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
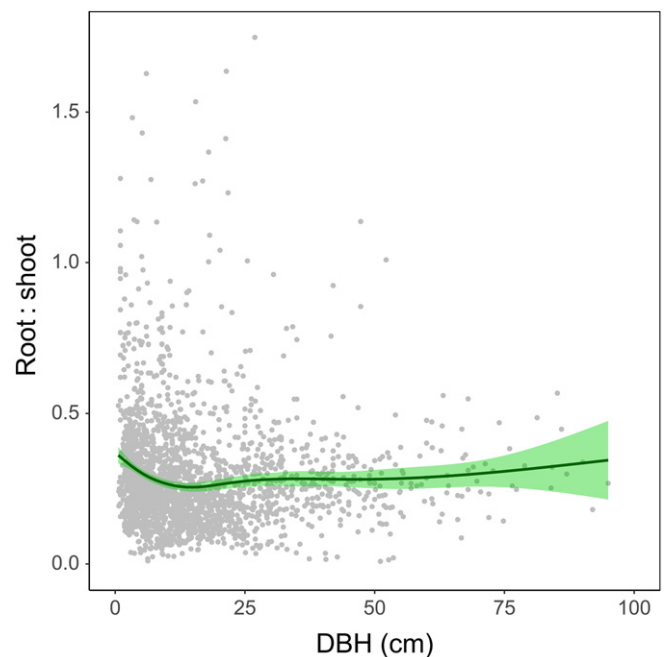

Fig. 1 Plot of individual root : shoot ($R:S$) ratios against tree diameter-at-breast height (DBH, in centimetres), including trees with DBH up to 1 m, for a better display. Each grey point corresponds to an individual value. The dark green line is the mean value of $R:S$ at that particular DBH, and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

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

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
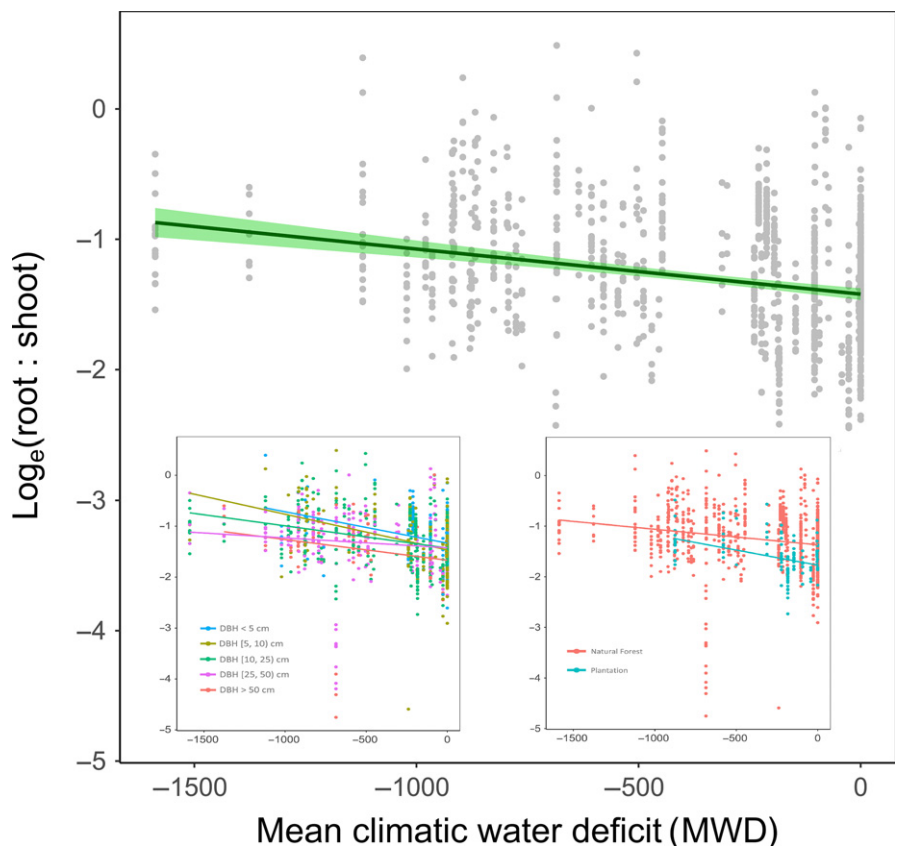

Fig. 2 Plot of $\log_e$ of individual root : shoot ratio ($R:S$) against the mean water deficit (MWD), where each point corresponds to an individual value. The green line is the linear trend and the green shading illustrates $\pm$ SE. Please note this is not the actual fitted curve. Inset right: plot 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.

Author contributions

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.figshare.5144164.

Notes S2 R code used in the analyses.

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Key words: aboveground biomass, aridity hypothesis, belowground biomass, carbon allocation, forest, plant biomass, trees.

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Notes S2 R code used in the analyses.

Figure S1: World map with sampling locations and details of the dataset

Contains:

FS1.1: Sampling locations (black asterisks), on mean climate water deficit (MWD).
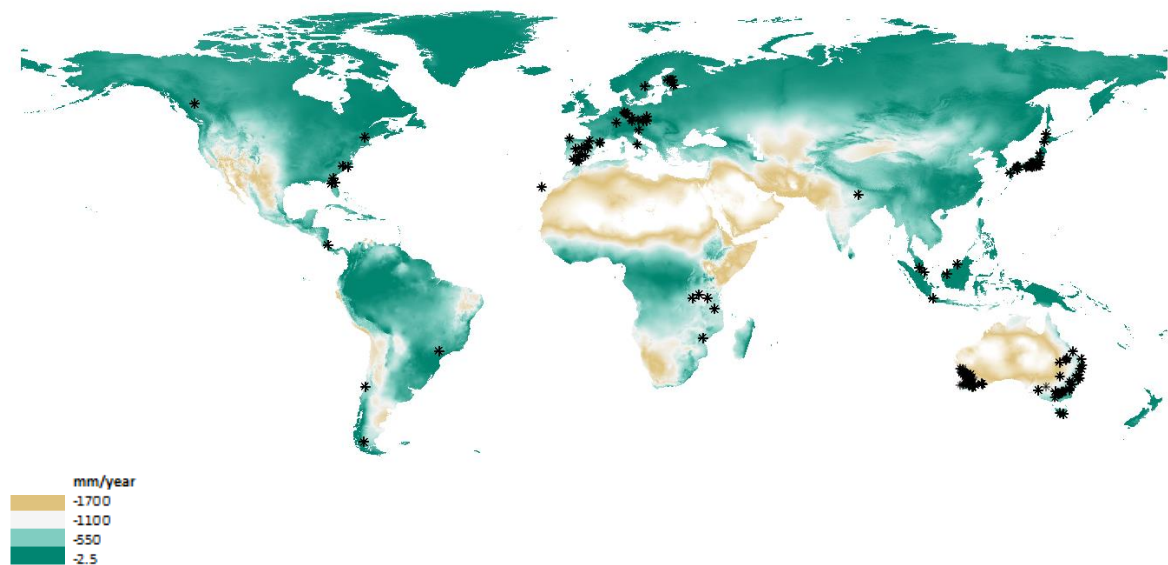
FS1.2: Details of the dataset

FS1.2.1. Database compilation

We compiled data on harvested trees that included the biomass of excavated roots from 409 sites distributed in forested biomes across much of the globe (Figure S1.1 above). For each individual tree, oven dry weight of both above ground biomass (AGB, or shoot, S) and below ground biomass (BGB, or roots, R) was directly assessed by destructive harvesting. The required data were available for 3,433 trees. Seventeen trees with R:S values greater than the mean for the entire dataset plus four times the standard deviation were considered as outliers and excluded, which left 3,416 trees available for analysis. The dataset is reproduced in Notes S1.

For each individual for which we had measurements of below ground biomass (BGB), we also compiled data on (i) above ground biomass (AGB), (ii) tree height (H), (iii) diameter at breast height (DBH), (iv) wood density (ρ), (v) species identity, (vi) biogeographical origin (defined as either temperate-plus-boreal, tropical dry or tropical wet), (vii) management type (either plantation or natural forest), phenology (evergreen, deciduous), clade (gymnosperm, dicot angiosperm or monocot angiosperm, i.e. palm), and geographical coordinates and the associated climatic data of this location (see below). For multi-stemmed individuals, a single, pooled DBH estimate was obtained from the quadratic mean diameter (= diameter of stem of mean basal area) of all stems in clump (Chojnacky and Milton 2008). When wood density was not present in the original database, we used the values from the Global Wood Density Database (Chave et al. 2009, Zanne et al. 2010).

Average climate data for the period 1950-2000 were acquired from the WorldClim dataset interpolated at a 2.5 arc min resolution (Hijmans et al. 2005). We selected the 19 available bioclimatic variables, which includes 11 variables related to temperature and eight related to precipitation, in both cases including annual values and those related to seasonality. Additionally, we downloaded the climatic water deficit parameter at 2.5 arc sec resolution (Chave et al. 2014). Climatic water deficit was computed by summing the difference between monthly rainfall from the Worldclim database, and monthly potential evapotranspiration (ET), from the FAO database at a 10 arc min resolution (http://www.fao.org/geonetwork/srv/en/main.home).

FS1.2.2. Characteristics of the dataset

After removing outliers, the dataset comprised 3,416 trees with DBH values ranging from 0.6 to 128 cm. The total number of species was 212, and 88% of the species had fewer than 20 individuals (Notes S1). Of the total number of trees, 60% of were from temperate and boreal regions and 40% from

the tropics; 30% from natural forests and 70% were planted. Of the trees with DBH >50 cm (n = 87) 57% of individuals were derived from temperate and boreal forests and the remainder from tropical forests. Most of these large trees (90%) were from natural forests and the remaining 10% were growing in plantations (Notes S1). The mean log(R:S) value of the dataset was -1.26058 (±0.6578964 sd), meaning that $\text{mean}(R\text{:}S) = e^{-1.26058 + 0.6578964^2}/2 = 0.3511 \pm 0.0669\ sd$.

FS1.2.3. Comments and caveats on the dataset

There were inevitable errors (mostly under-estimates) in the BGB dataset because the process of excavating and removing roots is generally incomplete, particularly for relatively large trees. In addition, data were derived from more than 400 studies (Notes S1), and there were methodological differences among studies that we could not control, such as whether the stump of the stem was included in the roots, methods for correcting measured fresh weights to dry weights (i.e. sub-sampling and drying temperature), minimum size of fine roots considered, and the depth or extent of excavation. There may be additional factors governing carbon allocation in plants that were not tested in this study due to a lack of data. These include soil nutrient availability, stand conditions such as mean stand DBH, and inter-tree competition.

FS1.3. References

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FIGURE S2: Boxplot of Root:Shoot (R:S) values for inter-group comparisons. The black lines of the middle of the boxes are the median values for each group, the boxes are the upper and lower 25 and 75 quantiles respectively, and the whiskers represent the extremes of the data, considered to be 1.5 times the interquartile range.

Figure S2a: including all the measured trees.

Figure S2b: including only trees with DBH from 10 to 50 cm and excluding plantations in panels a, b, c to account for differences in tree size and management differences.
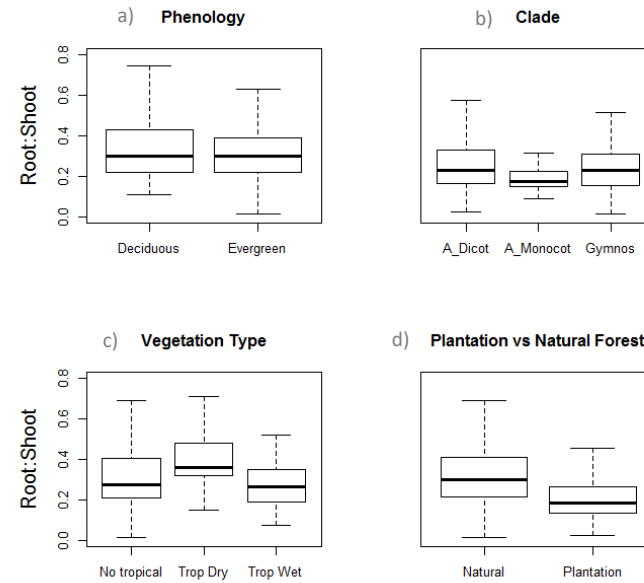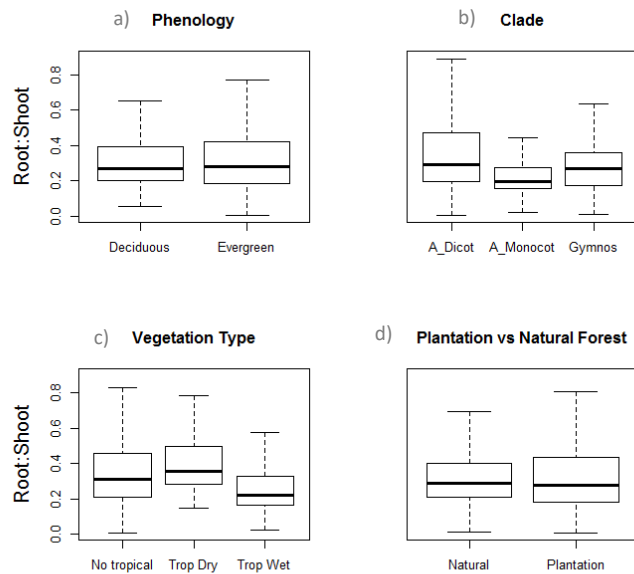
Methods S1: Extended description of methods, fitted models and model diagnosis

Contains:

MS.1.1 Extended description of methods

We fitted a series of models including different combinations of the available covariates (see Figure S1 for more details on the dataset and covariates and Section S.1.3 in this document for the list of fitted models). We added species as a random effect, to account for inter-specific differences. Therefore we fitted a series of General Linear Mixed Models (GLMM) with random intercepts:

$$\log(R\!:\!S) =\propto + \sum_{i=1}^{n} \beta_i\, F + \gamma_{sp} + \epsilon$$

where $\propto$ was the intercept, β_i were the coefficients of the explanatory variables (fixed effects, F), γ_{sp} was the random intercept that varied with species and ϵ was the error term, assumed to follow a normal distribution $N(0, \sigma^2)$. We used the *lme* function from the *nlme* package (Pinheiro et al. 2017) in the R statistical platform (R-Development-Core-Team 2008). We used restricted maximum likelihood (REML) to fit the models to our data. Although not all the species had the same number of individuals, techniques used in the *lme* function for parameter estimation nonetheless produce robust maximum likelihood estimation from unbalanced data (Pinheiro and Bates 2000).

The efficiency of the fitted model was checked and compared with nested models using the Akaike Information Criterion (AIC), which is given as an output by the *lme* function. The AIC gives information on the fit of alternative nested models given a dataset where lower AIC values are indicative of a more parsimonious model.

For model diagnosis, we checked the residuals for (i) absence of pattern, (ii) normality and (iii) whether they were centered (details in S1.3 in this document).

We calculated the conditional and marginal R^2_{GLMM} values for the final model (the best model in terms of AIC), using the method proposed by Nakagawa and Schielzeth (2013). The marginal R^2 (R^2_m)

gives the variance explained by the fixed factors and the conditional R^2 (R_c^2) the variance explained by the entire model, including both fixed and random effects (Vonesh et al. 1996).

$$R_m^2 = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_r^2 + \sigma_e^2 + \sigma_d^2} \quad \text{and} \quad R_c^2 = \frac{\sigma_f^2 + \sigma_r^2}{\sigma_f^2 + \sigma_r^2 + \sigma_e^2 + \sigma_d^2}$$

where σ_f^2 is the variance of the fixed effects components, σ_r^2 is the variance of the random effect (the species), σ_e^2 is the additive dispersion and σ_d^2 the is the distribution specific variance (Nakagawa and Schielzeth 2013).

In order to evaluate the contribution of each fixed effect to explained variance, we calculated the marginal R_m^2 values including sequentially the variance of each fixed component:

$$R_{m_i}^2 = \frac{\sigma_{f\,i}^2}{\sigma_f^2 + \sigma_r^2 + \sigma_e^2 + \sigma_d^2}$$

where $\sigma_{f\,i}^2$ is the variance of each fixed effect.

To obtain the values of the explained variance we used the *lmer* function from the "lme4" package. (Bates *et al.* 2015).

MS.1.2 Model diagnosis

Residuals versus fitted values: Residuals normality and outliers test:
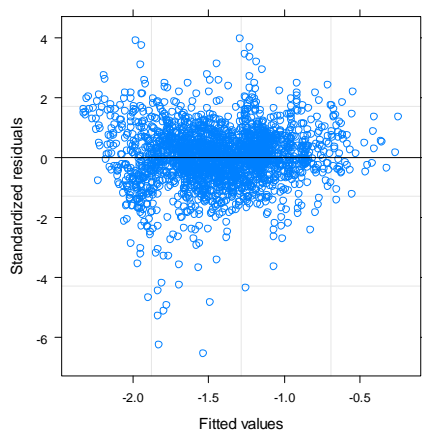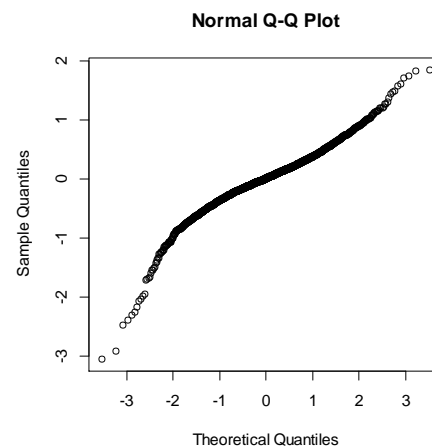
Values of residuals agains fitted are around zero (left). No particular problems arose in the Q-Q plot (right), despite random effect models are very sensitive to outliers (Faraway, 2005)

MS.1.3 List of fitted models

The included covariates where: Diameter at breast height (DBH) and its quadratic form (DBH^2), tree species, wood specific gravity (ρ), mean climate water deficit (MWD), phenology (Phen), clade, bioclimatic region (BCR), temperature (bio 1-11 following the worldClim classification, http://www.worldclim.org/bioclim), precipitation (bio 12-19 following the worldClim classification), whether the tree was growing in a natural forest or plantation (PlantYES).Additional details about the explanatory variables and methods are in the main document and in Methods S1. The selected model is highlighted in green.

Model	Random Variable	Fixed Variable(s)	Significant at 0.95	AIC	BIC	logLik
1	species	--		5244.1	5262.51	-2619.1
2	species	DBH	DBH	3540.15	3563.18	-1766.1
3	species	ρ	ρ	5090.85	5115.23	-2541.4
4	species	clade	--	5249.71	5292.64	-2617.9
5	species	DBH+DBH^2	DBH, DBH^2	3498.34	3527.13	-1744.2
6	species	$\rho + \rho^2$	--	5090.21	5120.69	-2540.1
7	species	Phen	--	5221.22	5307.06	-2596.6
8	species	BCR	BCR	5224.14	5254.81	-2607.1
9	species	PlantYES	PlantYES	5250.55	5275.08	-2621.3
10	species	bio1	bio1	5252.57	5277.11	-2622.3
11	species	bio2	bio2	5169.58	5194.12	-2580.8
12	species	bio3	--	5256.7	5281.24	-2624.4
13	species	bio4	--	5267	5291.54	-2629.5
14	species	bio5	bio5	5216.15	5240.69	-2604.1
15	species	bio6	--	5259.95	5284.48	-2626
16	species	bio7	bio7	5249.14	5273.68	-2620.6
17	species	bio8	bio8	5246.98	5271.52	-2619.5
18	species	bio9	bio9	5228.69	5253.23	-2610.3
19	species	bio10	bio10	5243.67	5268.21	-2617.8
20	species	bio11	--	5257.07	5281.61	-2624.5
21	species	bio12	bio12	5223.01	5247.55	-2607.5
22	species	bio13	bio13	5212.48	5237.01	-2602.2
23	species	bio14	bio14	5215.55	5240.09	-2603.8
24	species	bio15	--	5258.38	5282.92	-2625.2
25	species	bio16	bio16	5216.93	5241.47	-2604.5
26	species	bio17	bio17	5221.91	5246.45	-2607
27	species	bio18	bio18	5237.75	5262.29	-2614.9
28	species	bio19	bio19	5210.96	5235.5	-2601.5
29	species	MWD	MWD	5111.96	5136.49	-2552
30	species	DBH+ ρ	DBH	3395.31	3423.82	-1692.7
31	species	DBH+ clade	DBH	3531.55	3577.58	-1757.8
32	species	DBH+ $\rho + \rho^2$	DBH	3395.41	3429.62	-1691.7
33	species	DBH+ BCR	DBH	3470.75	3557.04	-1720.4
34	species	DBH+ Phen	DBH, clade	3493.96	3528.5	-1741
35	species	DBH+ PlantYES	DBH, PlantYES	3534.15	3562.94	-1762.1
36	species	DBH+bio1	DBH	5252.57	5277.11	-2622.3
37	species	DBH+bio2	DBH,bio2	5169.58	5194.12	-2580.8
48	species	DBH+bio5	DBH,bio5	5216.15	5240.69	-2604.1
49	species	DBH+bio7	DBH,bio7	5249.14	5273.68	-2620.6
40	species	DBH+bio8	DBH,bio8	5246.98	5271.52	-2619.5
41	species	DBH+bio9	DBH,bio9	5228.69	5253.23	-2610.3
42	species	DBH+bio10	DBH,bio10	5243.67	5268.21	-2617.8
43	species	DBH+bio12	DBH, bio12	5223.01	5247.55	-2607.5
44	species	DBH+bio13	DBH,bio13	5212.48	5237.01	-2602.2
45	species	DBH+bio14	DBH,bio14	5215.55	5240.09	-2603.8
46	species	DBH+bio16	DBH,bio16	5216.93	5241.47	-2604.5
47	species	DBH+bio17	DBH,bio17	5221.91	5246.45	-2607
48	species	DBH+bio18	DBH,bio18	5237.75	5262.29	-2614.9
49	species	DBH+bio19	DBH,bio19	5210.96	5235.5	-2601.5
50	species	DBH+MWD	DBH,MWD	5111.96	5136.49	-2552

Model	Random Variable	Fixed Variable(s)	Significant at 0.95	AIC	BIC	logLik
51	species	DBH+ PlantYES+bio2	DBH, PlantYES, bio2	3467.95	3502.49	-1728
52	species	DBH+ PlantYES+bio13	DBH, PlantYES, bio13	3502.81	3537.35	-1745.4
53	species	DBH+ PlantYES+MWD	DBH, PlantYES, MWD	3413.92	3448.46	-1701
54	species	DBH+ PlantYES+bio2+bio13+MWD	DBH, PlantYES, bio2, MWD	3436.18	3482.23	-1710.1
55	species	DBH+ PlantYES+bio2+bio14+MWD	DBH, PlantYES, bio2, MWD	3435.15	3481.2	-1709.6
56	species	DBH+ PlantYES+bio2+bio16+MWD	DBH, PlantYES, bio2, MWD	3438.28	3484.32	-1711.1
57	species	DBH+ PlantYES+bio2+bio17+MWD	DBH, PlantYES, bio2, MWD	3436.92	3482.97	-1710.5
58	species	DBH+ PlantYES+bio2+bio18+MWD	DBH, PlantYES, bio2, bio18, MWD	3427.67	3473.71	-1705.8
59	species	DBH+ PlantYES+bio2+bio19+MWD	DBH, PlantYES, bio2, bio19, MWD	3427.96	3474.01	-1706
60	species	DBH+ DBH^2+PlantYES+bio2+MWD +DBH:bio2	DBH, DBH^2, bio2, DBH:bio2	3400.52	3452.31	-1691.3
61	species	DBH+ DBH^2+PlantYES+bio2+MWD DBH:MWD	DBH, DBH^2,MWD, DBH:MWD	3407.57	3459.37	-1694.8
62	species	DBH+ DBH^2+PlantYES+bio2+MWD DBH: PlantYES	DBH, PlantYES	3400.89	3452.69	-1691.4
63	species	DBH+ PlantYES+bio2+MWD	DBH, PlantYES, bio2, MWD	3420.46	3460.75	-1703.2
64	species	DBH+ DBH^2+PlantYES+bio2+MWD	DBH, DBH^2,PlantYES, bio2,MWD	3388.46	3434.51	-1686.2
65	species	DBH+ DBH^2+PlantYES+bio18+MWD	DBH, DBH^2,PlantYES,bio18,MWD	3390.07	3436.11	-1687
66	species	DBH+DBH^2+PlantYES+bio2+bio18+MWD	DBH, DBH^2,PlantYES, Bio2+bio18,MWD	3398.08	3449.88	-1690
67	species	DBH+ PlantYES+bio2+bio18+MWD	DBH,PlantYES,T,P,MWD	3427.67	3473.71	-1705.8
68	species	DBH+ DBH^2+PlantYES+MWD	DBH+ DBH^2+PlantYES+MWD	3382.41	3422.7	-1684.2
69	species	DBH+ DBH^2+PlantYES+bio2+bio12+MWD	DBH, DBH^2,PlantYES, bio2,MWD	3408.99	3460.79	-1695.5
70	species	DBH+ DBH^2+PlantYES+bio2+bio13+MWD	DBH, DBH^2,PlantYES, bio2,MWD	3402.94	3454.74	-1692.5
71	species	DBH+ DBH^2+PlantYES+bio2+bio14+MWD	DBH, DBH^2,PlantYES, bio2,MWD	3403.3	3455.1	-1692.6
72	species	DBH+ DBH^2+PlantYES+bio2+bio16+MWD	DBH, DBH^2,PlantYES, bio2,MWD	3405.16	3456.96	-1693.6
73	species	DBH+ DBH^2+PlantYES+bio2+bio17+MWD	DBH, DBH^2,PlantYES, bio2,MWD	3405.73	3457.52	-1693.9
74	species	DBH+ DBH^2+PlantYES+bio2+bio19+MWD	DBH, DBH^2,PlantYES, bio2, bio19,MWD	3391.25	3443.05	-1686.6
75	species	DBH+ PlantYES+bio2+MWD	DBH, PlantYES, bio2, MWD	3420.46	3460.75	-1703.2
76	species	DBH+ DBH^2+PlantYES+bio2+MWD	DBH, DBH^2,PlantYES, bio2,MWD	3388.46	3434.51	-1686.2

MS.1.4 References

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Notes S1 R code used in the analyses.

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Date: 25 September 2017

Any concern/problem/bug, please email: aliciaedo@gmail.com

```r
#################################
#CONTENTS
#################################
# 1- Data reading and preparation
# 2- MODELS FITTING
# 3- MODEL DIAGNOSIS
# 4- VARIANCE EXPLAINED BY THE MODEL
# 5- Figures

library(nlme)
library(stats)
library(ggplot2)
library(gridExtra)
library(lme4)




####################################
# 1- data reading and preparation
####################################


#read data
rsdata<-read.table("RS_DATABASE.txt",h=T)
#remove unnecesary columns from the big original dataset
rsdata<-rsdata[,-4]
rsdata<-rsdata[,-6]
rsdata<-rsdata[,-7]
rsdata<-rsdata[,-7]
rsdata<-rsdata[,-10]
rsdata<-rsdata[,-14]
rsdata<-rsdata[,-15]
rsdata<-rsdata[,-15]
rsdata<-rsdata[,-15]
rsdata<-rsdata[,-17]
rsdata<-rsdata[,-17]
rsdata<-rsdata[,-17]
rsdata<-rsdata[,-19]
```

```r
colnames(rsdata)<-c("TreeID","Species","Family","H","DBH","AGB","BGB","RS","wd","v
egtyp","plantation","phenology","phylogen","dataset","latitude","longitude","RECVT
","RVT","bio1","bio2","bio3","bio4","bio5","bio6","bio7","bio8","bio9","bio10","bi
o11","bio12","bio13","bio14","bio15","bio16","bio17","bio18","bio19","CWD")


#remove values with RS=0 (from BGB=0)
rsdata<-subset(rsdata,rsdata$RS>0)
dim(rsdata)

#dataset
rsdat<-rsdata
#remove outliers
ourlier<-mean(rsdat$RS) + (4* sd(rsdat$RS))
rsdat<-subset(rsdat,rsdat$RS<ourlier)
dim(rsdat)

#target variable
rsdat$RES<-log(rsdat$RS)



###############################
#2 MODELS FITTING
###############################

#using species as a random effect
m1<-lme(RES~1,data=rsdat,random=~1|Species,na.action = na.omit)
#2.1 INDIVIDUAL FATORS
m2<-lme(RES~DBH,data=rsdat,random=~1|Species,na.action = na.omit)
m3<-lme(RES~wd,data=rsdat,random=~1|Species,na.action = na.omit)
m4<-lme(RES~phylogen,data=rsdat,random=~1|Species,na.action = na.omit)
rsdat$D2<-(rsdat$DBH)^2
rsdat$wd2<-(rsdat$wd)^2
m5<-lme(RES~DBH+D2,data=rsdat,random=~1|Species,na.action = na.omit)
m6<-lme(RES~wd+wd2,data=rsdat,random=~1|Species,na.action = na.omit)
#2.2 STAND TYPE
m7<-lme(RES~vegtyp,data=rsdat,random=~1|Species,na.action = na.omit)
m8<-lme(RES~RECVT,data=rsdat,random=~1|Species,na.action = na.omit)
m9<-lme(RES~plantation,data=rsdat,random=~1|Species,na.action = na.omit)
#2.3 CLIMATE FATORS
m10<-lme(RES~bio1,data=rsdat,random=~1|Species,na.action = na.omit)
m11<-lme(RES~bio2,data=rsdat,random=~1|Species,na.action = na.omit)
m12<-lme(RES~bio3,data=rsdat,random=~1|Species,na.action = na.omit)
m13<-lme(RES~bio4,data=rsdat,random=~1|Species,na.action = na.omit)
m14<-lme(RES~bio5,data=rsdat,random=~1|Species,na.action = na.omit)
m15<-lme(RES~bio6,data=rsdat,random=~1|Species,na.action = na.omit)
m16<-lme(RES~bio7,data=rsdat,random=~1|Species,na.action = na.omit)
m17<-lme(RES~bio8,data=rsdat,random=~1|Species,na.action = na.omit)
m18<-lme(RES~bio9,data=rsdat,random=~1|Species,na.action = na.omit)
m19<-lme(RES~bio10,data=rsdat,random=~1|Species,na.action = na.omit)
m20<-lme(RES~bio11,data=rsdat,random=~1|Species,na.action = na.omit)
m21<-lme(RES~bio12,data=rsdat,random=~1|Species,na.action = na.omit)
m22<-lme(RES~bio13,data=rsdat,random=~1|Species,na.action = na.omit)
m23<-lme(RES~bio14,data=rsdat,random=~1|Species,na.action = na.omit)
m24<-lme(RES~bio15,data=rsdat,random=~1|Species,na.action = na.omit)
m25<-lme(RES~bio16,data=rsdat,random=~1|Species,na.action = na.omit)
m26<-lme(RES~bio17,data=rsdat,random=~1|Species,na.action = na.omit)
m27<-lme(RES~bio18,data=rsdat,random=~1|Species,na.action = na.omit)
m28<-lme(RES~bio19,data=rsdat,random=~1|Species,na.action = na.omit)
```

```r
m29<-lme(RES~CWD,data=rsdat,random=~1|Species,na.action = na.omit)
#2.4 DBH + others
m30<-lme(RES~DBH+wd,data=rsdat,random=~1|Species,na.action = na.omit)
m31<-lme(RES~DBH+phylogen,data=rsdat,random=~1|Species,na.action = na.omit)
m32<-lme(RES~DBH+wd+wd2,data=rsdat,random=~1|Species,na.action = na.omit)
m33<-lme(RES~DBH+vegtyp,data=rsdat,random=~1|Species,na.action = na.omit)
m34<-lme(RES~DBH+RECVT,data=rsdat,random=~1|Species,na.action = na.omit)
m35<-lme(RES~DBH+plantation,data=rsdat,random=~1|Species,na.action = na.omit)
m36<-lme(RES~DBH+bio1,data=rsdat,random=~1|Species,na.action = na.omit)
m37<-lme(RES~DBH+bio2,data=rsdat,random=~1|Species,na.action = na.omit)
m38<-lme(RES~DBH+bio5,data=rsdat,random=~1|Species,na.action = na.omit)
m39<-lme(RES~DBH+bio7,data=rsdat,random=~1|Species,na.action = na.omit)
m40<-lme(RES~DBH+bio8,data=rsdat,random=~1|Species,na.action = na.omit)
m41<-lme(RES~DBH+bio9,data=rsdat,random=~1|Species,na.action = na.omit)
m42<-lme(RES~DBH+bio10,data=rsdat,random=~1|Species,na.action = na.omit)
m43<-lme(RES~DBH+bio12,data=rsdat,random=~1|Species,na.action = na.omit)
m44<-lme(RES~DBH+bio13,data=rsdat,random=~1|Species,na.action = na.omit)
m45<-lme(RES~DBH+bio14,data=rsdat,random=~1|Species,na.action = na.omit)
m46<-lme(RES~DBH+bio16,data=rsdat,random=~1|Species,na.action = na.omit)
m47<-lme(RES~DBH+bio17,data=rsdat,random=~1|Species,na.action = na.omit)
m48<-lme(RES~DBH+bio18,data=rsdat,random=~1|Species,na.action = na.omit)
m49<-lme(RES~DBH+bio19,data=rsdat,random=~1|Species,na.action = na.omit)
m50<-lme(RES~DBH+CWD,data=rsdat,random=~1|Species,na.action = na.omit)
#2.5 DBH,plantaiton + climate
m51<-lme(RES~DBH+plantation+bio2,data=rsdat,random=~1|Species,na.action = na.omit)
m52<-lme(RES~DBH+plantation+bio13,data=rsdat,random=~1|Species,na.action = na.omit
)
m53<-lme(RES~DBH+plantation+CWD,data=rsdat,random=~1|Species,na.action = na.omit)
#2.6 ALL FACTORS
m54<-lme(RES~DBH+plantation+bio2+bio13+CWD,data=rsdat,random=~1|Species,na.action
= na.omit)
m55<-lme(RES~DBH+plantation+bio2+bio14+CWD,data=rsdat,random=~1|Species,na.action
= na.omit)
m56<-lme(RES~DBH+plantation+bio2+bio16+CWD,data=rsdat,random=~1|Species,na.action
= na.omit)
m57<-lme(RES~DBH+plantation+bio2+bio17+CWD,data=rsdat,random=~1|Species,na.action
= na.omit)
m58<-lme(RES~DBH+plantation+bio2+bio18+CWD,data=rsdat,random=~1|Species,na.action
= na.omit)
m59<-lme(RES~DBH+plantation+bio2+bio19+CWD,data=rsdat,random=~1|Species,na.action
= na.omit)
#2.7 interactions
m60<-lme(RES~DBH+D2+plantation+bio2+CWD+DBH:bio2,data=rsdat,random=~1|Species,na.a
ction = na.omit)
m61<-lme(RES~DBH+D2+plantation+bio2+CWD+DBH:CWD,data=rsdat,random=~1|Species,na.ac
tion = na.omit)
m62<-lme(RES~DBH+D2+plantation+bio2+CWD+DBH:plantation,data=rsdat,random=~1|Specie
s,na.action = na.omit)
#2.8 defining final model
m63<-lme(RES~DBH+plantation+bio2+CWD,data=rsdat,random=~1|Species,na.action = na.o
mit)
m64<-lme(RES~DBH+D2+plantation+bio2+CWD,data=rsdat,random=~1|Species,na.action = n
a.omit)
m65<-lme(RES~DBH+D2+plantation+bio18+CWD,data=rsdat,random=~1|Species,na.action =
na.omit)
m66<-lme(RES~DBH+D2+plantation+bio2+bio18+CWD,data=rsdat,random=~1|Species,na.acti
on = na.omit)
m67<-lme(RES~DBH+plantation+bio2+bio18+CWD,data=rsdat,random=~1|Species,na.action
= na.omit)
```

```
m68<-lme(RES~DBH+D2+plantation+CWD,data=rsdat,random=~1|Species,na.action = na.omi
t) # BEST MODEL - SELECTED MODEL
m69<-lme(RES~DBH+D2+plantation+CWD+bio2+bio12,data=rsdat,random=~1|Species,na.acti
on = na.omit)
m70<-lme(RES~DBH+D2+plantation+CWD+bio2+bio13,data=rsdat,random=~1|Species,na.acti
on = na.omit)
m71<-lme(RES~DBH+D2+plantation+CWD+bio2+bio14,data=rsdat,random=~1|Species,na.acti
on = na.omit)
m72<-lme(RES~DBH+D2+plantation+CWD+bio2+bio16,data=rsdat,random=~1|Species,na.acti
on = na.omit)
m73<-lme(RES~DBH+D2+plantation+CWD+bio2+bio17,data=rsdat,random=~1|Species,na.acti
on = na.omit)
m74<-lme(RES~DBH+D2+plantation+CWD+bio2+bio19,data=rsdat,random=~1|Species,na.acti
on = na.omit)
m75<-lme(RES~DBH+D2+plantation+CWD+DBH:CWD,data=rsdat,random=~1|Species,na.action
= na.omit)
m76<-lme(RES~DBH+D2+plantation+bio2+bio19+DBH:CWD,data=rsdat,random=~1|Species,na.
action = na.omit)
m77<-lme(RES~DBH+D2+plantation+bio2:DBH+bio19:DBH,data=rsdat,random=~1|Species,na.
action = na.omit)
m78<-lme(RES~DBH+D2+plantation+bio2:DBH+bio19,data=rsdat,random=~1|Species,na.acti
on = na.omit)
m79<-lme(RES~DBH+D2+plantation+CWD+D2:CWD,data=rsdat,random=~1|Species,na.action =
na.omit)



######################################
# 3- MODEL DIAGNOSIS - only showed here for the selected model, m68
####################################################################

#3.1 Residuals testing

#residuals vs fitted values
plot(m68)

#normality and outliers
qqnorm(resid(m68))



######################################
# 4- VARIANCE EXPLAINED BY THE MODEL
######################################


##VARIANCE EXPLAINED BY EACH FIX EFFECT
lengths <- function (x, use.names = TRUE) vapply(x, length, 1L, USE.NAMES = use.na
mes)   #needs

#full model - best model
fullm<-lmer(RES~DBH+D2+CWD+plantation+(1|Species),data=rsdat,na.action = na.omit)


#R2 FULL MODEL
#variance random component
VarCorr(fullm)$Species[1]

#variance of each fixed
fixed_full<-fixef(fullm)[2]*getME(fullm,"X")[,2]+fixef(fullm)[3]*getME(fullm,"X")[
```

```
,3]+fixef(fullm)[4]*getME(fullm,"X")[,4] +fixef(fullm)[5]*getME(fullm,"X")[,5]
#variance of the fixed  effect
varF_null<-var(fixed_full)

# R2GLMM(m) - marginal R2GLMM    #following Nakagawa & Schielzeth 2013
R2mfull<-varF_null/(varF_null+VarCorr(fullm)$Species[1]+attr(VarCorr(fullm),"sc")^
2)

# R2GLMM(c) - conditional R2GLMM for full model
R2cfull<-(varF_null+VarCorr(fullm)$Species[1])/(varF_null+VarCorr(fullm)$Species[1
]+attr(VarCorr(fullm),"sc")^2)



#variance each factor
#######################

#variance fixed exCluding
#dbh
varF_DBH<-var(fixef(fullm)[2]*getME(fullm,"X")[,2])
R2mDBH<-varF_DBH/(varF_null+VarCorr(fullm)$Species[1]+attr(VarCorr(fullm),"sc")^2)
varF_D2<-var(fixef(fullm)[3]*getME(fullm,"X")[,3])
R2mD2<-varF_D2/(varF_null+VarCorr(fullm)$Species[1]+attr(VarCorr(fullm),"sc")^2)
#cwd
varF_CWD<-var(fixef(fullm)[4]*getME(fullm,"X")[,4])
R2mCWD<-varF_CWD/(varF_null+VarCorr(fullm)$Species[1]+attr(VarCorr(fullm),"sc")^2)
#plant
varF_plantY<-var(fixef(fullm)[5]*getME(fullm,"X")[,5])
R2mplantY<-varF_plantY/(varF_null+VarCorr(fullm)$Species[1]+attr(VarCorr(fullm),"s
c")^2)

#plor result
R2val<-c(R2mDBH,R2mD2,R2mCWD,varF_plantY)
names(R2val)<-c("DBH", "D2", "CWD", "plantY")

#percentage variance
PVMOD<-sum(R2val) # 0.5146425

R2vp<-c(R2mDBH/PVMOD,R2mD2/PVMOD,R2mCWD/PVMOD,R2mplantY/PVMOD)
names(R2vp)<-c("DBH", "D2", "CWD", "PlantY")

TOTALVAR<-c(R2mDBH*10,R2mD2*10,R2mCWD*10,R2mplantY*10,(VarCorr(fullm)$Species[1])*
10)
names(TOTALVAR)<-c("DBH", "D2", "CWD", "PlantY","Species")




#############################
#5- FIGURES
#############################

#FIGURE 1
plotdbh<-ggplot(rsdat, aes(DBH,RS)) + geom_point(col="grey",pch = 16) + geom_smoot
h(col=("darkgreen"),fill="green3",size=1)+ xlab("\nDBH (cm)")+ ylab("Root:Shoot\n"
)+  theme_bw() +theme(axis.line = element_line(colour = "black"),panel.grid.major
= element_blank(),panel.grid.minor = element_blank(), panel.background = element_b
lank(),axis.text = element_text(size=15),axis.title = element_text(size=20))
plot(plotdbh)
```

```
#FIGURE 2
rsdat$plantation<-as.character(rsdat$plantation)

#different DBH classes
rsdat$DBHCLASS=NA
rsdat$DBHCLASS<-as.character(rsdat$DBHCLASS)

rsdat<-subset(rsdat,rsdat$DBH!="NA", drop=T)
for (a in 1:dim(rsdat)[1]){if (rsdat$DBH[a]<300) rsdat$DBHCLASS[a]<-"over_50"}
for (b in 1:dim(rsdat)[1]){if (rsdat$DBH[b]<50) rsdat$DBHCLASS[b]<-"under_50"}
for (c in 1:dim(rsdat)[1]){if (rsdat$DBH[c]<25) rsdat$DBHCLASS[c]<-"under_25"}
for (d in 1:dim(rsdat)[1]){if (rsdat$DBH[d]<10) rsdat$DBHCLASS[d]<-"under_10"}
for (e in 1:dim(rsdat)[1]){if (rsdat$DBH[e]<5) rsdat$DBHCLASS[e]<-"under_5"}
rsclass<-subset(rsdat, rsdat$DBH!="NA",drop = T)
rsclass<-subset(rsclass, rsdat$DBHCLASS!="NA",drop = T)


fig2<-ggplot(rsclass,aes(CWD,RES))+  geom_point(colour="grey",pch = 16)+geom_smoot
h(method="lm",col=("darkgreen"),fill="green3",size=1) +  xlab("\nMWD")+ ylab("ln(R
oot:Shoot)\n")+  theme_bw() +theme(axis.line = element_line(colour = "black"),pane
l.grid.major = element_blank(),panel.grid.minor = element_blank(), panel.backgroun
d = element_blank(),axis.text = element_text(size=15),axis.title = element_text(si
ze=20))
plot(fig2)




fig2S1<-ggplot(rsclass, aes(CWD,RES, colour=DBHCLASS))+  geom_point()+geom_smooth(
method="lm",se=F) +  xlab("\nMWD")+ ylab("Root:Shoot\n")+  theme_bw() +theme(axis.
line = element_line(colour = "black"),panel.grid.major = element_blank(),panel.gri
d.minor = element_blank(), panel.background = element_blank(),axis.text = element_
text(size=15),axis.title = element_text(size=20))
plot(fig2S1)




fig2S2<-ggplot(rsclass, aes(CWD,RES,colour=plantation))+  geom_point()+geom_smooth
(method="lm",se=F) +  xlab("\nMWD")+ ylab("Root:Shoot\n")+  theme_bw() +theme(axis
.line = element_line(colour = "black"),panel.grid.major = element_blank(),panel.gr
id.minor = element_blank(), panel.background = element_blank(),axis.text = element
_text(size=15),axis.title = element_text(size=20))
plot(fig2S2)
```