

Summer rain pulse size and rainwater uptake by three dominant desert plants in a desertified grassland ecosystem in northwestern China

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Abstract

To examine the different effects of rain pulse size on uptake of summer rains by three dominant desert plants in field conditions of desertified grasslands on the Ordos Plateau of northwestern China, we studied relationships between precipitation event size and rainwater uptake using stable isotopes of hydrogen in plant and soil water. Four natural precipitation events that represented precipitation sizes of 5.3, 8.3, 13.3, and 65.3 mm in the summer were chosen for the experiment. The perennial grass *Stipa bungeana*, the shrub *Artemisia ordosia*, and the herb *Cynanchum komarovii* – the dominant species in the communities – were compared for their use of summer rains with different pulse sizes based on the changes in the hydrogen isotope ratios (δD) of their stem water 7 days following each natural rain event. We found that *S. bungeana* and *C. komarovii* took advantage of shallow water sources derived from small (<10 mm) rain events, *A. ordosia* took advantage of deeper soil water recharged by large (>65 mm) rain events, and *C. komarovii* relied primarily on rain events of intermediate (10–20 mm) size. These different responses to rain pulses among species suggested that more frequent small rain events will promote the dominance of *S. bungeana* and *C. komarovii*, medium-sized events will facilitate development of *C. komarovii*, and large events will advance *A. ordosia* in this community. The rainwater utilization patterns of the three species would allow the coexistence of *S. bungeana* and *A. ordosia* or the coexistence of *A. ordosia* and *C. komarovii* in various successional serals following the disturbances. With an increase in variability of summer rain pulse size as predicted by climate change models, we expect that the structure of this community will undergo significant change in the future. Altered precipitation regimes, especially in combination with anthropogenic-related disturbances such as over-grazing, are likely to accelerate rates of degradation in northwestern China.

Introduction

Water is the most important factor limiting ecosystem processes (e.g., carbon fixation, plant growth, respiration) and function (e.g., net primary production or NPP) in arid and semiarid regions (Sala et al. 1997; Ehleringer et al. 1999; Dube and Pickup 2001), where precipitation is the primary water source. Previous studies of arid and semiarid ecosystems suggested that the intensity and frequency of precipitation were critical in determining species survivorship, composition, structure and, therefore, functional assemblages in the landscape (Dodd et al. 1998; Lavee et al. 1998). Additionally, studies have shown that plant functional types (e.g., life forms) extract water from different depths in soil horizons and show different water use of winter-derived and summer-derived soil water (Burgess 1995; Sala et al. 1997; Dodd et al. 1998). Explorations of water use and patterns by different desert plants in arid and semiarid regions, as well as the differences in utilizing summer rains by precipitation size among plant life forms are necessary for understanding the function and dynamics of these ecosystems.

The “size” of precipitation events is an important issue in arid land ecology. The role of surface versus deep layer water and their effects on the coexistence of plant forms in savannahs was originally proposed by Walter (1971), who concluded that light rains effectively recharged the upper layers of the soil, thus, favoring shallow-rooted plants (e.g., grasses); whereas large rain events recharge deeper soil layers, which is essential for the survival of deep-rooted plants, such as shrubs. Gao and Reynolds (2003) also suggested that an increase in the number of large precipitation events would favor shrub establishment and growth; in contrast, small precipitation events (<10 mm) would tend to promote grass development. In the upper layers of the soil, each rain event generates a pulse of moisture that can last from a few hours to several weeks depending on rain event size and evaporative demand of the atmosphere (Sala et al. 1981), which is very important for plant growth during the hot summer period. In addition, Reynolds et al. (2004) showed the potential importance of soil texture to, for example, depth of recharge by rains and amounts of soil water taken-up by different life-forms. Clearly, a suite of complex factors governing the

interactions between the timing and amount of rainfall, its subsequent effects on soil water content, and the growth and reproduction of plants makes it difficult to make generalizations over a large scale (Gao and Reynolds 2003).

In arid and semiarid regions, plants of different life forms use water sources from dissimilar soil layers depending, in part, on the depth and degree of overlap of their roots (Schlesinger and Ehleringer 2001; Schenk and Jackson 2002). For example, the more herbaceous plants in arid and semiarid environments compete for resources in the upper soil layers, while woody plants have a larger proportion of roots in deeper layers, taking up significantly more soil water there (Schenk and Jackson 2002; Snyder and Williams 2003). With heavy and frequent disturbances (e.g., over grazing), plant communities in semiarid regions will be featured by the archetypical invasion of grasslands by desert shrubs (Schlesinger et al. 1996). Because grasses and shrubs often exhibit different water-use patterns (e.g., Flanagan and Ehleringer 1991; Dodd et al. 1998; Jackson et al. 1999), the pulse of shallow soil water and the diversification with respect to water use play important roles in determining the local patterns of species coexistence in arid ecosystems.

The Ordos plateau is a relatively independent physiographic unit and a complex, sensitive ecotone in the semiarid zone of northern China (Li 2001; Chen et al. 2002). *Stipa bungeana*, *Artemisia ordosia*, and *Cynanchum komarovii* are the three dominant species, all perennial and deciduous, those represent a series of successional stages of desertified communities in Ordos plateau (Zheng and Huang 1992; Yang et al. 1994; Cheng et al. 2001a, b; Cheng et al. 2004). *S. bungeana* is a shallow-rooted (<20 cm) meso-xerophytic grass found typically in steppe vegetation, and it is a preferred forage species of farm animals. *A. ordosia* is a deeply-rooted (50 cm) xerophyte shrub, which is less preferred by domestic animals. This species has extensive vertical roots for absorbing water and increases its dominance with an increase in grazing and drought intensity and, thus, has been used as an index of mid-level desertification (Cheng et al. 2004). *C. komarovii* is a shallowly-rooted xerophyte (30 cm) herb and not used by any domestic animals. Its presence in the ecosystem indicates serious desertification (Cheng et al. 2001a, b).

One of the most obvious features of the heavily-disturbed grassland ecosystems is that vegetation will be characterized by the loss or death of dominant grass species, or replacement of a desirable grass species by undesirable shrubs or alien weedy plants with poor forage quality (Zhang 1994). Drought and over-grazing have been the major causal factors leading to the “replacement” of the *S. bungeana* community (grass) by *A. ordosia* communities (shrubs) and further by toxic *C. komarovii* community (herbs) as desertification is intensified in the region (Zheng and Huang 1992; Yang et al. 1994; Cheng et al. 2001a, b; Cheng et al. 2004). Our previous studies have shown that the densities of *S. bungeana*, *A. ordosia* and *C. komarovii* in the same region were positively correlated with amount of summer precipitation (Cheng et al. 2001a, b). We have also found that plant biomass production was tightly correlated with precipitation during the growing season (Cheng et al. 2001a, b). Therefore, it is particularly important to understand rainwater use associated with rain pulse size by these species in grasslands of the Ordos Plateau.

To examine the different effects of rain pulse size on uptake of summer rains by the above three dominant plants in field conditions, we studied relationships between precipitation event size and rainwater uptake using stable isotopes of hydrogen in plant and soil water. We took advantage of the fact that stable isotope ratios of summer rains differ from those of other water sources and from one rain event to another. Specifically, we tested a hypothesis that the dominant plants representing different stages of degraded vegetation have immediately distinct responses to rainfall event size.

Materials and methods

Study area

This study was conducted at the Ordos Ecology Station (39°2′ N; 109°51′ E) of the Chinese Academy of Sciences located in Mu Us of the Ordos Plateau, China between May and August of 2001. Ordos Plateau lies between 37°27′–39°22′ N and 107°20′–111°30′ E. The elevation of the study site is 1355 m, with a typical continental semiarid climate. Between 1965 and 2001, annual precipitation

averaged 380 mm over 1965–2001, 60–80% of which occurred between June and August. The mean annual temperature varied between 6.0 and 8.5 °C, with monthly means of 22 °C for July and –11 °C for January. Shrub, steppe and meadow are the dominant vegetation types in the study area. Farmlands and forest plantations occur mostly along the riversides, but also as isolated patches across the sandy grassland landscapes (Zhang 1994).

Field sample collection

In early May 2001 (i.e., before the rainy season), samples of stem and rhizomes for *S. bungeana*, the fully suberized stem for *A. ordosia* and the stems near the soil surface for *C. komarovii* (Dodd et al. 1998), soil (to a depth of 20 cm), and groundwater (obtained from a nearby well, about 10 m depth) were collected for hydrogen isotopic analyses. These data reflected the moisture conditions of the dry season (i.e., no substantial precipitation for a long time). During the rainy season from late June to August, we collected rainwater from four individual precipitation events with a total event size of 5.3, 8.3, 13.3, and 65.3 mm (Table 1) that represented different precipitation pulses to obtain the baseline values of δD . For each precipitation event, we placed rainwater collectors outside the communities to collect rainwater throughout the event, and sampled and stored 50 ml in plastic bottles that were sealed immediately. Since we were not able to manipulate each rainfall, the order, size and interval between rain events varied but reflected the naturally occurring precipitation patterns in the region.

Three 1×1 m² plots in *S. bungeana* community, three 2×2 m² plots in *A. ordosia* community, and three 2×1 m² plots in *C. komarovii* community were established for sampling plant parts and soil. Three replicates of plant stems, each from separate plants, were taken in each plot at every sampling time. Plant samples for water source determination were taken on the same day of precipitation, and then again on days 2, 3, 4, 5, 6 and 7 after the precipitation events. Since all *S. bungeana* roots, *C. komarovii* roots and more than 80% of *A. ordosia* are distributed in the upper 20 cm of the soil (Cheng et al. 2001a), and the model prediction made by Barnes and Allison (1984) claimed that the δD values of soil water below 8 cm deep did

Table 1. Hydrogen isotope ratios (δD) and associated temperature of ground water, soil water, plant stem water and rain water on different summer days of 2001 in the Ordos grassland, China.

Description	Date	Rain amount (mm)	$\delta D(\text{‰})$	Air T ($^{\circ}\text{C}$)	Soil T ($^{\circ}\text{C}$)
Ground water	20 May		-79.6 ± 2.3	17.8 ± 2.4	19.1 ± 1.7
Soil water	20 May		-47.5 ± 1.8		
<i>Stipa bungeana</i>	20 May		-43.3 ± 1.2		
<i>Artemisia ordosia</i>	20 May		-45.6 ± 1.3		
<i>Cynanchum komarovii</i>	20 May		-44.4 ± 1.2		
Soil water before rain 1			-45.2		
Rain 1	23 Jun.	5.3	-26.1	26.4 ± 1.3	28.1 ± 1.8
Soil water before rain 2			-47.2		
Rain 2	9 Jul.	8.3	-30.1	22.2 ± 2.9	25.9 ± 1.9
Soil water before rain 3			-49.5		
Rain 3	24 Jul.	13.3	-38.6	23.9 ± 1.7	26.4 ± 1.9
Soil water before rain 4			-59.8		
Rain 4	19 Aug.	65.3	-77.6	20.1 ± 2.9	22.1 ± 1.4

Note: Air T – daily average air temperature at 2 m above the ground; Soil T – soil temperature.

not vary significantly, three replicates of soil samples from 0 to 20 cm depth were collected in each plot every day simultaneous to plant sampling to obtain the δD values of soil water. All samples were immediately stored in glass vials and kept frozen until the water was extracted using a cryogenic distillation method.

Measurements of environmental parameters

Air temperature (HMP45C Probe, Campbell Scientific, Inc., CSI, Logan UT, USA), soil moisture at 0–20 cm depth (CS616 water content reflectometry, CSI) and soil temperature at 20 cm depth (108 Soil and water temperature probe, CSI) were continuously recorded throughout the study period. Precipitation over a 36-year period from 1965 to 2001 was recorded at a nearby meteorological station, about 20 km from the study site, in Yijinhuoluo Banner, Inner Mongolia. The precipitation event size frequency distribution during the decades was calculated based on the 36-year data (Figure 1).

Stable isotope analysis

Hydrogen isotopic composition can be expressed as the hydrogen isotope ratio (δD) in units of ‰ as:

$$\delta D = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000\text{‰} \quad (1)$$

where R_{sample} and R_{standard} are the hydrogen stable isotopic composition (D/H molar ratio) of the

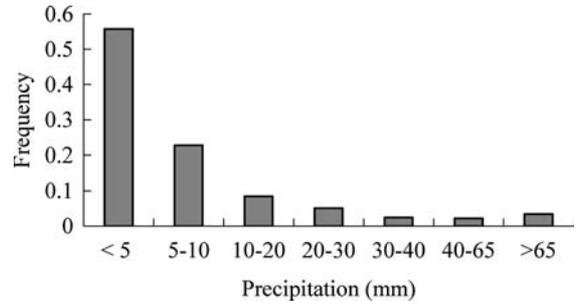


Figure 1. Frequency distribution of precipitation size between 1965 and 2001 in Ordos area, China.

sample and standard water (Standard Mean Ocean Water), respectively (Gonfiantini 1978). Approximately 3–5 ml of water was extracted from plant tissues and soil samples using a cryogenic vacuum distillation apparatus (Ehleringer et al. 1999). The extracted water was stored in a sealed glass tube under a slight vacuum. Sub-samples of the extracted water were prepared for analysis of hydrogen isotope composition by reacting a sub-sample of 3 μl of water with zinc in an evacuated Pyrex tube at 500 $^{\circ}\text{C}$. The hydrogen gas resulting from the combustion was analyzed for its isotopic composition with a gas isotope ratio mass spectrometer (Finnegan MAT-252, model delta E, San Jose, CA, USA).

Because the timing of natural rains is unpredictable, the δD of soil water prior to a rain event was not available. There is a potential way of estimating the δD of soil water prior to each rain

based on post-rain δD value and pre- and post soil water contents. A linear mixing model can also be used here: if δD_{SR} is the δD value of soil water immediately after rain event, δD_{SW} is the δD value of soil water immediately before rain event, δD_R is the δD value of the rain water, θ_{SW} is the absolute soil water content prior to the rain, and θ_{SR} is the absolute soil water content immediately after rain. Then the linear mixing model is:

$$\begin{aligned} \delta D_{SR} \\ = \left(\frac{\theta_{SW}}{\theta_{SR}} \right) \times \delta D_{SW} + \left(1 - \frac{\theta_{SW}}{\theta_{SR}} \right) \times \delta D_R \end{aligned} \quad (2)$$

where $\frac{\theta_{SW}}{\theta_{SR}}$ essentially describes the fraction of soil water that is derived from the previous soil water (i.e., soil water present before the rain), and $1 - \frac{\theta_{SW}}{\theta_{SR}}$ is the fraction input from the rain. This equation works if only a small amount of the total soil water was lost via evapotranspiration during the time immediately proceeding measurements, Equation (2) can be solved for δD_{SW} , yielding:

$$\delta D_{SW} = \delta D_R + (\delta D_{SR} - \delta D_R) \times \frac{\theta_{SR}}{\theta_{SW}} \quad (3)$$

Thus, δD_{SW} and δD_R should be used as the end-member signatures for soil water and rainfall immediately after each rain event.

The proportion of rainwater in a plant (P_C) is derived by the following linear mixing model:

$$\delta D_P = P_C \times \delta D_R + (1 - P_C) \times \delta D_{SW} \quad (4)$$

where δD_P is the δD value of plant water after precipitation, δD_R is the δD value of the rainwater; δD_{SW} is the δD value of soil water. For Day 1, δD_{SW} was estimated by Equation (3) and δD_{SW} on Days 2–7 after the rain event are based on δD measurements of soil water samples collected on each date. Solving this equation for P_C gives:

$$P_C = \frac{\delta D_P - \delta D_{SW}}{\delta D_R - \delta D_{SW}} \times 100\% \quad (5)$$

In this analysis, we assumed that groundwater was not a water source available to plants at the site. Groundwater in this region is about 10 m below the surface – a depth at which desert plants could not access it.

Data analysis

Frequency distribution of precipitation size was generated using the data between 1965 and 2000. To test the difference in temporal changes of plant δD and percentage of precipitation use, we performed an analysis of variance with repeated measures, where multiple measurements on a given plant species through time represent the repeated variables (see Williams and Ehleringer 2000). The interactive effects from temporal variation and species \times time (days after rain) were examined as within subject effects. Repeated ANOVA was performed to analyze the events simultaneously and to estimate each precipitation event effect, which would allow us to test for differences in water sources among rain events. Precipitation was treated as a categorical factor and time (i.e. day1–7) was treated as a continuous variable in repeated ANOVA analysis. Snapshot measurements of soil water indicated that the δD value of soil moisture at 20 cm depth was initially unaffected by immediate precipitation events. Treatment effects on the gravimetric soil water content were determined with separate analyses of variance for each combination of depth and sampling day. Because each precipitation event was found to have a different effect on soil water content, further treatment effects on air temperature and soil temperature were examined using independent ANOVAs for each combination of precipitation and sampling day. All the data were analyzed using Statistica statistical software for Windows (Version 6.0, StatSoft, Inc., 2001).

Results

Precipitation pattern, plant water sources and soil moisture

Precipitation at the study site over the past 36 years was characterized by many small events (e.g., <10 mm) and very few large ones (e.g., >65 mm) (Figure 1). Precipitation events of 0–5 and 5–10 mm rainfall accounted for 57.5 and 24.5% of all events, respectively. Medium rain events (10–20 mm) accounted for 9.1%, while heavy events (>65 mm) accounted for only 2.7% (Figure 1).

On May 20, 2001, just before the summer rain started, the δD values ($-79.6 \pm 2.3\text{‰}$) of groundwater were much lower than those of soil water ($-47.5 \pm 1.8\text{‰}$), which were similar to those of the stem water from the three dominant plants (Table 1). This suggested that soil water was the primary water source for plants that had not experienced a precipitation event for a prolonged time before the rainy season came in Mu Us sandy grasslands, and that the plants only used soil water, rather than groundwater. The δD values of precipitation varied significantly among four precipitation events differing in total rainfall and temperature (Table 1).

Clear vertical changes in soil moisture were recorded for the 5.3, 10.3 and 13.3 mm rain events with the greatest increase in water content occurring in the surface layer (Figure 2a–c). The 5.3, 8.3 and 13.3 mm precipitation events wet only the top 10 cm of the soil surface (Figure 2a–c), whereas the large rain event of 65.3 mm wet the soil as deep as 40 cm (Figure 2d). For precipitation events between 5.3 and 13.3 mm, soil water in the top 10 cm of soil increased a day after precipitation and then returned to the initial level within about 7 days. However, following the heavy rain event, the soil water at 20 and 40 cm depth was much

higher than initial levels 7 days after precipitation. This suggested that the shallow soil layers reached field capacity and additional water infiltrated to deeper layers after heavy rains.

Utilization of summer rains by dominant plants

Based on the soil δD values prior to each rain (Table 1), as calculated in Equation (4), we found great fluctuations in the δD values of soil water over time within 7 days after each precipitation event (Figure 3). The δD values of rain water during three small precipitation events (5.3, 8.3 and 13.3 mm) were much higher than those of stem and soil water (Figure 3a–c), while the δD value of rain water during the largest precipitation event (65.3 mm) was much lower than that of the stem and soil water (Figure 3d). The δD values of stem water from the three dominant plants differed significantly from those of the rain and soil water, and the plant δD values were, on average, about halfway between the soil and rain δD values (Figure 3).

A two-end member linear model (Equation 5) was used to calculate the percent of plant water uptake derived from precipitation for each species.

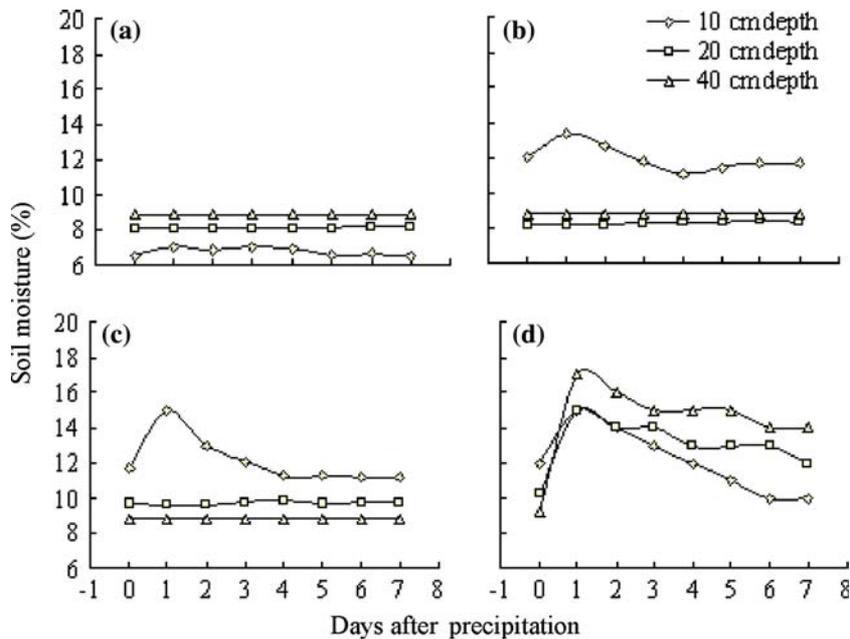


Figure 2. Change in volumetric soil water content (%) at different depths in the soil following each precipitation event in the Ordos grasslands. Accumulated rainfall was (a) 5.3 mm, (b) 8.3 mm, (c) 13.3 mm, and (d) 65.3 mm with each event.

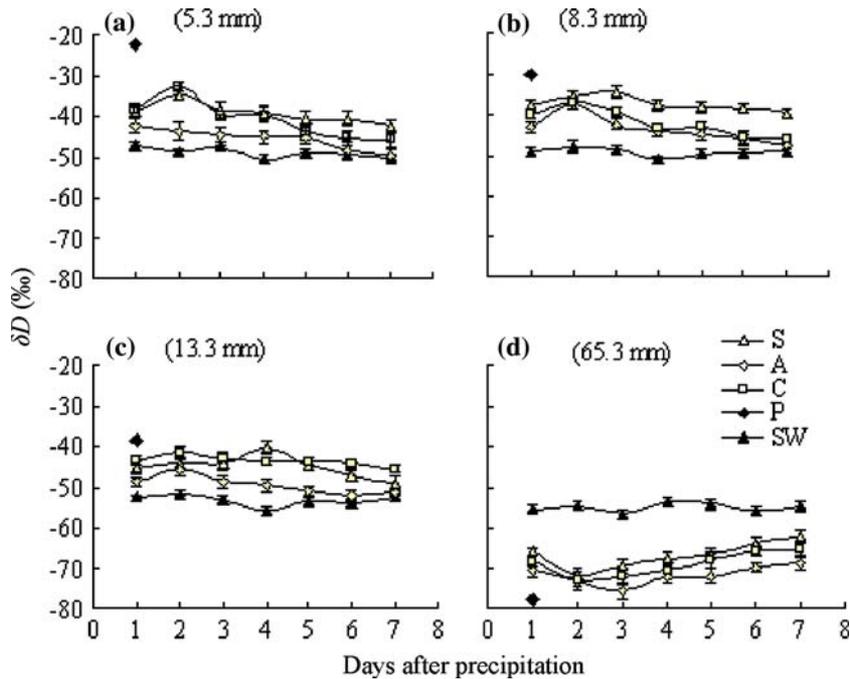


Figure 3. Changes of hydrogen isotopic composition (δD ‰) of stem and soil water over a 7-day study period following each precipitation event in the Ordos grasslands. The vertical bars represent the ± 1 SE of mean values ($n = 3$). Accumulated rainfall was (a) 5.3 mm, (b) 8.3 mm, (c) 13.3 mm, and (d) 65.3 mm with each event; *Stipa bungeana* (S), *Artemisia ordosia* (A), *Cynanchum komarovii* (C), Precipitation (P) and Soil water (SW).

After the 5.3 mm precipitation, the percent rainwater used by *S. bungeana* and *C. komarovii* was similar, while there were relatively smaller contributions of rainwater to the *A. ordosia* water source (Figure 4a). After the 8.3 mm precipitation events, the proportion of water used by *S. bungeana* was higher than those by *A. ordosia* and *C. komarovii* on all 7 days following the event (Figure 4b). Amount of rainwater used by *C. komarovii* was relatively higher than that that used by *S. bungeana* and *A. ordosia* following the 13.3 mm precipitation except on the fourth day (Figure 4c). Overall, all three species had similar responses to the largest rain event (Figure 4d), but there was a higher amount use of summer rainwater by *A. ordosia* than by *S. bungeana* and *C. komarovii* (Figure 4d). In most cases, amount of water uptake by the three dominant species reached the highest values on day 2 or 3, then decreased gradually following each rain event (Figure 4).

Repeated-measures analysis of variance showed that for all four individual precipitation events, δD values of stem water and percentage use of precipitation water differed among the plant species,

and were significantly affected by time (days after rain) and the interaction between species and time (Table 2). These significant interactions indicated that rainwater use from summer rain pulse sizes differed among the three species.

For *S. bungeana*, water uptake of summer rain reached a maximum when the rain pulse size was relatively small (8.3 or 10.3 mm) (Figure 5a). In contrast, *A. ordosia* increased summer rain uptake with increased rain pulse size and reached the highest values when the rain pulse size was at 65.3 mm (Figure 5b). *C. komarovii* appeared to increase uptake of summer rains when the pulse size increased from 5.3 to 13.3 mm but reached a plateau when the pulse size was 13.3 mm or higher (13.3 mm) (Figure 5c).

Discussion

Numerous researchers have applied the hydrogen isotope ratio method to quantify water acquisition by plants from soil water, groundwater and natural rains (Lin et al. 1996; Dodd et al. 1998;

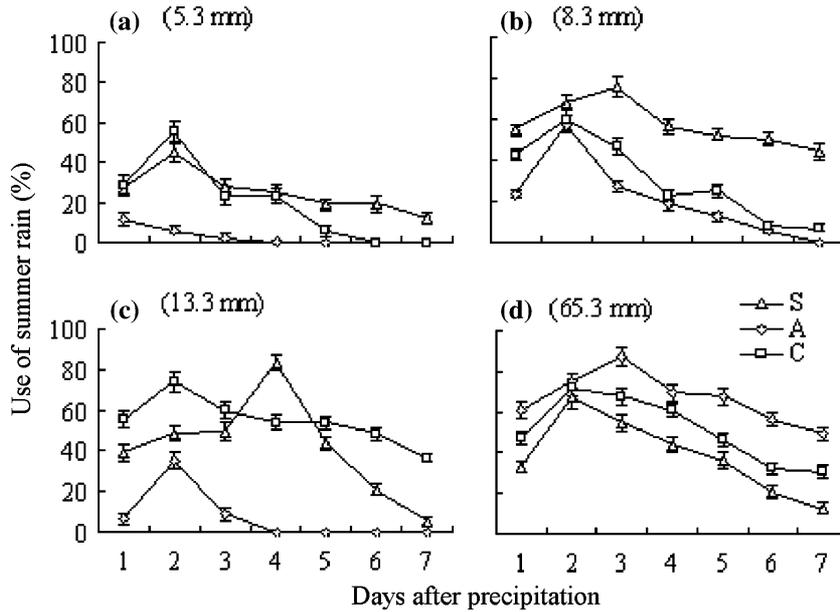


Figure 4. Change in the proportion of summer rainwater in the stems of three dominant plants during a 7-day study period following four rain events in the Ordos grasslands. Accumulated rainfall was (a) 5.3 mm, (b) 8.3 mm, (c) 13.3 mm, and (d) 65.3 mm with each event; *Stipa bungeana* (S), *Artemisia ordosia* (A) and *Cynanchum komarovii* (C).

Table 2. Results of repeated-measures analysis of variance for plant stem water isotopic composition (δD) and percentage use of summer rainwater by three desert plants in the Ordos grassland, China.

Source of variation	Plant water isotopic composition	Percentage rainwater use
Precipitation	****	****
Species	****	****
Days	****	****
Precipitation*Species	****	****
Days*Precipitation	****	****
Species*Days	**	****
Days*Precipitation*Species	**	****

Note: Data are for *Stipa bungeana*, *Artemisia ordosia* and *Cynanchum komarovii* from several sampling dates after each precipitation event. ** $p < 0.01$; **** $p < 0.0001$.

Golluscio et al. 1998). Based on the comparison of the δD values of stem water to those of soil water and groundwater, we believe that all three dominant species involved in this study had no access to groundwater during summer time, suggesting that soil water addition with summer rain was the only water source for the plants in Mu Us sandy grassland during their growing season (Table 1). However, the surface soil layers can have

highly variable δD values due to inputs from rains of variable signatures and evaporative enrichment (Lin et al. 1996), and thus can influence the δD values of the entire 0–20 cm layer (Figure 2). In comparing the δD value of soil water at a depth of 20 cm (Figure 3), it appeared that there existed some variations among the four different sampling periods, i.e., gradually decreasing from about -48 for the first (5.3 mm) to about -56 for the fourth (65.3 mm) event (Figure 3). Furthermore, roots distributions have played an important role in affecting the distribution of soil water and its availability to different plant functional types (Kemp et al. 1997; Reynolds et al. 2000). First, uptake by plants can alter δD of the “bulk” soil water if the roots are taking up water from a specific depth and thus removing water with a δD signature associated with that depth; this would cause the δD value of the bulk soil water to converge towards the δD values of layers from which plants are not actively taking up water. Second, hydraulic redistribution of water within the soil profile by roots would change the δD value of soil water (Yoder et al. 1998). Accordingly, the δD values of stem water of the three dominant plants would be influenced by the potential evaporative enrichment and rainwater contamination

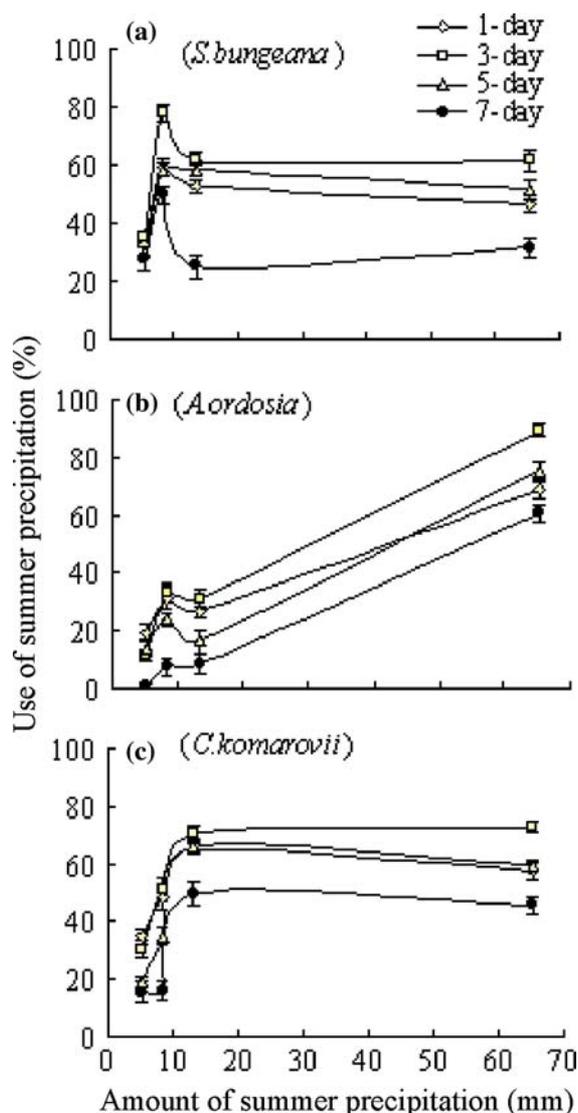


Figure 5. Percentage of summer precipitation use (%) by three dominant species, *Stipa bungeana*, *Artemisia ordosia* and *Cynanchum komarovii*, from one day to seven days after each precipitation event in the Ordos grasslands. The vertical bars on symbols represent the ± 1 SE of mean values ($n=3$).

(Lin et al. 1996; Reynolds et al. 2000). The evaporation would tend to enrich the plant water in deuterium and make δD less negative (Lin et al. 1996), while the δD of plant water would increase or decrease depending on the δD of precipitation inputs.

The three dominant plants showed different responses to the use of individual precipitation events according to the summer rain pulse size

(Figures 4, 5), as indicated by the changes in the δD values of stem water from the three dominant plants following each rain event (Table 2 and Figure 3). The shallow-rooted *S. bungeana* appeared to be more dependent on light rains (<10 mm) which accounted for 40–50 % of its water source following each rain event regardless of precipitation pulse size (Figures 4 and 5a). In contrast, *A. ordosia* was more deeply rooted and thus was more dependent of heavy rains (Figure 4d). For example, the relative contribution of precipitation to this species' water use increased with pulse size (Figure 5b). Similarly, *C. komarovii* showed more utilization of summer rains with medium rain sizes (10–20 mm) (Figures 4c and 5c). Previous studies have also demonstrated that light rainfall events might selectively favor populations of predominantly shallow-rooting grasses, and heavy rainfall events favor shrubs in arid ecosystems (Dodd et al. 1998; Golluscio et al. 1998; Schwinning et al. 2002, 2003). Our results were consistent with the conclusion that summer precipitation events of small size would favor shallow-rooting grasses (here *S. bungeana* and *C. komarovii*) rather than shrubs (*A. ordosia*). Additionally, we showed that moderate rain events would favor *C. komarovii*. Therefore, any shift in distribution of summer rain pulse size, even without a change in total annual precipitation in a given area, may have significant effects on species interactions and plant community composition.

The modified pulse-reserve theory presented by Reynolds et al. (2004) proposed that a suite of complex factors govern the interactions between the timing and amount of rainfall, its subsequent effects on soil water content and the growth of plants. This concept appears to be useful for explaining our results. Rainfall events produce biologically significant “pulses” of soil moisture recharged in soil depth associated with rainfall variability (Reynolds et al. 2004). In our study, small rain events usually wet only the surface layer of soil on fixed sand dunes (Figure 2a–c), while larger rains penetrated to the deep soil layer rapidly and complemented soil water (Figure 2d). The plant growth responses to soil moisture pulses were strongly affected by interactions between precipitation and antecedent soil moisture (Reynolds et al. 2004). We analyzed the responses of the three species to rainfall directly by examining uptake of rainwater during each 7-day period

following individual rain event, we found that there were significant differences in the proportional water uptake among the three species with rain events (Figures 4 and 5). The small rains, each separated by dry periods, resulted in short growth episodes associated with ephemeral soil moisture in soil surface (Figures 2a–c and 5); while the heavy rain resulted in longer growth episodes, which affected the extent and depth of soil water recharge (Figures 2d and 5). Our results further suggested that there is a little separation of soil with depth in our study area during summer (Figure 2). Thus, variability of precipitation over long periods determined differential water availability for coexistence of plant functional types. Although all three dominant species are perennials and deciduous, they could be more active in using rain water during the summer. It is possible that their abilities to use pulses of moisture are also adaptive, resulting from morphology (shallow- vs. deep-rooted). Grasses (*S. bungeana* and *C. komarovii*) have roots concentrated almost completely in the upper 20 cm depth soil layers and about 80% of shrubs (*Artemisia*) roots are distributed in the upper 20 cm depth soil layers while 20% of shrubs (*Artemisia*) roots reached the deeper 50 cm depth soil layers (Cheng et al. 2001b). The fact that the deeper layer soil water basically held constant would be of use to some deep-root plants later; *A. ordosia* may be one among the three plant species that could use a higher availability of deeper stored water. Therefore, integration of plant water use with soil water availability is helpful to understand the relationship between precipitation events and plant growth in arid and semiarid regions.

Differentiation in the capacity of plants to use precipitation water is critical to the dynamics of arid and semiarid ecosystem (Willian and Ehleringer 2000; Schwinning et al. 2002, 2003). The different ability to use summer rainwater among the three dominant species might greatly influence the composition and structure of the community in the region. Previous studies have shown that, under similar soil water conditions, transpiration of *A. ordosia* is higher than those of *C. komarovii* (Zheng et al. 1992) and *S. bungeana* (Cheng et al. 2001b). Our findings suggest that more frequent small rain events promote the growth of *S. bungeana*, more frequent medium rain events promote the growth of *C. komarovii*, and more frequent

heavy rain events advance the growth of both *A. ordosia* and *C. komarovii*. Over the past 36 years, the highest frequency rain events were small (<10 mm, Figure 1), which would advance the growth of *S. bungeana*, and promote the development of the grassland in Ordos Plateau. However, most grasslands in the region have been experiencing frequent and intensive disturbances during the past several decades. These introduced forces can control the dynamic trends of the grassland beyond precipitation patterns and changes over time. For example, the influences of overgrazing in this grassland ecosystem far exceeded the impact of precipitation change, which is reflected in the rapid decrease of *S. bungeana* in the region (Zheng and Huang 1992; Yang et al. 1994). Therefore, in addition to continuing exploration of precipitation change and its effects on plants' water use, it is also important to examine the coupled effects of disturbances, which can potentially change precipitation patterns as well. Finally, altered precipitation regimes, especially in combination with anthropogenic-related disturbances such as over-grazing (Zheng and Huang 1992; Yang et al. 1994; Cheng et al. 2001a, b), are likely to greatly accelerate rates of desertification in northwestern China.

It is important to note that the δD value of plant water estimated from the two-end member linear mixing model would be underestimated or overestimated, for the δD value of plant water should be effected by the potential evaporative enrichment and rainwater contamination (Lin et al. 1996; Reynolds et al. 2000). In our study, the δD_{SW} measured on Days 2–7 is contaminated with rainfall, and the rainwater δD_R is likely getting more and more depleted in D over time due to evaporation. This would mean that for the 5.3, 8.3 and 13.3 mm events, P_C may be overestimated (Figure 3a–c), but for 65.3, P_C may be underestimated (Figure 3d). Furthermore, we should acknowledge potential errors introduced by only sampling 0–20 cm soil layer to get δD values, although Barnes and Allison (1984) showed that the δD values of soil water below 8 cm deep did not vary significantly. As 20% of *A. ordosia*' roots are below 20 cm (Cheng et al. 2001a), they could potentially account for a large fraction of water uptake, especially when the surface soils are dry. Nevertheless, our results tentatively demonstrate the different effects of rain pulse size on uptake of

summer rains by three dominant desert plants in field conditions of desertified grasslands on the Ordos Plateau of northwestern China.

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