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# Variation in Organ Biomass with Changing Climate and Forest Characteristics across Chinese Forests

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**Abstract:** Forest biomass allocation patterns are important for understanding global carbon cycling and climate change, which might change with environmental conditions and forest characteristics. However, the effects of climate and forest characteristics on biomass allocation fractions (the fraction of total forest biomass distributed in organs) remains unknown. The authors use a large Chinese biomass dataset (1081 forests encompassing 10 forest types) to analyse the responses of biomass allocation fractions to biogeography, climate, and forest characteristics. The authors found that the stem mass fraction significantly increased with age and precipitation and significantly decreased with latitude and temperature. The branch mass fraction significantly decreased with age and density, but significantly increased with temperature and latitude. The leaf mass fraction significantly decreased with age and precipitation and significantly increased with temperature. The root mass fraction significantly increased with latitude and density, and significantly decreased with precipitation. The results suggest that latitude, temperature, precipitation, stand age and density are good predictors of biomass partitioning. These findings support the hypotheses that variation in resource availability constrains organ allocation and provides biogeographically explicit relationships between biomass allocation and both environmental and forest characteristics, which might be used for assessing the impact of changing environmental and forest characteristics on forest carbon dynamics and fixation.

**Keywords:** allometry; biogeography; biomass fraction; climate; forest characteristics

## 1. Introduction

Forests play an important role in the global carbon cycle [1] because their biomass stores over 80% of the global aboveground carbon [2]. The plant biomass allocation pattern is an important topic in ecology [3,4], due to its importance in global carbon cycling [2,5]. Forest biomass can be divided into stems, branches, leaves and roots. The process of proportional allocation of new carbon (C) to these organs can be influenced by climate [6–8]. The proportional growth of trees results in the proportional distribution of standing including the stem, branches, leaves and roots. Such distribution has important implications for the accuracy of global C cycle modeling and accounting [8]. Biomass allocation fractions (BAFs), defined as the ratio of plant biomass of organs (the stem, branches, leaves and roots) to total plant biomass, are well grounded in plant growth theory [9,10].

Changes in environmental conditions can have rapid and profound effects on vegetation biomass allocation [11,12]. The resource balance/optimal theory assumes that plants try to maximize their growth by allocating biomass to the organ that takes up the most limiting resource [13]. That is, plants allocate more biomass to roots if the limiting factor for growth is below ground, whereas they

allocate more biomass to shoots if the limiting factor is above ground [7]. Biomass distribution among tree organs can be influenced by climate due to the important influence of temperature, or precipitation, on biomass distribution for tree growth. Low temperatures in cold ecosystems limit many biological processes [14], whereas in dry environments plant growth is limited by water. Thus, it is reasonable to predict that a greater biomass allocation to roots and lower to stems and leaves should occur with decreasing temperature, and that precipitation would increase the uptake of water and nutrients. The fraction of total forest biomass in stems, branches and leaves should increase, and decrease in roots, as precipitation and/or temperature increases. During the past several decades, profound climatic change has occurred worldwide [15–17]. Increasing greenhouse gas emissions are expected to escalate the global atmospheric temperature by 2–7 °C by the end of this century due to the impacts of human population growth [18,19]. This temperature change is significantly altering the temporal variation of aboveground net primary productivity in terrestrial ecosystems [17], and the ecosystem carbon balance, because both ecosystem photosynthesis and respiration often increases with warming [19]. Many biological processes of trees are limited by low temperatures [14], which might affect forest growth. Conversely, precipitation is significantly altering the biomass of terrestrial ecosystems [17,20] due to its increase at high latitudes and decrease in most subtropical regions [16]. This, in turn, is expected to have a strong influence on the future of climate change [21–23]. Biomass allocation responses to large-scale spatial variations in temperature and precipitation has received increased attention due to its importance for several ecosystem processes, such as productivity, nutrient cycling, ecosystem fluxes and global carbon cycle modeling [21,24], and currently represents a major knowledge gap that hinders the understanding of carbon pool fluxes and below/above ground carbon storage at global scales. Consequently, researching biomass allocation responses to large-scale spatial variation in temperature and precipitation can strengthen the current understanding of responses to climate change.

Recently, many researchers have studied environmental effects on biomass allocation in many forest types with a focus on the root:shoot ratio, the allometric function relating root biomass and shoot biomass [14,25,26], or biomass allocation patterns to leaves, stems and roots [7,9,27–30], whereas research on BAFs has received little attention [8,10]. When different forest types are considered, the aforementioned studies have not been consistent, and consequently, relatively little is known about how the environment influences biomass allocation [26], especially on BAFs in forested ecosystems. Therefore, biomass allocation patterns in many forest types remains unclear. Thus, undertaking research to determine how environmental variation affects the shifts in forest biomass is required to understand the mechanisms of ecosystem adaptation and response to environmental change. Whether these allocation patterns vary systematically across environmental gradients remains unknown, and is a critical knowledge gap [24]. As a result, little is known about climate effects on tree organs. Moreover, the above studies have been focused on climate effects on tree organ allocation, but very little is known about climate effects on BAFs. Changes in BAFs that accompany climate changes include important implications for the global carbon cycle [8].

In addition, climatic factors, the growth environment, competition, plant age or size [31] also influence biomass allocation [7,28]. Although large data sets have been used to summarize the influence of forest characteristics on biomass allocation patterns, the understanding of BAFs in relation to effects of biogeography, environmental and forest characteristics is still unclear, and the large-scale pattern of BAFs in China's forests remains poorly understood [10].

Focusing on China, alpine temperate *Larix* Mill. and alpine *Picea abies* (L.) Karst. forest, temperate deciduous broadleaved forest, *Pinus tabulaeformis* Carriere forest, mixed coniferous broadleaved forest, montane *Populus* L.-*Betula* L. deciduous forest, subtropical evergreen broadleaved forest, *Pinus massoniana* Lamb. forest, *Cunninghamia lanceolata* (Lamb.) Hook. forest; and subtropical montane *Cupressus* Linn. and *Sabina* Mill. forest form both monospecific and mixed forests under a broad variety of temperate and subtropical climates and site conditions. These forest types have complicated stand conditions (such as, age and density), being widely distributed, geographically, over land-cover types with an area of 114 million ha and occupying approximately 80% of the Chinese forested area [30,32].

This allowed the authors to investigate the effects of biogeography, climate and stand characteristics on biomass allocation patterns of these forest types. Although a large organ biomass dataset of China has been used to evaluate temperature effect on biomass allocation in ten forest types [30], information about the effects of biogeographical, environmental and forest characteristics on BAFs of these forest types is still lacking.

During this study, the authors analyze the effects of longitude, latitude, temperature, precipitation, stand age and density on BAFs based on a large organ biomass data set (1081 sites) of the above forest types, which will be useful for assessing biogeographical, environmental and forest characteristic impacts on these forest carbon dynamics. The authors hypothesized that organ allocation fractions will change with site conditions, climate, and forest characteristics, since the ability of forest trees to utilize available resources is affected by environmental and biological factors.

## 2. Material and Methods

A large organ biomass dataset (comprising 1081 sites) was compiled from the literature, of which 916 sites were extracted from the database of Luo [33] and others collected from 21 sources [34–54]. The database was structured by geographic location, climate (temperature and precipitation), species, stand age and density. The sampled forests varied widely in age (from 3 to 317 years), density (from 125 to 20,535 trees ha<sup>-1</sup>) and size (with total forest biomass ranging from 3.86 to 657.30 Mg ha<sup>-1</sup>). The sampled forests also varied widely geographically (81°00′–134°00′ N, 18°70′–52°60′ E) and in mean annual temperature (MAT) (from –6.6 to 24.2 °C) and mean annual precipitation (MAP) (from 241.0 to 2989.1 mm) (Table 1).

**Table 1.** Site conditions (longitude, latitude), climate factors (mean annual temperature (MAT), mean annual precipitation (MAP)) and forest characteristics (stand age, stand density) of the studied forest types.

Forest Type	Latitude (°N)	Longitude (°E)	Mean Annual Temperature (°C)	Mean Annual Precipitation (mm)	Stand Age (years)	Stand Density (trees ha <sup>-1</sup> )
Larix forest	28.62–52.60	86.40–131.80	–6.2–12.9	357–1274	30–195	219–20,535
Alpine <i>Picea abies</i> forest	26.14–52.60	81.10–131.80	–6.6–13.9	370–1937	46–317	125–3967
Temperate <i>Pinus tabulaeformis</i> forest	32.60–42.60	103.79–129.50	2.9–18.7	380–1173	15–95	146–8506
Temperate mixed coniferous-broadleaved forest	40.88–50.70	123.90–133.50	–0.4–16.0	300–838	20–238	200–3920
Temperate typical deciduous broadleaved forest	28.25–51.70	103.00–134.00	–3.3–18.6	410–1142	20–157	166–8326
Temperate/subtropical montane <i>Populus–Betula</i> deciduous forest	25.75–52.50	85.20–134.00	–5.5–17.4	241–1283	25–222	149–7302
Subtropical montane <i>Populus</i> spp. and <i>Betula</i> spp. forest	25.50–33.59	85.20–113.10	2.7–18.2	370–1937	8–220	376–3450
Subtropical evergreen broadleaved forest	20.70–30.25	85.20–120.17	3.5–25.4	637–2323	3–200	150–9257
Subtropical <i>Pinus massoniana</i> forest	21.72–32.70	105.08–120.60	12.2–24.0	1020–2006	15–101	392–6700
Subtropical <i>Cunninghamia lanceolata</i> forest	18.7–32.33	103.37–121.57	9.4–22.4	720–2989	16–55	1018–4978

The size of these plots varied with stand condition and different forest types. Generally, the area of sample plots was 400–1000 m<sup>2</sup> for each forest with several replicates. Several “standard” trees within a plot were selected for felling and weighing of organs, then allometric equations were established, relating organ biomass to diameter at breast height and tree height. Organ mass was calculated using these allometric equations established for different organs in different plots. Organ biomass included stem, branch, leaf and root biomasses ( $M_{\text{stem}}$ ,  $M_{\text{bra}}$ ,  $M_{\text{leaf}}$  and  $M_{\text{root}}$ ) and total forest biomass ( $M_{\text{tot}} = M_{\text{stem}} + M_{\text{bra}} + M_{\text{leaf}} + M_{\text{root}}$ ) was estimated based on total tree numbers. The fraction of total biomass ( $M_{\text{tot}}$ ) in the stem ( $F_{\text{stem}} = M_{\text{stem}}/M_{\text{tot}}$ ), branches ( $F_{\text{bra}} = M_{\text{bra}}/M_{\text{tot}}$ ), leaves ( $F_{\text{lea}} = M_{\text{lea}}/M_{\text{tot}}$ ), and roots ( $F_{\text{root}} = M_{\text{root}}/M_{\text{tot}}$ ) was calculated [7]. The spatial variation allowed the organ fraction of biomass allocation to be evaluated in relation to longitude, latitude, temperature, precipitation,

stand age and stand density, potentially providing valuable information for understanding the effect of biogeography, climate and forest characteristics on biomass allocation patterns along temperature and precipitation gradients in China. This will enable better predictions of the regional carbon balance in response to future environmental change.

All data analyses were performed using statistical software SPSS 19.0 (SPSS Inc.: Chicago, IL, USA, 2004). Stepwise multiple regression (SMR) was used to identify the effects of climate (MAT and MAP), site condition (longitude, latitude) and forest characteristics (stand age and density) on BAFs. Pearson correlation analyses were performed to determine the relationships between the stem, branch, leaf, and root biomasses and site conditions (longitude and latitude).

### 3. Results

The average biomass of stems, branches, leaves and roots differed largely, ranging from 7.14 to 87.84 Mg ha<sup>-1</sup> (Table 2), meaning that BAFs varied markedly among organs, accounting for 60%, 14%, 6% and 20% of total forest biomass for the stem, branches, leaves and roots, respectively.

**Table 2.** Organ biomass and forest biomass (Mg ha<sup>-1</sup>) and organ mass fraction.

		Organ				Forest
		Stem	Branches	Leaves	Roots	
Biomass	Range	1.96–534.24	0.54–211.88	0.53–31.45	0.52–232.53	3.86–657.30
	Mean ± SD	87.84 ± 63.93	19.82 ± 18.82	7.14 ± 4.23	27.70 ± 19.38	142.31 ± 93.06
Organ/Forest	Range	0.34–0.87	0.02–0.37	0.01–0.28	0.06–0.45	
	Mean ± SD	0.60 ± 0.08	0.14 ± 0.06	0.06 ± 0.03	0.20 ± 0.06	

Data were taken from Luo (1996) and others.

All BAFs exhibited significant longitudinal trends ( $p < 0.01$ ; Table 3).  $F_{\text{stem}}$  significantly increased from east to west ( $p < 0.01$ ), whereas  $F_{\text{bra}}$ ,  $F_{\text{lea}}$  and  $F_{\text{root}}$  decreased from east to west ( $p < 0.01$  or 0.05). Except for  $F_{\text{lea}}$ , all BAFs exhibited significant latitudinal trends.  $F_{\text{stem}}$  and  $F_{\text{bra}}$  significantly decreased from south to north, whereas  $F_{\text{root}}$  significantly increased with increasing latitude ( $p < 0.01$ ).

**Table 3.** Pearson correlations between four biomass allocation fractions (BAFs) and site conditions.

Site Conditions	$F_{\text{stem}}$	$F_{\text{bra}}$	$F_{\text{lea}}$	$F_{\text{root}}$
Longitude (E, °C)	−0.259 **	0.145 **	0.081 *	0.185 **
Latitude (N, °C)	−0.176 **	−0.118 **	0.019	0.394 **

Note: (1)  $F_{\text{stem}}$ , stem mass fraction;  $F_{\text{bra}}$ , branch mass fraction;  $F_{\text{lea}}$ , leaf mass fraction;  $F_{\text{root}}$ , root mass fraction; (2) \* and \*\* represent  $p < 0.05$  and  $p < 0.01$ , respectively.

Stepwise multiple regression (SMR) analysis showed that the four BAFs exhibited different sensitivities to age (Table 4).  $F_{\text{stem}}$  was significantly positively correlated with age and precipitation and significantly negatively correlated with latitude and temperature.  $F_{\text{bra}}$  significantly decreased with age and density, but significantly increased with temperature and latitude. There were significant negative correlations between  $F_{\text{lea}}$  and age, as well as between  $F_{\text{lea}}$  and precipitation, and a significant positive correlation between  $F_{\text{lea}}$  and temperature. Significant positive correlations were also present between  $F_{\text{root}}$  and latitude and density, and the negative correlation between  $F_{\text{root}}$  and precipitation was also significant.

**Table 4.** Stepwise multiple regressions (SMR) between four biomass allocation fractions (BAFs) with stand characteristics and environmental factors in China's forests.

BAFs	Models	Equations	<i>p</i>	<i>R</i> <sup>2</sup>
F <sub>stem</sub>	1	Stem biomass fractions = 0.0010age + 0.555	0.000	0.136
	2	Stem biomass fractions = 0.0010age – 0.003latitude + 0.649	0.000	0.195
	3	Stem biomass fractions = 0.0010age – 0.005latitude – 0.030temperature + 0.751	0.000	0.202
	4	Stem biomass fractions = 0.0010age – 0.005latitude – 0.040temperature + 0.000023precipitation + 0.726	0.000	0.207
F <sub>bra</sub>	1	Branch biomass fractions = –0.0004age + 0.17	0.000	0.086
	2	Branch biomass fractions = –0.0005age – 0.000008density + 0.187	0.000	0.115
	3	Branch biomass fractions = –0.0004age – 0.000008density + 0.010temperature + 0.169	0.000	0.130
	4	Branch biomass fractions = –0.0003age – 0.000008density + 0.040temperature + 0.030latitude + 0.052	0.000	0.146
F <sub>lea</sub>	1	Leaf biomass fractions = –0.0002age + 0.072	0.000	0.132
	2	Leaf biomass fractions = –0.0002age – 0.000009precipitation + 0.082	0.000	0.151
	3	Leaf biomass fractions = –0.0004age – 0.000017precipitation + 0.010temperature + 0.082	0.000	0.157
F <sub>root</sub>	1	Root biomass fractions = 0.003latitude + 0.098	0.000	0.154
	2	Root biomass fractions = 0.003latitude + 0.000008density + 0.088	0.000	0.197

#### 4. Discussion

Significant changes in BAFs with latitude, temperature, precipitation and forest age and density were demonstrated in this study. These results support the hypothesis that different underlying environmental and biological factors affect the biogeographic patterns of biomass allocation. This study's results were consistent with some previous research [8,10]. Temperature drives global patterns of forest biomass distribution in leaves, stems, and roots [8,10,28,30], for example, which supports the resource balance/optimality theory stating that plants try to maximize their growth by allocating biomass to the organ requiring the most limited resource [55]. This indicates that the resource balance/optimality theory might be used to analyze forest biomass allocation in response to environmental change.

##### 4.1. Temperature Effects

During this study, F<sub>bra</sub> and F<sub>lea</sub> exhibited significantly positive responses to warming. Many biological processes of trees are limited by low temperatures [14]. Low temperature also impairs plant functions, such as photosynthesis, nutrient uptake, and growth [56]. Moreover, low temperatures can limit water viscosity, membrane permeability and metabolic processes, which affects root and microbial activity, decomposition and mineralization of organic matter, resulting in a reduced supply of nitrogen and phosphorus [30]. Zhou et al. [57] reported that low temperatures decrease the number of leaves due to competition for light, nutrients and water. Reich et al. [8] also found that leaves are a smaller proportion of standing biomass in forests in colder climates. Increasing temperature accelerates the metabolic rates of trees, stimulates microbial activity, enhances biologically driven processes such as soil nutrient mineralization [19,58,59], enhances plant growth by stimulating plant photosynthesis due to increased soil nutrient mineralization [60], extends the growing season [61,62] which increases aboveground biomass [63] and compensates for increased respiratory C losses [60], resulting in increased forest biomass [64,65]. Thus, the branch and leaf mass fractions increase. Many studies have shown a stimulation in biomass with warming in cold-temperate regions [14,66]. Different responses in forest biomass allocation to temperature might be partly regulated by turnover rate. Reich et al. [8] found that forests probably allocate a smaller proportion of new biomass to leaves in low temperature

environments due to low turnover rates, thus, increases in  $F_{bra}$  and  $F_{lea}$  might result in a decrease in  $F_{stem}$ .

#### 4.2. Precipitation Effects

Forest organ biomass varies across a large scale as a result of precipitation gradients [67]. During this study,  $F_{stem}$  significantly increased, whereas  $F_{lea}$  and  $F_{root}$  significantly decreased with increasing MAP, suggesting that the precipitation gradient is the critical control on  $F_{stem}$ ,  $F_{lea}$  and  $F_{root}$ . McCarthy and Enquist [31] found that stem mass increased with increased precipitation. Increased precipitation is favorable for plant growth [25]. Stem biomass increasing at the expense of root biomass will be favorable for competing for light resources, indicating that light is more limiting than water and nutrients in a warm and rainy climate. Decreased precipitation not only suppresses plant biomass and physiological processes, but also reduces nutrient availability due to water limitations on soil microbial processes [68,69].

Varying MAP did not alter the branch mass fraction. This result implies that precipitation is less important for limiting branch biomass in these forest types, and low temperature is more critical to limiting plant growth in cold-temperate regions [70,71]. Therefore, branch allocation patterns are fairly rigid and do not allow for acclimation in response to precipitation change. Inflexible allocation patterns might restrict the spatial distribution of branches, since they are incapable of adjusting biomass allocation to maximize resource acquisition in response to external factors [72].

Evidence for precipitation control of roots at a large scale is scarce [57,73]. A significantly negative correlation between  $F_{root}$  and MAP in this study suggested that trees in these forest types allocate a lower proportion of biomass to roots as water availability increases. This agrees with reports in other studies [5,13,74]. Mokany et al. [75] also showed that roots:shoot (stem + branches + leaves) was negatively related to precipitation for forests and woodlands worldwide [49]. These results are in line with the generally accepted idea that root biomass allocation is strongly correlated with available soil moisture, and with the common prediction that the root mass fraction increases with decreasing MAP [76] because soil water stress from low precipitation causes greater biomass allocation to roots [5,77]. The observed trend of root mass fraction in the Chinese forest types, along the precipitation gradient, is consistent with the prediction of the resource balance/optimality theory [7,13,28].

#### 4.3. The Effects of Forest Characteristics

Biomass allocation patterns are controlled by forest characteristics, such as, age and competition caused by high density [10,51,78]. During this study,  $F_{stem}$  significantly increased, whereas  $F_{lea}$  and  $F_{bra}$  significantly decreased, with age (Table 4). Plants invest proportionally more in support tissues with growth [7,27]. Stems, as support tissues, increase with tree growth [79]. Zewdie et al. [80] also concluded that  $F_{stem}$  increased, whereas  $F_{lea}$  decreased, with increasing stand age. Resource allocation from leaves and branches to stems with increasing stand growth has also been reported for *Pinus densiflora* [81] and *Eucalyptus urophylla* stands [82]. Considering tree growth, wood (dead cells) continuously accumulates in the stem, whereas branch and leaf biomass decreases as early death of lower branches, due to mutual shading, results in a lower amount of foliage [83,84]. Following canopy closure,  $F_{stem}$  continues to increase, whereas  $F_{lea}$  and  $F_{bra}$  decreases as trees grow. This is because older and taller trees entail greater expenditures for their construction and maintenance and expend more energy supplying leaves with the same amount of water, than do younger and shorter trees [82,85].

$F_{bra}$  decreases and  $F_{root}$  increases with stand density (Table 4). Canopy closure first occurs in the high-density stand, so its canopy growth is impeded. Conversely, the canopy of the low-density stand fully develops due to the broad growth space. The number of lateral branches gradually decreases and their length becomes shorter with increasing stand density [83], which results in  $F_{bra}$  decrease with increasing density. Weiner et al. [86] and Weiner and Fishman [87] also highlighted that branches are fewer in highly crowded stands than in low density stands. Zhang et al. [28] also observed low root biomass under low stand density. Resource acquisition and use is influenced by forest

density. Increasing stand density on a site might increase the acquisition and use of soil nutrients and water. Therefore,  $F_{\text{root}}$  increases with stand density even though the root growth rate of individual trees decreases.

#### 4.4. Latitude Effects

In this study, BAFs showed different latitude trends.  $F_{\text{stem}}$  revealed a significant negative longitudinal trend, whereas  $F_{\text{bra}}$  and  $F_{\text{lea}}$  displayed a significant positive latitudinal trend, which indicates that climate shapes the biogeographic patterns of forest biomass [29,78–89]. Climatically, the north-to-south gradients in China reflect shifts from cold and dry to warm and moist conditions, a phenomenon that appears to be consistent with latitudinal trends since temperature decreases with increasing latitude [10]. Forests in high-latitude conditions are influenced by low temperature, low water availability, and low nutrient supply [90,91]. Low MAT and low soil nutrients might result in an increase of root biomass, and low MAP might cause dramatic increases in root biomass at the expense of the stem [28].

Generally, biomass allocation displays a linear relationship with single climatic factors, such as, precipitation or temperature, though sometimes it shows a curvilinear relationship with the climatic factor [84]. When several influence factors were considered, SMR was generally used as the analysis method [10,28]. In the future, more feasible methods need to be developed to increase understanding of the ecological significance of climate and the effect of forest characteristics on patterns of forest biomass allocation.

## 5. Conclusions

This study analyzed changes of biomass allocation fractions with biogeography, climate, and forest characteristics. The results suggest that latitude, temperature, precipitation, stand age and density have significant effects on biomass partitioning, which provide biogeographically explicit relationships between biomass allocation and environment, as well as forest characteristics. This might influence the ability to improve management of forest ecosystems, understand regional patterns of biomass allocation and reduce the uncertainties in predicting forest carbon fixation.

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