

Letters

Tree size and climatic water deficit control root to shoot ratio in individual trees globally

Plants acquire carbon from the atmosphere and allocate it among different organs in response to environmental and developmental constraints (Hodge, 2004; Poorter *et al.*, 2012). One classic example of differential allocation is the relative investment into aboveground vs belowground organs, captured by the root : shoot ratio ($R : S$; Cairns *et al.*, 1997). Optimal partitioning theory suggests that plants allocate more resources to the organ that acquires the most limiting resource (Reynolds & Thornley, 1982; Johnson & Thornley, 1987). Accordingly, plants would allocate more carbon to roots if the limiting resources are belowground, that is water and nutrients, and would allocate more carbon aboveground when the limiting resource is light or CO_2 . This theory has been supported by recent research showing that the $R : S$ of an individual plant is modulated by environmental factors (Poorter *et al.*, 2012; Fatichi *et al.*, 2014). However, understanding the mechanisms underpinning plant allocation and its response to environmental factors is an active field of research (Delpierre *et al.*, 2016; Paul *et al.*, 2016), and it is likely that plant size and species composition have an effect on $R : S$. Accounting for these sources of variation is an important challenge for modelling (Franklin *et al.*, 2012).

The hypothesis that aridity controls $R : S$ is supported by experiments on tree seedlings, which report higher $R : S$ values in response to simulated drought treatments (Lambers *et al.*, 2008; Poorter *et al.*, 2012). This hypothesis is also consistent with the observation that trees in arid environments tend to allocate proportionally more biomass to roots, which may improve access to soil water (Nepstad *et al.*, 1994) and act as a protected reservoir of stored carbohydrates to facilitate rapid regrowth following disturbances such as fire that are common in arid regions (Ryan *et al.*, 2011). However, previous meta-analyses have led to contradictory results regarding the causes of stand-level variation in $R : S$. Mokany *et al.* (2006) found precipitation was the main control on $R : S$ values; by contrast, Reich *et al.* (2014) suggested that temperature was the main driver, with $R : S$ largely unrelated to aridity. Yet, previous studies used either data from soil cores (Reich *et al.*, 2014), or a limited amount of data on root biomass from individually excavated trees (Cairns *et al.*, 1997; Mokany *et al.*, 2006), making it impossible to explore individual patterns of $R : S$ variation in response to tree size and environmental conditions.

Using the largest global dataset of its kind, here we provide the first analysis of global patterns of variation in individual-tree $R : S$. We hypothesized that individual $R : S$ varies with environmental

conditions, namely climate and management type, and is also determined by intrinsic factors, namely tree size and species. We also aimed to rank the relative contribution of these factors to $R : S$ variation. The global dataset of individual $R : S$ values was compiled from whole-tree harvesting studies (Supporting Information Notes S1 and Fig. S1), the BAAD among them (Falster *et al.*, 2015) [correction added after online publication 23 October 2017: the reference Falster *et al.* (2015) has been inserted here and in the References section]. The dataset encompasses 409 sites and a total of 3416 trees of 212 species with oven dry weight measurements of both aboveground and belowground biomass, from which we computed the $R : S$ (Fig. 1). The destructively-sampled trees included in the database had diameter-at-breast height (DBH) values ranging from 0.6 to 128 cm (more details in Fig. S1). We fitted linear regression models, using the natural logarithm of $R : S$, $\log_e(R : S)$, as the response variable to reduce heteroscedasticity. The explanatory variables that we analysed were tree size, tree species, wood specific gravity, phenology (evergreen, deciduous), and clade (gymnosperm, dicot angiosperm or monocot angiosperm, i.e. palm). Additional factors in the models were bioclimatic region (tropical dry, tropical wet, non-tropical), temperature, precipitation, whether the tree was growing in a natural forest or plantation, and climatic water deficit (MWD, for mean water deficit, in mm yr^{-1}), which is the deficit between monthly rainfall and

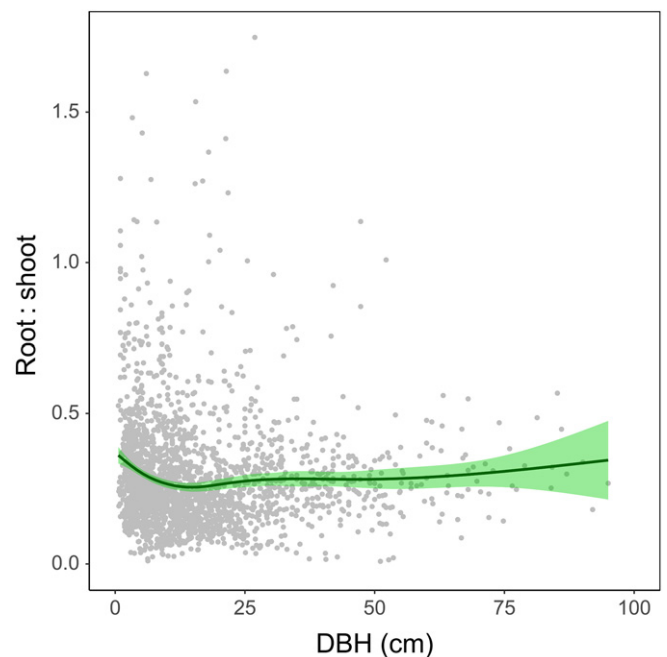


Fig. 1 Plot of individual root : shoot ($R : S$) ratios against tree diameter-at-breast height (DBH, in centimetres), including trees with DBH up to 1 m, for a better display. Each grey point corresponds to an individual value. The dark green line is the mean value of $R : S$ at that particular DBH, and the green shading illustrates \pm SE.

potential evapotranspiration (Aragão *et al.*, 2007). Additional details about the explanatory variables and methods are in Methods S1. We carried out a stepwise regression analysis, retaining the variables significant at 95%, and selected the best model based on Akaike information criterion (AIC) values. The conditional and marginal variances, R^2_{GLMM} values, for the final model and variances for each component were calculated using the method proposed by Nakagawa & Schielzeth (2013). All statistical analyses were conducted in R (code reproduced in Notes S2).

The following model, with species as a random effect, explained 62% of the variance of the data ($R^2_{\text{GLMM-C}}$ values):

$$\log_e(R : S) = -1.2312 - 0.0215 \text{ DBH} + 0.0002 \text{ DBH}^2 - 0.0007 \cdot \text{MWD} - 0.1631 \text{ plantation} + |\text{Species}|$$

where DBH is in centimetres, MWD is in millimetres, plantation is a binary 1/0 dummy variable and Species is a species specific random term.

The most important factor explaining global tree $R : S$ values was tree size: DBH and DBH^2 jointly accounted for 33% of the variance. Mean $R : S$ values decreased with tree size for trees with DBH up to 1 m. For instance, saplings < 2 cm DBH had a mean $R : S$ of 0.43, while trees with DBH 25–30 cm had a value of 0.28. For trees with DBH larger than 1 m, $R : S$ did not vary much (but the sample size for these was small, only 42 trees). Saplings and small trees presumably invest more biomass belowground to take up nutrients and water for fast growth and survival (Poorter *et al.*, 2012). The decline in $R : S$ with increasing DBH is also consistent

with the fact that as trees age, and DBH increases, nonconductive xylem accumulates disproportionately in aboveground tree parts. MWD accounted for 17% of the variance, and $R : S$ declined with decreasing MWD (Fig. 2). This suggests that plants experiencing water shortage allocate more biomass belowground, in agreement with Mokany *et al.* (2006) and observations from experiments (Hodge, 2004; Lambers *et al.*, 2008; Poorter *et al.*, 2012), but not with Reich *et al.* (2014). When MWD was included in the model, both precipitation and temperature became nonsignificant. MWD also explained more variance than precipitation or temperature when these variables were fitted separately in single-factor models (Methods S1). Importantly, the relationship between $R : S$ and both DBH and MWD was nonlinear, as has been observed previously (Mugasha *et al.*, 2013).

Many of the tested effects were not statistically significant, presumably because in some instances large variances precluded detection of true differences, and in others because of the absence of an effect. Our analysis does suggest that, after accounting for MWD, variation in $R : S$ did not differ across bioclimatic regions. We detected no correlation or significant interaction between tree size and MWD, which suggests that the effects of these two variables are independent (Methods S1). This is an interesting contrast with the findings of Bennett *et al.* (2015), who determined that larger trees are more vulnerable to drought than smaller trees: the influence of chronic water deficit (as expressed by MWD) on $R : S$ apparently does not translate to ability to respond to episodic drought. Species identity accounted for only 11% of the variance in $R : S$, and contrary to previous studies (Mokany

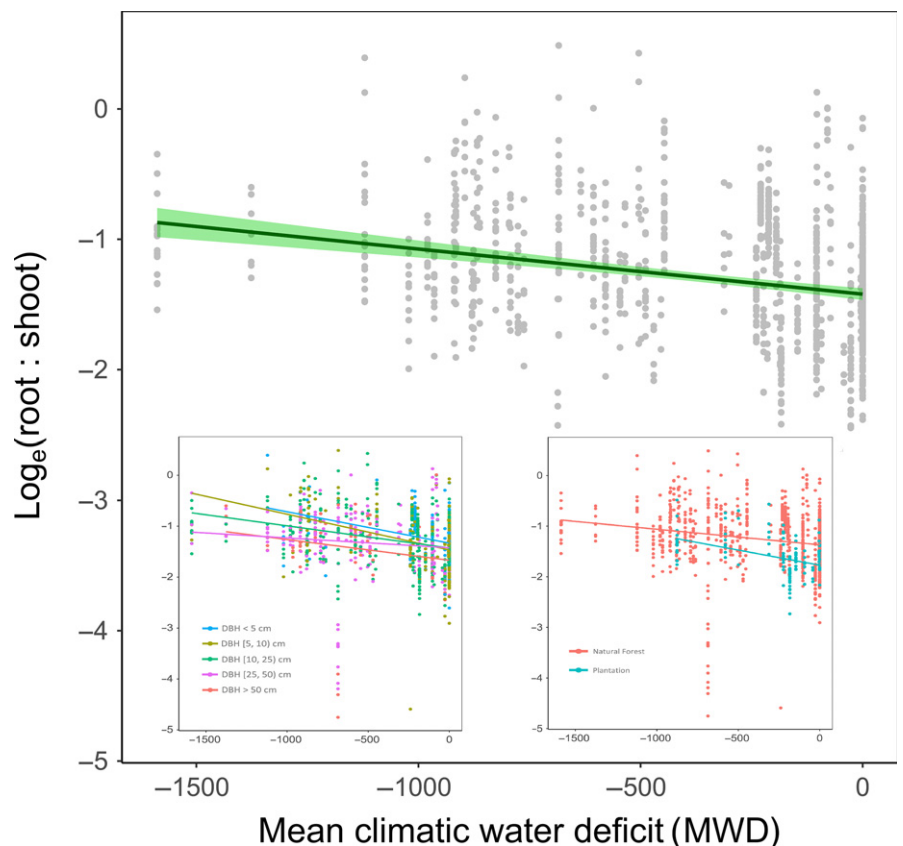


Fig. 2 Plot of \log_e of individual root : shoot ratio ($R : S$) against the mean water deficit (MWD), where each point corresponds to an individual value. The green line is the linear trend and the green shading illustrates \pm SE. Please note this is not the actual fitted curve. Inset right: plot of $\log_e(R : S)$ against MWD, where the red points and line correspond to natural forest and the blue ones to plantations. Inset left: plot of $\log_e(R : S)$ against MWD, where different colours represent different diameter classes (diameter-at-breast height (DBH) in centimetres) (see colour codes in the graph).

et al., 2006; Reich *et al.*, 2014), groupings of species by phenology or clade did not explain any additional variation in $R:S$ (Fig. S2), except that monocotyledons (palms) invest comparatively less biomass in roots. Species can have widely different root architectures (Lynch, 1995), therefore differences in $R:S$ values across species are not surprising. After accounting for species, wood specific gravity was not a significant predictor of $R:S$. Finally, trees in plantations had lower $R:S$ than trees in natural forests (Fig. S2b), although this effect explained only 2% of the variance in $R:S$. Plantations are sometimes fertilized, which may result in lower biomass allocation in belowground tissues in response to the greater nutrient availability. Moreover, species in plantations are typically fast-growing and selected for their capacity to produce aboveground biomass quickly. Finally, plantation trees may be more sheltered and the structural support of the roots is less necessary. The remaining 38% of variance that was unexplained may be due in part to soil fertility, which is known to influence $R:S$ (Reynolds & D'Antonio, 1996; Poorter *et al.*, 2012). Other possible sources of variance, not considered due to a lack of data here, include differences in micro-topography, soil properties, particular individual conditions like resprouting, and community structure. Further, differences in methodology for collecting root data (see Fig. S1(2.3)) among studies may account for some of the variance.

The main novel finding of this study is that globally, variation in individual tree $R:S$ is largely dominated by two effects: tree size and MWD, which largely support our hypothesis. The increase in $R:S$ in response to increasing climatic water deficit occurs independently of the size dependence in $R:S$, which supports the hypothesis that moisture availability drives global variation in $R:S$. With greater aridity, trees invest comparatively more resources to acquire soil water as it becomes a more limiting resource for growth and survival, and to provide a belowground reservoir of stored carbon for rapid regrowth following disturbance. Plasticity in $R:S$ has major implications for our understanding of the contribution of vegetation to the global carbon cycle and responses to climatic change. Some parts of the globe are predicted to experience drying trends, including longer dry seasons, and an increase in the frequency of extreme events and disturbances, while other regions may become wetter or less seasonal (Moss *et al.*, 2010; Intergovernmental Panel on Climate Change (IPCC), 2014). Our new results suggest that any change in water deficit, or in the relative abundance of smaller trees, may result in shifts in biomass allocation, with far-reaching consequences for the global carbon budget.

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A.L. and J. Chave initiated the study; A.L. analysed the data and J. Chave compiled the dataset; A.L., J. Chave, K.I.P. and D.F.R.P.B. designed the study and wrote the manuscript; A.L., K.I.P., D.F.R.P.B., J.J.E., C.B., M.B., K.B., J. Chave, T.H.E., J.R.E., A.F., J.J., M.M., K.D.M., G.M., W.A.M., E.P., S.R., C.M.R., R.R.P., S.S., A.S., D.W., C.W., A.Z. and J. Carter contributed ideas, provided written input, and/or data.

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Supporting Information

Additional Supporting Information may be found online in the
Supporting Information tab for this article:

Fig. S1 World map with data plots and details on the dataset.

Fig. S2 Boxplot of $R : S$ values for inter-group comparisons.

Methods S1 Extended description of methods, fitted models and
model diagnosis

Notes S1 Dataset used in the study: tree-by-tree root:shoot
dataset; also available in the Figshare achieve doi: 10.6084/m9.f
igshare.5144164.

Notes S2 R code used in the analyses.

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