Biomass partitioning and allometric relations of the *Reaumuria soongorica* shrub in Alxa steppe desert in NW China

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ABSTRACT

Allometry and partitioning of above- and below-ground biomass are needed to evaluate the sustainability of arid ecosystems. Biomass accumulation, allocation patterns, and allometric relationships for above- and below-ground components of the desert shrub *Reaumuria soongorica* were studied across five age classes (0–10, 11–20, 21–30, 31–40, and > 40 years) in Alxa desert steppe, northwestern (NW) China, where the biomass of each shrub component (i.e., leaves, branches, and coarse and fine roots) was harvested by destructive sampling and the allocation patterns between leaves (M_L), roots (M_R), branches (M_B) were studied by regression analysis of log_{10}-transformed data, and tested for data classified by age class and pooled data. By using basal diameter, age, height, and canopy area, we can predict the allometry properties of the *R. soongorica* shrub in terms of age class and/or entire age-sequence. The experimental results indicate that biomass accumulation has an obvious gradient across the five age classes, branch, and coarse root biomass were the main biomass pool as mature shrub. *R. soongorica* shrub partitioned a greater proportion of total biomass to roots with age in order to adapt to the extreme arid conditions. Shrub allometry was affected by variation of biomass partitioning, where the allometric relationships were strongly related to basal shrub diameter for almost all shrub components. Allometric biomass relationships were improved with the introduction of a second variable crown area.

1. Introduction

Reaumuria soongorica is the dominant shrub species in the Alxa steppe desert (37° to 42° N and 93° to 106° E) in northwestern (NW) China. Knowledge of the allometry and partitioning of shrub biomass are necessary for estimating carbon fixation and cycling (Vogt, 1991; Greaves et al., 2015; Jin et al. 2018), as well as for understanding shrub adaptive strategies to extreme arid environments (Nicola and Pickett, 1983; Zandler et al., 2015).

Biomass partitioning plays a critical role in carbon cycling by shifting the products of photosynthesis among different plant organs (stems, leaves and roots) (Niklas and Enquist, 2002; Ong et al., 2004; Yang et al., 2010; Yang et al., 2017). Currently, an incomplete understanding of carbon allocation has limited the ability to model ecosystem metabolism and accurately predict the impact of global change on the carbon cycle (Niklas and Enquist, 2002; Yang et al., 2010; Tian et al., 2015). Age is an important factor affecting biomass partitioning of perennial plants (Peichl and Arain, 2007; Gargaglione et al., 2010). In the single-species, even-aged plantation, results obtained through traditional growth and yield studies showed that the increment of height,

diameter, volume, and biomass gradually decrease with age, and the allocation of biomass also changes greatly (Peichl and Arain, 2007; Tian et al., 2015; Köhl et al., 2017), the decline in plant growth and changes in partitioning relationships over time may be due to variations in the required resources supply (light, nutrients, water), changes in the balance between photosynthesis and respiration, increased hydraulic resistance, and reduced nutritional supply, or genetic changes with meristem age (Ryan et al., 1997; Köhl et al., 2017). For many species, the small plants have a greater proportion of roots and leaves than older plants (Peichl and Arain, 2007; Tian et al., 2015). Thus, the study of the relationship between biomass partitioning and age is of great significance for understanding the biomass dynamics of perennial woody plants. However previous studies on biomass partitioning focus more on environmental and biological factors such as plant species, landform, soil texture, humidity, and nutrients and rarely paid attention to age factors (Yang et al., 2010; Gargaglione et al., 2010). In addition, due to influence of variation in regional climate and hydrological environment, coverage and age structure of *R. soongorica* have changed significantly in recent decades (Zhang et al., 2008; Wang et al., 2017). Thus, it is necessary to understand the present partitioning

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characteristics of above- and below-ground biomass for different age classes and to perform quantitative estimation of biomass and carbon storage at regional and/or global scale (Vogt, 1991; Gargaglione et al., 2010).

Allometric relationships among plant components have been extensively studied in various ecosystems or species (Niklas and Enquist, 2002; Enquist and Niklas, 2002; Gargaglione et al., 2010). Several conceptual models have been proposed to describe allometric relationships at the stage of stand development (Müller et al. 2000; Niklas and Enquist, 2002). A hypothesis "the canonical rules" was put forward to illustrate general allometric relationships (Niklas and Enquist, 2002; Enquist and Niklas, 2002). These allometric relationships are less affected by environmental factors (e.g., rainfall, temperature, and soil nutrients) and more related to species (Enquist and Niklas, 2002). This hypothesis has been widely investigated on spatial distribution (Gargaglione et al., 2010), however, information about temporal distribution is scarce, especially for shrubs. The temporal pattern of species allometric relationships may be different from the spatial pattern, as it may be more complex to combine site characteristics (Yang and Luo, 2011). Research is necessary to clarify the relationship between age and biomass allometric relationships among plant components. Optimal partitioning concept is another popular theory for biomass allocation, which suggests that plants preferentially partition more biomass to the tissue that acquires limited resources (Mccarthy and Enquist, 2007; Gargaglione et al., 2010). This indicates that plants adapt to stress environment by adjusting the allocation of biomass in various parts to obtain more limited resources such as light, water, and nutrients, and maintain a maximum growth rate (Ryser and Eek, 2000; Ong et al., 2004; Mokany et al., 2006; Bogeat-Triboulot et al., 2007; Herzog et al., 2013).

In general, biomass and carbon stock estimation at regional scale, is obtained by using allometric relationships (general allometric equations) on vegetation survey data at plot-level (Peichl and Arain, 2007). Previous research has reported plenty of allometric equations for various species in many geographical and ecological environmental, but age-specific equations are still lack for many species (Peichl and Arain, 2007; Kuyah et al., 2013; Yang et al. 2017). It is well known that biomass allocation of plant components varies throughout the life cycle, this may change the relationship between plant variables (e.g. tree diameter) and related biomass (Peichl and Arain, 2007; Gargaglione et al., 2010), and therefore, different allometric biomass equations may be required depending on the stage of plant development. The application of allometric equations without regard to age may bring considerable over- or under-estimation of plant biomass (Peichl and Arain, 2007). In addition, it is difficult to *trans*-use these existing biomass allotment equations due to inconsistent methodologies and definitions as well as the effects of specific factors that may affect the biomass allometry (Jenkins et al., 2003; Lambert et al., 2005). Therefore, it is necessary to establish and improve the specific biomass relationships for specific areas with typical plant species.

The objectives of this research are: (i) to quantify biomass partitioning for shrubs of the Alxa desert steppe, (ii) to clarify whether these allometric patterns follow canonical rules, and (iii) to provide allometric relationships for above- and below-ground components in terms of age class (0–10, 11–20, 21–30, 31–40, >50 years) as well as the whole age sequence.

2. Methods

2.1. Study site

The study was conducted at the southwestern margin of the Alxa Plateau (101° 34′ E, 38° 46′ N). The area is characterized as a transitional desert steppe with temperate continental extreme arid climate with low rainfall, abundant sunshine, strong wind, and deficient surface water. Meteorological data during 1999 to 2018 were obtained from the local Meteorological Authority. The mean annual precipitation is 119.5 mm, 80% of which occur between May and September. Pan evaporation is 2722 mm. The groundwater level is > 40 m below ground. The mean annual air temperature is 9.4 °C with a mean maximum air temperature of 24.2 °C in July and a mean minimum air temperature of −7.0 °C in January. The average annual sunshine duration is 2991.7 h, and the average annual frost-free period is 170 days. Northwestern winds prevail in spring, the maximum wind speed on record is > 24.5 m per second. The soil type is grey-brown desert soil with 62% sand, 20% silt, and 18% clay. The average organic matter content is about 4.84 g kg^{-1}. The predominant vegetation is *Reaumuria soongorica* (Pall.) Maxim, associated with *Salsola passerina*, *Kalidium foliatum,* and *Peganum harmala L.*

2.2. Field measurements

Vegetation investigation was carried out in three square plots of 100 m^2. Canopy cover (the ratio of total canopy projection area over the experimental plot area) of all ground vegetation was 18.6 ± 6.7% and that of *R. soongorica* shrubs was 11.5 ± 3.0% in the study area. In each plot, the total number of *R. soongorica* shrubs was counted, basal diameter (D), height (H), and crown area (C) of each *R. soongorica* shrub were measured (Table 1). In one of the three plots, we cut all *R. soongorica* shrubs from the base diameter and took high-definition (HD) photos of rings for analyzing age composition (Table 1). Shrubs were classified into five age classes, class I (0–10 years), II (11–20 years), III (21–30 years), IV (31–40 years), and V (>40 years). The oldest *R. soongorica* shrub observed was 56 years at our study site.

In the adjacent area of the above mentioned three vegetation investigation plots, we randomly selected and excavated 118 individuals of *R. soongorica* with base diameters spanning from the lower to the upper end during July to September (period of maximum biomass accumulation for *R. soongorica* during the growing season) 2018. Basal diameter (mean of two perpendicular measurements, buried stems by soil were cleared with a shovel), height (at center), and crown area (according to the calculation formula of ellipse area by taking the longest and shortest diameters through the center of the fullest part of the canopy) of selected shrubs were measured. Cut shrubs up to the ground with pruning shears and all above-ground components (branches and leaves) were placed in individual paper bags for transport and drying. HD photos of rings were taken for analyzing age on computer. Roots of individual shrubs were completely excavated with a shovel on a circular plot centered on stump until no roots were found (approximate maximum rooting depth 0.7 m for study area). Personnel were assigned to collect broken roots during excavation to minimize the loss of fine roots. In the laboratory, branch-leaf components were allowed to air-dry for several days to facilitate hand separation. The main stem of *R. soongorica* is very short and it is classified as branch biomass. Roots

Table 1
Basic characteristics of *R. soongorica* stands in the Alxa desert steppe.

Species	Canopy cover (%)	Plant density (shrubs ha^{-1})	Mean D (mm)	Mean H (cm)	Mean C (cm^2)	Age class (%)				
						I	II	III	IV	V
R. Soongorica	11.5 ± 3.0	5700 ± 1150	13.1 ± 8.1	23.9 ± 7.2	1807.9 ± 1194.6	15.8	28.1	26.3	19.3	10.5

Note: mean ± S.E.; n = 3 vegetation investigation plots.

Table 2
Biomass of *R. soongorica* components (g shrub^{-1}) according to age class.

Shrub component	Biomass (g shrub^{-1})				
	Age class I	Age class II	Age class III	Age class IV	Age class V
Foliage	1.32 ± 0.75	4.35 ± 1.60	10.30 ± 3.01	18.38 ± 3.17	23.40 ± 3.86
Branches	1.61 ± 1.37	11.36 ± 6.95	55.43 ± 22.80	129.75 ± 36.36	232.94 ± 61.62
Total above-ground	2.92 ± 2.06	15.71 ± 8.18	65.73 ± 25.63	148.13 ± 38.92	256.34 ± 65.09
Coarse roots	0.55 ± 0.41	3.87 ± 2.01	18.87 ± 8.03	44.87 ± 12.57	86.59 ± 33.29
Fine roots	0.27 ± 0.12	1.22 ± 0.64	3.81 ± 1.50	5.51 ± 1.15	8.51 ± 1.86
Total below-ground	0.82 ± 0.45	5.09 ± 2.61	22.68 ± 9.44	50.38 ± 13.48	95.09 ± 34.85
Total shrub	3.74 ± 2.52	20.80 ± 10.69	88.41 ± 34.93	198.51 ± 51.00	351.43 ± 97.62
Root to shoot ratio	0.28	0.32	0.34	0.34	0.37

Note: mean ± S.D.; n = 27, 31, 18, 25, and 17 individuals for age class I-V, respectively.

were sorted as fine roots (<2 mm in diameter, with a main function to absorb water and nutrients from soil) and coarse roots (>2 mm in diameter, with a major function to anchor plants to the soil and transport water and nutrients), and excavated roots were cleaned manually with a brush. All component materials were oven-dried at 65 °C to constant weight, allowed to cool for 4–6 h, and weighed by an electronic balance (0.01 g) for biomass calculation (Peichl and Arain, 2007). For harvested 118 shrubs, mean basal diameters were 3.7, 8.2, 14.3, 19.6, and 26.1 mm, mean ages were 6.8, 15.5, 25.7, 34.5, and 45.5 years, mean heights were 12.2, 15.9, 24.7, 32.5, and 33.3 cm, and mean crown areas were 112.6, 371.7, 1380.0, 3364.9, and 3481.1 cm^2 for age classes I-V respectively.

Carbon content of different components was determined using the dichromate oxidation method of Walkley and Black (1934); plant samples were crushed and sieved through 0.25 mm size, and heat-treated in standard potassium dichromate-sulfuric acid solution at 135 °C for 30 min, then the amount of oxidants remaining was determined. The growth rate was calculated by dividing the average of total biomass by average age. Relative share of different shrub components of each class age was calculated by dividing the component biomass by corresponding total biomass. Biomass of the *R. soongorica* shrub in Alxa steppe desert was calculated by biomass equations and characteristic parameters of *R. soongorica* stands in Table 1.

2.3. Biomass allometric scaling

Biomass data were log$_{10}$-transformed to apply a biomass allometric function between aboveground biomass (M$_A$), branch (M$_B$), root (M$_R$), and leaves (M$_L$). We verified "the canonical rules", predicting that the leaf biomass has a direct relationship to 3/4 power of branch (including stem) or root biomass and branch biomass is proportional to first power of root biomass. The analyses for allometric scaling were conducted on classified and pooled biomass data.

To estimate shrub biomass, two power equations were developed by stepwise regression of dry biomass data using basal diameter (D), age (A), height (H) and crown area (C) for all shrub components. One of them takes D as only input variable and is shown in Eqn. (1). Another equation has two input variables, the first is D with an explanatory variable (A, H or C) as described by Eqn. (2).

$$y_i = c(x_1)^a \qquad (1)$$

$$y_i = c(x_1)^a(x_2)^b \qquad (2)$$

where y_i is dry mass (g) of a shrub component (e.g., leaves, branches, total above-ground, fine-roots, coarse-roots, total below-ground, and total shrub); c is a constant; a and b are the power exponents of first and explanatory variable; x_1 is D (mm); x_2 is A (years), H (cm) or C (cm^2). When including the second variable improved the equation fit significantly, we use Eqn. (2) to give the biomass estimate, otherwise, Eqn. (1).

2.4. Statistical analysis

Statistical and regressive analyses for biomass partitioning pattern and allometric relationships were accomplished with SPSS 23.0 and Origin 9.0 software packages. We assessed the uncertainty in shrub biomass estimates as a result of finite precision of measuring equipment and sampling methods. The electronic balance (±0.01 g) may have caused an error of <1.0, 0.5, 0.1, 0.1, and 0.1% of individual shrub biomass for age classes I-V, respectively. Incomplete gathering of fine roots may have caused uncertainty errors. We compared the fine root biomass obtained by excavation method with soil coring method, which was conducted in the same plot at the time of study. It showed a potential underestimation of 5, 13, 15, 11, and 22% of fine root biomass that led to a total uncertainty of shrub biomass estimates of <1.3, 0.8, 0.6, 0.3, and 0.5% for age classes I-V, respectively. The error of branch (old branch + twig) and foliage biomass from the disturbance of new twigs which were easily sorted into leaves was estimated to be <2% of branch biomass and 5% of foliage biomass for all age classes. These errors did not affect estimates of total shrub biomass as we could calculate total shrub biomass using total above-ground biomass (old branch + twig + foliage). Similarly, the partition of coarse and fine roots did not affect the estimation of total shrub biomass. Based on the above mentioned error sources, the total error of the results will be <2.3, 1.3, 0.7, 0.4, and 0.6% of total shrub biomass across the five age classes. This may be considered as a small uncertainty in total shrub biomass estimate.

3. Results

3.1. Biomass partitioning

Dry mass of *R. soongorica* components is shown in Table 2. The first three age classes have a larger standard deviation than the older classes. The average biomass of each shrub component increased with age, most of the biomass was pooled in branches and coarse roots. Biomass accumulation increased with age. Total shrub biomass increased from 3.74 g shrub^{-1} in age class I to 20.80, 88.41, 198.51, and 351.43 g shrub^{-1} for age class II-V, respectively (Table 2). In age class V, the mean growth rate of total shrub biomass was 7.73 g year^{-1}.

Branches were the primary above-ground biomass pool containing 1.61, 11.36, 55.43, 129.75, and 232.94 g shrub^{-1} and contributing 55.1, 72.3, 84.3, 87.6, and 90.9% of above-ground biomass in age class I-V, respectively. Foliage biomass increased from 1.32 g shrub^{-1} in age class I to 4.35, 10.30, 18.38, and 23.40 g shrub^{-1} in age class II-V, respectively, while the proportion of leaf biomass to above-ground biomass dropped from 35.2 to 9.1% with age.

Belowground biomass accounted for about 1/4 of total biomass. The average root biomass increased from 0.82 g shrub^{-1} in age class I to 5.09, 22.68, 50.38, 95.09 g shrub^{-1} in age class II-V, respectively. Belowground component biomass rose with age. Coarse roots were the main belowground biomass pool containing 0.55, 3.87, 18.87, 44.87,
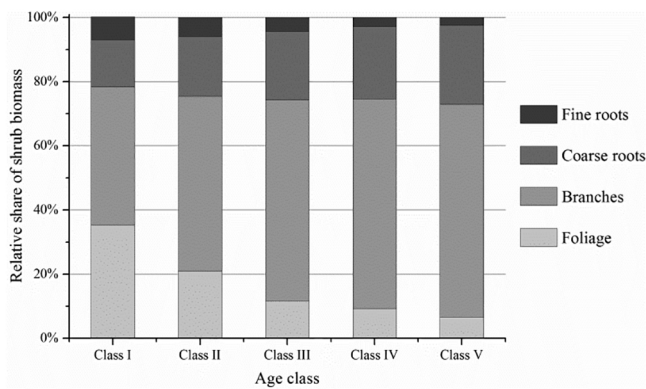
Fig. 1. Partitioning of biomass among different shrub components in age class I-V. Data from118 samples of destructive sampling.

86.59 g shrub^{-1} and contributing 67.1, 76.0, 83.2, 89.1, and 91.1% of total belowground biomass across five age classes. Fine root biomass increased from 0.27 g shrub^{-1} in age class I to 1.22, 3.81, 5.51, and 8.51 g shrub^{-1} in age class II-V, respectively, while the proportion of fine root biomass to belowground biomass decreased from 32.9 to 9.0% with age.

The relative proportions of shrub biomass components for different age class are shown in Fig. 1. The relative proportion of branch biomass to total shrub biomass rose from 43.0% in age class I to 54.6, 62.7, 65.4, and 66.3% in age class II-V, respectively. The relative proportion of leaf to total shrub biomass dropped from 35.2% in age class I to 20.9, 12.5, 9.3, and 6.7% in age class II, III, IV, and V, respectively. The relative portion of above-ground biomass dropped from 78.2% in age class I to 75.5, 74.4, 74.6, and 72.9% in age class II, III, IV, and V, respectively. The portion of coarse root biomass increased from 14.6% in age class I to 18.6, 21.3, 22.6, and 24.6% in age class II-V, respectively. The portion of fine root biomass dropped from 7.2% in age class I to 5.9, 4.3, 2.8, and 2.4% in age class II-V, respectively. The portion of belowground biomass increased with shrub age.

The mean root to shoot biomass ratios were 0.28, 0.32, 0.34, 0.34, and 0.37 in age class I-V, respectively (Table 2). The above- and below-ground biomass data of 118 harvested shrubs were analyzed by linear regression. Fig. 2 shows a fairly stable relationship throughout the whole age sequence with a regression slope corresponding to 0.37. The regression is mainly driven by the older shrubs.
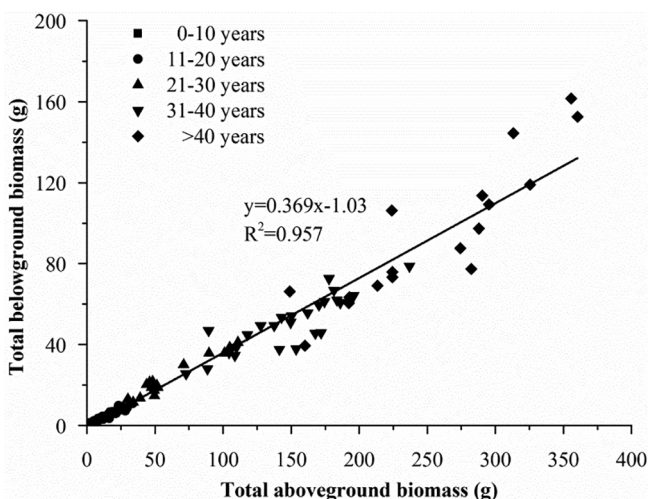

Fig. 2. Relationship between above- and below-ground biomass across five age classes.

Table 3
Scaling exponents (α) and allometric constants (β) for relations between *R. soongorica* above-ground biomass (M_A), leaf biomass (M_L), branch biomass (M_B), and total root biomass (M_R) for all pooled and classified data.

	α_P	α_O	95%CI	β_O.	95%CI	n	R^2
Across all pooled date							
M_A vs. M_R		0.97	0.95–0.99	3.19	2.99–3.39	118	0.98
M_B vs. M_R	1.00	1.10	1.07–1.13	1.69	1.56–1.81	118	0.98
M_L vs. M_R	0.75	0.64	0.61–0.66	1.46	1.35–1.57	118	0.95
M_L vs. M_B	0.75	0.58	0.55–0.60	1.08	1.00–1.17	118	0.96
Age class I							
M_A vs. M_R		1.11	0.89–1.34	3.44	2.91–3.96	27	0.80
M_B vs. M_R	1.00	1.41	1.15–1.66	1.87	1.54–2.19	27	0.83
M_L vs. M_R	0.75	0.87	0.60–1.14	1.52	1.24–1.79	27	0.62
M_L vs. M_B	0.75	0.60	0.44–0.75	1.03	0.89–1.18	27	0.70
Age class II							
M_A vs. M_R		1.03	0.91–1.15	2.90	2.36–3.48	31	0.92
M_B vs. M_R	1.00	1.23	1.09–1.38	1.46	1.12–1.80	31	0.91
M_L vs. M_R	0.75	0.59	0.41–0.77	1.67	1.20–2.15	31	0.60
M_L vs. M_B	0.75	0.46	0.32–0.60	1.46	0.99–1.94	31	0.60
Age class III							
M_A vs. M_R		0.93	0.78–1.08	3.23	1.76–4.70	18	0.911
M_B vs. M_R	1.00	1.00	0.85–1.15	2.12	1.13–3.12	18	0.92
M_L vs. M_R	0.75	0.61	0.37–0.85	1.55	0.42–2.68	18	0.63
M_L vs. M_B	0.75	0.61	0.41–0.82	0.96	0.20–1.71	18	0.70
Age class IV							
M_A vs. M_R		0.86	0.63–1.08	5.13	0.63–9.61	25	0.72
M_B vs. M_R	1.00	0.91	0.65–1.16	3.70	0.04–7.37	25	0.69
M_L vs. M_R	0.75	0.56	0.44–0.68	2.09	1.11–3.07	25	0.79
M_L vs. M_B	0.75	0.47	0.32–0.61	1.89	0.56–3.21	25	0.65
Age class V							
M_A vs. M_R		0.63	0.44–0.81	14.89	2.76–27.02	17	0.77
M_B vs. M_R	1.00	0.66	0.47–0.85	11.57	1.74–21.39	17	0.77
M_L vs. M_R	0.75	0.32	0.14–0.49	5.65	1.18–10.11	17	0.47
M_L vs. M_B	0.75	0.49	0.30–0.69	1.60	− 0.05–3.26	17	0.65

Note: Scaling exponents are for standardized major axis regression of $\log_{10}$-transformed data. α_P : predicted α; α_O : observed α; β_O : observed β.

3.2. Allometric relations for biomass partitioning

The linear relationship of biomass $\log_{10}$-transformed data was used to represent biomass partition pattern among shrub components. Converted R^2 varied from 0.46 to 0.98 (Table 3). For pooled data, the scaling exponent (α) for the relation with branch biomass (M_B) vs. root biomass (M_R), leaf biomass (M_L) vs. M_R, and M_L vs. M_B was 1.10, 0.64, and 0.58, respectively (Table 3, Fig. 3). Except for M_B vs. M_R, α was smaller than corresponding values by Niklas and Enquist (2002). The relationship between above- and below-ground biomass (M_A vs. M_R) gave α = 0.97 (Table 3, Fig. 3).

Most of the α values were different from values proposed by Niklas and Enquist (2002) when calculating according to classified biomass data (Table 3, Fig. 4). For root-related relationships (i.e., M_A vs. M_R, M_B vs. M_R, and M_L vs. M_R), α decreased significantly with age. The α for M_A vs. M_R was 1.11, 1.03, 0.93, 0.86, and 0.63, for M_B vs. M_R it was 1.41, 1.23, 1.00, 0.91, and 0.66, and for M_L vs. M_R it was 0.87, 0.59, 0.61, 0.55, and 0.31 for age class I-V, respectively (Table 3, Fig. 4). By comparison, effect of age class on the relation M_L vs. M_S was much smaller than for other relationships, the corresponding value was 0.60, 0.46, 0.61, 0.47 and 0.49 for age class I-V, respectively (Table 3, Fig. 4).

3.3. Allometric relationships

Biomass relationships developed for different age classes were significantly different (Table 4). Almost all shrub biomass components (i.e., foliage, branches, total above-ground, coarse roots, fine roots, total belowground, and total shrub) were significantly relevant to basal diameter (D). Compared to the four older age classes, correlation of shrub component biomass with D was weaker in the younger age class (R^2 = 0.70, 0.63, and 0.71 for above-, below-ground, and total shrub
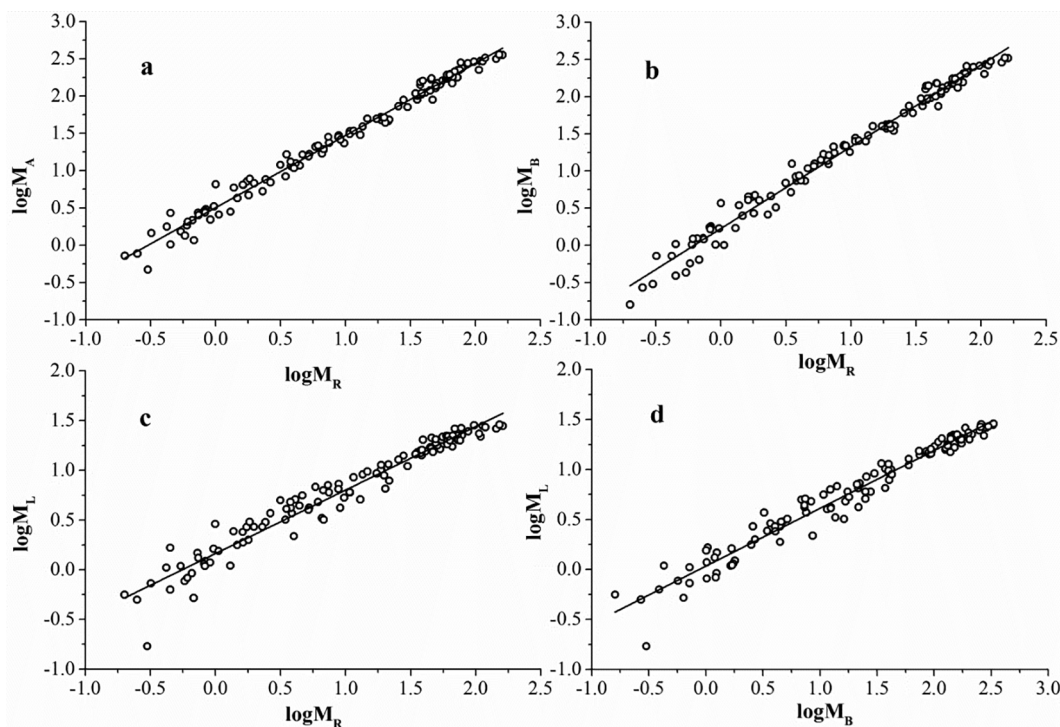
Fig. 3. Biomass partitioning of *R. soongorica* $\log_{10}$-transformed data across all age classes. Note: (a) above-ground biomass (M_A) vs. root biomass (M_R); (b) branch biomass (M_B) vs. M_R; (c) foliage biomass (M_L) vs. M_R and (d) M_L vs. M_B. $\log_{10}$-transformed data was analyzed using standardized major axis regression. Each circle on the graph represents one shrub.
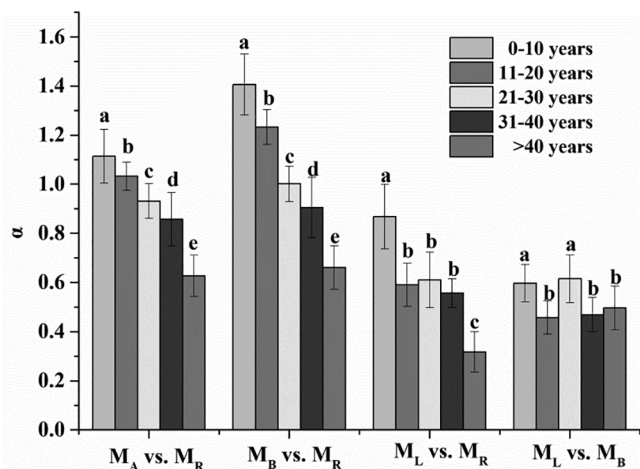

Fig. 4. Scaling exponents (α) of different biomass partitioning relations for five age classes. Note: Small letters indicate significant difference among age class ($P < 0.05$). The error bars indicate the standard errors of the scaling exponent per age class.

biomass, respectively) (Table 4). The addition of H as second variable only had a slight improvement for the fit in each class. Inclusion of C, by contrast, had a stronger effect, especially for canopy component for the two younger age classes (Table 4).

The shrub component biomass relationships with D as only input variable were stronger and had a lower standard error (S.E.) in the pooled equation ($R^2 = 0.93$, 0.92, 0.95, and 0.94 for branch, foliage, coarse-root, and fine-root, respectively) (Table 5). Fits with A as second input variable were hardly improved for the pooled equation. When adding H as second input variable, fits increased slightly. In contrast, addition of C had a major improvement ($R^2 = 0.98$, 0.97, and 0.98 for above-, below-ground, and total shrub biomass, respectively) (Table 5).

Relationships between shrub component biomass and D across five age classes are shown in Fig. 5. The figure reveals that all shrub biomass components are strongly correlated with D and independent of A (strong interlacing among different age classes).

The pooled relationships with D and C as first and second variable estimated biomass stored in *R. soongorica* shrubs to be 314.9 ± 63.5 and 94.3 ± 19.0 kg ha^{-1} for above- and below-ground, respectively. The biomass of branches, foliage, coarse roots, and fine roots was estimated to 260.7 ± 52.6, 54.9 ± 10.9, 78.4 ± 15.8, and 15.9 ± 3.2 kg ha^{-1}, respectively. Biomass estimates were transformed to carbon storage by carbon fractions 47.9, 32.3, 48.4, and 49.7% determined for branches, foliage, coarse roots, and fine roots by element analysis. The carbon storage of *R. soongorica* in Alxa desert steppe is about 147.3 ± 29.7 kg ha^{-1} in above-ground biomass, most of which is stored in branches 124.8 ± 25.1 kg ha^{-1}, and carbon in roots is about 45.8 ± 9.2 kg ha^{-1}. We observed stock carbon for R. soongorica of 189.5 ± 38.9 kg ha^{-1} in Alxa desert steppe.

4. Discussion

4.1. Biomass partitioning

We observed change of biomass partitioning among different shrub components with age. The samples were taken from the same habitat, limiting variability due to climate and soil factors. Consequently, variation of biomass partitioning was mainly affected by shrub age in our study. Previous studies have found that the relative proportion of branch biomass to total biomass increases with reduction of relative proportion of leaf biomass as shrubs age (Litton and Kaufman, 2008; Tian et al., 2015; Chen et al., 2016). For instance, a study conducted for a desert plant *Caragana intermedia* indicated that the proportion of branch to total shrub biomass increased from 28 to 48% and relative share of foliage biomass decreased from 32 to 9% in 3- and 37-year-old plantations (Tian et al., 2015). Litton and Kaufman (2008) reported that the proportion of leaf to above-ground biomass in young shrubs was larger than mature shrubs, while the relative proportion of stems was

Table 4

Biomass relationships for different shrub components: foliage, branches, total above-ground, coarse roots, fine root, total below-ground, and total shrub biomass in age class I-V, respectively.

Age class	Shrub component	X	c	a	S.E.(a)	$\bar{R}^2$	S.E.E	p-value	$\bar{R}^2_H$	$\bar{R}^2_C$
Age class I	Branches	D	0.011	3.663	0.653	0.689	0.764	<0.001	0.734	0.884
	Foliage	D	0.079	2.114	0.363	0.637	0.450	<0.001	0.631	0.738
	Total above-ground	D	0.055	2.933	0.471	0.703	1.125	<0.001	0.732	0.879
	Coarse roots	D	0.015	2.698	0.545	0.605	0.256	<0.001	0.633	0.711
	Fine roots	D	0.116	0.652	0.243	0.210	0.078	<0.001	0.261	0.218
	Total below-ground	D	0.058	1.989	0.351	0.628	0.276	<0.001	0.679	0.749
	Total shrub	D	0.098	2.704	0.423	0.706	1.346	<0.001	0.741	0.879
Age class II	Branches	D	0.097	2.230	0.208	0.827	2.851	<0.001	0.846	0.929
	Foliage	D	0.374	1.166	0.170	0.640	0.945	<0.001	0.655	0.671
	Total above-ground	D	0.221	1.996	0.150	0.883	2.798	<0.001	0.882	0.936
	Coarse roots	D	0.065	1.917	0.188	0.813	0.871	<0.001	0.807	0.843
	Fine roots	D	0.013	2.128	0.150	0.889	0.212	<0.001	0.888	0.888
	Total below-ground	D	0.077	1.963	0.161	0.860	0.975	<0.001	0.855	0.874
	Total shrub	D	0.298	1.988	0.141	0.894	3.487	<0.001	0.896	0.937
Age class III	Branches	D	0.138	2.183	0.126	0.853	4.962	<0.001	0.897	0.884
	Foliage	D	0.351	1.266	0.137	0.739	1.209	<0.001	0.787	0.788
	Total above-ground	D	0.262	2.019	0.118	0.851	5.695	<0.001	0.904	0.890
	Coarse roots	D	0.098	1.961	0.133	0.875	2.055	<0.001	0.882	0.884
	Fine roots	D	0.032	1.779	0.103	0.892	0.328	<0.001	0.908	0.907
	Total below-ground	D	0.128	1.929	0.105	0.907	1.855	<0.001	0.921	0.922
	Total shrub	D	0.388	1.994	0.104	0.900	6.981	<0.001	0.918	0.909
Age class IV	Branches	D	0.416	1.924	0.213	0.789	16.718	<0.001	0.803	0.804
	Foliage	D	0.645	1.124	0.148	0.714	1.692	<0.001	0.795	0.834
	Total above-ground	D	0.639	1.825	0.190	0.808	17.045	<0.001	0.829	0.830
	Coarse roots	D	0.126	1.967	0.195	0.824	5.277	<0.001	0.852	0.871
	Fine roots	D	0.067	1.479	0.139	0.832	0.471	<0.001	0.825	0.840
	Total below-ground	D	0.166	1.915	0.168	0.855	5.127	<0.001	0.879	0.892
	Total shrub	D	0.800	1.848	0.154	0.868	18.501	<0.001	0.894	0.897
Age class V	Branches	D	0.316	2.020	0.207	0.869	22.282	<0.001	0.875	0.912
	Foliage	D	0.416	1.235	0.131	0.854	1.475	<0.001	0.682	0.690
	Total above-ground	D	0.446	1.948	0.190	0.880	22.583	<0.001	0.885	0.920
	Coarse roots	D	0.006	2.930	0.373	0.819	14.177	<0.001	0.854	0.847
	Fine roots	D	0.0401	1.640	0.183	0.844	0.735	<0.001	0.838	0.864
	Total below-ground	D	0.010	2.811	0.337	0.834	14.180	<0.001	0.868	0.863
	Total shrub	D	0.286	2.176	0.185	0.907	29.849	<0.001	0.923	0.946

Note: Form of single input variable equation is $y = c(x)^a$, where y is dry mass (g) of shrub component; c is a constant; a is power exponent with the respective standard error (S.E.(a)); x is input variable basal diameter (D) (mm); n = 27, 31, 18, 25, and 17 in age class I-V, respectively. $\bar{R}^2$ is adjusted determination coefficient ($\bar{R}^2 = 1 - \frac{RSS/df_{Error}}{TSS/df_{Total}}$) with basal diameter as single input variable; S.E.E. (g) is standard error of estimate; p-value is the significance of regression. The two-input variable equation lists only adjusted determination coefficient $\bar{R}^2_H$ and $\bar{R}^2_C$ are adjusted determination coefficient with height (H) and crown area (C) as second input variable, respectively.

just opposite in one most ubiquitous native shrub, *Dodonaea viscosa* (Hawaii). Our study conforms to this rule, the proportion of branch to total biomass increased from 43 to 66%, while relative proportion of foliage biomass decreased from 35 to 7% with age. The relative proportion of branch and leaf biomass changed dramatically in the first 30 years, the proportion of branch to total biomass increased by 20% with relative proportion of leaf biomass decreasing by 23%, while the corresponding proportion varied very little after 30 years (3% for branch and 5% for leaf). This suggests that shrub biomass partitioning in early growth stage is more complex, which may largely depend on the plant physiological characteristics and this is consistent with the study by Tian et al. (2015) and Litton and Kauffman (2008). The diameter of branches increased with shrub size, which meets the biomechanical requirements for supporting the growing weight. However, although the above-ground biomass accounts for a considerable portion, the belowground components still hold about 1/4 of the total biomass. Thus, it needs to be included in biomass estimation.

Weiner (2004) and Peichl and Arain (2007) reported that young plants allocate more biomass to root to improve their early nutrient absorption capacity. Whereas, our study showed that roots in young shrubs accounted for a less proportion than mature shrubs. The relative proportion of root also varied greatly in first 30 years, the proportion in age class III was 1.2 times of that in class I, while the corresponding proportion of root in oldest age class only increased by 5% compared with age class III. The proportion of root biomass to total shrub biomass

had a differences of 9% between the oldest (class V) and the youngest class (class I). This can be the result of long-term natural selection. Arid environments may induce shrub to partition more biomass to the root system and expand the absorption range of water and nutrients. Our results are consistent with previous research by Ryser and Eek (2000) and Hartmann (2011). They reported that plants partition more biomass to their roots when water or nutrients are limiting factors. Although, fine root biomass was underestimated in our study due to the difficulty in harvesting the whole root biomass, missing fine roots only accounted for a small fraction of the total root biomass (e.g., Le and Ottorini, 2001). We assume that this had little effect on total root biomass calculations.

The root to shoot ratios of *R. soongorica* in our study ranged from 0.15 to 0.64, which are within the scope generally reported for this shrub and other arid region shrubs 0.07–1.55 (Wang et al., 2013). The mean root to shoot ratio (0.34) and the slope (0.37) of linear regression between above- and under-ground biomass from all harvested *R. soongorica* shrubs were smaller than root to shoot ratio of 0.69 and 1.05, respectively, reported for *R. soongorica* by Yang et al. (2017) and Dang et al. (2017). These differences may be caused by site-specific climatic and hydrogeologic conditions. Compared with two other study areas (Tengger Desert and Ordos), less annual precipitation (186 and 270 mm in Tengger Desert and Ordos, respectively) and lower groundwater level (4 and 15 m below ground, respectively) in our study area are probable main reasons. Affected by extreme arid environment, almost all plants

Table 5
Biomass relationships for shrub components: foliage, branches, total above-ground, coarse roots, fine roots, total below-ground, and total shrub across all five age classes.

	X_1	X_2	c	a	S.E.(a)	b	S.E.(b)	R^2	S.E.E	p-value
Branches	D		0.118	2.319	0.057			0.933	14.315	<0.001
		A	0.111	2.205	0.122	0.113	0.115	0.943	14.317	<0.001
		H	0.060	2.254	0.052	0.254	0.051	0.978	13.031	<0.001
		C	0.059	2.250	0.047	0.115	0.016	0.981	11.887	<0.001
Foliage	D		0.283	1.368	0.038			0.922	1.694	<0.001
		A	0.268	1.289	0.097	0.082	0.096	0.927	1.696	<0.001
		H	0.167	1.243	0.041	0.266	0.050	0.949	1.521	<0.001
		C	0.193	1.241	0.038	0.099	0.016	0.971	1.477	<0.001
Total above-ground	D		0.192	2.200	0.051			0.936	14.887	<0.001
		A	0.181	2.083	0.111	0.118	0.105	0.939	14.871	<0.001
		H	0.101	2.131	0.047	0.249	0.047	0.960	13.401	<0.001
		C	0.101	2.127	0.042	0.111	0.015	0.984	12.190	<0.001
Coarse roots	D		0.017	2.611	0.072			0.954	6.278	<0.001
		A	0.016	2.535	0.151	0.076	0.141	0.954	6.297	<0.001
		H	0.007	2.571	0.066	0.304	0.060	0.969	5.692	<0.001
		C	0.008	2.581	0.065	0.105	0.021	0.970	5.696	<0.001
Fine roots	D		0.048	1.591	0.035			0.937	0.472	<0.001
		A	0.055	1.805	0.082	−0.222	0.078	0.948	0.458	<0.001
		H	0.045	1.578	0.038	0.032	0.045	0.977	0.473	<0.001
		C	0.043	1.568	0.037	0.022	0.015	0.977	0.470	<0.001
Total below-ground	D		0.028	2.491	0.062			0.950	6.243	<0.001
		A	0.027	2.438	0.134	0.053	0.125	0.953	6.265	<0.001
		H	0.012	2.448	0.057	0.271	0.054	0.971	5.672	<0.001
		C	0.015	2.457	0.057	0.096	0.019	0.975	5.644	<0.001
Total shrub	D		0.210	2.271	0.045			0.951	17.789	<0.001
		A	0.199	2.170	0.098	0.102	0.093	0.959	17.773	<0.001
		H	0.107	2.209	0.040	0.521	0.039	0.976	15.333	<0.001
		C	0.111	2.209	0.036	0.106	0.012	0.979	13.860	<0.001

Note: Equation form is $y = c(x_1)^a$ or $y = c(x_1)^a(x_2)^b$, where y is dry mass (g) of shrub component; a and b are equation parameters with their respective standard error (S.E.a,b). $x_{1, 2}$ are equation variables with basal diameter (D), age (A), height (H) or crown area (C). S.E.E. (g) is standard error of estimate; p-value is the significance of regression; $\bar{R}^2$ is adjusted determination coefficient ($\bar{R}^2 = 1 - \frac{RSS / df_{Error}}{TSS / df_{Total}}$).

can only use a small amount of soil condensation water (Pan et al., 2018) and shallow soil water that intercepts by a shallow soil layer during rainfall. It is difficult to replenish water from the deep groundwater, additionally, thinner and poorer soil layer limits root development. As a result, the roots of *R. soongorica* in our study area were shallower and less than that in Tengger Desert and Ordos. Consequently, a smaller root to shoot biomass ratio is reasonable. In our study, the root to shoot biomass ratios increased with age, especially in early stages of growth, while studies by Yang et al. (2017) and Dang et al. (2017) did not show this trend. This indicates that biomass partitioning of *R. soongorica* changes with environment. The ability to alter biomass allocation according to environmental constraints may contribute to the distribution of *R. soongorica* over a wide range of site conditions (Yang et al., 2017; Dang et al., 2017; Jin et al., 2018).

The significant changes in biomass partitioning with shrub age help us understand the growth process and regional characteristics of *R. soongorica* in the study area. This implies that to get a more accurate estimate of carbon stock, the age structure and regional characteristics (e.g., site-specific of root to shoot ratios) of *R. soongorica* should be taken into account. Furthermore, the partitioning characteristic of *R. soongorica* at different growth stages also contributes to better understanding of the shrub adaptive strategies to environment. In addition, accurate estimation of the portion of grazing carbon may better quantify the carbon storage dynamics at the regional scale (Peichl and Arain, 2007; Gargaglione et al., 2010).

4.2. Allometric relations for biomass partitioning

Regression analysis of log_{10}-transformed biomass data indicated that biomass partitioning of *R. soongorica* follows allometric rules. Consequently, the allometric relationship among different shrub parts may effectively describe biomass allocation patterns of this species.

Determination coefficient of allometric relationships between different shrub components ranged from 0.47 to 0.92. Our data was used to test the specific scaling exponents suggested by Enquist and Niklas (2002). The hypothesis of the log-transformed plant data satisfies the following relationship, the allometric scaling of the leaves relative to stem (include branches) or root is 3/4 ($\alpha = 0.75$), that of stem to root is 1 ($\alpha = 1$) (Niklas and Enquist, 2002; Enquist and Niklas, 2002). Our results showed that predictions, especially for scaling exponent of above-ground components (M_L vs. M_B), were significantly different from observations for both pooled and classified data. In fact, the allometric relationships (1.12 for M_B vs. M_R, 0.91 for M_L vs. M_R and 0.81 for M_L vs. M_B) of *R. soongorica* in the southeastern edge of the Tengger Desert by Yang et al. (2017) are also different from the prediction by Enquist and Niklas (2002). This suggests that the difference of allometric relationship from "the canonical rules" may vary by species. Thus, we can conclude that the model proposed by Enquist and Niklas (2002) is not applicable to *R. soongorica* populations in arid desert areas of NW China. It should also be noted that the differences between the same species in different regions suggest that regional environments can also cause changes in allometric relationship.

Age class had a significant effect on all root-related scaling exponents (i.e., M_A vs. M_R, M_B vs. M_R, and M_L vs. M_R) in our study. Root-related scaling exponents decreased with age and were significantly different among different age classes. This indicates that *R. soongorica* partitions a greater biomass proportion to roots with age in order to adapt to extreme arid climate. This agrees with the optimal partitioning theory. In fact, plants tend to increase root biomass under drought conditions. This phenomenon has been confirmed by field and laboratory experiments (Mokany et al., 2006; Bogeat-Triboulot et al., 2007; Herzog et al., 2013). A *meta*-analysis of woody plants from temperate and tropical areas showed that the relative root part increased significantly with decrease of annual precipitation (Mokany et al., 2006).
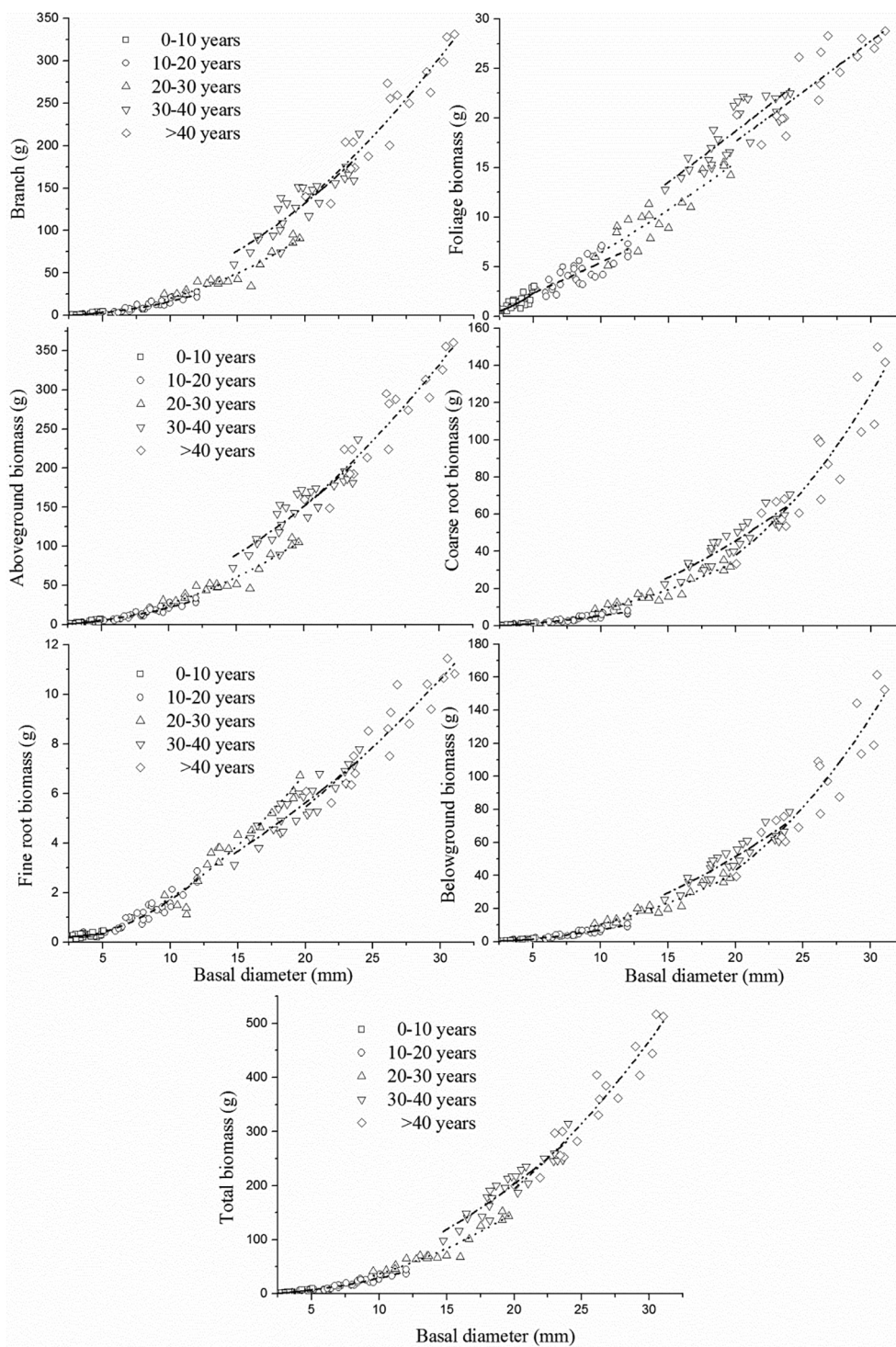
Fig. 5. Relationship between foliage, branches, aboveground, coarse roots, fine roots, belowground and total shrub biomass with basal diameter (D) across five age classes.

Likewise, Bogeat-Triboulot et al. (2007) reported that shoot growth of *Populus euphratica* decreased with gradual depletion of water, while root growth was maintained, leading to an increase in the root to shoot ratio. Paradoxically, Yang et al. (2013) reported that partitioning between above- and below-ground biomass of *R. soongorica* of different size displayed no significant difference in the southeastern margin of Tengger Desert. However, we speculate that their study area did not expose the drought tolerant shrub *R. soongorica* to severe water stress. In any case, we have not found any other studies on root biomass allocation of *R. soongorica* across the whole lifecycle for further comparison.

Interestingly, the relationship for M_L vs. M_B was almost unaffected by age class. Its scaling exponent varied little among age class compared with root-related relationships. This suggests that the relationship between foliage and branches may be independent of age.

4.3. Allometry

Shrub allometry was affected by variation of biomass partitioning. We found that relationships with D as a single input variable were

significantly different over different age classes. All shrub biomass components showed a close relationship with D except for fine root biomass at age class I ($R^2 = 0.21$). This is due to incomplete collection, rapid turnover, and uncertainty in root classification (distinguish root function by diameter is difficult in young shrubs). In accordance with our findings, Perkins and Owens (2003) and Kuyah et al. (2013) reported that accurate estimation of fine root biomass was difficult for plant seedlings. Compared with other biomass components, the relationship between leaf biomass and D was less obvious. This is reasonable in view of that foliage is a transient organ and more susceptible by disturbances such as grazing, which affects the allometric relationships (Rubilar et al., 2010). In agreement with our findings, Peichl and Arain (2007) found that foliage biomass had a relatively weaker positive relationship with diameter ($R^2 = 0.507$) for *white pine* forests in southern Ontario, Canada. Kuyah et al. (2013) reported that the relationship between foliage biomass and diameter at breast height was less significant than for other biomass components on *Eucalyptus* in Western Kenya. The relationships between shrub biomass components and D were less good for age class I compared to the other four classes probably due to more furious individual competition in the early growth stage of *R. soongorica*. Similar results have been reported for woody plants (Pérez-Cruzado and Rodríguez-Soalleiro, 2011; Kuyah et al., 2013; Chave et al., 2014). Kuyah et al. (2013 found that the biomass of young trees was difficult to estimate accurately. Chave et al. (2014) reported that the allometric coefficient of young plants varied greatly. Compared with age class specific relationships, pooled equations with D as single input variable had a smaller standard error (S.E.) for all shrub components. We assume that larger quantities of samples may be a main reason.

Some previous studies have explored to improve allometric relationships by adding a second variable. The results are inconsistent (Wagner and Ter-Mikaelian, 1999; Návar et al., 2004; Peichl and Arain, 2007). Peichl and Arain (2007) reported that tree age as a second variable only improved estimation for young *white pine* forests in north America, but not the estimation of total biomass. Wagner and Ter-Mikaelian (1999) found that using plant height as a second variable improved the estimation of stem biomass, rather than root biomass estimation. Návar et al. (2004) found that the inclusion of height led to an optimal biomass estimate for shrub species *Tamaulipan thornscrub* of north-eastern Mexico. Our study showed that shrub age or height as a second variable only slightly improved these relationships. In accordance with our results, Jenkins et al. (2003) and Peichl and Arain (2007) reported that plant age and height were inefficient variables because of their marginal improvement for diameter-based equations. In contrast, crown area is a more effective variable for estimating shrub biomass (Zeng et al., 2010; Zhang et al., 2016; Yang et al. 2017). Zeng et al. (2010) reported that canopy area could alone predict the shrub biomass of different components with an acceptable accuracy and precision. Zhang et al. (2016) found that crown area was a simple biomass predictor for two native shrubs in Tibet. We found that the inclusion of shrub crown area improved biomass estimation for both the entire age-sequence and each age class, and especially for the canopy biomass component at younger classes. We believe that this is due to that branches and leaves are more equally distributed horizontally than in the longitudinal direction. This results in a good correlation between crown area and canopy biomass components. In agreement with our findings, Yang et al. (2017) reported that crown area is a useful variable that can accurately estimate all biomass components of *R. soongorica* shrubs pooled in diameter classes. However, they did not include age information. Thus, we cannot make further comparisons.

Our allometric relationships were compared with other equations for *R. soongorica* growing in the southeastern edge of the Tengger Desert (Yang et al., 2017) and the western Ordos Basin in Inner Mongolia (Dang et al., 2017). Differences for all pooled biomass estimates were 9 (Yang et al., 2017) and 14% (Dang et al., 2017), and differences for different age class ranged from 38 to 454% (Yang et al., 2017; Dang

et al., 2017). Applying allometric equations reported by Yang et al. (2017) to our age class I and V caused a difference of 65 and 50% for above-ground biomass estimates and 461 and 9% for belowground biomass estimates, respectively. Such great differences can cause large errors in large-scale estimation of biomass and carbon stocks. Therefore, it is advised to apply site-specific equations or similar regional equations wherever possible to maximize accuracy in biomass estimation of *R. soongorica*.

When estimating carbon storage from biomass, the default value of 0.5 defined by IPCC is generally used. In fact, the carbon content varies among different plant species as well as the different organs of the same plant species. One recent study indicated that by using a carbon content of 0.5 in the same area may lead to errors of up to 10% (Fonseca et al., 2012). The carbon content of different component of *R. soongorica* shrubs varied from 32.3% to 49.7%, and the weighted average was 46.0%. The actual value of carbon reserves was 8.0% lower than the default value of 0.5. Using the measured values of different components in our study could greatly improve the estimation of carbon storage of the *R. soongorica* shrub. The biomass of different components of *R. soongorica* increased with age, and the carbon storage increased accordingly. The average carbon density of the *R. soongorica* shrub in Alxa steppe desert was 189.5 kg ha^{-1}, which is about 1/4 of the carbon density (800 kg ha^{-1}) of desert steppe of China estimated by Huang et al. (2006). This is a considerable amount for one single species in our study area, and much higher than other species. Compared with other desert areas, the carbon density of *R. soongorica* shrub in Alxa steppe desert is about 1/5 of temperate shrub desert in the Junggar Basin (Tao and Zhang, 2013), about 1/10 of central Asian desert (Tao and Zhang, 2013), and also much lower than the global average carbon density in desert areas (Houghton et al., 2009). However, as one of the dominate species in the Alxa steppe desert, *R. soongorica* is closely related to the carbon exchange in this region and plays an important role in maintaining the regional carbon pool.

5. Conclusions

Biomass partitioning and allometric relations of *R. soongorica* shrub were studied in the Alxa steppe desert. We may conclude that shrub age has a significant influence on shrub allometry and biomass partitioning. Biomass accumulation (both biomass components and total biomass) had an obvious gradient across five age classes (0–10, 11–20, 21–30, 31–40, and > 40 years). The main biomass pool, branch and coarse root, accounted for the greatest proportion of total shrub biomass as shrubs mature. Meanwhile, relative portion of foliage and fine root decrease with age. The contribution of total root to total biomass increases with age in order to adapt to the extreme arid conditions. The "canonical rules" proposed by Enquist and Niklas (2002) do not apply to *R. soongorica* populations. Our results are consistent with the optimal partitioning theory. Biomass functions were developed based on all pooled and classified data. Almost all shrub biomass components showed a significant correlation with basal diameter. In addition, allometric biomass equations were improved with the introduction of the second variable crown area. Our findings indicate that age factor and site characteristics in allometry and biomass partitioning should be considered to better estimate the regional material cycle and plant adaptability. Our research is important for accurately predicting biomass and carbon accumulation, and has great significance for understanding and protecting the eco-environment of the Alxa Plateau. The present study as well, shed light on the sustainability of *R. soongorica* shrubs in the Alxa plateau.

6. Author statement

Wang, X.P. designed research. Ma, X.Z. performed research. Ma, X.Z. and Wang, X.P. analyzed data and wrote the paper.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

Acknowledgments

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