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Relative growth rate variation of evergreen and deciduous savanna tree species is driven by different traits

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- **Background and Aims** Plant relative growth rate (RGR) depends on biomass allocation to leaves (leaf mass fraction, LMF), efficient construction of leaf surface area (specific leaf area, SLA) and biomass growth per unit leaf area (net assimilation rate, NAR). Functional groups of species may differ in any of these traits, potentially resulting in (1) differences in mean RGR of groups, and (2) differences in the traits driving RGR variation within each group. We tested these predictions by comparing deciduous and evergreen savanna trees.
- **Methods** RGR, changes to biomass allocation and leaf morphology, and root non-structural carbohydrate reserves were evaluated for juveniles of 51 savanna species (34 deciduous, 17 evergreen) grown in a common garden experiment. It was anticipated that drivers of RGR would differ between leaf habit groups because deciduous species have to allocate carbohydrates to storage in roots to be able to flush leaves again, which directly compromises their LMF, whereas evergreen species are not subject to this constraint.
- **Key Results** Evergreen species had greater LMF and RGR than deciduous species. Among deciduous species LMF explained 27 % of RGR variation (SLA 34 % and NAR 29 %), whereas among evergreen species LMF explained between 2 and 17 % of RGR variation (SLA 32–35 % and NAR 38–62 %). RGR and LMF were (negatively) related to carbohydrate storage only among deciduous species.
- **Conclusions** Trade-offs between investment in carbohydrate reserves and growth occurred only among deciduous species, leading to differences in relative contribution made by the underlying components of RGR between the leaf habit groups. The results suggest that differences in drivers of RGR occur among savanna species because these have different selected strategies for coping with fire disturbance in savannas. It is expected that variation in the drivers of RGR will be found in other functional types that respond differently to particular disturbances.

Key words: Carbohydrate storage, deciduous, ecological traits, evergreen, functional types, plant growth variation, relative growth rate, RGR, savanna trees.

INTRODUCTION

Relative growth rate (RGR) is an important trait distinguishing plant species' strategies (Grime and Hunt, 1975; Reich *et al.*, 2003*a*). Species with high growth rates are more competitive in acquiring resources, whereas species with low growth rates are more conservative with the scarce resources they have obtained (Grime, 1977; Berendse and Elberse, 1989; Reich *et al.*, 2003*b*; Poorter and Garnier, 2007) or are able to overcome disturbance events by allocating resources to storage rather than to growth (Kitajima, 1994; Poorter and Kitajima, 2007). Plant RGR depends on biomass allocation to leaves (leaf mass fraction, LMF), efficient construction of leaf surface area (specific leaf area, SLA) and biomass growth per unit leaf area (net assimilation rate, NAR) (Evans, 1972):

$$\mathrm{RGR} = \mathrm{LMF} \times \mathrm{SLA} \times \mathrm{NAR}. \quad (1)$$

This equation indicates that variation in one or more of the underlying components may lead to variation in RGR. It follows that if species of different functional groups differ in one or more of these components, then (1) the functional groups may differ in mean RGR, and (2) RGR variation across species within each group may be driven by different traits. In this paper we test these hypotheses by evaluating RGR of savanna tree species. We specifically focus on the role of leaf habit (i.e. deciduous versus evergreen phenology) of savanna tree species, as our previous studies have led us to conclude that these form different functional groups in savannas, whose ecological strategies may lead to different RGR determinants.

In previous studies (Tomlinson *et al.*, 2012, 2013*a*, *b*) we have analysed the seedling traits of 51 tropical savanna tree species from three continents (Africa, Australia, South America) in a common garden experiment. Those analyses suggested that RGR is lower in humid than in semi-arid environments in South America, where savannas are dominated by deciduous species, whereas RGR is greater in humid than in semi-arid environments in Australia, where savannas are dominated by evergreen species. Here we test specifically whether these trends are attributable to different strategies of evergreen and deciduous species, and whether differences in part relate to different patterns of below-ground allocation between the functional groups.

Leaf area ratio (LAR), the product of SLA and LMF, is highly positively correlated with RGR (Lambers and Poorter, 2004). Evergreen species are widely thought to be slower growing than deciduous species because evergreen species have lower SLA due their need to produce tough leaves that sustain long leaf lifespans (Cornelissen *et al.*, 1996; Swanborough and Westoby, 1996; Wright *et al.*, 2004). However, we have shown that among savanna tree seedlings, evergreen species have significantly greater LMF than deciduous species (Tomlinson *et al.*, 2013*a*). If LAR does not differ between leaf habit groups as a result of these different allocation patterns, mean RGR may not differ between evergreen and deciduous species.

The nature of the difference in biomass allocation between deciduous and evergreen savanna species suggests that the driving traits of RGR variation may differ between leaf habits. We found that while evergreen savanna species had greater mean LMF than deciduous savanna species, deciduous species had a substantially wider range of LMF values (range 0·19–0·76 g g^{-1} total mass) than evergreen species (range 0·42–0·67 g g^{-1}) (Tomlinson *et al.*, 2012) (see Supplementary Data Table S1). This suggests that variation in LMF may explain a substantially greater proportion of the variation in RGR among deciduous savanna species than RGR among evergreen savanna species. Conversely, RGR variation among evergreen species might be more substantially explained by SLA or NAR. Previously, Poorter *et al.* (2012) found that LMF made a small contribution to variation in RGR among eudicots.

The magnitude and variation of LMF across savanna tree species may be due substantially to differences in allocation to reserve storage in roots. Non-structural carbohydrate in roots can be an important sink for resources in juvenile trees of some species as it can constitute >50 % of the root biomass and >25 % of total plant biomass, and it appears to be much greater for deciduous than for evergreen species (Hoffmann *et al.*, 2004; Kobe *et al.*, 2010; Tomlinson *et al.*, 2013*b*). Deciduous species are thought to require greater root carbohydrate storage than evergreen trees to be able to flush new leaves after non-growing seasons (Walters and Reich, 1999; Hoffmann and Franco, 2003; Tomlinson *et al.*, 2013*b*). Because RMF is the sum of structural and non-structural biomass, RMF might be positively related to root carbohydrate storage, and hence LMF might be negatively related to root carbohydrate storage. This trade-off between storage and LMF describes the mechanism for how allocation to storage is at the expense of growth rate (Bloom *et al.*, 1985; Rappoport and Loomis, 1985). Importantly, as root storage of deciduous species shows a much greater range of values than evergreen species (Tomlinson *et al.*, 2013*b*), it may trade against RGR for deciduous species but not for evergreen species.

In this paper we evaluated RGR in relation to biomass allocation, leaf morphology and root carbohydrate content using data we had accumulated on 51 tropical savanna tree species differing in leaf habit (Tomlinson *et al.*, 2012, 2013*a*, *b*). We predicted that: (1) mean RGR of deciduous species and evergreen species does not differ significantly because they do not differ in LAR; (2) RGR variation is predominantly driven by LMF variation among deciduous species and by SLA or NAR variation among evergreen species; and (3) RGR and LMF are negatively related to root carbohydrate storage among deciduous species but not among evergreen species.

MATERIALS AND METHODS

Species selection

We sampled dominant or very abundant tropical and sub-tropical tree species from humid and semi-arid savannas in southern Africa (coastal and inland savannas in South Africa and Zimbabwe) (Frost, 1996; Mucina and Rutherford, 2006), north-eastern Australia (coastal and inland woodlands in Queensland) (Cole, 1986) and eastern South America (Cerrado and Caatinga biomes in Brazil) (Cole, 1986) (for a full description of the environments see Tomlinson *et al.*, 2012).

A total of 51 species were grown, including 18 species from Australia (eight humid, ten semi-arid), 21 species from Africa (ten humid, 11 semi-arid) and 12 species from South America (eight humid, four semi-arid), representing nine Angiosperm orders (APGIII), 13 families and 28 genera. Two plant orders formed the bulk of the species sample, namely Fabales and Myrtales. A full species list is provided in Supplementary Data Table S1, indicating their family and leaf habit.

Greenhouse experiment

We conducted a greenhouse experiment to evaluate whether the correlates of RGR differed between juveniles of deciduous and evergreen species. Plants were grown in a greenhouse chamber at Radix Research Farm, Wageningen University, the Netherlands (51°59′17″N, 5°39′45″E) between September 2008 and October 2010. Temperature in the greenhouse was set at 28 °C for 12 h (daytime) and 23 °C for 12 h (night time). Supplementary light (150 μmol m^{-2} s^{-1}) was provided for 12–16 h (seasonally adjusted) to ensure that the daily photon flux density exceeded 10 mol m^{-2} d^{-1}. Other studies have shown that the total daily photon flux density, rather than peak irradiance, is most important for plant growth (Poorter and Van der Werf, 1998). Although the total amount of light is low by comparison with full sun environments in the tropics, plant growth was substantial in some species and varied substantially among species, indicating that available light was sufficient to distinguish growth abilities of different species.

Tree seedlings were grown in plastic tubes of 10 cm diameter and 100 cm length, to allow the roots more space and to reduce pot limitation. Pots were filled with river sand mixed with slow-release fertilizer [Osmocote 18–6–12 (N–P–K) fertilizer (8–9 month mixture)] at a concentration of 5 kg fertilizer m^{-3} river sand. Water was supplied through irrigation three times per day at a rate of 40 ml per pot per day, equivalent to 800 mm of rainfall over 20 weeks of growth. This was a much more even water supply than most of these species would receive in their natural environment, but the intent was to ensure that all the plants were well watered while they grew, so that water limitation did not contribute to any trait variation between species.

Recently germinated seedlings were planted in pots and grown for either of two intervals, 5 and 20 weeks. A maximum of ten individuals per species were harvested after each growth interval (range 5–10 individuals; median ten individuals). Due to space limitations it was necessary to grow plants in three batches and individual species were therefore grown in one (ten individuals per time interval) or more usually two (five individuals per time interval) batch repetitions.

Biomass partitioning and morphological data

At each harvest date (5 or 20 weeks), biomass partitioning and morphological traits were measured or estimated that affect RGR (Lambers and Poorter, 2004). Morphological traits were estimated per individual using the following procedure. At harvest, up to six fully expanded fresh leaves were sampled from each plant. These were immediately scanned with a flatbed scanner (CanoScan LIDE 100, Canon) to obtain their surface area, dried at 70 °C for at least 48 h and weighed for their dry weight. The remaining plant biomass was separated into organ fractions (cotyledon, leaf, stem, root), dried and weighed to obtain dry mass estimates for cotyledon, leaf, stem, root and total (*Mass*). Organ mass fractions for leaf (LMF, g g^{-1}), stem (SMF, g g^{-1}) and root (RMF, g g^{-1}) were calculated as the mass of that organ divided by the plant total mass (*Mass*). SLA (cm^2 g^{-1}) was calculated as leaf area of the sampled leaves divided by their dry mass. Petioles and rachides of compound-leaved species were retained on the leaves for these measurements. Phyllodes of evergreen *Acacia* species were similarly treated as individual leaves of those species. LAR (leaf area per unit total plant mass, cm^2 g^{-1}) was calculated as the product of SLA and LMF. High SLA, LMF and LAR have all been associated with high RGR, while high RMF has been associated with low RGR (see Introduction). We calculated species' average trait values across the growing period (LMF_{ave}, SMF_{ave}, RMF_{ave}, SLA_{ave}, LAR_{ave}) by taking the average of the mean trait estimates for 5 and 20 weeks.

RGR (g g^{-1} d^{-1}) was calculated over the interval between Week 5 and Week 20 for each individual 20-week-old plant. RGR of individual 20-week-old plants was calculated as the difference between their natural-logged mass ($\ln Mass_{t2}$) and the mean value of natural logged initial masses of individuals of the same species harvested at 5 weeks ($\ln Mass_{t1}$), all divided by the interval of growth (days) (Hoffmann and Poorter, 2002).

$$\mathrm{RGR} = \frac{\ln Mass_{t2} - \overline{\ln Mass_{t1}}}{(t_2 - t_1)} \tag{2}$$

Mean NAR (g m^{-2} d^{-1}) was calculated over 5–20 weeks. The relationships between plant mass (*Mass*, g) and plant total leaf area (LA, cm^2) were non-linear within species such that plant mass was best represented by an exponential relationship with plant leaf area.

$$Mass = b\mathrm{LA}^{\alpha} \tag{3a}$$

Therefore, we used an equation that calculates NAR by incorporating the exponent, α, of the above relationship for each species (outlined in Radford, 1967). NAR was calculated per 20-week-old individual using mean data for 5-week-old individuals (as for RGR):

$$\mathrm{NAR} = \frac{\alpha}{\alpha - 1}\,\frac{(Mass_{t2} - \overline{Mass_{t1}})}{(t_2 - t_1)}\,\frac{(\mathrm{LA}_{t2}^{\alpha-1} - \overline{\mathrm{LA}_{t1}^{\alpha-1}})}{(\mathrm{LA}_{t2}^{\alpha} - \overline{LA_{t1}^{\alpha}})} \tag{3b}$$

All variables were measured or calculated per individual at the appropriate time period as described above. These individual values were averaged per species per time period, providing the species' data used for the statistical analysis described below (data provided in Supplementary Data Table S1).

Root carbohydrate data

Root non-structural carbon content was determined for a subset of 20 species, because of cost and time constraints. Nine evergreen and 11 deciduous species were selected from the larger sample. These were chosen to sample genetically as widely as possible within the 51 species, while also including more closely related species with different leaf habit in the Fabales, Myrtales and Asterids to ensure that phylogenetic biases between leaf habits were minimized. Root material was taken from the upper third of the central taproot of five plants of each species harvested at 20 weeks.

Root non-structural carbohydrate concentration (g carbohydrate g^{-1} root) was estimated per sample by separate estimation of its components, namely the starch concentration and soluble sugar concentration, using a revised procedure developed at the University of Florida (K. Kitajima, Kyoto University, Kyoto, Japan, pers. comm.). The method is identical to that described by Poorter & Kitajima (2007) except that starch and other complex sugars are hydrolysed to glucose using 1·1 % hydrochloric acid solution in place of amyloglucosidase.

Root carbohydrate storage might differ between species in terms of both carbohydrate concentration in roots and carbohydrate stored in roots as a fraction of total plant dry mass, the root non-structural carbohydrate (NSC) fraction (g carbohydrate g^{-1} total plant).

$$\text{Root NSC fraction} = \text{Root NSC concentration} \times \text{RMF} \tag{4}$$

This is a coarse approximation of fractional root carbon storage because it assumes equal carbon storage throughout the plant root. Most species considered here produced a thickened taproot which accounted for most of the root biomass (Tomlinson *et al.*, 2012), and therefore we were confident that this estimate was representative of differences between species. Root NSC fraction is also a measure of the cumulative partitioning to root storage, which is presumably at the expense of additional structural growth (see Bloom *et al.*, 1985). Species' mean estimates for root NSC concentration and root NSC fraction are provided in Supplementary Data Table S1.

Statistical analysis

To test Prediction 1, that mean RGR does not differ between leaf habits because they do not differ in LAR, we regressed RGR against the log of mean initial mass ($Mass_5$) and the interaction between initial mass and leaf habit (RGR∼ ln $Mass_5$ × Habit). We included initial mass in this regression because it is well known in studies of RGR that species with smaller initial masses often exhibit greater RGR because of scale effects (Turnbull *et al.*, 2008; Rees *et al.*, 2010), and thus any difference in mean seed mass between leaf habits might drive the pattern. We also checked whether mean $Mass_5$ differed between leaf habits, and whether mean values of LAR for each leaf habit at each age (5 weeks, 20 weeks) and averaged across each age (average) differed significantly between leaf habits (Table 1, Fig. 1).

To test Prediction 2 (variation in RGR is driven by different components for evergreen and deciduous species), we used

Table 1. *Comparisons of mean trait values of evergreen and deciduous seedlings of savanna tree species*

	Group means					
Variable	Deciduous	Evergreen	t	d.f.	*P*	λ
$\mathrm{RGR}_{5\to20}$	0·033	0·042	2·66	49	0·016*	
RMF_5	0·376	0·374	−0·05	49	0·956	0·976
RMF_{20}	0·361	0·209	−4·30	49	<0·001***	
$\mathrm{RMF}_{\mathrm{ave}}$	0·378	0·315	−2·14	49	0·037*	0·519
SMF_5	0·147	0·110	−2·36	49	0·021*	
SMF_{20}	0·241	0·229	−0·39	49	0·660	
$\mathrm{SMF}_{\mathrm{ave}}$	0·194	0·170	−1·25	49	0·217	
LMF_5	0·353	0·470	3·55	49	<0·001***	0·965
LMF_{20}	0·393	0·558	5·52	49	<0·001***	
$\mathrm{LMF}_{\mathrm{ave}}$	0·384	0·517	4·78	49	<0·001***	0·466
SLA_5	29·28	25·93	−1·20	45	0·237	
SLA_{20}	19·14	13·04	−3·98	49	<0·001***	
$\mathrm{SLA}_{\mathrm{ave}}$	23·86	19·48	−2·33	45	0·024*	
LAR_5	14·15	14·01	−0·07	45	0·945	
LAR_{20}	7·42	7·37	−0·05	49	0·956	
$\mathrm{LAR}_{\mathrm{ave}}$	10·64	10·69	0·04	45	0·965	
Root NSC $\mathrm{concentration}_{20}$	0·411	0·311	−1·83	18	0·083	
Root NSC $\mathrm{fraction}_{20}$	0·159	0·070	−2·39	18	0·028*	
$\mathrm{NAR}_{5\to20}$	4·015	4·810	−1·39	43	0·172	

Leaf habit group comparisons were conducted using the *pgls*() function of the *caper* package in R. Where phylogenetic signal was detected, estimated Pagel's lambda (λ) for that phylogenetic transformation is shown and results represent the group means under the optimal λ. Leaf habit means are calculated from individual species' means (Supplementary Data Table S1). These include: RGR over 5–20 weeks of growth, morphological traits measured at 5 and 20 weeks after planting and averaged across these measurements [LMF (leaf mass fraction), SMF (stem mass fraction), RMF (root mass fraction), SLA (specific leaf area) and leaf area ratio (LAR)], root non-structural carbohydrate concentration, root non-structural carbohydrate fraction, both measured at 20 weeks, and net assimilation rate (NAR) calculated over 5–20 weeks.

Significance levels: $*P \leq 0{\cdot}05$; $**P < 0{\cdot}01$; $***P < 0{\cdot}001$.

two tests. First, we wanted to know whether LMF differed significantly between deciduous and evergreen species, and importantly whether LMF decreased and RMF increased over time among deciduous species but not among evergreen species. This would provide evidence that deciduous species were allocating to roots, and thus presumably to storage, at the expense of RGR to a greater level than evergreen species. Simultaneously we explored how SLA developed over time in the functional groups, as it has long been known that evergreen species have lower SLA than deciduous species (Cornelissen *et al.*, 1996). We compared mean values of each trait for each leaf habit at each age (5 weeks, 20 weeks) and averaged means across each age (average) to determine whether they differed significantly between leaf habits (Table 1, Fig. 1). Correlations between all traits at both ages for all species, deciduous species only and evergreen species only are provided in Supplementary Data Table S2.

Secondly, we tested whether LMF, SLA and NAR explained different amounts of the variation in RGR associated with each leaf habit. For this, we first logged eqn (1) which gives a general linear form (see Rees *et al.*, 2010):

$$\ln \mathrm{RGR} = \ln \mathrm{LMF}_{\mathrm{ave}} + \ln \mathrm{SLA}_{\mathrm{ave}} + \ln \mathrm{NAR} + \varepsilon \qquad (5)$$

We ran a general linear model using this equation for all species and for each leaf habit group, after first standardizing all variables to mean 0 and variance 1. We used average SLA and LMF as measures of the mean value per species over the interval of growth. We were specifically interested in the proportion of variance accounted for by each component and in the effect sizes of each component on RGR, as represented by the coefficients of the standardized variables in the regression models (Table 2). It has been pointed out that using regression on eqn (5) can be naïve because in certain circumstances logNAR is calculated as logRGR − logLMF − logNAR and hence the equation is completely determined (Shipley, 2006; Rees *et al.*, 2010). However, we calculated NAR using the non-linear formula outlined in eqn (3), and thus independently of the above constraint. To confirm that the summed relationship was not fully deterministic for our data, we regressed logRGR (our estimated values) against the sum of (logLMF + logSLA + logNAR). Although this relationship was highly, positively significant, it accounted only for 60 % of the variation in logRGR ($R_a^2 = 0{\cdot}60$), indicating that our formula was not constrained, and thus that regression could be used with confidence. We also regressed RGR against SLA, LMF and NAR separately for deciduous and evergreen species using non-standardized data to visualize these relationships (Fig. 2).

Our regression analyses indicated that two species, *Eucalyptus erythrophloia* (E) and *Plathymenia reticulate* (D), had high leverage based on Cook's statistics from the analyses. Therefore we ran all analyses with and without the two high leverage species to see how different the results are.

To test Prediction 3 (RGR is negatively related to root carbohydrate storage among deciduous species but not among evergreen species) we regressed RGR, LMF_{20} and RMF_{20} against root NSC concentration (g carbohydrate g^{-1} root) and against root NSC fraction (g carbohydrate g^{-1} total) for each leaf habit group (Fig. 3). Both must be considered because savanna species appear to increase their capacity for storage through adjusted structural growth of roots that accommodates additional storage (Tomlinson *et al.*, 2013*b*). We regressed LMF_{20} and RMF_{20} against root NSC concentration and against root NSC fraction, because we had proposed that allocation to storage

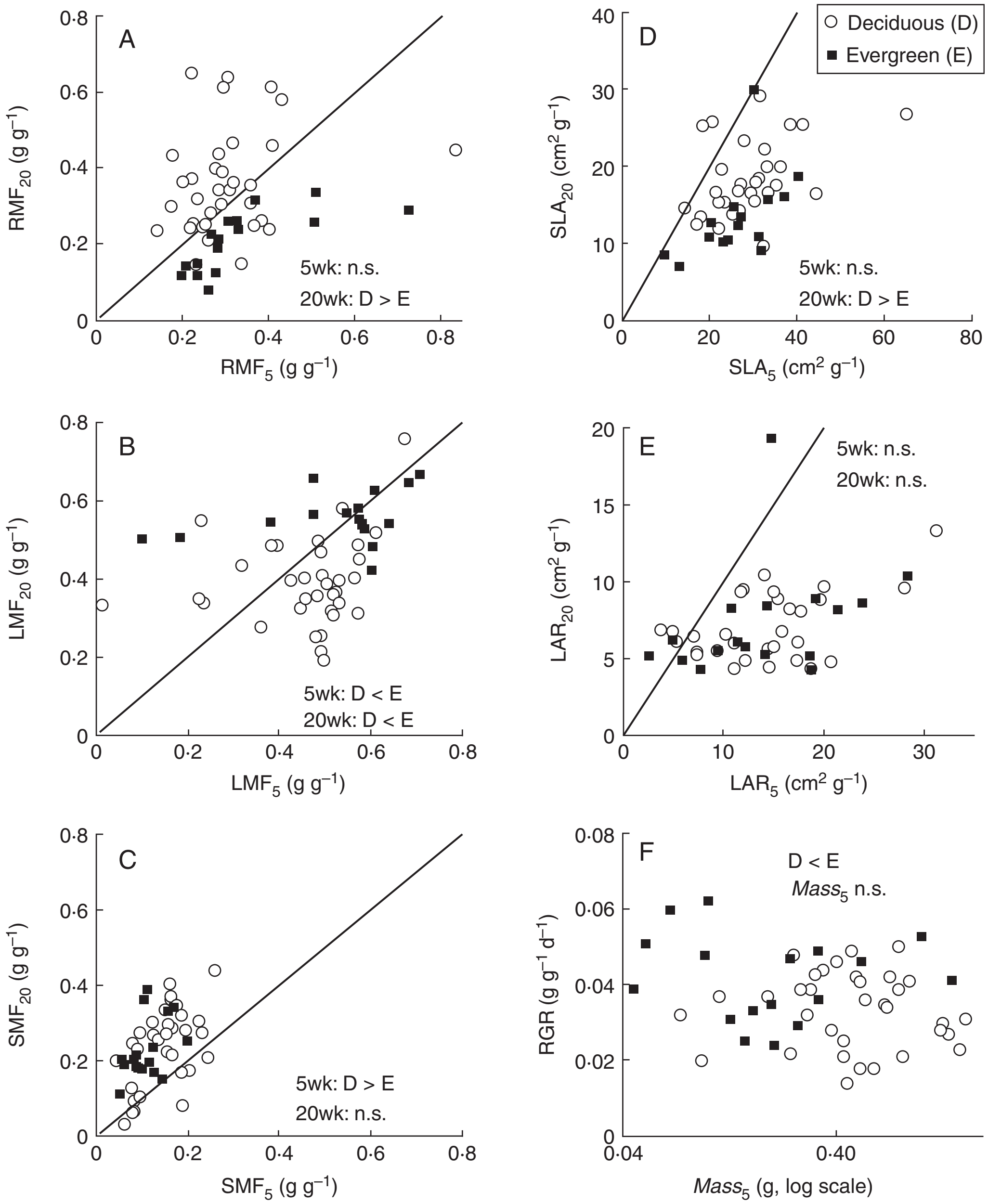

FIG. 1. Ontogenetic shifts in species' traits measured at 5 and 20 weeks after planting (A–E) and relative growth rate (RGR) over the same period (F) for 51 species of savanna trees of different leaf habit (deciduous, D; evergreen, E). Traits measured include (A–C) organ mass fractions (root, RMF; leaf, LMF; stem, SMF), (D) specific leaf area (SLA) and (E) leaf area ratio (LAR). A 1 : 1 line is indicated on each panel as reference to indicate how the traits have changed over time (species' symbols found above the line indicate that trait values have increased from 5 to 20 weeks, and vice versa). Significant differences ($P < 0{\cdot}05$) in traits between leaf habit groups at each age are also indicated on the panels (test results are provided in Table 1). RGR was uncorrelated with $Mass_5$ for either leaf habit group and across all species (Supplementary Data Table S2).

increased RMF and decreased LMF, thereby leading to decreased RGR.

All regression analyses and group comparisons were conducted using phylogenetically adjusted generalized least squares regression. We used the pgls() function of the R package *caper* (Orme *et al.*, 2013) to choose the best transformation based on the optimal value of Pagel's lambda (λ) (Freckleton *et al.*, 2002). Most variables did not show phylogenetic signal, and we indicate λ only when significant phylogenetic signal was detected.

RESULTS

Mean RGR of evergreen and deciduous savanna species

RGR of evergreen species was significantly greater than that of deciduous species but was unrelated to initial mass ($Mass_5$) (Fig. 1F, Table 1). At the initial harvest evergreen species were on average smaller than deciduous species (independent samples *t*-test: *t*-value = 3·5, $P = 0{\cdot}001$, d.f. = 49. Means: Deciduous: 0·465 g; Evergreen: 0·196 g). As there was no effect of initial mass (*Mass*$_5$) on RGR across species (Table 1 and Fig. 1F), we believe that initial size differences are not the cause of the greater RGR of evergreen species. LAR did not differ significantly between leaf habit groups at either age (Fig. 1E).

Trait changes over time

Leaf and root mass fractions of evergreen and deciduous species shifted in different directions over time (Fig. 1; Table 1). Most deciduous species increased allocation to roots (Fig. 1A) while most evergreen species increased allocation to leaves (Fig. 1B). Consequently, while at 5 weeks RMF$_5$ did not differ between leaf habits, after 20 weeks evergreen species had significantly smaller RMF$_{20}$ than deciduous species. Evergreen species had greater LMF than deciduous species at both ages, but the differences were even greater at 20 weeks (Table 1). The range of LMF values among evergreen species decreased over time (Fig. 1B). Species of both groups increased allocation to stems with increasing age (Fig. 1C). SLA decreased with age (Fig. 1D, E) (with the exception of *Eucalyptus erythrophloia*). At 5 weeks, SLA$_5$ did not differ significantly between leaf habits. However, the decline in SLA with age was more rapid among evergreens, such that they had significantly lower mean SLA than deciduous species at 20 weeks. NAR did not differ between deciduous and evergreen species (Table 1).

Across all species, traits measured at 5 weeks were not significantly correlated with mass at 5 weeks (Supplementary Data Table S2). The same was true for traits and mass measured at 20 weeks, with the exception of SMF$_{20}$, which was positively correlated with *Mass*$_{20}$. Overall, this suggests that plant size did not explain cross-species differences at a given moment in time.

RGR relationships with component traits for each leaf habit

For deciduous species, RGR was positively related to LMF$_{ave}$, SLA$_{ave}$ and LAR$_{ave}$ but unrelated to NAR (Fig. 2). For evergreen species, RGR was unrelated to any of the four variables. However, when the outlier, *Eucalyptus erythrophloia*, was excluded, RGR of evergreen species was positively related to SLA$_{ave}$ and LAR$_{ave}$ but still unrelated to LMF$_{ave}$ and NAR (Supplementary Data Fig. S1). When RGR was modelled as a function of LMF, SLA and NAR, all three components contributed significantly to the models among all species, among deciduous species and among evergreen species (Table 2). However, proportional variation explained by each component differed substantially between the deciduous and evergreen models, but somewhat differently from our expectations. Among deciduous species, RGR variation was similarly explained by LMF (27 %) and NAR (28 %) and slightly more so by SLA (34 %), whereas among evergreen species SLA explained almost 38 %, NAR 33 % and LMF only 17 % of the variation (Table 2). In most cases there was no evidence of phylogenetic signal. However, again the species with high leverage did affect the results for evergreen species quite substantially (Supplementary Data Table S3): when *Eucalyptus erythrophloia* was excluded, RGR of evergreen species did show significant phylogenetic signal and the resulting partitioning of variance was greatest for NAR (62 %), then SLA (35 %) and LMF only accounted for 2 % of the variation of RGR. The two analyses

TABLE 2. *Regression coefficients and ANOVA (Type II SS) results for general linear models of RGR modelled as a function of LMF, SLA and NAR (ln RGR = ln LMF + ln SLA + ln NAR + ε), for all species, deciduous species only and evergreen species only*

Variable	All species					Deciduous species					Evergreen species				
	β	s.e.	SS	η^2	*P*	β	s.e.	SS	η^2	*P*	β	s.e.	SS	η^2	*P*
LMF$_{ave}$	0·879	0·077	20·267	0·305	<0·001	0·819	0·101	8·981	0·273	<0·001	0·752	0·182	3·349	0·167	0·004
SLA$_{ave}$	0·706	0·066	17·902	0·269	<0·001	0·769	0·086	11·173	0·340	<0·001	0·665	0·115	6·543	0·327	< 0·001
NAR	0·836	0·071	21·846	0·328	<0·001	0·890	0·108	9·392	0·286	<0·001	0·734	0·118	7·562	0·378	< 0·001
Residual			6·515					3·328					2·547		
Total SS			66·530					32·874					20·001		
R^2_a	0·82					0·85					0·74				
Residual error	0·399					0·372					0·443				
d.f.	41					24					13				

All variables are standardized to mean 0 and variance 1. The effect sizes of the component variables are indicated by the coefficients of the regression models (β). The proportion of variance in RGR explained by each component is indicated (η^2). Analyses were conducted using the *pgls*() function of the *caper* package in R. No phylogenetic signal was detected for any analysis (λ = 0).

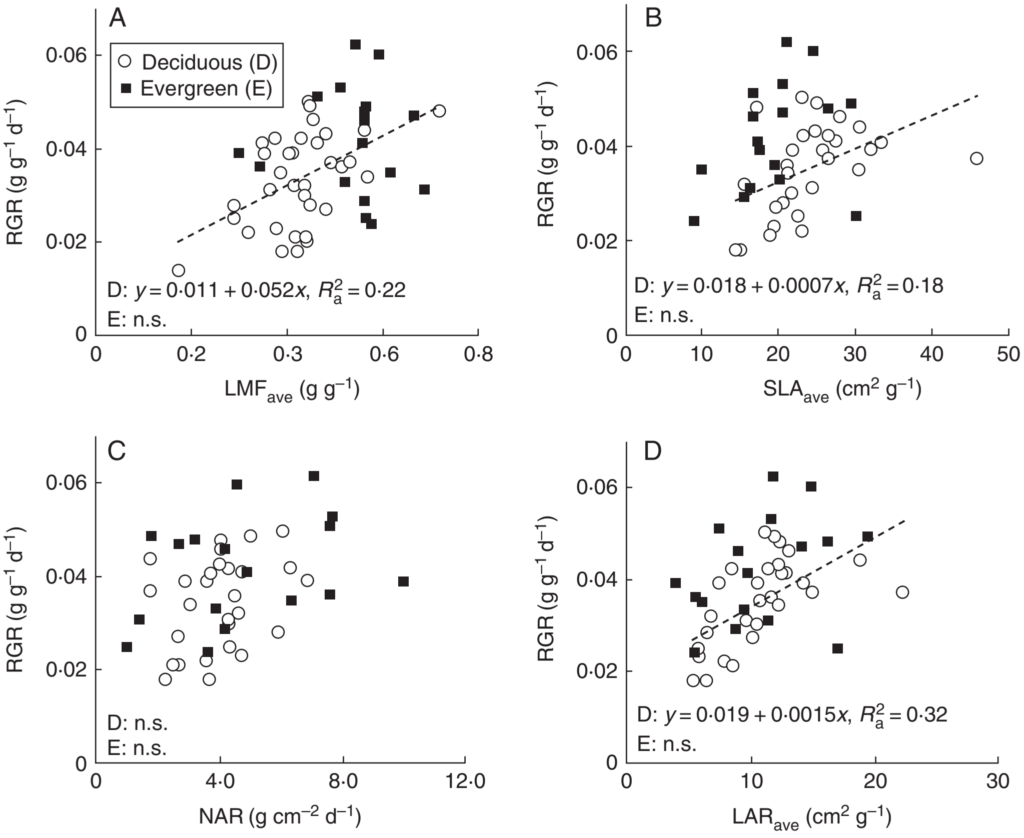

FIG. 2. RGR plotted against individual plant traits for juveniles of 51 savanna tree species. Species are distinguished by leaf habit (deciduous, $n = 17$; evergreen, $n = 34$). Significant regression relationships ($P < 0{\cdot}05$) between RGR and each plant trait for each leaf habit are indicated on each panel (dashed line = deciduous, solid line = evergreen). Regression analyses were estimated using the *pgls*() function of the *caper* package in R. No phylogenetic signal was detected for any of the four analyses shown.

indicate that LMF contributed much less to variation in RGR among evergreen species than among deciduous species. Effect sizes (model coefficients) were similar for each variable in each model.

RGR and LMF versus root carbohydrate storage

Root NSC *concentration* (g carbohydrate g^{-1} root) was not significantly different between leaf habits ($P = 0{\cdot}075$) whereas NSC *fraction* (g carbohydrate g^{-1} total) was greater for deciduous species than for evergreen species (Table 1). Among deciduous species, RGR, LMF_{20} and RMF_{20} were correlated with both root NSC concentration and root NSC fraction (Fig. 3). By contrast, among evergreen species, only RMF_{20} was correlated to either root NSC variable. LMF_{20} and RMF_{20} were highly negatively correlated among deciduous species ($\rho = -0{\cdot}69$, $P < 0{\cdot}001$) but uncorrelated among evergreen species ($\rho = -0{\cdot}39$, n.s.).

DISCUSSION

In this study, we compared RGR and traits related to RGR of seedlings of savanna tree species of different leaf habit taken from three continents. Surprisingly, RGR was greater among evergreen species than among deciduous species, which contradicts evidence from other plant communities (Cornelissen *et al.*, 1996; Swanborough and Westoby, 1996; Wright *et al.*, 2004). Furthermore, we observed that the contribution of drivers of RGR variation, LMF, SLA and NAR (Evans, 1972; eqn 1), differed between deciduous and evergreen species: RGR variation among evergreen species was mainly driven by SLA variation whereas RGR variation among deciduous species was more equally driven by SLA and LMF. We predicted that these differences in driving variables could be ascribed to differences in carbohydrate storage between evergreen and deciduous species, because allocation to storage compromises LMF. Our data support this prediction, as we found that LMF and RGR were negatively related to root NSC fraction among deciduous species but not among evergreen species.

Mean RGR is greater among evergreen than among deciduous savanna tree species

We found that mean RGR was greater for evergreen than for deciduous savanna species. This result contrasts with earlier studies suggesting that deciduous species are faster growing than evergreen species because they have greater SLA and nitrogen concentration per unit leaf mass (N_m) (Cornelissen *et al.*, 1996; Swanborough and Westoby, 1996; Wright *et al.*, 2004; Poorter and Garnier, 2007). In our study, deciduous savanna species indeed had higher SLA than evergreen savanna species (Fig. 1, Table 1). However, there was substantial overlap in the ranges of SLA_{ave} and of each leaf habit, and differences in mean SLA_{ave} were small. By contrast, LMF was substantially lower for deciduous species than for evergreen species (Table 1,

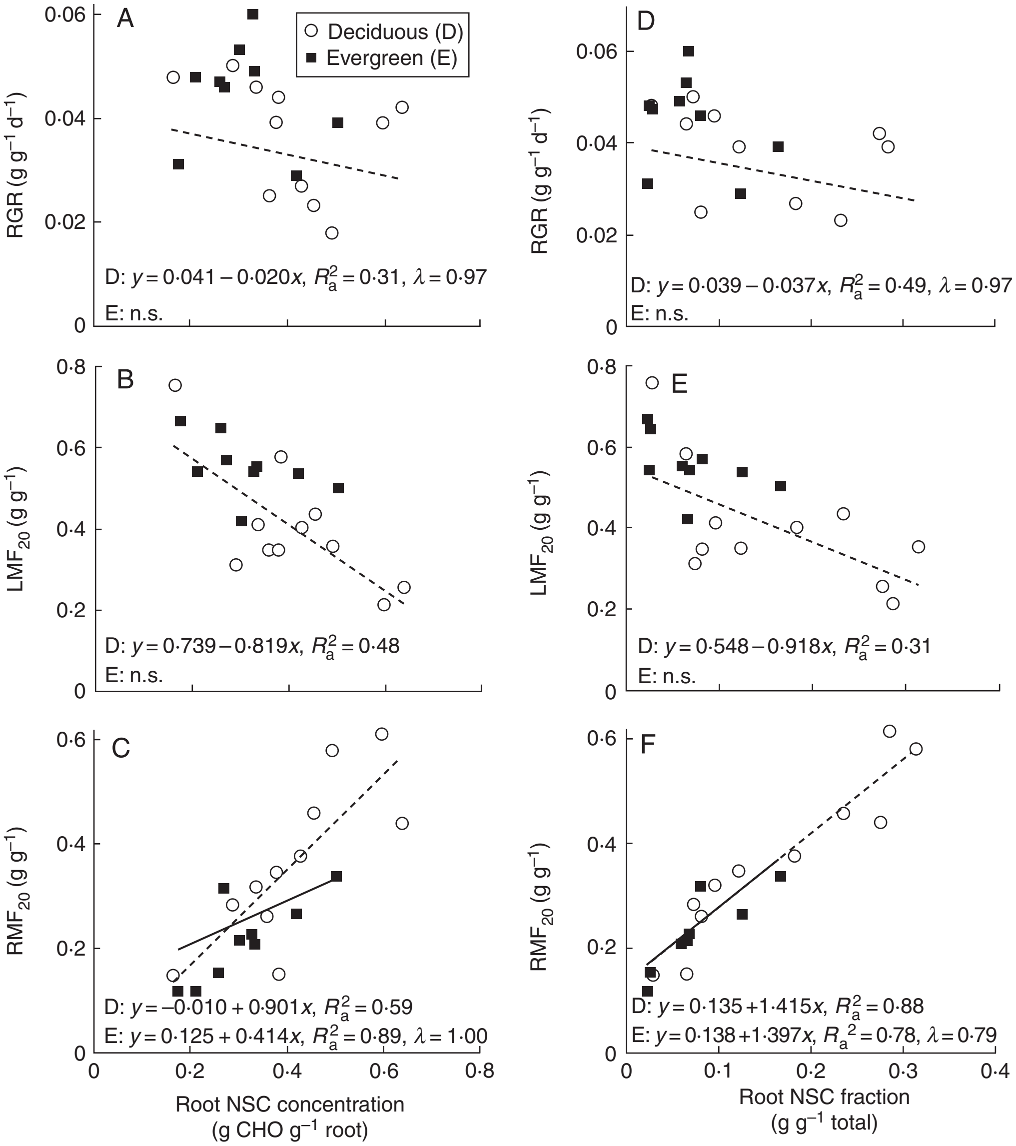

FIG. 3. RGR, LMF_{20} and RMF_{20} plotted against (A–C) root non-structural carbohydrate concentration (g carbohydrate g^{-1} root) and against (D–F) root non-structural carbohydrate fraction (g carbohydrate g^{-1} total). Non-structural carbohydrates were measured on 20-week-old plants. Species are distinguished by leaf habit (deciduous, $n = 11$; evergreen, $n = 9$). Significant regression relationships ($P < 0.05$) are indicated (dashed line = deciduous, solid line = evergreen). Regression analyses were estimated using the *pgls*() function of the *caper* package in R. Where phylogenetic signal was detected, estimated Pagel's lambda (λ) for that phylogenetic transformation is shown.

Fig. 2C), probably explaining why RGR was greater among evergreen than among deciduous species in our study. This result challenges previous interpretations that evergreen species are more conservative plants than deciduous species (Westoby *et al.*, 2002). Evergreens can dominate both productive and unproductive environments (Givnish, 2002). Our results suggest that at the very least evergreen species have equal RGR to deciduous species in savannas.

Traits that drive RGR differ between savanna trees of different leaf habit

We predicted that RGR variation is driven by LMF variation among deciduous species to a greater extent than among evergreen species. RGR variation was indeed being driven differently between groups: among deciduous species, LMF explained 27 % of the variation, whereas among evergreen species LMF explained between 2 % (without the outliers) and 17 % (including outliers) of the variation in RGR (Table 2). The contribution values we observed in this study lie within the ranges found across other studies (Poorter and Van der Werf, 1998; Shipley, 2006; Rees *et al.*, 2010). Estimated trait contributions to RGR differ depending on whether species are compared at a common size or variable sizes (Rees *et al.*, 2010): when species differ greatly in mass, this favours assigning RGR variation to NAR. When their RGRs are estimated for similar masses, then NAR is far less important. Our evergreen and deciduous species had substantial overlap in their initial mean masses and their range covers less than two orders of magnitude, so we think that our groups are comparable to one another.

We hypothesized that allocation to carbohydrate storage in deciduous species would compromise their allocation to LMF, and that because of the larger variation in LMF, LMF would be a stronger driver of RGR in deciduous species and not in evergreen species. This contention was indeed supported by our findings (Fig. 3) and contrasts with a previous global meta-analysis by Poorter *et al.* (2012), in which they found that LMF made a small contribution to RGR variation among eudicots. In the next section we argue that the reason for these differences in drivers may be due to different responses to an endemic disturbance in savanna systems. Our results also suggest that the relationships between RGR and root carbohydrate storage may not always be detectable among evergreen species (Myers and Kitajima, 2007; Poorter and Kitajima, 2007) because differences in storage are too small within the evergreens to generate variation in RGR.

Divergent driving traits of RGR among savanna species: a role for fire?

Our observations appear to be consistent with the growth–survival trade-off hypothesis, which proposes that species trade a high RGR by allocating resources to storage, which increases their ability to survive intermittent disturbance events (Kitajima, 1994; Poorter and Kitajima, 2007). Savannas are subject to regular fire disturbance of varying frequencies. Different fire adaptations of evergreen and deciduous species may explain why RGR variation is related to carbohydrate storage for deciduous but not for evergreen savanna tree species. Fire frequency changes substantially across savanna types (Barbosa *et al.*, 1999; Russell-Smith *et al.*, 2003; Daniau *et al.*, 2012), creating a gradient of selection for fire-responsive traits (e.g. Tomlinson *et al.*, 2012). In both functional groups, the amount of carbohydrates stored may be positively related to the severity of fire pressure. However, the overall carbohydrate amounts and range of amounts are much greater in deciduous than among evergreen species (Tomlinson *et al.*, 2013*b*). Because deciduous species must allocate substantial resources to storage for shoot regrowth, they may be predisposed to increased selection of this trait under fire pressure (Wigley *et al.*, 2008). This allocation to storage comes at the expense of RGR. By contrast, evergreen species retain their leaves through the non-growing season and are therefore not predisposed to enhanced allocation to storage in roots and possess much greater above-ground biomass than deciduous species (Tomlinson *et al.*, 2013*b*). Many of our evergreen species (*Eucalyptus*, *Melaleuca*, *Petalostigma*) possessed small lignotubers with large numbers of epicormic meristems. These meristems can expand rapidly following defoliation events (James, 1984; Canadell and Lopez-Soria, 1998), producing large leaf canopies very rapidly to recuperate lost resources. Therefore, the evergreen strategy may depend on rapid reshooting based on their remaining root reserves which are proportionately small, but significant (see also Hoffmann *et al.*, 2004), in turn explaining why evergreens have greater RGR than deciduous species in savanna systems.

Plant allometry and estimation of RGR drivers

Evergreen and deciduous savanna species show very different allocation patterns over time (Tomlinson *et al.*, 2013*b*; Fig. 2): deciduous species increase their allocation to roots with increasing size whereas evergreen species increase their allocation to leaves with increasing size. This pattern explains how the groups can have different drivers of RGR, as the deciduous group is consistently compromising growth through allocation to storage, whereas evergreens are not.

The different changes in allometries also suggests a potential weakness in existing methods of estimating RGR: if the drivers of RGR change with size/age, then surely what is affecting RGR across species is not just differences in their mean traits at some point in the period, but also the manner in which these traits change over the growing period. Methods of analysing contribution to RGR that are commonly used (Poorter and Van der Werf, 1998; Shipley, 2006; Rees *et al.*, 2010), and which we have followed here, typically use a single point estimate to calculate the contribution of LMF to RGR, whereas it may be necessary to incorporate an estimate of the change in value over the measurement period (ΔLMF, similarly for ΔSLA) to properly account for the contribution of the variable to RGR variation. In this sense we consider it possible that existing methods significantly underestimate the contribution of LMF variation and even SLA variation to RGR variation. This requires further investigation.

CONCLUSIONS

Our results indicate that drivers of RGR differ between evergreen and deciduous species, and that RGR can be greater for evergreens than for deciduous species, which contrasts with previous studies. Evergreen and deciduous tree species of savannas may employ fundamentally different strategies for coping with fire. Evergreens may have been selected for a fire-tolerance strategy that depends on rapidly establishing proportionately large leaf canopies (high LMF) to support rapid regrowth (high RGR), in contrast to high total carbohydrate storage below ground among deciduous species. This in turn suggests that where environmental disturbances select for different growth strategies between functional groups, these may also lead to different drivers of RGR variation between those groups.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Table S1: quantitative data of leaf traits of 51 savanna tree species from Africa, Australia and South America grown in a common greenhouse experiment. Table S2: Pearson correlations among RGR and measured plant morphological traits measured at 5 and 20 weeks. Table S3: regression coefficients and ANOVA results for general linear models of RGR modelled as a function of LMF, SLA and NAR. Figure S1: RGR plotted against individual plant traits for juveniles of 51 savanna tree species.

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