Allocation of forest biomass across broad precipitation gradients in China’s forests

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Forests act as major sinks for atmospheric CO₂. An understanding of the relationship between forest biomass allocation and precipitation gradients is needed to estimate the impacts of changes in precipitation on carbon stores. Biomass patterns depend on tree size or age, making it unclear whether biomass allocation is limited by tree age at regional scales. Using a dataset of ten typical forest types spanning a large age scale, we evaluated forest biomass allocation–precipitation correlations with the aim of testing whether biomass allocation patterns vary systematically in response to altered precipitation. With increasing mean annual precipitation, a significant quadratic increase occurred in ≤30 yr and >60 yr groups in stem biomass, >60 yr group in branch biomass, and >60 yr groups in leaf biomass; and a significant cubic increase occurred in 30–60 yr and all age forest groups in stem biomass, ≤30 yr, 30–60 yr and all age forest groups in branch biomass, ≤30 yr and all age forest groups in leaf biomass, and in each group in root biomass, indicating that organ biomass is strongly limited by precipitation. Thus, forest biomass responds predictably to changes in mean annual precipitation. The results suggest that forest organ biomass–precipitation relationships hold across independent datasets that encompass a broad climatic range and forest age.

Over the past several decades, the earth has experienced profound climatic change1,2, which affects forest growth. Forest biomass has thus received increased attention1 due to its major sinks for atmospheric CO₂. An understanding of the relationship between forest biomass and climate is needed to predict the impacts of climate change on carbon stores. Plants can differentially allocate biomass to leaves, stems and roots depending on tree size or age in a stand4, which follow ontogenetic trajectories that interact with the prevailing climate6. Enquist and Niklas7 predicted scaling relationships among organ masses by a general allometric model based on metabolic theory, and Zhang et al.8 studied the organ biomass-density relationship in Chinese forests. However, little information is available regarding the influence of climate on organ biomass in forests across different stages of age. Plant biomass allocation patterns are important for global carbon cycling9. At the forest community level, plant biomass allocation strategies are linked to environmental change10–13. When different forest types are considered, results are controversial. Some researchers suggested that biomass distribution can be influenced by climate6,12, whereas Cairns et al.14 found no relationship between global root biomass and climate. Whether these allocation patterns vary systematically across climatic gradients remains unknown, which represents a particularly critical knowledge gap15,16.

Precipitation is a crucial environmental factor in determining ecosystem biomass16 because the direct and indirect influence of moisture availability is important to growth and productivity17,18. Altered precipitation associated with climatic change is significantly altering the forest biomass of terrestrial ecosystems1. Consequently, studying forest responses to large-scale spatial variation in precipitation can strengthen our understanding of the mechanisms of ecosystem adaptation and response to climate change19. A growing number of studies have proposed that annual precipitation governs forest biomass20, but many forest biomass studies are based on empirical correlations restricted to a single forest type21. Although responses to precipitation were confirmed in some biomass patterns in these studies, whether the results of these studies can be extrapolated to a larger geographic scale remains unclear4. Moreover, many studies of large-scale precipitation variability have focused solely on shoot and root biomass, primarily root: shoot ratios of individual species or plant communities under specific environmental conditions22. Few studies have examined the relationship of biomass among organs, such as stem, branch,
leaf and root, with precipitation. Consequently, it is often unclear how the relative balance among organ biomass varies across a precipitation gradient. Such information is necessary for fine-tuning or constraining carbon stock estimates by vegetation type and precipitation zone23 and for improving our understanding of how precipitation affects forest biomass4.

Table 1. The best models for organ biomass of different age groups (quadratic: $y = C + b_1x + b_2x^2$ and cubic: $y = C + b_1x + b_2x^2 + b_3x^3$) and associated equations for data of forest-level organ biomass (stem biomass $w_s$, branch biomass $w_B$, leaf biomass $w_L$ and root biomass $w_R$) (Mg ha$^{-1}$) and mean annual precipitation MAP (mm). Data, grouped according to forest age, taken from Luo (1996) and others.

| Organ | Forest age group | Equation | Model Summary | $P$ | C   | Parameter Estimates | $b_1$ | $b_2$ | $b_3$ |
|-------|-----------------|----------|--------------|-----|-----|---------------------|-------|-------|-------|
| Stem  | ≤30 yr          | Quadratic| $0.18$ | $< 10^{-4}$ | 28.6 | 0.021 | 7.160E-06 | —    |
|       | 31–60 yr        | Cubic    | $0.50$ | $< 10^{-4}$ | 71.5 | −0.118 | 0.001165 | −0.000000044 |
|       | >60 yr          | Quadratic| $0.18$ | $< 10^{-4}$ | −50.3 | 0.333 | −0.000113 | —    |
|       | all age forests | Cubic    | $0.18$ | $< 10^{-4}$ | −32.7 | 0.257 | −0.000157 | 3.18E-08 |
| Branches | ≤30 yr         | Cubic    | $0.12$ | $< 10^{-4}$ | 17.5 | −0.028 | 2.95E-05 | −6.85E-09 |
|       | 31–60 yr        | Cubic    | $0.50$ | $< 10^{-4}$ | 23.6 | −0.0520 | 6.71E-05 | −1.73E-08 |
|       | >60 yr          | Quadratic| $0.41$ | $< 10^{-4}$ | 20.4 | −0.026 | 3.31E-05 | —    |
|       | all age forests | Cubic    | $0.19$ | $< 10^{-4}$ | 24.7 | −0.043 | 4.84E-05 | −1.14E-08 |
| Leaves | ≤30 yr          | Cubic    | $0.23$ | $< 10^{-4}$ | 1.8 | 0.015 | −9.75E-06 | 2.60E-09 |
|       | 31–60 yr        | Cubic    | $0.33$ | $< 10^{-4}$ | 4.7 | −0.0007 | 2.62E-06 | −2.68E-10 |
|       | >60 yr          | Cubic    | $0.17$ | $< 10^{-4}$ | 1.8 | 0.010 | −1.68E-06 | —    |
|       | all age forests | Cubic    | $0.18$ | $< 10^{-4}$ | −0.4 | 0.016 | −1.10E-05 | 2.92E-09 |
| Roots  | ≤30 yr          | Cubic    | $0.20$ | $< 10^{-4}$ | 32.9 | −0.046 | 3.30E-05 | −5.11E-09 |
|       | 31–60 yr        | Cubic    | $0.26$ | $< 10^{-4}$ | 29.0 | −0.036 | 4.15E-05 | −9.76E-09 |
|       | >60 yr          | Cubic    | $0.18$ | $< 10^{-4}$ | 19.6 | −0.015 | 8.09E-05 | −3.39E-08 |
|       | all age forests | Cubic    | $0.14$ | $< 10^{-4}$ | 2.3 | 0.057 | −3.88E-05 | 9.09E-09 |

Figure 1. Relationship between mean annual precipitation and stem biomass along a precipitation gradient in China. (a) ≤30 yr; (b) 31–60 yr group; (c) >60 yr group; (d) all age forests.
China has forest types across broad geographic regions and environmental gradients, which vary across a wide range of climatic regimes. These types include temperate and subtropical forests across North, Central and South China. Because of the wide distribution of these forests, there is a steep latitudinal gradient of precipitation for each type. Despite the importance of these forests for carbon cycling in China, influences of precipitation on biomass allocation among organs in these forests remain unclear.

Biomass allocation in young forests may be different from older forests. Thus, one approach to understand precipitation effects on biomass allocation in different growth stage forests is to compare biomass allocation patterns in forests of varying age along natural precipitation gradients. Data from across China provide an important opportunity to examine biomass allocation in relation to tree age and precipitation, which may contribute valuable insight toward understanding precipitation effects on carbon sequestration in forests. The objective of the present study is to test whether biomass allocation patterns of different age groups vary systematically across a mean precipitation gradient. Although many other environmental and climatic factors affect biomass allocation, we focused our analysis on mean annual precipitation (MAP) because of the availability of comprehensive data on this variable.

Results

Organ biomass had a quadratic or cubic response pattern to precipitation change. With MAP, stem biomass had a significant quadratic increase in ≤30 yr and >60 yr groups, and a significant cubic increase in 30–60 yr and all age groups (P < 10⁻⁶) (Table 1, Fig. 1). Adjusted R² for the two equations was ≥0.18. Branch biomass had a significantly positive cubic correlation with MAP in ≤30 yr, 30–60 yr and all age group groups, and a quadratic correlation in >60 yr group (P < 10⁻⁶) (Fig. 2). Adjusted R² for all equations was ≥0.12. Leaf biomass showed a significant cubic correlation with MAP in ≤30 yr and all age groups, and a quadratic correlation with MAP in 30–60 yr and >60 yr groups (P < 10⁻⁶) (Fig. 3). Adjusted R² for all equations was ≥0.17. Root biomass significantly cubic increased in ≤30 yr, 30–60 yr, >60 yr and all age groups (P < 10⁻⁶) (Fig. 4). Adjusted R² for all equations was ≥0.14.

Adjusted R² were characterized by this sequence: stem >branches >leaves >roots. The lower R² values for leaves and roots may reflect the smaller sample sizes for these organs. When predicting tree biomass, stem biomass is more stable than that of more short-lived leaves.

Figure 2. Relationship between mean annual precipitation and branch biomass along a precipitation gradient in China. (a) ≤30 yr; (b) 31–60 yr group; (c) >60 yr group; (d) all age forests.
Discussion

Forest organ biomass varies across a large scale as a result of precipitation gradients. Certain past studies have analyzed patterns of forest biomass in response to large-scale precipitation changes in China. However, most of these have focused on temperate forests, with few analyzing forest biomass allocation in subtropical regions. In this study, we showed that stem, branch, leaf and root biomasses increased significantly with increasing MAP in each age group. Saatchi et al. reported that total aboveground biomass increases with precipitation in moist and wet tropical forests of the Amazon Basin. McCarthy and Enquist found that stem mass increased with increased precipitation. These reports, together with our results, suggest that precipitation gradient is the critical variable driving forest biomass within these forest types. Greater annual precipitation is presumably favorable for vegetative shoot growth over the growing season. Reduced precipitation lowers nutrient availability due to water limitation of soil microbial processes, attenuates ecosystem photosynthesis, and ultimately results in an overall decrease of biomass and productivity.

Increasing root biomass favors uptake of nutrients and water. Despite greater attention over recent decades, knowledge of root biomass and its spatial distribution is much more limited than that of shoot biomass. Further, root dynamics remain largely uncertain because there have been few studies on responses of root biomass to spatial variations in precipitation. Our results show that root biomass was significantly related to MAP in each age group (cubic model), which indicates that increased precipitation promotes accumulation of root biomass of Chinese forests.

Plant ontogeny may also have a strong effect on biomass allocation patterns. With tree growth, wood (dead cells) continuously accumulates in stems and roots, whereas branch and leaf biomass decrease because crown growth is impeded and shade-intolerant leaves shed at the canopy base. Thus, emphasis in biomass allocation transitions over time from leaves and branches to stem and root. However, our analyses indicate that precipitation is consistently correlated with biomass allocation in forests of varying age stages. When data from forests of all ages were considered together, forest organ biomass was also correlated with MAP, which suggests that the decisive role of precipitation is consistent across forest age. As a result, it is possible to make general predictions concerning changes in biomass allocation in response to precipitation change, which may prove important for understanding forest biomass allocation patterns in the context of changing precipitation regimes.

Our data indicate that precipitation affects organ biomass allocation patterns, which indicates that the role of precipitation in determining biomass allocation is dependent on forest age, which is in line with the result of Zhang et al., who found that forest biomass varies with climatic variables, such as precipitation and temperature. Moreover, Reich et al. and Lie and Xue reported that organ biomass are also associated with temperature gradients, which implies that allocation patterns of organ biomass vary systematically as a result of climatic gradients, and will be useful for assessing climate change impacts on forest carbon stocks and cycles. By focusing on

Figure 3. Relationship between mean annual precipitation and leaf biomass along a precipitation gradient in China. (a) ≤30 yr; (b) 31–60 yr group; (c) >60 yr group; (d) all age forests.
In conclusion, this study examined biomass allocation patterns of forests in different age stages across China along precipitation gradients. With increasing MAP, organ biomass showed a significant quadratic increase in ≤30 yr and >60 yr groups for stem and in >60 yr group for branches and leaves; and a significant cubic increase in 30–60 yr and all age groups for stem; in ≤30 yr, >60 yr and all age groups for branches and leaves; and in ≤30 yr, 30–60 yr, >60 yr and all age groups for roots. Forest organ biomass–precipitation relationships hold across independent datasets that encompass a broad climatic range and forest age. These results could be used to predict precipitation influences on standing biomass. Such predictions will be essential for understanding feedbacks between climate change and forest community carbon storage.

Materials and Methods
Dataset. A 1193-large organ biomass and climatic dataset was compiled from the literature, in which 916 data points were extracted from the database of Luo. These originated from the inventories of the Forestry Ministry of China, and others collected from 21 sources. These data include alpine temperate Larix forest, alpine Picea-Abies forest, temperate typical deciduous broadleaved forest, temperate Pinus tabulaeformis forest, temperate mixed coniferous–broadleaved forest, montane Populus-Betula deciduous forest, subtropical evergreen broadleaved forest, subtropical montane Cupressus and Sabina forest, subtropical Pinus massoniana forest and subtropical Cunninghamia lanceolata forest. These are typical forest types from north to south in China and represent all the major forest types in China. These forest types are widely distributed land-cover types covering an area of 44.3 million ha, occupying about 80% of Chinese forest area.

Forest biomass of trees was measured by destructive harvesting in experimental plots. The size of these plots varied with stand condition and forest type but in general, the area of sample plots ranged from 400–1000 m² for each forest.

For each data point, we documented the following information, if available: (1) stem, branch, leaf, root and total biomass; (2) diameter-at-breast height (DBH) and tree height. The sampled forests varied widely in size.
Δ values indicating better fit (the best fitting model would have higher adjusted R² selection where the model with the lowest AIC indicates the best model\(^6\)). This criterion is based on Akaike information theory and has been widely used in variable and model selection\(^6\). To compare models, the ΔAIC was calculated as the difference in AIC values between each model and the model with the lowest AIC\(^6\) with smaller values indicating better fit (the best fitting model would have ΔAIC = 0 and all other models ΔAIC > 0)\(^6\), and then higher adjusted \(R^2\) values were considered. According to the ΔAIC results, quadratic or cubic equations fit better than linear equations against organ biomass data (Supplementary Table 1).

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Z.Y.L. collected and analyzed the data and prepared figures and tables, L.X. designed this study and wrote the main manuscript text, and D.F.J. reviewed the manuscript.

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