Full Length Article

Precipitation-Driven Changes in Biomass Allocation Pattern for Forests in China

Ming Yu, Wanqi Lin 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

Forests are main carbon pools in terrestrial ecosystems. Accurate estimation of forest biomass could improve estimation of the magnitude and distribution of carbon sinks. Precipitation-driven changes affect forest biomass, but the effects of precipitation on large-scale forest biomass patterns are still poorly understood in China. Here, biomass allocation patterns of eight typical forest types across China were studied to determine their biomass allocation patterns across broad precipitation. With increase of mean annual precipitation (MAP), stem, branch, leaf and shoot biomasses showed significant changes in seven of the eight forest types. Root biomass and MAP only had a significant relationship with four of the eight forest types. There was significant relationship between forest biomass and MAP in six of the eight forest types. Root: shoot ratios had a significant decline in four of the eight forest types. Root biomass was less limited by precipitation than shoot biomass. Precipitation affects biomass distribution patterns differentially in forest type, and the effects of future precipitation change on biomass are complex. © 2019 Friends Science Publishers

Key words: Allocation pattern; China; Forest biomass; Precipitation; Root: Shoot ratio

Introduction

Profound climatic change (IPCC, 2007; Ma *et al.*, 2010) affects forest growth and forest biomass (Barr *et al.,* 2007) due to its important function of CO_2 sink. The impact of climate change on the biomass allocation pattern of forests is not fully understood due to their long-life cycles (Rötzer *et al.,* 2009). An understanding on the both relationships is favorable to predict carbon storage with climate change (Lie *et al.,* 2018). Precipitation plays an important role in affecting forest biomass (Epstein *et al.,* 2002), and its change significantly alters net primary productivity (Fang *et al.*, 2018) and biomass of forest in terrestrial ecosystems (Ma *et al.,* 2010). Consequently, investigations on precipitation effect on forests can increase our knowledge on the response mechanisms of forest ecosystems to climate change (Fan *et al.,* 2009).

Some studies have proved that annual precipitation affects forest biomass (Sankaran *et al.,* 2005) based on data of a single forest type (Keith *et al.,* 2009). Although some biomass allocation patterns responses to precipitation are studied (e.g. Fang *et al.,* 2018; Lie *et al.,* 2018), the results of these studies have not been consistent, and therefore represent a particularly critical knowledge gap (Rötzer *et al.*, 2009; Reich *et al.*, 2014).

Plant biomass allocation has major effects on global carbon cycling (Houghton *et al.,* 2009) and has attracted much attention over the past decades (Yang *et al.,* 2010; Yang and Luo, 2011). Most studies are dedicated to shoot and root biomass, and most often root: shoot ratios in forests (Fan *et al.,* 2009). There are few studies on the relationship among organ biomass and precipitation. When different types of forest ecosystems are included, results have not been consistent (Yang and Luo, 2011). Consequently, it is unclear whether organ biomass changes with a precipitation gradient. How the forest allocates biomass to different organs remains uncertain (Roa-Fuentes *et al.,* 2012). Such information can improve our understanding of how precipitation affects the forest biomass (Stegen *et al.,* 2011).

Chinese forest types are distributed across a wide range of climatic regimes (Luo *et al.,* 2012). In these forests, there is a steep precipitation gradient. However, precipitation effects on their biomass allocations among tree organs remain unclear. The aim of this study is to examine whether biomass allocation patterns of main Chinese forest types vary across a mean precipitation gradient.

Materials and Methods

Dataset

A 1036-large organ biomass and climatic dataset was compiled from the literature (Tian and Pan, 1986; Hui *et al.*, 1988; Tian, 1989; Luo, 1996; Ding *et al.*, 1998; Ding, 2000,

2003; Chen *et al.*, 2001; Ding and Wang, 2001; Fang and Mo, 2002; Guo *et al.*, 2006; Peng, 2008; Li *et al.*, 2009; Xie *et al.*, 2009; Deng *et al.*, 2010; Li, 2010; Li, 2010; Tan, 2010; Zhang *et al.*, 2010; Cai, 2011; Wang *et al.*, 2011; Xiang *et al.*, 2011). These data were grouped into eight types: temperate Larix (*Larix principis-rupprechtii*, *L. gmelini* and *L. olgensis*) forest (TLF), temperate *Pinus tabulaeformis* forest (TPTF), temperate mixed coniferous-broadleaved forest (TCBF), temperate typical deciduous broadleaved forest (TDBF), temperate/subtropical montane Populus-Betula deciduous forest (TSPF), subtropical evergreen broadleaved forest (SEBF), subtropical *P. massoniana* forest (SPMF), and subtropical *Cunninghamia lanceolata* forest (SCLF). These are typical forest types from north to south in China (Luo, 1996). Table 1 shows, geographic ranges and distribution in the study area, for each forest type.

Forest biomass was determined using destructive harvesting method. In general, plot area ranged from 400 to 1 000 m^2 in these forest types. Organ allometric equations were established using organ biomass of standard trees to diameter at breast height (DBH) and tree height, and then organ mass in forests was estimated using these equations.

The information recorded for each data point was: (1) organ and total biomass; (2) DBH, tree height and forest age. Outlines of organ biomass, forest biomass and root: shoot ratio (R/S) for the eight forest types are given (Table 2).

Data Analysis

The slope α_{SMA}) and intercept β_{SMA}) of regressions, the biomass–MAP relationship (e.g., biomasses of organ, shoot (stem + branch + leaf) and forest (stem + branch + leaf + root), and R/S calculated from root and shoot biomasses against MAP were estimated by standardized major axis regression of data, using SMATR software Version 2.0 (Warton *et al.*, 2006).

Results

Mean values of stem, branch, leaf, root, shoot and forest biomasses in the eight forest types ranged from 39.6–113.4, 9.3–39.6, 4.5–9.9, 13.4–38.5, 54.7–161.4 and 68.1–199.9 Mg ha^{-1}, respectively. Stem, branch, leaf and root biomasses accounted for 53–78%, 9–20%, 3–10% and 16–26% of corresponding forest biomasses, respectively (Table 2). Forest biomass differed among the forest types (Table 2). Mean forest biomass decreased in the order of SEBF (199.9 Mg ha^{-1}) > TCBF (156.3 Mg ha^{-1}) > TLF (144.0 Mg ha^{-1}) > SPMF (130.4 Mg ha^{-1}) > SCLF (122.3 Mg ha^{-1}) > TSPF (116.8 Mg ha^{-1}) > TDBF (89.4 Mg ha^{-1}) > TPTF (68.1 Mg ha^{-1}). Among the eight forests, the percentage of stem biomass ranged from 53 to 61% in the four broadleaved forest types and from 58 to 78% in the four coniferous forests, while that of branch biomass ranged from 11 to 20%

in the four broadleaved forest types, which was generally greater than that in the four coniferous forest types. The percentage of leaf biomass was high in TPTF (9%) and SCLF (10%). Mean values of R/S ranged between 0.18 and 0.35. R/S had differences among the eight forest types, in the order: TSPF (0.35) > TLF (0.30) > TCBF (0.28) and TDBF (0.28) > TPTF (0.25) and SCLF (0.25) > SEBF (0.24) > SPMF (0.18).

Stem and branch biomasses had the same response patterns to precipitation change. With an increase of MAP, both biomasses showed a significant linear increase in seven forest types (P<0.049 and P<0.050; Table 3), except for TPTF. Leaf biomass had a significant linear increase for TLF, TSPF, SEBF, SPMF and SCLF (*P* < 0.002), and a significant linear decline in TPTF and TDBF (P<0.050). There was a significant relationship between root biomass and MAP in TDBF, TSPF, SPMF and SCLF (P<0.027). Shoot and forest biomasses increased significantly with MAP in TLF, TDBF, TSPF, SEBF, SPMF and SCLF (P<0.001), as did shoot biomass in TCBF (Table 3). R/S showed significantly linear decline in TLF, TPTF and SEBF (P<0.018), but had no trend in other forest types with increasing MAP (Table 3).

Discussion

The pattern of biomass allocation is strongly associated with species (Villar *et al.*, 1998). On the average, there were some differences of allocation into stem, branches and roots between coniferous and broadleaved forests. As regards stem, forest ratio in conifers was higher (63%) than in broadleaved forests (56%), whereas ratios of branch to forest (12%) and root to forest (19%) in conifers were smaller than corresponding ratios in broadleaved forests (18% and 22%). As regard to larger root: forest ratio in broadleaved forests than in coniferous forests was similar to that reported by Wang *et al.* (2008). Compared with coniferous trees, broadleaved trees with their higher growth rates and photosynthetic rates (Lusk *et al.*, 2003) frequently allocate more biomass to roots for acquiring greater nutrients and water, which is helpful for their survival and growth (Ruiz-Robleto and Villar, 2005).

In this study, with increasing MAP, stem, branch and shoot biomasses increased significantly in seven of the eight forest types and forest biomass increased significantly in six of the eight (P<0.05) (Table 3). This suggested that the precipitation gradient has important effect on these organ biomasses and forest biomass within these forest types. Increased in shoot biomass with an increase in MAP is in agreement with many early studies (e.g., Fan *et al.*, 2009). This suggests that water limitation imposes a common constraint on organ biomass or biomass of diverse forest types (Zhou *et al.*, 2009). Greater precipitation is favorable for tree growth (Wang and Gao, 2003). Reduced precipitation lowers soil nutrient availability, affects tree photosynthesis, and finally results in reduction in biomass

Table 1: Geographic and precipitation ranges for the eight forest types in data

Forest type	Latitude (°N)	Longitude (°E)	Altitude (m)	Mean annual temperature (°C)	Mean annual potential evapotranspiration (mm)	Mean annual precipitation (mm)
TLF	28.62–52.60	86.40–131.80	441–4240	–6.2–12.9	340–522	357–1274
TPTF	32.60–42.60	103.79–129.50	200–3200	2.9–18.7	432–821	380–1173
TCBF	40.88–50.70	123.90–133.50	233–770	–0.4–16.0	453–664	300–838
TDBF	28.25–51.70	103.00–134.00	177–2600	–3.3–18.6	429–926	410–1142
TSPF	25.75–52.50	85.20–134.00	150–3640	–5.5–17.4	358–940	241–1283
SEBF	20.70–30.25	85.20–120.17	80–4160	3.5–25.4	386–1132	637–2323
SPMF	21.72–32.70	105.08–120.60	10–1950	12.2–24.0	795–1130	1020–2006
SCLF	18.7–32.33	103.37–121.57	20–1910	9.4–22.4	679–1064	720–2989

Table 2: Organ biomass and forest biomass (Mg ha^{-1}) and organ: forest ratio (%), and root: shoot ratios (R/S) for the eight forest types

Forest type		Organ				Shoot	Forest	R/S
		Stem	Branches	Leaves	Root			
TLF	Range	10.2–249.8	3.0–33.7	0.5—13.0	3.1–92.0	17.6–294.4	20.8–384.6	0.09–0.69
	Mean±SD	95.4±54.8	12.9±7.2	4.6±2.7	31.1±19.0	112.9±62.9	144.0±77.4	0.30±0.16
	Organ/forest ratio	66	9	3	22			
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/forest ratio	58	14	9	20			
TCBF	Range	22.2–207.6	7.7–35.3	3.4–13.1	6.1–86.2	35.5–230.9	41.6–273.3	0.10–0.57
	Mean±SD	95.1±50.6	17.3±7.1	7.7±2.4	36.1±25.7	120.1±54.4	156.3±74.7	0.28±0.14
	organ/forest	61	11	5	23			
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/forest ratio	53	20	6	21			
TSPF	Range	11.7–181.8	2.1–48.8	1.5–10.6	3.4–87.1	15.3–240.2	18.7–315.6	0.09–0.50
	Mean±SD	66.4±29.9	15.4±7.8	4.5±2.2	30.5±15.1	86.3±37.5	116.8±51.5	0.35±0.08
	organ/forest	57	13	4	26			
SEBF	Range	30.2–329.7	4.2–211.9	2.8–28.5	10.0–232.5	37.2–570.1	47.4–657.3	0.09–0.81
	Mean±SD	113.4±52.2	39.6±28.5	8.4±4.4	38.5±24.9	161.4±81.7	199.9±101.2	0.24±0.08
	Organ/forest ratio	57	20	4	19			
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/forest ratio	65	15	5	16			
SCLF	Range	2.0–499.7	0.5–48.8	0.7–39.8	0.5–103.5	3.3–552.5	3.9–656.0	0.06–0.83
	Mean±SD	78.2±72.1	11.1±8.0	9.9±6.9	23.1±17.0	99.2±79.8	122.3±94.9	0.25±0.11

(Wu *et al.,* 2011). Stem, branch and forest biomasses of TPTF and forest biomass of TCBF were not correlated with MAP, which is in line with Dormann and Woodin (2002) and Wu *et al.* (2011) reports. Low temperature can seriously limit tree growth in cold regions (Peñuelas *et al.,* 2004), since the organ and forest biomasses of TPTF and TCBF types significantly increased with increasing mean annual temperature (data not shown). Warming accelerates metabolic rates, stimulates microbial activity and enhances organic matter mineralization (Shaver *et al.,* 2000), which consequently favors plant photosynthesis, growth and biomass accumulation (Rustad *et al.,* 2001).

Precipitation generally affects leaf biomass. This biomass increased significantly with mean precipitation in five of the eight forest types, and decreased significantly in two of the eight. Varying MAP did not significantly alter leaf biomass in TCBF (Table 3). This is in line with Poorter *et al.* (2012) who said that leaf biomass hardly changes with a water gradient. These varied patterns suggest that precipitation affect leaf biomass differently in Chinese forest types. It is therefore necessary to extend studies on

responses of leaf biomass for changes in precipitation change for understanding the mechanisms involved.

Root dynamics in response to precipitation remains largely uncertain, because of few studies are available on both the relationships (Zhou *et al*., 2009, 2012). Here, the eight forest types were divided into two groups according to MAP: a low annual precipitation group with MAP from 567–728 mm, including the four temperate forest types and one temperate-subtropical type; and a high annual precipitation group with MAP from 1395–1492 mm, including the three subtropical forest types. In the high MAP environment, forest types typically show small biomass allocation to roots (16–19%) and large allocation to shoots (81–85%). This is because competition for light is more important in such environments, which causes more shoot biomass. On the other hand, in the low MAP environment, forest types allocate large biomass to roots (20–26%) and small biomass to shoots (74–80%) relative to the high MAP environment, because forests with large root systems compete more for water (Villar *et al.,* 1998). The results showed that root biomass was significantly linearly related

Table 3: Standardized major axis regression (SMA) slopes and y-intercepts (α_{SMA} and β_{SMA}, respectively) for data of forest-level organ biomass, shoot biomass, forest biomass (Mg ha^{-1}) and mean annual precipitation (mm). Data, grouped according to forest types, were taken from Luo *et al.* (1996)

Forest type	Organ	α_{RMA} (95% CI)	β_{RMA} (95% CI)	n	R^2	P
TLF	Stem	0.3326 (0.2675, 0.4137)	-96.85 (-141.25, -52.44)	64	0.251	<0.001
	Branches	0.0439 (0.0349, 0.0551)	-12.45 (-18.59, -6.30)		0.179	<0.001
	Leaves	0.0163 (0.0129, 0.0205)	-4.792 (-7.116, -2.468)		0.149	0.002
	Root	0.1155 (0.0903, 0.1477)	-35.63 (-53.27, -17.99)		0.042	0.105
	Shoot	0.3818 (0.3070, 0.4747)	-107.7 (-158.7, -56.80)		0.252	<0.001
	Forest	0.4693 (0.3752, 0.5869)	-127.20 (-191.60, -62.80)		0.210	<0.001
	Root: shoot ratio	-0.0009 (-0.0012, -0.0007)	0.8481 (0.7082, 0.9881)		0.087	0.018
TPTF	Stem	0.2065 (0.1769, 0.2411)	-85.32 (-105.26, -65.38)	163	0.001	0.627
	Branches	0.0542 (0.0465, 0.0633)	-23.51 (-28.72, -18.31)		0.011	0.174
	Leaves	-0.0226 (-0.0264, -0.0194)	19.52 (17.37, 21.68)		0.024	0.050
	Root	-0.0607 (-0.0708, -0.0521)	50.10 (44.29, 55.91)		0.016	0.112
	Shoot	0.2686 (0.2300, 0.3136)	-107.7 (-133.7, -81.8)		0.001	0.629
	Forest	0.3245 (0.2779, 0.3789)	-128.2 (-159.6, -96.8)		0	0.917
	Root: shoot ratio	-0.0004 (-0.0005, -0.0004)	0.5013 (0.4642, 0.5383)		0.118	<0.001
TCBF	Stem	0.4850 (0.3555, 0.6618)	-258.1 (-371.3, -144.9)	39	0.101	0.049
	Branches	0.0676 (0.0499, 0.0914)	-31.89 (-47.22, -16.56)		0.149	0.015
	Leaves	0.0231 (0.01689, 0.0316)	-9.106 (-14.542, -3.671)		0.087	0.069
	Root	-0.2462 (-0.3415, -0.1775)	215.5 (154.6, 276.3)		0	0.981
	Shoot	0.5214 (0.3839, 0.7081)	-259.6 (-379.3, -139.8)		0.129	0.025
	Forest	0.7159 (0.5218, 0.9823)	-365.1 (-535.4, -194.8)		0.068	0.110
	Root: shoot ratio	-0.0014 (-0.0019, -0.0010)	1.271 (0.943, 1.6000)		0.042	0.210
TDBF	Stem	0.2215 (0.1925, 0.2548)	-93.23 (-113.36, -73.11)	180	0.094	<0.001
	Branches	0.0923 (0.0798, 0.1068)	-40.16 (-48.9, -31.42)		0.021	0.050
	Leaves	-0.0207 (-0.0239, -0.0178)	18.29 (16.3, 20.27)		0.961	<0.001
	Root	0.0721 (0.0624, 0.0834)	-26.94 (-33.74, -20.14)		0.027	0.027
	Shoot	0.2889 (0.2508, 0.3328)	-112.4 (-138.9, -86.0)		0.079	<0.001
	Forest	0.3404 (0.2954, 0.3922)	-126.3 (-157.6, -95.0)		0.075	<0.001
	Root: shoot ratio	-0.0009 (-0.0010, -0.0008)	0.8408 (0.7563, 0.9254)		0.006	0.290
TSPF	Stem	0.1654 (0.1413, 0.1937)	-40.8 (-58.72, -22.89)	137	0.132	<0.001
	Branches	0.0433 (0.0370, 0.0507)	-12.65 (-17.34, -7.95)		0.130	<0.001
	Leaves	0.0119 (0.0102, 0.0140)	-3.228 (-4.548, -1.908)		0.100	<0.001
	Root	0.0836 (0.0712, 0.0981)	-23.63 (-32.82, -14.43)		0.107	<0.001
	Shoot	0.2078 (0.1777, 0.2431)	-48.36 (-70.68, -26.05)		0.146	<0.001
	Forest	0.2851 (0.2437, 0.3337)	-67.9 (-98.62, -37.17)		0.141	<0.001
	Root: shoot ratio	0.0004 (0.0004, 0.0005)	0.0765 (0.0266, 0.1264)		0	0.850
SEBF	Stem	0.1723 (0.1522, 0.1952)	-129.9 (-161.4, -98.4)	240	0.044	0.001
	Branches	0.0940 (0.0838, 0.1055)	-93.15 (-108.94, -77.36)		0.185	<0.001
	Leaves	0.01439 (0.0129, 0.0161)	-11.93 (-14.25, -9.61)		0.246	<0.001
	Root	0.0821 (0.0723, 0.0932)	-77.46 (-92.83, -62.08)		0.006	0.225
	Shoot	0.2696 (0.2389, 0.3044)	-219.3 (-267.1, -171.5)		0.096	<0.001
	Forest	0.3339 (0.2954, 0.3775)	-271.6 (-331.6, -211.6)		0.073	<0.001
	Root: shoot ratio	-0.0003 (-0.0003, -0.0002)	0.5919 (0.5455, 0.6384)		0.029	0.009
SPMF	Stem	0.1756 (0.1484, 0.2078)	-160.7 (-203.0, -118.5)	240	0.290	<0.001
	Branches	0.0644 (0.0534, 0.0776)	-70.71 (-87.95, -53.47)		0.124	<0.001
	Leaves	0.0132 (0.0110, 0.0159)	-11.29 (-14.79, -7.79)		0.139	<0.001
	Root	0.0657 (0.0545, 0.0790)	-71.29 (-88.76, -53.81)		0.134	<0.001
	Shoot	0.229 0 (0.1934, 0.2711)	-209.0 (-264.3, -153.7)		0.284	<0.001
	Forest	0.2829 (0.2383, 0.3359)	-264.3 (-333.9, -194.8)		0.259	<0.001
	Root: shoot ratio	0.0002 (0.0002, 0.0003)	-0.1476 (-0.2149, -0.0804)		0	0.951
SCLF	Stem	0.1989 (0.1664, 0.2379)	-218.8 (-274.5, -163.1)	113	0.086	0.002
	Branches	0.0220 (0.0185, 0.0261)	-21.67 (-27.59, -15.75)		0.148	<0.001
	Leaves	0.0191 (0.0160, 0.0228)	-18.61 (-23.87, -13.36)		0.119	<0.001
	Root	0.0469 (0.0398, 0.0553)	-46.91 (-58.95, -34.87)		0.225	<0.001
	Shoot	0.2202 (0.1846, 0.2627)	-229.5 (-290.2, -168.7)		0.111	<0.001
	Forest	0.2617 (0.2199, 0.3115)	-268.4 (-339.6, -197.1)		0.134	<0.001
	Root: shoot ratio	0.0003 (0.0003, 0.0004)	-0.2423 (-0.3380, -0.1466)		0.026	0.085

to MAP in TDBF and three subtropical or temperate-subtropical forest types, and their shoot biomass increased concurrently (Table 3). This indicated increased accumulation of root biomass with precipitation in these forest types in China. Wang *et al.* (2008) also found

significant precipitation control of root biomass at large scale. Increasing root biomass favors nutrient uptake (Zhou *et al.,* 2012).

Root biomass did not significantly change along precipitation gradients in three temperate forest types and

SEBF (Table 3). Some studies also indicate that grassland roots may not respond to precipitation with enhanced root growth (Walter *et al.*, 2012). Cairns *et al.* (1997) did not find the relationship between root biomass and precipitation. Such lack of response of root biomass to precipitation is probably attributable to a decrease in the proportion of carbon allocation to roots and an increase in root turnover with precipitation (Zhou *et al.*, 2009). Zerihun *et al.* (2006) asserted that only when plants are subjected to severe drought, root biomass greatly increases in the cost of stems.

There are few studies on precipitation effect on R/S at large scale (Wang *et al.*, 2008; Zhou *et al.*, 2012). A significantly negative correlation between R/S and MAP was observed in TLF, TPTF and SEBF, suggesting that trees allocate less biomass to roots based on soil water condition (Table 3). This is coincident with other studies (Zerihun *et al.*, 2006; Wang *et al.*, 2008; Zhou *et al.*, 2009; Roa-Fuentes *et al.*, 2012). These results are in line with that available soil moisture strongly affects root biomass allocation (Chapin *et al.*, 1993), because drought leads to greater root biomass (Roa-Fuentes *et al.*, 2012).

The response of R/S to precipitation was inconsistent among forest types. Varying MAP did not alter the R/S of TCBF, TDBF, TSPF, SPMF and SCLF. Several reviews reported little or no link between MAP and R/S across various woody plant communities (Schenk and Jackson, 2002). This result implies that precipitation is less important in limiting root biomass in these forest types. Stiff allocation patterns may affect distribution of these forest types (Perkins and Owens, 2003).

Precipitation affects biomass distribution patterns differentially by forest type, some of which do not respond to changes in precipitation. This suggested that the effect of precipitation amount in determining biomass distribution depends to a large extent on the forests studied, and the effects of future precipitation change on biomass may be more complex than previously predicted. This confirms the importance of understanding forest biomass responses to future climate change over large scales to substantiate predictions of the effects of a changed climate on forest biomass.

Conclusion

This study examined biomass allocation patterns of eight typical forest types across China along precipitation gradients. With increase of MAP, stem, branch, leaf and shoot biomasses showed significant changes in seven of the eight forest types. These results indicate that precipitation is one of important factors explaining the global variation in biomass among forests. Precipitation affects biomass allocation differentially for different forest types, which suggests complexity and challenges in seeking general patterns of forest biomass accumulation in a future, precipitation change world.

References

Barr, A.G., T.A. Black, E.H. Hogg, T.J. Griffis, K. Morgenstern, N. Klujn, A. Theede and Z. Nesic, 2007. Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. *Glob. Change Biol.*, 13: 561–576

Cai, Q.L., 2011. Research on the Biomass of *Pinus massoniana* Plantations. *J. Anhui Agric.*, 39: 7122–7124

Chapin, F.S. III., K. Autumn and F. Pugnaire, 1993. Evolution of suites of traits in response to environmental stress. *Amer. Nat.*, 142: S72–92

Chen, Z.X., Y.J. He, F.M. Bai, J.H. Zhang and Z.H. Li, 2001. Effects of stand density on the biomass and productivity of *Pinus massoniana* air-sowing stands. *J. Cent South Univ. For. Technol.*, 21: 44–47

Deng, H.P., G. Geng and Z.C. Wang, 2010. Carbon storage and allocation of 35-years-old *Pinus massoniana* forest ecosystem in southern of Henan province. *J. Cent South Univ. For. Technol.*, 30: 6-9

Ding, G.J., 2000. Study on change laws of biomass and productivity of Masson pine forest plantation. III. Biomass and productivity of different site. *J. Mt. Agric. Biol.*, 19: 411–417

Ding, G.J., 2003. Study on biomass and productivity of Masson pine planting stand. I. Biomass and density effect of different planting density. *J. Fujian Coll. For.*, 23: 34–38

Ding, G.J. and P.C. Wang, 2001. Study on change laws of biomass and productivity of Masson pine forest plantation. II. Biomass and productivity of stand at different ages. *For. Res.*, 15: 54–60

Ding, G.J., P.C. Wang and R.F. Yang, 1998. Studies on the dynamic change of the commercial biomass of Masson pine pulpwood stands and its modeling. *Sci. Silvae Sin.*, 34: 33–41

Dormann, C.F. and S.J. Woodin, 2002. Climate change in the arctic: using plant functional types in a meta-analysis of field experiments. *Funct. Ecol.*, 16: 4–17

Epstein, H.E., I.C. Burke and W.K. Lauenroth, 2002. Regional patterns of decomposition and primary production rates in the US Great Plains. *Ecology*, 83: 320–327

Fan, J.W., K. Wang, W. Harris, H.P. Zhong, Z.M. Hu, B. Han, W.Y. Zhang and J.B. Wang, 2009. Allocation of vegetation biomass across a climate-related gradient in the grasslands of Inner Mongolia. *J. Arid. Environ.*, 73: 521–528

Fang, Y.R., X.J. Zou, Z.Y. Lie and L. Xue, 2018. Variation in organ biomass with changing climate and forest characteristics across Chinese forests. *Forests*, 9: 521

Fang, Y.T. and J.M. Mo, 2002. Study on carbon distribution and storage of a pine forest ecosystem in Dinghushan biosphere reserve. *Guihaia*, 22: 305–310

Guo, C.Y., J.L. Wu, Y.L. Tian and L.S. Guo, 2006. A study on the biomass of *Pinus tabulaeformis* forest on the different densities on Daqing Mountain. *J. Inner Mongolia Agri. Univ.*, 27: 29–33

Houghton, R.A., F. Hall and J.G. Scott, 2009. Importance of biomass in the global carbon cycle. *J. Geophys. Res.*, 114: 1–13

Hui, G.Y., S.Z. Tong, J.F. Liu and Y.W. Luo, 1988. Study on the afforestation density of *Cunninghamia lanceolata*. I. The effect of density on biomass of young growth of *C. lanceolata*. *For. Res.*, 1: 410–417

Intergovernmental Panel on Climate Change (IPCC), 2007. Climate change 2007: summary for policymakers. Contribution of Working Group I to the 4th Assessment Report of the IPCC. IPCC Secretariat, Geneva, Switzerland

Keith, H., B.G. Mackey and D.B. Lindenmayer, 2009. Reevaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proc. Natl. Acad. Sci. USA*, 106: 11635–11640

Li, B.B., W.H. Jian, Y. Qin, Y.Z. Zhang and Z.B. Wang, 2009. Relations of stand density and the biomass of the artificial young *Larix principis-upprechtii* forest. *Hebei J. For. Orchard Res.*, 24: 244–247

Li, Y., 2010. Carbon storage of *Cunninghamia lanceolata* mature plantation in Shaowu, Fujian Province. *Ph.D. Dissertation*. Chinese Academy of Forestry, Beijing, China

Li, Z., Zhou, W., Q.W. Guan, W. Wei, P. Dong and H.N. Zhang, 2010. Biomass and its influencing factors of *Platyclatdus orientalis* plantation in the limestone mountains of Xuzhou. *J. Anhui Agric. Univ.*, 37: 669–674

Lie, Z.Y., L. Xue and D.F. Jacobs, 2018. Allocation of forest biomass across broad precipitation gradients in China's forests. *Sci. Rep.*, 8: 10536

Luo, T.X., 1996. Patterns of Net Primary Productivity for Chinese Major Forest Types and their Mathematical Models. *Ph D. Dissertation*. Chinese Academy of Sciences, Beijing, China

Luo, Y.J., X.K. Wang, X.Q. Zhang, T.H. Booth and F. Lu, 2012. Root: shoot ratios across China's forests: Forest type and climatic effects. *For. Ecol. Manage.*, 269: 19–25

Lusk, C.H., I. Wright and P.B. Reich, 2003. Photosynthetic differences contribute to competitive advantage of evergreen angiosperm trees over evergreen conifers in productive habitats. *New Phytol.*, 160: 329–336

Ma, W.H., Z.L. Liu, Z.H. Wang, W. Wang, C.Z. Liang, Y.H. Tang, J.S. He and J.Y. Fang, 2010. Climate change alters interannual variation of grassland aboveground productivity: evidence from a 22-year measurement series in the Inner Mongolian grassland. *J. Plant Res.*, 123: 509–517

Peng, L.F., 2008. Preliminary study on the biomass of *Phoebe bournei* plantation with different density and site condition. *J. Fujian For. Sci. Technol.*, 35: 15–18

Peñuelas, J., C. Gordon, L. Llorens, T. Nielsen, A. Tietema, C. Beier, P. Bruna, B. Emmett, M. Estiarte and A. Gorissen, 2004. Nonintrusive field experiments show different plant responses to warming and drought among sites, seasons, and species in a north-south European gradient. *Ecosystems*, 7: 598–612

Perkins, St.R. and M.K. Owens, 2003. Growth and biomass allocation of shrub and grass seedlings in response to predicted changes in precipitation seasonality. *Plant Ecol.*, 168: 107–120

Poorter, H., K.J. Niklas, P.B. Reich, J. Oleksyn, P. Poot and L. Mommer, 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.*, 193: 30–50

Reich, P.B., Y.J. Luo, J.B. Bradford, H. Poorter, C.H. Perry and J. Oleksyn, 2014. Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proc. Natl. Acad. Sci. USA*, 111: 13721–13726

Roa-Fuentes, L.L., J. Campo and V. Parra-Tabla, 2012. Plant biomass allocation across a precipitation gradient: An approach to seasonally dry tropical forest at Yucatán, Mexico. *Ecosystems*, 15: 1234–1244

Rötzer, T., T. Seifert and H. Pretzsch, 2009. Modelling above and below ground carbon dynamics in a mixed beech and spruce stand influenced by climate. *Eur. J. For. Res.*, 128: 171–182

Ruiz-Robleto, J. and R. Villar, 2005. Relative growth rate and biomass allocation in ten woody species with different leaf longevity using phylogenetic independent contrasts (PICs). *Plant Biol.*, 7: 484–494

Rustad, L., J. Campbell, M. Marion, R. Norby, M. Mitchell, A. Hartley, J. Cornelissen, J. Gurevitch and GCTE-NEWS, 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126: 543–562

Sankaran, M., N.P. Hanan, R.J. Scholes, J. Ratnam, D.J. Augustine, B.S. Cade, J. Gignoux, S.I. Higgins, X. Le Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K.K. Caylor, M.B. Coughenour, A. Diouf, W. Ekaya, C.J. Feral, E.C. February, P.G. Frost, P. Hiernaux, H. Hrabar, K.L. Metzger, H.H. Prins, S. Ringrose, W. Sea, J. Tews, J. Worden and N. Zambatis, 2005. Determinants of woody cover in African savannas. *Nature*, 438: 846–849

Schenk, H.J. and R.B. Jackson, 2002. Rooting depths, lateral root spreads, and belowground/aboveground allometries of plants in water-limited environments. *J. Ecol.*, 90: 480–494

Shaver, G.R., J. Canadell, F.S.III. Chapin, J. Gurevitch, J. Harte, G. Henry, P. Ineson, S. Jonasson, J. Melillo, L. Pitelka and L. Rustad, 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bioscience*, 10: 871–882

Stegen, J.C., N.G. Swenson, B.J. Enquist, E.P. White, O.L. Phillips, P.M. Jørgensen, M.D. Weiser, A.M. Mendoza and P.N. Vargas, 2011. Variation in above-ground forest biomass across broad climatic gradients. *Global Ecol. Biogeogr.*, 20: 744–754

Tan, J.S., 2010. Biomass Dynamics in Successive Rotations of Chinese fir Plantation in Huitong. *Ph. D. Dissertation*. Central South University of Forestry Technology, Changsha, China

Tian, D.L., 1989. Studies on nutrient elements cycling and density effect of pole stage of *Pinus massoniana* stand. *Sci. Silvae Sin.*, 25: 106–112

Tian, D.L. and W.C. Pan, 1986. Preliminary discussion on biomass timber differentiation and density effect of masson's pine pole stands. *Chin. J. Plant Ecol.*, 10: 294–301

Villar, R., E.J. Veneklaas, P. Jordano and H. Lambers, 1998. Relative growth rate and biomass allocation in 20 *Aegilops* (Poaceae) species. *New Phytol.*, 140: 425–437

Walter, J., K. Grant, C. Beierkuhnlein, J. Kreyling, M. Weber and A. Jentsch, 2012. Increased rainfall variability reduces biomass and forage quality of temperate grassland largely independent of mowing frequency. *Agric. Ecosyst. Environ.,* 148: 1–10

Wang, R.Z. and Q. Gao, 2003. Climate-driven changes in shoot density and shoot biomass in *Leymus chinensis* (Poaceae) on the North-east China Transect (NECT). *Global Ecol. Biogeogr.*, 12: 249–259

Wang, X.P., J.Y. Fang and B. Zhu, 2008. Forest biomass and root–shoot allocation in northeast China. *For. Ecol. Manage.*, 255: 4007–4020

Wang, X.Y., Y.J. Sun and W. Ma, 2011. Biomass and carbon storage distribution of different density in *Larix olgensis* plantation. *J. Fujian Col. For.*, 31: 221–226

Warton, D.I., I.J. Wright, D.S. Falster and M. Westoby, 2006. Bivariate line-fitting methods for allometry. *Biol. Rev.*, 81: 259–291

Wu, Z.T., P. Dijkstra, G.W. Koch, J. Peñuelasa and B.A. Hungate, 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biol.*, 17: 927–942

Xiang, W.H., S.H. Liu, X.W. Deng, A.H. Shen, X.D. Lei, D.L. Tian, M.F. Zhao and C.H. Peng, 2011. General allometric equations and biomass allocation of *Pinus massoniana* trees on a regional scale in southern China. *Ecol. Res.*, 26: 697–711

Xie, W.D., S.M. Ye, M. Yang and L.J. Zhao, 2009. Biomass and distribution pattern of *Pinus massoniana* plantation in southeast area of Guanxi. *J. Beihua Univ.*, 10: 68–71

Yang, Y.H., J.Y. Fang, W.H. Ma, D.L. Guo and A. Mohammat, 2010. Large scale pattern of biomass partitioning across China's grasslands. *Global Ecol. Biogeogr.*, 19: 268–77

Yang, Y.H. and Y. Luo, 2011. Isometric biomass partitioning pattern in forest ecosystems: Evidence from temporal observations during stand development. *J. Ecol.*, 99: 431–437

Zerihun, A., K.D. Montagu, M.B. Hoffmann and S.G. Bray, 2006. Biomass in *Eucalyptus populnea* woodland communities of northeast Australia along a rainfall gradient. *Ecosystems*, 9: 501–515

Zhang, S.G., J. Liu, K.Y. Huang, R.L. Liang and X. Lan, 2010. Biomass and distribution patterns of *Pinus massoniana* plantation in northwest Guangxi. *Guangxi For. Sci.*, 39: 189–192

Zhou, X.H., S.F. Fei, R. Sherry and Y.Q. Luo, 2012. Root Biomass Dynamics under experimental warming and doubled precipitation in a tallgrass prairie. *Ecosystems*, 15: 542–554

Zhou, X.H., M. Talley and Y.Q. Luo, 2009. Biomass, litter, and soil respiration along a precipitation gradient in southern great plains, USA. *Ecosystems*, 12: 1369–1380