Patterns of biomass allocation in *Haloxylon persicum* woodlands and their understory herbaceous layer along a groundwater depth gradient

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ABSTRACT

To investigate above- and belowground biomass allocation patterns and the relationship of root distribution between different functional groups (shrubs vs. herbs) along a groundwater depth gradient, an experiment was carried out in a *Haloxylon persicum* woodland. Four sites were selected along the groundwater depth gradient. At each site, five sample plots (20×20 m) and 15 subplots (1×1 m) were established for a vegetation inventory of *Haloxylon persicum* and the herbaceous layer. The vegetation inventory included plant density, canopy coverage, height, and basal stem diameter of *H. persicum*. Allometric equations were established for *H. persicum* based on the biomass of 22 excavated trees, which were then applied to inventory data to provide stand estimates of aboveground biomass (AGB), belowground biomass (BGB), and total biomass (TB) of *H. persicum*. The AGB of the herbaceous layer was measured in subplots (1×1 m) and BGB was excavated and measured to a depth of 100 cm at 10-cm intervals. Our results indicated that the BGB-to-AGB ratio at the community level in the herbaceous layer increased notably along the gradient of declining groundwater depth. The depth of the soil horizon that contained 65% of the root surface area and 85% of the root biomass was shallower (0–2.5 m) in the deep end of the groundwater depth gradient than in the shallow end (0–3 m) of the gradient. *H. persicum* adjusted root distribution to capture water in the upper soil layers in response to the decline in groundwater depth. However, this adjustment was not sufficient to compensate for the decline in the water table; the BGB-to-AGB ratio showed no significant increase as AGB declined. On the contrary, herbaceous plants seemed better adapted to changes in the water table by effectively adjusting their BGB-to-AGB ratio. Use of BGB-to-AGB ratios that are specific to groundwater tables will significantly improve our estimates of BGB carbon stocks in these woodlands. Considering the scarcity of information on biomass stocks and partitioning in desert woodlands, our results might be applicable to other desert regions in Central Asia dominated by *H. persicum*.

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1. Introduction

Dryland is one of the largest terrestrial biomes, covering 41% of Earth's land surface and supporting over 38% of the global population (Reynolds et al., 2007). Dryland is also one of the most sensitive area to climate change and human activities (Huang et al., 2016). Because of low rainfall and high evapotranspiration in this region, groundwater is often an important water source for perennial plants (Imada et al., 2008; Cui and Shao, 2005; Naumburg et al., 2005). The dynamics and the availability of the groundwater plays an important role in defining vegetation composition and

distribution (Elmore et al., 2006; Naumburg et al., 2005), and in driving the vegetation dynamic and shifting the interactive balance between wooden species and herbaceous plants (McCluney et al., 2012; Cooper et al., 2006; Holzapfel et al., 2006). The unsustainable exploitation of groundwater associated with rapid population expansion and socio-economic development in these regions has aggravated the fluctuation of the groundwater table and influenced the availability of groundwater to desert plants (Orellana et al., 2012; Wang et al., 2011). Declining water tables decrease the accessibility to a permanent water source for some perennial plants, which can consequently result in water stress (Naumburg et al., 2005; Padilla and Pugnaire, 2007). However, there have been only few studies on the effects of lowering water table on vegetation dynamics and on the interaction balance between shrubs and

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herb species (Naumburg et al., 2005). Understanding the vegetation dynamics and interactions between shrubs and herbs in response to declining groundwater availability in dryland ecosystems is crucial for their sustainable management (Wu and Hobbs, 2002).

Belowground biomass (BGB) is an important component of global terrestrial ecosystem carbon stocks (Cairns et al., 1997; Reich, 2002; Wang et al., 2014). Knowledge of root profiles is essential for measuring and predicting ecosystem dynamics and ecosystem function (Hui and Jackson, 2006; Macinnis-Ng et al., 2010). Measuring root biomass and describing root distribution is labor-intensive and time-consuming (Metcalf et al., 2007; Xu and Li, 2008); therefore, detailed studies of belowground root biomass at the community level are sparse, especially for dryland vegetation. Consequently, it is often not clear how the relative balance between BGB and aboveground biomass (AGB) changes (both in magnitude and direction) across resource gradients (Zerihun et al., 2006).

The vegetation-specific root-to-shoot ratio (RS) is an effective parameter to describe the allocation between AGB and BGB, providing a practical tool to estimate BGB by the relatively easily measured AGB (Cairns et al., 1997; Mokany et al., 2006). RS changes with environmental factors (e.g., climate, CO₂, soil texture, soil moisture, and nitrogen), biotic factors (e.g., plant type, stand age, and leaf traits), and forest origins (Wang et al., 2014; Yu et al., 2012; Hollister and Flaherty, 2010; Cambui et al., 2011). Stand age affects allometry, wood density, and structure (Lehtonen et al., 2004; Wang et al., 2000) as well, which have a considerable impact on the quantitative analysis of forest biomass (Zhao et al., 2014). Only a few studies on biomass allocation patterns have been carried out on tree species in the field (Naidu et al., 1998; Shibuya et al., 2007; Peichl and Arain, 2007; Bolte and Löf, 2010), and there has been a scarcity of studies on biomass allocation patterns through the entire course of developmental stages for the desert shrub species. Failure to consider stand age may lead to considerable over- or underestimation of tree component biomass.

Research findings on shifts in biomass allocation above- and belowground along water gradients are inconsistent. Some studies have found that the BGB-to-AGB ratio declines as the environment becomes progressively hydric (Comeau and Kimmins, 1989; Schulze et al., 1996; Zerihun et al., 2006). However, other gradient studies (e.g., Compton et al., 1999) and several reviews (for example, Vogt et al., 1996; Cairns et al., 1997; Schenk and Jackson, 2002) have generally found a weak or no relationship between mean annual precipitation (MAP) and the BGB-to-AGB ratio in woody plants. The apparently conflicting evidence in these reports was summarized by Zerihun et al. (2006) and Yang et al. (2010), and the reason was attributed to one or two of the following factors: (a) Changes in species composition along a rainfall gradient (Schulze et al., 1996, 1998; Williams et al., 1996) could mask any effect of water availability on the BGB-to-AGB ratio; and (b) the gradients of MAP and a host of other environmental variables can affect the BGB-to-AGB ratio to different extent and direction (Yang et al., 2010). Therefore, a consistent pattern may be discerned if the species composition of communities and atmospheric demand are maintained while the water supply is varied.

The effect of water table depth on above/below ground biomass allocation in desert plant communities have been studied on small scales: with natural variations in water tables across micro-topographies (e.g., hummocks and hollows) (Vasander, 1982; Håland and Brække, 1989; Moore et al., 2002; Murphy et al., 2009a; Murphy et al., 2009b; Murphy and Moore, 2010), or in response to water table manipulations (Vasander, 1982; Brække, 1992; Laiho and Finér, 1996; Finér and Laine, 2000; Weltzin et al., 2000; Imada et al., 2008; Breeuwer et al., 2009). Few studies are available on the shifts in above- and belowground allocation

patterns among plant functional groups in response to natural water table gradients. Understanding the shifts of biomass allocation patterns and corresponding root distribution adjustments along water table depth gradients could not only help us to improve model prediction precision in relation to vegetation biomass (Hutchings and John, 2004) but also help us to recognize the interaction between shrubs and herbs (Michalet, 2006).

Haloxylon persicum Bunge ex Bois. et Buhse is distributed widely from the southern margins to the hinterlands of the Gurbantunggut Desert, especially in areas that have experienced a natural water table drawdown. Our previous research using hydrogen-oxygen stable isotope analysis showed that *H. persicum* mainly used deep soil water and limited amount of groundwater at the southern edge of the Gurbantunggut Desert (Dai et al., 2015). Based on the hypothesis that plants should maintain proportionally more biomass in the organ that acquires the most limiting resource (Reich et al., 2014), we anticipate that with the groundwater drawdown, the RS will increase at the community level. We hypothesized that due to the groundwater table drawdown, *H. persicum* trees and herbaceous plants will depend more on the shallow soil layer water and therefore adjust their root distribution for capturing the shallow soil moisture.

2. Materials and methods

2.1. Site description

The Gurbantunggut Desert (44°11'–46°20'N and 84°31'–90°00'E) is a typical temperate desert with vegetation cover up to 40% (Fan et al., 2014). This area has a continental arid climate with a dry, hot summer and a cold winter. In general, soil water in the Gurbantunggut Desert is recharged during early spring when the snow cover melts, and is consumed at the late spring and summer. Therefore, plants in this area experience frequent late summer water deficits, and the herbaceous layer only blooms in the spring. The vegetation layer is simple in this desert, including a shrub layer, herb layer, and primitive plant layer (moss, club moss, lichen, or fern). *Haloxylon ammodendron* (C.A.Mey.) Bunge and *H. persicum* (Chenopodiaceae), two sister taxa in the *Haloxylon* genus, are the dominant species in their respective communities. Ephemerals and annuals make up herb layer, with up to 70–80% of biomass of the herb layer made up of ephemerals from early spring to summer. On the southern edge of the Gurbantunggut Desert, *H. persicum* occurs mainly on dune crests, and *H. ammodendron* occupies inter-dune regions and the flat slopes of dunes, with both species rarely growing together. Moving from the southern edge to the interior of the Gurbantunggut Desert, the population size of *H. ammodendron* decreases, and *H. persicum* becomes the monospecific dominant species in the shrub layer. *H. ammodendron* is more salt tolerant and shows a higher affinity to groundwater (Xu and Li, 2008; Dai et al., 2015). In contrast, *H. persicum* is more drought resistant and less dependent on groundwater (Dai et al., 2015).

The current study was carried out in the southern part of the Gurbantunggut Desert, near the Fukang Station of Desert Ecology, Chinese Academy of Sciences (44°17'N, 87°56'E, 475 m above sea level). In this region, the air temperature ranges from a minimum of −42.2 °C in winter to a maximum of 44.2 °C in summer, with an annual mean temperature of 6.6 °C (Zhou et al., 2012). Annual mean precipitation is 70–180 mm, and annual pan evaporation is around 1000 mm. On the southern edge of the desert, the groundwater depth is over 5 m; while in the desert interior, the groundwater depth between the sand dunes is more than 16 m (Qian et al., 2004). At the range of our vegetation inventory, we assumed precipitation and evaporation were the same over the short distance (less than 20 km), where the groundwater drawdown

was significant. The natural existence of a groundwater gradient combined with similar species composition of community provides a suitable setting for studying shifting in the biomass allocation at the community level of *H. persicum* along groundwater depth gradient.

2.2. Sample plots inventory

The study was carried out from April to October 2009. Starting from the southern edge of the Gurbantunggut Desert, we selected four sites along a groundwater depth gradient at distance intervals of 4–5 km. The sample sites were located in a conservation area established in 2000. Detailed location information for the sites is shown in Fig. 1 and Table 1. The vegetation inventory included all the individuals of the *H. persicum* population in the sample plots and every single grass plant in subplots. We randomly chose five sample plots (20 × 20 m) at each site to investigate quantitative characteristics of the *H. persicum* population. The density, height, canopy width, and basal stem diameter of *H. persicum* were recorded with diameter tape and tapeline. Canopy width was the average of the major and minor axis length of each respective crown. Coverage was calculated using the formula of elliptical areas, $C = \pi XY/4$, where X and Y refer to the major and minor axis length (Phillips and MacMahon, 1981). To investigate the species composition and quantitative characteristics of the herb layer, three subplots (1 m × 1 m) were randomly selected within every sample plot. In total, there were 15 subplots at each site. Densities, coverage, species number, and height of the herb layer were recorded. Plant coverage of herb layers was visually estimated using a metal frame of 1 m × 1 m with 100 equally distributed grids above the subplots (Causton, 1988). The number of each species was counted in each subplot to obtain the densities and species number. The mean plant height was calculated from 3–5 random height measurements of each species in the subplot, with height measured from the base (ground level) to the top tip of the plant.

2.3. Biomass sampling and estimation

For the woody plant inventory, 22 trees representing the size range of *H. persicum* were harvested for the development of

allometric equations that relate tree diameter to AGB, BGB, and total plant biomass (TB). Tree height, canopy width, and basal stem diameter were measured before harvest with a diameter tape and tapeline. Destructive sampling was then carried out on the 22 live trees with different basal stem diameters (from 0.5 cm to 13.69 cm) in 2009. Around each selected plant, a ring ditch was dug with the inner diameter from 2 to 20 m (approximately 6–10 times the tree height). A large cylinder of soil around the root system was removed manually at 0.1 m intervals to progressively expose the roots layer by layer. All roots with diameter >0.1 mm were collected. The diameter and length of the lateral root segments were measured with a ruler and caliper. Since the shape of the root segment resembles a cylinder, we recorded diameters and lengths of all root segments within each 0.1-m deep section and then summed to determine the root surface area within each section. Details of the excavation and root surface area measurement methods have been reported previously (Xu and Li, 2006). To explore root distribution adjustments for water capture in upper soil layers, we investigated root distribution characteristics at both ends of the groundwater table depth gradient. Five adult *H. persicum* were selected at each end. The aboveground and belowground dry biomass of each tree was obtained by oven-drying the entire biomass at 65 °C until constant weight. The groundwater table was determined after root system excavation using a soil auger at the bottom of the pit.

To investigate herbaceous layer biomass, we randomly investigated 15 subplots (1 × 1 m) at each site within the *H. persicum* sample plots. Biomass harvesting was completed in the late spring and at the start of summer, a period when herbs were at peak biomass. For aboveground biomass, we removed the aerial biomass by cutting with scissors at ground level. For the belowground parts, we dug out the soil within the subplots at depth intervals of 10 cm to maximum rooting depths. Roots and other belowground plant biomass (e.g., rhizomes) contained within the excavated sample subplot were separated with water through a 0.3-mm-mesh sieve. Live roots were distinguished by their color, consistency, and attached fine roots (Vogt and Persson, 1991). The necromass was discarded from the measurement. The biomass samples were oven-dried at 65 °C to constant weight and weighed to the accuracy of 0.01 g.

Fig. 1. Study area and sampling plots in the southern part of Gurbantunggut Desert.

Table 1
Vegetation inventory at four sites along a groundwater table gradient. Note: GD, groundwater depth; H, average tree height; CW, canopy width; VG, coverage of *Haloxylon persicum*; SD, stand density (number of plants ha⁻¹); TN, total number of trees at each site for the 20 × 20 m plot (number of plants). Data are mean ± 1 SE.

Site	Sample location	GD (m)	H (m)	CW (m)	VG (%)	SD	TN
S1	44°2 0'06"N 87°53'04"E	12	1.87 ± 0.69	2.53a ± .53 n	13.24a ± 2.15	660a ± 33	128
S2	44°23'36"N 87°51'56"E	13	2.30 ± .304	4.66b ± .664	13.12a ± 2.04	450b ± 44	83
S3	44°27'29"N 87°50'26"E	16	1.93 ± .932	2.95a ± .952	9.24b ± 1.17	365b ± 37	73
S4	44°29'23"N 87°50'06"E	18	1.76 ± .767	2.10a ± .107	7.56b ± 1.01	455b ± 25	83

2.4. Data analysis

Descriptive statistics were used to calculate means and standard errors of each data set. Differences among density, coverage, species number, height, AGB, BGB, and TB of the *H. persicum* woodland communities and their components at each site along the groundwater depth gradient were tested using One-way Analysis of Variance (ANOVA), followed by the post hoc Tukey's HSD multiple comparison test. Allometric equations developed from sample trees (i.e., relating AGB, BGB, and TB to tree height, canopy width, and basal stem diameter at 2 cm above ground level) were applied to vegetation inventory data from the sample plots to provide stand estimates of AGB, BGB, and TB of *H. persicum* in each 20 × 20 m plot. Biomass data calculated for *H. persicum* from the 20 × 20 m quadrats and those of herbaceous biomass from the small plots (1 × 1 m) were transformed to standardize the biomass fractions as Mg/ha⁻¹. We examined the relationship between RS and the groundwater table, and the relationship between the components of herb layer biomass and shrub layers biomass by linear fitting. Figure preparation was done with Origin 8.0 (Origin Lab Corp., Northampton, MA, USA). All data analyses were performed using the SPSS software package (SPSS for Windows, Version 13.0, Chicago, IL, USA).

3. Results

3.1. Species composition and quantitative characteristics of the *H. Persicum* woodland community

Based on the inventory of *H. persicum* populations in five 20 × 20 m sample plots, the quantitative characteristics of the *H. persicum* population varied with the drawdown in groundwater depth. The canopy coverage of *H. persicum* was higher at the sites with shallow groundwater table (s1 and s2) than sites with deep groundwater table (Table 1). The stand density of *H. persicum* was also highest at the shallow end of the groundwater depth gradient (Table 1). At all sites, populations were dominated by trees of smaller size classes, suggestive a population that is recruiting in sufficient numbers to maintain itself (Fig. 2). However, there were differences in the distribution of basal stem diameter (BSD) classes among sites. The plant density also varied considerably among sites. *H. persicum* density was highest at the shallow groundwater site (average of 640 plants ha⁻¹). There were also more small and young trees at the shallow end of the groundwater depth gradient (Fig. 2). However, these differences were not linearly correlated to the groundwater table gradient (Fig. 2). Median BSDs for *H. persicum* along the groundwater depth gradient were 2.5, 7.0, 6.0, and 3.0 cm, respectively, presumably reflecting the average stand age and/or time since last major disturbance (e.g., human activity).

There were no significant variations in density, coverage, and height of the herbaceous layer across the groundwater depth gradient (Fig. 3). Only the species number showed a slight decrease at the third site with a groundwater depth of 16 m.

3.2. Aboveground, belowground, and total biomass

AGB, BGB, total biomass vs. basal stem diameter, tree height, and crown width were linearly related on a log-log scale (Fig. 4). As the adjusted r square and P value indicates, the linear regression equations can be used to predict the biomass of *H. persicum* from inventory data. We selected the best linear fitting equation of each biomass component to estimate the corresponding biomass of the inventory – specifically, the linear regression with the highest adjusted r square for each biomass component (Table 2). With the increase in diameter class, the total biomass of trees of that diameter class generally increased for each site (Fig. 5a and b).

On the southern edge of the desert, 90% of the belowground biomass was distributed at 0–80 cm; and in the desert hinterland, 90% of the belowground biomass was distributed at 0–50 cm (Fig. 6). Therefore, the belowground biomass distribution of the herbaceous layer tended to occupy the shallower layers with the decline in the groundwater table.

3.3. Biomass and BGB-to-AGB ratio of *H. Persicum* woodlands along a groundwater depth gradient

Except at the site with a groundwater table depth of 13 m, the AGB and BGB of the herbaceous layer showed no significant variation (Fig. 7a). The AGB of the *H. persicum* population showed a significant decline at the deep end of the groundwater gradient (Fig. 7c). Total BGB stocks of *H. persicum* woodland communities (shrubs and herbs combined) were constant along the declining groundwater gradient (about 4.55 ± 0.28 Mg ha⁻¹). Total AGB stocks of *H. persicum* woodland communities remained constant (about 2.38 ± 0.15 Mg ha⁻¹) as groundwater declined from 13 to 16 m, and decreased significantly (to 1.59 ± 0.15 Mg ha⁻¹) at the deepest end of the groundwater gradient (Fig. 7e). Even though there was no consistent variation in AGB and BGB along the groundwater depth gradient, the BGB-to-AGB ratio in the herbaceous layer and at the community level showed an increasing trend with the decline in groundwater depth.

3.4. Root distribution of *H. Persicum* and biomass relationship between shrubs and herbaceous layers

The *H. persicum* plants at the deepest groundwater depth developed more root surface area and rooted more deeply compared to the individuals at the shallowest groundwater depth site (Fig. 8). Furthermore, 65% of the root surface area was distributed at a depth of 0–3 m in the shallow end of the groundwater depth gradient; however, 65% of the root surface area was distributed at a depth of 0–2.5 m in the deep end of the groundwater depth gradient. The depth of the soil horizon containing 85% of the root system biomass (0–2.5 m) was shallower in the deep end of the groundwater depth gradient than in the shallow end of the groundwater depth gradient (0–3 m). The correlation analysis of total biomass

Fig. 2. Size distribution (based on BSD) of *Haloxylon persicum* at four studying sites. BSD, basal stem diameter at 2 cm above the ground surface. The groundwater depth was 12 m at (a), 13 m at (b), 16 m at (c), and 18 m at (d).

Fig. 3. Variation of density (a), coverage (b), species number (c), and height of herb layer (d) in *H. persicum* woodland communities along a groundwater depth gradient. The boxes denoted 25th and 75th percentiles. The whiskers denoted the 5th and 95th percentiles. The stars indicated the minimum and maximum value. The empty square is the mean ($n = 15$) and the line in the box is the median.

(TB) and BGB exhibited a weak negative relationship between shrubs and the herbaceous layer (Fig. 9).

4. Discussion

This study examined BGB, AGB, and vertical root distribution patterns in a *H. persicum* woodlands community along a groundwater depth gradient (12–18 m) in the Gurbantunggut Desert. A few similar studies have been carried out previously in this area (Tao et al., 2013; Xu et al., 2006). Typically, in these studies, the vegetation type (or its floristic composition) changes markedly in different microhabitats. A contrasting feature of this study was that, although groundwater depth varied, the vegetation (in terms of biomass) was dominated by one species, *H. persicum*, throughout

the groundwater depth gradient. This enabled evaluation of trends and relative balances in BGB and AGB, as well as root distribution, as a function of groundwater depth without the confounding effect of drastic changes in vegetation type and composition. Also, small individuals made up most of the population in terms of numbers, but the large individuals accounted for most of the population biomass.

4.1. Patterns of AGB and BGB in *H. Persicum* woodlands along a groundwater depth gradient

In developing the allometric equations for estimating *H. persicum* biomass, we used tree height, canopy area, and basal area as explanatory variables. Similar equations were previously

Fig. 4. *H. persicum* allometry across basal stem diameters. Allometric relationships shown are between $\ln(\text{BSD})$, $\ln(\text{H})$, $\ln(\text{CW})$ and measured $\ln(\text{AGB})$ in panel (a), (b), (c), between $\ln(\text{BSD})$, $\ln(\text{H})$, $\ln(\text{CW})$ and measured $\ln(\text{BGB})$ in panel (d), (e), (f), between $\ln(\text{BSD})$, $\ln(\text{H})$, $\ln(\text{CW})$ and measured $\ln(\text{TB})$ in panel (g), (h), (i). BSD, basal stem diameter at 2 cm above ground surface; H, tree height; CW, tree crown width; AGB, aboveground biomass; BGB, belowground biomass; TB, total plant biomass.

Table 2

Parameters estimated for the regression of $\ln(\text{AGB})$, $\ln(\text{BGB})$, $\ln(\text{TB})$ on $\ln(\text{BSD})$, $\ln(\text{H})$, $\ln(\text{CW})$ of *H. persicum*. Note: MSE, mean square error; df, degrees of freedom; AGB, aboveground biomass; BGB, belowground biomass; TB, total biomass; BSD, basal stem diameter; H, tree height; CW, tree crown width.

Relationship	Intercept $\pm$ SE	Slope $\pm$ SE	MSE, df	Range (cm)
$\ln(\text{AGB})$ on $\ln(\text{BSD})$	3.423 ± 0.231	2.255 ± 0.161	0.5487, 20	0.5–13.69
$\ln(\text{AGB})$ on $\ln(\text{H})$	-10.408 ± 1.104	3.381 ± 0.228	0.4976, 20	43–300
$\ln(\text{AGB})$ on $\ln(\text{CW})$	-3.207 ± 0.422	2.048 ± 0.094	0.2362, 20	20–290
$\ln(\text{BGB})$ on $\ln(\text{BSD})$	3.291 ± 0.185	2.325 ± 0.128	0.3477, 20	0.5–13.69
$\ln(\text{BGB})$ on $\ln(\text{H})$	-10.523 ± 1.212	3.393 ± 0.251	0.5997, 20	43–300
$\ln(\text{BGB})$ on $\ln(\text{CW})$	-3.202 ± 0.588	2.034 ± 0.130	0.4576, 20	20–290
$\ln(\text{TB})$ on $\ln(\text{BSD})$	4.120 ± 0.197	2.253 ± 0.137	0.3994, 20	0.5–13.69
$\ln(\text{TB})$ on $\ln(\text{H})$	-9.540 ± 1.056	3.345 ± 0.218	0.4553, 20	43–300
$\ln(\text{TB})$ on $\ln(\text{CW})$	-2.364 ± 0.444	2.015 ± 0.098	0.2621, 20	20–290

developed by Buras et al. (2012) for the estimation of AGB and BGB of *Haloxylon* species in central Asia, including regions under moderate to strong anthropogenic influence. However, Buras et al. (2012) findings on BGB were based on excavations of all visible roots within a cube of $2 \times 2 \times 2$ m, whereas our investigation revealed that the root systems of adult trees extended far beyond this volume.

The variation patterns of AGB and BGB (as well as their components) along the groundwater depth gradient were not consistent (compare Fig. 7a, c, and e). These patterns appeared to be determined as much by stand structure and growth features of *H. persicum* as by the groundwater depth gradient. The relatively low BGB of the *H. persicum* population on the shallow end of the groundwater depth gradient may be due to previous human activity near the southern edge of the desert (e.g., firewood collecting) before the reserve was established (Tian et al., 2014), which resulted in a larger number of small and young individuals in that *H. persicum* population (Fig. 2c). BGB at the community level showed no significant increase in relation to groundwater depth; meanwhile, AGB decreased significantly at the deepest end of the groundwater depth gradient (Fig. 7e). Since there was no significant decrease in AGB for the herbaceous layer at the deepest end of the groundwater gradient, the decrease of AGB for the community was mainly attributed

to the decrease of AGB in the *H. persicum* population. The lower herbaceous layer biomass at the second site with a groundwater depth of 13 m was due to over-grazing, as sheep manure was found during our field investigation at this site.

The overall average of AGB and BGB in China's grasslands has been estimated at 104.8 and 570.2 g m^{-2} , respectively (Yang et al., 2010). The average AGB and BGB of the desert herbaceous layer in our study were 53.9 and 157.5 g m^{-2} , respectively, and were lower than the overall average of AGB and BGB in China's grasslands. In addition, both the AGB and BGB of the herbaceous layer on the southern edge of the Gurbantunggut Desert were much smaller than the estimates for global grasslands by Jackson et al. (1996) (378.4 g m^{-2} for AGB and 1400 g m^{-2} for BGB) and by Mokany et al. (2006) (430.2 g m^{-2} for AGB and 1810.9 g m^{-2} for BGB). However, our estimation of AGB and BGB at the community level are within the range of values reported on *H. persicum* woodlands in central Asia (Thevs et al., 2013).

4.2. Variation of the BGB-to-AGB ratio of *H. Persicum* woodland communities along a groundwater depth gradient

The BGB-to-AGB ratio is an integrated measure of the relative balance between the BGB and AGB of plants. Although this ratio

Fig. 5. Biomass distribution and allocation across the basal stem diameter classes at each site of the water table gradient based on the developed allometric equations. Error bars indicate standard error of the mean.

Fig. 6. Distribution of total root biomass through the soil profile at each site along the groundwater table gradient. Error bars indicate standard error of the mean.

is primarily defined at the level of an individual plant, with appropriate sampling and inventory it can be readily aggregated to provide estimates at increasing levels of complexity, such as at community, ecosystem, or regional scales (Zerihun et al., 2006). Our results revealed community-level adjustments in the relative

balances of BGB and AGB stocks along the groundwater depth gradient.

As groundwater depth declined, the *H. persicum*-dominated plant community responded by increasing the proportion of whole system biomass apportioned to the belowground component.

Fig. 7. Changes in aboveground (AGB) and belowground (BGB) biomass and patterns of BGB-to-AGB ratios of *H. persicum* woodland communities along a groundwater depth gradient. Data are mean $\pm$ 1 SE. There are no significant differences for the BGB of *Haloxylon* and whole community among sites.

Accordingly, there was an approximate 77% increase in the BGB-to-AGB ratio from the shallow end to the deep end of the groundwater continuum. Because the BGB-to-AGB ratio of *H. persicum* population showed no significant trend with declining groundwater level, the allocation pattern of the herbaceous layer along the groundwater depth gradient and thus the corresponding BGB-to-AGB ratio had a greater contribution in shaping the pattern of the BGB-to-AGB ratio at the community level (Fig. 7a, b, e, and f). Based on the aboveground growth performance (Fig. 7a), there was no evidence of water stress in the grasses. Thus, the herbaceous layer species seemed to be better adapted to changes in water availability by effectively adjusting the root–shoot ratio, which aided in their efficient capture of rainfall (Fig. 7b). In contrast, *H. persicum* plants were not able to effectively adjust their root systems to declining groundwater availability, as signified by the decreased AGB of trees at the sites with lower groundwater tables (Fig. 7c and d).

The overall trend of the BGB-to-AGB ratio observed along the groundwater depth gradient is consistent with predictions of resource balance/optimality theory (Zerihun et al., 2006; Bloom et al., 1985; Friedlingstein et al., 1999), which predicts that plants adjust their biomass distribution to facilitate the acquisition of a growth-limiting resource: water in this instance. The average R/S of the herbaceous layer in our study was 3.3 (ranging from 2.6 to 4.2), which was smaller than that reported for China's grasslands (6.3, with 95% CIs of 5.9–6.7), but approached the value of 3.7 found by Jackson et al. (1996) for global grasslands. The BGB-to-AGB ratios of *H. persicum* vegetation were from 1.67 to 2.95, which fell within the value range reported by Thevs et al. (2013).

The *Haloxylon* woodlands cover a large area in the Central Asia and Middle-East Desert, including the border and sea floor of the Aral Sea, the Kyzylkum Desert (Uzbekistan), the Karakum Desert (Turkmenistan), Muryunkum Desert (Kazakhstan), South Sinai (Egypt), and the desert region of Mongolia and China (Thevs et al., 2013). Due to their natural dominance, *Haloxylon* are considered an ecologically key species that plays an important role in stabilizing sand surfaces (Breckle et al., 2001). Compared with other dryland forests, the Saxaul vegetation covers a larger area (Rachkovskaya et al., 2003). Their contribution to regional AGB and BGB and carbon stocks can be substantial (Buras et al., 2012; Thevs et al., 2013). However, previous research on the estimation of biomass and corresponding carbon stocks have scarcely considered the influence of limited resources or environmental conditions on biomass allocation, such as the natural existence of a salt gradient (Breckle, 2002) and a groundwater depth gradient in the areas bordering the Aral Sea as well as on the sea floor (Breckle et al., 2001). In this view, the allometric functions developed here may aid in more accurate estimations of AGB and BGB carbon stocks elsewhere in desert woodlands dominated by *H. persicum*.

4.3. Root distribution adjustments of *H. Persicum* and the herb–shrub biomass relationship

In water-limited environments, the availability of water to individual plants depends in part on local climatic and edaphic factors and also on the depth, lateral spread, and degree of overlap of plant root systems (Casper and Jackson, 1997). There are indications that desert shrubs may adjust their root systems toward the optimal phenotype that can maximize water availability (Schwinning and

Fig. 8. Vertical distributions of feeder roots surface area (a, b) and biomass (c, d) of *H. persicum* at the shallow and deep end of the groundwater table gradient. Error bars indicate standard error of the mean ($n = 5$). The dashed line marks 65% of the total surface root area (a, b) and 85% of the root biomass (c, d) distribution in the soil profile.

Ehleringer, 2001). The greater root surface area and root biomass in shallow soil layers for *H. persicum* located at the deep end of the groundwater table gradient indicated that *H. persicum* adjusted root distribution to facilitate uptake of soil moisture in the shallow soil layers (Fig. 8). However, the adjustment was not effective to maintain AGB production to a level of the sites with shallower water tables (Fig. 7c).

Shrub–herb interactions in arid ecosystems are most frequently reported as plant facilitation between the shrubs and the grasses under a shrub canopy (Flores and Jurado, 2003). The desert herbaceous species were usually shallow rooted with geometric mean rooting depths of 0.5 m in climates with 50–150 mm precipitation (Schenk and Jackson, 2002). A study on *Haloxylon ammodendron* and its understory grasses in our study showed that annual plants had higher aboveground biomass and lower R/S ratios when they were near shrubs, and invested less root biomass in deep soils than in interspace microhabitats (Li et al., 2010). However, the interaction relationship between shrubs and herbs may shift from facilitation to competition along the resource gradient (Maestre et al., 2003). Our findings revealed that BGB and TB of grasses tended to decline with an increase in biomass of trees (Fig. 9), suggesting a competitive interaction.

5. Conclusion

The BGB-to-AGB ratio of *H. persicum* community varied notably along groundwater depth. The shift of biomass allocation patterns along the water table gradient need to be considered for an accurate assessment of AGB and BGB of *H. persicum*. The allometric functions developed on this basis might be helpful for biomass estimation in similar vegetation communities in central Asian desert ecosystems.

H. persicum tended to optimize its root system by adjusting root distribution to facilitate uptake of shallower soil moisture when groundwater is deep. However, despite this adjustment the AGB declined with the groundwater depth drawdown. In contrast, herbaceous layer showed better adaptation to changes in water availability by effectively adjusting the BGB-to-AGB ratio and maintaining the AGB production levels.

This scaling exercise (albeit a coarse approximation) underscores the need for more targeted estimation of BGB-to-AGB ratios in major vegetation types along environmental/resource gradients, which are likely to impact BGB versus AGB partitioning patterns in the Central Asia desert area.

Fig. 9. The relationship of biomass between *H. persicum* trees and their understory herbaceous layer. (a) belowground biomass (BGB); (b) total biomass. There is no significant relationship between AGB of trees and grasses. The numbers adjacent to hollow circles represent the ground water depth. Data are mean $\pm$ 1 SE.

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