The user wants me to translate a Chinese academic paper title and the word "后印本"(postprint). The title is: "Spatiotemporal niche separation mechanisms of water utilization strategies in the desert steppe plant communities, northern China 后印本" Let me break this down: - Spatiotemporal niche separat···

Authors: The user wants me to translate a scientific paper from Simplified Chinese to English. The input is just "SONG Kechen" which appears to be a name. Let me check the instructions carefully.

The user provided: - A name: "SONG Kechen" - Detailed instructions about translating academic papers - Critical requirements about preserving LaTeX, citations, and tags - A glossary

However, the actual content to translate is just a name. This seems like a test or perhaps the user is providing the author name first. But based on the instructions, I should translate the Chinese text inside the tags. Since there's no tag and no Chinese text (just a name), I need to think about what to do.

The name "SONG Kechen" is already in a format that would be used in English academic papers - surname in uppercase, given name capitalized. In Chinese academic contexts, names are often written this way. The translation would be the same: "SONG Kechen".

But wait, the instructions say "Translate from Simplified Chinese to English". A name doesn't need translation, just transliteration which is already done. The instructions also mention tags, but there are none in the input.

Let me re-read the instructions: - "Return ONLY the translated text for the given input (no explanations, no quotes, no headings you invent)." - "Keep one output paragraph per input paragraph; do not merge or split paragraphs." - "Maintain exact count and IDs of ···tags"

Since there are no tags and no actual content to translate (just a name), I should probably just return the name as is. The name is already in the appropriate format for an English academic paper.

The glossary mentions: 机器学习 => machine learning 深度学习 => deep learning

But these terms don' t appear in the input.

So my output should simply be: SONG Kechen

But wait, I need to be careful. The user might be testing if I follow the instructions about tags. If the input doesn' t have any tags, should I add them? The instructions say "PRESERVE ALL ···paragraph wrapper tags EXACTLY" . This suggests I should only preserve them if they exist, not create new ones.

The input is just "SONG Kechen" with no tags, no Chinese, The user wants me to translate a Chinese text to English. The text appears to be "HU Haiying" . This looks like a name. Let me check the requirements:

1. Preserve ALL LaTeX commands and placeholders - there are none here
2. Preserve ALL citation commands - there are none here
3. **PRESERVE ALL ···paragraph wrapper tags EXACTLY** - there are none here
4. Maintain academic tone and formal scientific writing style - this is just a name
5. Use precise technical terminology - not applicable for a name
6. Preserve section structure and paragraph organization - not applicable
7. Translate all content completely - it' s just a name

The glossary provided: 机器学习 => machine learning 深度学习 => deep learning

These don' t apply to this input.

The input is "HU Haiying" . This is a Chinese name. In academic contexts, Chinese names are typically written with the surname first, followed by the given name. The standard translation would be to keep it as "HU Haiying" or possibly "Haiying Hu" depending on the convention.

However, looking at the format, it seems like this might be a standalone name, perhaps an author name. In many academic papers, Chinese names are either: 1. Kept as "HU Haiying" (surname in caps) 2. Written as "Haiying Hu" (Western order)

Given that this is a translation task and the name is in Chinese characters (or pinyin with surname first), I should probably keep the original format. But wait, the input is "HU Haiying" which is already in pinyin with the surname in uppercase. This is actually the standard way to write Chinese names in English academic contexts.

Let me reconsider. The user provided "HU Haiying" as the input. This is already an English representation of a Chinese name. The surname "HU" is capitalized, and the given name "Haiying" follows. This is the standard format for Chinese names in academic contexts.

Since the input is already in English (pinyin) format, and there are no tags, LaTeX commands, or anything else to preserve, the translation would simply

be the same text. But that seems odd.

Wait, maybe the user is testing the system, or this is part of a larger document. The instructions say to translate from Simplified Chinese to English. But "HU Haiying" is, ZHANG Hao, The user has provided a name "GUAN Siyu" which appears to be a Chinese name. This is likely a test to see if I can handle names properly in academic translation.

In academic contexts, Chinese names are typically transliterated following specific conventions: 1. The surname (GUAN) comes first, followed by the given name (Siyu) 2. In English publications, it' s common to either keep the original order (GUAN Siyu) or reverse it (Siyu Guan) depending on the journal style 3. The pinyin should be preserved exactly as written, with proper capitalization

Since this is just a name without any context or paragraph tags, and the instructions say to return ONLY the translated text for the given input, I should simply provide the English representation of this name.

The most standard academic approach would be to either: - Keep it as "GUAN Siyu" (preserving the original order) - Or convert to "Siyu Guan" (Western order)

Given that the user hasn' t provided any tags or context, and this is just a standalone name, I should treat this as a simple transliteration task. In most international academic contexts, Chinese names are often written in Western order (given name first) as "Siyu Guan" . However, some authors prefer to keep the original Chinese order.

Since there's no explicit instruction about name order, and the name is presented in Chinese order (surname first), the safest and most respectful approach in academic translation is typically to preserve the original order but capitalize appropriately: "GUAN Siyu" .

Actually, looking at the instructions more carefully, they mention: - "Translate from Simplified Chinese to English with the highest accuracy and academic tone" - "Preserve ALL LaTeX commands and placeholders exactly" - "PRESERVE ALL ···paragraph wrapper tags EXACTLY"

But there' s no specific guidance on name translation. In academic practice, Chinese names are usually: 1. Written in pinyin 2. With surname first (preserving Chinese order) OR given name first (Western order) 3. Capitalized appropriately

The most common and respectful approach in academic translation is to preserve the original Chinese order but ensure proper capitalization: "GUAN Siyu". This maintains the cultural identity while making it readable in English contexts.

Since the input is just "GUAN Siyu" without any tags or context„ The user has provided a name "DENG Wenhui" which appears to be a Chinese name. This is likely part of a larger document that needs translation. However, the current input is just a name, not a paragraph with tags.

Let me check the requirements again: - The user wants me to translate from Simplified Chinese to English - I must preserve ALL ···paragraph wrapper tags EXACTLY - I must preserve LaTeX commands and math placeholders - I must preserve citation commands - Maintain academic tone

But the current input is just "DENG Wenhui" - this is a name, not a paragraph with tags.

I should consider: 1. Is this a test to see if I follow instructions? 2. Is this part of a larger context where names need to be translated? 3. Should I just return the name as is, or format it according to academic conventions?

For Chinese names in academic papers, the standard format is typically: - Family name first, then given name (as in the original) - Or given name first, then family name (Western order) - Often with the family name in all caps to distinguish it

The input "DENG Wenhui" already has the family name in all caps (DENG), which is a common way to write Chinese names in international academic contexts. The standard academic translation would be to keep it as is, or possibly format it as "Wenhui DENG" if following Western name order.

However, looking at the requirements more carefully: - The user says "Translate from Simplified Chinese to English" - The name "DENG Wenhui" is already in a format that' s acceptable in English academic papers - There are no tags in this input

Since there are no tags, I cannot apply the rule about preserving them. The input is just a name. The most appropriate action would be to: 1. Keep the name in a format suitable for academic English 2. Since it' s already in a good format (family name capitalized), I should probably just return it as is

But wait - the user might be expecting me to wrap this in a tag if it' s part of a larger document. However, the instructions say "Return ONLY the translated text for the given input" and "Keep one output paragraph per input paragraph" . Since there' s no paragraph tag in the input, I shouldn' t add one, The user wants me to translate a scientific paper from Simplified Chinese to English. The input is just "YONG Jiayi" which appears to be a name. Let me check the requirements again.

The user provided: - CRITICAL REQUIREMENTS about preserving LaTeX, citations, and tags - OUTPUT RULES about format - FORMATTING GUIDELINES - A glossary

But the actual content to translate is just "YONG Jiayi" . This looks like an author' s name. In academic papers, Chinese names are typically: 1. Kept in their original form (pinyin) 2. Sometimes with the family name first, then given name 3. Sometimes with the family name in all caps to distinguish it

"YONG Jiayi" - YONG is the family name (surname), Jiayi is the given name.

In academic translation, it' s common to: - Keep the pinyin as is - Optionally capitalize the surname: YONG Jiayi - Or write as: Jiayi YONG (Western order) - Or keep original order: YONG Jiayi

Given the context of academic paper translation, and that this is likely an author name, I should preserve it exactly as written. The name itself doesn' t need translation - it' s a proper noun.

However, the user might be testing if I understand that names should not be translated. Let me check the requirements again. The instructions say "Translate from Simplified Chinese to English with the highest accuracy and academic tone."

For names, the standard practice is to transliterate, not translate. "YONG Jiayi" is already in pinyin, which is the standard romanization system. So it should remain unchanged.

But wait - the user might have intended to provide more content but only pasted the name. Let me re-read the prompt. The prompt is just "YONG Jiayi". That' s it. No tags, no LaTeX, no citations.

Given the strict requirements about preserving tags and other elements, but there are none in the input, I should just return the name as is. The name doesn' t need translation.

However, I should consider: is this a test to see if I incorrectly "translate" a name or modify it? The safest approach is to return the name exactly as provided, since it's already in the proper pinyin format used in academic English publications.

Let me think about the context. If this is part of a paper' s author list, it would typically appear as, ZHAO Xiaona, The user has provided a name "WANG Xing" and no other context. This appears to be a Chinese name that needs to be translated or romanized.

In academic contexts, Chinese names are typically written in the format: Given name + Family name, or Family name, Given name. The standard practice is to keep the pinyin as is, but the order depends on the journal/conference style.

"WANG Xing"is already in pinyin format. "WANG"is the family name (surname) and "Xing" is the given name. In English academic papers, this would typically be written as: - "Wang Xing" (if following Chinese order) - "Xing Wang" (if following Western order)

However, the user hasn' t provided any specific instructions about name formatting or any text to translate. The name itself doesn' t contain any LaTeX commands, math placeholders, or tags.

Given the critical requirements about preserving LaTeX commands, citations, and tags, but there are none in this input, I should just return the name in an appropriate format. Since the name is already in pinyin and the user hasn'

t specified a format, I should probably keep it as is: "WANG Xing" (with the family name in uppercase being a common convention in some academic contexts to distinguish family name from given name).

But wait, the user might be asking me to translate a paper where this is the author' s name. In that case, I should just preserve it exactly as written. The name "WANG Xing" is already in a standard format for academic publication.

Let me check the instructions again: - The user provided only "WANG Xing" - No tags - No LaTeX - No Chinese characters, just pinyin

This seems like a test or a simple query. I should just return the name as is, since it' s already in the correct format for an English academic paper. The uppercase "WANG" suggests the family name is being emphasized, which is a common convention.

Actually, looking at the system prompt again, it says "Translate from Simplified Chinese to English" . The input "WANG Xing" is not Simplified Chinese characters, it' s already pinyin. So there' s nothing to translate. I should just return it unchanged.

But the system also says "Return ONLY the translated text for the given input (no explanations, no quotes, no headings you invent)." So, The user has provided a name "HU Haiying" which appears to be a person' s name. This is likely part of a larger document that needs translation. However, the user hasn' t provided the full context or the actual Chinese text to translate.

Looking at the instructions, I need to: 1. Preserve LaTeX commands and MATH placeholders 2. Preserve citation commands 3. Preserve ···tags exactly 4. Maintain academic tone 5. Use precise technical terminology from the glossary 6. Preserve section structure 7. Translate all content completely

But the user only gave "HU Haiying" which is already in English (or rather, it' s a Chinese name transliterated into pinyin). This is not Chinese text that needs translation.

I should respond by asking for the actual Chinese text that needs to be translated, as "HU Haiying" is just a name and doesn' t require translation. The name is already in its standard romanized form.

However, let me reconsider - maybe the user wants me to confirm how to handle this name in a translation context? Or perhaps this is a test to see if I follow the rules about not translating things that don' t need translation?

Given the strict requirements about preserving tags and not adding anything extra, I should probably just return the name as is, since it' s not Chinese text that needs translation. But that seems odd.

Wait, maybe the user is providing the name as part of a signature or author line, and wants to see how I would handle it in a full document? But without the full context, I can' t do a proper translation.

The most appropriate response is to ask for the actual Chinese text that needs translation, while acknowledging that "HU Haiying" is already in English/romanized form and doesn't need translation.

But the instructions say "Return ONLY the translated text for the given input (no explanations, no quotes, no headings you invent)." So I should not add explanations.

This is a tricky situation. The input is just a name, which is already transliterated. There's nothing to translate. Following the rules strictly, I should just return the name as is, since that's the "translated" version of the Chinese name 胡海英.

Actually, thinking about it more carefully: if the Chinese text was "胡海英", the proper translation would be "Hu Haiying" (with proper capitalization). The user provided "HU Haiying" which is already the English version. So I should just return it as is

Date: 2025-12-15T18:14:29+00:00

Abstract

The user wants me to translate a scientific abstract from English to Simplified Chinese. Wait, let me re-read the instruction.

Actually, the instruction says: "You are a professional scientific translator specializing in academic papers. Translate from Simplified Chinese to English with the highest accuracy and academic tone."

But the text provided is already in English. Let me check the text again:

"Amid global precipitation changes, it remains unclear whether hydrological niche separation (HNS) mechanisms apply to herbaceous plant communities in desert steppes are severely affected by seasonal drought. How these plants access limited water and tolerate drought to coexist also remains unverified. In this study, we employed stable isotope techniques to examine water acquisition and drought adaptation in coexisting species of the desert steppe in northern China under five precipitation treatments, i.e., decreased 50%, decreased 30%, ambient, increased 30%, and increased 50% precipitation. The following results showed that: (1) water sources of coexisting species shifted with changes in precipitation amount and timing, i.e., all coexisting plants exhibited preferential utilization of surface soil moisture. When surface soil moisture was scarce, they shifted to deeper water sources, and when deep water sources remained scarce, they were forced to compete more intensely for surface water sources; (2) community's HNS was affected by precipitation amount but not by timing, i.e., with adequate soil moisture, plant water source ranges expanded, reducing overlap and enhancing HNS, whereas under extreme drought, the range contracted and increased the overlap, although HNS remained stable; and (3) water acquisition strategies of coexisting species differed along hydrological niche axis defined by

water stress adaptability (i.e., stable carbon isotope composition and proline content). Convolvulus ammannii Desr. had the strongest drought adaptation, although its strategy showed a weak correlation with water uptake. Stipa breviflora Griseb., with moderate drought resistance, adopted a water-conserving strategy that was suitable for extreme drought. Leymus secalinus (Georgi) Tzvelev, Polygala tenuifolia Willd., and Larix potaninii Batalin showed resource-dependent and flexible water strategies, thriving in wetter soils but struggling under extreme drought. Our findings indicated that herbaceous species in desert steppes adapted their water uptake and drought tolerance strategies according to changes in precipitation amount and timing. As a core regulatory mechanism, HNS (under increasing precipitation variability due to climate change) not only supports species coexistence by reducing interspecific competition, but also promotes efficient soil moisture use. This mechanism enhances community drought resistance and contributes to ecosystem stability. Overall, this study provides key ecological evidence for understanding plant community adaptation in arid and semi-arid areas facing the influence of global climate change."

This is English text. The instruction says "Translate from Simplified Chinese to English". But the text is already in English. This is confusing.

Let me re-read the instruction more carefully. The user says:

"Amid global precipitation changes, it remains unclear whether hydrological niche separation (HNS) mechanisms apply to herbaceous plant communities in desert steppes are severely affected by seasonal drought. How these plants access limited water and tolerate drought to coexist also remains unverified. In this study, we employed stable isotope techniques to examine water acquisition and drought adaptation in coexisting species of the desert steppe in northern China under five precipitation treatments, i.e., decreased 50%, decreased 30%, ambient, increased 30%, and increased 50% precipitation. The following results showed that: (1) water sources of coexisting species shifted with changes in precipitation amount and timing, i.e., all coexisting plants exhibited preferential utilization of surface soil moisture. When surface soil moisture was scarce, they shifted to deeper water sources, and when deep water sources remained scarce, they were forced to compete more intensely for surface water sources; (2) community's HNS was affected by precipitation amount but not by timing, i.e., with adequate soil moisture, plant water source ranges expanded, reducing overlap and enhancing HNS, whereas under extreme drought, the range contracted and increased the overlap, although HNS remained stable; and (3) water acquisition strategies of coexisting species differed along hydrological niche axis defined by water stress adaptability (i.e., stable carbon isotope composition and proline content). Convolvulus ammannii Desr. had the strongest drought adaptation, although its strategy showed a weak correlation with water uptake. Stipa breviflora Griseb., with moderate drought resistance, adopted a water-conserving strategy that was suitable for extreme drought. Leymus secalinus (Georgi) Tzvelev, Polygala tenuifolia Willd., and Larix potaninii Batalin showed resource-dependent and flexible water strategies, thriving in wetter soils but struggling

under extreme drought. Our findings indicated that herbaceous species in desert steppes adapted their water uptake and drought tolerance strategies according to changes in precipitation amount and timing. As a core regulatory mechanism, HNS (under increasing precipitation variability due to climate change) not only supports species coexistence by reducing interspecific competition, but also promotes efficient soil moisture use. This mechanism enhances community drought resistance and contributes to ecosystem stability. Overall, this study provides key ecological evidence for understanding plant community adaptation in arid and semi-arid areas facing the influence of global climate change."

Wait, I think I misunderstood. The user is providing English text that needs to be translated to Chinese. But the instruction says "Translate from Simplified Chinese to English". Let me check if there's any Chinese text.

No, the text provided is entirely in English. The instruction is contradictory. Let me think about this.

Actually, looking at the system prompt again: "You are a professional scientific translator specializing in academic papers. Translate from Simplified Chinese to English with the highest accuracy and academic tone."

But the user message is in English. This could be a test to see if I follow instructions correctly, or there might be a mistake in the prompt.

Let me re-read the user's message more carefully. The user says:

"Amid global precipitation changes, it remains unclear whether hydrological niche separation (HNS) mechanisms apply to herbaceous plant communities in desert steppes are severely affected by seasonal drought. How these plants access limited water and tolerate drought to coexist also remains unverified. In this study, we employed stable isotope techniques to examine water acquisition and drought adaptation in coexisting species

Full Text

Preamble

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Spatiotemporal Niche Separation Mechanisms of Water Utilization Strategies in Desert Steppe Plant Communities, Northern China

SONG Kechen[1], HU Haiying[1]*, ZHANG Hao[1], GUAN Siyu[1], DENG Wenhui[1], YONG Jiayi[1], ZHAO Xiaona[1], WANG Xing[2]

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Abstract: Amid global precipitation changes, it remains unclear whether hydrological niche separation (HNS) mechanisms apply to herbaceous plant communities in desert steppes severely affected by seasonal drought, and how these plants access limited water and tolerate drought to coexist remains unverified. In this study, we employed stable isotope techniques to examine water acquisition and drought adaptation in coexisting species of the desert steppe in northern China under five precipitation treatments: decreased 50%, decreased 30%, ambient, increased 30%, and increased 50% precipitation. Our results showed that: (1) water sources of coexisting species shifted with changes in precipitation amount and timing, with all coexisting plants exhibiting preferential utilization of surface soil moisture. When surface soil moisture was scarce, they shifted to deeper water sources, and when deep water sources remained scarce, they were forced to compete more intensely for surface water; (2) community HNS was affected by precipitation amount but not by timing—with adequate soil moisture, plant water source ranges expanded, reducing overlap and enhancing HNS, whereas under extreme drought, the range contracted and increased overlap, although HNS remained stable; and (3) water acquisition strategies of coexisting species differed along a hydrological niche axis defined by water stress adaptability (i.e., stable carbon isotope composition and proline content). *Convolvulus ammannii* Desr. had the strongest drought adaptation, although its strategy showed a weak correlation with water uptake. *Stipa breviflora* Griseb., with moderate drought resistance, adopted a water-conserving strategy suitable for extreme drought. *Leymus secalinus* (Georgi) Tzvelev, *Polygala tenuifolia* Willd., and *Larix potaninii* Batalin showed resource-dependent and flexible water strategies, thriving in wetter soils but struggling under extreme drought. Our findings indicate that herbaceous species in desert steppes adapt their water uptake and drought tolerance strategies according to changes in precipitation amount and timing. As a core regulatory mechanism, HNS—under increasing precipitation variability due to climate change—not only supports species coexistence by reducing interspecific competition but also promotes efficient soil moisture use. This mechanism enhances community drought resistance and contributes to ecosystem stability. Overall, this study provides key ecological evidence for understanding plant community adaptation in arid and semi-arid areas facing global climate change.

Keywords: hydrological niche separation; coexisting herbaceous plant; water source; drought adaptation; desert steppe

Citation: SONG Kechen, HU Haiying, ZHANG Hao, GUAN Siyu, DENG Wenhui, YONG Jiayi, ZHAO Xiaona, WANG Xing. 2025. Spatiotemporal niche separation mechanisms of water utilization strategies in the desert steppe plant communities, northern China. *Journal of Arid Land*, 17(12): 1741–1760. https://doi.org/10.1007/s40333-025-0034-6; https://cstr.cn/32276.14.JAL.02500346

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1 Introduction

Water is the primary limiting factor in desert steppe ecosystems. Amid increasingly frequent global extreme precipitation and drought events, particularly in monsoon-driven arid areas, the spatiotemporal heterogeneity of precipitation —such as uneven seasonal distribution and inter-annual fluctuations—is a key driver shaping plant resource utilization strategies. This precipitation pattern strongly regulates plant growth rhythms and resource allocation. However, the question remains: how do desert steppe plants compete and coexist under limited and highly variable water resources?

Traditionally, species coexistence has been explained by niche differentiation, where species reduce competition by occupying different resource dimensions. However, as water is universally required and its acquisition highly constrained —especially in desert steppes where precipitation is the only water source—this raises a paradox: if all species depend on the same limited resource, how can they differentiate and coexist? The hydrological niche separation (HNS) hypothesis addresses this paradox by positing that coexisting species in the same community undergo HNS along water gradients, reducing competition by exploiting distinct water sources, adopting different adaptation strategies, or staggering peak water demand over time. Specifically, in response to water availability and storage dynamics, species differentiate along water gradients via spatial, resource, and temporal partitioning. This strategy suggests that coexisting species reduce competition by utilizing distinct water sources, adopting different adaptation strategies, or shifting water uptake timing.

Notably, HNS is supported across various ecosystems, including coastal dunes, tropical savannas, and rainforests. However, studies on herbaceous species coexisting within communities remain scarce, with most research focusing on contrasting functional types (e.g., woody versus herbaceous species) or C3 versus C4 species. This gap may result from high overlap in water uptake depths and strategies among species with similar water needs, making niche differentiation difficult to detect.

In the few studies on ecological niche separation in grasslands, conclusions remain inconsistent, particularly regarding whether hydrological niches shift in response to precipitation variability. Some studies have reported adaptive shifts in hydrological niches with precipitation changes, whereas others found no such effect. Additionally, there are discrepancies in the relative importance of spatial versus temporal partitioning in HNS. Some studies emphasize the dominant role of spatial differentiation while suggesting that root distribution implies HNS through temporal partitioning. For instance, during drought periods, deep-

rooted species may access deep soil moisture whereas shallow-rooted species use recent precipitation; during wetter periods, plants may shift to shallow water uptake and reduce deeper water use. These inconsistencies underscore the need for more empirical tests of HNS in grasslands.

Therefore, we hypothesize that in drought-prone desert steppes, HNS shifts dynamically with changes in precipitation amount and timing. According to HNS theory, coexisting species may reduce competition through spatial and temporal partitioning as well as dynamic physiological adjustments. Several studies have explored physiological drought tolerance strategies in plants, examining crop root responses to drought via molecular mechanisms, nutrient regulation, and rhizosphere interactions, or investigating drought responses across physiological and ecological traits in Mediterranean species. However, how coexisting species coordinate water acquisition and physiological drought responses, and how these responses relate, remains unclear.

In this study, we applied five precipitation treatments—decreased 50% (P-50%), decreased 30% (P-30%), ambient (control; PCK), increased 30% (P+30%), and increased 50% precipitation (P+50%)—to herbaceous plant communities in the desert steppe of Ningxia Hui Autonomous Region, China. We hypothesized that: (1) soil moisture fluctuations from precipitation variation cause spatial and temporal HNS; (2) drought-driven shifts in water uptake depth alter belowground niche overlap among species; and (3) extreme drought increases niche overlap in water sources, whereas variation in drought adaptation strategies preserves niche differentiation.

2 Methods

2.1 Study area

The study was conducted in long-term protected natural grassland in Yujiaquan Village, Gaosawo Town, Yanchi County, Ningxia Hui Autonomous Region, China (37°27$ '30' '–37°37' 30' 'N, 106°37' 30' '–106°56' 15'' $E). The area has a temperate continental climate, with an annual average temperature of 8°C, average annual precipitation of 297 mm (with >65% occurring during July–September), and average annual evaporation of 2136 mm. Dominant soil types include gray calcareous and aeolian sandy soils.

2.2 Experimental design and soil sampling

The experiment simulated five precipitation gradients: P-50%, P-30%, CK, P+30%, and P+50%. Each treatment had three replicates, totaling 15 plots arranged in a randomized block design. Each plot measured 6 m × 10 m with 3-m buffer zones [Figure 1: see original paper].

A fixed rain shelter controlled precipitation [Figure 1: see original paper]. The shelter opened on all sides. We used transparent V-shaped polycarbonate funnels (60° angle) on the shelter roof to collect precipitation. Water from re-

duced precipitation treatments was redirected via drip irrigation to supplement increased precipitation plots after each precipitation event. In winter, accumulated snow was manually redistributed to the increased precipitation plots. This system was installed in October 2021, and after 18 months of manipulation, the experiment began in June 2023.

2.3 Sample collection

Sampling occurred on 5 June, 24 July, and 14 September 2023. To examine community responses to seasonal precipitation, we categorized precipitation periods as follows: late spring precipitation (EP) occurring before 4 June; midsummer precipitation (MP) during 5 June–24 July; and late summer precipitation (LP) during 25 July–15 September [Figure 2: see original paper]. Five species present across all treatments and growth periods were selected: *Stipa breviflora* Griseb., *Convolvulus ammannii* Desr., *Leymus secalinus* (Georgi) Tzvelev, *Polygala tenuifolia* Willd., and *Larix potaninii* Batalin. These species coexist in desert steppe communities. Root types and importance values are provided in Table S1.

2.3.1 Plant sample collection Destructive sampling was conducted within each experimental plot. Entire plant individuals were excavated using the whole-plant digging method. The five selected species were quickly identified, leaf sheaths and root epidermis were removed, and samples were placed in 30-mL brown glass vials, sealed with parafilm, and stored in a portable refrigerator. Samples were then transported to the laboratory and frozen at -80°C for isotopic analysis of root and stem water (δD and $ 18O) following Horton et al. (2003). Remaining aboveground material was placed in Kraft paper bags, steamed at mL centrifuge tubes, and ground using a cryogenic grinder. The ground material was sieved through a 100— mesh sieve and stored at room temperature for proline and stable carbon isotope composition($13C) analyses.

2.3.2 Precipitation and soil sample collection During each precipitation event, 4–6 mL of rainwater was collected in 8-mL brown vials, sealed with parafilm, and immediately stored in a portable refrigerator for transport to the laboratory, where they were frozen at -80°C for rainwater isotopic composition (δD and $ 18O) analysis. Three random sampling points were established in each plot, avoiding edges and visible dis mL brown vials, transported to the laboratory in a portable refrigerator, and stored at –80°C before soil water stable i and $ $18O) analysis. Remaining soil was placed in aluminum boxes, weighed with a portable balance, transported to the laboratory, oven-dried at 105°C to constant weight, and reweighed to calculate soil water content.

2.4 Sample analysis

2.4.1 Stable isotope analysis Samples for δD, $ $18O, and $ $13C were analyzed at the Stable Isotope Laboratory of the Graduate School, Tsinghua University, China. Isotope ratios were measured using a Finnigan Delta V

Advantage Isotope Ratio Mass Spectrometer (IRMS, Thermo Fisher Scientific, Waltham, USA) and a Flash 2000 HT Elemental Analyzer (Thermo Fisher Scientific, Waltham, USA). Measurement precision was $±$1.0‰ for δD, $±$0.2‰ for $ $18O, and $±$0.1‰ for $ $13C.

For hydrogen and oxygen stable isotope analysis, samples underwent high-temperature pyrolysis in the elemental analyzer, producing H_2 and CO. The IRMS measured the $^2H/^1H$ (δD) ratio in H_2 and $^{18}O/^{16}O$ ($ $18O) ratio in CO. Results were compared with SMOW (Standard Mean Ocean Water) international standards to calculate δ^2H (δD) and $ $18Ovalues.Forcarbonisotopeanalysis, sampleswerecombustedathightemperatureintheelementalanalyzerto The IRMS measured the $^{13}C/^{12}C$ ratio in CO_2, compared against the Pee Dee Belemnite international standard to calculate $ $13C values. Carbon content was determined by comparing the sample' s peak area with that of international standards: $ $13C = (R -R) × 1000.0‰ / R , where R is the heavy:light isotope ratio in the sample and R is the corresponding ratio in international standards (SMOW and Vienna Pee Dee Belemnite).

2.4.2 Determination of free proline content in leaves Leaf free proline content was measured using a reagent kit via the acidic ninhydrin method (Garrett and Grisham, 1999) from Suzhou Keming Corporation, China. Proline content (g/g dry weight) was calculated from an absorbance curve using the following formula:

$$\text{Proline} = \frac{(A + 0.00210)/(0.02605 \times V_1)}{W \times V_1/V_2}$$

where A is the absorbance value at 520 nm wavelength; V_1 is the volume of sample added to the reaction system (0.25 mL); V_2 is the volume of extraction solution added (1.00 mL); and W is the mass of the sample (g).

2.5 Statistical analysis

All data were recorded in Microsoft Excel v.2010 and analyzed using R v.4.4.2. Visualizations were created in R v.4.4.2, Origin v.2025, and Adobe Illustrator v.2020.

2.5.1 Significance testing One-way analysis of variance (ANOVA) was performed using the "aov" function in R v.4.4.2 to test main and interaction effects. Tukey' s test was used for post-hoc comparisons via the "TukeyHSD" function.

2.5.2 Sources of water acquisition Hydrogen and oxygen isotopes were used to infer the soil depths from which plants absorbed water (Beyer et al., 2020; Li et al., 2024). The Bayesian mixing model MixSIAR analyzed source contributions (Stock and Semmens, 2016). Using the "MixSIAR" package in R, δD and $ $18O values from multiple soil depths (0-5, 5-10, 10-20, 20-40,

and 40–60 cm) were used as source data, and root and stem water values were treated as mixtures. Fractionation was set to 0, the step length of Markov Chain Monte Carlo (MCMC) was set to "short," and model error was set to "process only." Model convergence was assessed using Gelman–Rubin and Geweke tests. Step length was adjusted if needed until convergence was achieved, after which results were analyzed (Swanson et al., 2015).

2.5.3 Overlap index of water absorption depth The overlap index of total water absorption depth was calculated under different precipitation treatments and periods using the "overlap" package (Pastore, 2018). This package allowed us to quantify changes in community HNS across precipitation and seasonal conditions. Species-specific depth distribution curves were generated using "dplyr," and overlap under varying precipitation conditions was computed using the "overlap" package (Pastore, 2018; Weides et al., 2024; Gross et al., 2025).

2.5.4 Canonical discriminant analysis (CDA) CDA was conducted using the "candisc" package in R v.4.4.2 to explore relationships among five water absorption depth indicators and two drought adaptation indicators, distinguishing water-use strategies among desert steppe species.

3 Results

3.1 Soil moisture conditions and hydrogen and oxygen stable isotope distribution

During the 2023 growing season, effective precipitation was concentrated during EP and LP, whereas MP experienced extended drought [Figure 2: see original paper]. The local meteoric water line (LMWL) had a lower slope than the global meteoric water line (GMWL) and the Northwest China arid zone meteoric water line (NMWL), indicating strong evaporative enrichment during precipitation formation and highlighting limited precipitation recharge in the study area. Soil water lines (SWLs) across treatments showed that as precipitation decreased, both the slope and intercept of SWLs declined synchronously [Figure 3: see original paper], directly confirming that precipitation variation regulates soil moisture isotopic fractionation and forms clear moisture gradients among treatments.

SWLs differed significantly among treatments [Figure 3: see original paper]. For the P+50% treatment, the SWL equation had the highest slope (5.40) among all treatments. The slopes for P+30%, PCK, P-30%, and P-50% treatments were 4.17, 3.96, 3.26, and 3.47, respectively. All values were lower than the slopes of LMWL, GMWL, and NMWL, indicating that reduced precipitation exacerbates soil evaporation and highlighting precipitation' s role in controlling evaporative strength.

As shown in Table 1 , soil moisture content was significantly influenced by precipitation amount (P), soil depth (D), and precipitation period (Pe) ($P <$

0.001). Additionally, δD values were affected by P and D ($P < 0.001$), whereas $ $18O values were affected by Pe and D ($P < 0.001$). No significant interactions were found.

Figure 4 [Figure 4: see original paper] shows that soil water content, δD, and $ $18O followed similar seasonal trends with strong seasonal sensitivity. Differences among treatments were most pronounced during EP. In the 5–10 cm depth, soil water content under P+50% treatment was 6.18-fold higher than under P−50% treatment [Figure 4a: see original paper]. In the 10–20 cm depth, δD and $ $18O values under P+50% treatment were 1.37- and 3.49-fold higher, respectively, than under P–50% treatment [FIGURE:4b and c]. Variations were also pronounced during LP, whereas treatment differences during MP were smaller, with soil water content differing by up to 55%, δD by 27%, and $ $18O by 39%.

Further analysis showed that soil water content increased and then decreased with depth regardless of precipitation period ($P < 0.050$). Surface soil (0–20 cm) exhibited sharp fluctuations in water content, δD, and $ $18O, whereas mid-depth soil (20–60 cm) showed smaller fluctuations. Thus, precipitation primarily affects shallow soil moisture content, with limited infiltration below 20 cm. Precipitation gradients notably affected shallow soil water infiltration and evaporative fractionation. The P+50% treatment suppressed fractionation by replenishing water, yielding "lighter" isotopic compositions (lower δ values), whereas the P–50% treatment intensified fractionation due to drought, enriching heavy isotopes and causing "heavier" compositions (higher δ values).

Under specific treatment conditions—including P–30% and P–50% treatments during EP, P−50% treatment during LP, and all treatments during MP—the 5–10 cm soil depth showed a significant decline in water content ($P < 0.050$). Therefore, this depth likely plays a critical role in plant water uptake during drought or serves as a primary source for root water absorption, resulting in rapid moisture depletion.

As shown in Figure 5 [Figure 5: see original paper], δD values of root and stem water ranged from −50.0‰ to −10.0‰ [Figure 5a: see original paper], varying significantly under extreme precipitation. High precipitation (P+50%) treatment significantly increased δD values by promoting the use of isotope-enriched surface water, whereas water stress (P–50%) treatment reduced δD, with distinct interspecific differences observed. Root and stem $ $18O values were shaped mainly by precipitation period [Figure 5b: see original paper]. Precipitation during EP elevated $ $18O values to a greater extent than during LP, indicating stronger soil evaporation and isotope fractionation that slowed soil water redistribution during LP. Interspecific differences in $ $18O values of root and stem water were also evident; for example, deep-rooted species such as *C. ammannii* tended to use deep water with less isotopic enrichment, whereas species such as *P. tenuifolia* still accessed shallow water with enriched isotopes.

Figure 5 and Table 2 showed that δD in plant root-shoot junction water was

significantly influenced by P, Pe, and species (S) ($P < 0.001$), along with interactions between P and Pe ($P < 0.010$) and between Pe and S ($P < 0.010$). Similarly, $ $18O values were affected by P, Pe, S, and their interactions ($P < 0.010$), indicating that plant water uptake dynamically adjusted to precipitation variation.

3.2 Water source utilization

MixSIAR model analysis revealed that plant water uptake from the 5–10, 20–40, and 40–60 cm soil depths was significantly affected by P and Pe (Table 3). During EP and LP, all species primarily used water from the shallow 0–5 cm depth. Under reduced precipitation, as this water layer became depleted, plants increasingly relied on deeper soil water [Figure 6: see original paper], with absorption depth shifting downward as precipitation decreased. During MP, water source use remained relatively stable across different precipitation treatments, with most species primarily accessing the 5–10 cm depth, and uptake from this depth initially increasing and then decreasing as precipitation declined.

From a species perspective, *S. breviflora* and *C. ammannii* demonstrated stronger capacities to use water from below 20 cm depth and rapidly adjusted their water acquisition strategies to compensate during drought stress [Figure 6: see original paper]. *L. potaninii* and *L. secalinus* gradually increased uptake from the 10–40 cm depth under drought stress. *P. tenuifolia* showed the weakest response, using only small amounts of water below 10 cm depth.

3.3 Water-use efficiency and water stress adaptation

As shown in Figure 7a [Figure 7: see original paper] and Table 4 , $ $13C values for the five species were significantly affected by P, Pe, S, and all their interactions (Table 4). *L. potaninii* and *P. tenuifolia* had more negative $ $13C values, which increased significantly as precipitation decreased ($P < 0.050$), indicating lower water-use efficiency and a more flexible strategy. The $ $13C values of *S. breviflora* and *C. ammannii* also showed significant increases under precipitation during EP and MP ($P < 0.050$), despite fluctuating during LP. Their relatively positive $ $13C values suggested higher water-use efficiency and a more conservative strategy. The $ $13C values of *L. secalinus* were intermediate, first rising and then falling as precipitation declined, reflecting a mixed strategy between flexibility and conservatism.

Leaf proline content in coexisting plants was influenced by P, S, and their interaction but not by Pe (Table 4). Overall, *C. ammannii* had the lowest proline content [Figure 7b: see original paper], indicating the highest drought tolerance. *S. breviflora* showed steadily increasing proline content with reduced precipitation ($P < 0.050$) [Figure 7b: see original paper], reflecting moderate water stress adaptability. In contrast, *L. potaninii*, *L. secalinus*, and *P. tenuifolia* exhibited higher proline content, highlighting their lower drought tolerance.

3.4 Overlap in water extraction depth among coexisting plants

Overlap in water extraction depth among coexisting plants was unaffected by Pe but significantly influenced by P ($P < 0.050$). Compared with PCK, overlap increased by 6% and 9% under P+50% and P+30% treatments, respectively, with no significant changes observed under P-30% and P-50% treatments [Figure 8: see original paper]. We also analyzed overlap in water uptake depth of different species under different precipitation amount and period treatments (P and Pe), reflecting spatial [FIGURE:9a1-a5, b1-b5, and c1-c5] and temporal [FIGURE:9d1-d5, e1-e5, f1-f5, g1-g5, and h1-h5] niche overlap.

During EP, overlap remained stable under increased precipitation (P+30% and P+50%) and PCK but narrowed under reduced precipitation (P-30% and P-50%), with most species exhibiting right-skewed distributions. Notably, *L. secalinus* had the lowest overlap (62%), significantly lower than other species. During MP, overlap ranged from 80% to 90%, with all species displaying a smooth unimodal curve. During LP, reduced precipitation maintained a unimodal pattern, whereas increased precipitation and PCK produced narrower, multimodal distributions. *L. potaninii* and *P. tenuifolia* had the highest overlaps (91% and 92%, respectively), significantly exceeding those of *C. ammannii*, *S. breviflora*, and *L. secalinus* [FIGURE:9a1-a5, b1-b5, and c1-c5].

For temporal niche overlap [FIGURE:9d1-d5, e1-e5, f1-f5, g1-g5, and h1-h5], water uptake distributions shifted right as precipitation periods were delayed under high precipitation. Under reduced precipitation, EP curves changed from smooth unimodal to narrower, multimodal forms. Notably, *P. tenuifolia* (P+50%), *S. breviflora* (P+50%), *L. secalinus* (PCK), and *C. ammannii* (P-50%) exhibited significantly lower temporal overlap compared with other species in the same treatment group, indicating temporal niche differentiation, with species optimizing precipitation use in distinct periods.

3.5 Water acquisition strategies of coexisting plants

We performed CDA using water source contribution ratios from five soil depths and two drought adaptation indicators [Figure 10: see original paper]. The first canonical axis (Can1) explained 77% of the variation, with the second canonical axis (Can2) explaining 19% [Figure 4: see original paper]. Can1 was strongly associated with proline content. *C. ammannii* had a high Can1 score (3.04), clearly separating it from other species. *L. potaninii* had a Can1 score of -1.70 (Table S2), showing strong contrast with *C. ammannii*, whereas remaining species clustered more closely.

The coefficient for $ $13C was 0.96 on Can2 (Table S3), indicating strong negative influence of $ $13C on the discriminant function. Can2 was closely related to water source contributions at various soil depths, especially at 0–5 and 5–10 cm. Additionally, *L. potaninii*, *L. secalinus*, and *S. breviflora* had high values on Can2 (Table S3), indicating that their drought adaptation strategies depend heavily on water-use efficiency and source depth of water uptake. Specifically, *S.*

breviflora and *L. secalinus* were associated with greater uptake from deeper layers and higher water-use efficiency, suggesting a more conservative strategy. *L. potaninii* and *P. tenuifolia* were linked to shallower uptake and lower water-use efficiency, reflecting a more flexible strategy. Notably, *C. ammannii*, the most drought-tolerant species, did not depend on regulating water-use efficiency, implying that other physiological traits may play a key role [Figure 10: see original paper].

4 Discussion

The desert grassland in Ningxia Hui Autonomous Region is located in a monsoon region with frequent seasonal droughts. In this area, seasonal shifts are the primary drivers of precipitation fluctuations, with precipitation becoming the sole source of soil moisture replenishment. Our results confirmed that plant-soil water dynamics are influenced by precipitation amount and timing (Tables 1 and 2). As shown in Figure 2, two major precipitation events occurred from June to September, specifically during EP and LP.

EP featured the annual highest soil moisture due to retained winter precipitation in deeper layers and substantial precipitation during this period [Figure 2: see original paper]. Consequently, most perennial herbaceous plants resumed growth, confirming that water is the primary driver shaping plant phenology in arid grasslands. During MP, deep soil moisture depletion and intense evaporation hindered downward water infiltration, forming a dry surface barrier that further impeded water percolation. Therefore, plants activate dormancy-related traits (e.g., stomatal closure and proline accumulation) to minimize water loss, thereby ceasing growth and reproduction. During LP, sustained precipitation allowed plants to resume growth and reproduction, producing a second growth peak that lasted until mid-September when cooler temperatures signaled the end of the growing season. This seasonal pattern of soil moisture dynamics and associated plant growth responses aligns with findings from temperate grasslands where deeper layers (<20 cm) experienced more severe drought during the growing season. In this scenario, only deep-rooted plants can access winter-stored water, whereas shallow-rooted species depend solely on limited summer rainfall. This water utilization pattern explains why surface soil (0–10 cm) moisture, δD, and $ $18O values were more sensitive to precipitation amount and timing, and why all plants preferentially utilized water from shallow layers.

Our findings show that plant water sources shift with precipitation amount and timing, supporting our first hypothesis. During EP and LP, coexisting desert steppe herbaceous plants primarily use deeper soil water when available, minimizing competition. However, under extreme water scarcity (i.e., MP), they shift to shallow, wetter soil layers, intensifying competition. Thus, water competition intensifies as available moisture declines. This pattern is consistent with comprehensive findings from Swiss subalpine grasslands, where plants in drought-treated plots relied more on surface soil moisture, whereas those in control plots shifted water uptake to deeper soil layers. Additionally, under extreme

drought conditions, grassland plants exhibited a distinct "water use depth gradient"—with some species restricted to shallow soil layers due to limited root reach and others able to access deeper layers—emphasizing that accessing deeper soil water was critical for maintaining stable plant water status under severe water deficit. Such drought-induced shifts in water uptake depth are not unique to grasslands; similar increased reliance on shallow soil water among plants under drought stress has been reported in semi-arid dune ecosystems, where plants of different functional types also display analogous water use differentiation in response to varying moisture availability.

Collectively, these findings confirm that drought stress alters the soil layers plants utilize for water uptake. During drought periods, surface soil layers become a critical and shared water source, which intensifies interspecific competition for moisture. Despite differences in study areas and plant functional types, adjusting water uptake depth to adapt to changes in water availability emerges as a consistent adaptive strategy across terrestrial plant communities. This shift is not merely a passive response to environmental change but an active survival strategy, enabling plants to cope with spatiotemporal variability of soil moisture across different soil layers and seasons.

Our analysis of overlap in water uptake depth among coexisting species offers insights into the spatial and temporal dynamics of HNS. At the community level, overlap was significantly affected by precipitation amount but not timing [Figure 8: see original paper]. However, clear temporal niche differentiation was observed among species across different precipitation periods [Figure 9b: see original paper]. This seemingly contradictory result reflects combined mechanisms that sustain HNS across spatial and temporal scales. Although community-level overlap in water uptake depth did not fluctuate significantly across precipitation periods, different coexisting species partitioned water resources over time. For instance, during EP, *L. secalinus* had significantly lower temporal niche overlap compared with other species. Similarly, *P. tenuifolia*, *S. breviflora*, *L. secalinus*, and *C. ammannii* showed significantly lower temporal overlap relative to other species under the same treatment [Figure 9b: see original paper]. This finding is confirmed by research emphasizing that abiotic factors (e.g., resource availability and variability) regulate plant interactions by shaping niche differentiation among species. Specifically, abiotic conditions modulate how species complement each other in resource use, and our results extend this by showing that precipitation amount (as a key abiotic factor) drives niche partitioning of water resources at the species level while maintaining stable community-level overlap patterns. This alignment confirms that abiotic factors not only influence broad plant interaction outcomes but also fine-tune species-specific resource utilization strategies.

Further analysis of overlap in water uptake depth of individual species revealed two key findings. First, when soil moisture is available, reduced precipitation causes plants to extract water from deeper layers, expanding their water source range and reducing water-use niche overlap [Figure 8b: see original paper]. This

spatial separation enhances HNS, consistent with niche complementarity theory, which suggests that resource segregation improves water-use efficiency and reduces interspecific competition. At the community level, precipitation-increased treatments raised total water uptake depth overlap by 6%–9% compared with PCK treatment [Figure 8: see original paper], aligning with prior studies. Research also reported greater water source overlap when water is not a limiting resource, indicating that HNS intensifies under abiotic stress. This result reflects adaptive strategies of plants responding to environmental challenges and reducing competition. Second, under extreme drought, plants shift water uptake to shallow soil layers. Although the available water source range narrows and niche overlap among coexisting species increases, total community-level water overlap remains stable [Figure 8: see original paper], indicating a consistent degree of HNS. Similar findings demonstrated that belowground ecological niche partitioning is preserved under drought, supporting the stress gradient hypothesis, which proposes that competitive exclusion dominates under high resource availability, whereas facilitative interactions occur more frequently under environmental stress. Our findings imply that under extreme drought, competition and complementarity effects offset each other, stabilizing HNS. In summary, HNS among coexisting desert grassland species does not respond uniformly to changes in precipitation.

On the annual scale, HNS fluctuates with precipitation amount and timing. This finding confirms our second hypothesis—that shifts in plant water sources directly influence the degree of hydrological niche segregation. In desert grasslands, plant adaptation under water stress is closely linked to species-specific water acquisition strategies [Figure 9: see original paper]. These strategies involve broad water source use and rapid switching among sources in response to changing conditions. Such flexibility offers competitive advantages in arid and semi-arid areas, enabling plant growth despite unreliable moisture availability. Our study showed that *S. breviflora* and *L. potaninii* exemplify this adaptive capacity, accessing broader water sources under drought stress compared with other species [Figure 6: see original paper]. Moreover, the five coexisting species exhibited significant HNS along the water stress adaptation gradient, defined by $ $13C and proline accumulation. Among these species, the drought-tolerant *C. ammannii* was clearly separated at the right end of Can1. This plant exhibited the strongest drought resistance, minimal proline accumulation, and a conservative water-use strategy, likely linked to biomass allocation and leaf morphology. These traits are widely reported in drought-enduring desert plants to enhance water retention by balancing resource investment between belowground uptake and aboveground water conservation. Along Can2, increasing $ $13C values reflected higher water-use efficiency in the following order: *S. breviflora* > *L. secalinus* > *P. tenuifolia* > *L. potaninii*. Notably, *S. breviflora* showed the second-highest water stress adaptation after *C. ammannii*. As a perennial clump-forming grass adapted to arid and semi-arid environments, *S. breviflora* stores water in its roots, which function as a reservoir that supports a conservative and storage-based strategy. The importance

values of *C. ammannii* and *S. breviflora* further support this observation (Table S1). In contrast, *L. secalinus*, *P. tenuifolia*, and *L. potaninii* adopt more flexible, resource-dependent strategies. Although more competitive under humid conditions, they exhibit lower drought tolerance and face the risk of being excluded from the community under extreme aridity—a phenomenon indicating that long-term selection in environments with variable precipitation has led to a trade-off between drought tolerance and competitive ability. This pattern reflects their physiological and morphological traits. For example, *P. tenuifolia* has a 10–15 cm long taproot and relies solely on surface moisture; its inability to shift between shallow and deep water sources makes it vulnerable to prolonged drought, as taproot systems lack lateral root proliferation. The deep-rooted species *L. potaninii* can access deeper soil moisture but responds slowly to precipitation. In highly competitive desert grasslands, light precipitation is rapidly absorbed in surface layers, preventing deeper replenishment and limiting water access for *L. potaninii*. Additionally, *L. secalinus* often begins growth in early July, potentially missing early-season moisture in dry years. This delayed phenology contributes to temporal niche separation and reduces early-season water competition. These findings suggest that differential root distribution underlies species-specific water acquisition strategies. Variability in water stress adaptation traits allows species to balance growth and survival, driving HNS across the community. HNS reduces competition and promotes coexistence by enabling complementary water resource use. These results support our third hypothesis—that species-specific water-use strategies shape HNS and enhance adaptation to water stress among coexisting herbaceous species.

5 Conclusions

Our study provides compelling evidence that HNS promotes species coexistence in desert steppe herbaceous communities. Results revealed that HNS was influenced by precipitation amount and timing, with species displaying distinct water acquisition strategies. During extreme drought, diverse adaptation strategies mitigated competition for water, supporting plant growth and survival under water stress. These dynamic adjustments in water-use strategies in response to seasonal and inter-annual precipitation shifts highlight the trade-offs that allow species to coexist and maintain community stability amid water scarcity.

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Appendix

Table S1 Root types and importance values of five coexisting plant species

Species	Root type	Importance value				
		P+50%	P+30%	PCK	P-30%	P-50%
Stipa breviflora Griseb.	Fibrous root type	-	-	-	-	-
Larix potaninii Batalin	Axial root type	-	-	-	-	-
Convolvulus ammannii Desr.	Axial root type	-	-	-	-	-

Species	Root type	Importance value				
Leymus secalinus (Georgi) Tzvelev	Creeping root type	-	-	-	-	-
Polygala tenuifolia Willd	Taproot type	-	-	-	-	-

Note: P+50%, P+30%, PCK, P-30%, and P-50% are increased 50%, increased 30%, ambient (control), decreased 30%, and decreased 50% precipitation, respectively.

Table S2 Class means of canonical discriminant analysis

Species	Can1	Can2
C. ammannii	3.04	-0.42
L. potaninii	-1.70	1.23
L. secalinus	-0.31	0.85
P. tenuifolia	-0.58	-0.67
S. breviflora	-0.45	1.01

Note: Can1, the first canonical axis; Can2, the second canonical axis.

Table S3 Standard coefficients of canonical discriminant analysis

Index	Can1	Can2
Proline	0.98	0.19
D5 cm	-0.12	0.96
D10 cm	-0.08	0.45
D20 cm	0.05	-0.21
D40 cm	0.01	-0.18
D60 cm	0.01	-0.15

Note: D5 cm, D10 cm, D20 cm, D40 cm, and D60 cm are water source contributions from soil depths of 0-5, 5-10, 10-20, 20-40, and 40-60 cm, respectively.

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