

## ***New Phytologist* Supporting Information**

Article title: **How does biomass allocation change with size and differ among species? An analysis for 1200 plant species from five continents**

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Article acceptance date: 15 June 2015

The following Supporting Information is available for this article:

**Fig. S1** Residuals of the allometric relationships after fitting a SMA regression through log-log transformed organ mass data.

**Fig. S2** Phylogenetic tree of the Leaf Mass Fraction (LMF) data.

**Fig. S3** Distribution of the deviations from the overall allometric log-log curves for various functional groups.

- **Note S1** Methodological assumptions

**Note S2** Inference value of  $r^2$  in plant allometric analyses

**Note S3** Explanation of a very simple model that shows dynamic scaling exponents as a consequence of physiological or environmental constraints.

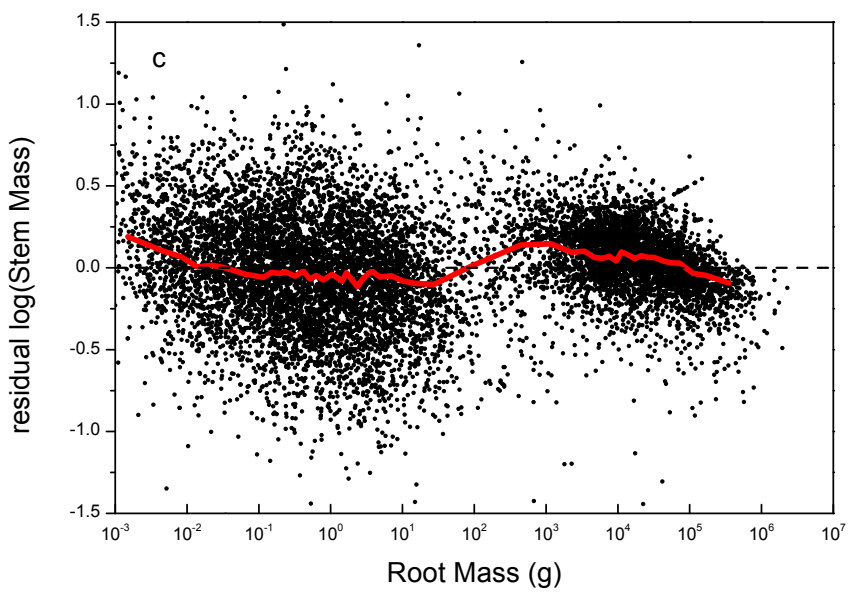
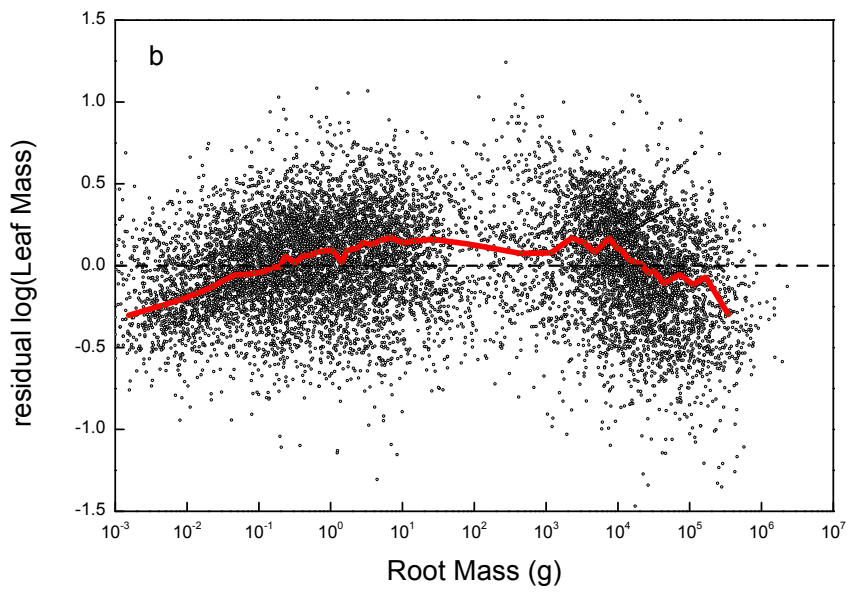
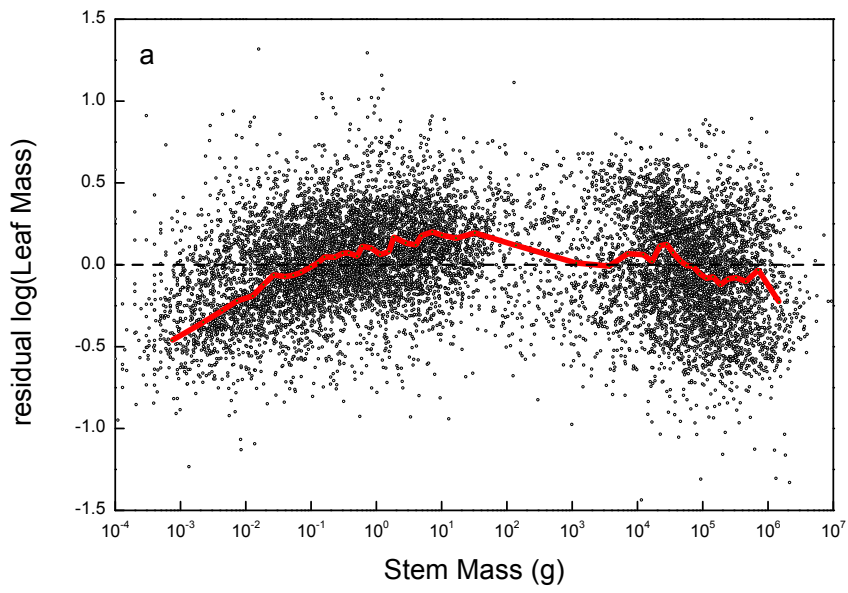
**Table S1** Literature references on which the database is built.

**Table S2** Biomass data for leaves, stems and roots as well as biomass distribution patterns (LMF, SMF and RMF) and deviations from the overall trends in biomass distribution (pLMF, pSMF and pRMF) as used for the current analyses.

**Table S3** Overview of the representation of various plant groups in the database.

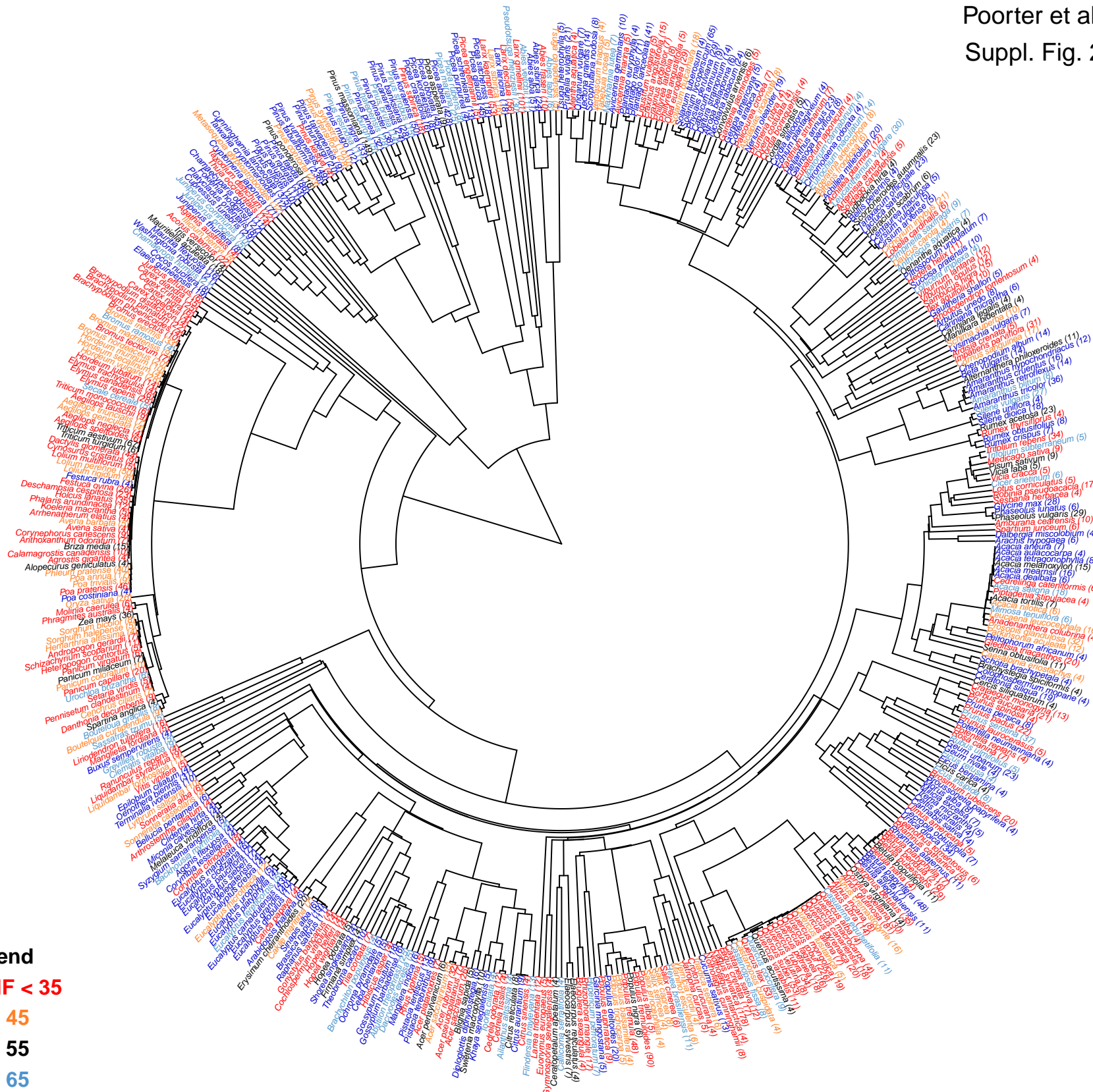
**Table S4** Allometric scaling exponents as given for all records of all species, and for herbaceous and woody species separately.

**Fig. S1** Residuals after fitting a SMA regression through log-log transformed organ mass data. For clarity, the residuals are binned for the 50 size classes, and the median residuals for each size class are connected with a red line.

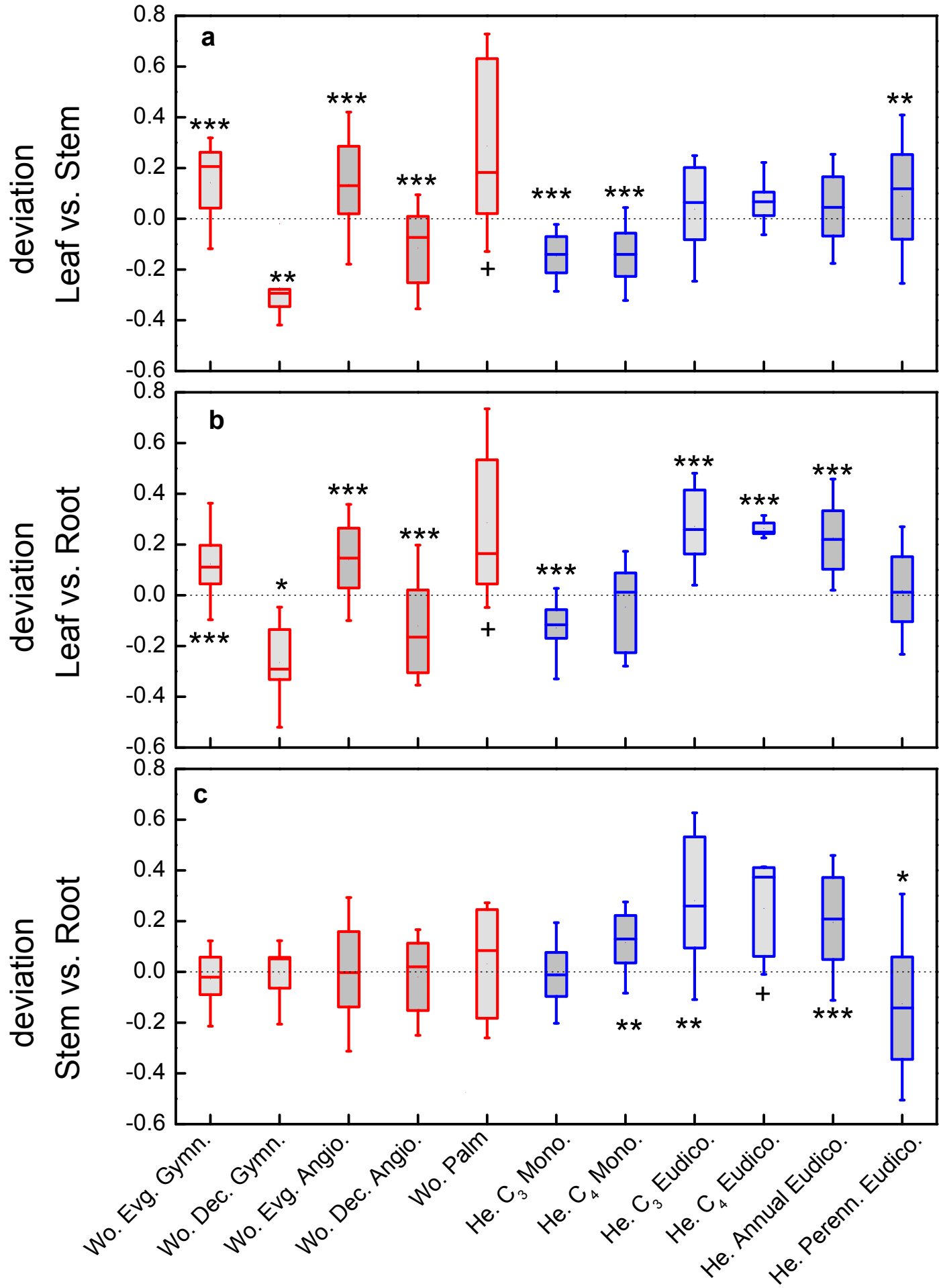


**Fig. S2** Phylogenetic tree of the Leaf Mass Fraction (LMF) data. Data are based on the deviations of the LMF of each record from the median trend line (pLMF) as shown in Fig. 2a, expressed as percentiles and calculated per size class (see Methods). Note that a pLMF of 50 indicates that the species does not deviate from the median trend. The total number of species included is 482. The species colour indicates the average pLMF for that species, for explanation of the colour code see the legend of the figure.

**Legend**  
**pLMF < 35**  
**35 – 45**  
**45 – 55**  
**55 – 65**  
**> 65**



**Fig. S3** Distribution of the deviations from the overall allometric log-log curves for various functional groups for (a) Leaf mass vs. stem mass scaling (b) Leaf mass vs. Root mass scaling and (c) Stem mass vs. Root mass scaling. The overall allometric curves were first determined by a Loess fit, and for all observations the deviations from the fitted line were calculated and averaged over species. Species averages were then used to determine boxplots of the distribution of values per species. The boxplot indicates the 10<sup>th</sup>, 25<sup>th</sup>, 50<sup>th</sup>, 75<sup>th</sup> and 90<sup>th</sup> percentile. Wo.: woody; He.: herbaceous; Evg.: evergreen; Dec.: deciduous; Perenn.: perennial; Gymn.: gymnosperms; Angio.: angiosperms; Mono: monocotyledons; Eudico.: Eudicotyledons. Significance values indicate t-tests for significant deviation from 0, which indicates no deviation from the overall allometric curve. +,  $0.05 < P < 0.10$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ).



## **Note S1.** Methodological assumptions

There were four important assumptions in our methodology, shared with previous studies. First, we assumed that differences among studies in how the whole plant was separated into leaf, stem and root would have only a small effect on the patterns analysed. Not all investigators followed exactly the same protocol, and not all described their specific protocol. Ideally, organs would be consistently defined by function; for example, leaf lamina, as the organ most active in photosynthesis, would ideally be consistently separated from petioles and, in grasses, from leaf sheaths, which mainly function to position the leaf blades in a favourable location and for water and sugar transport (Pérez-Harguindeguy et al., 2013 and references therein). However, in a number of reports petioles and/or leaf bases were included in the leaf fraction. We made a correction only in the case of palm trees, where leaves can be up to 8 meters long with petioles as thick as small branches of dicotyledonous trees (Corley & Tinker, 2003). In those cases we subtracted petiole and rachis from total leaf mass, using supplementary data of other publications as necessary. We also presumed that differences among studies in the separation of stems and roots would not have a strong effect on the analyses.

Our second assumption was that root mass was accurately measured. The extraction of roots from solid substrates can be challenging (Mokany et al., 2006). On the one hand, root mass can be overestimated if roots are not cleaned well enough of adhering soil particles; on the other hand, root mass is underestimated if not all roots are recovered. Based on sophisticated methods where the root diameter of various roots were taken into account, the fraction of unrecovered root mass or volume for a *Pinus* root system was estimated to be 17% in young plants but only 4% in older ones (Danjon et al., 2013; Chmura et al., 2013). The effect of such error would be relatively modest, though for large field-grown trees no estimates are available.

Third, we assumed that total plant biomass is a far more important driver for biomass distribution than the age or – for trees – the ontogenetic stage of a plant. Some studies focused on size-related changes within species, while others, especially in zoology, have focused on differences across species when measured at the adult reproductive stage. In plants, modular and indeterminate growth generates far more variability in size at any ontogenetic stage than in animals, and size imposes a variety of functional constraints. It is also a strong determinant in competition. We therefore decided to include both younger and older plants, as long as they matched the criteria given in Material and Methods. Ontogeny will be an important factor, especially when flowering occurs in monocarpic species. We therefore excluded all herbs as well as monocarpic woody species in the generative phase. Consequently, the overall database has both ontogenetic and interspecific components, and total plant size is considered to be the main driver.



Our fourth assumption was that the plants for each size class in the dataset constitute a representative subsample with respect to growth conditions, functional group, and phylogeny. That is, for all sizes of plants there are individuals grown at various environmental conditions (high/low temperature, nutrients, densities, etc.). Larger trees were only grown and harvested in the field, so we also assume that the mix of conditions for small trees (partly experimental, partly field) was not very different from those of larger trees (partly plantations, partly natural). Thus, we supposed environmental effects to be randomly and equally distributed over the full range of data, adding noise to the data set, but without driving any substantial systematic deviations.

## References

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- **Mokany K, Raison RJ, Prokushkin AS. 2006.** Critical analysis of root:shoot ratios in terrestrial biomes. *Global Change Biology* **12**: 84-96.
- **Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE et al. 2013.** New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**: 167-234.

**Note S2.** Inference value of  $r^2$  in plant allometric analyses

Sensitivity analysis of the effect of a predefined range in Root Mass Fraction (RMF: fraction of Total Plant Mass (TM) invested in roots) on the explained variance ( $r^2$ ) of the relationship between  $\log(\text{root mass})$  and  $\log(\text{shoot mass})$ . The predefined ranges were chosen to be narrow from a biological perspective ( $0.4 < \text{RMF} < 0.6$ ), realistic ( $0.07 < \text{RMF} < 0.70$ ; as observed for the current data set based on the 0.5<sup>th</sup> and 99.5<sup>th</sup> percentile), very wide ( $0.01 < \text{RMF} < 0.99$ ) and improbably wide ( $0.001 < \text{RMF} < 0.999$ ). Each correlation was based on 20,000 random drawings as explained below. Overall variation in simulated plant mass was either 10 orders of magnitude, or 1 order of magnitude.

Range in RMF	$r^2$	
	10 <sup>10</sup> -fold range in TM	10-fold range in TM
0.40 – 0.60	0.999	0.886
0.07 – 0.70	0.982	0.170
0.01 – 0.99	0.941	0.011
0.001 – 0.999	0.932	0.020

*Simulations*

To evaluate the meaning to be attached to the actual value of  $r^2$  in allometric relationships, we simulated a population of plants with substantial variation in biomass, drawing randomly from a uniform distribution of  $\log$ -transformed total plant mass, for a range that comprised 10 orders of magnitude in biomass. This is more or less similar to the current dataset. For each of these plants, root mass was then calculated, after simulating a Root Mass Fraction by randomly drawing from a uniform distribution with values ranging from – in the first scenario – 0.40 to 0.60. Shoot mass was then simply the difference between the mass of the total plant and the roots. We drew samples for 20,000 simulated plants in total, and subsequently calculated the  $r^2$  of the allometric relationship between the  $\log$ -transformed shoot and root mass for all 20,000 observations. The analysis was then repeated with three other scenarios with increasingly wider intervals for the RMF.

The compiled data showed very tight relationships between organs ( $r^2 \geq 0.932$ ; see table above), and between each organ and total plant biomass ( $r^2 \geq 0.992$ ). We analysed how such high  $r^2$  values for the relationships between the biomass of two organs should be interpreted, and whether it permits the inference of a fixed scaling exponent, in principle. We simulated cases with various ranges in RMF. In the case of relatively narrow variation in RMF (0.40-0.60), we found that the allometric relationship yielded an  $r^2$  higher than 0.99. However, when allowing

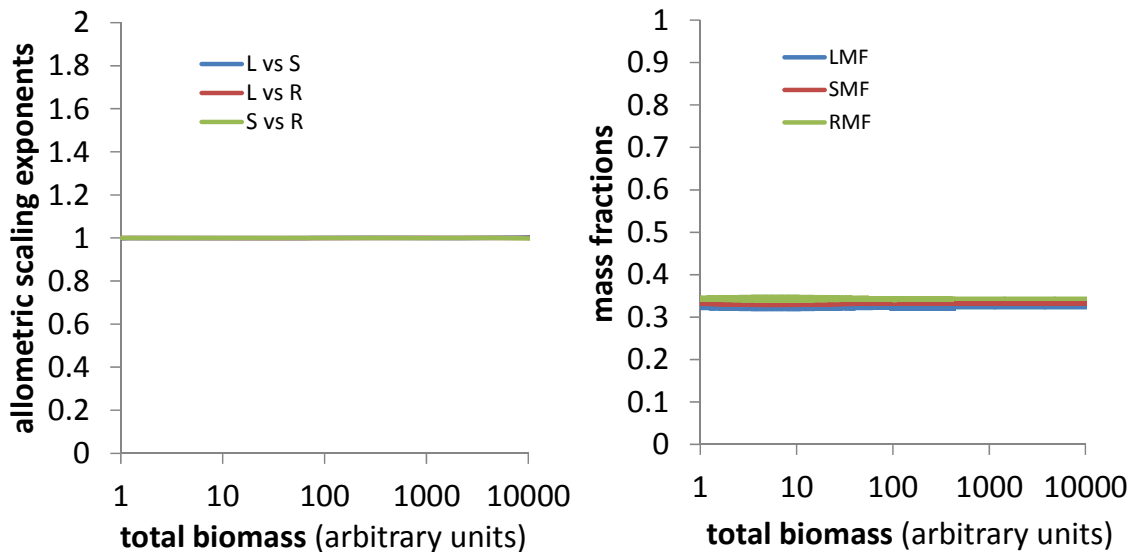
RMF to vary randomly across the range actually observed in our compiled dataset (99% of the cases were in the 0.07-0.70 range), the  $r^2$  still exceeded 0.98. Only in simulations when the range in allocation became much larger than normally observed (0.01 – 0.99 or wider) was the  $r^2 < 0.95$ . Indeed, even if the shoot and root system of plants showed highly variable proportionality, that is when RMF ranged between 0.01 and 0.99 (and thus, shoot:root ratios were confined between 0.01 and 99), the correlation between log-transformed shoot and root biomass was still around 0.94 or higher. The high  $r^2$ s were predominantly due to the large range of biomass considered; the  $r^2$  dropped dramatically with increasing range of RMF when the same allometric relationship is considered over one rather than ten orders of magnitude in plant size (Table above). Hence, the fact that an allometric equation “explains” ~97% of the variation in shoot and root mass according to its  $r^2$ , does not allow the inference of the central tendency of biomass allocation. Direct examination of the allometries, and potential shifts in the allometries are necessary to establish the central trend, and whether it is fixed or dynamic.

**Note S3.** Accounting for changes in the economics of C allocation during growth

The central features of the economics of plant carbon allocation are that the effect of C investment in any pool on growth must be saturating – i.e., growth rate  $G$  approaches a finite limit as C in any pool approaches infinity – and that the effects of each C investment on growth rate are not independent: if investment is high in one pool, this increases the return on investment in other pools due to their mutual influence on photosynthesis. Perhaps the simplest implementation of these features is

$$G \propto \left( \frac{c_s}{c_s + k_s} \right) \left( \frac{c_r}{c_r + k_r} \right) \left( \frac{c_l}{c_l + k_l} \right)$$

Apart from the saturation constants  $k_j$ , the carbon pools are indistinguishable in this model. When carbon allocation is optimised in this model (by modulating allocation over time, during growth, so that the marginal products for each pool remain equal:  $\partial G/\partial c_s = \partial G/\partial c_r = \partial G/\partial c_l$ ), allocation is isometric:



(The lines for LMF and RMF have been shifted up by 0.01 and down by 0.01, respectively, to make them visible.) To capture what happens during height growth, we must incorporate the effect of height, which influences the economics of allocation to stems, roots and leaves differently. Suppose that height growth brings diminishing returns because its benefits for light capture are counteracted by its negative impact on water transport. This can be expressed qualitatively by multiplying  $G$  by a hyperbolic function of height analogous to the terms for the carbon pools:

$$G \propto \left( \frac{c_s}{c_s + k_s} \right) \left( \frac{c_r}{c_r + k_r} \right) \left( \frac{c_l}{c_l + k_l} \right) \left( \frac{h}{h + k_h} \right)$$

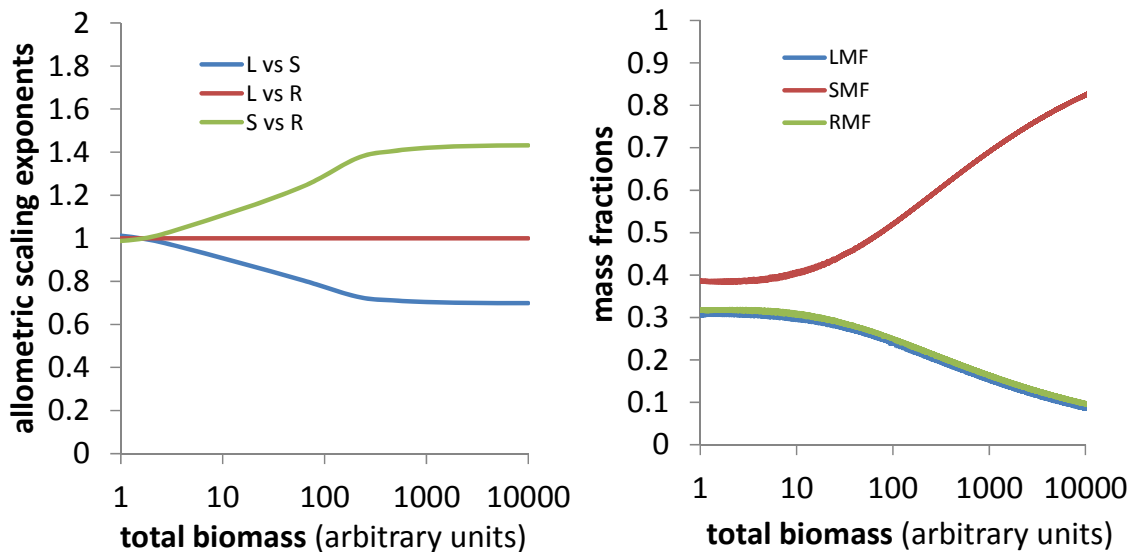
where  $h$  is height. Height also depends on stem carbon. Supposing that height is proportional to the  $2/3$  power of stem diameter as specified by buckling theory, and that stem carbon is proportional to the product of height and diameter, it follows that  $h \propto c_s^{1/(1+1/(2/3))} = c_s^{2/5} = c_s^{\alpha/(\alpha+1)} = c_s^\beta$  where  $\beta = \alpha/(\alpha+1)$  and  $\alpha = 2/3$  and  $\beta = 2/5$  nominally. Then

$$\frac{h}{h + k_h} = \frac{c_s^\beta}{c_s^\beta + k_h}$$

and

$$G \propto \left( \frac{c_s^{\beta+1}}{(c_s + k_s)(c_s^\beta + k_h)} \right) \left( \frac{c_r}{c_r + k_r} \right) \left( \frac{c_l}{c_l + k_l} \right)$$

This model predicts increasing scaling exponents for stem relative to roots, decreasing exponents for leaf relative to stem, increasing SMF and decreasing RMF and SMF -- as observed:



### Interpretation

We do not suggest that this model should be directly interpreted as a mechanistic model for predicting changes in allometry during plant growth and neither should be the exact values of scaling exponents or mass fractions. For one, it omits many important features that may influence the economics of carbon allocation, such as the mechanical demands for below-ground anchorage, the effect of leaf investment on hydraulic conductance, the respiratory and hydraulic costs of height growth, the loss of leaf and fine root investments to senescence and the conversion of sapwood to heartwood, and the return of nutrients to the soil from leaf litter

during growth. To incorporate all of these features requires a radically more detailed and mechanistically explicit model, and it is unlikely that any such model will apply generally enough across types of plants and environments to permit general theories of allometric scaling to be deduced. Instead, the analysis above shows that when MST's fundamental assumption about plant carbon economics – namely, that growth is directly proportional to leaf biomass – is minimally elaborated to include qualitative features of the economics of stem and root carbon investment, it quickly emerges that allometric scaling constants should vary continuously and in complex fashion during plant growth.

### *Simulation methods*

We simulated the growth model described above using  $k_s = k_r = k_l = 1$  with initial biomass pool sizes equal to  $1/6$  so that the total initial biomass was 0.5. For simulations including the saturating positive effect of height, we set  $k_h = 1$ . In each time step, the marginal product for each biomass pool was computed numerically using a small biomass increment ( $10^{-5}$ ), and the biomass pool with the greatest marginal product was incremented by the biomass available for allocation, which was computed as the product of  $G$  and an arbitrary timestep of 0.3. This ensured that the marginal products remained approximately equal across biomass pools during the simulated growth period.

**Table S1. Literature references on which the database is built.**

**Herbaceous species:**

**A-E**

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**Table S3** Overview of the representation of various plant groups in the database. Data are provided for the total number of observations for herbaceous and woody species, the % of the total observations related to each phylogenetic class, the % of all observations of a phylogenetic class that were made in the field (rather than in a growth chamber, a glasshouse, an Open Top Chamber or in an experimental field), and the total number of species represented by the observations in a phylogenetic class.

<b>Functional Type</b>	<b># of observations in the database</b>	<b>Phylogenetic class</b>	<b>% of total observations</b>	<b>% of the # of observations made in the field</b>	<b># of species per phylogenetic class</b>
Herbaceous	2954	Monocots	12.2	0	192
		Eudicots	14.2	0	210
Woody	8178	Gymnosperms	33.4	80	108
		Basal Angiosperms	0.8	54	23
		Monocots	1.2	55	14
		Eudicots	37.7	35	643
Intermediate	69	Eudicots	0.6	1	15



**Table S4** Allometric scaling exponents as given for all records of all species, and for herbaceous and woody species separately. (a) Standard Major Axis regression (SMA; model 2 regression) for the intercept ( $\alpha$ ) and slope ( $\beta$ ) of the regression of leaf mass (LM) vs. root mass (RM), stem mass (SM) vs. root mass, and leaf mass vs. stem mass, all based on log<sub>10</sub>-transformed values. The 95% confidence interval for the slope, as well as the  $r^2$  of the equation are given. (b) Ordinary least square regression (OLS), tested for linear and quadratic relationships.  $a$  is the value for the intercept,  $b_1$ ,  $b_2$  and  $b_3$  are the values for the linear, the quadratic and the cubic component, respectively. The degrees of freedom was >3000 for herbaceous species and >8,200 for woody species.

(A) Species	Regression	$\alpha$	$\beta$	95% CI for $\beta$	$r^2$
All	LM vs. SM	0.113	0.740	0.738 - 0.742	0.978
	LM vs. RM	0.070	0.849	0.847 - 0.851	0.977
	SM vs. RM	-0.058	1.147	1.145 - 1.149	0.988
Herbaceous	LM vs. SM	0.239	0.864	0.855 - 0.872	0.928
	LM vs. RM	0.192	0.985	0.972 - 0.991	0.931
	SM vs. RM	-0.054	1.140	1.128 - 1.153	0.904
Woody	LM vs. SM	0.127	0.728	0.725 - 0.730	0.971
	LM vs. RM	0.077	0.834	0.831 - 0.837	0.970
	SM vs. RM	-0.069	1.146	1.143 - 1.149	0.987

(B) Species	Regression	$a$	$b_1$	$b_2$	$b_3$	$r^2$
All	LM vs. SM	0.213	0.795	-0.0177	-	0.981
	LM vs. RM	0.151	0.897	-0.0184	-	0.979
	SM vs. RM	-0.126	1.144	0.0318	-0.00606	0.989
Herbaceous	LM vs. SM	0.216	0.819	-0.0082		0.926
	LM vs. RM	0.173	0.918	-0.0219		0.931
	SM vs. RM	-0.102	1.081	-		0.901
Woody	LM vs. SM	0.225	0.790	-0.0221	0.00094	0.977
	LM vs. RM	0.110	0.897		-0.00356	0.975
	SM vs. RM	-0.147	1.138	0.0408	-0.00748	0.990