

Isometric biomass partitioning pattern in forest ecosystems: evidence from temporal observations during stand development

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Summary

1. Knowledge of biomass partitioning is essential for estimating spatial patterns and temporal dynamics of root biomass in terrestrial ecosystems. The isometric hypothesis predicts that above-ground biomass scales isometrically with belowground biomass across both individual plants and community types (i.e. the slope of the log–log relationship between above- and belowground biomass is not significantly different from 1.0), and that the isometric pattern is independent of variation in environmental conditions. However, current evidence primarily comes from observations over space. It is still unknown whether biomass partitioning patterns occurring over time are similar to those observed over space.

2. In this study, we explored biomass partitioning patterns in forest ecosystems over space and time by synthesizing biomass measurements made in 112 stands extracted from 16 age sequences around the world. We characterized biomass partitioning patterns in forest ecosystems using both root:shoot ratio and the relationship between above- and belowground biomass. Data across various individual studies were organized to reflect biomass partitioning patterns over space, while data within each individual study were used to illustrate biomass allocation patterns over time.

3. Our results showed that root:shoot ratio did not exhibit any significant trend with stand age over space. Similarly, root:shoot ratio remained relatively constant over time in 10 out of 16 age sequences.

4. Reduced major axis analysis indicated that the slope of the log–log relationship between above- and belowground biomass did not reveal a significant difference from 1.0 over space, supporting the isometric hypothesis. Likewise, the slope was not statistically different from 1.0 in 10 out of 16 age sequences, nor did it show any significant change with climatic factors and stand age. Thus, the isometric hypothesis also most probably holds true during forest stand development.

5. Synthesis. Our results demonstrate that biomass partitioning patterns occurring over time are consistent with those observed over space, suggesting that belowground biomass dynamics in forest ecosystems may be reliably estimated from aboveground biomass using biomass partitioning patterns generated over space.

Key-words: aboveground biomass, age sequence, belowground biomass, ecophysiology, isometric pattern, root:shoot ratio, space, time

Introduction

Biomass partitioning, commonly described by the root:shoot (R:S) ratio or the allometric function relating belowground biomass (M_B) and aboveground biomass (M_A), can be a critical indicator of plant physiological processes (Wilson 1988; Cannell & Dewar 1994; van Wijk *et al.* 2003; Mokany, Raison & Prokushkin 2006). It reflects the different investment of photosynthates in above- and belowground organs (Shipley &

Meziane 2002), and its variation is a response to differential selection for adaptations to different environmental conditions (Bazzaz & Grace 1997). For instance, growth-limiting conditions usually lead to greater biomass partitioning to those organs that are constrained (Reynolds & Thornley 1982; Luo, Field & Mooney 1994; Luo, Hui & Zhang 2006; Wang & Taub 2010). Biomass partitioning is also an important parameter for estimating M_B from the more easily measured M_A (Cairns *et al.* 1997; Mokany, Raison & Prokushkin 2006; Yang *et al.* 2010) and has been incorporated into terrestrial ecosystem modelling (Friedlingstein *et al.* 1999; Landsberg 2003).

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Therefore, quantitative assessments of biomass partitioning are essential for evaluating the responses of vegetation growth to ambient environmental conditions (Niklas 2005) and for understanding root biomass distributions in terrestrial ecosystems (Hui & Jackson 2005; King *et al.* 2007; Yang *et al.* 2009, 2010).

Biomass partitioning has been widely examined across various ecosystems (e.g. Jackson *et al.* 1996; Titlyanova *et al.* 1999; Hui & Jackson 2005; Mokany, Raison & Prokushkin 2006; Litton, Raich & Ryan 2007; Li, Luo & Lu 2008; Fan *et al.* 2009; Yang *et al.* 2009, 2010; Ma *et al.* 2010; Wang *et al.* 2010). More importantly, an isometric hypothesis has been developed to characterize the allometric relationship between M_A and M_B (Enquist & Niklas 2002; Cheng & Niklas 2007). This hypothesis predicts that M_A scales isometrically with M_B across both individual plants and community types (i.e. the slope of the log–log relationship between M_A and M_B is not significantly different from 1.0), and that the scaling slope does not vary with environmental factors (Enquist & Niklas 2002; Cheng & Niklas 2007). Specifically, the isometric model states that standing leaf biomass (M_L) scales as the 3/4 power of standing stem biomass (M_S), M_L scales as the 3/4 power of standing root biomass (M_R), and M_R scales isometrically with respect to M_S (Enquist & Niklas 2002; McCarthy & Enquist 2007). Considering this point, $M_L = \beta M_S^{3/4} = \beta_1 M_R^{3/4}$ and $M_S = (\beta_1/\beta)^{4/3} M_R$, where β_1 and β are allometric constants (i.e. the y -intercept of the log–log regression relationship) (Niklas 2005; Cheng & Niklas 2007). Given that M_A is the sum of leaf and stem biomass (i.e. $M_A = M_L + M_S$) and M_B is only comprised of roots (i.e. $M_R = M_B$), the relationship between M_A and M_B can be expressed as $M_A = \beta_1 M_B^{3/4} + (\beta_1/\beta)^{4/3} M_B$. If $(\beta_1/\beta)^{4/3} > \beta_1$, M_A can be expected to scale isometrically with respect to M_B (Niklas 2005; Cheng & Niklas 2007).

The isometric hypothesis has been validated across both individual plants (e.g. Enquist & Niklas 2002; Niklas 2005) and community types (e.g. Cheng & Niklas 2007; Yang *et al.* 2009, 2010); however, current evidence is primarily derived from observations over space, with little information available over time. The ecological patterns occurring over time may differ from those observed over space since geographic patterns usually reflect the contribution of vegetation types, while temporal patterns within site may be more complicated, incorporating interannual variation in climatic and other site-specific factors (Lauenroth & Sala 1992; Jobbágy, Sala & Paruelo 2002; Fisher, Frank & Legget 2010). Thus, it remains unknown whether the isometric pattern between M_A and M_B observed over space also exists over time and whether the scaling slope over time is insensitive to variation in environmental conditions.

In this study, we examined partitioning patterns between M_A and M_B across various forest ecosystems around the world by synthesizing biomass measurements made in 112 stands and described in 16 published studies which documented changes in M_A and M_B during stand development. More specifically, this study aimed at testing the following four hypotheses: (i) the R:S ratio exhibits similar trends with stand age over

space and time, (ii) M_A scales isometrically with M_B across various individual studies, (iii) an isometric pattern between M_A and M_B also exists during stand development and (iv) the slope of the log–log relationship between M_A and M_B over an age sequence is independent of environmental conditions.

Materials and methods

DATA SOURCES

We collected biomass measurements made in 112 stands from 16 published studies that quantified aboveground biomass (M_A) and belowground biomass (M_B) in forest ecosystems during stand development (see Appendix S1, Table S1 in Supporting Information). These papers were assembled from a range of literature sources according to the following three criteria: (i) both coarse and fine roots were included in M_B , (ii) stand age was quantitatively described and (iii) at least five age stages were involved. We were then able to statistically examine the relationship between M_A and stand age, between M_B and stand age, between root:shoot (R:S) ratio and stand age, and between M_A and M_B over an age sequence. The raw data were either extracted from published tables or obtained by digitizing graphs using the software Originpro 7.5 (OriginLab, Northampton, MA, USA). Our database consisted of geographic location (longitude and latitude), climatic information (mean annual temperature and mean annual precipitation), stand age, forest type and three target variables (M_A , M_B and R:S ratio). The age range exhibited large differences among various studies, varying from 1–5 to 9–316 years (see Table S1).

DATA ANALYSES

Data were processed by the following four steps. First, we examined changes of M_A , M_B and R:S ratio with respect to stand age across two levels: across site (a test of site and age effects) and within site (a test of age effect alone). As in other studies (e.g. Lauenroth & Sala 1992; Jobbágy, Sala & Paruelo 2002; Hui & Jackson 2005), the ‘*across site*’ analysis was performed to explore biomass partitioning patterns over space, while the ‘*within site*’ analysis was conducted to investigate biomass partitioning patterns over time. Specifically, the ‘*across site*’ analysis combined all observations at each age stage from each sequence to examine the relationships of M_A , M_B and R:S ratio with stand age across the 16 chronosequence studies. By contrast, the ‘*within site*’ analysis investigated the relationships of M_A , M_B and R:S ratio with stand age for each individual sequence.

Second, to examine whether M_A and M_B scale isometrically, we performed reduced major axis (RMA) regression (e.g. Enquist & Niklas 2002; Niklas 2005; Yang *et al.* 2009, 2010; Wang *et al.* 2010) to examine M_A – M_B relationships across various sites and within each site. The regression relationship of the form $\log y = a + b(\log x)$ was used to describe the allometric relationship between M_A and M_B , where x is M_B (Mg ha^{-1}), y is M_A (Mg ha^{-1}), a is the intercept, and b is the scaling slope (Enquist & Niklas 2002; Niklas 2005, 2006; Yang *et al.* 2009, 2010; Wang *et al.* 2010). The scaling slope and y -intercept of the allometric function were determined using the software package ‘Standardized Major Axis Tests and Routines’ (Falster, Warton & Wright 2003). If 95% confidence interval of the scaling slope covered 1.0, the relationship between M_A and M_B was considered to be isometric.

Third, to test whether the slope of the relationship between M_A and M_B over time is independent of environmental factors, we first estimated the scaling slope of the M_A – M_B relationship for each

individual sequence, and then investigated the relationship between the scaling slope and mean annual temperature (MAT), mean annual precipitation (MAP) and mean stand age over each sequence. A significant relationship between the scaling slope and environmental factors would indicate that biomass partitioning patterns were sensitive to variations in environmental conditions. Otherwise, we could deduce that environmental factors did not exert profound effects on above- and belowground biomass partitioning patterns.

Fourth, we conducted ordinary least squares (OLS) regression to explore the relationship between M_B and M_A across sites. Specifically, all biomass measurements made in 112 stands were used to establish the allometric function between M_B and M_A across 16 chronosequence studies. Like other studies (e.g. Cairns *et al.* 1997; Mokany, Raison & Prokushkin 2006; Yang *et al.* 2009, 2010), a power function was used to fit the relationship between M_B and M_A . To test whether M_B dynamics during stand development could be reliably estimated from M_A using the allometric function generated over space, the power function between M_B and M_A generated across sites was then used to predict M_B from M_A within site. All statistical analyses, with the exception of RMA regression, were conducted using the software package R (R Development Core Team 2007).

Results

Both M_A and M_B increased with stand age and then levelled off across sites (Fig. 1a,b). These changes could be well fitted by logarithmic functions of $M_A = 98.8 \log(\text{age}) - 93.1$ and $M_B = 23.5 \log(\text{age}) - 18.5$, respectively. The slopes of M_A vs. stand age and M_B vs. stand age were significantly larger than zero in most individual studies ($P < 0.05$) (Fig. 1c,d), showing that both M_A and M_B exhibited increasing trends dur-

ing stand development. However, R:S ratio did not show any significant trend with stand age across sites ($r^2 = 0.01$, $P = 0.35$) (Fig. 2a). Moreover, the trend was still not significant even if we excluded the three data points where stand age was over 150 years ($P > 0.05$). Likewise, no significant trend was observed for the R:S ratio dynamics in 10 out of 16 individual studies (Fig. 2b), indicating that the R:S ratio also most probably remained relatively constant during stand development. Nevertheless, the R:S ratio declined with stand age in five sequences while it increased in one sequence (see Fig. S1).

Reduced major axis (RMA) analysis indicated that M_A scaled isometrically with M_B over space (Fig. 3a). Specifically, the scaling slope of the relationship between M_A and M_B across sites was estimated at 1.01, with 95% confidence intervals of 0.94–1.09 (Fig. 3a), indicating that the scaling exponent was not significantly different from 1.0 over space. Likewise, the slope of the M_A – M_B relationship was not statistically different from 1.0 in 10 out of 16 individual studies ($P > 0.05$) (Fig. 3b), consistent with the isometric pattern observed over space (Fig. 3a). Of those studies inconsistent with the isometric pattern, the scaling slope was observed to be significantly larger than 1.0 in five sequences while it was lower than 1.0 in one sequence (Fig. 3b). However, the scaling slope did not exhibit any significant trend with climatic factors (MAT: $r^2 = 0.07$, $P = 0.33$; MAP: $r^2 = 0.08$, $P = 0.30$) or stand age ($r^2 = 0.01$, $P = 0.94$) (Fig. 4). Conversely, the ordinary least squares (OLS) relationship between M_B and M_A across sites could be well characterized by a power function of $M_B = 0.38M_A^{0.92}$ ($r^2 = 0.86$, $P < 0.001$) (Fig. 5a). Interestingly, the M_B estimated from M_A using this power function

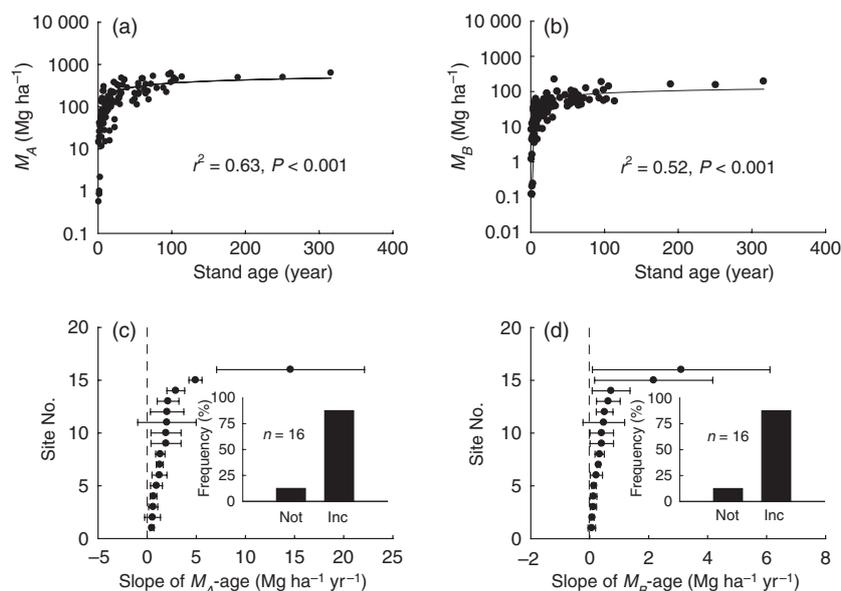


Fig. 1. Changes in aboveground biomass (M_A) and belowground biomass (M_B) with stand age across site (a–b) and within site (c–d). The x-axis in panel c–d is the slope of the relationship between target variables (i.e. M_A and M_B) and stand age. The y-axis in panel (c–d), site number, denotes various individual studies used in this study as shown in Table S1. The dashed line in panel (c–d) denotes the constant slope (equal to zero). If zero is covered by the 95% confidence interval of the slope, the target variable does not change significantly over time. The slope is ordered to clearly illustrate whether it is significantly different from zero. The inset in panel c–d shows the percentage of published studies exhibiting various patterns of M_A and M_B over time. Not: no trend, Inc: increase.

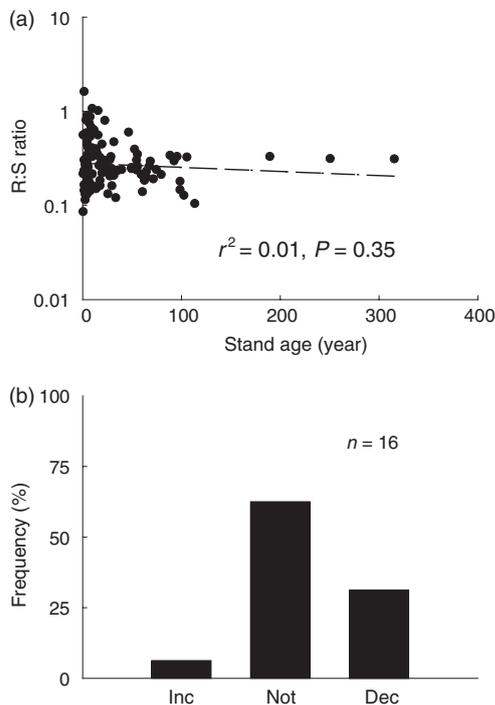


Fig. 2. Changes in root:shoot (R:S) ratio with stand age across site (a) and within site (b). The change in R:S ratio over stand age within site is illustrated by the percentage of published studies exhibiting various patterns of R:S ratio over time. Inc: increase, Not: no trend, Dec: decrease.

accorded well with measured values, with a mean relative difference of 9.6% (Fig. 5b).

Discussion

The R:S ratio did not show significant changes with stand age over space (Fig. 2a) or over time at most sites (Fig. 2b). These results differed from those obtained by Mokany, Raison & Prokushkin (2006), who found that the R:S ratio exhibited a decreasing trend with stand age across forests and woodlands from around the world ($r^2 = 0.05, P = 0.003$). Our results also differed from those of Wang, Fang & Zhu (2008), who observed that the R:S ratio decreased with stand age in forests of northeastern China ($r^2 = 0.04, P < 0.05$). However, our results concurred with an earlier analysis by Cairns *et al.* (1997) which demonstrated that the R:S ratio did not change with stand age across forest ecosystems from around the world. Taken together, these comparisons suggest that stand age alone cannot explain a large proportion of variation in the R:S ratio across a broad geographic gradient (Cairns *et al.* 1997; Mokany, Raison & Prokushkin 2006; Wang, Fang & Zhu 2008) or a long-term age gradient.

Though R:S ratio was relatively stable across stand age when we examined it across sites, it is possible that our analysis hid small differences that existed due to forest types. To test this possibility, we examined trends in R:S ratio over time in temperate and tropical forests separately. Our results demonstrated that R:S ratio did not exhibit any significant trend with

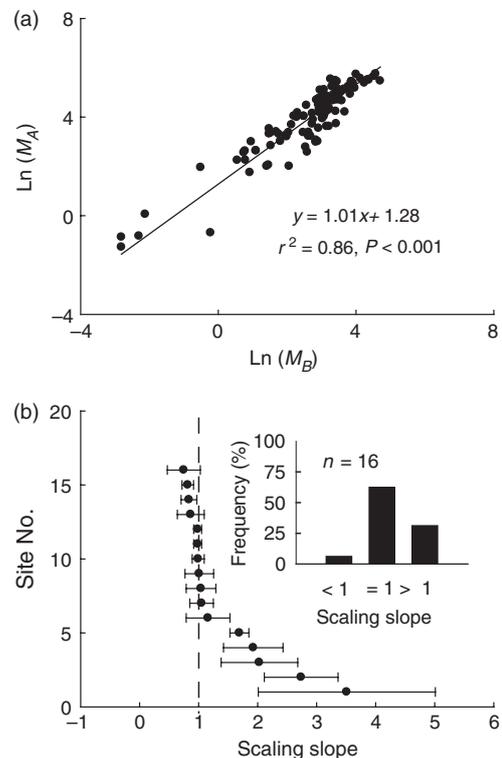


Fig. 3. Reduced major axis (RMA) regression between M_A and M_B across site (a) and within site (b). The x-axis in panel (b), the scaling slope, indicates the slope of the log–log relationship between M_A and M_B . The y-axis in panel b, site number, denotes various individual studies used in this study as shown in Table S1. The dashed line in panel b denotes the constant slope (equal to 1.0) predicted by the isometric hypothesis. If 1.0 is covered by the 95% confidence interval of the slope, biomass partitioning between M_A and M_B follows the isometric prediction. The inset in panel b shows the frequency distribution of the scaling slope within site.

stand age in temperate forests ($r^2 = 0.01, P = 0.63$) or tropical forests ($r^2 = 0.01, P = 0.74$) (see Fig. S2 in Supporting information). These results were consistent with previous observations by Cairns *et al.* (1997), who reported no significant change of R:S ratio with stand age in tropical, temperate or boreal forests.

The slope of the relationship between M_A and M_B across various individual studies was not significantly different from 1.0 (Fig. 3a), supporting the isometric hypothesis (Enquist & Niklas 2002; Niklas 2005; Cheng & Niklas 2007). Moreover, the scaling slope did not reveal a significant difference from 1.0 in 10 out of 16 individual studies (Fig. 3b) and did not exhibit any significant change with environmental factors (Fig. 4). These results also accorded well with the isometric prediction (Enquist & Niklas 2002; Niklas 2005; Cheng & Niklas 2007). The isometric M_A – M_B relationship observed in this study concurred with previous observations across various forest types (Cheng & Niklas 2007) and grassland biomes (Yang *et al.* 2009, 2010). Specifically, Cheng & Niklas (2007) demonstrated that the scaling slope of the relationship between M_A and M_B was indistinguishable from 1.0 in most forest types of China. Likewise, Yang *et al.* (2009) reported that M_A scaled

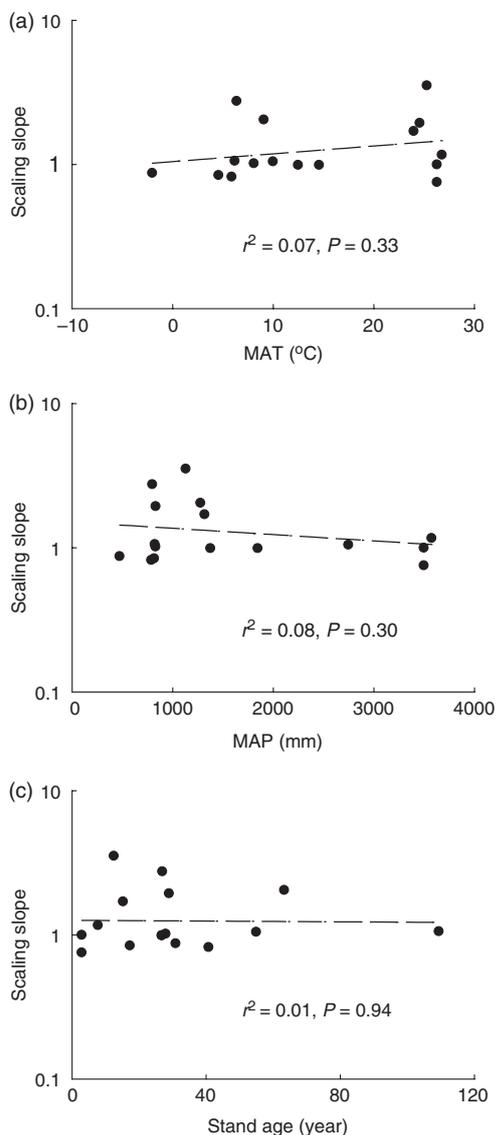


Fig. 4. Relationships of the slope of M_A - M_B relationship with mean annual temperature (a), mean annual precipitation (b) and mean stand age over each sequence (c).

isometrically with respect to M_B in the Tibetan alpine grasslands. Moreover, the isometric pattern observed in the Tibetan alpine grasslands also occurred in other grassland types of northern China (Yang *et al.* 2010). More interestingly, the isometric relationship did not differ significantly between temperate and alpine grasslands or between steppe and meadow (Yang *et al.* 2010). These isometric patterns between M_A and M_B observed in various ecosystems suggest that plants invest their annual growth proportionally above- and belowground with increasing body size (Enquist & Niklas 2002).

Theoretically, the isometric relationship between M_A and M_B during stand development is consistent with the relatively constant R:S ratio observed over age sequences (McConnaughay & Coleman 1999). Then, an interesting question arises why the R:S ratio does not show significant changes with stand age in most sequences? First, the non-significant change of the

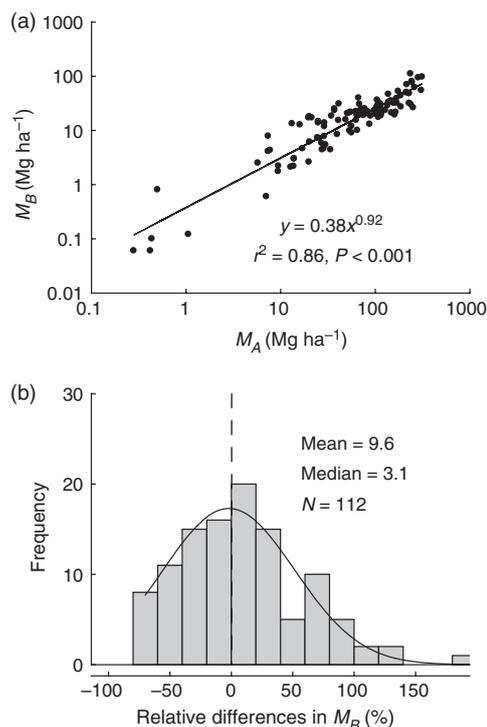


Fig. 5. Ordinary least squares (OLS) regression between M_B and M_A across site (a), and frequency distribution of the relative difference between predicted and measured M_B during stand development (b). M_B within site is predicted from M_A using the M_B - M_A relationship generated across site. The dashed line denotes the relative difference between predicted and measured M_B is equal to zero. The solid curve is a Gaussian distribution fitted to the frequency data.

R:S ratio may be due to diverse patterns of biomass partitioning among various individual tree species. For instance, McConnaughay & Coleman (1999) reported that biomass allocation patterns in various plant species exhibited diverse ontogenetic drifts, including increasing, decreasing and non-significant change of the R:S ratio with increases in plant age. Consequently, the diverse patterns of biomass partitioning among different individual species over time may lead to a non-significant change in the R:S ratio in forest ecosystems during stand development. Second, the non-significant change of the R:S ratio may be driven by changes in nutrient availability over age sequence. Nutrient availability in mineral soils is usually high at the beginning of stand development due to accelerated mineralization after a stand-replacing disturbance (Covington 1981; Zak *et al.* 1990), but may decrease with stand age following forest regrowth (Kutsch *et al.* 2009). The decrease of nutrient availability may stimulate biomass partitioning in favour of M_B (Bloom, Chapin & Mooney 1985; Chapin *et al.* 1987; Shipley & Meziane 2002), thus obscuring the ontogenetic decrease of the R:S ratio over time. Third, the non-significant change in the R:S ratio may also be ascribed to the altered species composition over time. During stand development, forest ecosystems usually experience significant changes in species composition (Wirth & Lichstein 2009). It is well known that different species may have different R:S ratios (Bazzaz & Grace 1997). Therefore, changes in species

composition over time may also obscure the pattern of the R:S ratio dynamics with stand age.

In summary, this study examined biomass partitioning patterns in forest ecosystems over space and time by synthesizing biomass measurements made in 112 stands from 16 age sequences. Our results indicated that the R:S ratio did not exhibit any significant change with stand age both across 16 chronosequence studies (a test of site and age effects) and within 10 out of 16 individual studies (a test of age effect alone). Moreover, M_A scaled isometrically with M_B both across various individual studies and within 10 out of 16 individual studies. These results demonstrated that biomass partitioning patterns over time were similar to those observed over space, suggesting that M_B dynamics during stand development may be reliably estimated from M_A using the allocation function generated over space. The results observed in this study, together with those of previous studies (Enquist & Niklas 2002; Cheng & Niklas 2007; Yang *et al.* 2009, 2010) provide a framework for estimating spatial patterns and temporal dynamics of M_B from M_A in terrestrial ecosystems.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. A list of papers from which data were extracted for this study.

Table S1. Characteristics of the 16 age sequences collected in this study.

Figure S1. Changes in root:shoot (R:S) ratio with stand age in six forest ecosystems.

Figure S2. Relationships between root:shoot (R:S) ratio and stand age in temperate and tropical forests.

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