

With the exception of Alice Mulga, each site was visited on two occasions. The timing of the visits was designed, within logistical constraints, to provide the widest possible seasonal contrast. The prevailing climate conditions leading up to each campaign are provided in Table S1 (Supporting Information). Each visit to a site was designated as either the 'Favourable' or 'Unfavourable' season based on a local assessment of growing conditions. Our study focused on the impact of seasonal contrasts (i.e. sub-annual) on leaf metabolic traits and so the monthly scale has been adopted here to present corresponding time-averaged climate conditions, on the basis that 30 days is likely to provide sufficient time for acclimation to occur within pre-existing leaves of long-lived broadleaved species (Zaragoza-Castells *et al.* 2008).

## Leaf gas exchange

The plants measured (407 individuals of 80 species, Table S6), were selected to include locally dominant species and to provide a wide range of leaf morphology. At each visit, we chose young, fully developed leaves from two sun exposed branches. Leaf gas exchange measurements were concentrated in the morning and performed using portable photosynthesis systems (Li-Cor 6400, Li-Cor, Lincoln, NE, USA), using a 6 cm<sup>2</sup> chamber fitted with a red-blue light source (Li-Cor 6400-02B LED, Li-Cor, Lincoln, NE, USA). Upper canopy branches were excised using forestry shears on telescopic poles and the cut end of the branches immediately placed in a bucket and then recut under water to re-establish the xylem water column (Domingues *et al.* 2010). Performing gas exchange measurements on excised branches can affect subsequent calculations where stomatal conductance is heavily depressed; our initial data exploration was designed to identify any such outliers. For each leaf, approximately light-saturated (1500  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) measurements of net photosynthesis were taken at ambient CO<sub>2</sub> concentration, 400  $\mu\text{mol mol}^{-1}$  (ppm) ( $A_{400}$ ). The leaf was next wrapped in aluminium foil for 30 minutes before  $R_{\text{dark}}$  was measured, still at 400 ppm CO<sub>2</sub>. Air flow was held constant and a constant chamber block temperature ( $T_{\text{Block}}$ ) was adopted for all measurements at a given site and season, set marginally (*ca.* 1°C) higher than expected morning air temperatures to counter the effect of transpirational cooling and to ensure leaf and ambient air temperatures were similar.  $T_{\text{Block}}$  settings ranged from 10°C for the winter visit to Warra to 32°C for the summer visit to Calperum, reflecting the wide range of air temperatures experienced. The Li-Cor 6400 system is capable of maintaining  $T_{\text{Block}}$  values  $\pm 6^\circ\text{C}$  from ambient and this operating constraint precluded measuring gas exchange at a common temperature across all sites and seasons. With a constant flow rate, chamber humidity conditions varied and mean vapour pressure deficits within the chamber ranged from 0.51 kPa for the winter visit to Warra to 3.16 kPa for the summer visit to Calperum, mirroring differences in ambient conditions across sites and seasons.

When assessing whether photosynthesis shows seasonal acclimation, concurrent seasonal changes in  $g_s$  might confound analysis - an important consideration in semi-arid zones. Unlike net photosynthesis,  $V_{\text{cmax}}$  (classically estimated as the slope of the  $A-C_i$  response curve in the initial CO<sub>2</sub> limited region) is theoretically independent of  $g_s$  (Farquhar & Sharkey 1982). In the absence of  $A-C_i$  response curves, we estimated  $V_{\text{cmax}}$  based on our light-saturated  $A_{400}$  values using the ‘one point method’, whose accuracy was established by de Kauwe *et al.* (2016). Mitochondrial respiration in the light ( $R_{\text{day}}$ ) was here assumed to be equivalent to  $R_{\text{dark}}$  (but this simplifying assumption has only a very minor effect on the estimation of  $V_{\text{cmax}}$ ). To allow comparisons of metabolic rates across sites and seasons, we calculated rates at both a standard

temperature (25°C) and at the prevailing air temperature for the 30-day period leading up to the end of each field campaign (Table S1). From the flux recorded at a given measurement temperature, normalised  $R_{\text{dark}}$  was calculated by applying a temperature-dependent  $Q_{10}$  function (Tjoelker, Oleksyn & Reich 2001). Normalised  $V_{\text{cmax}}$  was calculated from the original estimate by applying the Arrhenius function (Medlyn *et al.* 2002) assuming an activation energy of 64.8 kJ mol<sup>-1</sup> (Badger & Collatz 1977).

### Leaf morphology and nutrient determination

On completion of the gas exchange measurements leaves were weighed for fresh mass and scanned for leaf area before being dried in an oven at 70 °C for a minimum of 48 hours, after which their dry mass was recorded. The ratio of leaf dried mass to surface area ( $M_a$ , gm<sup>-2</sup>) allows interconversion between area- and mass-based leaf parameters. Oven-dried leaf material was used for determination of total concentrations of leaf N and P: dried ground leaf material was hot-digested in acid-peroxide before colorimetric analysis using a flow injection system (QuikChem 8500, Lachat Instruments, Loveland, Colorado, USA).

### Plasticity index and statistical analyses

A plasticity index (PI) ranging from 0 to 1 was calculated for each leaf trait and site as the absolute difference between the favourable and unfavourable seasonal means divided by the maximum trait value observed across all species (Zunzunegui *et al.* 2011). This index permits plasticity comparisons among traits recorded in different units and with variable ranges.

Our study design included repeat measurements of the same plants and so a mixed effects modelling approach was adopted to infer trait differences between seasons or among sites and site clusters (Pinheiro *et al.* 2012). The random intercept term adopted for such models was plant identity nested within species. Post-hoc differences were assigned using Tukey's Honest Significant Differences (HSD). To draw inferences from trait-trait plots, standardised major axis (SMA) analysis was used to determine the best-fitting lines ( $\alpha = 0.05$ ) (Warton *et al.* 2012). We also used linear mixed effects models to partition trait variation by adopting a structure that reflected the combination of crossed and partially nested factors in our sampling design. The dataset provided five hierarchical terms: season, site, site:season, species:site:season and plant\_number:species:site:season (here an interaction is denoted term1:term2). Mixed models adopting this structure as the random intercept term were fitted using restricted maximum likelihood estimation where the response variable was the trait in question and no predictor (fixed) variables were included. Any residual variation in the model was assigned between



branches within a given plant. All statistical analysis and modelling was performed using the open-source statistical environment R (R Development Core Team 2017) employing the packages: *dplyr*, *ggplot2*, *lme4* and *smatr*.

## Results

### Spatial differences at the plant community level

Differences between the site clusters were observed for traits of both leaf structure and chemistry.  $M_a$  was largest and most variable in the arid sites (Fig. 1) while the high leaf N:P ratios were all indicative of plant communities growing on relatively P-impooverished soils (Güsewell 2004). Overall, we found that trait values relating to leaf chemistry and construction were consistent with global patterns reported in the worldwide leaf economic spectrum (Wright *et al.* 2004) (Fig. S4).

### Metabolic acclimation to seasonal changes in temperature

Marked seasonal differences in mean leaf metabolic traits were observed for certain species, but the direction of change depended on whether rates were normalised to the prevailing temperature or to a common reference of 25°C (Fig. 2, Table S7). For species at non-tropical sites,  $V_{\text{cmax}}$  at the prevailing temperature was most frequently higher in summer than in winter. However, our expectation of faster metabolic rates at a common reference temperature in winter versus summer was not consistently borne out. At GWW, for example, only one species showed a significantly faster  $V_{\text{cmax},25}$  in winter. At Warra, where differences existed, the  $R_{\text{dark},25}$  rates were generally faster in summer (three of four cases; Fig. S5). Nonetheless, where seasonal mean values were statistically distinguishable (13 of 41 species), the trend at the non-tropical sites was for  $V_{\text{cmax}}$  at 25°C to be faster in winter than in summer, which is opposite to the pattern for  $V_{\text{cmax}}$  at the prevailing growth temperature. Clear seasonal patterns in leaf metabolic traits were not detectable at the tropical sites.

### Seasonal plasticity

The degree of seasonal plasticity observed across the sites was highly trait-specific. Seasonal plasticity in  $M_a$  and total  $N_{\text{area}}$  were broadly similar across all sites, but P contents per unit leaf area ( $P_{\text{area}}$ ) were much more plastic for the tropical compared with the arid sites (Fig. 3). For the leaf metabolic traits, normalised to 25°C, plasticity scores for individual species varied widely at many sites and this was especially true at Warra. Our plasticity index, by grouping species, is essentially a site measure that combines inter- and intraspecific variability. For a given trait, we

can attempt to unravel this by partitioning variation among successive hierarchical terms (see below).

### Seasonal and spatial flexibility in trait-trait relationships

We found extensive flexibility in the scale and direction of seasonal mean  $V_{\text{cmax}25}$  and  $R_{\text{dark}25}$  relationships with total  $N_{\text{area}}$  (Fig. 4). Whilst overall positive trends were observed for the tropical and temperate sites, there was wide variation among the species. Few consistent trends emerged: faster metabolic rates in a given season were not associated with concurrent changes in levels of  $N_{\text{area}}$ . Importantly, the patterns here did not support either of the hypothesised models of thermal acclimation (Fig. S1); i.e. separate relationships for the two seasons, or a shift along a perennial relationship driven by seasonal changes in  $N_{\text{area}}$ .

Our dataset included four species measured at two different sites (Fig. 5). These data were used to explore whether leaf trait-trait relationships altered under different environments. Here again the anticipated  $V_{\text{cmax},25} - N_{\text{area}}$  relationships proved weak, even when combining both sites and seasons for a given species (e.g. *Cryptocarya mackinnoniana*:  $r = 0.44$ ,  $p = 0.030$ ). Only in the case of *Cardwellia sublimis* did SMA analysis confirm different  $V_{\text{cmax},25} - N_{\text{area}}$  slopes at the two sites: steeper at Robson Creek (Likelihood ratio = 7.826,  $p = 0.005$ ); however, the small sample sizes meant that the regression line fits for the two sites lacked predictive power (e.g.  $r^2 = 0.27$ ,  $n = 12$ ,  $p = 0.083$  at Daintree). For *Acacia aneura*, faster levels of  $V_{\text{cmax}}$  for a given  $N_{\text{area}}$  at GWW compared to Alice Mulga suggest differences between the two sites in patterns of either leaf N allocation or the Rubisco activation state.

Given such wide variability in  $V_{\text{cmax},25} - N_{\text{area}}$  relationships for individual sites and species, we next attempted a multiple regression type model designed to predict values of  $V_{\text{cmax},25}$  at the site cluster level. Model performance was improved by inclusion of  $P_{\text{area}}$  as well as  $N_{\text{area}}$ , but not in interaction with site clusters i.e. the common positive relationship between foliar P and  $V_{\text{cmax},25}$  did not vary at these broad spatial scales (Table 2). There was limited support for retaining different  $V_{\text{cmax},25} - N_{\text{area}}$  slopes for the different clusters (steeper for the moist tropical forests), but in selecting a parsimonious model knowledge of  $P_{\text{area}}$  was a more valuable predictive term (compare models 6 and 7, Table 2). At this clustered site scale, differentiating between favourable and unfavourable seasons did not improve model performance.

### Partitioning trait variation

Under our schema (Fig. 6), ITV is composed of variation among branches, conspecific trees and between seasons (Branches + Trees + Seasons). After controlling for site and taxonomic effects,

seasonal variation accounted for less than 14% of total variation for traits related to leaf structure and chemistry, but 31% of variation in  $R_{\text{dark}}$  normalised to the prevailing air temperature. For  $M_a$  and  $N_{\text{area}}$ , a greater proportion of total variation was explained by inter-specific variation than ITV. For the metabolic traits and  $P_{\text{area}}$  the reverse was true and ITV was highest for  $R_{\text{dark}, 25}$  accounting for 69% of total variation. Variation partitioning for the metabolic traits depended, to some extent, on the temperature normalisation adopted: variation between seasons was much less pronounced when rates were normalised to a common reference of 25°C. Combined ITV, however, was broadly similar under the two approaches: e.g. 51% of total for  $V_{\text{cmax, Prevailing}}$  versus 46% for  $V_{\text{cmax}, 25}$ .

## Discussion

### *The relative importance of intraspecific trait variation*

The timing of our repeat field visits was designed to provide pronounced seasonal contrasts in growing conditions. Our leaf trait seasonal plasticity (PI) scores appeared low, however, against a comparable index reported for seedlings of 16 congeneric shrubs native to the Panamanian rainforest: mean PI scores of 0.41 for  $M_a$ , 0.59 for photosynthetic capacity and 0.61 for  $R_{\text{dark}}$  (Valladares *et al.* 2000). Our combined PI (mean of the five individual leaf traits, Fig. 3a) ran from a low (0.09-0.10) at the arid sites of GWW and Calperum to a high (0.23) at Warra; a ranking that broadly coincides with gradients of increasing LAI and canopy stature, suggesting that leaf seasonal plasticity for these communities may be driven by radiation differences mediated through LAI and the more diverse light environments created by taller stands (Rozendaal, Hurtado & Poorter 2006). For a given trait, our site PI scores reflected underlying diversity (the number of species included ranged from 8 at GWW to 16 at Daintree) and emphasised community composition rather than the characteristics of dominant species. We next consider ITV whilst controlling for species biodiversity.

The design of our variance partitioning model (although unable to account fully for variation between populations) allowed us to attribute trait variation to discrete ITV components whilst controlling for spatial and taxonomic terms. Consistent with earlier studies (e.g. Albert *et al.* 2010), we found that the pattern of variance partitioning changed from trait to trait. To our surprise, seasonal differences (greatest for  $R_{\text{dark, Prevailing}}$  at 31%) had little explanatory power for three of the five traits considered here:  $M_a$ ,  $N_{\text{area}}$  and  $P_{\text{area}}$ . In a recent study of leaf trait variation in 12 woody species in Chile, Fajardo & Siefert (2016) also found that the partitioning of variation was highly trait specific and that interspecific variation was much higher than temporal

ITV for  $M_a$ . For species with long-lived leaves that must still contend with seasonal changes in the growing environment, relatively fixed traits of morphology and chemistry may necessitate greater variability within the metabolic traits like photosynthesis and respiration.

Across our sites, inter-specific variation was highest for  $N_{\text{area}}$  (43% of total) and this may reflect the range of N fixation capabilities exhibited by Australian flora (Sprent, Ardley & James 2017) – a trait influenced in turn by soil P conditions (Houlton *et al.* 2008). The dominance of phylogenetic variation (32.8%) over site (26.4%) for  $P_{\text{area}}$  is surprising given the closed nature of the P-cycle, and converse findings in the Amazon (Fyllas *et al.* 2009). It may be that plant-available soil P is so low across much of Australia (Kooyman, Laffan & Westoby 2017) that genetic adaptations have been necessary for the viability of a great many species (e.g. Sulpice *et al.* 2014).

In a meta-analysis of variation in plant communities, Siefert *et al.* (2015) reported typical ITV proportions at 25% of total: with higher ITV for chemical than morphological traits, but with ITV less than interspecific variation in all cases. Whilst there are important differences between our analysis and the Siefert *et al.* study (which did not include leaf metabolic traits, seasonal contrasts, or attempt to distinguish the sources of ITV), our results provide partial confirmation with ITV greater for  $N_{\text{area}}$  (18%) than for  $M_a$  (12%) and ITV less than interspecific variation for both those traits. Refuting our hypothesis, we found that ITV outweighed interspecific variation for  $R_{\text{dark}}$ ,  $V_{\text{cmax}}$  and  $P_{\text{area}}$ ; this was true whether metabolic rates were normalised to the prevailing temperature or to a common reference temperature. For the metabolic traits, levels of variation within individual plants (18% for  $V_{\text{cmax Prevailing}}$  and 20% for  $R_{\text{dark Prevailing}}$ ) were lower than reported in a recent study in coffee crops which found that variation among leaves within an individual branch accounted for approximately 25% of total variation in light saturated photosynthesis (Martin *et al.* 2016). Overall, our results indicate that ITV can be an important, even dominant, component of leaf trait variation, especially for metabolic processes. Our field study of mature plants provided an opportunity to assess how far leaves that experience both favourable and unfavourable growing conditions acclimate their physiology to seasonal changes in the environment.

### *Thermal acclimation of leaf metabolism*

Compelling evidence for seasonal acclimation in leaf metabolic traits will require modification to the standard temperature responses implemented in DGVMs (Smith & Dukes 2013; Huntingford *et al.* 2017). In a study of juvenile trees of ten species native to temperate and boreal forests in North America, Reich *et al.* (2016) found that for both forest types seasonal

acclimation (late spring vs. summer vs. early autumn) offset anticipated increases in leaf  $R_{\text{dark}}$  of non-acclimated plants by as much as 80%. Plant or leaf developmental stage might be an important consideration here since previous studies have demonstrated that thermal acclimation is more fully achieved by newly developed (e.g. ‘cold grown’) rather than pre-existing plant tissue (e.g. Hurry *et al.* 1995). It has been shown, however, that fully-expanded, long-lived leaves can show a high degree of thermal acclimation over timescales of weeks to months (Campbell *et al.* 2007). Indeed, the ability to acclimate might be particularly important at sites dominated by species with long-lived leaves where there may be little benefit in producing leaves tailored to transient seasonal climatic conditions (Kitajima, Mulkey & Wright 1997).

At sites other than the tropical forests, we found that metabolic rates normalised to the prevailing growing temperature were not homeostatic and, where seasonal differences emerged (the majority of species), rates were always faster in summer than in winter. A different picture emerged when those same rates were normalised to a common reference temperature of 25°C; in this case many fewer species exhibited seasonal differences (only 13 of the 41 species), but for those that did (with a single exception) rates of  $V_{\text{cmax},25}$  were faster in winter than summer. Our hypothesis of faster 25°C-standardised rates in the cooler season was not universally supported, however; for species at Warra, for example, normalised rates of  $R_{\text{dark}}$  were either unchanged or faster in summer than in winter, suggesting that seasonality in metabolic rates can respond to signals other than temperature.

In a recent study that explored leaf trait coordination and optimisation, Dong *et al.* (2017) tested the predictability of  $N_{\text{area}}$  across sites and species using explanatory factors that included  $M_a$ , the ratio of intercellular to ambient  $\text{CO}_2$  and environmental variables of irradiance and MAT. The authors argue that whereas both  $V_{\text{cmax},25}$  and  $N_{\text{area}}$  allocated to photosynthetic machinery should decrease with increasing growth temperature,  $V_{\text{cmax}}$  assessed at growth temperature should increase with increasing growth temperature (albeit less steeply than would be predicted simply from enzyme kinetics). The study of Dong *et al.* also found that major patterns of variation observed in  $N_{\text{area}}$  could be accounted for if both an optimised metabolic component and a structural component proportional to  $M_a$  were combined. Our results extend the analysis of Dong *et al.* to seasonal variations and support the general idea, embodied in the widely used Lund-Potsdam-Jena (LPJ) DGVM (e.g. Sitch *et al.* 2003), that variation in  $V_{\text{cmax}}$  across species and sites may be adaptive.

### Seasonal effects on trait-trait relationships

Our results showed that the seasonal effect on individual leaf traits was species-dependent, with site (or community) based trait-trait relationships showing no consistent seasonal patterns. Anticipated relationships between key metabolic traits and total  $N_{\text{area}}$  were unconvincing (Fig. 4) while the lack of a uniform seasonal signal appears consistent with earlier studies that have reported a relatively minor role for climate in influencing leaf trait relationships. Wright *et al.* (2004) and Reich *et al.* (2007), for example, found that including climate variables within multiple regression models improved trait prediction by less than 15%.

Why were the leaf trait-trait relationships observed in our study so weak? One possibility is that our site-based analyses (e.g. Fig. 4) are at too fine a spatial scale to conform to a worldwide leaf economic spectrum (Messier *et al.* 2017). Yet the site with the broadest range in species-averaged values of  $N_{\text{area}}$  in our dataset (Alice Mulga: 2.7 to 7.2 g m<sup>-2</sup>) provided approximately half the coverage reported in Glopnet (0.3 to 9.1 g m<sup>-2</sup>) (Wright *et al.* 2004); and extending our analysis to include all seven sites did not reveal an underlying relationship for species-averaged values of  $V_{\text{cmax},25}$  -  $N_{\text{area}}$  ( $r = 0.20$ ,  $p=0.07$ ; data not shown). Broad variability in  $A$ - $N$  relationships has been widely reported (e.g. Evans 1989) and interspecific variability in photosynthetic N use efficiency will be influenced by environmental conditions such as light and nutrient availability manifested through physiological mechanisms including CO<sub>2</sub> diffusion, light interception and enzyme kinetics (Hikosaka 2004). Allocation of N within the leaf is likely to play a crucial role and whilst available data lend support to an hypothesised trade-off between photosynthetic capacity and longevity, up to half of leaf N may be invested in pools other than the proteins associated with photosynthesis and cell walls (Onoda *et al.* 2017). We infer that the premise of a universal relationship linking leaf N content to photosynthetic capacity is questionable. For tropical systems in particular, P has been invoked as an important co-limiting factor for rates of photosynthesis (Domingues *et al.* 2010) and the same constraint is likely to apply over much of Australia. But despite uniformly high foliar N:P ratios across our study sites, we did not find support for the notion that foliar P content influences the slope of the  $A$ - $N$  relationship (cf Kattge *et al.* 2009; Reich, Oleksyn & Wright 2009). The N:P ratio is itself a plastic trait and provides only an approximate measure of relative ‘limitation’ – due, for example, to storage of P in the vacuole. Irrespective of stoichiometry, leaf metabolism is heavily dependent on N-rich proteins, but equations that ignore environmentally or phylogenetically mediated variations in trait-trait relationships may have limited predictive power (Adams *et al.* 2016).

A more fruitful approach for DGVMs would be to avoid prescribing the values of photosynthetic traits for a given PFT or biome and instead allow these traits to vary adaptively in time and space. This alternative approach has a long history since Haxeltine & Prentice (1996) and Dewar (1996) first noted the existence of an optimal photosynthetic capacity for any given growth temperature and light environment (see also Hirose & Werger 1987). This optimality assumption underlies the LPJ model and its successors. Further empirical research is required to quantitatively evaluate such optimality hypotheses across different biomes and climates.

## Conclusion

The aim of our study was to explore seasonal and spatial drivers of intraspecific leaf trait variation and how seasonal changes across environmental gradients might affect trait-trait relationships that are incorporated in many current DGVMs. Most species at the non-tropical sites showed faster metabolic rates in summer than in winter, but variable responses amongst co-occurring species and differing degrees of plasticity for selected traits frustrated attempts to find clear seasonal differentiation in leaf trait-trait relationships. These results question the common practice in DGVMs of assigning constant trait values to PFTs or assuming fixed trait-trait relationships (e.g. between  $V_{\text{cmax}}$  and  $N_{\text{area}}$ ). Instead, our results support the idea that metabolic traits vary within species through acclimation in both space and time. This is a key point for the design of trait-based DGVMs, with important implications for modelling species' responses to a changing environment.

## Acknowledgments

We would like to thank Alex Cheesman and Georg Wiehl for logistical support in the field, Jared Streich and Ian Marang for their help with analysis of the climate variables and Teresa Neeman for advice on statistical techniques. This work would not have been possible without the support and collaboration of facilities within the Australian Government's Terrestrial Ecosystem Research Network ([www.tern.org.au](http://www.tern.org.au)): the SuperSite network, the OzFlux network and the eMAST facility. The project was made possible, in part, by a TERN Supplemental Grant to ICP and OKA. The support of the Australian Research Council to OKA (DP130101252 and CE140100008) and DE (DP140101150) is acknowledged. HFT was supported by a Macquarie University International Research Scholarship (iMQRES). KJB was hosted by the University of Exeter during the writing of this manuscript.

## Data accessibility

The data are freely available on the TERN SuperSites portal. ([www.supersites.net.au/knb](http://www.supersites.net.au/knb)).



## References

- Adams, M.A., Turnbull, T.L., Sprent, J.I. & Buchmann, N. (2016) Legumes are different: Leaf nitrogen, photosynthesis, and water use efficiency. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, 4098-4103.
- Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G. & Violle, C. (2011) When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology Evolution and Systematics*, **13**, 217-225.
- Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P. & Lavorel, S. (2010) Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, **98**, 604-613.
- Atkin, O.K., Atkinson, L.J., Fisher, R.A., Campbell, C.D., Zaragoza-Castells, J., Pitchford, J.W., Woodward, F.I. & Hurry, V. (2008) Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate-vegetation model. *Global Change Biology*, **14**, 2709-2726.
- Atkin, O.K., Holly, C. & Ball, M.C. (2000) Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. *Plant Cell and Environment*, **23**, 15-26.
- Badger, M.R. & Collatz, G.J. (1977) Studies on the kinetic mechanism of ribulose-1, 5-bisphosphate carboxylase and oxygenase reactions, with particular reference to the effect of temperature on kinetic parameters. *Carnegie Institute of Washington Yearbook*, **76**, 355-361.
- Beadle, N.C.W. (1962) Soil phosphate and delimitation of plant communities in Eastern Australia II. *Ecology*, **43**, 281-288.
- Beringer, J., Hutley, L.B., McHugh, I., Arndt, S.K., Campbell, D., Cleugh, H.A., Cleverly, J., Resco de Dios, V., Eamus, D., Evans, B., Ewenz, C., Grace, P., Griebel, A., Haverd, V., Hinko-Najera, N., Huete, A., Isaac, P., Kanniah, K., Leuning, R., Liddell, M.J., Macfarlane, C., Meyer, W., Moore, C., Pendall, E., Phillips, A., Phillips, R.L., Prober, S., Restrepo-Coupe, N., Rutledge, S., Schroder, I., Silberstein, R., Southall, P., Sun, M., Tapper, N.J., van Gorsel, E., Vote, C., Walker, J. & Wardlaw, T. (2016) An introduction to the Australian and New Zealand flux tower network - OzFlux. *Biogeosciences Discuss.*, **2016**, 1-52.
- Campbell, C., Atkinson, L., Zaragoza-Castells, J., Lundmark, M., Atkin, O. & Hurry, V. (2007) Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. *New Phytologist*, **176**, 375-389.
- Carlucci, M.B., Debastiani, V.J., Pillar, V.D. & Duarte, L.D.S. (2015) Between- and within-species trait variability and the assembly of sapling communities in forest patches. *Journal of Vegetation Science*, **26**, 21-31.
- De Kauwe, M.G., Lin, Y.S., Wright, I.J., Medlyn, B.E., Crous, K.Y., Ellsworth, D.S., Maire, V., Prentice, I.C., Atkin, O.K., Rogers, A., Niinemets, U., Serbin, S.P., Meir, P., Uddling, J., Togashi, H.F., Tarvainen, L., Weerasinghe, L.K., Evans, B.J., Ishida, F.Y. & Domingues, T.F. (2016) A test of the 'one-point method' for estimating maximum carboxylation capacity from field-measured, light-saturated photosynthesis. *New Phytologist*, **210**, 1130-1144.
- Dewar, R.C. (1996) The correlation between plant growth and intercepted radiation: An interpretation in terms of optimal plant nitrogen content. *Annals of Botany*, **78**, 125-136.
- Domingues, T.F., Meir, P., Feldpausch, T.R., Saiz, G., Veenendaal, E.M., Schrodte, F., Bird, M., Djagbletey, G., Hien, F., Compaore, H., Diallo, A., Grace, J. & Lloyd, J. (2010) Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. *Plant Cell and Environment*, **33**, 959-980.

- Dong, N., Prentice, I.C., Evans, B.J., Caddy-Retalic, S., Lowe, A.J. & Wright, I.J. (2017) Leaf nitrogen from first principles: field evidence for adaptive variation with climate. *Biogeosciences*, **14**, 481-495.
- Eamus, D., Myers, B., Duff, G. & Williams, D. (1999) Seasonal changes in photosynthesis of eight savanna tree species. *Tree Physiology*, **19**, 665-671.
- Evans, J.R. (1989) Photosynthesis and nitrogen relationships in leaves of C<sub>3</sub> plants. *Oecologia*, **78**, 9-19.
- Fajardo, A. & Siefert, A. (2016) Phenological variation of leaf functional traits within species. *Oecologia*, **180**, 951-959.
- Farquhar, G.D. & Sharkey, T.D. (1982) Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, **33**, 317-345.
- Farquhar, G.D., von Caemmerer, S. & Berry, J.A. (1980) A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta*, **149**, 78-90.
- Fyllas, N.M., Patino, S., Baker, T.R., Nardoto, G.B., Martinelli, L.A., Quesada, C.A., Paiva, R., Schwarz, M., Horna, V., Mercado, L.M., Santos, A., Arroyo, L., Jimenez, E.M., Luizao, F.J., Neill, D.A., Silva, N., Prieto, A., Rudas, A., Silveira, M., Vieira, I.C.G., Lopez-Gonzalez, G., Malhi, Y., Phillips, O.L. & Lloyd, J. (2009) Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences*, **6**, 2677-2708.
- Güsewell, S. (2004) N : P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, **164**, 243-266.
- Haxeltine, A. & Prentice, I.C. (1996) A general model for the light-use efficiency of primary production. *Functional Ecology*, **10**, 551-561.
- Hikosaka, K. (2004) Interspecific difference in the photosynthesis-nitrogen relationship: patterns, physiological causes, and ecological importance. *Journal of Plant Research*, **117**, 481-494.
- Hirose, T. & Werger, M.J.A. (1987) Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia*, **72**, 520-526.
- Houlton, B.Z., Wang, Y.P., Vitousek, P.M. & Field, C.B. (2008) A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature*, **454**, 327-U334.
- Huntingford, C., Atkin, O.K., Martinez-de la Torre, A., Mercado, L.M., Heskell, M.A., Harper, A.B., Bloomfield, K.J., O'Sullivan, O.S., Reich, P.B., Wythers, K.R., Butler, E.E., Chen, M., Griffin, K.L., Meir, P., Tjoelker, M.G., Turnbull, M.H., Sitch, S., Wiltshire, A. & Malhi, Y. (2017) Implications of improved representations of plant respiration in a changing climate. *Nature Communications*, **8**.
- Hurry, V., Tobiaeson, M., Kromer, S., Gardestrom, P. & Oquist, G. (1995) Mitochondria contribute to increased photosynthetic capacity of leaves of winter rye (*Secale-Cereale* L.) following cold-hardening. *Plant Cell and Environment*, **18**, 69-76.
- Hutchinson, M.F., McKenney, D.W., Lawrence, K., Pedlar, J.H., Hopkinson, R.F., Milewska, E. & Papadopol, P. (2009) Development and testing of Canada-wide interpolated spatial models of daily minimum-maximum temperature and precipitation for 1961-2003. *Journal of Applied Meteorology and Climatology*, **48**, 725-741.
- Jung, V., Albert, C.H., Violle, C., Kunstler, G., Loucougaray, G. & Spiegelberger, T. (2014) Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology*, **102**, 45-53.
- Karan, M., Liddell, M., Prober, S.M., Arndt, S., Beringer, J., Boer, M., Cleverly, J., Eamus, D., Grace, P., Van Gorsel, E., Hero, J.M., Hutley, L., Macfarlane, C., Metcalfe, D., Meyer, W., Pendall, E., Sebastian, A. & Wardlaw, T. (2016) The Australian SuperSite Network: A continental, long-term terrestrial ecosystem observatory. *Science of the Total Environment*, **568**, 1263-1274.
- Kattge, J., Diaz, S., Lavorel, S., Prentice, C., Leadley, P., Bonisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., van Bodegom,

- P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernandez-Mendez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kuhn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusia, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Muller, S.C., Nadrowski, K., Naeem, S., Niinemets, U., Nollert, S., Nuske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordonez, J., Overbeck, G., Ozinga, W.A., Patino, S., Paula, S., Pausas, J.G., Penuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negre, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E. & Wirth, C. (2011) TRY - a global database of plant traits. *Global Change Biology*, **17**, 2905-2935.
- Kattge, J. & Knorr, W. (2007) Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. *Plant Cell and Environment*, **30**, 1176-1190.
- Kattge, J., Knorr, W., Raddatz, T. & Wirth, C. (2009) Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology*, **15**, 976-991.
- Kitajima, K., Mulkey, S.S. & Wright, S.J. (1997) Seasonal leaf phenotypes in the canopy of a tropical dry forest: Photosynthetic characteristics and associated traits. *Oecologia*, **109**, 490-498.
- Kooyman, R.M., Laffan, S.W. & Westoby, M. (2017) The incidence of low phosphorus soils in Australia. *Plant and Soil*, **412**, 143-150.
- Lin, Y.S., Medlyn, B.E., De Kauwe, M.G. & Ellsworth, D.S. (2013) Biochemical photosynthetic responses to temperature: how do interspecific differences compare with seasonal shifts? *Tree Physiology*, **33**, 793-806.
- Martin, A.R., Rapidel, B., Roupsard, O., Van den Meersche, K., de M. Virginio Filho, E., Barrios, M. & Isaac, M.E. (2016) Intraspecific trait variation across multiple scales: the leaf economics spectrum in coffee. *Functional Ecology*, n/a-n/a.
- Medlyn, B.E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P.C., Kirschbaum, M.U.F., Le Roux, X., Montpied, P., Strassmeyer, J., Walcroft, A., Wang, K. & Loustau, D. (2002) Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant Cell and Environment*, **25**, 1167-1179.
- Messier, J., McGill, B.J., Enquist, B.J. & Lechowicz, M.J. (2017) Trait variation and integration across scales: is the leaf economic spectrum present at local scales? *Ecography*, **40**, 685-697.
- Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838-848.
- Misson, L., Tu, K.P., Boniello, R.A. & Goldstein, A.H. (2006) Seasonality of photosynthetic parameters in a multi-specific and vertically complex forest ecosystem in the Sierra Nevada of California. *Tree Physiology*, **26**, 729-741.
- Onoda, Y., Wright, I.J., Evans, J.R., Hikosaka, K., Kitajima, K., Niinemets, U., Poorter, H., Tosens, T. & Westoby, M. (2017) Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytologist*, **214**, 1447-1463.

- Pavlick, R., Drewry, D.T., Bohn, K., Reu, B. & Kleidon, A. (2013) The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. *Biogeosciences*, **10**, 4137-4177.
- Pinheiro, J., Bates, D., Debroy, S., Sarkar, D. & R Development Core Team (2012) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-105.
- Prentice, I.C. & Cowling, S.A. (2013) Dynamic global vegetation models. *Encyclopedia of Biodiversity* (ed. S.A. Levin), pp. 670-689. Academic Press, Waltham, MA, USA.
- Prentice, I.C., Dong, N., Gleason, S.M., Maire, V. & Wright, I.J. (2014) Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology. *Ecology Letters*, **17**, 82-91.
- Prior, L.D., Eamus, D. & Duff, G.A. (1997) Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetradonta* saplings in a wet-dry savanna in northern Australia. *Australian Journal of Botany*, **45**, 241-258.
- R Development Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reich, P.B., Oleksyn, J. & Wright, I.J. (2009) Leaf phosphorus influences the photosynthesis-nitrogen relation: a cross-biome analysis of 314 species. *Oecologia*, **160**, 207-212.
- Reich, P.B., Sendall, K.M., Stefanski, A., Wei, X.R., Rich, R.L. & Montgomery, R.A. (2016) Boreal and temperate trees show strong acclimation of respiration to warming. *Nature*, **531**, 633-+.
- Reich, P.B., Wright, I.J. & Lusk, C.H. (2007) Predicting leaf physiology from simple plant and climate attributes: A global GLOPNET analysis. *Ecological Applications*, **17**, 1982-1988.
- Restrepo-Coupe, N., Levine, N.M., Christoffersen, B.O., Albert, L.P., Wu, J., Costa, M.H., Galbraith, D., Imbuzeiro, H., Martins, G., da Araujo, A.C., Malhi, Y.S., Zeng, X., Moorcroft, P. & Saleska, S.R. (2017) Do dynamic global vegetation models capture the seasonality of carbon fluxes in the Amazon basin? A data-model intercomparison. *Global Change Biology*, **23**, 191-208.
- Rozendaal, D.M.A., Hurtado, V.H. & Poorter, L. (2006) Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology*, **20**, 207-216.
- Scheiter, S., Langan, L. & Higgins, S.I. (2013) Next-generation dynamic global vegetation models: learning from community ecology. *New Phytologist*, **198**, 957-969.
- Schulze, E.D., Turner, N.C., Nicolle, D. & Schumacher, J. (2006) Leaf and wood carbon isotope ratios, specific leaf areas and wood growth of Eucalyptus species across a rainfall gradient in Australia. *Tree Physiology*, **26**, 479-492.
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W., Baraloto, C., Carlucci, M.B., Cianciaruso, M.V., Dantas, V.D., de Bello, F., Duarte, L.D.S., Fonseca, C.R., Freschet, G.T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V., Kamiyama, C., Katabuchi, M., Kembel, S.W., Kichenin, E., Kraft, N.J.B., Lagerstrom, A., Le Bagousse-Pinguet, Y., Li, Y.Z., Mason, N., Messier, J., Nakashizuka, T., McC Overton, J., Peltzer, D.A., Perez-Ramos, I.M., Pillar, V.D., Prentice, H.C., Richardson, S., Sasaki, T., Schamp, B.S., Schob, C., Shipley, B., Sundqvist, M., Sykes, M.T., Vandewalle, M. & Wardle, D.A. (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, **18**, 1406-1419.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K. & Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161-185.
- Smith, N.G. & Dukes, J.S. (2013) Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO<sub>2</sub>. *Global Change Biology*, **19**, 45-63.

- Sprent, J.I., Ardley, J. & James, E.K. (2017) Biogeography of nodulated legumes and their nitrogen-fixing symbionts. *New Phytologist*, **215**, 40-56.
- Sulpice, R., Ishihara, H., Schlereth, A., Cawthray, G.R., Encke, B., Giavalisco, P., Ivakov, A., Arrivault, S., Jost, R., Krohn, N., Kuo, J., Laliberté, E., Pearse, S.J., Raven, J.A., Scheible, W.R., Teste, F., Veneklaas, E.J., Stitt, M. & Lambers, H. (2014) Low levels of ribosomal RNA partly account for the very high photosynthetic phosphorus-use efficiency of Proteaceae species. *Plant Cell and Environment*, **37**, 1276-1298.
- Tjoelker, M.G., Oleksyn, J. & Reich, P.B. (2001) Modelling respiration of vegetation: evidence for a general temperature-dependent Q(10). *Global Change Biology*, **7**, 223-230.
- Valladares, F., Wright, S.J., Lasso, E., Kitajima, K. & Pearcy, R.W. (2000) Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology*, **81**, 1925-1936.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, **27**, 244-252.
- Warton, D.I., Duursma, R.A., Falster, D.S. & Taskinen, S. (2012) smatr 3-an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, **3**, 257-259.
- Way, D.A. & Yamori, W. (2014) Thermal acclimation of photosynthesis: on the importance of adjusting our definitions and accounting for thermal acclimation of respiration. *Photosynthesis Research*, **119**, 89-100.
- Wright, I.J., Reich, P.B. & Westoby, M. (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, **15**, 423-434.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821-827.
- Zaragoza-Castells, J., Sanchez-Gomez, D., Hartley, I.P., Matesanz, S., Valladares, F., Lloyd, J. & Atkin, O.K. (2008) Climate-dependent variations in leaf respiration in a dry-land, low productivity Mediterranean forest: the importance of acclimation in both high-light and shaded habitats. *Functional Ecology*, **22**, 172-184.
- Zunzunegui, M., Barradas, M.C.D., Ain-Lhout, F., Alvarez-Cansino, L., Esquivias, M.P. & Novo, F.G. (2011) Seasonal physiological plasticity and recovery capacity after summer stress in Mediterranean scrub communities. *Plant Ecology*, **212**, 127-142.

## Supporting information

Additional Supporting information may be found in the online version of this article:

Fig. S1. Conceptual diagram for a leaf trait-trait relationship of two possible thermal acclimation responses to seasonal variation

Fig. S2. Australian map with location and key climate indicators for each of the study sites

Fig. S3. Unrooted (phylogenetic-type) tree of the study sites based on spatial analysis using bioclimatic indices

Fig. S4. Three-way scatterplot showing the associations between total leaf phosphorus concentration, leaf mass per unit area and total leaf nitrogen concentration.

Fig. S5 Two-way interaction plots (Season : Species) contrasting dark respiration per unit leaf area normalised to the prevailing air temperature and to a common reference temperature of 25°C.

Table S1. Climate conditions for each fieldwork campaign

Table S2. Leaf traits by site, averaged across both seasons and all species

Table S3. Photosynthetic parameters by site, averaged across both seasons and all species

Table S4. Leaf traits by site and season, averaged across all species

Table S5. Photosynthetic parameters by site and season, averaged across all species

Table S6. Leaf traits by site and season and species

Table S7. Photosynthetic parameters by site and season and species

## TABLES

Table 1 Site location and descriptors. The sites are listed in order of latitude. An Australian map with the site locations indicated is included in Supporting Information (Fig. S2). Leaf traits of nitrogen, phosphorus and dried leaf mass per unit area ( $M_a$ ) are averaged across all species and both seasons (Table S2, Supporting Information). Leaf area index is the ratio of leaf to ground surface area. Climate indices are annual long-term averages of interpolated data obtained from the TERN eMAST website ([www.emast.org.au](http://www.emast.org.au)). Moisture index is shown as the ratio of precipitation to potential evapotranspiration. Additional details for each site may be found on the TERN SuperSites website ([www.supersites.net.au](http://www.supersites.net.au)).

Site	Lat	Long	Biome	Vegetation	Leaf area	Canopy	Leaf N	Leaf P	$M_a$	Soil type	Soil texture	MAT	Annual	Moisture
					index	height							Precip	index
					ratio	m							mm	ratio
Daintree	16.103	145.447	Tropical moist forest	Closed forest	2.65	25.0	2.34	92.5	118.5	Acidic, dystrophic, brown Dermosol	37 : 36 : 27	24.3	3,671	3.36
Robson Creek	17.117	145.630	Tropical moist forest	Closed forest	3.19	28.0	1.82	94.7	110.8	Acidic, dystrophic, brown Dermosol	61 : 09 : 30	20.4	1,813	1.65
Alice Mulga	22.400	133.250	Tropical savanna	Low, open, arid woodland	0.34	6.5	4.48	206.6	252.2	Eutrophic, red Kandosol	74 : 11 : 15	22.5	357	0.22
Great Western Woodlands	30.191	120.654	Mediterranean woodland	Semi-arid woodland	1.07	18.0	4.70	154.8	256.0	Kandosol	51 : 17 : 32	18.9	291	0.31
Cumberland Plain	33.619	150.738	Temperate forest	Dry woodland	1.20	23.0	2.71	94.8	171.9	Grey podsol	33 : 47 : 20	17.7	788	0.83
Calperum Mallee	34.003	140.588	Mediterranean woodland	Sparse, mallee woodland	0.88	3.0	3.21	144.6	258.3	Tenosol (Calcisol)	90 : 01 : 09	17.4	268	0.32
Warra	43.095	146.654	Temperate forest	Tall, wet forest	5.84	55.0	2.07	78.2	133.5	Kurosolic, redoxic Hydrosol	24 : 48 : 28	9.8	1,591	4.41

Table 2 Stepwise selection of explanatory terms in a multiple regression type model with carboxylation capacity ( $V_{\text{cmax } 25}$ ) as the response variable. Explanatory terms are site cluster, levels of nitrogen and phosphorus expressed per unit leaf area and season. Interaction between two terms is denoted  $:$ . The effect of dropping sequential terms was tested by comparing the nested model variants. Model variants were all run using the maximum likelihood method; the model's random component was identical in all variants (plant id nested in species). Test parameters and statistics are  $df$ , degrees of freedom; AIC, Akaike information criteria; BIC, Bayesian information criteria; logLik, maximum likelihood; the likelihood ratio statistic and associated probability,  $p$  value.

Model	Explanatory terms	$df$	AIC	BIC	logLik	Test	$L$ ratio	$p$ value
1	Cluster : $N_{\text{area}}$ : $P_{\text{area}}$	15	8,710.4	8,784.2	-4340.2			
2	Cluster : $N_{\text{area}}$ + Cluster : $P_{\text{area}}$ + $N_{\text{area}}$ : $P_{\text{area}}$	13	8,706.5	8,770.5	-4340.3	1 vs 2	0.16	0.9254
3	Cluster : $N_{\text{area}}$ + Cluster : $P_{\text{area}}$	12	8,706.0	8,765.0	-4341.0	2 vs 3	1.49	0.2223
4	Cluster : $N_{\text{area}}$ + $P_{\text{area}}$	10	8,707.6	8,756.8	-4343.8	3 vs 4	5.60	0.0608
5	Cluster : $N_{\text{area}}$ + $P_{\text{area}}$ + Season	11	8,708.3	8,762.4	-4343.1	4 vs 5	1.35	0.2449
6	Cluster + $N_{\text{area}}$ + $P_{\text{area}}$	8	8,709.9	8,749.3	-4347.0	4 vs 6	6.31	0.0427
7	Cluster : $N_{\text{area}}$	9	8,716.3	8,760.6	-4349.2	4 vs 7	10.72	0.0011



## Figure captions

Fig. 1 Box plots by site cluster for leaf mass per unit area ( $M_a$ , plot a) and the ratio of total leaf nitrogen to phosphorus (plot b). Boxes indicate the interquartile range and median values. Whiskers extend to the largest or smallest observations that fall within 1.5 times the box size; any observations outside these values are shown as individual points. Boxes which share the same letter correspond to cluster mean trait values that were not significantly different (Tukey's HSD). The dashed horizontal line in Fig. 1b shows the N:P ratio of 20 and indicates a threshold above which conditions may be considered phosphorus limited (Güsewell 2004).

Fig. 2 Two-way interaction plots (Season : Species) for species' mean estimates of maximal carboxylation capacity per unit leaf area normalised to: the prevailing air temperature at the time of the measurement campaign (Table S1) ( $V_{\text{cmax Prevaling}}$ , top panel) and to a common reference temperature of 25°C ( $V_{\text{cmax 25}}$ , bottom panel). Paired plots are shown for each of the sites (Alice Mulga is not included because only a single visit was made to that site). Individual species for a given site, ranked in alphabetical order, are labelled numerically (0 through 9) and then with letters (a, b, c etc.). Trace lines connecting the two seasonal means for a given species are only shown where the seasonal means were significantly different. Site\_Season\_Species mean trait values are shown in Table S7, Supporting Information. Notice that axes ranges vary to accommodate seasonal temperature variability from site to site.

Fig. 3 Community-level leaf trait plasticity by site (Calperum CAL; Great Western Woodlands GWW; Cumberland Plain CBLP; Warra WAR; Robson Creek RCR; Daintree DRO; Alice Mulga is not included because only a single visit was made to that site). For a given trait, the Site\_Species Plasticity Index (PI) is calculated as the absolute index of the difference between favourable and unfavourable seasonal means divided by the maximum trait value observed. The box and whiskers plots show the range of individual species' PIs at a given site; the number of species included for each site is indicated above the boxes in panel (a). Separate panels are shown for (b) leaf mass per unit area ( $M_a$ ); (c) total nitrogen content per unit leaf area ( $N_{\text{area}}$ ); (d) total phosphorus content per unit leaf area ( $P_{\text{area}}$ ); (e) maximal rate of carboxylation per unit leaf area and normalised to a common reference temperature of 25°C ( $V_{\text{cmax 25}}$ ); (f) leaf dark respiration per unit leaf area and normalised to 25°C ( $R_{\text{dark 25}}$ ) and (a) a combined index for each Site\_Species taken as the mean of the five trait PIs. Boxplot construction is explained in Fig. 1. Boxes which share the same letter correspond to site mean indices that were not significantly different (Tukey's HSD); the six sites showed comparable levels of plasticity for  $M_a$  and  $N_{\text{area}}$ .

Fig. 4 Flexibility in leaf trait-trait relationships: scatterplots of maximal carboxylation capacity ( $V_{\text{cmax 25}}$ , left hand panels) and dark respiration ( $R_{\text{cmax 25}}$ , right hand panels), both rates expressed per unit leaf area and normalised to a common reference temperature of 25°C and each plotted against leaf Nitrogen per unit area. Paired plots are shown for one site from each of the three spatial clusters: Daintree (Tropical, plots a and b); Great Western Woodlands (Arid, plots c and d) and Warra (Temperate, plots e and f). Each point represents a species average ( $n \sim 5$ ) for distinct seasons: red for favourable and blue for unfavourable. The blue trace lines connect the two seasonal means for a given species; the dashed black line shows the overall trend combining all species and both seasons. Site\_Season\_Species mean trait values are shown in Table S7.

Fig. 5 Spatial variation in leaf trait-trait relationships. Scatterplot of the maximal rate of carboxylation per unit leaf area normalised to a common reference temperature of 25°C in relation to total leaf nitrogen per unit leaf area ( $[N]_a$ ). Separate panels are shown for each of four species measured at more than one site. Each point represents a single leaf; sites are differentiated by colour and seasons by shape. Points for Alice Mulga relate to the single winter visit to that site. Pearson correlation coefficients are shown where the association was significant ( $\alpha = 0.05$ ).

Fig. 6 Bar chart showing partitioning of leaf trait variation around the overall mean as derived from a multilevel model with separate random effects for the following factors: Season; Site; Site\_within\_Season; Species\_within\_Site\_within\_Season and Tree.number\_within\_Species\_within\_Site\_within\_Season. Any residual variation in the model was assigned to individual branches within a given plant. The leaf traits considered are leaf dry mass per unit area ( $M_a$ ,  $\text{g m}^{-2}$ ); total leaf nitrogen ( $\text{gN m}^{-2}$ ); total leaf phosphorus ( $\text{mgP m}^{-2}$ ); maximum rate of carboxylation of Rubisco per unit leaf area, normalised to the prevailing air temperature at the time of the campaign **and** to a common reference temperature of 25°C ( $V_{\text{cmax Prevaling}}$  **and**  $V_{\text{cmax25}}$  both  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); dark respiration per unit leaf area ( $R_{\text{dark Prevaling}}$  **and**  $R_{\text{dark 25}}$  both  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).

Figure 1

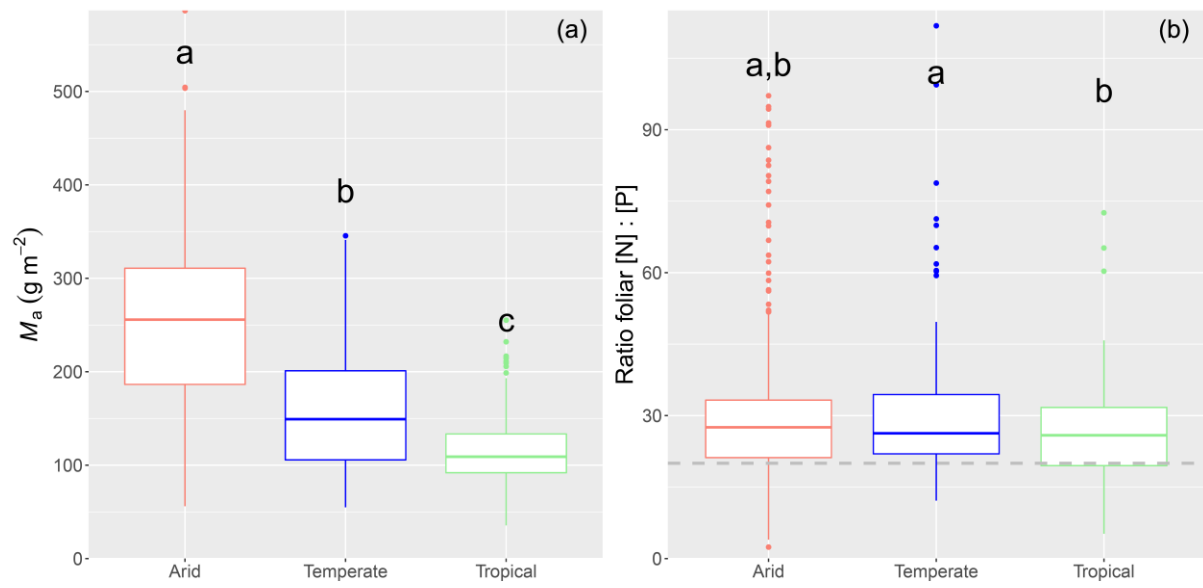


Figure 2

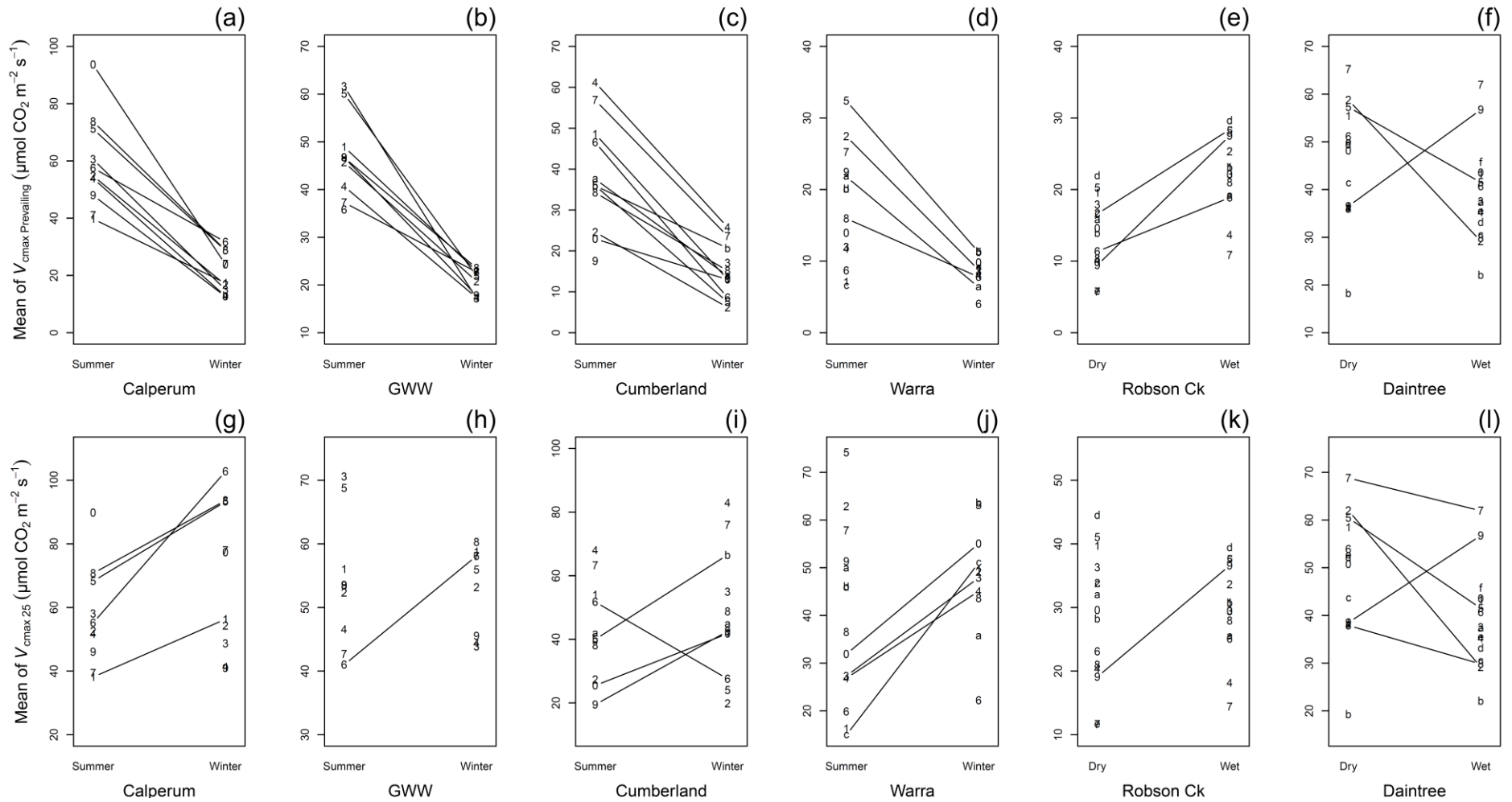


Figure 3

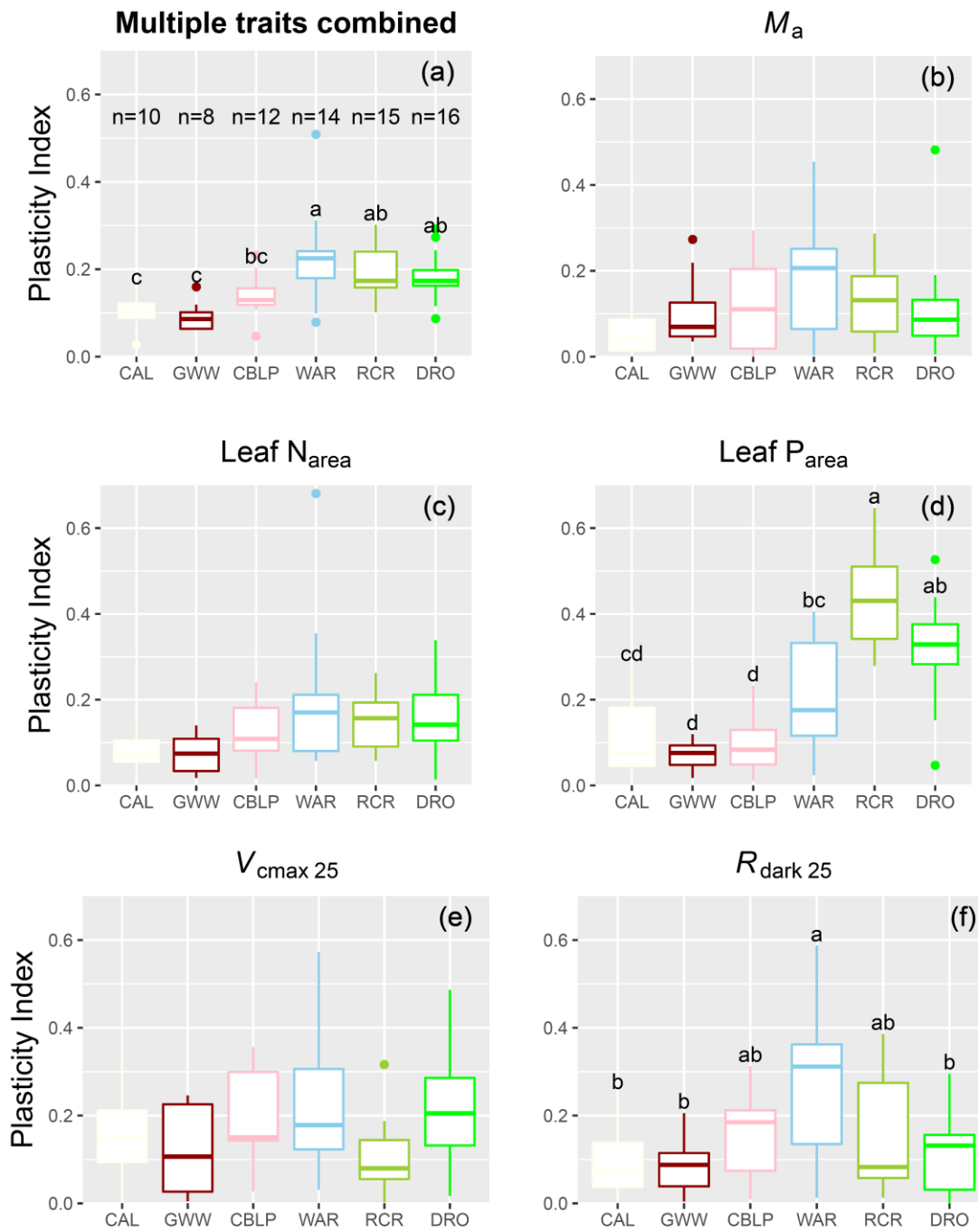


Figure 4

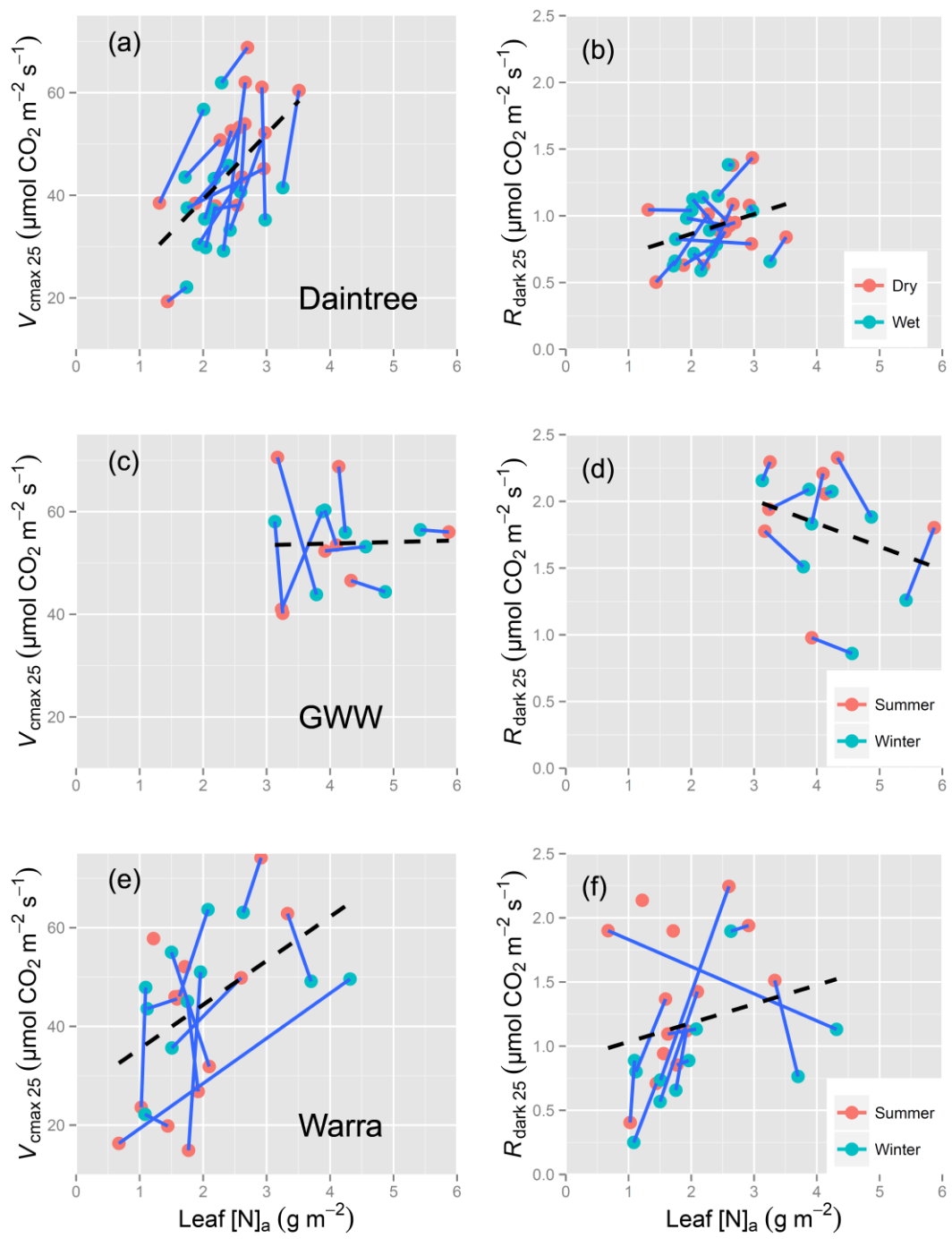


Figure 5

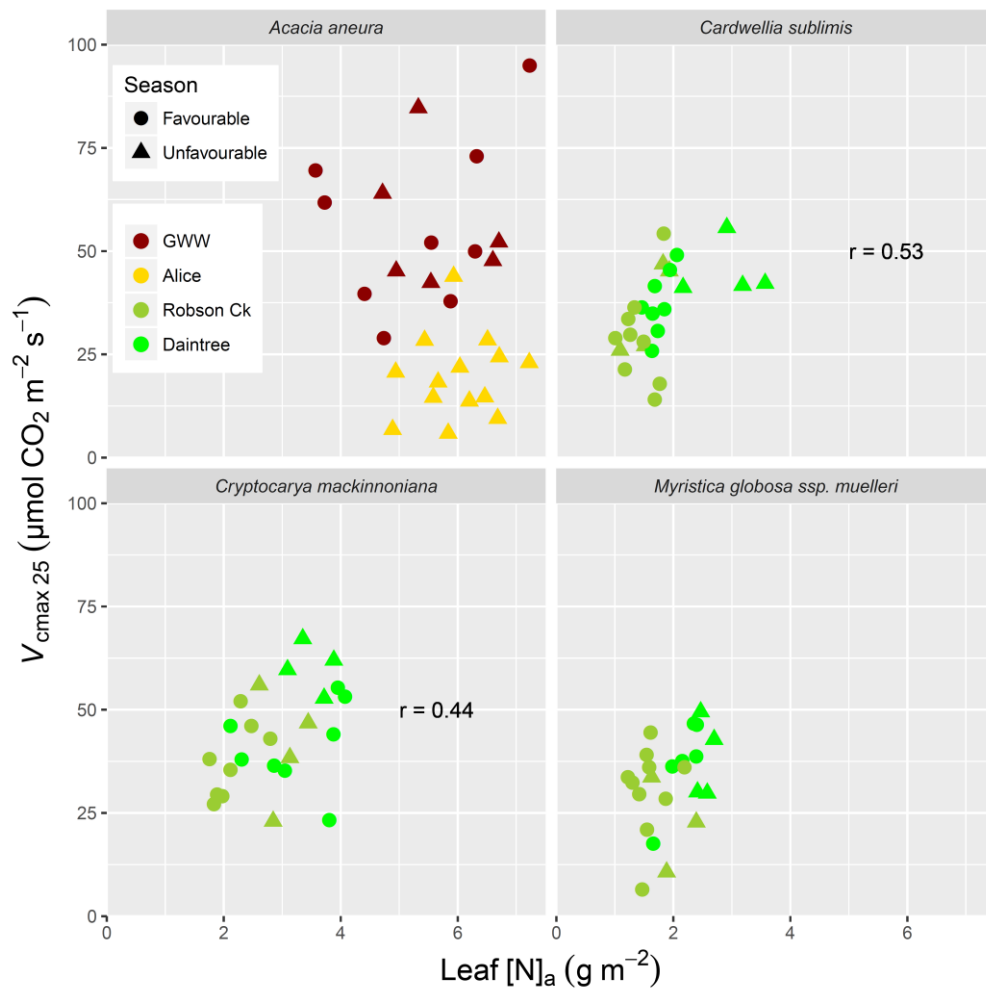
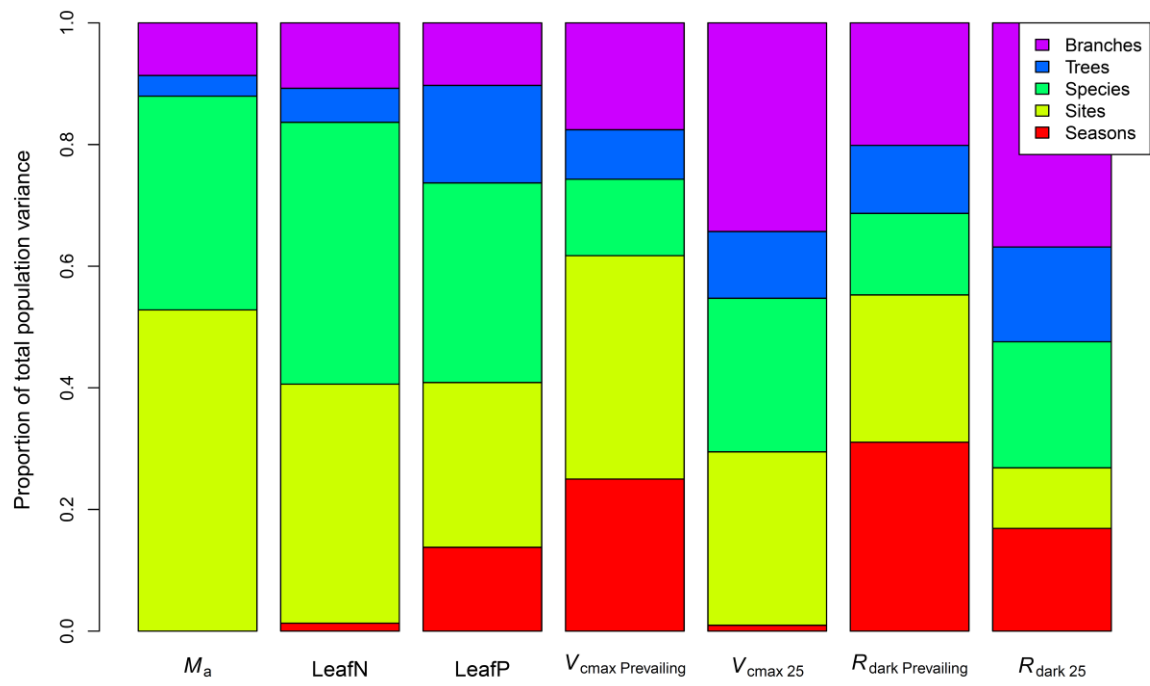
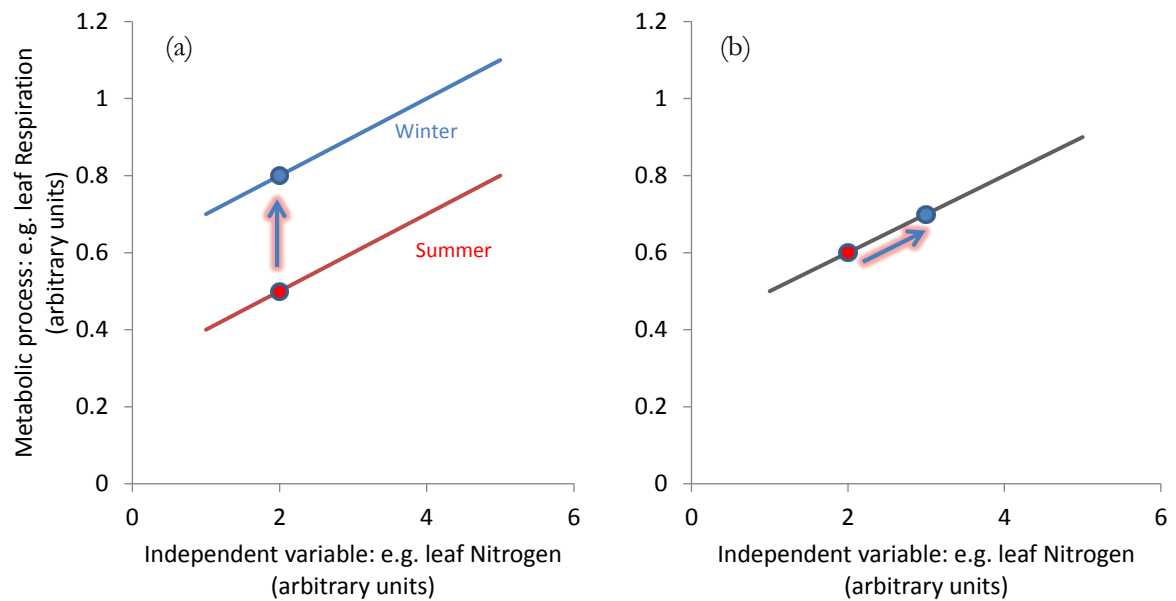


Figure 6



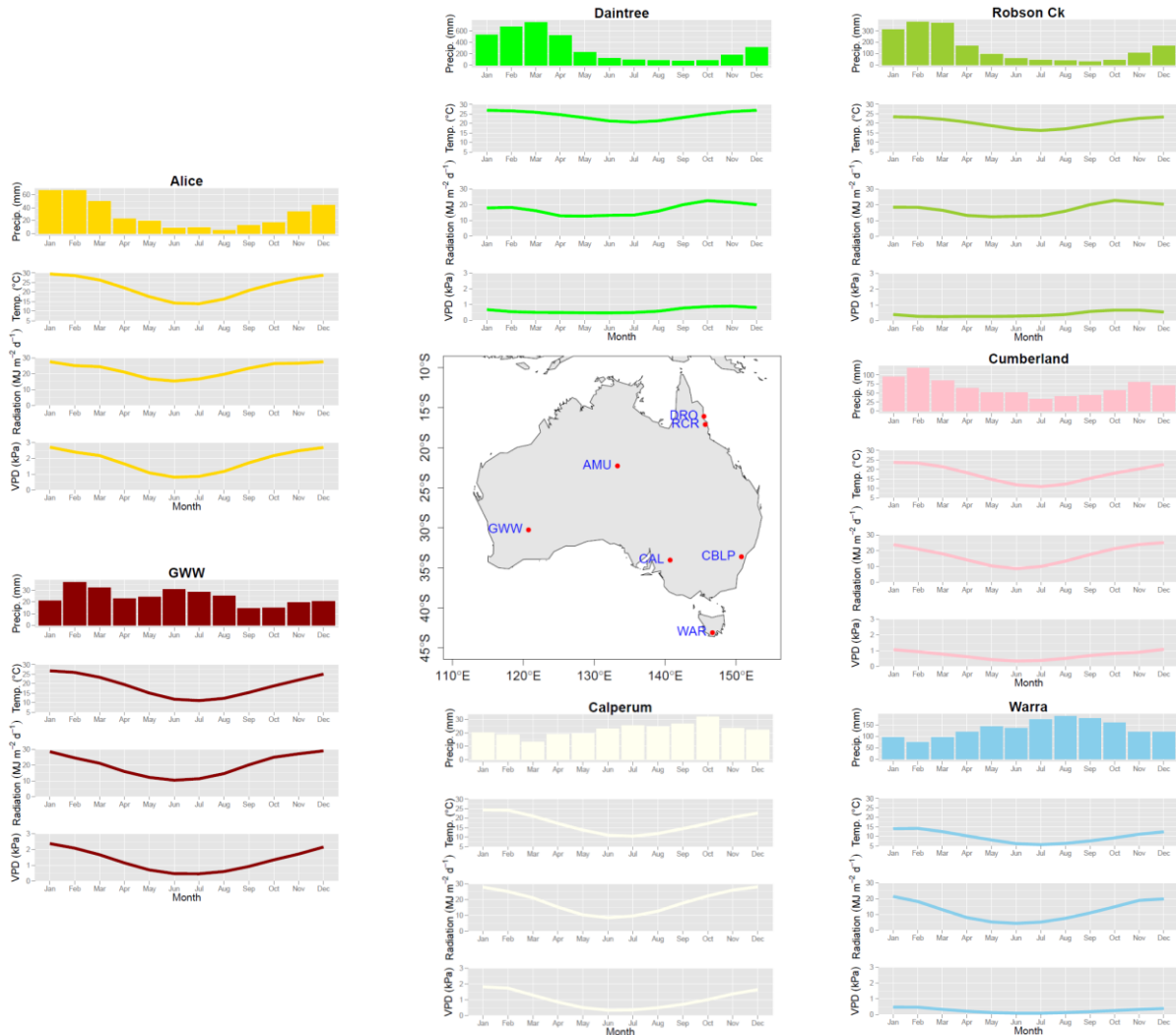
## Supporting information

**Fig. S1** Conceptual diagram for a leaf trait-trait relationship of two possible thermal acclimation responses to seasonal variation: (a) different response curves for the contrasting seasons reflecting a change in elevation (y intercept); (b) a common relationship holds, but seasonal effects cause a shift along the response curve. In both cases, temperature-standardised metabolic rates (e.g.  $R_{\text{dark}}$  at 25°C) would be faster in winter than summer, but with the underlying factors responsible for the seasonal change differing between the two scenarios.

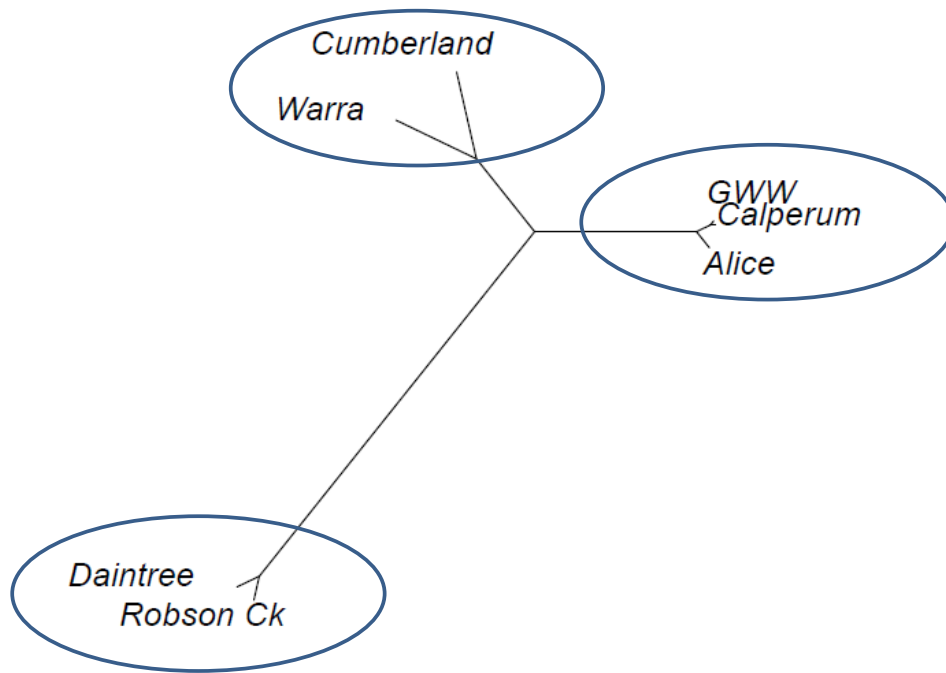




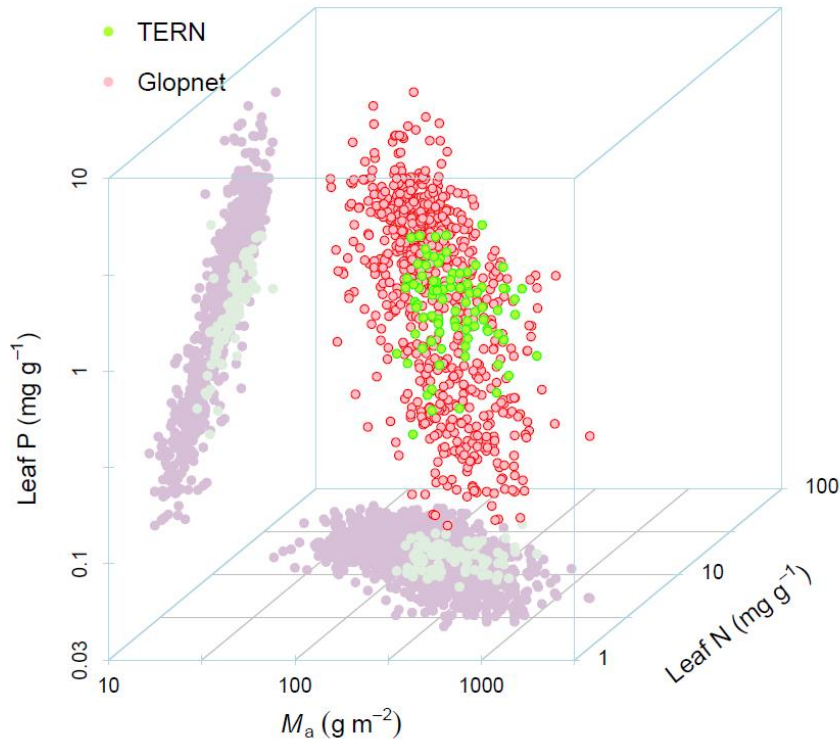
**Fig. S2** Map and key climate indicators for each of the study sites (**Table 1**): Alice Mulga (AMU), Calperum Mallee (CAL), Cumberland Plain (CBLP), Daintree (DRO), Great Western Woodlands (GWW), Robson Creek (RCR) and Warra (WAR). Climate variables are interpolated long-term monthly averages (1970–2012) generated by a spatial model: TERN eMAST ([www.emast.org.au](http://www.emast.org.au)). Precipitation (monthly total, mm); air temperature ( $^{\circ}\text{C}$ ); net radiation ( $\text{MJ m}^{-2} \text{ day}^{-1}$ ); vapour pressure deficit (kPa). Precipitation axes vary for the seven climate sites.



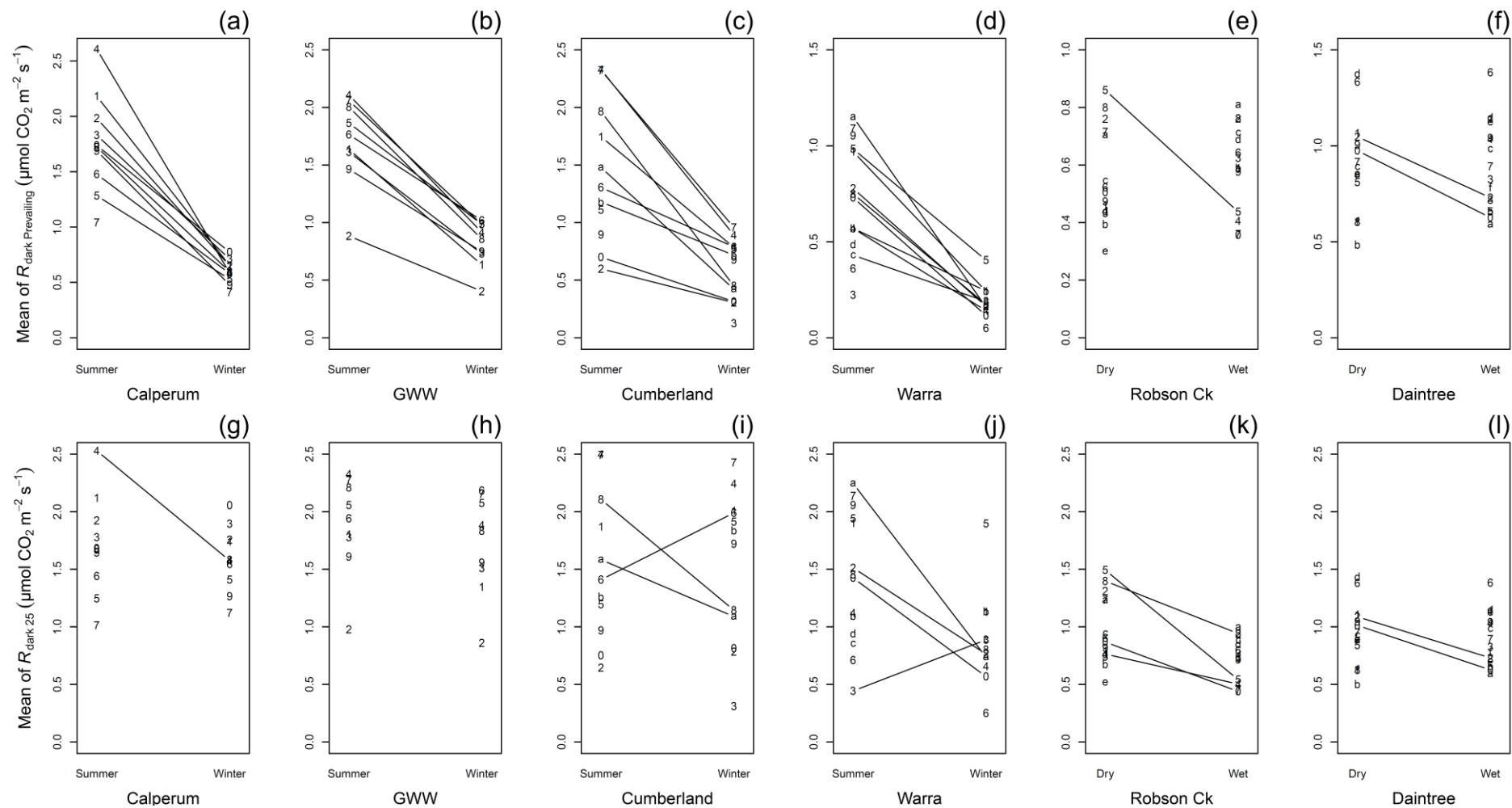
**Fig. S3** Unrooted ('phylogenetic') tree of the study sites based on a spatial analysis using bioclimatic indices (interpolated long-term averages taken from WorldClim (Hijmans *et al.* 2005)). Six indices were included in the spatial matrix, selected to place an emphasis on water availability and seasonality: BIO12 Annual precipitation, BIO15 Precipitation seasonality (Coefficient of variation), BIO16 Precipitation of wettest quarter, BIO17 Precipitation of driest quarter, BIO18 Precipitation of warmest quarter, BIO19 Precipitation of coldest quarter. Sites that have similar patterns across these indices will appear closer together on the branching tree. We have assigned three clusters (blue ovals): 'Arid' - comprising Alice Mulga, Calperum Mallee and Great Western Woodlands; 'Temperate' comprising Cumberland Plain and Warra; 'Tropical' - comprising Daintree and Robson Creek. Qualitatively similar tree patterns were obtained when the bioclimatic indices were broadened to include temperature variables.



**Fig. S4** Three-way scatterplot showing the associations between total leaf phosphorus (P) concentration, leaf mass per unit area ( $M_a$ ) and total leaf nitrogen (N) concentration. The direction of the data cloud in three-dimensional space can be ascertained from the shadows projected on the floor and wall of the cube (back wall not shown). All axes are on a log scale. Each dot represents a Site\_Species average, no seasonal contrasts are presented. Red dots (mauve in shadow) denote the Glopnet dataset (n=2548, Wright *et al.* 2004), green dots (grey in shadow) denote the current TERN SuperSite study (n=84, Table S2)



**Fig. S5** Two-way interaction plots (Season : Species) for species' mean estimates of dark respiration per unit leaf area normalised to: the prevailing air temperature at the time of the campaign (Table S1) ( $R_{\text{dark Prevailing}}$ , top panel) and to a common reference temperature of 25°C ( $R_{\text{dark } 25}$ , bottom panel). Paired plots are shown for each site (Alice Mulga is not included because only a single visit was made to that site). Individual species for a given site, ranked in alphabetical order, are labelled numerically (0 through 9) and then with letters (a, b, c etc.). Trace lines connecting the two seasonal means for a given species are only shown where the seasonal means were significantly different. Site\_Season\_Species mean trait values are shown in Table S7. Notice that axes ranges vary in the top panel to accommodate seasonal temperature variability from site to site.



**Table S1** Climate conditions for each campaign (Site\_Season) for the 30 day period ending on the final day of fieldwork. Air temperature (Ta), precipitation, net radiation (Fn), vapour pressure deficit (VPD), soil water fraction (Sws, top layer), short-wave down-welling radiation (Fsd). Rainfall figures are totals, other values are means. In most cases the climate data have been obtained from instruments located on flux towers at each site and managed under the OzFlux network ([www.ozflux.org.au](http://www.ozflux.org.au)). In three cases our fieldwork campaigns were made before the flux towers were fully operational and in these instances we have used interpolated data obtained from ANUClimate ([www.emast.org.au/our-infrastructure/observations/anuclimate\\_data/](http://www.emast.org.au/our-infrastructure/observations/anuclimate_data/)). As we prepared the manuscript, daily radiation data for the periods of interest were not available within ANUClimate and so those radiation data have been obtained for the nearest automated weather station operated by the Australian Bureau of Meteorology ([www.bom.gov.au](http://www.bom.gov.au)). The designation of Favourable and Unfavourable seasons is based on a local assessment of growing conditions.

Site	Visit	Season	Source	Ta °C	Precip mm	Fn W m <sup>-2</sup>	VPD Kpa	Sws fraction	Fsd W m <sup>-2</sup>
Calperum Mallee	Summer	Unfavourable	OzFlux	25.5	42.9	133.8	2.24	0.044	256.6
Calperum Mallee	Winter	Favourable	OzFlux	12.2	31.4	41.9	0.54	0.041	115.6
Great Western Woodlands	Summer	Unfavourable	OzFlux	23.5	26.4	116.2	1.89	0.209	239.6
Great Western Woodlands	Winter	Favourable	OzFlux	14.7	27.2	83.1	0.83	0.117	185.0
Alice Mulga	Winter	Unfavourable	OzFlux	15.5	-	92.9	1.29	0.059	227.5
Cumberland Plain	Summer	Favourable	OzFlux	23.8	13.2	180.4	1.15	0.054	257.0
Cumberland Plain	Winter	Unfavourable	OzFlux	12.3	7.0	52.6	0.62	0.052	129.1
Warra	Summer	Favourable	ANUClimate	15.9	72.9	106.2	0.52	NA	NA
Warra	Winter	Unfavourable	OzFlux	6.6	57.6	6.4	0.21	0.178	41.0
Robson Creek	Dry	Unfavourable	ANUClimate	17.2	46.0	64.0	0.34	NA	NA
Robson Creek	Wet	Favourable	OzFlux	21.8	238.3	129.5	0.38	0.325	174.0
Daintree	Dry	Unfavourable	ANUClimate	24.4	209.6	85.5	0.62	NA	NA
Daintree	Wet	Favourable	OzFlux	25.0	1,287.2	90.9	0.63	0.385	127.2

**Table S2** Leaf traits by site, averaged across both seasons and all species: number of observations (*n*), standard deviation (*sd*). For a given trait, sites that do not share the same letter indicate significant differences between the mean values (Tukey's HSD). Traits suffixed *\_a* expressed per unit leaf area, suffixed *\_m* expressed per unit leaf dried mass. Light saturated net photosynthesis at [CO<sub>2</sub>] 400 ppm (*A*<sub>400,a</sub>, μmol m<sup>-2</sup> s<sup>-1</sup>; *A*<sub>400,m</sub>, nmol g<sup>-1</sup> s<sup>-1</sup>); leaf dark respiration at [CO<sub>2</sub>] 400 ppm (*R*<sub>dark,a</sub>, μmol m<sup>-2</sup> s<sup>-1</sup>; *R*<sub>dark,m</sub>, nmol g<sup>-1</sup> s<sup>-1</sup>); leaf temperature in the measuring chamber (*T*<sub>leaf</sub>, °C); leaf dried mass per unit area (*M*<sub>a</sub>, g m<sup>-2</sup>); total leaf nitrogen (*N*<sub>a</sub>, g m<sup>-2</sup>; *N*<sub>m</sub>, mg g<sup>-1</sup>); total leaf phosphorus (*P*<sub>a</sub>, mg m<sup>-2</sup>; *P*<sub>m</sub>, mg g<sup>-1</sup>).

Site	<i>A</i> <sub>400,a</sub>		<i>A</i> <sub>400,m</sub>		<i>R</i> <sub>dark,a</sub>		<i>R</i> <sub>dark,m</sub>		<i>T</i> <sub>leaf</sub>
	<i>n</i>	Mean (sd)	<i>n</i>	Mean (sd)	<i>n</i>	Mean (sd)	<i>n</i>	Mean (sd)	Mean (sd)
Calperum	145	8.94 (4.27) c, d	145	39.57 (24.51) a, b, c	142	1.70 (1.12) d	142	8.38 (9.46) a, b	24.64 (7.58)
GWW	163	6.47 (2.63) b, c	163	28.67 (17.32) a, b	161	1.81 (0.97) d	161	7.97 (5.69) a, b	25.18 (4.57)
Alice	62	2.21 (2.15) a	62	8.89 (7.38) a	59	1.31 (0.84) c, d	59	5.81 (4.73) a, b	23.84 (2.46)
Cumberland	207	6.99 (4.03) b, c	207	46.50 (33.15) b, c	203	1.67 (1.21) d	203	10.71 (8.54) b	26.28 (6.36)
Warra	134	5.77 (2.73) a, b	133	47.00 (23.82) b, c	132	0.51 (0.45) a	131	3.82 (3.37) a	14.65 (5.51)
Robson Ck	181	6.66 (3.16) b	180	63.42 (31.68) c	181	0.83 (0.36) a, b	180	8.03 (4.12) b	27.04 (1.89)
Daintree	179	10.33 (3.92) d	177	94.41 (45.26) d	176	1.22 (0.48) b, c, d	176	11.33 (6.26) b	31.47 (0.94)

Site	<i>M</i> <sub>a</sub>		Leaf <i>N</i> <sub>a</sub>		Leaf <i>N</i> <sub>m</sub>		Leaf <i>P</i> <sub>a</sub>		Leaf <i>P</i> <sub>m</sub>
	<i>n</i>	Mean (sd)	<i>n</i>	Mean (sd)	<i>n</i>	Mean (sd)	<i>n</i>	Mean (sd)	<i>n</i> Mean (sd)
Calperum	146	258.3 (106.4) c	146	3.21 (0.98) b	146	13.53 (3.99) a	146	144.59 (56.42) a, b, c	146 0.621 (0.282) a, b
GWW	165	256.0 (74.4) c	165	4.70 (2.42) b, c	165	19.36 (8.85) a, b	165	154.84 (72.12) b, c	165 0.620 (0.235) a, b
Alice	62	252.2 (75.4) c	62	4.48 (1.7) c	62	18.20 (5.33) a, b	62	206.57 (197.19) c	62 0.826 (0.704) b, c
Cumberland	207	171.9 (63) b	207	2.71 (1.35) a, b	207	16.78 (6.7) a, b	207	94.76 (36.05) a, b	207 0.598 (0.223) a, b
Warra	133	133.5 (42.7) a, b	133	2.07 (1) a, b	134	15.77 (6.32) a	133	78.22 (39.42) a	134 0.602 (0.279) a
Robson Ck	181	110.8 (29.9) a	181	1.82 (0.5) a	181	17.11 (5.04) a, b	181	94.67 (59.38) a, b	181 0.853 (0.417) c
Daintree	177	118.5 (36.3) a, b	177	2.34 (0.59) b	178	20.81 (5.76) b	177	92.54 (38.16) a, b	178 0.846 (0.419) b, c

**Table S3** Leaf physiological parameters by site, averaged across both seasons and all species: number of observations (n), standard deviation (sd). Rates have been normalised on two bases: to the prevailing air temperature at the time of the campaign (**Table S1**); or to a reference temperature of 25°C. For a given parameter, sites that do not share the same letter indicate significant differences between the mean values (Tukey’s HSD). Parameters suffixed \_a expressed per unit leaf area, suffixed \_m expressed per unit leaf dried mass. Point estimates of maximal carboxylation rate based on light saturated net photosynthesis at [CO<sub>2</sub>] 400 ppm ( $V_{\text{cmax}_a}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ;  $V_{\text{cmax}_m}$ ,  $\text{nmol g}^{-1} \text{s}^{-1}$ ); leaf dark respiration at [CO<sub>2</sub>] 400 ppm ( $R_{\text{dark}_a}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ;  $R_{\text{dark}_m}$ ,  $\text{nmol g}^{-1} \text{s}^{-1}$ ).

Site	$V_{\text{cmax}_a, \text{prevailing}}$			$V_{\text{cmax}_a, 25}$			$V_{\text{cmax}_m, 25}$			$R_{\text{dark}_a, \text{prevailing}}$			$R_{\text{dark}_a, 25}$			$R_{\text{dark}_m, 25}$		
	n	Mean (sd)		Mean (sd)		Mean (sd)		n	Mean (sd)		Mean (sd)		Mean (sd)		Mean (sd)			
Calperum	139	39.17 (25.29) d		61.77 (26.45) c		272.8 (137.1) a, b, c		142	1.18 (0.79) c, d		1.66 (0.64) b		8.22 (7.19) a					
GWW	159	33.14 (18.23) c, d		52.92 (19.52) b, c		233.5 (132.9) a, b		161	1.26 (0.68) d		1.81 (0.75) b		7.66 (3.78) a					
Alice	54	9.79 (9.16) a		23.25 (21.75) a		92.8 (83.6) a		59	0.75 (0.46) b, c		1.44 (0.88) b		6.38 (4.99) a					
Cumberland	200	25.91 (18.74) b, c		44.18 (22.83) b		295.3 (196.6) b, c		203	0.99 (0.7) c, d		1.54 (0.82) b		9.55 (5.20) a					
Warra	132	12.58 (8.06) a		47.01 (19.82) b		383.7 (184.9) b, c		132	0.38 (0.34) a		1.09 (0.65) a		8.40 (4.80) a					
Robson Ck	180	20.33 (9.2) a, b		30.26 (12.46) a		287.2 (125.8) b, c		181	0.59 (0.26) a, b		0.81 (0.38) a		7.76 (4.04) a					
Daintree	176	41.46 (14.21) d		42.33 (14.78) b		386.0 (173.0) c		176	0.89 (0.34) c		0.91 (0.35) a		8.41 (4.69) a					

**Table S4** Leaf traits by site and season, averaged across all species: number of observations (n), standard deviation (sd). We made only a single visit to Alice Mulga. For a given trait and site, differences between seasons (Yes/No) were tested with a linear mixed effects model with a random term of plant id nested in species. Trait descriptions and units as shown in [Table S2](#).

Site	Season	$A_{400, a}$		$A_{400, m}$		$R_{dark, a}$		$R_{dark, m}$		$Tleaf$
		n	Mean (sd)	n	Mean (sd)	n	Mean (sd)	n	Mean (sd)	Mean (sd)
Alice	Winter	62	2.21 (2.15)	62	8.89 (7.38)	59	1.31 (0.84)	59	5.81 (4.73)	23.8 (2.5)
Calperum	Summer	73	9.57 (4.16) Yes	73	44.52 (30.53) Yes	71	2.53 (1.01) Yes	71	12.75 (11.7) Yes	31.6 (3.8)
Calperum	Winter	72	8.29 (4.31)	72	34.56 (14.92)	71	0.88 (0.36)	71	4.01 (2.19)	17.6 (1.8)
GWW	Summer	82	6.9 (2.6) Yes	82	34.35 (19.5) Yes	78	2.4 (0.87) Yes	78	11.57 (5.94) Yes	29 (2.6)
GWW	Winter	81	6.03 (2.6)	81	22.91 (12.48)	83	1.25 (0.67)	83	4.58 (2.48)	21.3 (2.3)
Cumberland	Summer	103	7.46 (4.38) Yes	103	53.84 (39.09) Yes	99	2.27 (1.38) Yes	99	15.51 (9.74) Yes	32.3 (2.4)
Cumberland	Winter	104	6.52 (3.6)	104	39.24 (24.04)	104	1.1 (0.61)	104	6.15 (3.12)	20.3 (1.8)
Warra	Summer	50	6.48 (3.59) No	49	46.63 (27.42) No	50	0.92 (0.48) Yes	49	6.73 (3.85) Yes	21.5 (1.8)
Warra	Winter	84	5.34 (1.95)	84	47.21 (21.61)	82	0.26 (0.15)	82	2.08 (1.11)	10.6 (1.2)
Robson Ck	Dry	57	5.87 (3.14) No	56	51.14 (28.02) Yes	57	0.83 (0.4) No	56	7.31 (4.14) No	24.6 (0.8)
Robson Ck	Wet	124	7.03 (3.12)	124	68.96 (31.78)	124	0.84 (0.35)	124	8.36 (4.09)	28.2 (1)
Daintree	Dry	61	12.02 (3.38) Yes	60	108.09 (42.29) Yes	60	1.18 (0.47) No	60	10.95 (6.99) No	30.6 (0.8)
Daintree	Wet	118	9.46 (3.91)	117	87.4 (45.29)	116	1.24 (0.48)	116	11.53 (5.87)	31.9 (0.6)

Site	Season	$M_a$		Leaf $N_a$		Leaf $N_m$		Leaf $P_a$		Leaf $P_m$	
		n	Mean (sd)	n	Mean (sd)	n	Mean (sd)	n	Mean (sd)	n	Mean (sd)
Alice	Winter	62	252.2 (75.4)	62	4.48 (1.7)	62	18.2 (5.33)	62	206.6 (197.2)	62	0.826 (0.704)
Calperum	Summer	74	265.9 (112.2) No	74	3.21 (1.06) No	74	13.14 (3.98) No	74	142.6 (63.7) No	74	0.612 (0.332) No
Calperum	Winter	72	250.5 (100.3)	72	3.22 (0.9)	72	13.92 (4)	72	146.6 (48.1)	72	0.631 (0.221)
GWW	Summer	82	228.5 (70.8) Yes	82	4.17 (1.05) Yes	82	20.43 (9.58) Yes	82	149.4 (71.9) No	82	0.666 (0.24) Yes
GWW	Winter	83	283.2 (67.9)	83	5.23 (3.17)	83	18.31 (7.99)	83	160.2 (72.3)	83	0.575 (0.221)
Cumberland	Summer	103	160.6 (64.5) Yes	103	2.5 (1.34) Yes	103	16.98 (7.31) No	103	94.1 (32) No	103	0.647 (0.231) Yes
Cumberland	Winter	104	183 (59.7)	104	2.91 (1.34)	104	16.59 (6.07)	104	95.4 (39.8)	104	0.55 (0.205)
Warra	Summer	49	146.6 (38.6) Yes	49	1.95 (0.82) No	50	13.4 (5.66) Yes	49	66.1 (43) Yes	50	0.447 (0.264) Yes
Warra	Winter	84	125.9 (43.4)	84	2.14 (1.09)	84	17.18 (6.29)	84	85.3 (35.5)	84	0.695 (0.246)
Robson Ck	Dry	56	121.1 (36.5) Yes	56	2.01 (0.61) Yes	56	17.19 (4.78) No	56	161.3 (64.9) Yes	56	1.335 (0.361) Yes
Robson Ck	Wet	125	106.2 (25.3)	125	1.74 (0.42)	125	17.07 (5.17)	125	64.8 (18.6)	125	0.637 (0.207)
Daintree	Dry	60	119.4 (37) No	60	2.52 (0.63) Yes	61	22.28 (5.51) Yes	60	124.4 (39.6) Yes	61	1.128 (0.476) Yes
Daintree	Wet	117	118 (36.1)	117	2.24 (0.54)	117	20.05 (5.75)	117	76.2 (24.9)	117	0.698 (0.294)



**Table S5** Leaf physiological parameters by site and season, averaged across all species: number of observations (n), standard deviation (sd). Rates have been normalised on two bases: to the prevailing air temperature at the time of the campaign (**Table S1**); or to a reference temperature of 25°C. We made only a single visit to Alice Mulga. For a given parameter and site, differences between seasons (Yes/No) were tested with a linear mixed effects model with a random term of plant id nested in species. Parameter descriptions and units as shown in Table S3.

Site	Season	$V_{cmax, a, 25}$		$V_{cmax, a, prevailing}$		$V_{cmax, m, 25}$	
		n	Mean (sd)	Mean (sd)	n	Mean (sd)	
Alice	Winter	54	23.25 (21.75)	9.79 (9.16)	54	92.76 (83.61)	
Calperum	Summer	68	56.03 (21.3) Yes	58.43 (22.2) Yes	68	261.22 (159.14) No	
Calperum	Winter	71	67.26 (29.7)	20.72 (9.14)	71	283.82 (112.15)	
GWW	Summer	78	52.64 (19.66) No	45.96 (17.17) Yes	78	267.05 (157.78) Yes	
GWW	Winter	81	53.19 (19.51)	20.80 (7.63)	81	201.16 (93.5)	
Cumberland	Summer	99	41.80 (21.79) No	37.60 (19.6) Yes	99	300.74 (193.18) No	
Cumberland	Winter	101	46.51 (23.68)	14.45 (7.35)	101	290.00 (200.71)	
Warra	Summer	50	42.82 (22.34) Yes	18.71 (9.75) Yes	49	304.97 (160.42) Yes	
Warra	Winter	82	49.56 (17.77)	8.84 (3.17)	82	430.77 (183.43)	
Robson Ck	Dry	57	29.52 (13.53) No	14.55 (6.67) Yes	56	259.42 (128.72) No	
Robson Ck	Wet	123	30.60 (11.98)	23.01 (9)	123	299.87 (122.88)	
Daintree	Dry	60	48.91 (13.83) Yes	46.37 (13.11) Yes	60	438.44 (168.68) Yes	
Daintree	Wet	116	38.92 (14.14)	38.92 (14.15)	116	358.92 (169.6)	

Site	Season	$R_{dark, a, 25}$		$R_{dark, a, prevailing}$		$R_{dark, m, 25}$	
		n	Mean (sd)	Mean (sd)	n	Mean (sd)	
Alice	Winter	59	1.44 (0.88)	0.75 (0.46)	59	6.38 (4.99)	
Calperum	Summer	71	1.70 (0.71) No	1.75 (0.73) Yes	71	8.90 (9.35) No	
Calperum	Winter	71	1.62 (0.57)	0.61 (0.22)	71	7.53 (3.95)	
GWW	Summer	78	1.92 (0.65) No	1.74 (0.59) Yes	78	9.11 (3.92) Yes	
GWW	Winter	83	1.72 (0.83)	0.81 (0.4)	83	6.30 (3.10)	
Cumberland	Summer	99	1.48 (0.82) No	1.38 (0.77) Yes	99	10.14 (5.85) Yes	
Cumberland	Winter	104	1.59 (0.83)	0.62 (0.33)	104	8.99 (4.45)	
Warra	Summer	50	1.34 (0.69) Yes	0.69 (0.36) Yes	49	9.78 (5.54) Yes	
Warra	Winter	82	0.94 (0.57)	0.20 (0.12)	82	7.58 (4.12)	
Robson Ck	Dry	57	0.96 (0.49) Yes	0.55 (0.28) No	56	8.39 (4.81) No	
Robson Ck	Wet	124	0.75 (0.30)	0.61 (0.25)	124	7.47 (3.63)	
Daintree	Dry	60	0.93 (0.37) No	0.90 (0.35) No	60	8.66 (5.52) No	
Daintree	Wet	116	0.89 (0.34)	0.89 (0.34)	116	8.28 (4.21)	

**Table S6** Leaf traits by site and season and species: the number of branches measured (*n*, typically two per plant), standard deviation (sd). Trait descriptions and units as per Table S2.

Site	Season	Species	<i>n</i>	<i>A</i> <sub>400, a</sub>	<i>R</i> <sub>dark, a</sub>	TL <sub>leaf</sub>	<i>M</i> <sub>a</sub>	Leaf <i>N</i> <sub>a</sub>	Leaf <i>P</i> <sub>a</sub>
				Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)
Calperum	Summer	<i>Beyeria opaca</i>	7	6.14 (1.51)	3.34 (0.99)	32.4 (4.4)	165.9 (55)	2.29 (0.93)	104.89 (52.51)
Calperum	Summer	<i>Dodonaea angustissima</i>	8	9.58 (3.73)	2.49 (1.21)	30.7 (3.6)	145.5 (45.9)	2.31 (0.67)	124.00 (48.43)
Calperum	Summer	<i>Dodonaea bursariifolia</i>	8	12.00 (3.85)	2.59 (0.63)	31 (2.4)	201.9 (36.9)	3.07 (1.07)	100.73 (31.94)
Calperum	Summer	<i>Eremophila glabra</i>	8	9.15 (3.19)	3.14 (0.77)	28 (4)	162.2 (35.6)	2.72 (0.47)	170.98 (72.63)
Calperum	Summer	<i>Eucalyptus dumosa</i>	8	10.38 (5.08)	1.94 (0.43)	33.3 (2.5)	417.3 (23.9)	3.62 (0.76)	133.11 (43.06)
Calperum	Summer	<i>Eucalyptus socialis</i>	8	7.49 (4.63)	2.69 (0.98)	35.9 (2.6)	348.6 (58.4)	3.29 (0.49)	121.51 (46.84)
Calperum	Summer	<i>Grevillea huegelii</i>	8	8.24 (3.6)	1.44 (0.88)	29.8 (1.3)	397.2 (120.3)	3.51 (1.26)	116.2 (39.96)
Calperum	Summer	<i>Myoporum platycarpum</i>	6	13.07 (3.03)	2.22 (0.46)	32 (2.9)	217.4 (33.5)	3.29 (0.6)	126.42 (42.73)
Calperum	Summer	<i>Senna artemisioides ssp. filifolia</i>	6	8.76 (1.9)	3.02 (1.54)	34.4 (2.7)	303.3 (46.3)	4.8 (1.3)	236.81 (74.46)
Calperum	Summer	<i>Triodia irritans</i>	6	11.64 (6.12)	1.97 (0.37)	27.9 (2.7)	284.5 (50.2)	3.36 (0.52)	211.98 (19.74)
Calperum	Winter	<i>Beyeria opaca</i>	8	6.11 (2.36)	0.93 (0.44)	18.2 (0.9)	174.5 (11.3)	2.55 (0.39)	92.33 (13.28)
Calperum	Winter	<i>Dodonaea angustissima</i>	8	5.41 (1.38)	0.86 (0.22)	16 (0.9)	144.9 (14)	2.69 (0.38)	127.44 (39.15)
Calperum	Winter	<i>Dodonaea bursariifolia</i>	8	5.86 (2.42)	1.04 (0.41)	18 (1.4)	180.3 (48.1)	2.73 (0.86)	95.13 (32.13)
Calperum	Winter	<i>Eremophila glabra</i>	8	5.49 (1.75)	0.81 (0.28)	16.9 (1.2)	165.7 (12.5)	2.61 (0.16)	147.71 (27.79)
Calperum	Winter	<i>Eucalyptus dumosa</i>	8	11.63 (1.57)	0.79 (0.19)	18.8 (2.4)	411.1 (32)	3.93 (0.49)	176.4 (40.42)
Calperum	Winter	<i>Eucalyptus socialis</i>	8	14.99 (3.15)	0.84 (0.21)	17.7 (1.2)	349.7 (42.3)	3.58 (0.5)	167.54 (20.98)
Calperum	Winter	<i>Grevillea huegelii</i>	2	11.35 (6.24)	0.55 (0.32)	15.2 (0.3)	346.3 (223.6)	2.81 (1.72)	112.75 (75.73)
Calperum	Winter	<i>Myoporum platycarpum</i>	8	12.93 (2.03)	0.9 (0.56)	18.1 (1.9)	229.4 (24.1)	3.55 (0.6)	163.89 (27.14)
Calperum	Winter	<i>Senna artemisioides ssp. filifolia</i>	8	5.22 (2.48)	0.72 (0.28)	18.2 (2.5)	264.5 (57)	4.55 (1.02)	210.38 (45.84)
Calperum	Winter	<i>Triodia irritans</i>	6	5.57 (2.59)	1.12 (0.53)	17.3 (0.7)	331.1 (59.7)	2.72 (0.39)	147.25 (28.76)

Table S6 contd.

Site	Season	Species	n	$A_{400, a}$	$R_{dark, a}$	Tileaf	$M_a$	Leaf $N_a$	Leaf $P_a$
				Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)
GWW	Summer	<i>Acacia aneura</i>	9	7.68 (2.81)	2.21 (0.82)	28.7 (1.3)	293 (36.2)	5.87 (0.88)	181.23 (36.04)
GWW	Summer	<i>Acacia hemiteles</i>	8	6.77 (2.58)	1.15 (0.35)	29.1 (0.5)	141.5 (22)	3.92 (0.43)	115.28 (14.59)
GWW	Summer	<i>Atriplex nummularia</i>	7	6.61 (0.99)	2.37 (0.65)	29.5 (2.8)	131.1 (13.1)	3.17 (0.66)	91.59 (18)
GWW	Summer	<i>Eremophila scoparia</i>	10	7.05 (2)	2.8 (0.49)	27.4 (2.4)	276.3 (26.1)	4.33 (0.55)	302.33 (73.48)
GWW	Summer	<i>Eucalyptus clelandii</i>	8	9.1 (2.48)	2.7 (0.68)	29.3 (2.9)	296.6 (27.7)	4.14 (0.45)	141.94 (19.36)
GWW	Summer	<i>Eucalyptus salmonophloia</i>	10	5.62 (2.7)	2.53 (0.67)	28.5 (2.6)	235.9 (19.3)	3.24 (0.51)	115.25 (28.71)
GWW	Summer	<i>Eucalyptus salubris</i>	10	5.73 (2.77)	2.67 (0.47)	27.5 (2.4)	246.3 (27.4)	3.25 (0.32)	142.79 (15.13)
GWW	Summer	<i>Eucalyptus transcontinentalis</i>	10	5.7 (2.51)	2.72 (1.2)	30.3 (2.3)	282.2 (27.3)	4.1 (0.68)	150.39 (24.52)
GWW	Summer	<i>Maireana sedifolia</i>	10	8.23 (2.49)	2.19 (1.08)	31 (3.5)	126.9 (16.2)	5.28 (0.66)	81.53 (23.28)
GWW	Winter	<i>Acacia aneura</i>	9	5.63 (2.37)	0.9 (0.41)	20.5 (1.3)	312.6 (33.9)	5.42 (1.25)	153.08 (32.24)
GWW	Winter	<i>Acacia hemiteles</i>	8	7.33 (3.37)	0.58 (0.23)	19.8 (1.1)	205.7 (16.2)	4.56 (0.87)	111.93 (35.45)
GWW	Winter	<i>Atriplex nummularia</i>	8	4.54 (2.25)	1.26 (0.34)	23.2 (1.4)	178.3 (30.8)	3.79 (0.55)	107.31 (25.98)
GWW	Winter	<i>Eremophila scoparia</i>	10	4.68 (1.41)	1.66 (0.71)	23.2 (3)	289.7 (75.6)	4.87 (1.1)	287.02 (116.21)
GWW	Winter	<i>Eucalyptus clelandii</i>	10	7.39 (3.32)	1.56 (1.05)	22.1 (0.9)	335.4 (33.3)	4.24 (0.85)	157.37 (48.94)
GWW	Winter	<i>Eucalyptus salmonophloia</i>	8	6.46 (1.71)	1.41 (0.75)	21.3 (2.3)	259.8 (18.4)	3.88 (0.7)	133.44 (44.36)
GWW	Winter	<i>Eucalyptus salubris</i>	10	6.15 (2.01)	1.2 (0.46)	18.8 (1.9)	259.1 (27.7)	3.13 (0.45)	161.6 (27.36)
GWW	Winter	<i>Eucalyptus transcontinentalis</i>	10	6.87 (3.17)	1.25 (0.44)	20.7 (1.6)	301 (46.5)	3.92 (0.91)	136.96 (26.6)
GWW	Winter	<i>Maireana sedifolia</i>	8	5.08 (2.11)	1.32 (0.77)	22.6 (2.1)	375.3 (29.8)	13.39 (2.81)	168.16 (52.59)
Alice	Winter	<i>Acacia aneura</i>	19	1.9 (0.86)	0.77 (0.63)	24.1 (2.7)	278.2 (25.4)	5.87 (0.74)	174.74 (27.28)
Alice	Winter	<i>Acacia dictyophleba</i>	9	1.02 (0.51)	0.73 (0.37)	20.6 (1.8)	177.8 (11.5)	2.97 (0.35)	78.24 (20.87)
Alice	Winter	<i>Corymbia terminalis</i>	8	1.62 (2.25)	1.21 (0.66)	25.4 (0.6)	285.7 (25.6)	2.83 (0.57)	640.03 (280.84)
Alice	Winter	<i>Eremophila latrobei</i>	10	1.97 (1.06)	2.22 (0.62)	24.1 (0.6)	158.7 (17)	3.87 (0.45)	137.54 (22.59)
Alice	Winter	<i>Eucalyptus camaldulensis</i>	6	4.59 (1.9)	2.38 (0.6)	27 (0.5)	241.6 (37.3)	2.71 (0.23)	144.9 (44.02)
Alice	Winter	<i>Hakea leucoptera</i>	6	5.22 (3.95)	1.55 (0.64)	21.9 (0.7)	408.6 (51.3)	7.22 (1.61)	140 (32.63)
Alice	Winter	<i>Psyrax latifolia</i>	4	0.09 (0.04)	1.48 (0.61)	24.3 (0.8)	243.3 (12.9)	4.6 (0.4)	144.5 (9.79)

Table S6 contd.

Site	Season	Species	n	$A_{400, a}$	$R_{dark, a}$	Tileaf	$M_a$	Leaf $N_a$	Leaf $P_a$
				Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)
Cumberland	Summer	<i>Acacia parramattensis</i>	8	9.86 (4.27)	3.08 (1.26)	34.5 (1.3)	228.8 (75.4)	6.03 (1.79)	143.44 (55.68)
Cumberland	Summer	<i>Breyenia oblongifolia</i>	10	5.56 (1.49)	0.88 (0.29)	30.2 (1)	65.2 (7)	1.49 (0.25)	52.27 (7.29)
Cumberland	Summer	<i>Eucalyptus amplifolia</i>	8	12.04 (5.49)	4.02 (1.31)	33.9 (0.6)	122.8 (28.8)	2.38 (0.55)	96.53 (20.33)
Cumberland	Summer	<i>Eucalyptus fibrosa</i>	10	6.6 (3.2)	1.62 (0.81)	31 (2.4)	219 (15.4)	2.21 (0.34)	97.2 (23.91)
Cumberland	Summer	<i>Eucalyptus moluccana</i>	10	10.51 (2.78)	1.83 (0.62)	30.4 (0.5)	210.3 (19.9)	2.43 (0.32)	96.85 (10.99)
Cumberland	Summer	<i>Eucalyptus tereticornis</i>	9	12.43 (4.67)	3.96 (0.98)	34 (0.8)	152.7 (25.4)	2.5 (0.72)	115.78 (26.52)
Cumberland	Summer	<i>Hakea sericea</i>	9	5.82 (2.99)	3.38 (1.43)	32.8 (1)	257.7 (33.3)	1.69 (0.3)	90.71 (28.96)
Cumberland	Summer	<i>Jacksonia scoparia</i>	10	4.18 (1.8)	1.15 (0.65)	28.5 (0.5)	152.4 (35)	3.52 (0.89)	106.34 (21.33)
Cumberland	Summer	<i>Melaleuca decora</i>	10	5.35 (1.55)	1.13 (0.34)	32.7 (0.3)	133 (12.3)	1.37 (0.17)	65.78 (7.56)
Cumberland	Summer	<i>Melaleuca nodosa</i>	9	4.56 (1.6)	2.66 (0.83)	33.6 (2.5)	142.9 (28.3)	2.3 (0.32)	92.27 (14.18)
Cumberland	Summer	<i>Ozothamnus diosmifolius</i>	10	6.6 (5.63)	2.09 (0.67)	34.5 (2.7)	94.6 (11.6)	2.15 (0.33)	89.99 (19.64)
Cumberland	Winter	<i>Acacia parramattensis</i>	9	5.66 (3.06)	1.33 (0.54)	20.2 (2.3)	222.3 (38)	5.88 (0.98)	140.97 (30.74)
Cumberland	Winter	<i>Breyenia oblongifolia</i>	10	2.47 (1.17)	0.51 (0.17)	20.1 (0.7)	78.2 (12)	1.64 (0.3)	46.84 (8.33)
Cumberland	Winter	<i>Bursaria spinosa</i>	2	7.72 (0.29)	0.2 (0.01)	20.8 (0.2)	96 (3.5)	1.49 (0.2)	65.4 (8.34)
Cumberland	Winter	<i>Eucalyptus amplifolia</i>	10	11.36 (3.6)	1.55 (0.54)	21 (1.1)	186.6 (30.6)	3.34 (0.55)	131.89 (24.3)
Cumberland	Winter	<i>Eucalyptus fibrosa</i>	8	3.06 (1.57)	1.49 (0.72)	22.2 (2.5)	223.7 (23.4)	2.7 (1.07)	91.75 (19.76)
Cumberland	Winter	<i>Eucalyptus moluccana</i>	10	3.43 (1.57)	1.43 (0.53)	21.6 (3.5)	212 (20.3)	2.51 (0.4)	95.35 (15.8)
Cumberland	Winter	<i>Eucalyptus tereticornis</i>	9	11.48 (3.06)	1.78 (0.37)	21.1 (1.1)	209.5 (16.5)	3.34 (0.48)	124.91 (22.33)
Cumberland	Winter	<i>Hakea sericea</i>	10	7.37 (3.03)	0.79 (0.22)	20.3 (0.6)	257.1 (40.8)	2.04 (0.49)	56.79 (16.66)
Cumberland	Winter	<i>Jacksonia scoparia</i>	6	5.87 (1.74)	1.19 (0.6)	19.6 (1.8)	220.3 (43.8)	4.58 (1.18)	128.65 (39.06)
Cumberland	Winter	<i>Melaleuca decora</i>	10	7.16 (0.96)	0.49 (0.18)	18.6 (0.3)	147.5 (12)	1.92 (0.6)	71.2 (14.19)
Cumberland	Winter	<i>Melaleuca nodosa</i>	10	6.25 (2.02)	0.68 (0.27)	19.8 (0.5)	183.4 (28.8)	2.6 (0.37)	76.28 (17.89)
Cumberland	Winter	<i>Ozothamnus diosmifolius</i>	10	6.84 (2.13)	1.21 (0.53)	19.3 (0.8)	119.8 (46.6)	2.71 (0.95)	110.94 (54.71)

Table S6 contd.

Site	Season	Species	n	$A_{400, a}$	$R_{dark, a}$	Tileaf	$M_a$	Leaf $N_a$	Leaf $P_a$
				Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)
Warra	Summer	<i>Acacia dealbata</i>	1	2.67	1.28	21.87	73.34	0.67	8.50
Warra	Summer	<i>Acacia melanoxylon</i>	5	10.35 (3.81)	1.08 (0.48)	22.4 (2)	132.4 (13.3)	3.33 (0.45)	89.52 (17.34)
Warra	Summer	<i>Anopterus glandulosus</i>	4	3.83 (2.33)	0.24 (0.05)	21 (0.2)	120.8 (17.6)	1.03 (0.13)	37.33 (13.77)
Warra	Summer	<i>Atherosperma moschatum</i>	4	3.12 (2.04)	0.74 (0.38)	23.1 (1.1)	105.1 (19.7)	1.92 (0.21)	67.7 (27.55)
Warra	Summer	<i>Eucalyptus obliqua</i>	5	9.81 (2.1)	1.24 (0.62)	20.5 (0.7)	205.9 (28.3)	2.91 (0.2)	126.26 (15.27)
Warra	Summer	<i>Eucryphia lucida</i>	4	2.48 (1.61)	0.46 (0.18)	23.5 (0.9)	155.3 (25.2)	1.44 (0.19)	41.58 (21.04)
Warra	Summer	<i>Leptospermum lanigerum</i>	3	8.79 (0.46)	1.45 (0.24)	18.5 (0.2)	124.3 (22.7)	1.22 (0.42)	26.57 (22.38)
Warra	Summer	<i>Melaleuca squarrosa</i>	3	7.96 (3.18)	1.02 (0.29)	20.8 (0.4)	101.5 (9.3)	1.59 (0.55)	65 (28.87)
Warra	Summer	<i>Notelaea ligustrina</i>	4	7.65 (2.19)	1.32 (0.51)	23 (2)	142.4 (24.2)	1.71 (0.75)	36.65 (27.54)
Warra	Summer	<i>Nothofagus cunninghamii</i>	4	3.91 (2.38)	0.97 (0.33)	20.7 (3.1)	151.7 (16.1)	2.1 (1.08)	78.65 (92.45)
Warra	Summer	<i>Phyllocladus aspleniifolius</i>	2	6.46 (1.48)	1.56 (0.35)	22.7 (0.6)	225.2 (14.1)	2.6 (0.68)	125.5 (21.36)
Warra	Summer	<i>Pittosporum bicolor</i>	4	9.12 (2.88)	0.87 (0.14)	22 (0.6)	172.3 (12.5)	1.63 (0.22)	74.83 (12.07)
Warra	Summer	<i>Pomaderris apetala</i>	3	2.23 (1.86)	0.53 (0.05)	21.5 (0.6)	132.9 (10.6)	1.77 (0.21)	36.97 (10.6)
Warra	Summer	<i>Tasmannia lanceolata</i>	4	7.51 (1.92)	0.69 (0.23)	19.5 (0.6)	155.6 (28.7)	1.56 (0.53)	51.13 (28.11)
Warra	Winter	<i>Acacia dealbata</i>	8	5.19 (2.81)	0.32 (0.16)	10.6 (0.3)	156 (18.4)	4.31 (0.65)	134.1 (16.04)
Warra	Winter	<i>Acacia melanoxylon</i>	8	5.51 (1.51)	0.21 (0.05)	11 (1.3)	148.4 (14.9)	3.7 (0.78)	131.01 (25)
Warra	Winter	<i>Anopterus glandulosus</i>	8	5.97 (1.27)	0.25 (0.09)	11.7 (0.5)	85 (12.6)	1.1 (0.09)	43.26 (7.8)
Warra	Winter	<i>Atherosperma moschatum</i>	10	4.59 (1.22)	0.18 (0.09)	10.5 (0.9)	76.3 (9.2)	1.75 (0.27)	83.48 (14.17)
Warra	Winter	<i>Eucalyptus obliqua</i>	10	5.93 (2.25)	0.51 (0.12)	10.5 (1.1)	192.6 (24.7)	2.63 (0.44)	106.77 (20.98)
Warra	Winter	<i>Eucryphia lucida</i>	1	2.47	0.08	12.51	147.64	1.08	71.00
Warra	Winter	<i>Melaleuca squarrosa</i>	8	5.38 (0.95)	0.23 (0.1)	11.1 (0.5)	101.1 (8.4)	1.12 (0.11)	30.91 (5.82)
Warra	Winter	<i>Nothofagus cunninghamii</i>	10	5.1 (1.78)	0.13 (0.14)	8.4 (0.7)	99 (6.1)	1.5 (0.19)	73.43 (11.86)
Warra	Winter	<i>Phyllocladus aspleniifolius</i>	8	3.97 (2.2)	0.21 (0.13)	11.1 (0.5)	164.6 (47)	1.51 (0.45)	97.59 (27.13)
Warra	Winter	<i>Pittosporum bicolor</i>	3	6.93 (4.02)	0.3 (0.12)	9.3 (0.1)	158.4 (4.9)	2.08 (0.43)	78.53 (23.28)
Warra	Winter	<i>Pomaderris apetala</i>	10	6.12 (1.65)	0.25 (0.1)	10.9 (0.7)	103.7 (15.1)	1.96 (0.21)	72.62 (14.74)

Table S6 contd.

Site	Season	Species	n	$A_{400, a}$	$R_{dark, a}$	TL <sub>leaf</sub>	$M_a$	Leaf $N_a$	Leaf $P_a$
				Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)
Robson Ck	Dry	<i>Alphitonia whitei</i>	4	8.78 (2.54)	0.73 (0.31)	24.6 (0.8)	129.6 (29)	2.3 (0.52)	154.45 (14.11)
Robson Ck	Dry	<i>Alstonia muelleriana</i>	3	6.9 (3.37)	1.14 (0.44)	24.7 (0.5)	82.7 (23.4)	1.93 (0.44)	130.87 (60.25)
Robson Ck	Dry	<i>Cardwellia sublimis</i>	4	7.69 (3.43)	0.67 (0.54)	24.7 (0.7)	104.5 (25.1)	1.59 (0.38)	133.3 (75.56)
Robson Ck	Dry	<i>Ceratopetalum succirubrum</i>	3	3.91 (1.73)	0.64 (0.12)	24 (0.5)	126.9 (39.9)	1.52 (0.36)	129.6 (71.28)
Robson Ck	Dry	<i>Cryptocarya mackinnoniana</i>	4	7.73 (2.65)	1.24 (0.66)	24.9 (1.6)	193.5 (8.5)	3.01 (0.36)	283.15 (65.73)
Robson Ck	Dry	<i>Daphnandra repandula</i>	4	4 (0.88)	0.81 (0.65)	25.1 (0.5)	62.3 (8.7)	1.7 (0.35)	114.08 (19.08)
Robson Ck	Dry	<i>Doryphora aromatica</i>	3	2.26 (1.37)	0.95 (0.42)	24.4 (0.6)	106.3 (5.3)	2.24 (0.53)	161.93 (25.77)
Robson Ck	Dry	<i>Ficus leptoclada</i>	4	4.12 (2.25)	1.14 (0.24)	24.3 (1.1)	115.9 (19.3)	2.48 (0.53)	175.68 (68.14)
Robson Ck	Dry	<i>Flindersia bourjotiana</i>	3	3.92 (2.02)	0.74 (0.18)	25 (0.8)	134.9 (23.4)	2.13 (0.2)	198.8 (17.79)
Robson Ck	Dry	<i>Gillbeea adenopetala</i>	5	6.2 (2.84)	0.81 (0.35)	24.9 (1)	129.1 (10.8)	1.53 (0.07)	169.78 (85.99)
Robson Ck	Dry	<i>Litsea leefeana</i>	4	5.54 (1.49)	0.89 (0.54)	24.7 (0.3)	125.7 (27.6)	2.22 (0.68)	162.23 (67.28)
Robson Ck	Dry	<i>Myristica globosa ssp. muelleri</i>	3	3.8 (2)	0.71 (0.2)	25.3 (0.6)	119 (24.4)	1.97 (0.39)	159.8 (53.27)
Robson Ck	Dry	<i>Polyscias elegans</i>	5	7.18 (1)	0.85 (0.22)	24.5 (0.4)	124.7 (55.2)	2.03 (0.97)	133.02 (74.18)
Robson Ck	Dry	<i>Prunus turneriana</i>	5	9.55 (4.48)	0.65 (0.15)	24.6 (1)	134.3 (21)	2.16 (0.29)	176.28 (35.02)
Robson Ck	Dry	<i>Syzygium johnsonii</i>	3	2.04 (0.09)	0.45 (0.19)	23.7 (0.6)	110.3 (21.1)	1.15 (0.24)	121.03 (37.46)
Robson Ck	Wet	<i>Alphitonia whitei</i>	10	7.29 (2.4)	0.77 (0.4)	27.9 (1.3)	108 (21.8)	1.89 (0.47)	60.36 (11.57)
Robson Ck	Wet	<i>Alstonia muelleriana</i>	7	7.77 (3.9)	1.04 (0.42)	27.8 (1)	91.9 (11.4)	1.71 (0.3)	49.21 (11.66)
Robson Ck	Wet	<i>Cardwellia sublimis</i>	9	7.09 (3.3)	0.82 (0.39)	28.5 (0.9)	105.7 (14.4)	1.48 (0.33)	59.58 (16.96)
Robson Ck	Wet	<i>Ceratopetalum succirubrum</i>	7	3.67 (0.88)	0.55 (0.06)	29 (0.5)	128.6 (16.3)	1.38 (0.15)	42.16 (5.55)
Robson Ck	Wet	<i>Cryptocarya mackinnoniana</i>	9	8.58 (2.24)	0.59 (0.19)	27.7 (0.9)	134.6 (20.4)	2.11 (0.35)	84.66 (15.07)
Robson Ck	Wet	<i>Daphnandra repandula</i>	10	5.72 (1.62)	0.9 (0.21)	28.7 (1.1)	79.3 (12.5)	2.24 (0.29)	75.96 (16.63)
Robson Ck	Wet	<i>Doryphora aromatica</i>	3	3.23 (0.59)	0.48 (0.23)	27.7 (0.5)	85.4 (4.6)	1.75 (0.07)	63.5 (11.87)
Robson Ck	Wet	<i>Ficus leptoclada</i>	10	6.52 (3.29)	1.03 (0.23)	28.4 (0.7)	85.1 (14.2)	1.84 (0.28)	64.06 (8.84)
Robson Ck	Wet	<i>Flindersia bourjotiana</i>	9	8.44 (2.64)	0.74 (0.27)	27.7 (0.5)	142.6 (18.2)	1.8 (0.34)	57.74 (9.16)
Robson Ck	Wet	<i>Gillbeea adenopetala</i>	10	7.78 (3.16)	0.49 (0.13)	28.5 (0.4)	111.8 (24.7)	1.21 (0.22)	40.05 (7.62)
Robson Ck	Wet	<i>Litsea leefeana</i>	10	5.59 (2.5)	1.19 (0.39)	28.5 (1.6)	117.7 (22.2)	2.02 (0.26)	85.65 (16.33)
Robson Ck	Wet	<i>Myristica globosa ssp. muelleri</i>	10	6.15 (2.64)	0.82 (0.26)	28.2 (0.9)	101.1 (12.6)	1.58 (0.28)	83.17 (12.13)
Robson Ck	Wet	<i>Polyscias elegans</i>	10	8.53 (3.21)	1 (0.27)	27.9 (1)	81.5 (17.3)	1.41 (0.37)	58.52 (10.3)
Robson Ck	Wet	<i>Prunus turneriana</i>	10	8.89 (4.25)	0.96 (0.37)	27.5 (0.6)	107.6 (16)	1.89 (0.34)	71.87 (12.29)

Table S6 contd.

Site	Season	Species	n	$A_{400, a}$	$R_{dark, a}$	Tileaf	$M_a$	Leaf $N_a$	Leaf $P_a$
				Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)
Daintree	Dry	<i>Syzygium graveolens</i>	4	12.72 (3.38)	1.84 (0.56)	30.9 (0.5)	152.4 (42.5)	2.97 (0.88)	187.88 (78.56)
Daintree	Dry	<i>Alstonia scholaris</i>	4	12.64 (2.29)	1.24 (0.45)	31.4 (0.6)	113.6 (20.6)	2.57 (0.22)	149.13 (54.77)
Daintree	Dry	<i>Argyrodendron peralatum</i>	4	15.08 (0.69)	1.44 (0.24)	30.6 (0.1)	172.1 (19.1)	2.66 (0.16)	140.6 (10.64)
Daintree	Dry	<i>Cardwellia sublimis</i>	4	12.34 (1.48)	0.99 (0.38)	31.1 (0.5)	124 (12.9)	2.96 (0.59)	93.25 (8.84)
Daintree	Dry	<i>Castanospermum australe</i>	4	13.31 (1.21)	1.29 (0.47)	29.2 (0.4)	94 (16)	2.93 (0.76)	151.53 (23.33)
Daintree	Dry	<i>Cryptocarya mackinnoniana</i>	4	15.16 (0.7)	1.04 (0.39)	29.7 (0.3)	187.2 (20.6)	3.51 (0.36)	159.53 (27.54)
Daintree	Dry	<i>Dysoxylum papuanum</i>	4	13.62 (0.94)	1.78 (0.34)	30.8 (0.8)	90.3 (2.1)	2.66 (0.19)	122.67 (11)
Daintree	Dry	<i>Elaeocarpus grandis</i>	4	18.16 (0.74)	1.15 (0.27)	29.4 (0.2)	109.8 (7.3)	2.7 (0.49)	133.58 (19.58)
Daintree	Dry	<i>Endiandra leptodendron</i>	4	10.43 (1.11)	0.78 (0.31)	30.4 (0.4)	88.2 (10)	2.2 (0.19)	92.7 (3.06)
Daintree	Dry	<i>Ficus variegata</i>	2	9.59 (0.3)	1.33 (0.63)	31.2 (0.6)	38.4 (4)	1.31 (0.03)	119.25 (23.97)
Daintree	Dry	<i>Gillbeea whypallana</i>	4	11.85 (4.15)	1.25 (0.35)	30.5 (0.8)	147.4 (19.7)	2.27 (0.23)	93.15 (8.47)
Daintree	Dry	<i>Myristica globosa ssp. muelleri</i>	4	8.75 (2.85)	1.15 (0.69)	31 (0.1)	118.9 (12.4)	2.54 (0.13)	126.63 (14.36)
Daintree	Dry	<i>Rockinghamia angustifolia</i>	4	5.61 (1.52)	0.62 (0.26)	30.2 (0.3)	75.3 (7.4)	1.44 (0.14)	70.43 (9.84)
Daintree	Dry	<i>Synima cordierorum</i>	4	10.99 (0.94)	1.21 (0.39)	31.7 (0.4)	113.9 (6)	2.61 (0.18)	128.4 (21.52)
Daintree	Dry	<i>Syzygium sayeri</i>	4	11.09 (0.63)	1.15 (0.32)	31.3 (0.4)	116.3 (9.6)	2.45 (0.31)	118.45 (19.57)
Daintree	Dry	<i>Xanthophyllum octandrum</i>	3	9.12 (2.77)	0.78 (0.24)	30.9 (0.4)	121.4 (2.4)	1.88 (0.19)	91.5 (5.16)
Daintree	Wet	<i>Syzygium graveolens</i>	7	7.59 (3.72)	1.62 (0.51)	31.8 (0.5)	134.3 (21.2)	2.42 (0.28)	101.93 (31.03)
Daintree	Wet	<i>Alstonia scholaris</i>	8	9.34 (3.39)	1.62 (0.36)	32.3 (0.6)	131.9 (17)	2.18 (0.35)	74.65 (20.33)
Daintree	Wet	<i>Argyrodendron peralatum</i>	7	5.6 (2.71)	1 (0.32)	32.2 (0.7)	155.4 (21.4)	2.32 (0.4)	81.9 (18.54)
Daintree	Wet	<i>Cardwellia sublimis</i>	8	9.7 (2.48)	1.19 (0.24)	32.2 (0.7)	123.2 (14.6)	1.75 (0.19)	55.25 (7.15)
Daintree	Wet	<i>Castanospermum australe</i>	8	6.82 (3.92)	1.46 (0.46)	32.3 (0.7)	102.2 (12.3)	2.98 (0.51)	94.16 (16.36)
Daintree	Wet	<i>Cryptocarya mackinnoniana</i>	8	10.78 (2.85)	0.9 (0.32)	31.8 (0.6)	198.2 (40.6)	3.25 (0.78)	93.95 (15.36)
Daintree	Wet	<i>Dysoxylum papuanum</i>	8	9.56 (2.96)	1.94 (0.55)	32.2 (0.7)	83.7 (9.6)	2.59 (0.35)	81.4 (10.21)
Daintree	Wet	<i>Elaeocarpus grandis</i>	8	15.83 (2.8)	1.25 (0.47)	31.8 (0.7)	103.9 (5.7)	2.29 (0.11)	88.71 (8.31)
Daintree	Wet	<i>Endiandra leptodendron</i>	8	8.11 (0.92)	1 (0.41)	31.8 (0.4)	83.5 (11.8)	2.04 (0.2)	87.06 (21.55)
Daintree	Wet	<i>Ficus variegata</i>	6	14.79 (2.98)	1.38 (0.2)	31.8 (0.1)	82.5 (5.2)	2.01 (0.22)	68.27 (4.22)
Daintree	Wet	<i>Gillbeea whypallana</i>	8	12.76 (1.7)	0.87 (0.3)	31.2 (0.4)	149.5 (38.8)	1.72 (0.48)	38.68 (10.28)
Daintree	Wet	<i>Myristica globosa ssp. muelleri</i>	6	8.67 (2.34)	0.84 (0.21)	31.7 (0.3)	102.1 (11.3)	2.16 (0.3)	69.52 (9.79)
Daintree	Wet	<i>Rockinghamia angustifolia</i>	8	5.87 (2.34)	0.92 (0.28)	32.2 (0.4)	98.3 (14.3)	1.74 (0.18)	46.28 (7.71)
Daintree	Wet	<i>Synima cordierorum</i>	8	6.92 (2.87)	1.37 (0.52)	32 (0.7)	101 (10.6)	1.93 (0.23)	105.33 (32.63)
Daintree	Wet	<i>Syzygium sayeri</i>	4	6.86 (2.91)	1.52 (0.35)	32.2 (0.5)	137.5 (12.5)	2.03 (0.34)	60.38 (11.31)
Daintree	Wet	<i>Xanthophyllum octandrum</i>	8	11.26 (2.1)	1.05 (0.16)	31.2 (0.7)	102.6 (13.1)	2.4 (0.14)	66.59 (6.57)

**Table S7** Leaf physiological variables by site and season and species: number of observations ( $n$ , typically two per plant), standard deviation (sd). Rates have been normalised on two bases: to the prevailing air temperature at the time of the campaign (**Table S1**); or to a reference temperature of 25°C. Parameter descriptions and units as per Table S3.

Site	Season	Species	$V_{\text{cmax, a, prevailing}}$		$V_{\text{cmax, a, 25}}$	$R_{\text{dark, a, prevailing}}$		$R_{\text{dark, a, 25}}$
			$n$	Mean (sd)	Mean (sd)	$n$	Mean (sd)	Mean (sd)
Calperum	Summer	<i>Beyeria opaca</i>	7	39.74 (5.88)	38.11 (5.65)	7	2.18 (0.46)	2.12 (0.45)
Calperum	Summer	<i>Dodonaea angustissima</i>	8	57.08 (16)	54.74 (15.34)	8	1.81 (1)	1.76 (0.97)
Calperum	Summer	<i>Dodonaea bursariifolia</i>	8	60.56 (17.44)	58.06 (16.75)	8	1.83 (0.53)	1.78 (0.52)
Calperum	Summer	<i>Eremophila glabra</i>	8	53.9 (18.15)	51.68 (17.41)	8	2.61 (0.88)	2.53 (0.85)
Calperum	Summer	<i>Eucalyptus dumosa</i>	8	71.16 (24.03)	68.26 (23.04)	8	1.28 (0.23)	1.25 (0.22)
Calperum	Summer	<i>Eucalyptus socialis</i>	8	57.29 (20.76)	54.93 (19.92)	8	1.57 (0.47)	1.54 (0.46)
Calperum	Summer	<i>Grevillea huegelii</i>	5	41.04 (21.96)	39.38 (21.05)	5	1.04 (0.53)	1.01 (0.52)
Calperum	Summer	<i>Myoporum platycarpum</i>	6	71.2 (5.59)	68.28 (5.37)	6	1.53 (0.41)	1.48 (0.4)
Calperum	Summer	<i>Senna artemisioides ssp. filifolia</i>	6	47.98 (15.25)	46.02 (14.63)	7	1.77 (0.88)	1.72 (0.86)
Calperum	Summer	<i>Triodia irritans</i>	4	93.63 (37.48)	89.8 (35.97)	6	1.56 (0.39)	1.51 (0.37)
Calperum	Winter	<i>Beyeria opaca</i>	8	17.35 (6.57)	56.31 (21.39)	8	0.65 (0.26)	1.74 (0.69)
Calperum	Winter	<i>Dodonaea angustissima</i>	8	16.71 (3.73)	54.28 (12.09)	8	0.65 (0.17)	1.76 (0.47)
Calperum	Winter	<i>Dodonaea bursariifolia</i>	8	15 (6.07)	48.65 (19.7)	8	0.71 (0.22)	1.9 (0.56)
Calperum	Winter	<i>Eremophila glabra</i>	8	12.74 (3.88)	41.34 (12.66)	8	0.59 (0.18)	1.58 (0.49)
Calperum	Winter	<i>Eucalyptus dumosa</i>	8	28.71 (5.31)	93.26 (17.3)	8	0.53 (0.12)	1.41 (0.33)
Calperum	Winter	<i>Eucalyptus socialis</i>	8	31.66 (7.51)	102.76 (24.41)	8	0.58 (0.13)	1.55 (0.35)
Calperum	Winter	<i>Grevillea huegelii</i>	2	24 (13.44)	77.95 (43.77)	2	0.41 (0.24)	1.12 (0.64)
Calperum	Winter	<i>Myoporum platycarpum</i>	7	28.84 (4.17)	93.64 (13.59)	7	0.6 (0.27)	1.58 (0.66)
Calperum	Winter	<i>Senna artemisioides ssp. filifolia</i>	8	12.61 (5.31)	40.95 (17.2)	8	0.48 (0.14)	1.27 (0.35)
Calperum	Winter	<i>Triodia irritans</i>	6	23.82 (9.87)	77.32 (32.09)	6	0.77 (0.36)	2.06 (0.97)
GWW	Summer	<i>Acacia aneura</i>	6	48.93 (13.92)	56.03 (15.95)	6	1.64 (0.48)	1.8 (0.53)
GWW	Summer	<i>Acacia hemiteles</i>	8	45.71 (17.42)	52.34 (19.97)	8	0.88 (0.27)	0.98 (0.3)
GWW	Summer	<i>Atriplex nummularia</i>	7	61.61 (23.47)	70.57 (26.87)	7	1.61 (0.38)	1.78 (0.42)
GWW	Summer	<i>Eremophila scoparia</i>	10	40.66 (11.26)	46.57 (12.9)	10	2.11 (0.51)	2.33 (0.57)
GWW	Summer	<i>Eucalyptus clelandii</i>	8	60.06 (11.8)	68.78 (13.51)	8	1.87 (0.41)	2.06 (0.46)
GWW	Summer	<i>Eucalyptus salmonophloia</i>	9	35.78 (16.64)	40.99 (19.07)	9	1.76 (0.35)	1.94 (0.38)
GWW	Summer	<i>Eucalyptus salubris</i>	10	35.11 (15.49)	40.2 (17.72)	10	2.08 (0.29)	2.3 (0.32)
GWW	Summer	<i>Eucalyptus transcontinentalis</i>	10	46.68 (15.35)	53.47 (17.55)	10	2 (0.76)	2.21 (0.84)
GWW	Summer	<i>Maireana sedifolia</i>	10	46.74 (14.65)	53.53 (16.78)	10	1.46 (0.61)	1.61 (0.67)
GWW	Winter	<i>Acacia aneura</i>	9	22.07 (8.07)	56.46 (20.62)	10	0.59 (0.26)	1.26 (0.55)
GWW	Winter	<i>Acacia hemiteles</i>	8	20.78 (6.71)	53.18 (17.15)	8	0.4 (0.16)	0.86 (0.34)
GWW	Winter	<i>Atriplex nummularia</i>	8	17.16 (10.53)	43.85 (26.93)	8	0.73 (0.18)	1.51 (0.38)
GWW	Winter	<i>Eremophila scoparia</i>	10	17.34 (4.67)	44.38 (11.9)	10	0.92 (0.31)	1.88 (0.61)
GWW	Winter	<i>Eucalyptus clelandii</i>	10	21.88 (9.15)	55.94 (23.4)	10	0.99 (0.63)	2.08 (1.31)
GWW	Winter	<i>Eucalyptus salmonophloia</i>	8	23.48 (3.99)	60.03 (10.25)	8	0.98 (0.44)	2.09 (0.91)
GWW	Winter	<i>Eucalyptus salubris</i>	10	22.71 (5.9)	58.06 (15.08)	10	0.98 (0.37)	2.16 (0.81)
GWW	Winter	<i>Eucalyptus transcontinentalis</i>	10	23.55 (7.69)	60.28 (19.67)	10	0.86 (0.29)	1.83 (0.62)
GWW	Winter	<i>Maireana sedifolia</i>	8	17.46 (9.46)	44.66 (24.21)	9	0.78 (0.41)	1.62 (0.82)
Alice	Winter	<i>Acacia aneura</i>	14	8.25 (4.27)	19.59 (10.1)	18	0.42 (0.31)	0.81 (0.59)
Alice	Winter	<i>Acacia dictyophleba</i>	8	4.06 (1.69)	9.68 (4.05)	9	0.49 (0.32)	0.98 (0.65)
Alice	Winter	<i>Corymbia terminalis</i>	8	8.94 (13.82)	21.24 (32.8)	8	0.67 (0.36)	1.29 (0.69)
Alice	Winter	<i>Eremophila latrobei</i>	8	7.5 (2.92)	17.79 (6.92)	8	1.24 (0.33)	2.38 (0.64)
Alice	Winter	<i>Eucalyptus camaldulensis</i>	6	21.38 (9.06)	50.8 (21.5)	6	1.21 (0.3)	2.3 (0.56)
Alice	Winter	<i>Hakea leucoptera</i>	6	18.4 (10.81)	43.67 (25.68)	6	0.98 (0.44)	1.94 (0.87)
Alice	Winter	<i>Psyrax latifolia</i>	4	2.63 (0.89)	6.2 (2.05)	4	0.9 (0.32)	1.74 (0.61)



Table S7 contd.

Site	Season	Species	$V_{\text{cmax, a, prevailing}}$		$V_{\text{cmax, a, 25}}$	$R_{\text{dark, a, prevailing}}$		$R_{\text{dark, a, 25}}$
			<i>n</i>	Mean (sd)	Mean (sd)	<i>n</i>	Mean (sd)	Mean (sd)
Cumberland	Summer	<i>Acacia parramattensis</i>	8	48.59 (17.09)	54 (19)	8	1.75 (0.78)	1.87 (0.84)
Cumberland	Summer	<i>Breynea oblongifolia</i>	10	24.58 (8.02)	27.34 (8.93)	10	0.6 (0.2)	0.65 (0.22)
Cumberland	Summer	<i>Eucalyptus amplifolia</i>	8	61.19 (22.26)	68.03 (24.75)	8	2.33 (0.72)	2.5 (0.77)
Cumberland	Summer	<i>Eucalyptus fibrosa</i>	9	35.98 (16.71)	39.99 (18.58)	9	1.11 (0.49)	1.19 (0.53)
Cumberland	Summer	<i>Eucalyptus moluccana</i>	9	46.54 (8.74)	51.74 (9.71)	9	1.31 (0.46)	1.41 (0.49)
Cumberland	Summer	<i>Eucalyptus tereticornis</i>	9	56.87 (14.12)	63.22 (15.68)	9	2.32 (0.55)	2.49 (0.59)
Cumberland	Summer	<i>Hakea sericea</i>	8	34.24 (12.37)	38.08 (13.75)	8	1.97 (0.81)	2.11 (0.87)
Cumberland	Summer	<i>Jacksonia scoparia</i>	10	17.95 (6.44)	19.95 (7.14)	10	0.87 (0.5)	0.94 (0.54)
Cumberland	Summer	<i>Melaleuca decora</i>	10	22.92 (6.95)	25.47 (7.73)	10	0.7 (0.22)	0.75 (0.23)
Cumberland	Summer	<i>Melaleuca nodosa</i>	9	37.54 (22.93)	41.74 (25.52)	9	1.48 (0.47)	1.58 (0.5)
Cumberland	Summer	<i>Ozothamnus diosmifolius</i>	9	35.93 (21.54)	39.97 (23.94)	9	1.18 (0.35)	1.26 (0.38)
Cumberland	Winter	<i>Acacia parramattensis</i>	9	13.06 (5.95)	42.01 (19.22)	9	0.78 (0.28)	2.01 (0.71)
Cumberland	Winter	<i>Breynea oblongifolia</i>	10	6.17 (3.98)	19.85 (12.86)	10	0.31 (0.1)	0.78 (0.26)
Cumberland	Winter	<i>Bursaria spinosa</i>	2	17.05 (1.49)	54.9 (4.81)	2	0.13 (0.01)	0.31 (0.01)
Cumberland	Winter	<i>Eucalyptus amplifolia</i>	8	25.78 (3.8)	82.96 (12.23)	10	0.85 (0.29)	2.13 (0.72)
Cumberland	Winter	<i>Eucalyptus fibrosa</i>	8	7.46 (3.86)	24 (12.45)	8	0.77 (0.37)	1.91 (0.91)
Cumberland	Winter	<i>Eucalyptus moluccana</i>	10	8.56 (4.33)	27.55 (13.95)	10	0.79 (0.27)	1.99 (0.67)
Cumberland	Winter	<i>Eucalyptus tereticornis</i>	8	23.59 (3.6)	75.93 (11.64)	9	1 (0.21)	2.52 (0.54)
Cumberland	Winter	<i>Hakea sericea</i>	10	15.14 (4.65)	48.73 (15)	10	0.45 (0.12)	1.14 (0.31)
Cumberland	Winter	<i>Jacksonia scoparia</i>	6	13.2 (4.34)	42.52 (14)	6	0.68 (0.35)	1.72 (0.88)
Cumberland	Winter	<i>Melaleuca decora</i>	10	12.99 (1.84)	41.78 (5.9)	10	0.31 (0.11)	0.81 (0.29)
Cumberland	Winter	<i>Melaleuca nodosa</i>	10	13.88 (5.26)	44.69 (16.86)	10	0.42 (0.17)	1.09 (0.44)
Cumberland	Winter	<i>Ozothamnus diosmifolius</i>	10	20.66 (6.43)	66.54 (20.68)	10	0.72 (0.31)	1.84 (0.78)
Warra	Summer	<i>Acacia dealbata</i>	1	7.10	16.30	1	0.97	1.90
Warra	Summer	<i>Acacia melanoxylon</i>	5	27.44 (10.66)	62.86 (24.48)	5	0.78 (0.34)	1.51 (0.66)
Warra	Summer	<i>Anopterus glandulosus</i>	4	10.35 (4.39)	23.6 (10.03)	4	0.21 (0.04)	0.41 (0.08)
Warra	Summer	<i>Atherosperma moschatum</i>	4	11.73 (6.7)	26.83 (15.28)	4	0.57 (0.3)	1.12 (0.58)
Warra	Summer	<i>Eucalyptus obliqua</i>	5	32.4 (8.01)	74.16 (18.33)	5	0.98 (0.43)	1.94 (0.84)
Warra	Summer	<i>Eucryphia lucida</i>	4	8.68 (7.36)	19.83 (16.84)	4	0.36 (0.15)	0.71 (0.29)
Warra	Summer	<i>Leptospermum lanigerum</i>	3	25.23 (0.4)	57.8 (0.95)	3	1.09 (0.17)	2.14 (0.33)
Warra	Summer	<i>Melaleuca squarrosa</i>	3	19.9 (7.27)	45.57 (16.64)	3	0.71 (0.2)	1.37 (0.4)
Warra	Summer	<i>Notelaea ligustrina</i>	4	22.78 (5.9)	52.1 (13.48)	4	0.97 (0.4)	1.9 (0.79)
Warra	Summer	<i>Nothofagus cunninghamii</i>	4	13.93 (5.08)	31.88 (11.65)	4	0.73 (0.26)	1.43 (0.5)
Warra	Summer	<i>Phyllocladus aspleniifolius</i>	2	21.8 (1.84)	49.85 (4.17)	2	1.15 (0.24)	2.25 (0.46)
Warra	Summer	<i>Pittosporum bicolor</i>	4	20.13 (5.48)	46.1 (12.5)	4	0.57 (0.09)	1.1 (0.17)
Warra	Summer	<i>Pomaderris apetala</i>	3	6.53 (4.94)	14.9 (11.35)	3	0.43 (0.04)	0.85 (0.09)
Warra	Summer	<i>Tasmannia lanceolata</i>	4	20.1 (4.64)	46 (10.62)	4	0.49 (0.17)	0.94 (0.34)
Warra	Winter	<i>Acacia dealbata</i>	8	8.84 (4.43)	49.6 (24.75)	8	0.24 (0.12)	1.13 (0.58)
Warra	Winter	<i>Acacia melanoxylon</i>	8	8.76 (2.85)	49.15 (15.98)	8	0.16 (0.04)	0.76 (0.21)
Warra	Winter	<i>Anopterus glandulosus</i>	8	8.55 (1.95)	47.89 (10.94)	8	0.19 (0.07)	0.89 (0.33)
Warra	Winter	<i>Atherosperma moschatum</i>	10	8.03 (2.03)	45.08 (11.34)	10	0.14 (0.07)	0.66 (0.32)
Warra	Winter	<i>Eucalyptus obliqua</i>	10	11.24 (3.2)	63.1 (17.96)	10	0.4 (0.1)	1.9 (0.45)
Warra	Winter	<i>Eucryphia lucida</i>	1	4.00	22.20	1	0.05	0.25
Warra	Winter	<i>Melaleuca squarrosa</i>	7	7.79 (1.11)	43.59 (6.3)	7	0.17 (0.08)	0.8 (0.35)
Warra	Winter	<i>Nothofagus cunninghamii</i>	9	9.8 (2.8)	55.02 (15.73)	9	0.12 (0.13)	0.57 (0.64)
Warra	Winter	<i>Phyllocladus aspleniifolius</i>	8	6.35 (3.57)	35.64 (19.95)	8	0.16 (0.1)	0.74 (0.46)
Warra	Winter	<i>Pittosporum bicolor</i>	3	11.37 (6.75)	63.67 (37.9)	3	0.24 (0.1)	1.13 (0.46)
Warra	Winter	<i>Pomaderris apetala</i>	10	9.1 (2.12)	51.01 (11.75)	10	0.19 (0.08)	0.89 (0.38)

Table S7 contd.

Site	Season	Species	$V_{\text{cmax, a, prevailing}}$		$V_{\text{cmax, a, 25}}$	$R_{\text{dark, a, prevailing}}$		$R_{\text{dark, a, 25}}$
			<i>n</i>	Mean (sd)	Mean (sd)	<i>n</i>	Mean (sd)	Mean (sd)
Robson Ck	Dry	<i>Alphitonia whitei</i>	4	19.55 (4.72)	39.7 (9.52)	4	0.46 (0.18)	0.79 (0.3)
Robson Ck	Dry	<i>Alstonia muelleriana</i>	3	16.7 (7.63)	33.83 (15.49)	3	0.76 (0.31)	1.31 (0.55)
Robson Ck	Dry	<i>Cardwellia sublimis</i>	4	17.9 (5.56)	36.3 (11.29)	4	0.43 (0.32)	0.74 (0.54)
Robson Ck	Dry	<i>Ceratopetalum succirubrum</i>	3	10.07 (4.19)	20.37 (8.42)	3	0.44 (0.11)	0.76 (0.2)
Robson Ck	Dry	<i>Cryptocarya mackinnoniana</i>	4	20.25 (6.89)	41.05 (14.02)	4	0.86 (0.5)	1.49 (0.87)
Robson Ck	Dry	<i>Daphnandra repandula</i>	4	11.35 (3.24)	23.08 (6.57)	4	0.52 (0.42)	0.9 (0.72)
Robson Ck	Dry	<i>Doryphora aromatica</i>	3	7.77 (4.21)	15.7 (8.47)	3	0.66 (0.32)	1.13 (0.56)
Robson Ck	Dry	<i>Ficus leptoclada</i>	4	10.35 (4.76)	20.98 (9.62)	4	0.8 (0.19)	1.4 (0.34)
Robson Ck	Dry	<i>Flindersia bourjotiana</i>	3	9.43 (4.01)	19.1 (8.14)	3	0.47 (0.14)	0.82 (0.24)
Robson Ck	Dry	<i>Gillbeea adenopetala</i>	5	14.58 (6.74)	29.58 (13.69)	5	0.51 (0.18)	0.87 (0.31)
Robson Ck	Dry	<i>Litsea leefeana</i>	4	15.1 (4.09)	30.68 (8.34)	4	0.62 (0.4)	1.08 (0.69)
Robson Ck	Dry	<i>Myristica globosa ssp. muelleri</i>	3	11.07 (5.65)	22.4 (11.51)	3	0.45 (0.12)	0.77 (0.21)
Robson Ck	Dry	<i>Polyscias elegans</i>	5	17.3 (3.11)	35.12 (6.27)	5	0.56 (0.18)	0.97 (0.32)
Robson Ck	Dry	<i>Prunus turneriana</i>	5	21.98 (8.13)	44.56 (16.56)	5	0.44 (0.11)	0.76 (0.2)
Robson Ck	Dry	<i>Syzygium johnsonii</i>	3	5.7 (1.47)	11.6 (3.05)	3	0.3 (0.15)	0.52 (0.26)
Robson Ck	Wet	<i>Alphitonia whitei</i>	10	22.86 (4.94)	30.42 (6.57)	10	0.56 (0.29)	0.69 (0.36)
Robson Ck	Wet	<i>Alstonia muelleriana</i>	7	25.31 (11.33)	33.64 (15.06)	7	0.76 (0.3)	0.94 (0.37)
Robson Ck	Wet	<i>Cardwellia sublimis</i>	9	22.1 (8.9)	29.4 (11.83)	10	0.58 (0.3)	0.72 (0.37)
Robson Ck	Wet	<i>Ceratopetalum succirubrum</i>	7	13.67 (3.94)	18.17 (5.24)	7	0.41 (0.05)	0.5 (0.06)
Robson Ck	Wet	<i>Cryptocarya mackinnoniana</i>	8	28.24 (6.74)	37.58 (8.96)	8	0.44 (0.13)	0.54 (0.17)
Robson Ck	Wet	<i>Daphnandra repandula</i>	10	18.87 (4.51)	25.08 (6.03)	10	0.64 (0.15)	0.8 (0.18)
Robson Ck	Wet	<i>Doryphora aromatica</i>	3	10.83 (2.06)	14.4 (2.78)	3	0.36 (0.16)	0.45 (0.2)
Robson Ck	Wet	<i>Ficus leptoclada</i>	10	21 (9.87)	27.94 (13.14)	10	0.76 (0.17)	0.94 (0.21)
Robson Ck	Wet	<i>Flindersia bourjotiana</i>	9	27.51 (8.05)	36.59 (10.75)	9	0.58 (0.21)	0.72 (0.26)
Robson Ck	Wet	<i>Gillbeea adenopetala</i>	10	22.15 (8.95)	29.46 (11.91)	10	0.36 (0.1)	0.44 (0.13)
Robson Ck	Wet	<i>Litsea leefeana</i>	10	19.13 (5.52)	25.46 (7.39)	10	0.81 (0.25)	1 (0.3)
Robson Ck	Wet	<i>Myristica globosa ssp. muelleri</i>	10	23.11 (7.99)	30.75 (10.63)	10	0.59 (0.18)	0.73 (0.22)
Robson Ck	Wet	<i>Polyscias elegans</i>	10	28.39 (9.95)	37.73 (13.24)	10	0.71 (0.19)	0.88 (0.23)
Robson Ck	Wet	<i>Prunus turneriana</i>	10	29.69 (11.53)	39.48 (15.33)	10	0.69 (0.26)	0.85 (0.32)

Table S7 contd.

Site	Season	Species	$V_{\text{cmax, a, prevailing}}$		$V_{\text{cmax, a, 25}}$		$R_{\text{dark, a, prevailing}}$		$R_{\text{dark, a, 25}}$	
			<i>n</i>	Mean (sd)	Mean (sd)	Mean (sd)	<i>n</i>	Mean (sd)	Mean (sd)	
Daintree	Dry	<i>Syzygium graveolens</i>	4	49.48 (10.55)	52.18 (11.12)	4	1.38 (0.44)	1.44 (0.46)		
Daintree	Dry	<i>Alstonia scholaris</i>	4	50.48 (10.88)	53.25 (11.45)	4	0.93 (0.34)	0.96 (0.36)		
Daintree	Dry	<i>Argyrodendron peralatum</i>	4	58.78 (3.68)	62 (3.87)	4	1.05 (0.13)	1.09 (0.14)		
Daintree	Dry	<i>Cardwellia sublimis</i>	4	42.88 (6.63)	45.2 (7.01)	4	0.76 (0.3)	0.79 (0.31)		
Daintree	Dry	<i>Castanospermum australe</i>	4	57.9 (9.6)	61.05 (10.14)	4	1.04 (0.37)	1.08 (0.38)		
Daintree	Dry	<i>Cryptocarya mackinnoniana</i>	4	57.28 (5.69)	60.43 (5.97)	4	0.81 (0.29)	0.84 (0.3)		
Daintree	Dry	<i>Dysoxylum papuanum</i>	3	51.1 (1.4)	53.9 (1.48)	3	1.33 (0.26)	1.38 (0.27)		
Daintree	Dry	<i>Elaeocarpus grandis</i>	4	65.23 (4.11)	68.8 (4.28)	4	0.92 (0.22)	0.95 (0.23)		
Daintree	Dry	<i>Endiandra leptodendron</i>	4	35.95 (4.62)	37.9 (4.86)	4	0.6 (0.24)	0.63 (0.25)		
Daintree	Dry	<i>Ficus variegata</i>	2	36.5 (0.14)	38.5 (0.14)	2	1.01 (0.5)	1.05 (0.52)		
Daintree	Dry	<i>Gillbeea whypallana</i>	4	48.15 (10.37)	50.78 (10.96)	4	0.98 (0.26)	1.01 (0.28)		
Daintree	Dry	<i>Myristica globosa ssp. muelleri</i>	4	36.05 (9.26)	38.05 (9.75)	4	0.85 (0.51)	0.88 (0.53)		
Daintree	Dry	<i>Rockinghamia angustifolia</i>	4	18.3 (4.88)	19.3 (5.18)	4	0.49 (0.2)	0.5 (0.21)		
Daintree	Dry	<i>Synima cordierorum</i>	4	41.3 (1.61)	43.58 (1.7)	4	0.89 (0.29)	0.93 (0.3)		
Daintree	Dry	<i>Syzygium sayeri</i>	4	49.9 (1.9)	52.58 (1.99)	4	0.85 (0.25)	0.89 (0.25)		
Daintree	Dry	<i>Xanthophyllum octandrum</i>	3	36.43 (9.59)	38.43 (10.14)	3	0.61 (0.19)	0.63 (0.2)		
Daintree	Wet	<i>Syzygium graveolens</i>	7	33.21 (14.37)	33.21 (14.37)	7	1.15 (0.35)	1.15 (0.35)		
Daintree	Wet	<i>Alstonia scholaris</i>	8	43.25 (17.27)	43.25 (17.27)	8	1.14 (0.26)	1.14 (0.26)		
Daintree	Wet	<i>Argyrodendron peralatum</i>	7	29.17 (11.65)	29.17 (11.65)	7	0.73 (0.24)	0.73 (0.24)		
Daintree	Wet	<i>Cardwellia sublimis</i>	8	37.51 (7.62)	37.51 (7.62)	8	0.83 (0.17)	0.83 (0.17)		
Daintree	Wet	<i>Castanospermum australe</i>	7	35.21 (15.75)	35.21 (15.75)	7	1.04 (0.32)	1.04 (0.32)		
Daintree	Wet	<i>Cryptocarya mackinnoniana</i>	8	41.49 (10.45)	41.49 (10.45)	8	0.66 (0.24)	0.66 (0.24)		
Daintree	Wet	<i>Dysoxylum papuanum</i>	8	40.68 (11.28)	40.68 (11.28)	8	1.38 (0.4)	1.38 (0.4)		
Daintree	Wet	<i>Elaeocarpus grandis</i>	8	61.94 (4.78)	61.94 (4.78)	8	0.89 (0.34)	0.89 (0.34)		
Daintree	Wet	<i>Endiandra leptodendron</i>	8	29.83 (4.76)	29.83 (4.76)	8	0.72 (0.29)	0.72 (0.29)		
Daintree	Wet	<i>Ficus variegata</i>	6	56.73 (9.76)	56.73 (9.76)	6	1.04 (0.13)	1.04 (0.13)		
Daintree	Wet	<i>Gillbeea whypallana</i>	8	43.53 (6.02)	43.53 (6.02)	8	0.63 (0.21)	0.63 (0.21)		
Daintree	Wet	<i>Myristica globosa ssp. muelleri</i>	6	37.23 (10.62)	37.22 (10.6)	6	0.59 (0.14)	0.59 (0.14)		
Daintree	Wet	<i>Rockinghamia angustifolia</i>	8	22.1 (7.93)	22.1 (7.93)	8	0.66 (0.22)	0.66 (0.22)		
Daintree	Wet	<i>Synima cordierorum</i>	8	30.43 (11.78)	30.43 (11.78)	8	0.98 (0.39)	0.98 (0.39)		
Daintree	Wet	<i>Syzygium sayeri</i>	4	35.38 (15.08)	35.38 (15.08)	4	1.12 (0.26)	1.12 (0.26)		
Daintree	Wet	<i>Xanthophyllum octandrum</i>	7	45.8 (5.27)	45.8 (5.27)	7	0.78 (0.11)	0.78 (0.11)		

## Reference

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965-1978.