Biocrust-induced partitioning of soil water between grass and shrub in a desert steppe of Northwest China (Postprint)

Authors: YANG Xinguo, WANG Entian, Wenjie Qu, WANG Lei

Date: 2023-02-07T00:00:00+00:00

Abstract

Maintaining the stability of exotic sand-binding shrub has become a large challenge in arid and semi-arid grassland ecosystems in northern China. We investigated two kinds of shrublands with different BSCs (biological soil crusts) cover in desert steppe in Northwest China to characterize the water sources of shrub (Caragana intermedia Kuang et H. C. Fu) and grass (Artemisia scoparia Waldst. et Kit.) by stable 18O isotopic. Our results showed that both shrublands were subject to persistent soil water deficiency from 2012 to 2017, the minimum soil depth with CV (coefficient of variation) <15% and SWC (soil water content) <6% was 1.4 m in shrubland with open areas lacking obvious BSC cover, and 0.8 m in shrubland covered by mature BSCs. For C. intermedia, a considerable proportion of water sources pointed to the surface soil. Water from BSCs contributed to averages 22.9% and 17.6% of the total for C. intermedia and A. scoparia, respectively. C. intermedia might use more water from BSCs in rainy season than dry season, in contrast to A. scoparia. The relationship between shrub (or grass) and soil water by $ $18O shown significant differences in months, which partly verified the potential trends and relations covered by the high variability of the water source at seasonal scale. More fine roots at 0–5 cm soil layer could be found in the surface soil layer covered by BSCs (8000 cm/m3) than without BSCs (3200 cm/m3), which ensured the possibility of using the surface soil water by C. intermedia. The result implies that even under serious soil water deficiency, C. intermedia can use the surface soil water, leading to the coexistence between C. intermedia and A. scoparia. Different with the result from BSCs in desert areas, the natural withdrawal of artificial C. intermedia from desert steppe will be a long-term process, and the highly competitive relationship between shrubs and grasses also determines that its habitat will be maintained in serious drought state for a long time.

Full Text

Preamble

Biocrust-induced partitioning of soil water between grass and shrub in a desert steppe of Northwest China

YANG Xinguo[1],[2],[3]*, WANG Entian[1],[2],[3], QU Wenjie[1],[2],[3], WANG Lei[1],[2],[3]

[1] Northwest National Key Laboratory Breeding Base for Land Degradation and Ecological Restoration, Ningxia University, Yinchuan 750021, China
[2] Key Laboratory of Restoration and Reconstruction of Degraded Ecosystems, Ministry of Education, Ningxia University, Yinchuan 750021, China
[3] Ecology and Environment College, Ningxia University, Yinchuan 750021, China

Abstract

Maintaining the stability of exotic sand-binding shrubs has become a major challenge in arid and semi-arid grassland ecosystems of northern China. We investigated two shrublands with different biological soil crust (BSC) cover in a desert steppe of Northwest China to characterize the water sources of shrub (*Caragana intermedia* Kuang et H. C. Fu) and grass (*Artemisia scoparia* Waldst. et Kit.) using stable δ^{18}O isotopic analysis. Our results showed that both shrublands experienced persistent soil water deficiency from 2012 to 2017. The minimum soil depth with coefficient of variation (CV) <15% and soil water content (SWC) <6% was 1.4 m in shrubland with open areas lacking obvious BSC cover, and 0.8 m in shrubland covered by mature BSCs. For *C. intermedia*, a considerable proportion of water sources originated from surface soil. Water from BSCs contributed an average of 22.9% and 17.6% of the total water for *C. intermedia* and *A. scoparia*, respectively. *C. intermedia* might use more water from BSCs in the rainy season than in the dry season, in contrast to *A. scoparia*. The relationship between shrub (or grass) and soil water as indicated by δ^{18}O showed significant differences across months, which partly verified the potential trends and relationships obscured by high variability in water sources at the seasonal scale. More fine roots were found in the surface soil layer (0–5 cm) covered by BSCs (8000 cm/m^3) than without BSCs (3200 cm/m^3), which ensured the possibility of using surface soil water by *C. intermedia*. The result implies that even under severe soil water deficiency, *C. intermedia* can utilize surface soil water, leading to coexistence between *C. intermedia* and *A. scoparia*. Unlike results from BSCs in desert areas, the natural withdrawal of artificial *C. intermedia* from desert steppe will be a long-term process, and the highly competitive relationship between shrubs and grasses also determines that its habitat will be maintained in a serious drought state for a long time.

Keywords: desert steppe; biological soil crusts; water resource; *Caragana intermedia*; *Artemisia scoparia*

Introduction

In northern China, arid and semi-arid grassland ecosystems are threatened by desertification, and the use of desert shrubs as sand-binding vegetation to restore such areas has been implemented across approximately 6$×10^{6}$ hm^2 over the past 60 years. However, sand-binding vegetation can reduce soil water content in deep soil layers, leading to dieback and mortality due to water stress (Li et al., 2014). Thus, maintaining the stability of exotic sand-binding shrubs has become a major challenge (Li et al., 2013).

The senescence of exotic sand-binding species and the reappearance of native species may be inevitable (Li et al., 2014), though the process varies among regions. For example, the inflection point of shrub-grass replacement—wherein the senescence of exotic shrubs is followed by the reappearance of native grasses—has been recorded at around 30–40 years after shrub planting where annual precipitation is about 200 mm (Li, 2005), or 10–20 years where annual precipitation is around 400 mm (Zuo et al., 2009). However, in desert steppes with precipitation of around 300 mm where shrub (*C. intermedia*) has been replanted to restore sandy grassland, the shrub has remained the dominant species for more than 40 years without a significant increase in plant diversity (Yang et al., 2015). As a result, a binary vegetation structure dominated by the shrub and grass (*A. scoparia*) is common in the region (Zhao et al., 2015; Chen et al., 2019).

Soil water deficiency drives competition between shrubs and grasses for shallow soil water (Ehleringer et al., 1991), weakening the upper and lower layer coexistence strategy (Le Roux et al., 1995). As a result, shrub degradation is not always avoidable. However, differences in root configuration among different shrub species and across life stages lead to variable use of water sources among individual shrubs adapting to arid and semi-arid grassland ecosystems (Jia et al., 2012; Huang and Zhang, 2015; Zheng et al., 2015). For example, shrubs growing in the Mu Us Sandy Land of China can successfully compete to delay the emergence of grasses as the dominant species during later successional stages (Liu et al., 2010). In addition, the succession process is also related to disturbances, environmental factors such as precipitation, soil type, and other variables, indicating specificity of eco-hydrologic processes in different regions (Li et al., 2017). These different succession processes reflect possible differences in the intensity and mode of shrub-grass competition for shallow soil water among regions.

To our knowledge, however, few studies have examined the water source and competitive relationship between exotic *C. intermedia* and native grasses, especially in combination with stable isotope studies. In arid regions, biological soil crusts (BSCs) are important factors affecting hydrological processes and vegetation succession. Studies have shown that compared with bare soil, soil water infiltration decreases when soil is covered by BSCs, with more water from precipitation being constrained in shallow soil layers (i.e., shallowing soil hydrological processes) (Li et al., 2010; Zhang et al., 2015). In the Tengger Desert of China, the appearance of BSCs accelerates the decline of re-vegetated shrubs and the recovery of local shallow-rooted grasses (Li, 2005). However, in the Negev Desert of Southern Israel, moss crusts scarcely influence precipitation infiltration and do not lead to shrub death (Kidron, 2014a). During severe droughts, BSCs can even provoke the death of certain annual plant species (Kidron, 2014b). Due to differences in soil properties and crust types, the influence of BSCs on vegetation-hydrological processes is highly variable across regions (Li et al., 2010; et al., 2012), and debate remains regarding the vegetation-hydrological effects of BSCs. The effects of BSCs on the exotic shrub *C. intermedia* and native species in the desert steppe of China have yet to be specifically analyzed.

C. intermedia is an important species for restoring sandy grassland that now also faces the challenge of stability maintenance in the desert steppe. The different processes of shrub-grass replacement reflect potential specificity of ecological-hydrological mechanisms in this region. To investigate these mechanisms, we selected two examples of exotic *C. intermedia* shrublands with notable differences in BSC coverage and examined soil hydrological processes and water sources for the shrub and dominant grass *A. scoparia*. We aimed to describe the effect of BSCs on water sources of *C. intermedia* and *A. scoparia* and to deeply understand the stability of the exotic shrub in the region.

2.1 Study Area

The study area was located in a semi-arid desert steppe of Yanchi County, Ningxia Hui Autonomous Region of China (37°47 -37°57 N, 107°22 -107°33 E; Fig. 1 [Figure 1: see original paper]). The annual mean temperature is 8.1°C and mean annual precipitation ranges from 250 to 350 mm, with more than 62% of total precipitation occurring between July and September. Annual sunlight is 3124 h and potential evaporation is 2897 mm. The frost-free period lasts about 165 days. The main soil types of the region are sierozem, loess, and aeolian sandy soil. In general, the plant growth season is from April to October, and precipitation and soil water conditions often change significantly before and after July. The period before July is called the dry season with little precipitation and shallow soil water deficiency, except for more water in deep soil from precipitation in the previous year. The period after July is therefore called the rainy season with more precipitation and good soil water conditions in shallow layers.

The region is a typical transition zone between the Mu Us Sandy Land and the Loess Plateau. While there is considerable heterogeneity of climate, soil, and plants in the region, there has also been serious environmental destruction caused by human activity such as livestock overgrazing. *C. intermedia* was extensively planted to restore these areas beginning in the 1970s, and the areas presently exceed 2$×10^{5}$ hm^{2}. Most *C. intermedia* planted before the 1990s have reached maturity, and soil water deficiency and individual senescence have followed (Song et al., 2014; Yang et al., 2015).

C. intermedia is typically planted in belts with two lines, spaced 1 m apart and

6–8 m between belts, and oriented perpendicular to the primary wind direction in winter and spring (Zuo et al., 2006). The native vegetation of the area varies greatly due to differences in the degree of desertification and grazing disturbance. In general, most native species are annual plants adapted to sandy environments, such as *A. scoparia*. Most perennial grasses are only found in small soil patches scattered within the sandy grassland matrix.

2.2 Sampling Design

Two *C. intermedia* shrublands with different BSC coverage were considered (Fig. 1). One shrubland lacked obvious BSC cover (S-CK), while open areas of another shrubland were covered with BSCs (S-BSC). Shrub coverage was 23.5% in S-CK and 21.8% in S-BSC, without obvious differences (Table S1). Reduction of shrub individuals was more obvious in S-BSC, with light damage to the canopy. *A. scoparia* was the dominant grass species in both shrublands, forming a single binary community with *C. intermedia*. Both shrublands had sandy calcareous soil at the surface with similar qualities (Table S2). BSCs in S-BSC were composed primarily of moss, with traces of lichen, and covered 57% of the ground with an average thickness of 2 cm. Their color differed between the arid and rainy seasons, becoming gray in the dry season and green in the rainy season.

Within each shrubland, we selected three 100 m\$ $\times 100 msamplingplotsandrandomlychosefive*$ $C.intermedia*individualsandfivesubplotswithindifferentbelts(oneeveryotherbelt), 1.5mfromtheedgeofthel$ this varied widely over space and time. According to our investigation, when herders rely on livestock as their main income, higher grazing intensity is common and BSCs in the shrubland are rare, such as in S-CK. However, some herders may give up grazing temporarily due to economic or other factors, or may sublease meadows to achieve rotational grazing. Therefore, these shrublands may be temporarily idle, giving BSCs a chance to develop, such as in S-BSC.

2.3 Soil Moisture Monitoring

In the sampled plots, six transparent plastic pipes for time-domain reflectometry (TDR) probes (HD2-TRIME/T3, IMKO Device Ltd., Ettlingen, Germany) were vertically installed in the soil, 1.5 m from the edge of the belt, to measure soil moisture from 0–300 cm in 20 cm intervals. Measurements were made every 15 days during the growing seasons from 2012 to 2017. Natural grassland without *C. intermedia* was also sampled to serve as a control (CK). At the same sites, surface soil moisture was monitored from August 2015 at layers of 3 and 8 cm. These measurements were used to obtain average soil moisture at 0–5 and 5–10 cm, respectively. These sensors have a resolution of 0.001 m^3/m^3, estimated accuracy of 0.02 (\$ $\pm 0.03) m^{\{3\}/m}\{3\}, andrangefrom0to1m^{\{3\}/m}\{3\}$\$. Installation of probes followed a protocol outlined in Chamizo et al. (2013) and was completed in August 2015. At each site, a U30 Soil Moisture Logger system was installed, and data were collected every 30 minutes using a HOBO Micro

Station system (Onset Co., Bourne, Massachusetts, USA). Standard calibration equations were used to obtain measures of volumetric water content (Cobos and Chambers, 2010). Daily soil moisture was considered the average of the 30-minute soil moisture records in a day.

2.4 Water Sources for *C. intermedia* and *A. scoparia*

To further determine the role of BSCs in water sources, and according to the main sources of soil water for plants based on pre-test results and the limitation of the linear mixed model (sources should be less than five; Dawson, 1993), we adjusted the sampling method of soil water during 2016–2017 based on four sources: (1) BSCs at 0–2 cm layer, (2) shallow soil from 2–30 cm layer, (3) middle soil from 30–70 cm layer, and (4) deep soil deeper than 70 cm, until reaching the impermeable parent material horizon. During 2016–2017, nine sampling events in different months were completed. The sampling dates in the dry season were May, June, and early July, while in the rainy season were late July, August, and September. For each sampling event, three replicate samples of plants or soil were collected, yielding 27 samples in total.

During each sampling event, nine xylem samples were collected from two-year-old *C. intermedia* twigs without green parts. Nine xylem samples of root and stem joints from different *A. scoparia* individuals were also randomly selected. All bark and phloem were removed, and samples were pooled, transferred to glass vials sealed with parafilm, and stored in a portable cooler. At the same time, different layers of soil were sampled using a hand auger with 35 mm diameter, sealed, and stored. All samples were subsequently kept in a -20°C freezer prior to water extraction.

Water extraction and isotopic δ^{18}O analyses were performed at the China Academy of Forestry. Eighteen samples for *C. intermedia* (seven in the dry season and eleven in the rainy season) and twelve samples for *A. scoparia* (five in the dry season and seven in the rainy season) were used to analyze water sources, meeting the requirements of the linear mixed model. The IsoSource software package (Phillips and Gregg, 2003) was used to quantify the contributions of multiple water sources from different soil layers for *C. intermedia* or *A. scoparia*.

2.5 Fine Root Distribution in 0-10 cm Soil Layer for *C. intermedia*

The fine root distribution of *C. intermedia* in S-BSC at layers of 0–5 and 5–10 cm was investigated in 2016. To examine the relative effects of BSCs, we established two types of root sampling plots away from the shrub belts used in the above experiments. One used three replicate 4 m$×*4mplotswithBSCsreserved, andtheotherusedthreereplicateplotswithBSCsremovedcompletelyinApril*20
m subplots in each plot were established, and whole soil samples from 0–5 and 5–10 cm layers were collected. Fresh fine roots of *C. intermedia* with 0.5-2.0 mm diameter were extracted, and root length was measured in the field. Fine

root parts less than 0.5 mm in diameter were discounted due to the associated difficulty in recognizing and collecting them (Fig. S1).

2.6 Statistical Analyses

Statistical analyses were performed using SPSS v.20.0 statistical software (SPSS Inc., Chicago, USA). T-tests were used to determine statistically significant differences (α=0.05) in root length between plots and differences in δ^{18}O among soil and plants. A time-depth contour map of soil moisture in different years was created using Surfer v.13.0 software (Golden Software Inc., Colorado, USA) and used to analyze dynamics and trends in soil moisture during the study period.

CV (coefficient of variation) values of soil moisture in the upper layers were generally greater than in deeper layers due to disturbance from seasonal precipitation. We defined soil moisture in a given layer as relatively stable when the average value of CVi (the coefficient of variation in soil moisture at the ith soil layer) during 2012–2017 was lower than 15%. According to the variation of soil moisture in the 0–300 cm layer during 2012–2017, the depth of the uppermost soil layer whose average CVi during 2012–2017 was lower than 15% and SWC was lower than 6% was considered empirically as the maximum depth affected by precipitation, or the starting depth for soil water deficiency in the study area. When this depth was lower, soil water deficiency was regarded as more serious.

The daily difference in soil moisture in surface soil (0–5 cm layer) relative to the lower layer (5–10 cm layer) was calculated as follows:

$$ISSM = \frac{SWC_5 - SWC_{10}}{SWC_{10}} \times 100$$

where ISSM is the daily increment of surface soil moisture (%); SWC_5 is the percent volumetric soil water content at 0–5 cm layer, and SWC_{10} is the percent volumetric soil water content at 5–10 cm layer. When surface soil has higher water-holding capacity, precipitation infiltration will be delayed, leading to higher water content relative to the lower layer for a certain duration. Under continuous monitoring of soil moisture, ISSM could be considered a simple indicator to measure dynamic changes in hydrological states in the surface soil, e.g., shallowing soil hydrological processes.

3.1 Soil Moisture Dynamics in 0–300 cm Layer from 2012 to 2017

There were significant spatial and temporal differences among S-CK, S-BSC, and CK (grassland) (Fig. 2 [Figure 2: see original paper]). From 2012 to 2017, soil water contents in both S-CK and S-BSC showed continuous decreasing trends, while natural grassland did not show similar changes. Soil water content in the 0–60 cm layer in S-BSC was higher than that in S-CK, but the relationship was reversed when the layer was deeper than 60 cm. Mean values during 2012–2017 indicated that the minimum soil layer with CV<15% and SWC<6% was 1.4 m for S-CK and 0.8 m for S-BSC (Fig. S2). During most of the observation period, soil water deficiency was most evident in S-BSC, where the moisture of soil layers below 1.0 m was consistently <6%.

3.2 Daily Surface Soil Moisture Dynamics

The relative water content of the surface soil layer (0–5 cm) was consistently higher than the lower layer (5–10 cm) in S-BSC, but was lower or nearly equal to the lower layer in S-CK (Fig. 3 [Figure 3: see original paper]). The relative increment in ISSM was higher under BSC cover (S-BSC: 14.67% on average, varying from -59.26% to 355.19%), indicating that BSCs retained more precipitation and led to greater relative residence time of water at the surface. Where there was no BSC cover, ISSM was greatly reduced (S-CK: -5.08% on average, varying from -32.74% to 37.49%). This was a typical case of shallowing soil hydrological processes under BSC cover.

3.3 Water Uptake for *C. intermedia* and *A. scoparia*

To further understand the role of BSCs in water resource use by *C. intermedia* and *A. scoparia*, we collected water samples from BSCs (0–2 cm layer) and restricted soil water sampling to shallow (2–30 cm layer), middle (30–70 cm layer), and deep (>70 cm) layers from 2016 to 2017 (Table 1). On average, BSCs were a source of 22.9% of water for *C. intermedia* and 17.9% for *A. scoparia*. Water from 0–30 cm contributed nearly 60% of the resources for both *A. scoparia* and *C. intermedia*.

More variation in *C. intermedia* water resource use was observed in the dry season than in the rainy season (Fig. 4 [Figure 4: see original paper]). On average, more water was taken up from BSCs by *C. intermedia* in the rainy season, but not by *A. scoparia*. Greater uptake by *A. scoparia* from BSCs occurred in the dry season. The differences in water sources of *A. scoparia* between rainy and dry seasons were related to its root growth dynamics (Fig. S3). However, the water resources in the dry season between *C. intermedia* and *A. scoparia* were significantly different (P<0.05; Fig. S4).

3.4 Root Length Distribution of *C. intermedia* in 0–10 cm Soil Layer

BSCs also affected root distribution of *C. intermedia* (Figs. 5 and S1). More fine roots occurred in the 0–5 cm layer in the presence of BSCs than without them (P<0.05), but this difference was not observed in the 5–10 cm layer (P>0.05). Overall, more fine roots were found in the 0–5 cm layer than in the 5–10 cm layer in both plots, but the difference was not significant (P>0.05).

4.1 Surface Soil Water Use by *C. intermedia*

Whether *C. intermedia* can use more surface soil water when BSCs are present depends on two conditions: water availability and fine roots in surface soil. First, the relative availability of surface soil water increased when BSCs were present (Fig. 2), as similarly observed in desert regions (Li et al., 2010). Second, more fine roots of *C. intermedia* were found in the 0–5 cm layer when BSCs were present (Fig. 5). Although BSCs exacerbated the degree of soil water deficiency in the 0–300 cm layer, they also increased the possibility for *C. intermedia* to use more surface soil water, just as *Caragana korshinskii* Kom. does in the desert (Zhang et al., 2006) and *C. intermedia* does in a loess region (Lu et al., 2017).

The hydrological role of BSCs and their ecological impacts on plant communities in arid and semi-arid grassland ecosystems are still under debate (Kowaljow and Fernández, 2011; Kidron et al., 2012). The water use pattern of *C. intermedia* induced by BSCs in the desert steppe, like previous debates, reflects the complexity and particularity of the relationship between soil and vegetation across different regions where BSCs exist. Moss, as the main component of BSCs, is often associated with high water-holding capacity, which increases the residence time of water in surface soil, resulting in greater availability for plants with shallow roots (Li et al., 2010). However, *C. intermedia* is a typical shrub with distinct vertical and horizontal roots that are highly plastic in their response to different soil and water conditions (functionally dimorphic root system, Grossiord et al., 2017). Many shrub species develop horizontal roots in drier soil habitats (Zhang et al., 2010; Zhu et al., 2010) to utilize shallower soil water (Jia et al., 2012; Liu et al., 2012). As previously reported (Zhou et al., 2013; Lu et al., 2017), water used by both shrubs and grasses may be obtained from different soil layers according to changes in water availability during different seasons. In our study, the distribution of fine roots in the 0–5 cm soil layer indicates that *C. intermedia* also has the ability to use surface soil water.

Due to limitations in observational techniques, we do not have direct evidence of the existence of *C. intermedia* fine roots within BSCs themselves. It is also possible that the dense structure of moss does not allow the roots of *C. intermedia* to enter (Galun et al., 1982). In fact, the isotopic δ^{18}O signal between BSCs (0–2 cm) and the surface soil layer (0–5 cm) may be indistinguishable due to the close physical and hydrological connection between them (Chamizo et al., 2012). Therefore, the water source indicated by isotope analysis may reflect the utilization of water in the surface soil layer (possibly including BSCs) by *C. intermedia*, which is more consistent with the distribution of water and roots.

4.2 Seasonal Water Use Patterns of Coexisting Plants

In arid regions, most plants preferentially use shallow soil water, while deep soil water might be used only as a supplementary source (Eggemeyer et al., 2009; Liu et al., 2014), depending on the relationship between supply (distribution of soil water) and demand (distribution of root system). At the same time, extensive distribution of roots in the surface layer can compensate for relative deficiency of soil water and minimize energy expenditure (Ogle and Reynolds, 2004; Schenk, 2008). That is, spatial overlap of water sources for most species in arid regions generally cannot be avoided (Ehleringer et al., 1991). In our study, water in the 0–30 cm soil layers is the main source for both *C. intermedia* and *A. scoparia*, accounting for close to 60% of total usage. This indicates spatial overlap in the shallow soil layer and therefore water competition between the shrub and grass is not avoided.

However, there are obvious differences in water sources between dry and rainy seasons for both *C. intermedia* and *A. scoparia*. For *C. intermedia*, 13.7% of water was obtained from BSCs and 33.5% from the shallow soil layer during the dry season; the same values are 30.2% and 31.9% for *A. scoparia*. Meanwhile, in the rainy season, these values are 31.8% and 25.7% for *C. intermedia*, and 10.5% and 48.1% for *A. scoparia*. The competitive relationship between species for water resources is related to the soil hydrological environment and seasonal changes in precipitation in arid areas, as well as to life history characteristics of various species (Asbjornsen et al., 2007). In the dry season, *C. intermedia* sprouts earlier than *A. scoparia* (Liang et al., 2008) and has opportunities to use deeper soil water from precipitation storage in late autumn (Niu et al., 2003; Lu et al., 2017). However, the early growth of *A. scoparia* mainly occurs in the roots as an annual plant (Chen et al., 2019), and its soil water use gradually increases by layer. Therefore, there may not be many opportunities for the fine roots of the two plants to directly interact in the early dry season. Other studies have shown that under drought conditions, herbs generally adopt physiological adaptations to reduce water consumption, while shrubs search for more water sources to respond more actively to drought (Angert et al., 2009; Chen et al., 2017; Lu et al., 2017). Therefore, in cases of spatial water source overlap, *C. intermedia* and *A. scoparia* may still coexist through various mechanisms such as seasonal water partitioning and life history differences.

At the same time, the presence of BSCs significantly affected the hydrological characteristics and water environment of surface soil, which made it possible to further divide the shared soil water resource for *C. intermedia* and *A. scoparia*. In the study area, the biological activity and hydrological characteristics of BSCs were significantly different between the arid and rainy seasons. In general, the water-holding capacity of BSCs is greater in the dry season, while the water-infiltrating capacity of BSCs is greater in the rainy season (Zhang et al., 2014; Yang et al., 2018). More precipitation may be retained in surface soil in the dry season, giving *A. scoparia* an opportunity to use this water rather than *C. intermedia*. However, for both *C. intermedia* and *A. scoparia*, more fine roots are invested in the surface soil layer during the rainy season to intercept water filtering through the BSCs, with improved surface soil moisture conditions.

Here, unlike the classic shrub-grass coexistence mechanism of “upper and lower layers”(where shrubs use water in lower soil layers and grasses use water in upper soil layers), the division of water resources between the shrub and grass can still be realized based on differences in their life history when BSCs are present, even if the main water sources for shrubs and grasses are highly concentrated in shallow soil layers.

5 Conclusions

When surface soil was covered by BSCs, it exacerbated the average degree of soil drought in the 0–300 cm layer as a whole, but the relative availability of water in the surface soil layer (0–5 cm) also increased, since more water was retained in this layer. The surface soil, including BSCs where possible, might be a key water source used by *C. intermedia*. In cases where the main water sources for *C. intermedia* and *A. scoparia* were both concentrated in the shallow soil layer (0–30 cm), division of water resources could still be achieved for *C. intermedia* and *A. scoparia* based on differences in life history. The coexistence of *C. intermedia* and *A. scoparia* around the competition for shallow soil water with BSC cover breaks through the "up and down" mode of shrub-grass coexistence in arid areas. Unlike results from BSCs in desert areas, the natural withdrawal of artificial *C. intermedia* from desert steppe will be a long-term process, and the highly competitive relationship between shrubs and grasses also determines that its habitat will be maintained in a serious drought state for a long time.

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Appendix

Table S1 Shrub morphological characters and biodiversity in S-CK and S-BSC

Shrub morphological characters	Biodiversity index
CA (m^2)	SH (m)

2.87$±0.30|1.25±0.43|1.79±0.63|23.5±4.08|2.33±0.30|3.38±0.36|0.23±0.17|1.25±0.12||2.51±0.45|0.99±0.28|1.4

Note: CA, canopy area; SH, shrub height; BD, base diameter of branch; CD, covering degree; R, richness index; H, Shannon-Wiener index; D, dominance index; E, evenness index; S-CK, shrubland without BSCs cover; S-BSC, shrubland with BSCs cover. Mean±SD.

Table S2 Information of surface soil (0-20 cm) in S-CK and S-BSC

	Silt and clay (%)	SOC (g/kg)	TN (g/kg)	TP (g/kg)
S-CK	11.08$±5.08*a*	3.94±0.35*a*	0.29±0.07*a*	0.29±0.06*a*
S−BSC	15.44±7.04*a*	4.04±0.27*a*	0.23±0.06*a*	0.33±$0.02a

Note: Different lowercase letters within the column represent significant differences between S-CK and S-BSC at P<0.05 level. S-CK, shrubland without BSCs cover; S-BSC, shrubland with BSCs cover. Mean±SD.

Fig. S1 Upper-direct growth of roots in 0-20 cm soil layer for *C. intermedia* in the rainy season in 2018

Fig. S2 Soil water content and its CV (coefficient of variation) values in different soil layers during 2012-2017. CV-S1, CV values of soil water contents during 2012-2017 in S-CK plot; CV-S2, CV values of soil water contents during 2012-2017 in S-BSC plot; CV-CK, CV values of soil water contents during 2012-2017 in CK plot; AV-S1, average values of soil water contents during 2012-2017 in S-CK plot (shrubland without BSCs cover); AV-S2, average values of soil water contents during 2012-2017 in S-BSC plot (shrubland with BSCs cover); AV-CK, average values of soil water contents during 2012-2017 in CK plot (grassland without shrub).

Fig. S3 Root growth of *A. scoparia* from May to September

Fig. S4 Percentage of water uptake from four potential soil water sources for *Caragana intermedia* and *Artemisia scoparia* in the rainy and dry seasons during 2016-2017. Water sources were defined as BSCs (biological soil crusts) ranging from surface (0-2 cm), shallow (2-30 cm), middle (30-70 cm) to deep (>70 cm). Different uppercase letters indicate significant differences between *C. intermedia* and different water sources at P<0.05 level. Different lowercase letters indicate significant differences between *A. scoparia* and different water sources at P<0.05 level. * indicates significant differences between *C. intermedia* and *A. scoparia* at P<0.05 level. Bars are standard errors.

Note: Figure translations are in progress. See original paper for figures.