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

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

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

27   Using the largest global dataset of its kind, here we provide the first analysis of global patterns
28   of variation in individual-tree R:S. We hypothesized that individual R:S varies with environmental
29   conditions, namely climate and management type, and is also determined by intrinsic factors, namely
30   tree size and species. We also aimed to rank the relative contribution of these factors to R:S variation.
31   The global dataset of individual R:S values was compiled from whole-tree harvesting studies (Dataset
32   S1, Figure S1). The dataset encompasses 409 sites and a total of 3,416 trees of 212 species with oven
33   dry weight measurements of both above- and below-ground biomass, from which we computed the

34   R:S (Fig. 1). The destructively-sampled trees included in the database had diameter at breast height

35   (DBH) values ranging from 0.6 to 128 cm (more details in Figure S1). We fitted linear regression

36   models, using the natural logarithm of R:S, ln(R:S), as the response variable to reduce

37   heteroscedasticity. The explanatory variables that we analysed were tree size, tree species, wood

38   specific gravity, phenology (evergreen, deciduous), and clade (gymnosperm, dicot angiosperm or

39   monocot angiosperm, i.e. palm). Additional factors in the models were bioclimatic region (tropical dry,

40   tropical wet, non-tropical), temperature, precipitation, whether the tree was growing in a natural

41   forest or plantation, and climatic water deficit (MWD, for mean water deficit, in mm/year), which is

42   the deficit between monthly rainfall and potential evapotranspiration (Aragão *et al.*, 2007). Additional

43   details about the explanatory variables and methods are in Methods S1. We carried out a stepwise

44   regression analysis, retaining the variables significant at 95%, and selected the best model based on

45   AIC values. The conditional and marginal variances, R^2_{GLMM} values, for the final model and variances

46   for each component were calculated using the method proposed by Nakagawa & Schielzeth (2013).

47   All statistical analyses were conducted in R (code reproduced in Note S1).

48   The following model, with species as a random effect, explained 62% of the variance of the

49   data ($R^2_{\text{GLMM-C}}$ values):

50   $$\ln(R\!:\!S) = -1.2312 - 0.0215DBH + 0.0002DBH^2 - 0.0007 \cdot MWD - 0.1631\,plantation + |Species|$$

51   Where DBH is in cm, MWD is in mm, plantation is a binary 1/0 dummy variable and Species is a species

52   specific random term.

53   The most important factor explaining global tree R:S values was tree size: DBH and DBH^2

54   jointly accounted for 33% of the variance. Mean R:S values decreased with tree size for trees with DBH

55   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

56   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

57   these was small, only 42 trees). Saplings and small trees presumably invest more biomass below

58   ground to take up nutrients and water for fast growth and survival (Poorter *et al.*, 2012). The decline

59   in R:S with increasing DBH is also consistent with the fact that as trees age and DBH increases non-

60   conductive xylem accumulates disproportionately in aboveground tree parts. Mean water deficit

61   accounted for 17% of the variance, and R:S declined with decreasing MWD (Fig. 2). This suggests that

62   plants experiencing water shortage allocate more biomass belowground, in agreement with Mokany

63   et al. (2006) and observations from experiments (Hodge, 2004; Lambers *et al.*, 2008; Poorter *et al.*,

64   2012), but not with Reich *et al.* (2014). When MWD was included in the model, both precipitation and

65   temperature became non-significant. MWD also explained more variance than precipitation or

66 temperature when these variables were fitted separately in single-factor models (Methods S1).
67 Importantly, the relationship between R:S and both DBH and MWD was nonlinear, as has been
68 observed previously (Mugasha *et al.*, 2013).

69 Many of the tested effects were not statistically significant, presumably because in some
70 instances large variances precluded detection of true differences, and in others because of the
71 absence of an effect. Our analysis does suggest that, after accounting for MWD, variation in R:S did
72 not differ across bioclimatic regions. We detected no correlation or significant interaction between
73 tree size and MWD, which suggests that the effects of these two variables are independent (Methods
74 S1). This is an interesting contrast with the findings of Bennett et al. (2015), who determined that
75 larger trees are more vulnerable to drought than smaller trees: the influence of chronic water deficit
76 (as expressed by MWD) on R:S apparently does not translate to ability to respond to episodic drought.
77 Species identity accounted for only 11% of the variance in R:S, and contrary to previous studies
78 (Mokany *et al.*, 2006; Reich *et al.*, 2014), groupings of species by phenology or clade did not explain
79 any additional variation in R:S (Figure S2), except that monocotyledons (palms) invest comparatively
80 less biomass in roots. Species can have widely different root architectures (Lynch 1995), therefore
81 differences in R:S values across species are not surprising. After accounting for species, wood specific
82 gravity was not a significant predictor of R:S. Finally, trees in plantations had lower R:S than trees in
83 natural forests (Figure S2b), although this effect explained only 2% of the variance in R:S. Plantations
84 are sometimes fertilized, which may result in lower biomass allocation in belowground tissues in
85 response to the greater nutrient availability. Moreover, species in plantations are typically fast-
86 growing and selected for their capacity to produce aboveground biomass quickly. Finally, plantation
87 trees may be more sheltered and the structural support of the roots is less necessary. The remaining
88 38% of variance that was unexplained may be due in part to soil fertility, which is known to influence
89 R:S (Reynolds & D'Antonio, 1996; Poorter *et al.*, 2012). Other possible sources of variance, not
90 considered due to a lack of data here, include differences in micro-topography, soil properties,
91 particular individual conditions like resprouting, and community structure. Further, differences in
92 methodology for collecting root data (see S2.2.3) among studies may account for some of the variance.

93 The main novel finding of this study is that globally, variation in individual tree R:S is largely
94 dominated by two effects: tree size and mean water deficit, which largely support our hypothesis. The
95 increase in R:S in response to increasing climatic water deficit occurs independently of the size
96 dependence in R:S, which supports the hypothesis that moisture availability drives global variation in
97 R:S. With greater aridity, trees invest comparatively more resources to acquire soil water as it becomes
98 a more limiting resource for growth and survival, and to provide a below-ground reservoir of stored

99 carbon for rapid regrowth following disturbance. Plasticity in R:S has major implications for our
100 understanding of the contribution of vegetation to the global carbon cycle and responses to climatic
101 change. Some parts of the globe are predicted to experience drying trends, including longer dry
102 seasons, and an increase in the frequency of extreme events and disturbances, while other regions
103 may become wetter or less seasonal (Moss *et al.*, 2010; IPCC, 2014). Our new results suggest that any
104 change in water deficit or in the relative abundance of smaller trees may result in shifts in biomass
105 allocation, with far-reaching consequences for the global carbon budget.

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107 **Authors' contributions.** AL and JC initiated the study; AL analysed the data and JC compiled the
108 dataset; AL, JC, KIP and DRFPB designed the study and wrote the manuscript; all authors contributed
109 ideas, provided written input, and/or data**.**

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SUPPORTING INFORMATION

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

Figure S2: Boxplot of R:S values for inter-group comparisons, including (a) all the measured trees and (b) only trees with DBH from 10 to 50 cm and excluding plantations in panels i,ii,iii to account for differences in tree size and management differences.

Notes S1: R code used in the analyses.

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

Dataset S1: Tree-by-tree R:S dataset. Also available in the figshare achieve doi *<to be given>*

FIGURE LEGENDS

Figure 1: Plot of individual root:shoot ratios (R:S) against tree diameter at breast height (DBH, in cm), including trees with DBH up 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 greed shade illustrates the standard error.

Figure 2: Plot of the natural logarithm (ln) of individual root:shoot ratios (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 greed shade illustrates the standard error. Please, note this is not the actual fitted curve. Bottom, right: Plot of ln(R:S) against MWD, where the red points and line correspond to natural forest and the green ones to plantations. Bottom, left: Plot of ln(R:S) against MWD, where different colours represent different diameter classes (see colour codes in the graph).