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Full Length Article

Forest Biomass Allocation vary with Temperature in Five Forest Types of China

Wanqi Lin, Yiran Fang and Li Xue*
College of Forestry and Landscape Architecture, South China Agricultural University, Guangzhou, 510642, P.R. China
*For correspondence: forxue@scau.edu.cn

Abstract

Currently global warming is an inevitable phenomenon and its effects on forests are palpable. In this study, temperature effect on biomass allocation was examined using biomass data for five forest types. Stem, branch, leaf and root biomasses comprised 53–71%, 8–20%, 4–9% and 15–21% of the overall stand biomasses, respectively. Mean values for the root: shoot ratio increased in the order of subtropical montane *Cupressus* and *Sabina* forest (SCSF) (0.18) = subtropical *Pinus massoniana* forest (SPMF) (0.18) < alpine *Picea abies* forest (APAF) (0.21) < temperate *P. tabulaeformis* forest (TPTF) (0.25) < temperate typical deciduous broadleaved forest (TDBF) (0.28). Warming significantly enhanced the stem, shoot and forest biomasses in APAF and SPMF, and significantly decreased in TDBF, TPTF and SCSF. With increasing temperature, branch biomass decreased significantly in TDBF and increased significantly in SPMF; leaf biomass decreased significantly in APAF and TDBF and increased significantly in SPMF; root biomass showed a significant increase in APAF and SPMF. The root: shoot ratio decreased significantly in APAF and increased significantly in TPTF and SCSF, but did not change significantly in TDBF and SPMF. Thus, due to warming, the biomass allocation was observed to be changed with forest types.

Keywords: Biomass; China; Distribution pattern; Forest; Root: Shoot ratio; Temperature gradient

Introduction

By the end of this century, the global atmospheric temperature is expected to increase by 2–7℃ due to the emission of greenhouse gasses (IPCC, 2014). This temperature change is significantly altering forest growth (Ma *et al.*, 2010; Poorter and Sack, 2012), net primary productivity (Fang *et al.,* 2018) and carbon balance in the ecosystem (Wu *et al.,* 2011). Forests are important carbon pools (Zhang *et al.,* 2010). The plant biomass allocation pattern is important for understanding global carbon cycle and climate change (Shipley and Meziane, 2002; Fang *et al.,* 2018). Accordingly, changes in environmental conditions can have profound effects on plant biomass allocation (Fan *et al.,* 2009) and have significant effects at the forest community level (Niklas, 2005).

In recent years, ecologists have studied the warming effect on the root: shoot ratio or the allometric function relating root and shoot biomasses (Stegen *et al.,* 2011; Wu *et al.,* 2011). For instance, Reich *et al.* (2014), Zhang *et al.* (2015a, b), Lie and Xue (2016) and Fang *et al.* (2018) studied the allocation patterns of Chinese forests biomass across temperature gradients. However, these results have not been consistent (Roa-Fuentes *et al.,* 2012), and as a consequence, the biomass allocation patterns in many forest types are still unclear (Stegen *et al.,* 2011), and represent a particularly critical knowledge gap (Reich *et al.,* 2014; Lie *et al.,* 2018).

The major forest types in China include Alpine *Picea-abies* forest (APAF), temperate typical deciduous broadleaved forest (TDBF), temperate *Pinus tabulaeformis* forest (TPTF), subtropical montane *Cupressus* and *Sabina* forest (SCSF) and subtropical *P. massoniana* forest (SPMF), which spread in temperate and subtropical climates with varying site conditions. Currently, studies on biomass allocations between organs (such as stems, branches, leaves, and roots) in these forest types along temperature gradients are lacking. The objectives of the present study were to (1) study the effect of temperature on biomass allocations among tree organs, and (2) examine whether biomass allocations vary systematically with temperature in the above-mentioned forest types.

Materials and Methods

Studied Regions

The studied forests originate from natural forests and seeding plantations. APAF, TDBF and TPTF were distributed in temperate climate regions, whereas SCSF and SPMF were distributed in subtropical climate regions. Soils are classified as brown coniferous forest soils for APAF, brown coniferous forest soils and cinnamon soils for TDBF, TPTF, yellow brown earths

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and yellow cinnamon soils for SCSF, and yellow earths, red earth and lateritic red earth for SPMF, respectively (Unified Soil Classification System).

Datasets

We compiled biomass dataset from 730 sites of five forest types – APAF, TDBF, TPTF, SCSF and SPMF (Luo, 1996). Data on organs included stem, branch, leaf and root biomasses. Biomass of trees in forest was measured by destructive harvesting in experimental plots. For each selected data point, we obtained data on latitude, longitude, elevation, mean annual temperature and mean annual precipitation (Table 1). General statistics on the organ biomass for the five forest types are given in Table 2.

Data Analysis

The slope (α_{SMA}) and intercept (β_{SMA}) of regressions of forest organ biomass to mean annual temperature (MAT) relationships, and R/S ratio against MAT were determined using a standardized major axis regression of the data, with SMATR software Version 2.0 (Warton *et al.,* 2006). Differences were deemed significant at $P < 0.05$.

Results

Biomass and R/S Ratios of Different Forest Types

Stem, branch, leaf and root biomasses accounted for 53–71%, 8–20%, 4–9% and 15–21% of the overall forest biomasses, respectively (Table 2). Among the five forests, stem biomass comprised the highest percentage in APAF (71%) and the lowest in the broadleaved forest (TDBF) (53%), whereas the branch and leaf biomasses were the lowest in the APAF (8 and 4%, respectively), while the branch and root biomasses were highest in the TDBF (20 and 21%, respectively). The leaf biomass percentage was low in both forests with the lowest MAT (APAF), as well as the highest MAT (SPMF), whereas the root biomass percentage was generally high in forest types with low MATs (APAF, TDBF, and TPTF) ($P < 0.05$). The mean R/S values were between 0.18 and 0.28, in the order of SCSF (0.18) = SPMF (0.18) < APAF (0.21) < TPTF (0.25) < TDBF (0.28) ($P < 0.05$). Generally, forest types with low MATs were observed to have higher R/S values.

Effects of Warming on Forest Biomass

The stem, shoot and forest biomasses had significant correlations with MAT in APAF and SPMF ($P \leq 0.005$), and were significantly decreased in TDBF, TPTF and SCSF ($P \leq 0.05$) (Table 3). The branch biomass decreased significantly in TDBF and increased significantly in SPMF, but did not change significantly in APAF, TPTF, and SCSF with warming. Warming significantly decreased the leaf biomass in APAF and TDBF ($P \leq 0.007$) while it increased significantly in SPMF ($P = 0.001$) and did not change significantly in TPTF and SCSF. The root biomass showed significant increases in APAF and SPMF ($P \leq 0.021$), but no trend was observed in the other forest types with increasing temperature. Finally, the R/S significantly decreased with increasing temperature in APAF and significantly increased in TPTF and SCSF, but did not change significantly in TDBF and SPMF (Table 3).

Discussion

Biomass allocation greatly alters with changes in temperature (Xiao *et al.*, 2003), and across temperature gradients, the biomass in forest organs varies greatly (Wu *et al.*, 2011). Moreover, the organ biomass changes with forest types in response to warming, which suggests that temperature affects biomass allocation of forests (Lin *et al.*, 2010). In this study, the overall forest biomass of the coolest and hottest forest types (APAF and SPMF, respectively) exhibited significantly positive responses, while the other forest types showed obviously negative responses to warming (Table 3). In cold ecosystems, many biological processes of forests are limited by low temperatures (Sebastià, 2007), thus, making temperature potentially the most critical factor affecting biomass allocation in APAF.

Warming can enhance plant productivity (Luo *et al.*, 2009) by promoting photosynthesis in plants, prolonging the growth season (Majdi and Ohrvik, 2004) and enhancing nutrient availability (Lin *et al.*, 2010; Wu *et al.*, 2011). An increase in temperature accelerates the metabolic rates of trees, stimulates microbial activity and enhances soil nutrient mineralization, resulting in increased forest biomass, which is the reason for increasing MAT for APAF. Many studies have shown a biomass increase with increasing temperature in cold-temperate regions (Sebastià, 2007). With increasing MAT leaf biomass significantly decrease in APAF. Low temperature can limit many biological processes. Lambers *et al.* (2008) reported that low temperature impaired photosynthesis, nutrient uptake and the growth of plants leading to decreased leaf biomass. Conversely, increasing temperature enhances plant growth by stimulating plant photosynthesis due to increased soil nutrient mineralization (Melillo *et al.*, 2002) and extending the growth season (Zhou *et al.*, 2012), which ultimately results in increased leaf mass fractions. Increasing temperatures in winter may increase plant growth, because of enhanced plant metabolism, water absorption, and nutrient supply, as were observed in SPMF. A high mean annual precipitation range for SPMF (1012 to 2006 mm; Table 1) indicates that water availability is sufficient for tree growth, thus the sensitivity of the whole SPMF to soil water availability may be reduced (Ma *et al.*, 2010).

Table 1: Geographic and climatic data ranges for the five forest types in China

Forest type	Latitude (°N)	Longitude (°E)	Altitude (m)	Mean annual precipitation (mm)	Mean annual potential evapotranspiration (mm)	Mean annual Temperature (℃)
APAF	26.14 - 52.60	81.10 - 131.80	410 - 4200	370 - 1937	329 - 739	–6.6 - 13.9
TDBF	28.25 - 51.70	103.00 - 134.00	177 - 2600	410 - 1142	429 - 926	–3.3 - 18.6
TPTF	32.60 - 42.60	103.79 - 129.50	200 - 3200	403 - 1173	432 - 821	2.9 - 18.7
SCSF	25.50 - 33.59	85.20 - 113.10	65 - 3500	370 - 1937	382 - 967	2.7 - 18.2
SPMF	21.72 - 32.70	105.08 - 120.60	10 - 1950	1020 - 2006	795 - 1130	12.2 - 24.0

Data was adapted from Luo (1996)

Table 2: Organ biomass and stand biomass (Mg ha^{-1}); organ: stand percentage (%); and root: shoot ratios (R/S) for the five forest types in China

Forest Type		Organ				Shoot	Forest	R/S
		Stem	Branches	Leaves	Root			
APAF	Range	45.0 - 1280.3	6.5 - 116.2	3.3 - 38.7	8.7 - 131.3	55.9 - 1435.2	68.5 - 156.65	0.09 - 0.39
	Mean±SD	177.5 ± 119.5	19.3 ± 11.8	10.4 ± 5.4	43.0 ± 19.0	207.1 ± 129.3	250.1 ± 144.9	0.22 ± 0.05
	organ/stand	71	8	4	17			
TDBF	Range	12.2 - 129.9	2.8 - 62.7	1.6 - 9.4	3.6 - 40.5	16.6 - 198.8	20.1 - 239.2	0.11 - 0.52
	Mean±SD	47.1 ± 21.9	18.3 ± 9.1	5.2 ± 2.0	18.8 ± 7.1	70.6 ± 28.5	89.4 ± 33.6	0.28 ± 0.09
	organ/stand	53	20	6	21			
TPTF	Range	10.9 - 166.5	2.1 - 47.2	1.9 - 13.8	4.6 - 60.0	14.9 - 218.8	19.8 - 278.8	0.12 - 0.38
	Mean±SD	39.6 ± 20.9	9.3 ± 5.5	5.8 ± 2.3	13.4 ± 6.2	54.7 ± 27.2	68.1 ± 32.9	0.25 ± 0.04
	organ/stand	58	14	9	20			
SCSF	Range	15.3 - 208.6	6.4 - 57.8	3.4 - 21.1	3.8 - 71.2	25.1 - 240.6	28.9 - 280.4	0.10 - 0.34
	Mean±SD	76.6 ± 57.0	14.9 ± 9.9	9.5 ± 4.0	17.7 ± 14.6	100.9 ± 63.7	118.6 ± 75.9	0.18 ± 0.05
	organ/stand	65	12	8	15			
SPMF	Range	9.8 - 208.8	1.5 - 86.5	0.69 - 17.54	2.9 - 90.2	15.0 - 306.5	17.9 - 396.8	0.09 - 0.48
	Mean±SD	84.2 ± 44.1	19.1 ± 16.2	7.1 ± 3.3	20.3 ± 16.5	110.4 ± 57.6	130.3 ± 71.1	0.18 ± 0.06
	organ/stand	65	15	5	16			

The negative impacts of warming on biomass accumulation in TDBF, TPTF and SCSF may be attributed to an increased plant respiration/photosynthesis ratio and warming-aggravated water limitations (Clark, 2004). Wu *et al.* (2011) reported that although both ecosystem photosynthesis and respiration may be stimulated by increasing temperature, respiration eventually surpasses photosynthesis with sustained high temperatures. De Boeck *et al.* (2008) reported that warming-induced moisture stress may reduce biomass accumulation. Water availability limits biomass accumulation and affects forests responses to warming because the high temperature can aggravate water limitations by increasing evapotranspiration and lowering the soil water (Lin *et al.*, 2010). Concurrently, warming although increases biomass accumulation in some cases (Welker *et al.*, 2004; Sullivan *et al.*, 2008), the sensitivity of respiration to warming may eventually surpass ecosystem photosynthesis (Wu *et al.*, 2011). Thus, warming can decrease forest biomass due to moisture stress induced by high temperature (De Boeck *et al.*, 2008). This may explain the significant decrease in forest biomass with increasing MAT in TDBF, TPTF, and SCSF. This result is consistent with predictions of earlier reports (Wu *et al.*, 2011).

The R/S ratio is an index of energy allocation between roots and shoots (Fan *et al.*, 2008). In this study, the mean R/S value in the broadleaved forest (TDBF) was 0.25 and ranged from 0.18 to 0.25 in the four coniferous forest types. Furthermore, Jackson *et al.* (1996) and Wang *et al.* (2008) also found lower R/S ratios for coniferous forests than that of the broadleaved forests. However, Mokany *et al.* (2005) did not find a significant difference in the R/S ratio between coniferous and broadleaf forests. Thus, there are still many uncertainties concerning the R/S ratio of forests.

The high R/S ratio was observed in the low MAT forest types (Table 2), which is regarded as an adaptation to cold (Fan *et al.*, 2008; Song *et al.*, 2012). In cold environments, a lower root turnover results in the accumulation of more root biomass, to facilitate increased nutrient absorption of roots at higher soil temperatures (Fan *et al.*, 2009). Low temperatures can reduce the photosynthetic rate and also reduce respiratory losses, a condition favorable for biomass accumulation (Song *et al.*, 2012). Thus, the higher R/S ratios in the low MAT forest types may be explained by lower root turnover, more efficient nutrient absorption by roots, the balance between photosynthesis and respiration, and the partitioning photosynthate between shoots and roots.

Plants maintain a balanced functional economy by photosynthate partitioning and nutrient allocation between roots and shoots. Therefore, the R/S ratio balances the photosynthetic rate: absorption rate, thus, limiting plant

Table 3: Standardized major axis (SMA) regression slopes and y-intercepts represented as α_{SMA} and β_{SMA}, respectively, for data of forest-level organ biomasses (stem, branch, leaf and root biomasses), shoot biomass, forest biomass (M_T) (Mg ha^{-1}) and mean annual temperature (organ biomass = α_{SMA} MAT + β_{SMA}). Data, grouped according to stand types, were taken from Luo (1996)

Forest	Organ	α_{RMA} (95% CI)	β_{RMA} (95% CI)	*n*	R^2	*P*
APAF	Stem	39.47 (34.37, 45.33)	34.9 2 (7.09, 62.75)	168	0.178	< 0.001
	Branches	-3.884 (-4.524, -3.335)	33.28 (30.00, 36.56)		0.002	0.566
	Leaves	-1.788 (-2.076, -1.54)	16.87 (15.46, 18.29)		0.044	0.007
	Root	6.591 (5.676, 7.654)	19.17 (13.92, 24.41)		0.041	0.009
	Shoot	42.72 (37.08, 49.21)	52.86 (21.84, 83.88)		0.142	< 0.001
	Forest	47.87 (41.52, 55.18)	77.23 (42.19, 112.27)		0.133	< 0.001
	Root: shoot ratio	-0.0180 (-0.0209, -0.0155)	0.2814 (0.2617, 0.2956)		0.049	0.004
TDBF	Stem	-5.911 (-6.839, -5.109)	87.17 (79.95, 94.38)	180	0.021	0.050
	Branches	-2.463 (-2.847, -2.131)	35.02 (32.06, 37.99)		0.036	0.011
	Leaves	-0.5513 (-0.6358, -0.478)	8.933 (8.284, 9.581)		0.064	0.001
	Root	-1.925 (-2.228, -1.662)	31.8 (29.43, 34.18)		0.011	0.153
	Shoot	-7.71 (-8.911, -6.671)	122.9 (113.6, 132.2)		0.036	0.011
	Forest	-9.085 (-10.501, -7.86)	151 (140, 161.9)		0.034	0.013
	Root: shoot ratio	0.0236 (0.0204, 0.0274)	0.1193 (0.0899, 0.1488)		0.004	0.382
TPTF	Stem	-6.538 (-7.603, -5.622)	83.69 (75.9, 91.48)	163	0.053	0.003
	Branches	1.717 (1.471, 2.004)	-2.289 (-4.427, -0.151)		0.006	0.345
	Leaves	-0.7161 (-0.8361, -0.6132)	10.67 (9.77, 11.57)		0	0.856
	Root	-1.922 (-2.243, -1.647)	26.34 (23.96, 28.73)		0.007	0.287
	Shoot	-8.503 (-9.908, -7.297)	112.1 (101.7, 122.4)		0.027	0.037
	Forest	-10.27 (-11.98, -8.81)	137.4 (124.9, 150)		0.023	0.050
	Root: shoot ratio	0.0130 (0.0112, 0.0151)	0.1655 (0.1501, 0.1810)		0.055	0.002
SCSF	Stem	-12.95 (-18.55, -9.04)	236.1 (173.2, 298.9)	24	0.31	0.005
	Branches	2.238 (1.46, 3.43)	-12.7(-26.08, 0.68)		0.008	0.68
	Leaves	-0.9117 (-1.3947, -0.596)	20.7 (15.29, 26.1)		0.019	0.526
	Root	-3.313 (-5.075, -2.163)	58.54 (38.80, 78.27)		0.012	0.606
	Shoot	-14.46 (-21.06, -9.93)	279 (205.3, 352.7)		0.243	0.014
	Forest	-17.16 (-25.28, 11.64)	329.9 (239.3, 420.5)		0.191	0.033
	Root: shoot ratio	0.0122 (0.0083, 0.0180)	0.0256 (-0.0391, 0.0902)		0.186	0.035
SPMF	Stem	16.52 (13.64, 20.00)	-203.4 (-259.8, -147)	100	0.077	0.005
	Branches	6.054 (5.002, 7.329)	-86.36 (-106.99, -65.73)		0.081	0.004
	Leaves	1.24 (1.027, 1.497)	-14.50 (-18.67, -10.33)		0.104	0.001
	Root	6.175 (5.087, 7.496)	-87.25 (-108.62, -65.88)		0.053	0.021
	Shoot	21.54 (17.82, 26.03)	-264.7 (-337.4, -192)		0.097	0.002
	Forest	26.61 (22, 32.18)	-333.1 (-423.4, 242.8)		0.088	0.003
	Root: shoot ratio	0.0219 (0.0180, 0.0268)	-0.2044 (-0.2827, -0.1261)		0	0.885

responses (Sebastià 2007). The R/S ratio decreased with increasing MAT in APAF, indicating that root proportion decreases with increase in temperature (Mokany *et al.*, 2005). A large proportion of photosynthates are allocated to the shoots, which, in turn, allow this forest type to capture more photons (Mokany *et al.*, 2005). The R/S ratio increases significantly with increasing temperature in TPTF and SCSF. Under a dry environment, plants allocate more biomass to roots (Sebastià, 2007). High temperature decreases soil water content due to enhanced evapotranspiration, which may increase the proportional biomass allocation toward the roots (Wan *et al.*, 2002), leading to significant increases in the R/S ratio in TPTF and SCSF. In a warm and dry environment, plants allocating more biomass to roots are favorable for coping with drought stress and nutrient uptake. The impact of warming on root biomass is smaller than that of shoot biomass in TDBF, TPTF and SCSF. Likewise, Cairns *et al.* (1997) also did not find any correlation between root biomass and temperature. Overall, warming has a significantly greater effect on shoot biomass than on root biomass (Lin *et al.*, 2010).

Conclusion

In this study, biomass allocation responses to warming were observed to be dependent upon forest type. The results suggest that temperature has a significant effect on biomass partitioning, but that organ biomass–temperature relationship may vary according to forest type. The overall forest biomass of the coolest and hottest forest types (APAF and SPMF, respectively) exhibited significantly positive responses to warming, while the other forest types (TDBF, TPTF, and SCSF) showed distinct negative responses to warming. The broadleaf forest (TDBF) had a higher R/S ratio than the other four coniferous forests, and a higher R/S ratio was observed in the low MAT forest types. This information may be useful in improving our knowledge of forest ecosystem management, and in reducing the uncertainties in predicting forest carbon fixation at a regional level.

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