Above- and below-ground biomass and its allometry of Salsola passerina shrub in Alxa steppe desert in NW China

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Abstract

Knowledge of the biomass allometry and partitioning is essential for understanding shrub adaptive strategies to extreme arid environments as well as for estimating organic carbon storage. We studied biomass accumulation, allocation patterns, and allometric models of Salsola passerina shrub in Alxa desert steppe, northwestern (NW) China. We measured above- and below-ground biomass accumulation across different ages (0-50 years) by destructive sampling. The biomass allocation patterns between aboveground biomass (MA), leaves (ML), branches (MB) and roots (MR) were studied by fitting allometric functions for both pooled and age-classed data. Allometric biomass models were developed by regressing on single-input variable of basal diameter (D), crown area (C), height (H), and age (A) alone or on the pairwise variables of above four parameters. Biomass accumulation increased with age, aboveground components represented 86–89% of the total biomass, root to shoot biomass ratios increased with shrub age. Allometry patterns of S. passerina is relatively constant, the growth rate of root was faster than that of aboveground components. Allometric models with two-input variables were obviously better than single variable models. C and D were the best predictors for biomass of S. passerina shrub.

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Knowledge of the biomass allometry and partitioning is essential for understanding shrub adaptive strategies to extreme arid environments as well as for estimating organic carbon storage. We studied biomass accumulation, allocation patterns, and allometric models of *Salsola passerina* shrub in Alxa desert steppe, northwestern (NW) China. We measured above- and below-ground biomass accumulation across different ages (0-50 years) by destructive sampling. The biomass allocation patterns between aboveground biomass (M_A), leaves (M_L), branches (M_B) and roots (M_R) were studied by fitting allometric functions for both pooled and age-classed data. Allometric biomass models were developed by regressing on single-input variable of basal diameter (D), crown area (C), height (H), and age (A) alone or on the pairwise variables of above four parameters. Biomass accumulation increased with age, aboveground components represented 86–89% of the total biomass, root to shoot biomass ratios increased with shrub age. Allometry patterns of *S. passerina* is relatively constant, the growth rate of root was faster than that of aboveground components. Allometric models with two-input variables were obviously better than single variable models. C and D were the best predictors for biomass of*S. passerina* shrub.

Keywords: Allocation; Biomass partitioning; Allocation pattern; Allometric model; Alxa

1 Introduction

Affected by climate change and human activities, Alxa steppe desert has become one of the most severely desertified regions in China (Wan et al, 2018). As the dominant plant type, shrubs are of great significance in fixing sand dunes and improving soil, and beneficial to the ecological restoration of degraded desert ecosystems (Wang, Schaffer, Yang, & Rodriguez-Iturbe, 2017). *Salsola passerina* , featured by strong salinity, drought, and cold resistance, is one of the most widely distributed species in Alxa steppe desert (37° to 42° N and 93° to 106° E). Knowledge of the biomass allometry and partitioning of this shrub has important significance for understanding the process of carbon allocation among organs and estimation of organic carbon storage, as well as shrub adaptive strategies to extreme arid environments (Jin et al., 2018; Peichl & Arain, 2007).

Previous studies on biomass partitioning of different plant species have been carried out throughout most ecosystems, and a number of environmental and biological factors, such as species, landform, soil texture, humidity, and nutrients, are likely to affect biomass partitioning (Niklas & Enquist, 2002; Ong, Gong, & Wong, 2004; Yang, Wang, Tan, & Gao, 2017). However, age, due to the difficulty of sampling, is rarely studied in naturally growing shrubs. It is well known that biomass allocation of plant components varies throughout the life cycle (Peichl & Arain, 2007). Studies in even-aged plantation showed that biomass allocation changed greatly with age (Köhl, Neupane, & Lotfiomran, 2017; Peichl & Arain, 2007). For many species, the young plants have a greater proportion of roots and leaves than older plants (Peichl & Arain, 2007; Tian et al, 2015). Thus, it is necessary to understand the biomass partitioning characteristics for different age to more accurately quantify biomass and carbon storage at regional scale.

Optimal partitioning theory suggests that plants preferentially partition more biomass to the tissue that acquires limited resources (Gargaglione, Peri, & Rubio, 2010). This means that if light becomes more limited, plants will partition more biomass to leaves and branches, and if water or nutrients become limited, plants will partition more biomass to roots (Mokany, Raison, & Prokushkin, 2006; Ryser & Eek, 2000). While the allometric theory suggests that the allocation of plant biomass is restricted only by the size of the individual, and the accumulation of biomass in different organs has an allometric relationship which is determined by a power function of the form$\mathrm{Y}_1 = \beta \mathrm{Y}_2^{\alpha}$, where Y_1 and Y_2 are interdependent variables (e.g. above- and below-ground biomass), α and β are allometric coefficient and allometric constant respectively. When $\alpha = 1$ the expression of the model becomes a linear equation describing the isometric relation, and when α [?] 1 the model expresses the allometric relationship. Some studies have pointed out that the allometric theory and optimal partitioning theory may be complementary to each other instead of independent in explaining plant biomass allocation (Chen, Zhao, He, & Fu, 2016).

In the past few decades, plenty of allometric biomass equations have been reported for various species in many geographical and ecological environmental. However, few researches were conducted on shrub species in arid regions (Buras et al., 2012; Wang, Schaffer, Yang, & Rodriguez-Iturbe, 2017), and most studies only focus on aboveground biomass, especially in Alxa steppe desert. In addition, due to the differences in sampling methods, definitions, and specific factors influencing the biomass allometry, these existing biomass allocation equations are difficult to trans-use (Jenkins, Birdsey, & Pan, 2001; Lambert, Ung, & Raulier, 2005). Therefore, it is necessary to develop biomass equations for typical plant species in specific areas.

The objectives of this research are: (i) to provide biomass partitioning information of *S. passerina* over the entire lifetime, (ii) to clarify the allometric patterns between different biomass components of*S. passerina* , and (iii) to develop biomass equations for above- and below-ground as well as total biomass of *S. passerina* in Alxa desert steppe.

2 Methods

2.1 Study site

The study was conducted in the southwestern margin of the Alxa Plateau (101° 34' E, 38deg 46' N). The area is characterized as a transitional desert steppe. 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. Precipitation is the only source of soil water. The groundwater level is greater than 40 meters below ground. Pan evaporation is 2722 mm. The mean annual air temperature is 9.4 degC. The average annual frost-free period is 170 days. 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 native vegetation is*Reaumuria soongorica (Pall.) Maxim, Salsola passerina* ,*Kalidium foliatum* , and *Peganum harmala L* . etc., with*S. passerina* and *R. soongorica* are the dominant shrubs.

2.2 Field measurement and biomass sampling

Vegetation investigation was carried out in three square plots of 100 m^2. In each plot, the total number of *S. passerina* shrubs was counted, and the shrub density was 1070 +- 750 plants ha^{-1}, basal diameter (D), height (H), and crown area (C) of each *S. passerina* shrub were measured, and were 14.1 +- 0.5 mm, 12.4 +- 0.5 cm and 389.3 +- 42.2 cm^{2}respectively. In the adjacent area of the above mentioned three vegetation investigation plots, a total of 143 individuals of *S. passerina* were randomly selected and excavated in 2018 and 2019. Basal diameter, height, and crown area of harvested shrubs were measured. Basal diameter was the mean of two perpendicular diameter of stem base, height was the vertical distance from the highest point of the canopy to the surface ground, and crown area was calculated by taking the longest and shortest diameters through the center of the fullest part of the canopy. 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. 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 0.4 m for study area). Special 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 *S. passerina* was classified as branch biomass. Roots were sorted into fine roots ([?]2 mm in diameter, with a main function to absorb water and nutrients from soil) and coarse roots (>2 mm in diameter), and excavated roots were cleaned manually with a brush. All component materials were oven-dried at 65 degC to constant weight, allowed to cool for 4-6 h, and weighed by an electronic balance (0.01 g) for biomass calculation. Carbon content of different components was determined using the dichromate oxidation method of Walkley and Blac (1934). For 56 individuals harvested in 2019, HD photos of rings were taken for analyzing age on computer, and their ages varied from 0 to 50 years, dividing them into three age classes, 0-20, 21-30 and 31-50 years. Due to the large sample size of 21-30 years, they were classed separately. Basic characteristics of each group are shown in Table 1.

2.3 Biomass scaling relations

Biomass partitioning patterns were studied by logarithmically transformed allometric function with $\log_{10}$ transformed data. The analyses for allometric scaling of aboveground biomass (M_A) vs. root biomass (M_R), branch biomass (M_B) vs. M_R, leaves biomass (M_L) vs. M_R and M_L vs. M_B. were conducted on classified and pooled biomass data.

Data from 143 harvested shrubs were used to develop biomass equations. Different biomass components were regressed on single shrub variable, crown area (C), basal diameter (D), height (H) and age (A), and also on the pairwise variables of above four parameters to obtain biomass equations. Age-related equation only used biomass data harvested in 2019. The allometric equation of the form $Y = c \bullet X^a$ was used for plant biomass modeling, where Y is shrub biomass component (e.g. leaf, branch, coarse root, fine root), X is a predictor (i.e., crown area, basal diameter, height and age), a and c are allometric coefficients. The equation was logarithmically transformed into a linear equivalent, $ln(Y) = ln(c) + a \bullet ln(X)$. The equation with two input variables was described by$Y = c \bullet X_1^a \bullet X_2^b$, with logarithmically transformed form$ln(Y) = ln(c) + a \bullet ln(X_1) + b \bullet ln(X_2)$, where Y is shrub biomass component, X_1 and $X_2$are predictors (i.e., crown area, basal diameter, height and age), a, b and c are model parameters.

Models with one parameter were assessed by coefficient of determination (R^2), while models with multiple input variables were assessed by adjusted coefficient of determination (R^2_{adj}).The relative error (RE) defined as the error of predicted biomass (B_P) relative to measured biomass (B_M),$RE = (B_P - B_M)/B_M$ (Chave et al., 2005), the Akaike information criterion (AIC) (Akaike, 1974), and R^2 orR^2_{adj} were used to select the most suitable model with the highest R^2 or R^2_{adj}, and lowest RE and AIC values.

3 Result

3.1 Biomass partitioning

Dry biomass of *S. passerina* components classified by age (data from harvested shrubs in 2019) is shown in Table 2. The average biomass of each shrub component increased with age, most of the biomass was pooled in aboveground components. Total shrub biomass increased from 43.9 g shrub^{-1}in 0-20 years to 89.8 and 143.4 g shrub^{-1} in two older classes, respectively (Table 2). The mean growth rate of total shrub biomass was 2.6, 3.6, 3.6 g year^{-1} across the three age classes.

Branches were the main above-ground biomass pool containing 23.8, 53.4, and 89.0 g shrub^{-1} and contributing 60.8, 66.9, and 71.5% of above-ground biomass in age class 0-20, 21-30, and 31-50 years, respectively. Foliage biomass increased from 15.3 g shrub^{-1} to 26.4, and 35.5 g shrub^{-1}across three age classes, respectively, while the proportion of leaf biomass to above-ground biomass dropped from 39.2 to 28.5%.

The root biomass increased from 4.8 g shrub^{-1} in age class 0-20 years to 10.0 and 18.9 g shrub^{-1}in two older classes, respectively. Coarse roots were the main underground biomass pool containing 4.2, 8.5 and 16.6 g shrub^{-1}and contributing 88.0, 84.8, and 87.7% of total underground biomass across three age classes. Fine root biomass increased from 0.6 g shrub^{-1} in age class 0-20 years to 1.5, and 2.3 g shrub^{-1} in age class 21-30 and 31-50 years, respectively, the proportion of fine root biomass to underground biomass were 12.0, 15.2 and 12.3% across three age classes.

The relative proportions of shrub biomass components in different age class are shown in Fig. 1. The relative proportion of branch biomass to total shrub biomass rose from 54.1% in age class 0-20 years to 59.4 and 62.1% in age class 21-30 and 31-50 years, respectively. The relative proportion of leaf to total shrub biomass dropped from 35.0 to 24.7% across three age classes. The relative portion of above-ground biomass dropped from 89.1% in the youngest age class to 86.8% in age class 31-50 years, respectively. The portions of coarse root biomass were 9.6, 9.5, and 11.6%, and corresponding portions of fine root biomass were 1.3, 1.7, and 1.6% across three age classes. The portion of belowground biomass increased from 10.9% to 13.2% with shrub age.

The mean root to shoot biomass ratios were 0.12, 0.13, and 0.18 in three age classes. The root to shoot for all pooled data (including data of undetermined age) was 0.20. The above- and below-ground biomass of 143 harvested shrubs was analyzed by linear regression. Figure 2 shows a fairly stable relationship with a regression slope corresponding to 0.20.

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. For pooled data, R^2varied from 0.42 to 0.73 (Fig. 3). The allometric scaling for above- and underground biomass (M_A vs. M_R) was 0.757 with 95% CI 0.681 to 0.834. The allometric relationships of branch biomass (M_B) vs. root biomass (M_R), leaf biomass (M_L) vs. M_R, and M_L vs. M_B were 0.851 (95% CI: 0.758 to 0.944), 0.562 (95% CI: 0.451 to 0.673), and 0.570 (95% CI: 0.464 to 0.677), respectively (Fig. 3).

For age-specific data (from harvested shrubs in 2019), the allometric scaling for M_A vs. M_R was 0.88 (95% CI: 0.56 to 1.12), 0.90 (95% CI: 0.72 to 1.07), and 0.92 (95% CI: 0.34 to 1.50) across three age classes, for M_B vs. M_R was 1.00 (95% CI: 0.69 to 1.30), 0.92 (95% CI: 0.66 to 1.17), and 1.01 (95% CI: 0.36 to 1.66), for M_L vs. M_R was 0.83 (95% CI: 0.31 to 1.35), 0.69 (95% CI: 0.49 to 0.89) and 0.53 (95% CI: 0.08 to 0.98), and for $M_L$vs. M_B was 0.71 (95% CI: 0.41 to 1.01), 0.59 (95% CI: 0.28 to 0.90), and 0.62 (95% CI: 0.26 to 0.98) (Fig. 4). The allometry coefficient of three age classes has no significant difference.

3.3 Allometric biomass models

Empirical allometric coefficients for estimating biomass of different components based on crown area (C), basal diameter (D), height (H), and age (A) are presented in Table 3. R^2 of total biomass varied from 0.24 to

0.72 (Table 3). The shrub component biomass relationships with C or D as only input variable were stronger than that with H or A. C was significant predictor variable for all components ($P < 0.001$) and estimated branch, leaf and aboveground biomass with least RE (9, 10, and 6% for branch, leaf and aboveground biomass), and also had a relatively small RE (7%) in estimating total biomass (Table 3). However, C underestimated fine root biomass by 25%, coarse root biomass by 37%, and belowground biomass by 17% (Table 3). D also was a significant predictor variable for all biomass components ($P < 0.001$) and estimated branch and belowground components with least RE (9, 6, and 4% for branch, coarse root, and underground biomass, respectively), the total biomass estimated by D had a minimum RE of 5%, D underestimated leaf biomass by 14%, aboveground biomass by 7%, and fine root biomass by 39% (Table 3). It seemed that C was better at estimating aboveground biomass components, while D was better at estimating belowground biomass components. H and A, by contrast, showed a bad estimation for almost all components, and underestimated the biomass of all components by over 10%. All predictors failed to accurately estimate fine root biomass, the range of $R^2$was 0.15 to 0.26, and the minimum RE for fine root was 30% (Table 3).

When including two input variables, model fits were sharply improved. R^2 of aboveground, underground, and total biomass were 0.53 to 0.87, 0.41 to 0.82, and 0.54 to 0.87 (Table 4). For aboveground biomass, fit of aboveground biomass with C-D as two input variables reached the highest R^2 (0.76), and the corresponding RE was the least value (2%), and these values were significantly better than other combinations of input variables (e.g. C-H, C-A, and D-A). For belowground biomass, equation with D-H as input variables was best, with highest R^2 (0.82) and least RE value (3%). R^2 (0.81) and RE (4%) with C-D as input variables was slightly worse than that with D-H in estimating belowground biomass. Other combinations of input variables, by contrast, were less good. Model with C-D as input variables had highest R^2 (0.87) and least RE value (2%) for estimating total shrub biomass. AIC values supported the above results, the best variable combination for biomass estimation of above-, under-ground, and total biomass were C-D (AIC = -364.16), D-H (AIC = -284.00) or C-D (AIC = -280.67), and C-D (AIC = -372.37), respectively. Thus, C-D was the best variables for two-input variable equation in biomass estimation of *S. passerina*shrub.

The biomass equations with D and C as first and second variable, aboveground biomass=$0.119\text{x}C^{0.621}\text{x}D^{0.849}$, belowground biomass=$0.042\text{x}C^{0.134}\text{x}D^{1.834}$, estimated biomass stored in *S. passerina* shrubs to be 48.4 +- 34.0, 12.6 +- 8.8, and 61.0 +- 42.8 kg ha^{-1} for above- and below-ground as well as total biomass, respectively. Biomass estimates were transformed to carbon storage by carbon fractions 40.5 and 45.2% determined for above- and under-ground components by element analysis. The carbon storage was about 19.6 +- 13.8 kg ha^{-1} in aboveground biomass, and 5.7 +- 4.0 kg ha^{-1} in root biomass. In total, *S. passerina*shrubs dominated desert steppe in Alxa Plateau were estimated to stock carbon 25.3 +- 17.8 kg ha^{-1} in live *S. passerina*shrub biomass, on average.

Discussion

4.1 Biomass partitioning

Biomass partitioning among different shrub components varied with age in our study. Considering that these samples were collected from the same habitat, the difference of biomass partitioning may be mainly affected by shrub age. The relative proportion of branch to total biomass increased from 54 to 62% with reduction of relative proportion of leaf from 35 to 25%. Consistent with our findings, Tian et al. (2015) and Litton and Kauffman (2010) also confirmed this rule.

Some previous studies reported more resources were allocated to plant root in early stage of growth, in order to improve nutrient absorption capacity of young plant (Peichl & Arain, 2007; Weiner, 2004). In our study, roots of young shrubs held a less proportion than old shrubs, which may be caused by the drought conditions. As the shrubs grow, the water demand continues to increase, and water restriction causes plants to invest more biomass into the root system to absorb more water to maintain growth and reproduction, which has led to a continuous increase of root during the life cycle. Consistent with our findings, Ryser and Eek (2000) and Hartmann (2011) reported that plants partitioned more biomass to their roots when water was limiting factors. In fact, other shrubs in our study area also showed similar characteristics, sampling of *Reaumuria soongorica* found that the ratio of root to total biomass increased from 21.8% in age class 0-10 years to 27.1% in in age class >40 years. Although the collection of fine roots was incomplete, missing fine roots only accounted for a small fraction of total root biomass (e.g., Peichl & Arain, 2007), thus, it has no effect on calculations of total root biomass.

The root to shoot ratios of *S. passerina* in our study ranged from 0.08 to 0.47, which met other arid land shrubs 0.07-1.55 in northern China (Wang, Su, Yang, & Yang, 2013). The mean root to shoot ratio (0.20) of all harvested *S. passerina* shrubs were lower than that reported for *S. passerina* by Yang et al. (2013). The differences may be caused by site-specific climatic and hydrogeologic conditions. Affected by extreme arid environment of our study area, plants can only use a small amount of precipitation and soil condensation water (Pan, Wang, Zhang, & Hu, 2018). Additionally, thinner and poorer soil also limits root development. While Tengger desert, by contrast, has more annual precipitation (186 mm), higher groundwater level (4 below ground) and more fertile soil. Consequently, a smaller root to shoot biomass ratio in our study is reasonable. The root to shoot biomass ratios increased with age in our study. Although not much, it indicates that biomass partitioning of *S. passerina* change with shrub size. The ability to alter biomass allocation according to environmental constraints and individual size may contribute to the distribution of *S. passerina* over a wide range of site conditions.

4.2 Allometric relations for biomass partitioning

Regression analysis of $\log_{10}$-transformed biomass data indicated that biomass partitioning of *S. passerina* follows allometric rules. Consequently, the biomass allocation patterns can be described by allometric relationship. Enquist and Niklas (2002) suggested the log-transformed plant data satisfies the following relationship, the allometric scaling of the leaves relative to stem (include branches) or root was 0.75, that of stem to root was 1 (Enquist & Niklas, 2002; Niklas & Enquist, 2002). Our results showed that predictions were significantly different from observations for pooled data. However, the data classified by age did not reject the hypothesis suggested by Enquist and Niklas (2002). The confidence intervals of the allometric scaling of classified data were very wide, which may be caused by the large variation of biomass in each age class. The pooled data avoided this problem because of the larger sample size, and their allometric scaling seemed to stand for actual values. The allometric relationships of *S. passerina* in the southeastern edge of the Tengger desert by Yang et al. (2017) were also different from the prediction by Enquist and Niklas (2002). This suggests that the difference of allometric relationship with prediction may be mainly caused by the species. Age factor had no significant effect on all scaling exponents in our study, which indicates that the allometry relationship of*S. passerina*is relatively constant.

In our study, the scaling exponents of aboveground biomass components relative to roots were all less than 1, indicating that the growth rate of root is faster than that of branches, leaves and the sum of them. In fact, the relative proportion of root to total shrub biomass in 30-50 years is 1.2 times that in 0-20 years in our study. This also meets the optimal partitioning theory. Previous studies have suggested that plants tend to increase root biomass under drought conditions (Bogeat-Triboulot et al., 2007; Mokany, Raison, & Prokushkin,, 2006). Mokany et al. (2006) reported relative proportion of root increase with decrease of annual precipitation in woody plants. Bogeat-Triboulot et al. (2007) found that the root to shoot ratio of *Populus euphratica* increase in a drought treatment. The biomass allocation of *S. passerina*can be well explained by optimal allocation theory and allometric theory, indicating that the two theories complement each other (Chen, Zhao, He, & Fu, 2016; Gargaglione, Peri, & Rubio, 2010).

4.3 Allometric biomass models

We found that shrub biomass components showed a different correlation with single input variable. Aboveground biomass components, by contrast, had good correlation with crown area; this may be due to equal distribution of branches and leaves in horizontal direction. In agreement with our findings, Yang et al. (2017) reported that crown area is a useful variable for estimating aboveground biomass components of*R.*

soongorica shrubs. Belowground biomass components had good correlation with basal diameter, and this may be due to a closer relationship that the base of main stem connected to the root. Kuyah et al. (2013) reported that basal diameter fitted root biomass with a coefficient of determination as high as 0.971 in farmed eucalyptus species. Research on *Elaeagnus mollis* also confirmed the close correlation between root biomass and basal diameter (Liu, Bi, & Zhao, 2009). In contrast, total biomass had the highest correlation with base diameter ($R^2 = 0.72$) or canopy area ($R^2 = 0.72$). In fact, many previous studies have corroborated this result (Kuyah et al., 2013; Peichl & Arain, 2007; Zeng, Liu, Feng, & Ma, 2010; Zhang, Cui, Shen, & Liu, 2016). Zhang et al. (2016) and Zeng et al. (2010) found that crown area was a simple biomass predictor for desert shrubs. Peichl and Arain (2007) and Kuyah et al. (2013) reported that there was a strong correlation between diameter and total biomass of woody plant. Leaf and fine root showed a bad correlation with all predictors. The best correlation with leaf biomass was crown area with $R^2 = 0.57$. 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 results, Peichl and Arain (2007) and Kuyah et al. (2013) reported that the relationship between foliage biomass and predictor was less significant than for other biomass components. The determination coefficients related to fine root biomass were all less than 0.25, which indicates that fine root biomass is difficult to predict accurately. This may be due to incomplete collection, rapid turnover, and uncertainty in fine-root classification. In addition, the spatial heterogeneity of water caused by micro-topography is also an important reason. In accordance with our findings, Perkins and Owens (2003) and Kuyah et al. (2013) reported that accurate estimation of fine root biomass was difficult. The relationships between shrub biomass component and shrub height or age were less good in our study. Consistent with our findings, Peichl and Arain (2007) reported that age only improved biomass estimation of young *white pine* , while not biomass of all age class. Yang et al. (2017) found height was not the best variable for biomass estimation of 12 desert shrub species in northern China. Tong et al. (2018) reported that crown area was a more effective variable than height for 3 common shrubs in Horqin sandy land. In fact, heights of different sizes of *S. passerina* were not much different, and the relationship between biomass and age was rough (biomass classed by age showed a large variability). Although the crown area and basal diameter were both the best variable for estimating biomass of *S. passerina* , there were still some deviations. This may be due to difficulties in quantifying crown area and basal diameter, crown area can only be measured roughly based on the major and minor axes of canopy, and the basal diameter tends to show more fluted cross sections, this even becomes more apparent as increase of shrub size, but there is no more suitable single predictor.

The addition of age as second variable in crown area or basal diameter based equations had a slight improvement for the equations of few biomass components. In accordance with our results, Peichl and Arain (2007) reported that plant age were inefficient variables because of their marginal improvement for diameter-based equations. The addition of height as second variable in basal diameter-based equations had obviously improvement for model fit of aboveground biomass, but only slight improvement for belowground and total shrub biomass. In accordance with our results, Wagner and Ter-Mikaelian (1999) found that height as a second variable improved the estimation of stem biomass, rather than root biomass. Kuyah et al. (2013) reported that the inclusion of height hardly improved the model fit in farmed eucalyptus species. When the equation took crown area and basal diameter as two input variables, the fits of above-, under-ground, and total biomass had been significantly improved, and the RE of biomass estimation was the smallest. This may be due to the complementation of the two variables. C and D were the best predictors for above- and below-ground biomass, respectively. Consistent with our findings, Kuyah et al. (2013) reported that crown area improved the biomass prediction model based on basal diameter.

Our biomass models were compared with models of the same species developed for the southeastern edge of the Tengger desert (Yang, Wang, Tan, & Gao, 2017). Allometric models reported by Yang et al. (2017) caused RE of 16% and 126% for above- and below-ground biomass, respectively. Differences of all pooled biomass estimate was 13%, which can cause great errors in large-scale estimation of biomass and carbon stocks in our study area. Thus, site-specific or similar regional models should be applied in order to more accurately estimate biomass.

The default value of 0.5 defined by IPCC was often used to estimate carbon storage from biomass. While the carbon contents vary greatly in different species and organs. Fonseca et al. (2012) reported that the use of default value may lead to an error of 10% in estimating carbon storage. In our study, the carbon content of above- and below-ground components were 40.5% and 45.2%, respectively, with a weighted average of 41.5%. The actual carbon storage was 17.0% less than the default value. The average carbon density of the *S. passerina* was 25.3 kg ha^{-1} in Alxa steppe desert, which only accounts for a small fraction of the carbon density (800 kg ha^{-1}) of desert steppe of China (Huang, Ji, Cao, & Li, 2006). However, *S. passerina* , as one of the dominate species, is closely related to the carbon exchange in the Alxa steppe desert and plays an important role in maintaining the regional carbon pool.

5 Conclusions

Biomass partitioning and allometric relations of *S. passerina*shrub were studied in the Alxa steppe desert. Total biomass of individual shrub increased with age, most of the biomass was pooled in aboveground components. The relative proportion of branch to total biomass increased as shrubs age, with reduction of relative proportion of leaf. The proportion of root increased with age due to the drought conditions. Root to shoot biomass ratios varied with environmental constraints and individual size, which contributed to the distribution of *S. passerina* over a wide range of site conditions. Biomass partitioning of*S. passerina* followed allometric rules. Allometric relations were relatively constant, and regardless of age. The root growth rate of*S. passerina* was faster than that of aboveground components, which met optimal partitioning theory. The allometric theory and optimal partitioning theory complemented each other in explaining biomass allocation of *S. passerina* . Allometric models with two-input variables were obviously better than single variable models. C and D were the best predictors for two-input variable models in estimating biomass of *S. passerina* shrub. Our research contributes to accurately predict biomass and carbon storage of*S. passerina* shrub, and is important for understanding shrub adaptive strategies to extreme arid environments. The present study, as well, is beneficial to the protection and sustainability of eco-environment of the Alxa Plateau.

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Tables

TABLE 1 Basic characteristics of *S. passerina* stands in the Alxa desert steppe (mean +- S.E.).

Age class	Crown areas (cm^2)	Basal diameters (mm)	Heights (cm)	Ages (years)	sample size
0-20	513.0±147.7	9.0±0.9	17.3±0.6	16.7±1.5	12

Age class	Crown areas (cm^2)	Basal diameters (mm)	Heights (cm)	Ages (years)	sample size
21-30	1134.1±95.2	12.6±0.6	21.3 ±0.9	24.8±0.5	31
31-50	1520.8±233.3	21.3±1.7	23.0±2.3	40.2±1.5	13
Total (0-50)	1090. 8±92.4	12.5±0.5	20.7±0.8	26. 8±1.2	56

TABLE 2 Biomass of *S. passerina* components (g shrub^{-1}) according to age class.

Shrub component	Biomass (g shrub^{-1})	Biomass (g shrub^{-1})	Biomass (g shrub^{-1})
	0-20 years	21-30 years	31-50 years
Branch	23.8±7.6	53.4±5. 5	89.0±16.7
Leaf	15.3±3.1	26.4±2.6	35.5±5.4
Total above-ground	39.1±10.3	79.8±7.4	124.5±20.7
Fine root	0.6±0.1	1.5±0.2	2.3±0.4
Coarse root	4.2±1.3	8.5±0.9	16.8±2.5
Total below-ground	4.8±1.3	10.0±1.0	18.9±2.7
Total shrub	43.9±11.6	89.8±8.3	143.4±23.1

Note: mean ± S.E; n=12, 31 and 13 individuals for age class 0-20, 21-30, and 31-50 years, respectively.

TABLE 3 Biomass equations with single variable for shrub components: foliage, branches, total above-ground, coarse roots, fine root, total below-ground, and total shrub biomass.

	X	ln(c)	S.E.(ln(c))	a	S.E.(a)	R^2	p-value	RE
Branch	C	-2.87	0.37	1.00	0.06	0.69	¡0.001	-0.09
Leaf	C	-2.09	0.37	0.78	0.06	0.57	¡0.001	-0.10
Aboveground	C	-1.84	0.28	0.91	0.04	0.76	¡0.001	-0.06
Fine-root	C	-5.86	0.84	0.88	0.13	0.25	¡0.001	-0.37
Coarse-root	C	-2.66	0.55	0.76	0.08	0.37	¡0.001	-0.20
Belowground	C	-2.56	0.50	0.76	0.08	0.42	¡0.001	-0.17
Total	C	-1.47	0.30	0.88	0.05	0.72	¡0.001	-0.07
Branch	D	-1.05	0.29	1.83	0.11	0.65	¡0.001	-0.09
Leaf	D	0.00	0.34	1.16	0.13	0.36	¡0.001	-0.14
Aboveground	D	-0.01	0.25	1.60	0.10	0.66	¡0.001	-0.07
Fine-root	D	-3.96	0.65	1.48	0.25	0.20	¡0.001	-0.39
Coarse-root	D	-2.99	0.25	2.05	0.09	0.77	¡0.001	-0.06
Belowground	D	-2.71	0.21	2.00	0.08	0.81	¡0.001	-0.04
Total	D	0.03	0.23	1.66	0.09	0.72	¡0.001	-0.05
Branch	H	-0.32	0.65	1.34	0.22	0.21	¡0.001	-0.23
Leaf	H	-0.54	0.55	1.19	0.18	0.23	¡0.001	-0.17
Aboveground	H	0.33	0.55	1.27	0.18	0.25	¡0.001	-0.17
Fine-root	H	-4.96	0.98	1.62	0.33	0.15	¡0.001	-0.42
Coarse-root	H	-0.77	0.71	1.03	0.24	0.12	¡0.001	-0.28
Belowground	H	-0.60	0.67	1.02	0.22	0.13	¡0.001	-0.25
Total	H	0.66	0.55	1.23	0.18	0.24	¡0.001	-0.18
Branch	A	-1.52	0.95	1.62	0.29	0.36	¡0.001	-0.16
Leaf	A	-0.37	0.84	1.06	0.26	0.24	¡0.001	-0.14
Aboveground	A	-0.39	0.84	1.40	0.26	0.35	¡0.001	-0.13
Fine-root	A	-5.51	1.55	1.68	0.48	0.19	¡0.001	-0.30

	X	ln(c)	S.E.(ln(c))	a	S.E.(a)	R^2	p-value	RE
Coarse-root	A	-4.05	0.79	1.86	0.24	0.52	¡0.001	-0.11
Belowground	A	-3.62	0.77	1.78	0.24	0.51	¡0.001	-0.10
Total	A	-0.44	0.81	1.46	0.25	0.39	¡0.001	-0.12

Note: Form of single input variable equation is$ln(Y) = ln(c) + a \bullet ln(X)$, where Y is dry mass (g) of shrub component; ln(c) is a constant with the standard error S.E.(ln(c)); a is power exponent with the standard error S.E.(a); X is crown area (C), basal diameter (D), height (H), or age (A); n = 143 except for A-related equation (n = 56); R^2 is determination coefficient; p-value is the significance of regression; RE is the relative error.

TABLE 4 Biomass equations with two-input variables for shrub components: foliage, branches, total above-ground, coarse roots, fine root, total below-ground, and total shrub biomass.

	X	ln(c)	S.E.(ln(c))	a	S.E.(a)	b	S.E.(b)	R^2(adj)	p-value	AIC	RE%
Aboveground	C-H	-1.88	0.34	0.91	0.05	0.03	0.13	0.76	¡0.001	-278.46	-0.06
	C-D	-2.13	0.21	0.62	0.04	0.85	0.08	0.87	¡0.001	-364.16	-0.02
	C-A	-2.51	0.46	0.80	0.06	0.40	0.15	0.83	¡0.001	-133.58	-0.04
	D-H	-1.81	0.35	1.44	0.09	0.75	0.11	0.74	¡0.001	-269.83	-0.04
	D-A	-0.92	0.70	1.44	0.28	0.47	0.28	0.56	¡0.001	-78.84	-0.09
	H-A	-2.53	0.85	1.04	0.22	1.11	0.23	0.53	¡0.001	-75.22	-0.09
Belowground	C-H	-2.49	0.59	0.77	0.09	-0.04	0.22	0.41	¡0.001	-117.04	-0.17
	C-D	-3.16	0.29	0.13	0.06	1.83	0.11	0.81	¡0.001	-280.67	-0.04
	C-A	-5.10	0.63	0.56	0.09	1.07	0.21	0.72	¡0.001	-98.03	-0.07
	D-H	-3.48	0.33	1.93	0.08	0.32	0.11	0.82	¡0.001	-284.00	-0.03
	D-A	-4.20	0.56	1.60	0.22	0.74	0.22	0.75	¡0.001	-104.46	-0.06
	H-A	-4.91	0.86	0.63	0.22	1.60	0.23	0.56	¡0.001	-73.43	-0.09
Total	C-H	-1.49	0.36	0.88	0.06	0.02	0.14	0.72	¡0.001	-258.22	-0.07
	C-D	-1.80	0.21	0.54	0.04	1.01	0.08	0.87	¡0.001	-372.39	-0.02
	C-A	-2.44	0.46	0.75	0.06	0.51	0.15	0.83	¡0.001	-132.01	-0.04
	D-H	-1.60	0.32	1.51	0.08	0.68	0.10	0.78	¡0.001	-296.72	-0.03
	D-A	-0.97	0.66	1.44	0.26	0.52	0.26	0.60	¡0.001	-85.60	-0.08
	H-A	-2.45	0.82	0.98	0.21	1.18	0.22	0.54	¡0.001	-78.42	-0.09

Note: Equation form is$ln(Y) = ln(c) + a \bullet ln(X_1) + b \bullet ln(X_2)$, where Y is dry mass (g) of shrub component; a, b and ln(c) are equation parameters with their respective standard error S.E.(a, b, ln(c)); X_1 and X_2 are equation variables with crown area (C), basal diameter (D), height (H), or age (A). R^2 (adj): is the adjusted coefficient of determination; p-value is the significance of regression; AIC is the Akaike information criterion, and RE is the relative error.

Figure legends

FIGURE 1 Partitioning of biomass among different shrub components in age class 0-20, 21-30, and 31-50 years, respectively. n=12, 31 and 13 individuals for age class 0-20, 21-30, and 31-50 years, respectively.

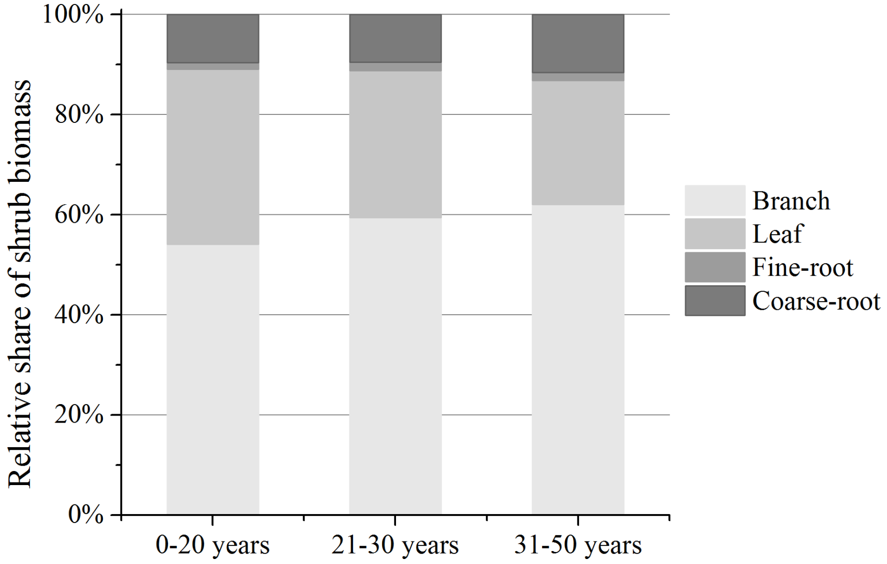
FIGURE 2 Relationship between above- and below-ground biomass.

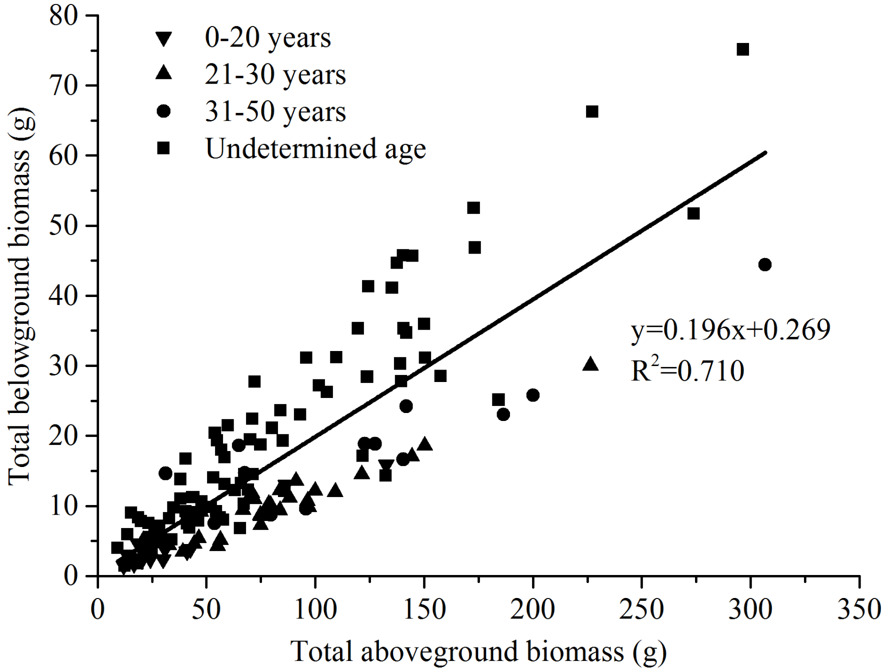
FIGURE 3 Biomass partitioning of *S. passerina*$\log_{10}$-transformed data.

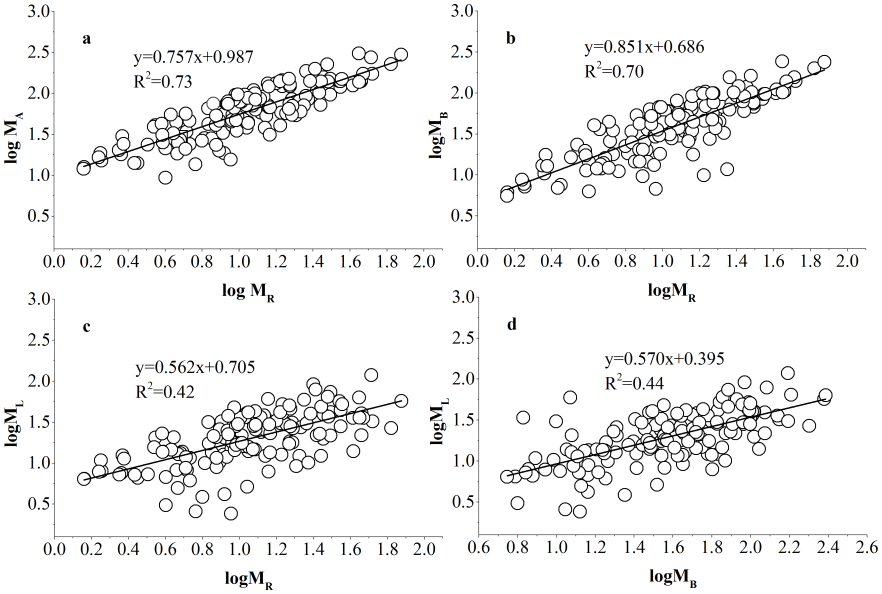
Note: (a) above-ground biomass (M_A) vs. root biomass (M_R); (b) branch biomass (M_B) vs. M_R; (c) foliage biomass (M_L) vs. M_R and (d) M_L vs. M_B. Each circle on the graph represents one shrub.

FIGURE 4 Scaling exponents of different biomass partitioning relations for three 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.






a
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R²=0.73
log M_A
log M_R
b
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R²=0.70
logM_B
logM_R
c
y=0.562x+0.705
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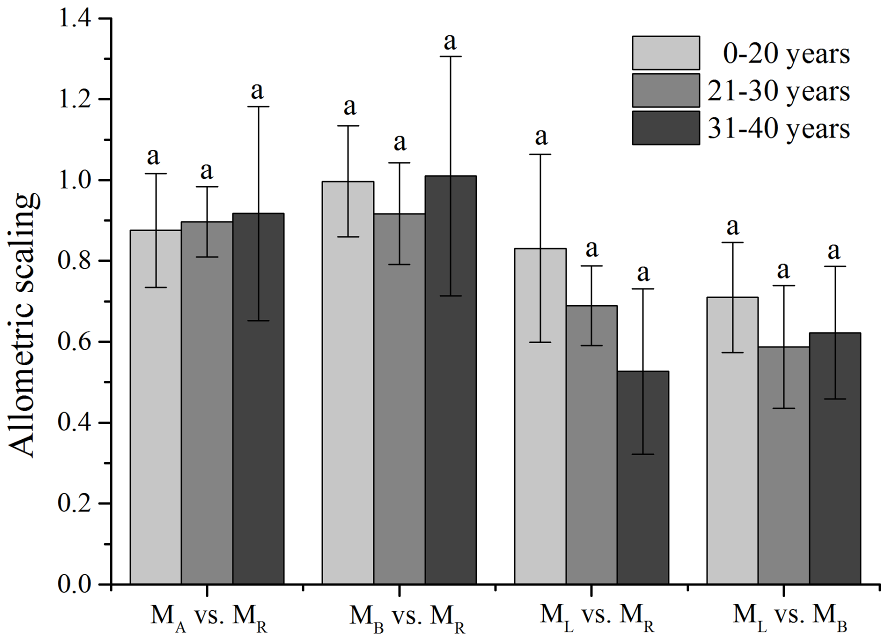
logM_B


Allometric scaling
0-20 years
21-30 years
31-40 years
a
M_A vs. M_R
M_B vs. M_R
M_L vs. M_R
M_L vs. M_B
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4