





# Stem diameter growth rates in a fire-prone savanna correlate with photosynthetic rate and branch-scale biomass allocation, but not specific leaf area

IAN J. WRIGHT,<sup>1\*</sup>  JULIA COOKE,<sup>1,2</sup>  LUCAS A. CERNUSAK,<sup>3</sup>   
 LINDSAY B. HUTLEY,<sup>4</sup>  MARINA C. SCALON,<sup>1,5</sup> WADE C. TOZER<sup>1</sup> AND  
 CAROLINE E. R. LEHMANN<sup>1,6</sup>

<sup>1</sup>Department of Biological Sciences, Macquarie University, North Ryde, New South Wales 2109, Australia (Email: [ian.wright@mq.edu.au](mailto:ian.wright@mq.edu.au)); <sup>2</sup>School of Environment, Earth & Ecosystem Sciences, The Open University, Milton Keynes, UK; <sup>3</sup>College of Science and Engineering, James Cook University, Cairns, Queensland; <sup>4</sup>School of Environmental and Life Sciences, Charles Darwin University, Darwin, Northern Territory, Australia; <sup>5</sup>School of Geography and the Environment, Environmental Change Institute, University of Oxford, Oxford; <sup>6</sup>School of Geosciences, The University of Edinburgh, Edinburgh, UK

**Abstract** Plant growth rates strongly determine ecosystem productivity and are a central element of plant ecological strategies. For laboratory and glasshouse-grown seedlings, specific leaf area (SLA; ratio of leaf area to mass) is a key driver of interspecific variation in growth rate (GR). Consequently, SLA is often assumed to drive GR variation in field-grown adult plants. However, there is an increasing evidence that this is not the general case. This suggests that GR – SLA relationships (and perhaps those for other traits) may vary depending on the age or size of the plants being studied. Here we investigated GR – trait relationships and their size dependence among 17 woody species from an open-canopy, fire-prone savanna in northern Australia. We tested the predictions that SLA and stem diameter growth rate would be positively correlated in saplings but unrelated in adults while, in both age classes, faster-GR species would have higher light-saturated photosynthetic rate ( $A_{\text{sat}}$ ), higher leaf nutrient concentrations, higher branch-scale biomass allocation to leaf *versus* stem tissues and lower wood density (WD). SLA showed no relationship to stem diameter GR, even in saplings, and the same was true of leaf N and P concentrations, and WD. However, branch-scale leaf:stem allocation was strongly related to GR in both age groups, as was  $A_{\text{sat}}$ . Together, these two traits accounted for up to 80% of interspecific variation in adult GR, and 41% of sapling GR.  $A_{\text{sat}}$  is rarely measured in field-based GR studies, and this is the first report of branch-scale leaf:stem allocation (analogous to a benefit:cost ratio) in relation to plant growth rate. Our results suggest that we may yet find general trait-drivers of field growth rates, but SLA will not be one.

**Key words:** leaf, leaf economic spectrum, plant functional traits, relative growth rate, specific leaf area, stem allocation.

## INTRODUCTION

Growth rate differences between species are critical in determining the outcome of competition, while forest, shrubland and grassland yields – and carbon sequestration – are driven by growth rates. Since the 1970s, seedling relative growth rate (RGR; the dry mass increase per unit dry mass per unit time) has been treated as a key element of plant ecological strategies (Grime & Hunt 1975; Lambers & Poorter 1992; Grime *et al.* 1997; Lambers *et al.* 1998). A chief focus in that literature has been on identifying the key drivers of RGR variation. Although other

formulations are possible (Lambers & Poorter 1992; Enquist *et al.* 2007; Cernusak *et al.* 2008), RGR is most commonly mathematically decomposed as follows:

$$\text{RGR} = \text{NAR} \times \text{SLA} \times \text{LMF}; \quad (1)$$

where NAR is net assimilation rate (dry mass growth rate per unit leaf area), LMF is leaf mass fraction (leaf dry mass/plant dry mass) and SLA is specific leaf area (leaf area/leaf dry mass). A meta-analysis of 111 studies concerning herbaceous species found SLA to account for 64% of RGR variation, whereas NAR and LMF accounted for just 26% and 11%, respectively (Poorter & van der Werf 1998). For woody species, meta-analyses have shown LMF has

\*Corresponding author.

Accepted for publication October 2018.

only a weak influence on RGR, with NAR and SLA being the dominant terms (Veneklaas & Poorter 1998; Shipley 2006). For seedlings, NAR variation is thought to largely reflect photosynthetic rate; for older plants, other factors presumably become increasingly influential on NAR, most especially carbon losses from tissue turnover, tissue respiration and root exudates (Konings 1989; Poorter & Garnier 2007; Li *et al.* 2016).

But do high SLA species achieve faster growth rates also as adults? Intuitively one might think so. After all, high SLA species typically have high leaf N and P concentrations and various other traits indicative of a 'fast' lifestyle (Reich 2014). However, it seems increasingly apparent that SLA and field-measured growth rates are most commonly unrelated (Gower *et al.* 1993; Coomes & Grubb 1998; Poorter *et al.* 2008; Aiba & Nakashizuka 2009; Easdale & Healey 2009; Martínez-Vilalta *et al.* 2010; Hérault *et al.* 2011; Rüger *et al.* 2012; Paine *et al.* 2015). In only a minority of cases – mostly for saplings or small trees – has a positive SLA-growth relationship been reported and even then, only weakly (Reich *et al.* 1992; Prior *et al.* 2004; Poorter & Bongers 2006; Rossatto *et al.* 2009; Wright *et al.* 2010). This raises the question, how is it that, through ontogeny – or with increasing plant size – variation in SLA becomes less strongly correlated with plant growth rate? This is an important question, with species-dimensions running from slow to fast growth rates, and low to high SLA, being widely accepted as pivotal in plant ecological strategies (Grime *et al.* 1997; Westoby *et al.* 2002; Reich 2014).

One potential explanation is that low SLA species accumulate more massive canopies over time (because of their longer leaf lifespan), and this counteracts their slower per-gram metabolic rates such that annual productivity can be as high as that of a high SLA species (Chabot & Hicks 1982; Matyssek 1986; Reich *et al.* 1992). Another potential explanation was outlined by Gibert *et al.* (2016). In their first-principles plant growth model, SLA always had a positive influence on growth rate but, as plants grow, this effect becomes increasingly masked by leaf turnover costs (which are higher in high SLA species, because of short leaf lifespan) and by increasing sapwood respiration costs – because larger plants have relatively more sapwood (King 1999; Poorter *et al.* 2012). Other predictions from this model were that, irrespective of plant size, light-saturated photosynthetic rate ( $A_{\text{sat}}$ ) should correlate positively with growth rate, and wood density negatively. Meta-analysis across a range of trait – growth studies showed broad support for these predictions, though low sample size (number of studies) was a recurring problem for the analysis (Gibert *et al.* 2016).

Considering plant growth as an outcome of the balance between sapwood respiration and leaf photosynthesis is not new. For example, slower growth rates in larger (older) trees are likely a result of whole-plant sapwood volume increasing more rapidly over time than canopy leaf area (Ryan 1989). Of particular interest for this study, one can make a related argument at branch-scale. That is, species (or indeed, individuals) deploying more leaf relative to stem wood and bark on terminal branches (i.e. with higher branch-scale LMF) should – all else equal – achieve faster whole-plant growth rates (Pickup *et al.* 2005). This intriguing proposition remains untested.

In this study we investigated the size-dependence of relationships between growth rate and several key plant functional traits (including branch-scale leaf:stem allocation), for a range of woody species from a fire-prone savanna in northern Australia. We chose this vegetation type because we expected the predicted relationships to be most clearly expressed in a situation where competition for light is minimal, and potential photosynthetic benefits are more likely to be realized. For each species we sampled traits both on small-DBH individuals and on larger-DBH individuals (henceforth called 'saplings' and 'adults'), and matched the trait data to previously reported long-term, stem-diameter growth rate data, re-calculated separately for small and large individuals. We tested the following predictions: (i) The GR – SLA relationship would be positive in saplings but absent among adult plants; (ii)  $A_{\text{sat}}$  (expressed per unit leaf area) would explain substantial variation in GR, both in saplings and adults; (iii) Trends in leaf N and P would mirror those in  $A_{\text{sat}}$  (e.g. because N-rich proteins and P-rich energetic molecules play key roles in plant metabolism); (iv) Sapwood tissue density would be negatively related to GR both in saplings and adults and (v) Branch-scale leaf:stem biomass allocation would correlate positively with GR, both in saplings and adults.

## MATERIALS AND METHODS

### Trait dataset: Site and species selection

We sampled species at Howard Springs Nature Reserve, 30 km east from Darwin. The savanna vegetation there is typical of the region, with an overstorey dominated by eucalypts and an understorey dominated by C<sub>4</sub> grasses. Overstorey leaf area index ranges between about 0.6 in the dry season to 1 in the wet season (Hutley *et al.* 2001). At Darwin airport (20 km to the west), long-term annual rainfall is 1736 mm, typically with >95% of rain falling during the wet season (October–April). Mean annual temperature is 27.6°C (data from [www.bom.gov.au](http://www.bom.gov.au)). Fires occur regularly in the dry season; typical fire return intervals in the region are 1–3 years (Russell-Smith *et al.* 2003). Soils at the site

are sandy and low in nutrients: mean (and standard deviation) nutrient concentrations in eight soil samples (0–20 cm depth) collected in September 2010 were as follows: total C = 2.7% (1.8), total N = 0.093% (0.074), total P = 72.7 mg kg<sup>-1</sup> (22.6).

Deciduous, semi-deciduous and evergreen species are all present in this savanna. Hence, we sampled plant traits at two time points: at the end of one dry season (September 2010), when deciduous species are leafless and the canopies of semi-deciduous species are at their thinnest; and right at the end of the subsequent wet season (early May 2011), when most species still tend to have full or nearly-full canopies (Williams *et al.* 1997). We selected 17 species to study, based on available growth rate data and their availability across two nearby sub-sites (12°27'10"S, 131°6'30"E; 12°27'57"S, 131°6'51"E). This species-set represents a range of functional types (trees and shrubs; nitrogen-fixers and non-fixers; deciduous, semi-deciduous and evergreen species; Table 1). We used diameter at breast height (DBH) to identify 'adults' *versus* 'saplings' for each species, but we use these terms informally (i.e. not necessarily reflecting degree of reproductive maturity), and synonymously with 'small individuals' and 'large individuals' of each species (Prior *et al.* 2006). For species that are large trees at maturity we used a DBH cut-off of 6 cm to distinguish saplings from adults; for smaller trees and shrub species we used a 3 cm cut-off, with the exception of the small, short-lived and fast growing species *Acacia difficilis*, for which we used a cut-off of 1.5 cm DBH (Table 1). When choosing plants to sample we prioritized individuals of each species which clearly fell into these size-defined 'sapling' and 'adult' categories, so as to minimize ambiguity in this regard. For each age/size class of each species we aimed to make trait measurements on each of five individuals.

### Leaf traits

Five recently-matured, fully-expanded and undamaged leaves (including petioles) were collected from each individual for determination of one-sided projected leaf area (flatbed scanner), oven-dried mass (70°C for at least 48 h) and thus SLA (area per dry mass; cm<sup>2</sup> g<sup>-1</sup>). Total N concentration of leaf and soil samples was measured with a LECO TruSpec CHN analyser; total P by ICP-OES, on nitric acid digests (analyses run at Appleton Lab, University of Queensland). Area-based leaf N and P concentrations were calculated from mass-based concentrations and the mean SLA value for each species/age class.

Light-saturated rates of photosynthesis ( $A_{sat}$ ) and stomatal conductance to water vapour ( $g_s$ ) were measured during the wet season only, using a Li-Cor 6400XT portable infra-red gas analyser (5–8 replicate plants per species/age class). These measurements were made on leaves held on detached branches, >1 m in length; branch-ends were recut and kept in water post-harvest until photosynthesis was measured (within 5 min of harvesting). Cuvette block temperature was kept at 26–27°C, reference CO<sub>2</sub> was set to 400 ppm and cuvette photosynthetic photon flux density was maintained at 2000 μmol m<sup>-2</sup> s<sup>-1</sup>. Cuvette vapour pressure deficit was only loosely controlled, averaging

1.22 kPa across all measurements (standard deviation 0.28). Leaf lamina material used in photosynthetic measurements was oven-dried and pooled per species/age class, then analysed for <sup>13</sup>C/<sup>12</sup>C stable isotope composition (hereafter 'δ<sup>13</sup>C') at the Stable Isotopes Laboratory, Australian National University, Canberra. The δ<sup>13</sup>C provides an integrated measure of the extent of CO<sub>2</sub> drawdown during photosynthesis (Farquhar *et al.* 1982). We also measured δ<sup>13</sup>C on representative whole-leaf (including petiole) samples collected during September 2010 (dry season).

### Branch traits

A single terminal branch, 80 cm in length, was sampled from each of several individuals of each species/age class (average, 4.8 branches per species/age). These were divided into segments cut at 5, 10, 20, 40 and 80 cm from the terminal end and oven-dried at 70°C for at least 5 days. For each 80 cm branch (and including material on any side-branches) we calculated (i) total leaf dry mass, (ii) total stem dry mass, (iii) the ratio of leaf:stem dry mass for this 80 cm segment (hereafter LM:SM), (iv) the ratio of leaf area: stem dry mass (by multiplying leaf mass by the appropriate SLA value; hereafter LA:SM) and (v) the allometric slope describing leaf mass accumulation *versus* stem mass accumulation (hereafter a\_LMSM). This slope was estimated for accumulations from the tip going back down the stem, expressed at the 5, 10, 20, 40 and 80 cm sampling points. These allometries were calculated as standardized major axis slopes (Warton *et al.* 2006) fitted to log-transformed data. The 'static ratio' (LM:SM, LA:SM) and allometric (a\_LMSM) descriptors were of course correlated, but sufficiently weakly (mean  $r^2$  across age/season datasets = 0.37) that they contained substantial independent information about branch-scale leaf:stem allocation.

Stem tissue density (dry mass per fresh volume) was measured on 2 cm long branch segments of approximately 1 cm over-bark diameter. For dry season samples, density was measured on whole stems, including bark. For wet season samples, the bark was first removed, allowing us to measure relative dry mass allocation to bark *versus* sapwood. For these samples, stem density refers to that of the sapwood only (plus any pith, if present). Hereafter we refer to these quantities as 'WD' (wood density). At each date, five samples were taken per species/age class. Sample volumes were measured using standard procedure (via displacement), and dry masses after oven-drying at 70°C for 7 days.

### Growth rates

The stem increment (growth rate) data were not measured as part of this study. Data for northern Australian savanna species came from two sources: (i) The 'Kapalga' dataset and (ii) the 'Three Parks' dataset (Murphy *et al.* 2010). Kapalga (12°50'S, 132°50'E) is located 200 km east of Darwin in Kakadu National Park. It was run as a CSIRO research station from the mid-1970s to the mid-1990s. Various combinations of fire frequency and severity were generated between 1990 and 1995 (Cook & Corbett 2003; Williams *et al.* 2003). Stem diameters at 1.3 m height

**Table 1.** List of study species, some key life history characteristics, the stem diameter cut-offs (at 1.3 m height) used to distinguish small plants ('saplings') from large plants ('adults') and the sample size (number of data points) used for estimating stem-diameter growth rates

Species	Family	Leaf phenology	Habit	N <sub>2</sub> fixer	DBH cut-off (cm)	GR sample size (saplings, adults)
<i>Acacia difficilis</i>	Fabaceae	Evergreen	Shrub	Yes	1.5	–, 19
<i>Acacia latescens</i>	Fabaceae	Evergreen	Shrub	Yes	3	77, 67
<i>Acacia mimula</i>	Fabaceae	Evergreen	Shrub	Yes	3	15, 31
<i>Buchanania obovata</i>	Anacardiaceae	Semi-deciduous	Tree	No	6	31, 95
<i>Cochlospermum fraseri</i>	Bixaceae	Deciduous	Tree	No	3	8, 21
<i>Corymbia bleeseri</i>	Myrtaceae	Semi-deciduous	Tree	No	6	44, 220
<i>Corymbia porrecta</i>	Myrtaceae	Semi-deciduous	Tree	No	6	207, 752
<i>Erythrophleum chlorostachys</i>	Fabaceae	Semi-deciduous	Tree	Yes	6	273, 741
<i>Eucalyptus miniata</i>	Myrtaceae	Evergreen	Tree	No	6	635, 1559
<i>Eucalyptus tetradonta</i>	Myrtaceae	Evergreen	Tree	No	6	346, 1810
<i>Grevillea decurrens</i>	Proteaceae	Semi-deciduous	Shrub	No	3	–, 9
<i>Grevillea pteridifolia</i>	Proteaceae	Semi-deciduous	Shrub	No	3	12, 94
<i>Lophostemon lactifluus</i>	Myrtaceae	Semi-deciduous	Tree	No	6	34, 159
<i>Persoonia falcata</i>	Proteaceae	Semi-deciduous	Shrub	No	3	4, 36
<i>Petalostigma pubescens</i>	Picrodendraceae	Evergreen	Tree	No	6	24, 48
<i>Planchonia careya</i>	Lecythidaceae	Deciduous	Tree	No	3	4, 147
<i>Xanthostemon paradoxus</i>	Myrtaceae	Semi-deciduous	Tree	No	6	207, 168

Semi-deciduous species are evergreen, but exhibit a noticeable thinning of the canopy during the dry season.

(DBH) were measured every 12 months. The 'Three Parks' dataset contains repeat-measured DBH data for savanna vegetation in Kakadu, Litchfield and Nitmiluk National Parks (Northern Territory, Australia). At each of 163 locations, all individuals with DBH  $\geq 5$  cm were initially measured between 1994 and 1997, then re-measured twice, each time approximately 5 years apart. DBH measurements were made during the wet season only (to avoid the stem shrinkage that may occur during dry conditions). Fire severity and frequency was determined for each location/census period *post hoc*, using survey data and aerial photographs (Murphy *et al.* 2010). Annual rainfall ranges from 900 mm at Nitmiluk to 1470 mm at Kakadu (including Kapalga), with sites showing similar seasonality (Murphy *et al.* 2010). Murphy *et al.* (2010) – one of our two sources of growth rate data – showed that DBH growth rate was unrelated to rainfall across this region, suggesting that the GR data should be broadly representative of our study species, despite Howard Springs receiving higher rainfall.

In savanna, fire damage to stems may result in very low or even negative stem diameter increments between censuses. We took three steps to counter this issue. First, we discarded all DBH data from sites designated as having experienced 'severe' (Kapalga) or 'frequent, severe' (Three Parks) fire. Second, all negative increment data were discarded. This resulted in a dataset with 7897 rows, each row describing a stem diameter increment for some individual plant, for some census period. (Data from Kapalga contributed 5155 rows; from Three Parks, 1340 rows from Kakadu NP, 765 from Litchfield NP, 637 from Nitmiluk NP). Finally, we summarized the set of stem increment data for each species/age class using 80th percentiles, rather than a measure of central tendency (Clark & Clark 1999; Rozendaal *et al.* 2010; Wright

*et al.* 2010). Doing so should minimize the influence of fire-damaged plants and better facilitate quantifying trait-growth relationships of 'successful' individuals of each species and age class (by analogy, we measured traits such as photosynthetic rates on recently-matured leaves which are near their peak physiological condition). There were too few data to confidently estimate GR for saplings of *A. difficilis* and *Grevillea decurrens*, meaning that we had GR data for 17 species as adults, and 15 species as saplings. Trait data were averaged to give a single value for saplings and for adults, for each species, for each sampling period (Appendices S1–S3). Almost all individuals of the two deciduous species were leafless during dry season sampling, limiting analyses of GR-trait relationships for that period to 16 species as adults and 13 species as saplings (Table 2).

In this study we were working across species with very different sizes at maturity. Consequently we chose to use absolute rather than relative growth rate as our preferred growth index, relative growth rates being strongly size-dependent (Rees *et al.* 2010; Iida *et al.* 2014), systematically decreasing with increasing plant size. By contrast, absolute growth rates are generally relatively stable across broad ranges in plant size (Prior *et al.* 2004, 2006).

## Analyses

Ordinary least squares regression (including multiple regressions, with interaction terms) was used to quantify relationships between GR and the various plant traits. For key bivariate relationships we tested for heterogeneity among regression slopes fitted to each age-season group. Where deemed non-heterogeneous (slope test,  $P > 0.05$ ) a

**Table 2.** Tests for correlation between stem-diameter growth rates and various plant functional traits for the four age-season datasets

Trait	Saplings (dry season) $r^2$ , $P$ , $n$ , sign	Saplings (wet season) $r^2$ , $P$ , $n$ , sign	Adults (dry season) $r^2$ , $P$ , $n$ , sign	Adults (wet season) $r^2$ , $P$ , $n$ , sign
log SLA (cm <sup>2</sup> g <sup>-1</sup> )	0.02, 0.664, 13	0.002, 0.870, 15	0.02, 0.633, 16	0.03, 0.492, 17
log N <sub>mass</sub> (%)	0.06, 0.425, 13	0.03, 0.536, 15	0.04, 0.499, 15	0.13, 0.149, 17
log N <sub>area</sub> (g m <sup>-2</sup> )	0.05, 0.468, 13	0.05, 0.409, 15	0.08, 0.315, 15	0.07, 0.302, 17
log P <sub>mass</sub> (%)	0.15, 0.193, 13	0.11, 0.226, 15	0.02, 0.606, 15	0.05, 0.397, 17
log P <sub>area</sub> (g m <sup>-2</sup> )	0.04, 0.526, 13	0.11, 0.223, 15	0.04, 0.487, 15	<0.001, 0.997, 17
log $A_{\text{sat}}$ (μmol m <sup>-2</sup> s <sup>-1</sup> )		<b>0.23, 0.071, 15, +</b>		<b>0.32, 0.017, 17, +</b>
log $g_s$ (mmol m <sup>-2</sup> s <sup>-1</sup> )		<b>0.20, 0.095, 15, +</b>		<b>0.17, 0.095, 17, +</b>
Leaf δ <sup>13</sup> C (‰)	0.03, 0.59, 12	<b>0.25, 0.056, 15, -</b>	0.01, 0.736, 16	0.13, 0.157, 17
log LM (g)	0.22, 0.101, 13	0.03, 0.520, 15	0.02, 0.613, 16	0.09, 0.252, 17
log SM (g)	0.13, 0.225, 13	0.09, 0.290, 15	<b>0.27, 0.039, 16, -</b>	<b>0.32, 0.019, 17, -</b>
log LM:SM (g g <sup>-1</sup> )	<b>0.65, 0.001, 13, +</b>	0.16, 0.134, 15	<b>0.18, 0.097, 16, +</b>	<b>0.44, 0.004, 17, +</b>
a <sub>LM</sub> /SM	<b>0.51, 0.006, 13, +</b>	<b>0.32, 0.027, 15, +</b>	<b>0.41, 0.008, 16, +</b>	<b>0.32, 0.017, 17, +</b>
log LA:SM (cm <sup>2</sup> g <sup>-1</sup> )	<b>0.66, 0.001, 13, +</b>	0.08, 0.313, 15	0.15, 0.132, 16, +	<b>0.35, 0.013, 17, +</b>
Bark % mass		0.05, 0.443, 15		<b>0.30, 0.024, 17, -</b>
Wood density (g cm <sup>-3</sup> )	0.002, 0.896, 13	<0.001, 0.947, 15	0.001, 0.923, 15	0.03, 0.473, 17

Correlations at least marginally significant ( $P < 0.1$ ) are shown in bold, and the sign of these relationships is also indicated. Note, ‘wood density’ refers to whole-stem tissue density for dry season sampling, and density of sapwood only for the wet season. a<sub>LM</sub>/SM, allometric slope describing leaf mass allocation relative to stem mass allocation;  $A_{\text{sat}}$ , light-saturated photosynthetic rate;  $g_s$ , stomatal diffusional conductance to water; LA, leaf area; LM, leaf mass; N<sub>mass</sub>, N<sub>area</sub>, leaf N per mass and area; P<sub>mass</sub>, P<sub>area</sub>, leaf P per mass and area; SLA, specific leaf area; SM, stem mass.

common slope can be fitted, and whole-model explanatory power ( $r^2$ ) and statistical significance can be reported. All analyses were run in IBM SPSS Statistics v. 22, with the General Linear Model module used for testing slope heterogeneity and calculating descriptors of common slopes.

An additional analysis is reported in Supplementary Appendix S4. There we report results from an analysis of phylogenetically independent contrasts (PICs) calculated for GR in relation to key traits, for the wet season – adult data subset only (this subset including all 17 species, and all traits including photosynthetic rates).

## RESULTS

Sapling GR varied *ca.* 3-fold, from 0.37 cm year<sup>-1</sup> (*Corymbia bleeseri*) to 1.0 cm year<sup>-1</sup> (*Grevillea pteridifolia*), median = 0.50 cm year<sup>-1</sup> (Appendix S3). Adult GR varied *ca.* 6-fold, from 0.25 cm year<sup>-1</sup> (*Persoonia falcata*) to 1.56 cm year<sup>-1</sup> (*A. difficilis*, for which we lacked data for saplings), median 0.42 cm year<sup>-1</sup>. Leaf-level traits (Appendix S3) varied 9-fold or less among species. By contrast, leaf mass on terminal branches varied 16-fold among species, wood mass 34-fold, and their ratio, 17-fold.

### Growth rate – leaf trait relationships

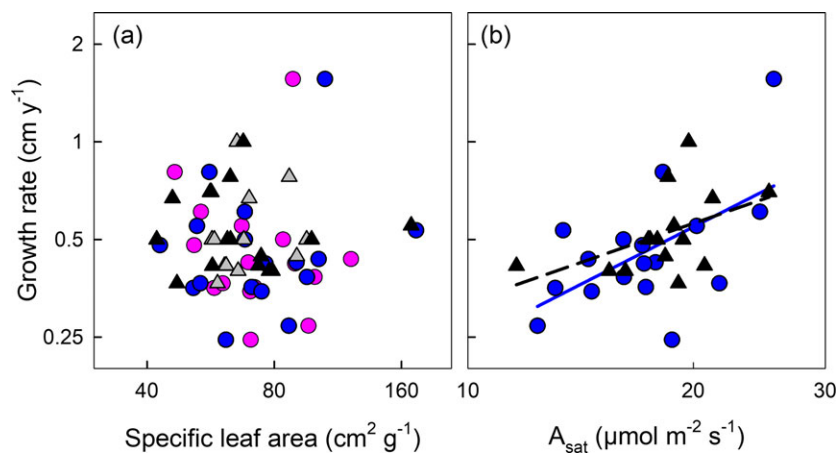
Specific leaf area was unrelated to GR in any of the four comparisons (two age classes, two sampling

periods; all  $r^2 \leq 0.03$ ,  $P > 0.4$ ; Fig. 1a, Table 2). Leaf N and P, expressed either per mass or per area, were also unrelated to GR in every case (all  $r^2 \leq 0.15$ , with most  $r^2 \leq 0.07$ , and all  $P > 0.14$ ; Table 2). By contrast,  $A_{\text{sat}}$  explained a substantial proportion of growth rate variation in adults ( $r^2 = 0.32$ ;  $P = 0.017$ ) as well as saplings ( $r^2 = 0.23$ ;  $P = 0.071$ ; Fig. 1b). The common fitted slope of log<sub>10</sub>GR on log<sub>10</sub> $A_{\text{sat}}$  was 1.0 (whole-model  $r^2 = 0.31$ ), indicating direct proportionality: on average, a two-fold increase in  $A_{\text{sat}}$  corresponded to a two-fold increase in stem diameter growth rate.

Variation in  $A_{\text{sat}}$  can be underpinned by variation in stomatal conductance to water ( $g_s$ ) and by the extent of CO<sub>2</sub> drawdown during photosynthesis, indexed here via leaf δ<sup>13</sup>C. The observed GR –  $A_{\text{sat}}$  relationships were seemingly underpinned more by variation in  $g_s$  than by CO<sub>2</sub> drawdown,  $g_s$  being more consistently related to GR than was δ<sup>13</sup>C (Table 2) and relationships between  $A_{\text{sat}}$  and  $g_s$  being tighter than those between  $A_{\text{sat}}$  and δ<sup>13</sup>C ( $r^2 = 0.63$ – $0.70$  vs.  $0.25$ – $0.35$ , respectively).

### Growth rate – stem trait relationships

Growth rate was unrelated to either sapwood or whole-stem tissue density (Fig. 2a; Table 2). Fractional bark allocation varied from *ca.* 20% to 60% by mass and was unrelated to GR in saplings, and negatively correlated with GR among adults ( $r^2 = 0.30$ ,  $P = 0.024$ ; Fig. 2b). That said, the sapling and adult



**Fig. 1.** Relationships between stem diameter growth rate and (a) specific leaf area, and (b) light-saturated photosynthetic assimilation rate,  $A_{\text{sat}}$ , for each of the age-season datasets (note, photosynthesis measurements were made during the wet season only). Each data point represents a different species. Significant regression slopes ( $P < 0.05$ ) shown as solid lines; marginally significant slopes ( $0.05 < P < 0.10$ ) with dashed lines (full details given in Table 2). Symbols: pink circles: adults, dry season; blue circles: adults, wet season; grey triangles: saplings, dry season; black triangles: saplings, wet season. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

slopes were deemed not significantly different from one another (slope test,  $P = 0.223$ ), with the common fitted slope significantly negative ( $P = 0.016$ ; model  $r^2 = 0.21$ ). This suggests some tendency for species with higher relative investment in bark to have slower stem diameter growth rates.

### Relationships between GR and branch-scale biomass allocation

Total leaf mass was unrelated to GR in each of the four comparisons (Fig 3a; all  $P > 0.1$ ). For adult plants, stem mass was negatively related to growth rate ( $r^2 = 0.27\text{--}0.32$ ; Fig. 3b); for saplings, no relationship was observed (Table 2). Nonetheless, the four stem mass – GR slopes did not differ significantly from one another ( $P = 0.731$ ), with the common slope explaining 25% of GR variation (significantly negative,  $P < 0.001$ ).

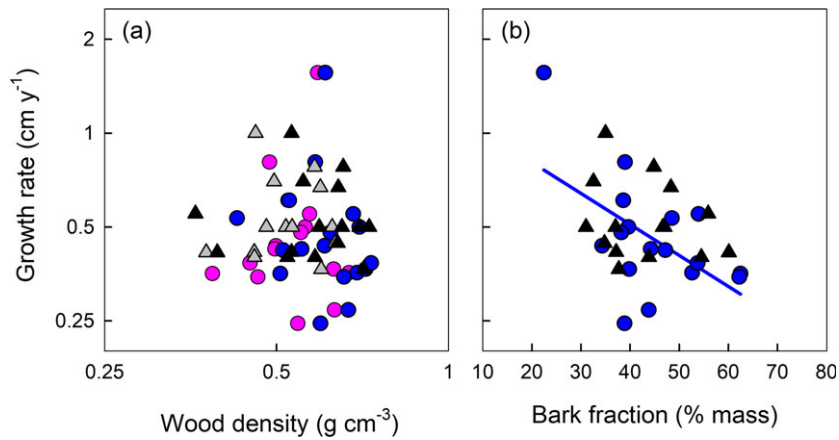
Leaf and stem mass tended to explain more variation in growth rate when considered together, rather than one at a time. LM:SM explained between 16% and 65% variation in GR, depending on plant age and season (Fig. 3c). The four GR – LM:SM regression slopes were deemed non-heterogeneous ( $P = 0.414$ ), with the common fitted slope explaining 33% variation in GR (significantly positive slope,  $P < 0.001$ ). The allometric descriptor  $a_{\text{LMSM}}$  explained between 32% and 51% variation in GR (Fig. 3d; Table 2). The four GR –  $a_{\text{LMSM}}$  regressions were deemed non-heterogeneous ( $P = 0.300$ ), with a common fitted slope explaining 36% variation (significantly positive slope,  $P < 0.001$ ).

### Combined explanatory power of leaf:stem allocation and photosynthesis

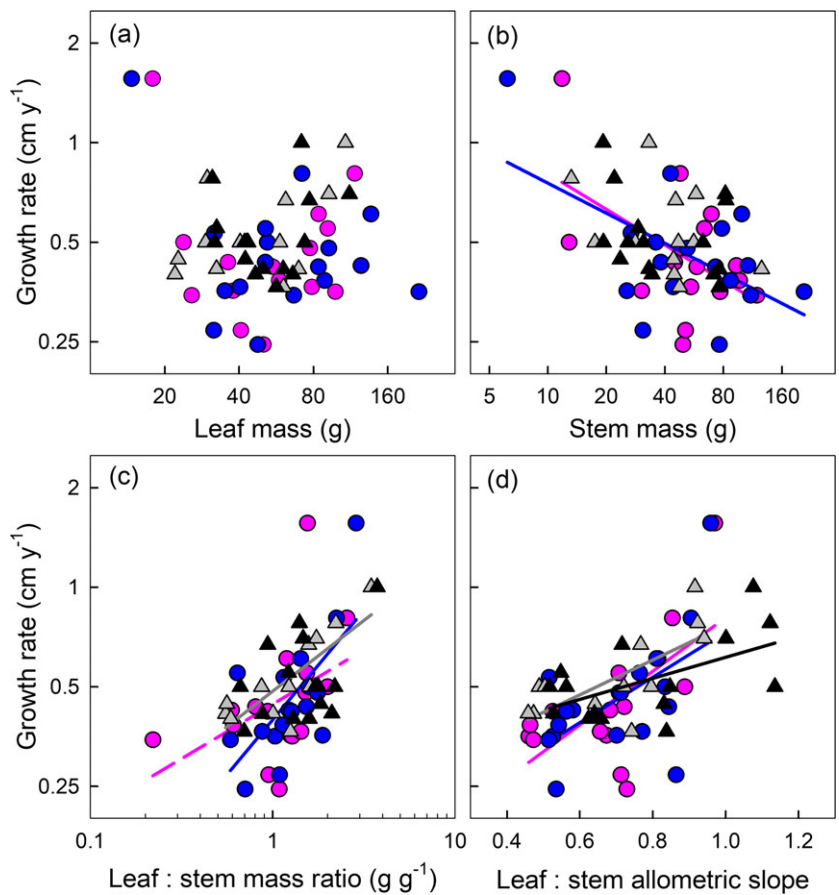
To be consistent with treating photosynthetic rate ( $A_{\text{sat}}$ ) on a per area basis, for this analysis we used the ratio of leaf *area* to stem mass (LA:SM), rather than LM:SM. Regression models including an interaction term between  $A_{\text{sat}}$  and LA:SM were run first. With these interactions deemed non-significant for both saplings and adults (both  $P > 0.2$ ), we next ran models including main effects only. For adults,  $A_{\text{sat}}$  and LA:SM together explained 64% of GR variation, with each variable contributing similar explanatory power (as judged by their respective  $F$ -statistics; Table 3). For saplings, the two traits explained 28% of GR variation, just a modest improvement over  $A_{\text{sat}}$  on its own ( $r^2 = 0.23$ ; Table 2), and in this case the coefficient for LA:SM was non-significant and that for  $A_{\text{sat}}$  just marginally so (Table 3).

For the allometric descriptor we continued to use  $a_{\text{LMSM}}$  (the mass-basis allometry). For adults,  $A_{\text{sat}}$  and  $a_{\text{LMSM}}$  explained 80% of GR variation, in a regression model that included a highly significant, positive interaction between the traits (Table 3). This interaction term indicated that the effect of higher  $A_{\text{sat}}$  on GR was stronger in species with higher  $a_{\text{LMSM}}$ , and vice versa. For saplings, the two traits explained 41% of GR variation (Table 3), just a modest improvement of  $a_{\text{LMSM}}$  on its own ( $r^2 = 0.32$ ; Table 2), and in this case the coefficient for  $A_{\text{sat}}$  was non-significant (Table 3).

For the adult dataset these relationships were strongly influenced by *A. difficilis*. Re-running the analyses with this species removed,  $A_{\text{sat}}$  and  $a_{\text{LMSM}}$



**Fig. 2.** Relationship between stem diameter growth rate and properties of 1 cm diameter terminal stems. (a) Whole-stem (dry season) or sapwood (wet season) tissue density. (b) Percentage of stem mass allocated to bark (wet season only). Solid regression line indicates the relationship was significant ( $P < 0.05$ ); see Table 2. Symbols. Pink circles: adults, dry season; blue circles: adults, wet season; grey triangles: saplings, dry season; black triangles: saplings, wet season. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**Fig. 3.** Relationship between stem diameter growth rate and leaf *versus* stem deployment on terminal branches. (a) Total leaf mass; (b) Total stem mass (including bark); (c) Ratio of leaf:stem mass; (d) Allometric coefficient describing the rate of leaf mass accumulation *versus* stem mass accumulation along the branch. Significant regression slopes ( $P < 0.05$ ) shown as solid lines; marginally significant slopes ( $0.05 < P < 0.10$ ) with dashed lines (full details given in Table 2). Symbols. Pink circles: adults, dry season; blue circles: adults, wet season; grey triangles: saplings, dry season; black triangles: saplings, wet season. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**Table 3.** Multiple regressions exploring the interactive effects of photosynthetic rate and leaf:stem allocation on plant growth rates

Variable	<i>F</i>	Coefficients	<i>P</i>
GR ~ $A_{\text{sat}}$ , LA:SM (interaction was never significant)			
Adults ( $r^2 = 0.64$ , $P < 0.001$ , d.f. = 16)			
Intercept	29.83	-2.53 (-3.52, -1.54)	<0.001
log $A_{\text{sat}}$	11.29	1.12 (0.41, 1.84)	0.005
log LA:SM	12.25	0.41 (0.16, 0.66)	0.004
Saplings ( $r^2 = 0.28$ , $P = 0.022$ , d.f. = 14)			
Intercept	6.945	-1.43 (-2.61, -0.25)	0.022
log $A_{\text{sat}}$	3.261	0.75 (-0.16, 1.66)	0.096
log LA:SM	0.766	0.10 (-0.15, 0.35)	0.399
GR ~ $A_{\text{sat}}$ , a_LMSM, $A_{\text{sat}} \times \text{a\_LMSM}$ (where significant)			
Adults (model $r^2 = 0.80$ , $P < 0.001$ , d.f. = 16)			
Intercept	13.36	6.27 (2.56, 9.98)	0.003
log $A_{\text{sat}}$	16.45	-5.76 (-8.84, -2.69)	0.001
a_LMSM	20.22	-9.64 (-14.27, -5.01)	0.001
log $A_{\text{sat}} \times \text{a\_LMSM}$	22.44	8.34 (4.54, 12.14)	<0.001
Saplings (model $r^2 = 0.41$ , $P = 0.042$ , d.f. = 14)			
Intercept	5.86	-1.15 (-2.18, -0.12)	0.032
log $A_{\text{sat}}$	1.78	0.53 (-0.34, 1.4)	0.207
a_LM:SM	3.69	0.26 (-0.03, 0.55)	0.079

together still explained 57% of GR variation (multiple regression with interaction term; not shown), and  $A_{\text{sat}}$  and LA:SM explained 34% (main effects only; not shown).

A supplementary analysis, incorporating phylogenetic information as Phylogenetically Independent Contrasts (Appendix S4), gave additional strength to our results. In those analyses also, variation in growth rate was clearly (significantly) connected to variation in leaf: stem allometry,  $A_{\text{sat}}$  and fractional bark allocation, but not to variation in either SLA or wood density.

## DISCUSSION

### Photosynthetic rate as a driver of GR variation

Light-saturated photosynthetic rate,  $A_{\text{sat}}$ , explained roughly 30% of interspecific variation in stem diameter growth rates. This mirrors the generally positive  $A_{\text{sat}}$  – growth rate relationship known from controlled-environment seedling studies (Kruger & Volin 2006) and older seedlings grown for 2 years in a shade house (Li *et al.* 2016). By contrast, there have been rather few field-based tests of GR –  $A_{\text{sat}}$  relationships, especially for sapling or adult plants. A positive relationship has been reported across several vegetation types in northern Australia (Prior *et al.* 2004), from open forest in Hawaii (Stratton & Goldstein 2001), and from saplings of 53 species growing in high-light gaps within a Bolivian rainforest (Poorter & Bongers 2006). No relationship was observed among 24 savanna and forest species in Brazil (Rossatto *et al.* 2009).

A generally positive GR –  $A_{\text{sat}}$  relationship makes intuitive sense, especially in high-light situations. That said, species with higher  $A_{\text{sat}}$  could in principle deploy less total leaf area, or have higher leaf replacement costs (shorter leaf lifespan), or have higher belowground or sapwood respiration costs, and these costs could potentially cancel out the growth benefit of higher  $A_{\text{sat}}$ . However, for both adults and saplings of the 17 species examined here this was seemingly not the case, in support of the prediction that the GR –  $A_{\text{sat}}$  relationship does not vary with plant stature (Gibert *et al.* 2016).

### Leaf:stem allocation as a driver of GR variation

This study represents the first test of the proposition that higher relative allocation to leaf *versus* stems, considered at branch level, should drive faster growth at the whole-plant level (Pickup *et al.* 2005). Those authors argued that higher allocation to leaf represented greater potential for photosynthetic benefits, while higher allocation to stem would incur higher costs for maintenance respiration. All else equal, a more positive carbon balance at branch-level should lead to more carbon exported to other parts of the plant, and thus faster growth (Pickup *et al.* 2005). Our results are consistent with this interpretation. However, as it turned out, the positive influence of leaf:stem allocation on growth rate was more strongly driven by stem allocation (which was negatively correlated with GR) than by leaf mass (which was unrelated to GR).

Higher investment in stem tissues must also have benefits, for example it may represent more biomechanical

support and hydraulic supply to leaves, greater potential for water storage in sapwood and the living inner bark layers (Rosell 2016), and greater protection against fire, especially from the outer bark layers (Pausas 2014). Presumably, all of these features can be important in seasonally dry, frequently burnt savannas, such as that studied here.

### No general relationship between GR and SLA for field-grown plants

The other key finding from this study is the null result that SLA failed to explain variation in GR for either saplings or adult plants. The size-dependence of GR – SLA relationships has been investigated in several recent studies, but conclusions have varied. SLA and stem diameter growth rate were: positively correlated among Puerto Rico rainforest species, with no size-related trend in relationship strength (Lasky *et al.* 2015); unrelated across all size classes in a very detailed study of Panamanian rainforest species (Visser *et al.* 2016); unrelated across all size classes except mid-size trees (DBH = 16–18 cm) in a seasonally dry forest, Brazil (Prado-Junior *et al.* 2016); and positively correlated among adult rainforest trees in Taiwan, but *negatively* correlated among juveniles (Iida *et al.* 2014). Mostly these studies have focused on forests with a marked vertical light gradient and (at least partially as a result) marked shifts in leaf traits between young and old plants. Our study represents an important contrast, coming from open vegetation with little vertical light gradient, and where leaf and wood traits of saplings were indistinguishable from adults (Appendix S1).

### GR unrelated to stem tissue density and leaf nutrient concentrations

Other hypotheses detailed in the Introduction receiving no support were the predictions that GR would be negatively related to WD, and positively related to leaf N and P concentrations. A negative relationship between stem diameter growth rates and trunk wood density has been reported many times (King *et al.* 2006; Poorter *et al.* 2008; Martínez-Vilalta *et al.* 2010; Wright *et al.* 2010; Iida *et al.* 2014; Lasky *et al.* 2015), although null relationships have also been reported (Russo *et al.* 2010). Even when statistically significant the explanatory power is generally rather low in these studies, typically <10% (but see Martínez-Vilalta *et al.* 2010), and sample size (number of species) is usually far higher than used here. Perhaps we lacked sufficient power to detect a relationship between growth rate and wood density, if indeed there is a general tendency for this to be true among Australian savanna

species. Here we measured tissue density on terminal branches rather than main trunks; however, these properties would likely be related (Swenson & Enquist 2008), and their relationships to GR therefore similar.

Growth rates were also unrelated to leaf N and P concentrations (considered per unit leaf area or mass). Perhaps this should not be surprising since  $A_{\text{sat}}$  was at best marginally correlated with  $N_{\text{area}}$  (in saplings,  $r = 0.46$ ,  $P = 0.062$ ) and unrelated to  $P_{\text{area}}$  in both age groups ( $P > 0.140$ ; not shown), and the causal pathway between leaf N (and P) and GR arguably flows via their respective links to photosynthesis. Considered on a leaf mass basis, leaf N, leaf P and photosynthetic rate were all correlated with SLA (not shown). Covariation in this suite of traits can be thought of representing variation along a ‘leaf economic spectrum’ (Wright *et al.* 2004). Hence, the finding that all of SLA,  $N_{\text{mass}}$  and  $P_{\text{mass}}$  were unrelated to GR (Table 2) can also be taken to illustrate how strategy variation along the leaf economic spectrum does not necessarily map on to variation in growth rate of field-grown plants.

### Successful growth – trait strategies

Our results help us understand the biology underpinning differences among species in their growth rates. For example, the short-lived, fire-sensitive species *A. difficilis* was the fastest growing species, with this high GR seemingly driven by the combination of high leaf:stem mass ratio (1.6–2.9 g g<sup>-1</sup> depending on season; Appendix S3), low fractional allocation to bark (23%) and fast  $A_{\text{sat}}$  (26 μmol m<sup>-2</sup> s<sup>-1</sup>), itself associated with profligate photosynthetic water use ( $g_s$ ; 1087 mmol m<sup>-2</sup> s<sup>-1</sup>). *Grevillea pteridifolia* seemingly achieves its fast GR by teaming high LM:SM (ca. 3.6 g g<sup>-1</sup> in saplings, 2.4 g g<sup>-1</sup> in adults) with medium-high  $A_{\text{sat}}$  (18.2–19.7 μmol m<sup>-2</sup> s<sup>-1</sup>), while *Eucalyptus miniata* does so by teaming very rapid  $A_{\text{sat}}$  (ca. 25 μmol m<sup>-2</sup> s<sup>-1</sup>) with mid-range LM:SM (1.2–1.7 g g<sup>-1</sup>). Conversely, the slow GR of adult *Petalostigma pubescens* was associated with the lowest mean  $A_{\text{sat}}$  value (12.4 μmol m<sup>-2</sup> s<sup>-1</sup>), slow  $g_s$  (392 mmol m<sup>-2</sup> s<sup>-1</sup>) and low LM:SM (ca. 1.0 g g<sup>-1</sup>). The slow GR of sapling *Buchanania obovata* was associated with the lowest  $A_{\text{sat}}$  values (11.6 μmol m<sup>-2</sup> s<sup>-1</sup>) seen for saplings, the lowest  $g_s$  (301 mmol m<sup>-2</sup> s<sup>-1</sup>), low LM:SM (0.6–0.9 g g<sup>-1</sup>, depending on season) and the highest fractional allocation to bark (60%).

That these species vary widely in stem diameter growth rate yet still co-occur indicates that there are many equally successful growth and survival strategies in this system. Of particular importance, not addressed in this study, is the need for sufficient individuals of each species to overcome the demographic bottleneck that frequent, intense fires create

– the so-called sapling ‘fire trap’ (Bond 2008; Prior *et al.* 2010). For investigating that aspect of the growth strategy, additional data for height growth rate would be especially valuable.

## Synthesis

Our results suggest that branch-level biomass allocation is a property deserving serious attention in future studies of plant growth. Here we presented two types of indices: static ratios (LM:SM, LA:SM) and an allometric descriptor ( $a_{\text{LMSM}}$ ). Not surprisingly  $a_{\text{LMSM}}$  and LM:SM were correlated, but weakly enough that each variable contains considerable independent information. Besides explaining considerable variation in GR, branch-level biomass allocation also has the virtue of being easy to measure.

Together,  $A_{\text{sat}}$  and leaf:stem deployment explained up to 41% GR variation in saplings and up to 80% in adults (57% with *A. difficilis* excluded). These results are remarkable given that we did not consider interspecific variation in, for example, canopy architecture, below-ground allocation, or tissue turnover rates. Of course, the extent to which these results generalize to other savannas or other vegetation types will require further study. On the face of it, one might predict lower explanatory power for these traits in vegetation types where many individuals are shaded, or where many individuals are very large (i.e. situations where the benefits of higher  $A_{\text{sat}}$  are likely muted, and where sapwood respiration costs begin to dominate GR variation). Testing this hypothesis would be a useful next step.

Currently we lack clear demonstration (i.e. within a single empirical study) that SLA – growth rate relationships flip as predicted, from positive in small plants to null in large plants. Nonetheless we suggest that this is likely the case, given the wealth of seedling studies showing strong positive relationships and the increasing number of sapling-adult studies showing little if any relationship. Even so, it is as yet unclear at what plant size these shifts occur and whether they occur systematically earlier or later in particular light environments or vegetation types, or in plants with particular architectures or growth strategies.

That SLA is often unrelated to growth rates of field-grown plants has been disappointing for authors expecting plant functional traits to neatly explain demographic variation (Wright *et al.* 2010; Paine *et al.* 2015). Nonetheless, SLA remains a key trait for understanding leaf economic variation (Westoby *et al.* 2002); a key descriptor of how canopy mass interconverts with canopy light-capturing area (and thus an important property in plant growth models);

and it is related to important ecological variation at other scales – for example, herbivory rates, flammability and litter decomposition rate (Poorter *et al.* 2009). But, it seems increasingly clear that SLA and plant growth rate are generally correlated only in very small plants, and this fact should be more widely appreciated.

## ACKNOWLEDGEMENTS

We thank Mick Brand, Martina Ripcke and Ian Davidson for their enthusiasm and hard work in the field and lab; Matthew Norwood, CDU, for helping prepare equipment; Graeme Patch for organizing use of drying ovens at DPI Berrimah; Dick Williams (CSIRO Darwin) for access to the Kapalga growth rate data; Jeremy Russell-Smith (Bushfire NT) for access to the ‘Three Parks’ dataset. Saskia Grootemaat helped prepare several figures and Amy Zanne generated the phylogenetic tree. This work was made possible by funding from Macquarie University and from the Australian Research Council (DP120103284).

## AUTHOR CONTRIBUTIONS

IJW and CEL designed the study. All authors contributed to fieldwork and discussion of results. IJW analysed the data and drafted the manuscript. All authors contributed to subsequent versions.

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## SUPPORTING INFORMATION

Additional supporting information may/can be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Comparison of growth rate and trait values of adults and saplings for each of the study species.

**Appendix S2.** Comparison of trait values between the two seasons sampled (wet season, May 2011; dry season September 2010) for both adults (orange circles) and saplings (purple triangles) of 17 species.

**Appendix S3.** Growth rate and trait data used in this study.

**Appendix S4.** Phylogenetic analysis.