



# Overlooking what is underground: Root:shoot ratios and coarse root allometric equations for tropical forests



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## ARTICLE INFO

### Article history:

Received 16 September 2016

Received in revised form 29 October 2016

Accepted 5 November 2016

### Keywords:

Allometry

Belowground

Coarse roots

Rooting depth

Tropical forest

## ABSTRACT

Coarse roots are a major belowground carbon (C) pool, yet we know little about the factors controlling coarse root distributions in tropical forests, the biome where belowground biomass stocks are largest. We conducted a literature survey to identify potential environmental controls on the root:shoot biomass ratio (R:S) across tropical forests worldwide. Moreover, to aid efforts to extrapolate aboveground biomass measurements to belowground C stocks, we also compiled a list of allometric equations for coarse root biomass.

Across our large and geographically comprehensive dataset, we found that R:S is negatively correlated with mean annual precipitation, and positively linked with stand age. However, information on root biomass allocation is still scarce in comparison with the wealth of available data on aboveground plant biomass in tropical forests, and more data will be necessary to understand the drivers of belowground biomass allocation. Moreover, the available root allometric equations show tremendous variation in mathematical form, which is likely related to the many different methods that have been used to quantify root biomass and its distribution with depth. A better understanding of belowground dynamics in tropical forests will require systematic surveys of root biomass along gradients of soil type, climate, and stand age, along with a streamlined protocol for developing root allometric equations.

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## 1. Introduction

The influence of roots on terrestrial biogeochemical cycles is increasingly appreciated (Warren et al., 2015), and evidence suggests that root carbon (C) stocks are larger than previously thought (Robinson, 2007). Roots are the sites of interaction among plants, symbiotic organisms such as mycorrhizal fungi, and free-living rhizosphere microorganisms (Bardgett et al., 2014). Due to the close physical proximity of roots and soil minerals, root-derived C appears to be preferentially stabilized in comparison with shoot-derived C (Rasse et al., 2005), and up to 70% of soil organic matter may be derived from roots and their associated fungi in some ecosystems (Clemmensen et al., 2013). Additionally, deep roots play a direct role in mineral weathering and soil formation (Maeght et al., 2013). Finally, because coarse roots turn over slowly (Clark et al., 2001) and can comprise well over 80% of total root biomass (Butnor et al., 2003), coarse roots themselves constitute an important belowground C pool (Moble et al., 2013).

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Because roots mediate plant nutrient uptake and growth, they also have significant impacts on aboveground C cycling. Interspecific variation in root biomass or root:shoot ratios mediates competitive interactions among species (Casper and Jackson, 1997), thereby structuring plant community composition. Roots also play an important ecohydrological role: deeply rooted species cause movement of water into shallower soil layers in a process known as hydraulic redistribution (Neumann and Cardon, 2012). In fact, hydraulic redistribution can enhance plant productivity at the ecosystem scale during dry seasons or droughts.

Although moderately strong associations between root stocks, plant community structure, and climate emerge at global scales (Vogt et al., 1996; Cairns et al., 1997; Schenk and Jackson, 2002a; Mokany et al., 2006), controls on root biomass at regional scales are less well resolved. In particular, little is known about root biomass, root:shoot ratios, and rooting depth in tropical ecosystems (Schenk and Jackson, 2002a; Mokany et al., 2006), despite the fact that tropical evergreen forests have the highest belowground biomass stocks in comparison with other biomes (Jackson et al., 1996). Yet there are a number of reasons to expect high heterogeneity in root biomass distributions among tropical forests. First, although all lowland tropical forests tend to have high mean annual temper-

ature (MAT), there is enormous variation in the quantity and timing of mean annual precipitation (MAP), ranging from dry tropical forests with eight or nine-month dry seasons and less than 1000 mm of rainfall annually, to wet, aseasonal tropical rainforests with MAP over 5000 mm. Variation in rainfall regime is likely to have large consequences for plant biomass allocation and rooting depth (Schenk and Jackson, 2002b). Next, tropical forests are characterized by extraordinary plant species diversity, which is manifested in the high heterogeneity in plant chemical composition and architecture within and among forests (Townsend et al., 2008; Hallé et al., 1978). It is reasonable to hypothesize that the complexity of the forest canopy may be mirrored by strong inter-specific variation in root architecture belowground.

Changes in temperature, rainfall, or nutrient deposition are likely to affect plant biomass allocation and root stocks within tropical forests. However, uncertainties associated with representing roots in ecosystem models constrain our ability to predict forest responses to climate change (Warren et al., 2015; Smithwick et al., 2014). Moreover, there are few empirical data against which to test model predictions of coarse root C pools. Aboveground C stocks can be estimated from forest inventory data with allometric equations (Chave et al., 2005), and these estimates can be validated using remote sensing data (Saatchi et al., 2011). In this way, measurements made at the scale of individual trees can be linked with ecosystem-level C stocks. However, it is much more difficult to develop and test allometric models of belowground biomass, as this requires destructive harvests of root biomass – a challenging and time-consuming endeavor.

In this review, we synthesized information on plant biomass allocation and root allometric equations across tropical forest biomes. Our aims were threefold: first, we compiled a list of allometric equations used for predicting coarse or total root biomass from simple, tree-level measurements (e.g. diameter at breast height, or DBH). Second, we leveraged the associated allometric datasets in order to examine changes in root:shoot biomass ratios (R:S) across gradients of climate and stand age. Finally, we analyzed discrepancies among different methodologies for quantifying root biomass, pointing out areas especially in need of further study. Our synthesis provides an important benchmark for understanding regional-scale drivers of coarse root biomass in tropical forests, and is a useful guide for both modeling efforts and data collection.

## 2. Methods

### 2.1. Literature search and data extraction

Because data on root allometry in tropical ecosystems are relatively sparse, we extensively searched four separate databases. First, we performed two searches on Web of Science using the terms “belowground AND allometry” and “belowground AND allometric.” We also explored the U.S. Forest Service’s online database TreeSearch and the SciELO database using the terms “belowground,” “allometry,” “allometric” and “root” (these search engines do not allow Boolean operators). We also extracted all data from the Biomass And Allometry Database (BAAD, Falster et al., 2015) that matched our search criteria.

For each database, search results were reviewed to identify studies that matched our search criteria. We retained studies that reported root biomass data collected in forested ecosystems in the tropics (between 25°N and 25°S) on tree individuals >1 year. All included studies directly quantified total (coarse, or >2 mm diameter, and fine) or coarse root biomass via excavation of individual trees or a known volume of soil. Although the inclusion of fine roots in some studies could potentially introduce additional unexplained variance into the dataset, there was no difference in R:S

between studies that quantified total vs. coarse root biomass only (means of  $0.360 \pm 0.090$  vs.  $0.313 \pm 0.021$ , respectively), likely because fine roots make up only a small fraction of total root weight. We did not include studies that reported fine (<2 mm) root biomass only, or studies performed in a glasshouse or shadehouse.

For each study, we recorded latitude and longitude of the study site, MAP, MAT, dry season length, stand age, the species under study (if applicable), and information about how root measurements were made. Some studies reported precise stand ages in years, while others only reported descriptive categories (e.g., “mature forest.”) Therefore, we binned all sites into one of three stand age categories: young (<20 y), intermediate (between 20 and 40 y), and mature (>40 y). Stand age categories were determined based on the empirical relationship between aboveground biomass recovery and stand age described in Becknell et al. (2012). We also recorded allometric equations for predicting belowground biomass, which were parameterized using data from harvests of individual trees. In some studies, individuals of multiple abundant species were harvested to parameterize allometric equations; in this case, we recorded the species identity as “various.” We also calculated root:shoot biomass ratios (R:S) as the ratio between belowground (root) biomass and total aboveground biomass (leaves, branches, and stems).

### 2.2. Statistical analysis

We used multiple linear regression to examine relationships between R:S and MAT, MAP, and dry season length. A one-way ANOVA (using MAP as a covariate; see Section 3) was used to test the relationship between stand age category and R:S, while a *t*-test was used to examine the dependence of R:S on forest type (plantation vs. unmanaged or natural forest). The dependent variable was log-transformed to meet conditions of normality. We did not examine relationships between root biomass and climate, as studies reported very different units (e.g., kg root biomass tree<sup>-1</sup>, Mg biomass ha<sup>-1</sup>, Mg biomass kg<sup>-1</sup> soil) and it was not possible to convert reported values to a common metric without unreported information such as soil bulk density. All analyses were performed in R Version 3.2.1.

## 3. Results

Our final database contained 195 observations of R:S ratios from 19 countries in Central and South America, Africa, and Asia (Fig. 1, Supplementary Information). Of these observations, 132 were collected in native, unmanaged forests, whereas 63 were collected in plantations. The observations spanned a broad range of forest types and climatic conditions (Table 1), from very dry forests with less than 1000 mm of rainfall annually and marked seasonality, to wet, aseasonal rainforests with over 5000 mm of rainfall annually. Across the entire dataset, R:S ratios ranged from 0.07 (for a 16-year old *Hyeronima alchorneoides* plantation in wet forest) to 5.57 (for a *Jacaratia* spp. sapling in a seasonally dry forest), with a mean of 0.54.

There was a significant negative relationship between mean annual precipitation and the ratio of belowground to aboveground biomass (Table 2, Fig. 2a), although most of the variance was unexplained ( $R^2 = 0.114$ ). The relationship between R:S and MAP was robust even when the wettest sites were removed from the analysis ( $P < 0.001$ ,  $R^2 = 0.101$ ). Mean annual temperature and dry season length were not significant predictors of R:S. The ratio of belowground to aboveground biomass also varied significantly among forest age categories ( $F_{2,103} = 21.78$ ,  $P < 0.001$ ) and was two times greater in mature vs. young or intermediate-aged forests (Tukey’s HSD test,  $P < 0.003$ ; Fig. 2b). Root:shoot ratios were two

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