

Deciduous and evergreen trees differ in juvenile biomass allometries because of differences in allocation to root storage

Kyle W. Tomlinson^{1,2,*}, Frank van Langevelde¹, David Ward², Frans Bongers³, Dulce Alves da Silva^{4,5}, Herbert H. T. Prins^{1,2}, Steven de Bie¹ and Frank J. Sterck³

¹Resource Ecology Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands, ²School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa, ³Forest Ecology and Management Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands, ⁴Departamento de Botânica, Universidade de Brasília, Brasília, DF 70910-970, Brazil and ⁵Empresa Brasileira de Pesquisa Agropecuária, Cenargen, Parque Estação Biológica, Av. W5 Norte, CP 02372, Brasília, DF 70770-917, Brazil

* For correspondence. E-mail kyle.tomlinson@wur.nl or kylewtomlinson@gmail.com

Received: 15 January 2013 Revision requested: 19 March 2013 Accepted: 22 April 2013

- **Background and Aims** Biomass partitioning for resource conservation might affect plant allometry, accounting for a substantial amount of unexplained variation in existing plant allometry models. One means of resource conservation is through direct allocation to storage in particular organs. In this study, storage allocation and biomass allometry of deciduous and evergreen tree species from seasonal environments were considered. It was expected that deciduous species would have greater allocation to storage in roots to support leaf regrowth in subsequent growing seasons, and consequently have lower scaling exponents for leaf to root and stem to root partitioning, than evergreen species. It was further expected that changes to root carbohydrate storage and biomass allometry under different soil nutrient supply conditions would be greater for deciduous species than for evergreen species.
- **Methods** Root carbohydrate storage and organ biomass allometries were compared for juveniles of 20 savanna tree species of different leaf habit (nine evergreen, 11 deciduous) grown in two nutrient treatments for periods of 5 and 20 weeks (total dry mass of individual plants ranged from 0.003 to 258.724 g).
- **Key Results** Deciduous species had greater root non-structural carbohydrate than evergreen species, and lower scaling exponents for leaf to root and stem to root partitioning than evergreen species. Across species, leaf to stem scaling was positively related, and stem to root scaling was negatively related to root carbohydrate concentration. Under lower nutrient supply, trees displayed increased partitioning to non-structural carbohydrate, and to roots and leaves over stems with increasing plant size, but this change did not differ between leaf habits.
- **Conclusions** Substantial unexplained variation in biomass allometry of woody species may be related to selection for resource conservation against environmental stresses, such as resource seasonality. Further differences in plant allometry could arise due to selection for different types of biomass allocation in response to different environmental stressors (e.g. fire vs. herbivory).

Key words: Carbohydrate storage, leaf habit, nutrients, plant allocation theory, plant growth, savanna, trees.

INTRODUCTION

Constraints on plant allometric scaling potentially frame plant form, function, ecology and diversity, and there is strong evidence to suggest that several prominent organismal-, community- and ecosystem-level properties of plants emerge from relatively few allometric and biomechanical rules (Enquist, 2004). However, existing general models explaining allometric patterns in plants (West *et al.*, 1997, 1999) do not account for a substantial amount of variation in plant organ allometry (Enquist and Niklas, 2002; McCarthy and Enquist, 2007). Research into biomass partitioning and allometry has been led by the notion that partitioning functionally supports resource capture because plants collect different resources with different organs (Brouwer, 1962; Tilman, 1988; Enquist and Niklas, 2002; Poorter *et al.*, 2012). There is a substantial body of evidence that biomass partitioning affects the ability of plants to tolerate and respond to disturbance, such as for instance species growing in fire-prone environments store substantial resources in roots

beyond the reach of fires (Raunkiaer, 1934; Bellingham and Sparrow, 2000; Hoffmann *et al.*, 2004; Tomlinson *et al.*, 2012). This indicates that biomass allocation is also selected for resource conservation, which may go beyond selected responses to disturbance, as we will demonstrate below. Importantly, the cumulative effects of this altered biomass allocation could result in different organ biomass allometries among species with different levels of allocation to storage. Biomass partitioning to storage may explain a significant amount of this unaccounted for variation, providing an avenue for improvement in the predictive power of such models as well as our understanding of plant biomass allometry. As a first step, it is necessary to demonstrate that differences in biomass allometry between groups of plants can be related to differences in their reserve storage patterns.

Resource conservation through storage may be selected in environments with strong seasonality in resource supply because those stored resources can support survival through non-growing seasons and support regrowth at the start of growing seasons. Given the extent of seasonal environments across the globe

(Kottek *et al.*, 2006), selection for both resource capture and storage may explain a substantial amount of interspecific variation in biomass partitioning and allometry. Leaf habit, i.e. whether a species is evergreen or deciduous, has been linked to divergent plant strategies in seasonal climates (Reich and Borchert, 1984; Walters and Reich, 1999; Marksteijn and Poorter, 2009; Tomlinson *et al.*, 2012). Walters and Reich (1999) demonstrated that for juvenile trees growing under light-limited conditions (<12% light), tropical evergreen and temperate deciduous species partition resources differently with increasing size: evergreen species increase allocation to leaf and stem, while deciduous species increase allocation to root. They postulated that deciduous species require greater allocation to reserve storage in roots than evergreen species for rapid growth during windows of high light availability at the start of each subsequent growing season, and that evergreen species require much less storage because they retain leaves throughout the year. They further postulated that these resources are conserved in the roots, thereby explaining the greater root mass fractions of deciduous species in temperate environments. Unfortunately, their study leaves a lot of room for speculation because they compared growth of species of two different leaf habits that were selected from quite different environments (evergreen species from the tropics and deciduous species from the temperate zone). Therefore, there is a need to compare evergreen and deciduous species from the same habitat to establish these differences properly. Further, their explanation for the differences is specific to the conditions of forest environments, and we believe that a simpler explanation can be provided that predicts differences in partitioning of evergreen and deciduous species in general: deciduous species need to retain stored reserves for re-establishing leaf canopies in subsequent growing seasons. Thus deciduous species may allocate more resources to roots than evergreen species in any seasonal environment, defining distinct biomass partitioning patterns between the leaf habits (e.g. Espelta *et al.*, 2005). There is evidence that for juvenile trees, carbohydrate reserves are stored in roots (Hoffmann *et al.*, 2004; Kobe *et al.*, 2010), but it has yet to be formally demonstrated that root carbohydrate storage differs for evergreen and deciduous species.

In this study, we investigated whether leaf habit distinguishes root carbohydrate storage and biomass allometry of juveniles of tree species abundant in savanna systems, and whether allocation to root carbohydrate storage can predict biomass allometry among these species. Savannas are seasonal environments with marked wet and dry seasons (Cole, 1986; Sarmiento, 1992; Kottek *et al.*, 2006) where light is usually non-limiting to growth while water stress and defoliation by fire (disturbance) during the non-growing season are more pressing hazards to seedling survival and growth (Hoffmann *et al.*, 2004; Tomlinson *et al.*, 2012). If differences in biomass allometry between leaf habits can be found that are qualitatively similar to the patterns found by Walters and Reich (1999), this would underpin the proposition that biomass allocation and biomass allometry are fundamentally different between leaf habits.

Biomass allometry of species of different leaf habit might further differ in the species' response to different nutrient supply conditions if they have different carbohydrate partitioning patterns. Kobe *et al.* (2010) observed that much of the variation in cumulative root to shoot partitioning between plants grown under high and low nutrient conditions is due to differences in root carbon storage: plants allocate more carbon to

storage in roots when grown under low nutrient conditions than under high nutrient conditions, rather than to increased root branching and extension for resource capture. Given that evergreen and deciduous species may differ in the rate at which they allocate resources to storage, differences in storage, and consequently in allometries, between the leaf habits may be accentuated under nutrient deficiency.

We hypothesized that deciduous and evergreen trees differ in juvenile biomass allometries because of differences in allocation to root storage. We made the following specific predictions. (1) Biomass allocation to stems and leaves over roots increases with plant size at a faster rate among evergreen species than deciduous species (indicated by higher scaling exponents for stem to root and leaf to root partitioning). (2) Deciduous species store more carbohydrates in roots than evergreen species. (3) Across species, scaling exponents for stem to root and leaf to root biomass partitioning are negatively related to root carbohydrate storage. (4) Under low nutrient conditions, biomass partitioning to roots and carbohydrate storage in roots increases in plants, and both effects are greater for deciduous species than for evergreen species.

We tested these predictions by considering root carbohydrate storage and biomass allometry of juveniles of 20 savanna tree species (all angiosperms) of different leaf habit (nine evergreen, 11 deciduous) grown in two soil nutrient treatments for up to 20 weeks.

MATERIALS AND METHODS

A list of variables discussed in the text, together with their acronyms and units of measurement, is provided in Table 1.

Species selection

We selected 20 abundant tree species (nine evergreen, 11 deciduous) from savannas in Africa, Australia and South America (Tomlinson *et al.*, 2012). Species were sampled in southern Africa (Miombo in Zimbabwe, Lowveld and Coastal Belt in South Africa; Frost, 1996; Mucina and Rutherford, 2006), *Eucalyptus* and *Acacia* woodlands in north-eastern Australia (coastal and inland woodlands in Queensland; Cole, 1986) and in eastern South America (Cerrado and Caatinga biomes in Brazil; Cole, 1986). Two plant orders form the bulk of the species sample, Fabales (Fabaceae) and Myrtales (Combretaceae, Myrtaceae) (a species list with descriptions is provided in Supplementary Data Table S1).

Experimental design

We conducted a greenhouse experiment to compare the organ biomass allometries of tree species' juveniles grown for 5 and 20 weeks under different nutrient treatments. A pot trial was conducted in a greenhouse chamber at UNIFARM, Wageningen University, The Netherlands. The temperature in the greenhouse was set at 28 °C for 12 h (daytime) and 23 °C for 12 h (nighttime). Supplementary light (150 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was provided in order to supply sufficient light to ensure that the daily supply of photon flux density exceeded 10 $\text{mol m}^{-2} \text{d}^{-1}$.

The trees were grown in plastic pipes of 10 cm diameter and 100 cm depth, to allow the roots more space to grow in an effort to reduce any changes in organ allocation caused by pot

soil volume. Water was supplied through irrigation three times per day at a rate of 40 mL per pipe per day, equivalent to 800 mm of rainfall over 20 weeks of growth. Soil nutrients were supplied using slow-release fertilizer [Osmocote 18-6-12 fertilizer (8–9 month mixture)] mixed into the growing medium (river sand). The plants were grown at two nutrient levels. The high nutrient treatment was applied at a rate of 5 kg fertilizer m⁻³ river sand, and the low nutrient treatment was applied at a rate of 1 kg fertilizer m⁻³ river sand.

Allometric data

Seedlings were planted into the pipes a few days after germination, and then grown for a further 5 or 20 weeks, at which time they were harvested. Five plants per species per nutrient treatment were grown for each time period (5 and 20 weeks) in each batch run of the experiment. Each species was grown in two of three batch runs of the experiment, yielding a maximum replication of ten plants per nutrient treatment per time period for each species, or 20 plants per nutrient treatment for each species, which provided a range of plant sizes per species covering five orders of magnitude (total dry mass of individual plants ranged from 0.003 to 258.724 g) on which allometric relationships could be calculated. Some plants did not thrive after transplanting into pipes; those individuals were destroyed. Leaf mass (M_L), stem mass (M_S) and root mass (M_R) were measured on each plant harvested at 5 and 20 weeks after planting (all masses in g dry matter).

Scaling allometries are usually represented using a power function (Snell, 1892; Peters, 1983; Enquist and Niklas, 2002):

$$Y = \beta X^\alpha \quad (1)$$

which can also be written in the logarithmic form:

$$\log_{10} Y = \log_{10} \beta + \alpha \log_{10} X \quad (2)$$

where α is the allometric exponent, describing the change in scaling with increasing size, β is the allometric constant, and X

TABLE 1. List of variables discussed in the text, with their acronyms and units of measure

Variable	Abbreviation	Units
Leaf habit (E, evergreen, D, deciduous)	H	Factor
Soil nutrient treatment [high (H) and low (L) nutrient supply]	N	Factor
Biomass allometry variables		
Allometric scaling exponent	α	g g ⁻¹
Allometric scaling constant	β	g
Individual data		
Individual leaf mass	M_L	g
Individual stem mass	M_S	g
Individual root mass	M_R	g
Individual total mass	M_T	g
Individual root non-structural carbohydrate concentration	$[C]_R$	g carbohydrate g ⁻¹ root
Individual plant root non-structural carbohydrate fraction	$C_{R/T}$	g carbohydrate g ⁻¹ total
Species mean data		
Mean total mass of individuals of species	M_{species}	g

and Y are the two biomass components being related to one another. When α does not differ significantly from 1, this indicates that the biomass relationship between the two components does not change with size. When comparing allometric relationships for two groups, significant differences between the intercepts, β , are difficult to interpret if the exponents, α , differ significantly, because the position of each intercept depends on the slope of that line. However, when differences in α are non-significant, differences in β may indicate fixed partitioning differences between groups (Enquist and Niklas, 2002; McCarthy and Enquist, 2007).

Allometric coefficients, α and β , for each species grown under each nutrient treatment were estimated for M_L vs. M_S (leaf to stem allometry), M_L vs. M_R (leaf to root allometry) and M_S vs. M_R (stem to root allometry), using reduced major axis (RMA) regression on the log₁₀-transformed organ mass data measured at the two harvesting dates (see Sokal and Rohlf, 1981). The derived coefficient estimates are presented in Tables 2 and 3.

Root carbohydrate data

Root material was taken from the upper third of the central taproot of five plants harvested at 20 weeks grown under each nutrient treatment (thus ten plants per species). Root non-structural carbohydrate concentration ($[C]_R$, g carbohydrate g⁻¹ root) was estimated per sample by separate estimation of the components of $[C]_R$, namely the starch concentration and soluble sugars concentration, using a revised procedure developed at the University of Florida (Kaoru Kitajima, pers. comm.). The method is identical to that described in Poorter and Kitajima (2007) except that starch and more complex sugars are hydrolysed to glucose using 1.1 % hydrochloric acid solution in place of amyloglucosidase.

Root carbohydrate storage might differ between species both in terms of concentration in roots ($[C]_R$) and in terms of total carbohydrate stored in roots, i.e. the plant root non-structural carbohydrate fraction ($C_{R/T}$, g carbohydrate g⁻¹ total). The latter depends on the plant root mass (M_R) to total mass (M_T) fraction:

$$C_{R/T} = [C]_R \times (M_R/M_T) \quad (3)$$

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, and therefore we were confident that this estimate was representative of differences between species. $C_{R/T}$ is also a measure of the cumulative partitioning to root storage.

Mean root non-structural carbohydrate concentration ($[C]_R$) per species ranged from 16 to 64 % in the high nutrient treatment and from 22 to 59 % in the low nutrient treatment (Table 4), which is similar to ranges found by Hoffmann *et al.* (2004) for seedlings of forest and savanna species measured at 21 weeks of growth (approx. 5–55 %).

Statistical analysis

We adopted a mixed modelling approach to evaluate whether allometries and root carbohydrate storage differed between

TABLE 2. Allometric coefficients α and β for biomass partitioning of 20 savanna tree species grown in the high nutrient treatment

Species	Leaf habit	<i>n</i>	Total mass (g)			M_L vs. M_S					M_L vs. M_R					M_S vs. M_R				
			Mean	Max	Min	α	s.e.	$\log_{10} \beta$	s.e.	ρ	α	s.e.	$\log_{10} \beta$	s.e.	ρ	α	s.e.	$\log_{10} \beta$	s.e.	ρ
<i>Acacia aulacocarpa</i>	E	19	1.948	72.517	0.125	0.832	0.014	0.629	0.020	0.998	1.051	0.055	0.600	0.061	0.976	1.263	0.078	-0.034	0.086	0.967
<i>Acacia shirleyi</i>	E	20	0.660	45.064	0.051	0.829	0.027	0.532	0.043	0.991	1.007	0.048	0.684	0.068	0.980	1.215	0.081	0.183	0.115	0.959
<i>Acacia sieberiana</i>	D	19	4.164	94.636	0.177	0.825	0.027	0.248	0.023	0.991	0.685	0.050	-0.027	0.052	0.954	0.83	0.072	-0.333	0.076	0.935
<i>Acacia tortilis</i>	D	20	3.740	60.062	0.155	0.793	0.023	0.131	0.023	0.993	0.771	0.029	0.029	0.030	0.987	0.972	0.036	-0.129	0.038	0.987
<i>Aspidosperma macrocarpon</i>	D	20	4.828	28.433	1.029	1.109	0.044	0.598	0.029	0.985	1.064	0.113	-0.089	0.075	0.892	0.96	0.095	-0.62	0.063	0.907
<i>Aspidosperma pyrifolium</i>	D	18	1.539	10.748	0.206	0.912	0.027	0.007	0.024	0.993	1.352	0.111	0.051	0.069	0.945	1.482	0.108	0.048	0.067	0.957
<i>Atalaya hemiglauca</i>	E	17	1.397	14.753	0.188	0.784	0.039	0.464	0.046	0.981	1.056	0.093	0.332	0.075	0.940	1.347	0.11	-0.168	0.088	0.949
<i>Brachylaena discolor</i>	E	20	0.872	50.837	0.015	0.811	0.023	0.562	0.043	0.993	1.006	0.029	0.396	0.042	0.993	1.24	0.037	-0.204	0.053	0.992
<i>Brachystegia spiciformis</i>	D	20	1.458	10.533	0.398	0.952	0.075	0.730	0.083	0.942	0.849	0.082	-0.106	0.043	0.911	0.891	0.086	-0.878	0.045	0.913
<i>Colophospermum mopane</i>	D	20	4.728	65.421	0.631	0.753	0.019	0.396	0.015	0.994	0.729	0.034	0.256	0.028	0.980	0.968	0.04	-0.186	0.032	0.985
<i>Combretum apiculatum</i>	D	16	1.895	41.697	0.115	0.774	0.022	0.218	0.026	0.994	0.916	0.042	0.090	0.040	0.985	1.183	0.037	-0.166	0.035	0.993
<i>Combretum molle</i>	D	19	3.991	70.957	0.156	0.854	0.015	0.325	0.017	0.997	0.906	0.033	0.221	0.035	0.989	1.061	0.032	-0.122	0.034	0.992
<i>Eucalyptus crebra</i>	E	20	1.009	29.949	0.022	0.875	0.019	0.292	0.026	0.996	1.117	0.049	0.642	0.062	0.982	1.277	0.058	0.4	0.073	0.981
<i>Eucalyptus platyphylla</i>	D	20	2.610	66.796	0.042	0.886	0.016	0.449	0.020	0.997	1.216	0.077	0.477	0.072	0.963	1.372	0.082	0.032	0.077	0.967
<i>Eucalyptus shirleyi</i>	E	18	6.387	147.874	0.079	0.766	0.032	0.433	0.046	0.986	1.014	0.047	0.317	0.051	0.983	1.325	0.057	-0.123	0.061	0.984
<i>Eucalyptus tessellaris</i>	E	20	2.419	67.978	0.055	0.904	0.024	0.480	0.032	0.993	1.098	0.071	0.434	0.077	0.962	1.215	0.07	-0.051	0.076	0.97
<i>Euclea divinorum</i>	E	9	0.319	2.686	0.017	1.417	0.114	0.816	0.163	0.977	1.643	0.105	0.413	0.108	0.986	1.159	0.05	-0.285	0.057	0.993
<i>Grevillea pteridifolia</i>	E	19	3.662	109.099	0.053	0.867	0.026	0.794	0.031	0.993	1.027	0.071	0.237	0.074	0.956	1.121	0.073	-0.601	0.074	0.963
<i>Mimosa clausenii</i>	D	20	2.138	52.164	0.045	0.999	0.033	0.925	0.043	0.990	1.110	0.077	0.694	0.083	0.956	1.111	0.072	-0.231	0.077	0.961
<i>Mimosa tenuiflora</i>	D	20	9.369	240.290	0.304	0.755	0.015	0.315	0.021	0.996	0.881	0.022	0.240	0.027	0.994	1.167	0.024	-0.099	0.03	0.996

Leaf mass M_L vs. stem mass M_S , leaf mass M_L vs. root mass M_R , and stem mass M_S vs. root mass M_R . These coefficients were derived from RMA regression (see Sokal and Rohlf, 1981).

Pearson correlations (ρ) between regression variables are also presented.

The number of individuals per species (n) used to derive each relationship is shown. Plant mean size and extremes of sampled individuals are also shown. Leaf habit of each species is indicated (E, evergreen; D, deciduous).

TABLE 3. Allometric coefficients α and β for biomass partitioning of 20 savanna tree species grown in the low nutrient treatment

Species	Leaf habit	<i>n</i>	Total mass (g)			M_L vs. M_S					M_L vs. M_R					M_S vs. M_R				
			Mean	Max	Min	α	s.e.	$\log_{10} \beta$	s.e.	ρ	α	s.e.	$\log_{10} \beta$	s.e.	ρ	α	s.e.	$\log_{10} \beta$	s.e.	ρ
<i>Acacia aulacocarpa</i>	E	20	0.859	22.669	0.061	0.890	0.022	0.643	0.032	0.995	1.142	0.049	0.605	0.057	0.984	1.284	0.068	-0.042	0.078	0.976
<i>Acacia shirleyi</i>	E	19	0.413	10.734	0.038	0.891	0.028	0.627	0.044	0.992	1.148	0.064	0.772	0.086	0.973	1.288	0.087	0.163	0.117	0.96
<i>Acacia sieberiana</i>	D	20	2.636	41.831	0.297	0.874	0.035	0.269	0.028	0.985	0.687	0.043	-0.236	0.036	0.964	0.785	0.068	-0.577	0.057	0.93
<i>Acacia tortilis</i>	D	20	1.638	20.284	0.178	0.757	0.023	0.143	0.024	0.992	0.781	0.029	-0.106	0.027	0.988	1.031	0.039	-0.329	0.036	0.987
<i>Aspidosperma macrocarpon</i>	D	20	4.038	17.918	1.232	1.275	0.078	0.618	0.044	0.966	1.053	0.114	-0.190	0.062	0.888	0.825	0.084	-0.634	0.045	0.903
<i>Aspidosperma pyrifolium</i>	D	17	0.939	4.119	0.125	1.167	0.120	0.050	0.114	0.918	1.840	0.267	-0.113	0.146	0.828	1.237	0.156	-0.195	0.108	0.863
<i>Atalaya hemiglauca</i>	E	20	0.378	5.702	0.031	0.933	0.030	0.618	0.051	0.990	1.091	0.064	0.167	0.071	0.968	1.169	0.085	-0.484	0.094	0.951
<i>Brachylaena discolor</i>	E	18	0.148	11.435	0.003	1.103	0.071	0.822	0.152	0.966	1.172	0.097	0.469	0.175	0.944	1.059	0.097	-0.317	0.171	0.936
<i>Brachystegia spiciformis</i>	D	19	1.156	3.874	0.283	0.953	0.151	0.721	0.185	0.759	0.607	0.108	-0.298	0.052	0.677	0.636	0.113	-1.069	0.055	0.68
<i>Colophospermum mopane</i>	D	20	2.819	23.379	0.367	0.820	0.026	0.410	0.019	0.991	0.761	0.046	0.089	0.031	0.966	0.928	0.063	-0.392	0.042	0.957
<i>Combretum apiculatum</i>	D	17	1.351	11.385	0.173	0.805	0.028	0.241	0.029	0.991	0.889	0.051	0.015	0.040	0.975	1.103	0.045	-0.281	0.036	0.987
<i>Combretum molle</i>	D	20	0.685	15.238	0.054	1.057	0.046	0.435	0.071	0.983	1.229	0.088	0.082	0.101	0.952	1.163	0.048	-0.334	0.055	0.984
<i>Eucalyptus crebra</i>	E	20	0.743	22.470	0.022	0.900	0.044	0.287	0.069	0.979	1.267	0.060	0.613	0.075	0.981	1.407	0.081	0.363	0.102	0.971
<i>Eucalyptus platyphylla</i>	D	20	1.803	32.648	0.020	0.941	0.019	0.451	0.028	0.996	1.059	0.049	0.312	0.060	0.981	1.122	0.051	-0.146	0.062	0.982
<i>Eucalyptus shirleyi</i>	E	19	3.977	181.072	0.082	0.814	0.015	0.466	0.022	0.997	1.014	0.026	0.333	0.030	0.994	1.253	0.045	-0.17	0.051	0.989
<i>Eucalyptus tessellaris</i>	E	20	1.210	28.599	0.025	0.935	0.026	0.538	0.038	0.993	1.018	0.056	0.428	0.071	0.972	1.089	0.052	-0.118	0.066	0.98
<i>Euclaea divinorum</i>	E	11	0.096	0.495	0.043	2.116	0.449	2.239	0.839	0.771	1.391	0.269	0.236	0.384	0.814	0.658	0.125	-0.946	0.178	0.822
<i>Grevillea pteridifolia</i>	E	20	6.047	101.446	0.133	0.872	0.018	0.843	0.023	0.996	0.955	0.047	0.155	0.054	0.978	1.095	0.059	-0.789	0.069	0.973
<i>Mimosa clausenii</i>	D	20	0.776	13.177	0.035	1.017	0.035	0.883	0.049	0.989	1.158	0.087	0.847	0.106	0.948	1.139	0.092	-0.035	0.112	0.939
<i>Mimosa tenuiflora</i>	D	20	2.903	258.724	0.100	0.734	0.034	0.391	0.055	0.980	1.077	0.054	0.154	0.057	0.977	1.466	0.039	-0.322	0.04	0.994

Leaf mass M_L vs. stem mass M_S , leaf mass M_L vs. root mass M_R , and stem mass M_S vs. root mass M_R . These coefficients were derived from RMA regression (see Sokal and Rohlf, 1981).

Pearson correlations (ρ) between regression variables are also presented.

The number of individuals per species (*n*) used to derive each relationship is shown. Plant mean size and extremes of sampled individuals are also shown. Leaf habit of each species is indicated (E, evergreen; D, deciduous).

TABLE 4. Mean species root non-structural carbohydrate storage of 20-week-old juveniles of 20 savanna tree species grown in the two nutrient treatments

Species	Leaf habit	High nutrient treatment								Low nutrient treatment							
		Total mass, M_T (g)		Root mass fraction (g g^{-1})		$[C]_R$ (g g^{-1})		$C_{R/T}$ (g g^{-1})		Total mass, M_T (g)		Root mass fraction (g g^{-1})		$[C]_R$ (g g^{-1})		$C_{R/T}$ (g g^{-1})	
		Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
<i>Acacia aulacocarpa</i>	E	31.159	22.241	0.152	0.103	0.260	0.040	0.026	0.008	9.992	5.425	0.160	0.048	0.278	0.033	0.043	0.016
<i>Acacia shirleyi</i>	E	12.710	16.077	0.119	0.046	0.175	0.028	0.023	0.010	3.344	3.237	0.136	0.045	0.243	0.054	0.036	0.017
<i>Acacia sieberiana</i>	D	37.317	23.949	0.612	0.189	0.599	0.099	0.285	0.120	15.571	11.270	0.677	0.117	0.496	0.112	0.287	0.072
<i>Acacia tortilis</i>	D	35.318	15.760	0.438	0.108	0.638	0.140	0.275	0.057	12.298	5.411	0.494	0.096	0.504	0.169	0.280	0.122
<i>Aspidosperma macrocarpon</i>	D	16.725	5.628	0.457	0.104	0.455	0.066	0.233	0.046	10.437	3.530	0.521	0.107	0.510	0.023	0.262	0.062
<i>Aspidosperma pyriformis</i>	D	6.094	2.158	0.261	0.051	0.361	0.055	0.081	0.017	2.668	0.774	0.392	0.084	0.327	0.051	0.108	0.023
<i>Atalaya hemiglauca</i>	E	7.185	5.263	0.265	0.092	0.418	0.090	0.125	0.040	2.365	1.540	0.378	0.122	0.537	0.067	0.215	0.046
<i>Brachylaena discolor</i>	E	20.583	14.304	0.226	0.068	0.328	0.019	0.068	0.017	4.425	4.274	0.163	0.137	0.396	0.018	0.039	0.032
<i>Brachystegia spiciformis</i>	D	4.599	3.247	0.579	0.094	0.492	0.147	0.313	0.072	2.350	0.702	0.701	0.102	0.516	0.085	0.336	0.099
<i>Colophospermum mopane</i>	D	26.144	20.133	0.374	0.109	0.429	0.103	0.183	0.080	10.552	6.422	0.462	0.110	0.446	0.104	0.206	0.062
<i>Combretum apiculatum</i>	D	16.980	12.658	0.346	0.061	0.377	0.034	0.122	0.028	5.180	3.458	0.394	0.075	0.374	0.068	0.166	0.054
<i>Combretum molle</i>	D	37.756	17.791	0.318	0.076	0.335	0.053	0.095	0.030	5.094	4.332	0.398	0.046	0.308	0.055	0.114	0.024
<i>Eucalyptus crebra</i>	E	14.453	8.904	0.118	0.034	0.212	0.017	0.025	0.007	11.009	6.984	0.133	0.032	0.221	0.032	0.029	0.006
<i>Eucalyptus platyphylla</i>	D	35.324	24.370	0.150	0.050	0.382	0.089	0.065	0.028	25.288	6.393	0.248	0.073	0.320	0.033	0.086	0.018
<i>Eucalyptus shirleyi</i>	E	87.292	38.328	0.215	0.077	0.302	0.025	0.065	0.017	62.784	47.104	0.227	0.064	0.272	0.024	0.056	0.015
<i>Eucalyptus tessellaris</i>	E	35.717	23.764	0.209	0.096	0.333	0.039	0.059	0.036	16.572	7.061	0.217	0.056	0.315	0.041	0.070	0.030
<i>Euclea divinorum</i>	E	1.453	0.731	0.336	0.029	0.503	0.030	0.166	0.021	0.185	0.172	0.512	0.143	0.593	0.093	0.283	0.081
<i>Grevillea pteridifolia</i>	E	48.247	36.328	0.316	0.175	0.270	0.078	0.081	0.057	72.693	19.625	0.407	0.160	0.290	0.030	0.076	0.015
<i>Mimosa clausenii</i>	D	24.782	12.432	0.148	0.093	0.164	0.022	0.028	0.023	6.087	4.039	0.123	0.072	0.215	0.027	0.021	0.016
<i>Mimosa tenuiflora</i>	D	132.206	43.023	0.283	0.059	0.288	0.066	0.073	0.036	64.934	76.095	0.257	0.067	0.302	0.044	0.061	0.010

Carbohydrate measures presented include root non-structural carbohydrate concentration, $[C]_R$ (g carbohydrate g^{-1} root) and plant root non-structural carbohydrate fraction, $C_{R/T}$ (g carbohydrate g^{-1} total).

Mean total mass (g) and mean root mass fraction (g g^{-1}) of plants are also presented. Leaf habit of each species is indicated (E, evergreen; D, deciduous).

Estimates represent means of five sampled individuals per species per nutrient treatment.

individuals of different leaf habit (H; deciduous or evergreen) and across different nutrient treatments (N; high nutrient supply or low nutrient supply) (Predictions 1, 2 and 4), and whether allometries could be related to root carbohydrate storage (Prediction 3). Species was included as a random component in the models, such that each species could have separate intercepts and separate slopes if these accounted for significant variation in the data.

All analyses were conducted using the *lmer* function of lme4 in R (Pinheiro and Bates, 2000). Equations (4–6) below indicate model statements in lme4. The resulting regression models were also plotted to allow visual interpretation of the patterns. We tested all main effects and all interactions between the main effects. Likelihood ratio tests (LRTs) on unrestricted maximum likelihoods (MLs) were used to evaluate fixed and random effects in the model, following the procedure described in Baayen *et al.* (2008). Random effects were first evaluated using the full model. Fixed effects were subsequently evaluated using ML with the chosen random model. Final estimates for parameters of the chosen models were estimated using restricted maximum likelihood (REML).

Allometric partitioning across leaf habits and nutrient treatments. First, we used our entire individual data set to test whether organ mass allometries differed between individuals of different leaf habit (H) (Prediction 1), and whether they changed in response to different nutrient treatments (N) (Prediction 4).

$$M_L \sim M_S \times H \times N + (1 + M_S | \text{Species}) \quad (4)$$

The model above represents allometric scaling between leaf (M_L) and stem (M_S) organs. Similar models were used for M_L vs. M_R and M_S vs. M_R . We used deciduous species growing in the high nutrient treatment as the default case. Therefore, the scaling exponent of this group is represented by the coefficient of the main effect M_S . Changes to the scaling exponent due to evergreen leaf habit and the low nutrient treatment are indicated by the coefficients of the interactions involving M_S with leaf habit ($M_S:H$) and nutrient treatment ($M_S:N$), respectively. The interaction $M_S:H:N$ discerns whether allometric scaling differs between nutrient treatments for each leaf habit. The remaining terms (H, N, H:N) affect the position of the scaling constant (β). $M_S \times \text{Species}$ was included in the random component to account for variation in the scaling exponent due to individual species. The chosen regression models are provided in Table 5 (these are visualized in Supplementary Data Fig. S1).

The differences between allometric slopes could be quite small even if they were significant (Table 5). This is in part because they are derived using log-transformed data. Therefore, to visualize these changes more clearly, we ran an additional set of regression models where we regressed the leaf:stem ratio, leaf:root ratio and stem:root ratio against total plant mass (M_T), habit and nutrient treatment, which we subsequently plotted (Fig. 1) (the underlying regression model estimates are provided in Supplementary Data Table S2). Here the chosen models selected using the allometric models [eqn (4)] were simply rerun substituting the appropriate organ mass ratio for the dependent variable and M_T in place of the predictor organ mass.

$$\text{Mass ratio} \sim M_T \times H \times N + (1 + M_T | \text{Species}) \quad (4)$$

Root carbohydrate storage across leaf habits and nutrient treatments. Secondly, we tested whether root carbon storage differed between individuals of different leaf habits (H) (Prediction 2) and across different nutrient treatments (N) (Prediction 4). Total plant mass (M_T) was included in this model to account for size effects on storage. We tested all main effects and all interactions between the main effects.

$$[C]_R \sim M_T \times H \times N + (1 | \text{Species}) \quad (5)$$

The chosen regression models are visualized in Fig. 2 (the underlying regression model estimates are provided in Supplementary Data Table S3).

Relationship between organ allometry and root carbohydrate storage. Thirdly, we tested whether species' organ scaling coefficients (α) differed systematically with stored carbohydrate in roots (Prediction 3). We regressed the estimated scaling coefficients for each species on each nutrient treatment (data provided in Tables 2 and 3) against mean $[C]_R$ estimates for those species (data provided in Table 4; $n = 40$ for 20 species). We included mean species mass (M_{species}) as a covariate to account for the effect of mean plant size on the scaling coefficient. Species was included as a random effect.

$$\alpha \sim M_{\text{species}} \times [C]_R + (1 | \text{Species}) \quad (6)$$

The chosen regression models are provided in Table 6 and visualized in Fig. 3.

RESULTS

Plant biomass allometry

The allometric models obtained using the individual data are presented in Table 5 and visualized in Fig. 1. Leaf habit significantly distinguished organ scaling exponents (α) involving roots and supported Prediction 1. Allocation to leaves over roots (Fig. 1B) and stems over roots (Fig. 1C) increased with size at a greater rate among evergreen species than among deciduous species, as indicated by their greater scaling exponents.

Nutrient treatment affected scaling of organ relationships involving stems, with increased allocation towards leaves and roots at the expense of stems with increasing size under low nutrient conditions (Fig 1A, C; Table 5). All species also increased allocation to roots at the expense of leaves across plant sizes in the low nutrient treatment [significant effect of N on the allometric constant (β) of leaf vs. root allometry, Fig. 1B; Table 5]. Species of different leaf habit did not differ in their partitioning response to different nutrient treatments ($M_S:H:N$ non-significant for all three relationships). Thus biomass scaling patterns did not support Prediction 4.

Root carbohydrate storage

Root non-structural carbohydrate concentration ($[C]_R$) and root non-structural carbohydrate fraction (C_{RT}) were significantly lower among evergreen than deciduous species with increasing size (Fig. 2), supporting Prediction 2. The relative differences in

TABLE 5. Regression results of mixed models testing for the effects of leaf habit (*H*) [levels: deciduous and evergreen (*E*)] and nutrient treatment (*N*) (levels: high and low) on the organ biomass scaling relationships of juveniles of 20 savanna tree species, harvested between 5 and 20 weeks after planting as recently germinated seedlings [eqn (4)]

(A) Random effects														
M_L vs. M_S					M_L vs. M_R					M_S vs. M_R				
Effect	s.d.				Effect	s.d.				Effect	s.d.			
Species (Intercept)	0.222				Species (Intercept)	0.229				Species (Intercept)	0.282			
Species (M_S)	0.129				Species (M_R)	0.168				Species (M_R)	0.155			
Residual	0.159				Residual	0.250				Residual	0.265			
(B) Fixed effects (regression estimates)														
M_L vs. M_S					M_L vs. M_R					M_S vs. M_R				
Parameter	Estimate	s.e.	<i>t</i> *	<i>P</i>	Parameter	Estimate	s.e.	<i>t</i>	<i>P</i>	Parameter	Estimate	s.e.	<i>t</i>	<i>P</i>
Intercept														
β_0	0.462	0.050	9.18	<0.001	β_0	0.142	0.071	2.00	<0.05	β_0	-0.271	0.085	-3.19	<0.01
H(Evergreen)	–	–	–	–	H(Evergreen)	0.310	0.106	2.93	<0.01	H(Evergreen)	0.163	0.127	1.28	NS
N(low)	–	–	–	–	N(low)	-0.114	0.019	-6.15	<0.001	N(low)	-0.132	0.021	-6.44	<0.001
H(E):N(low)	–	–	–	–	H(E):N(low)	–	–	–	–	H(E):N(low)	–	–	–	–
Slope														
M_S (α)	0.867	0.030	28.91	<0.001	M_R (α)	0.915	0.053	17.16	<0.001	M_R (α)	1.040	0.050	20.63	<0.001
M_S :H(E)	–	–	–	–	M_R :H(E)	0.160	0.079	2.02	<0.05	M_R :H(E)	0.150	0.074	2.03	<0.05
M_S :N(low)	0.052	0.009	5.81	<0.001	M_R :N(low)	–	–	–	–	M_R :N(low)	-0.048	0.019	-2.45	<0.05
M_S :H(E):N(low)	–	–	–	–	M_R :H(E):N(low)	–	–	–	–	M_R :H(E):N(low)	–	–	–	–

Allometric slopes tested were leaf mass to stem mass (M_L vs. M_S), leaf mass to root mass (M_L vs. M_R) and stem mass to root mass (M_S vs. M_R). All masses were \log_{10} -transformed prior to modelling. The default factor levels are deciduous leaf habit and high nutrient treatment. ($n = 753$).

Models were chosen using likelihood ratio tests following the procedure outlined in Baayen *et al.* (2008). Final parameter estimates were evaluated with non-conservative *t*-tests (see Baayen *et al.*, 2008).

*Critical *t*-values for $n-8$ d.f. $t_{0.05}$ (745 d.f.) = 1.96; $t_{0.01}$ (745 d.f.) = 2.58; $t_{0.001}$ (745 d.f.) = 3.30.

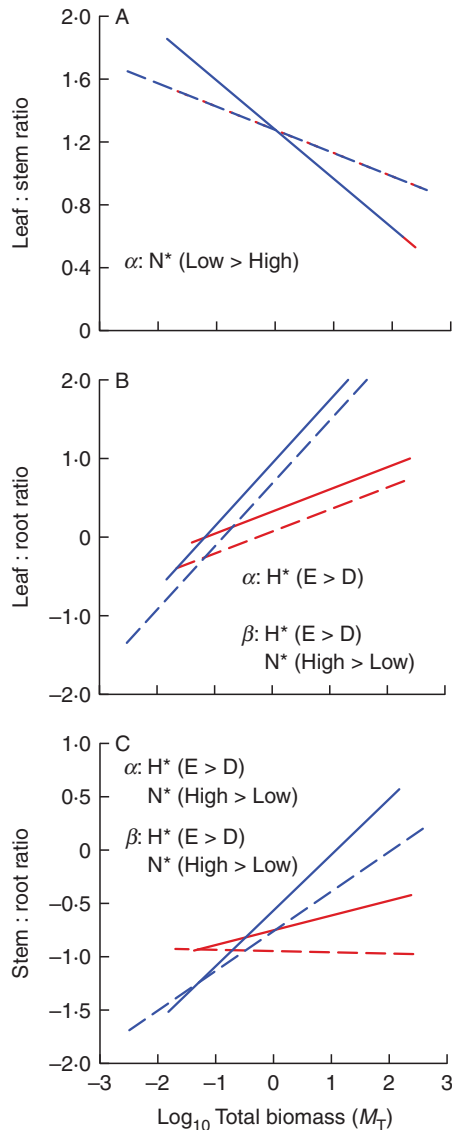


FIG. 1. Illustration of estimated allometric organ mass relationships for juveniles of 20 savanna tree species of different leaf habit (H) (evergreen, E = blue lines; deciduous, D = red lines) grown in two soil nutrient treatments (N) (high nutrient supply = solid lines; low nutrient supply = dashed lines). Significant differences between leaf habits and nutrient treatments are indicated on the plots (* $P < 0.05$). (A–C) The derived organ type to organ type allometric models using organ mass ratios plotted against plant total mass (M_T) [eqn (4)]. (Details of the underlying statistical models are provided in Supplementary Data Table S2.) (A) Leaf:stem ratio. High nutrients, $M_L:M_S = -0.313 M_T + 1.281$; low nutrients, $M_L:M_S = -0.147 M_T + 1.281$. (B) Leaf:root ratio, D, high nutrients, $M_L:M_R = -0.118 M_T + 0.364$; low nutrients, $M_L:M_R = -0.118 M_T + 0.118$. E, high nutrients, $M_L:M_R = 0.248 M_T + 0.942$; low nutrients, $M_L:M_R = 0.248 M_T + 0.696$. (C) Stem:root ratio. D, high nutrients, $M_S:M_R = 0.179 M_T - 0.750$; low nutrients, $M_S:M_R = 0.080 M_T - 0.961$. E, high nutrients: $M_S:M_R = 0.495 M_T - 0.555$; low nutrients, $M_S:M_R = 0.396 M_T - 0.765$.

$C_{R/T}$ were larger than for $[C]_R$ because evergreen species had much lower root mass fractions than deciduous species (see species' mean estimates in Table 4). $[C]_R$ did not change between nutrient treatments, while $C_{R/T}$ increased under low nutrient conditions. This indicates that tree juveniles increased allocation to storage under nutrient stress, but that this additional storage occurred through structural adjustment (root thickening) rather

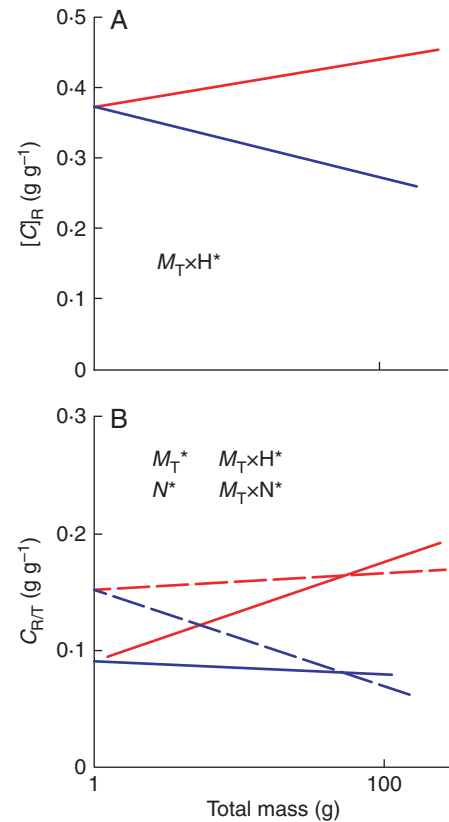


FIG. 2. Estimated root carbohydrate storage relationships to total plant mass (M_T) for juveniles of 20 savanna tree species of different leaf habit (H) (evergreen, E = blue lines; deciduous, D = red lines) grown in two soil nutrient treatments (N) (high nutrient supply = solid lines; low nutrient supply = dashed lines). Significant differences between leaf habits and nutrient treatments are indicated on the plots (* $P < 0.05$). (Details of the statistical models are provided in Supplementary Data Table S3.) (A) Root non-structural carbohydrate concentration, $[C]_R$ (g carbohydrate g^{-1} root). D, $[C]_R = 1.456 M_T + 37.227$; E, $[C]_R = -2.161 M_T + 37.227$. (B) Root non-structural carbohydrate fraction, $C_{R/T}$ (g carbohydrate g^{-1} total). D, high nutrients, $C_{R/T} = 1.836 M_T + 9.103$; low nutrients, $C_{R/T} = 0.316 M_T + 15.155$. E, high nutrients, $C_{R/T} = -0.253 M_T + 9.103$; low nutrients, $C_{R/T} = -1.773 M_T + 15.155$.

than through increased cellular concentrations of non-structural carbohydrates. Also, for small plant sizes, storage differences under high and low nutrient treatments were much greater than for larger plant sizes (Fig. 2B). Deciduous and evergreen species did not differ in their carbohydrate storage response to nutrient stress. Thus carbohydrate storage patterns did not support Prediction 4.

Relationships between organ scaling and root carbohydrate storage

Allometric scaling relationships differed across species (Tables 2 and 3). Species' allometric scaling relationships (α) were significantly related to root non-structural carbohydrate concentration ($[C]_R$) (Table 6, Fig. 3), supporting Prediction 3. Leaf to stem scaling ($\alpha: M_L$ vs. M_S) increased and stem to root scaling ($\alpha: M_S$ vs. M_R) decreased in relation to increases in $[C]_R$. Leaf to root scaling ($\alpha: M_L$ vs. M_R) was not related to $[C]_R$. Most evergreen species were restricted to high values of stem to root scaling and low values of root carbohydrate

TABLE 6. Regression results for a mixed model testing for the effects of root carbohydrate concentration, $[C]_R$, measured at 20 weeks on allometric scaling coefficients (α) of juveniles of 20 savanna tree species calculated on individuals harvested between 5 and 20 weeks after planting as recently germinated seedlings

(A) Random effects (variance)												
	$\alpha: M_L$ vs. M_S				$\alpha: M_L$ vs. M_R				$\alpha: M_S$ vs. M_R			
Species	0.020				0.041				0.008			
Residual	0.007				0.016				0.016			
(B) Fixed effects (regression)												
	$\alpha: M_L$ vs. M_S				$\alpha: M_L$ vs. M_R				$\alpha: M_S$ vs. M_R			
	Estimate	s.e.	<i>t</i> -value	<i>P</i> ($> t $)*	Estimate	s.e.	<i>t</i> -value	<i>P</i> ($> t $)	Estimate	s.e.	<i>t</i> -value	<i>P</i> ($> t $)
Intercept	0.664	0.101	6.57	<0.001	1.033	0.032	32.62	<0.001	1.516	0.089	16.98	<0.001
M_{species}	0.138	0.073	1.89	NS	-0.055	0.024	-2.28	<0.05	–	–	–	–
$[C]_R$	0.862	0.250	3.45	<0.01	–	–	–	–	-1.064	0.229	-4.64	<0.001
$M_{\text{species}} \times [C]_R$	-0.659	0.166	-3.97	<0.001	–	–	–	–	–	–	–	–

Allometric scaling coefficients regressed against $[C]_R$ were leaf to stem mass ($\alpha: M_L$ vs. M_S), leaf to root mass ($\alpha: M_L$ vs. M_R) and stem to root mass ($\alpha: M_S$ vs. M_R). Individual species' allometric estimates are provided in Tables 2 and 3 and individual species root carbohydrate contents are provided in Table 4 ($n = 40$).

Models were chosen using likelihood ratio tests following the procedure outlined in Baayen *et al.*, (2008). Final parameter estimates were evaluated with non-conservative *t*-tests (see Baayen *et al.*, 2008).

*Critical *t*-values for $n-4$ d.f. $t_{0.05}$ (36 d.f.) = 2.03; $t_{0.01}$ (36 d.f.) = 2.72; $t_{0.001}$ (36 d.f.) = 3.58.

storage, while deciduous species were distributed across a much wider range of stem to root scaling values and root storage values (Fig. 3).

DISCUSSION

We tested the hypothesis that deciduous and evergreen trees differ in juvenile biomass allometries because of differences in allocation to root storage. Our results provide support for the hypothesis. There were significant differences in the allometric exponents of evergreen and deciduous species involving roots (Table 5, Fig. 1): allocation to leaves and stems over roots increased with plant total biomass at a greater rate among evergreen species than among deciduous species (Fig. 1). Species of different leaf habit differed in their allocation of resources to reserve storage in roots: allocation to non-structural carbohydrate in roots increased with plant total biomass at a greater rate among deciduous species than evergreen species (Fig. 2). Finally, we showed that species' scaling exponents could be significantly explained by their root carbohydrate concentrations (Table 6, Fig. 3).

Biomass allometry across leaf habits

Our study showed that juveniles of evergreen species allocate more biomass to stems and leaves over roots than deciduous species with increasing plant total biomass. This corroborates the findings of Walters and Reich (1999), but suggests further that biomass allocation is fundamentally different between trees with different leaf habits. Whereas Walters and Reich (1999) used species from different environments (deciduous species from temperate forests and evergreen species from tropical forests), we have shown differences in biomass allocation of species of different leaf habit from the same environment, (sub-) tropical savannas. For both studies, it appears that biomass allometry of juveniles of deciduous and evergreen species differs in environments with strong seasonality. It remains to be

established whether deciduous species and evergreen species growing in less seasonal environments also show differences in biomass allometry. In less seasonal environments where brevi-deciduous species (leaf-exchanging species; Borchert, 1994) exchange their old leaves for new ones, resources may be directly shifted from old leaves into new growth, reducing the requirement for below-ground storage. Hence, deciduous and evergreen species from less seasonal environments may not differ in their partitioning patterns.

We considered scaling allometries in juvenile trees grown for up to 20 weeks. Our data covered five orders of magnitude in size (individuals ranged in mass from 0.003 to 258.724 g), but the maximum sizes recorded are much less than tree species are able to attain (e.g. Enquist and Niklas, 2002). It is apparent from previous work that plant organ allometric slopes change with plant size (Enquist and Niklas, 2002; Enquist *et al.*, 2007). Therefore, a question that arises is whether our observations on juvenile trees carry over to adult trees? A comparison of root to shoot ratios among different forest biomes found greater allocation to roots for deciduous- than evergreen-dominated communities (Jackson *et al.*, 1996), suggesting that differences in biomass partitioning between leaf habits do persist into adult plants. Although the fractional contribution of leaf material to total plant biomass can decline to <5% of total mass in large trees (Poorter *et al.*, 2012), most of this biomass is constituted by inert wood in stem and root. Partitioning of live material may not change nearly as dramatically. Seasonal leaf resprouting remains a constraint on deciduous species for the entirety of their lives, so they may continue to allocate resources storage at a greater rate than evergreen species. Architectural adjustment for carbohydrate storage in roots may partly explain these long-term differences in root to shoot partitioning between evergreen- and deciduous-dominated communities (Jackson *et al.*, 1996).

The divergent patterns of allocation to stem material over root material between evergreen and deciduous savanna species (Fig. 1) can also explain the quite disparate physiognomy of

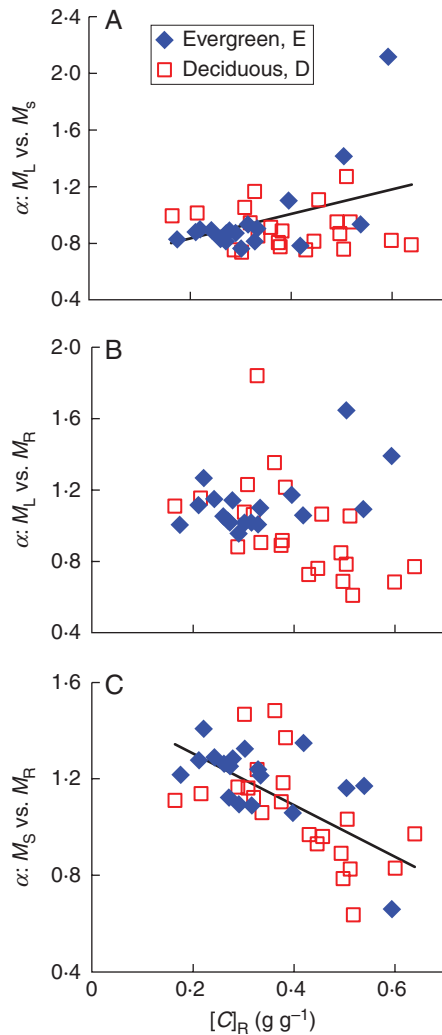


FIG. 3. Relationships between the estimated species' scaling coefficients and species' root carbohydrate concentration, $[C]_R$, measured at 20 weeks for juveniles of 20 savanna tree species grown under two nutrient treatments (hence 40 data points; see the Materials and Methods for details). Allometric relationships illustrated are: (A) leaf to stem partitioning ($\alpha: M_L$ vs. M_S); (B) leaf to root partitioning ($\alpha: M_L$ vs. M_R); and (C) stem to root partitioning ($\alpha: M_S$ vs. M_R). The regression relationships are calculated across all species (lines) and significant relationships ($P < 0.05$) are projected in two-dimensional space. Line equations: (A) $\alpha = -0.659 [C]_R + 0.664$; (B) NS; (C) $\alpha = -1.064 [C]_R + 1.515$. (Details of the regression models are provided in Table 6.) Individual species' mean data are also plotted and distinguished by leaf habit, as indicated in the key.

adult trees in frequently burnt savannas in Australia (dominated by very tall, straight evergreen trees) vs. those in Africa and South America (dominated by much shorter, deciduous trees) (Cole, 1986). Fire is a severe disturbance pressure that can remove leaf and stem material and inhibit trees from progressing to adulthood (Bond and Van Wilgen, 1996; Higgins *et al.*, 2000). Fires typically occur at the end of the dry season when deciduous species have no live leaves. Among deciduous species, increased fire frequency may select for increased allocation to storage in roots, and hence increased allocation to root biomass, so that they can conserve resources beyond the reach of fires. Among evergreen species, increased fire frequency may select for increased growth rates and height extension, and hence increased

allocation to stem mass, so that they can overtop fires (Tomlinson *et al.*, 2012).

Species' partitioning responses to nutrient treatments

Across species, biomass partitioning towards the leaves and roots at the expense of stems increased with plant size under soil nutrient stress (Fig. 1, Table 5). In addition, there was a shift to lower leaf to root partitioning in the low nutrient treatment (indicated by a significant shift in the allometric constant for M_L vs. M_R in Fig. 1). Deciduous species showed a greater increase in partitioning to roots over stems and leaves than evergreen species with increasing soil nutrient stress (Fig. 1). These differences were restricted to the allometric constants, so did not accumulate with increasing plant size.

As the change in scaling in response to nutrient supply was associated with a trade-off between allocation to stems and other organs (Table 5), allocation to stems appeared to be secondary to allocation to roots and leaves when resources were limiting. Possibly this was related to the ontogenetic stage of our plants, which were all young (harvested at 20 weeks of growth). Stems mostly serve a structural function, while roots and leaves both acquire plant resources. For very young plants, allocation towards increasing resource accumulation may be selected at the expense of structural strength. Thus, under low nutrient conditions, more resources are diverted towards roots and leaves to build additional structures to increase access to resources and therefore to improve growth potential (Brouwer, 1962; Poorter and Nagel, 2000; Poorter *et al.*, 2012). With increasing size, as the importance of structural support for the shoot increases, this difference across nutrient treatments might fade.

Our results confirmed that total non-structural carbohydrates stored in roots ($C_{R/T}$) increased in plants under low nutrient conditions (Kobe *et al.*, 2012) (Fig. 2). Interestingly, root non-structural carbohydrate concentration ($[C]_R$) did not increase in the low nutrient treatment, which indicates that plants accommodated the additional carbohydrates through increased root volume. Hence resource supply affects carbohydrate storage in roots, which in turn can alter organ biomass partitioning across resource gradients. This indicates that the standing paradigm that biomass adjustment under nutrient stress improves access to limiting soil resources (Brouwer, 1962; Poorter and Nagel, 2000; Poorter *et al.*, 2012) is only partly correct. A significant portion of the biomass adjustment is due to allocation to storage, as asserted by Kobe *et al.* (2010).

So why does nutrient stress lead to increased carbohydrate storage in plants? A plausible explanation may be that increased allocation to root structure for soil volume exploration does not yield a sufficient nutrient return on investment in low nutrient environments because most nutrient resources are only available during temporal pulses (Blair *et al.*, 1998; Mamolos, 2006). Hence allocating resources to reserve storage retains these resources for rapid root expansion during future resource pulses. There is already evidence that plants can rapidly expand root systems into spatiotemporal nutrient patches when these are encountered (Robinson, 1994). In addition, carbohydrate storage in roots might be directly supplied to arbuscular mycorrhizal fungi when water is available to stimulate root activity and fungal growth (Bago *et al.*, 2003), when soil nutrients are

low (Bohrer *et al.*, 2003). Therefore, retaining carbohydrate stores in roots allows plants to respond rapidly to external resource supplies when and where these are encountered.

Further speculations on the role of resource conservation in plant organ allometries

We focused on how selection for resource conservation distinguished biomass allometry of species of different leaf habits growing in seasonal environments through differences in allocation to storage in roots. Selection for structural adjustment that supports resource conservation might also be important in environments subject to severe defoliation pressure. For instance, species growing in environments with severe fire pressure might be selected to allocate more resources to roots to conserve them against fires relative to species growing in environments with lower fire pressure (at least among deciduous species) (Bellingham and Sparrow, 2000; Hoffmann *et al.*, 2004; Tomlinson *et al.*, 2012). Similarly, structural modifications selected to reduce herbivory such as reduced leaf size and divaricate growth (Bond *et al.*, 2004) may lead to quite different biomass allometries with both constitutive and induced effects on partitioning (Ward, 2010). It is clear that a substantial amount of variation in organ biomass allometries of woody species may be related to selection for resource conservation.

Conclusions

Our data provide strong support for the hypothesis that deciduous and evergreen trees differ in juvenile biomass allometries because of differences in allocation to root storage.

This indicates that biomass allometry in plants reflects selection on biomass allocation for resource capture and for resource conservation. Therefore, future research into the mechanisms underlying plant allometry should consider these dual functions of biomass partitioning. Substantial unexplained variation in biomass allometry of woody species may be related to selection for resource conservation against environmental stresses, such as resource seasonality. Further differences in plant allometry could arise due to selection for different types of biomass allocation in response to different environmental stressors (e.g. fire, herbivory), and in response to the severity of those environmental stressors.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxford-journals.org and consist of the following. Table S1: list of 20 species used in analysis, including names, families, continent of origin and leaf habit. Table S2: regression results of mixed models testing for the effects of leaf habit, nutrient treatment and total plant mass on the organ biomass ratios of juveniles of 20 savanna tree species. Table S3: regression results of mixed models testing for the effects of leaf habit, nutrient treatment and species' plant size on root non-structural carbohydrate concentration and root non-structural carbohydrate fraction of juveniles of 20 savanna tree species. Figure S1: estimated allometric organ mass relationships for juveniles of 20 savanna tree species of different leaf habit grown in two soil nutrient treatments.

ACKNOWLEDGEMENTS

We thank the staff of UNIFARM and the Resource Ecology Group, Wageningen University, especially André Maassen, Jia Wu and Ainara Ballesteros-Larranaga for technical support for the experiment, and Anne-Marie van den Driessche and Loes Jacobs for the root carbohydrate analyses. Everardo Sampaio, Giovanna Carramaschi, Tony Grice, Patricia Tomlinson and Peggy Wiseman provided seeds for the experiment. This work and K.W.T. were supported by Shell Research Foundation. We thank four anonymous referees, and B. J. Enquist and T. DeJong for helpful comments on earlier drafts of this manuscript.

LITERATURE CITED

- Baayen RH, Davidson DJ, Bates DM. 2008. Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language* **59**: 390–412.
- Bago B, Pfeffer PE, Abubaker J, *et al.* 2003. Carbon export from arbuscular mycorrhizal roots involves the translocation of carbohydrate as well as lipid. *Plant Physiology* **131**: 1496–1507.
- Bellingham PJ, Sparrow AD. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* **89**: 409–416.
- Blair JM, Seastedt TR, Rice CW, Ramundo RA. 1998. Terrestrial nutrient cycling in tallgrass prairie. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL, eds. *Grassland dynamics: long-term ecological research in tallgrass prairie*. New York: Oxford University Press, 222–243.
- Bohrer G, Kagan-Zur V, Roth-Bejerano N, Ward D, Beck G, Bonifacio E. 2003. Effects of different Kalahari-Desert VA mycorrhizal communities on mineral acquisition and depletion from the soil by host plants. *Journal of Arid Environments* **55**: 193–208.
- Bond WJ, Lee WG, Craine JM. 2004. Plant structural defences against browsing birds: a legacy of New Zealand's extinct moas. *Oikos* **104**: 500–508.
- Bond WJ, Van Wilgen BW. 1996. *Fire and plants*. London: Chapman and Hall.
- Borchert R. 1994. Water status and development of tropical trees during seasonal drought. *Trees* **8**: 115–125.
- Brouwer R. 1962. Nutritive influences on the distribution of dry matter in the plant. *Netherlands Journal of Agricultural Science* **10**: 399–408.
- Cole MM. 1986. *The savannas: biogeography and geobotany*. London: Academic Press.
- Enquist BJ. 2004. Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiology* **22**: 1045–1064.
- Enquist BJ, Niklas KJ. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* **295**: 1517–1520.
- Espelta JM, Cortés P, Mangirón M, Retana J. 2005. Differences in biomass partitioning, leaf nitrogen content, and water use efficiency ($\delta^{13}\text{C}$) result in similar performance of seedlings of two Mediterranean oaks with contrasting leaf habit. *Ecoscience* **12**: 447–454.
- Frost PGH. 1996. The ecology of Miombo woodlands. In: Campbell B, ed. *The Miombo in transition: woodlands and welfare in Africa*. Bogor: Center for International Forestry Research (CIFOR), 11–57.
- Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**: 389–411.
- Higgins SI, Bond WJ, Trollope WSW. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology* **88**: 213–229.
- Hoffmann WA, Orthen B, Franco AC. 2004. Constraints to seedling success of savanna and forest trees across the savanna–forest boundary. *Oecologia* **140**: 252–260.
- Kobe RK, Iyer M, Walters MB. 2010. Optimal partitioning theory revisited: nonstructural carbohydrates dominate root mass responses to nitrogen. *Ecology* **91**: 166–179.
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F. 2006. World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* **15**: 259–263.
- Mamolos AP. 2006. Temporal differentiation in maximum biomass and nutrient accumulation rates in two coexisting annual plant species. *Journal of Arid Environments* **64**: 377–389.

- Markesteijn L, Poorter L. 2009.** Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology* **97**: 311–325.
- McCarthy MC, Enquist BJ. 2007.** Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology* **21**: 713–720.
- Mucina L, Rutherford MC. eds. 2006.** *The vegetation of South Africa, Lesotho and Swaziland, Strelitzia 19*. Pretoria: South African National Biodiversity Institute.
- Peters RH. 1983.** *The ecological implications of body size*. Cambridge: Cambridge University Press.
- Pinheiro JC, Bates DM. eds. 2000.** *Mixed-effects models in S and S-PLUS*. New York: Springer-Verlag.
- Poorter L, Kitajima K. 2007.** Carbohydrate storage and light requirements of tropical moist and dry forest tree species. *Ecology* **88**: 1000–1011.
- Poorter H, Nagel O. 2000.** The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology* **27**: 595–607.
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012.** Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* **193**: 30–50.
- Raunkiaer C. 1934.** *The life forms of plants and statistical plant geography, being the collected papers of C. Raunkiaer*. Oxford: Clarendon Press.
- Reich PB. 2002.** Root–shoot relations: optimality in acclimation and adaptation or the ‘emperor’s new clothes’? In: Waisel Y, Eshel A, Kafkafi U. eds. *Plant roots: the hidden half*. New York: Marcel Dekker, 205–220.
- Reich PB, Borchert R. 1984.** Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology* **72**: 61–74.
- Robinson D. 1994.** The responses of plants to non-uniform supplies of nutrients. *New Phytologist* **127**: 635–674.
- Sarmiento G. 1992.** A conceptual model relating environmental factors and vegetation formations in the lowlands of tropical South America. In: Furley PA, Proctor J, Ratter JA. eds. *Nature and dynamics of forest–savanna boundaries*. London: Chapman & Hall, 583–601.
- Sokal RR, Rohlf FJ. 1981.** *Biometry: the principles and practice of statistics in biological research*, 2nd edn. New York: Freeman.
- Snell O. 1892.** Die abhängigkeit des hirngewichts von dem körporgewicht und den geistigen Fähigkeiten. *Archiv für Psychiatrie und Nervenkrankheiten* **23**: 436–446.
- Sterck F, Markesteijn L, Schieving F, Poorter L. 2011.** Functional traits determine trade-offs and niches in a tropical forest community. *Proceedings of the National Academy of Sciences, USA* **108**: 20627–20632.
- Tilman D. 1988.** *Plant strategies and the dynamics and structure of plant communities*. Princeton, NJ: Princeton University Press.
- Tomlinson KW, Sterck FJ, Bongers F, et al. 2012.** Biomass partitioning and root morphology of savanna trees across a water gradient. *Journal of Ecology* **100**: 1113–1121.
- Walters MB, Reich PB. 1999.** Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? *New Phytologist* **143**: 143–154.
- Ward D. 2010.** The effects of apical meristem damage on growth and defenses of two *Acacia* species in the Negev desert. *Evolutionary Ecology Research* **12**: 589–602.
- West GB, Brown JH, Enquist BJ. 1997.** A general model for the origin of allometric scaling laws in biology. *Science* **276**: 122–126.
- West GB, Brown JH, Enquist BJ. 1999.** A general model for the structure and allometry of plant vascular systems. *Nature* **400**: 664–667.