Changes and determinants of belowground bud banks of a rhizomatous clonal plant Sophora alopecuroides L. in the desert steppe, northern China (postprint)

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Abstract

Belowground bud banks are crucial for the regeneration of plant populations in arid desert regions, and their responses to environmental change can reflect plant adaptive strategies to desert habitats. However, the size and composition of belowground bud banks, as well as their responses to environmental factors in the desert steppe zone, remain poorly understood, which poses challenges for desertification control in arid desert areas. In this study, we investigated the density and vertical distribution of horizontal and vertical rhizome buds of the rhizomatous leguminous herb Sophora alopecuroides L., together with its population characteristics and soil physicochemical properties, across three habitat types—interdune lowland (IL), flat sandy land (FSL), and desert steppe (DS)—in a desert steppe zone of northern China. The results showed that: (1) total rhizome bud density and horizontal rhizome bud density of S. alopecuroides differed significantly among the three habitats ($P<0.05$), with the highest total rhizome bud density in IL (177 buds/m^2) and the lowest in DS (63 buds/m^2); (2) in IL, horizontal rhizome buds were predominantly distributed in deeper soil layers, whereas in DS, vertical rhizome buds were mainly concentrated in the topsoil; and (3) soil coarse sand content, soil nutrient content, and population density were the primary factors influencing the bud bank density of S. alopecuroides. Specifically, horizontal rhizome buds were largely dependent on soil coarse sand content, while vertical rhizome buds were more closely associated with soil organic matter content and population density. These findings indicate that horizontal rhizome buds play a more important role in IL, where aeolian disturbance is frequent, whereas vertical rhizome buds are more important in DS, where water and nutrient resources are relatively abundant. The plastic responses and survival strategies of the S. alopecuroides bud bank across different habitats provide valuable insights for the effective implementation of desertification control measures and the management of desert steppe ecosystems.

Full Text

Preamble

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Changes and determinants of belowground bud banks of a rhizomatous clonal plant *Sophora alopecuroides* L. in the desert steppe, northern China

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Abstract: Belowground bud banks are essential for plant population regeneration in arid desert areas, and their response to environmental changes reflects adaptive strategies of plants to desert habitats. However, the size and composition of belowground bud banks and their response to environmental factors in the desert steppe zone remain poorly understood, challenging desertification control efforts in arid regions. This study examined the density and vertical distribution of horizontal and vertical rhizome buds of the rhizomatous legume herb *Sophora alopecuroides* L., its population characteristics, and soil physical-chemical properties across three habitats (interdune lowland (IL), flat sandy land (FSL), and desert steppe (DS)) in a desert steppe zone of northern China. Our findings revealed that: (1) total and horizontal rhizome bud densities of *S. alopecuroides* differed significantly among the three habitats ($P<0.05$), with the largest total rhizome bud density (177 buds/m^2) in IL and the smallest (63 buds/m^2) in DS; (2) horizontal rhizome buds distributed in deep soil layers were dominant in IL, while vertical rhizome buds in the topsoil layer were predominant in DS; and (3) soil coarse sand, nutrient content, and population density were the primary factors affecting bud bank density of *S. alopecuroides*. Specifically, horizontal rhizome buds depended largely on soil coarse sand content, while vertical rhizome buds tended to be more related to soil organic matter content and population density. Our results indicated that horizontal rhizome buds were more important in IL with frequent aeolian disturbance, whereas vertical rhizome buds were more important in DS with abundant water and nutrient resources. The plastic responses and survival strategies of *S. alopecuroides* bud banks to different habitats provide valuable information for effective implementation of desertification control measures and management of desert steppe ecosystems.

Keywords: belowground bud bank; soil coarse sand content; soil nutrient; population density; desert steppe

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1 Introduction

Clonal plants are widely distributed across various ecosystems and predominate in those with harsh natural conditions such as drought, poor nutrition, or low productivity (Klimeš et al., 1997; Hartnett et al., 2006). Clonal plants spread through both sexual reproduction and vegetative propagation (Benson and Hartnett, 2006). Vegetative propagation has been demonstrated to be more advantageous for plant population recruitment and vegetation development in desert ecosystems than sexual reproduction (Liu et al., 2014; Luo and Zhao, 2019). As a potential source of vegetative propagation for clonal plants, the belowground bud bank is the foundation for desert plant population regeneration and maintenance, playing a vital role in post-disturbance vegetation restoration and reconstruction in arid desert areas (Yu et al., 2002; Wu et al., 2021a; Luo et al., 2023).

Different types of bud banks serve distinct ecological functions and exhibit diverse adaptive strategies in response to disturbances (Wang et al., 2010; Qian et al., 2017). Rhizome buds, serving as reserve resources for horizontally oriented colonization, represent the guerrilla growth form of clonal plants, while tiller buds, acting as vertically oriented growth potential, represent the phalanx growth form (Liu et al., 2014; Dong et al., 2023). Changes in the number and proportion of these two bud bank types can reflect shifts in clonal growth architectures (guerrilla or phalanx). Clonal plants modulate growth patterns to adapt to resource heterogeneity and environmental disturbances by regulating bud bank size and composition (Hutchings and Kroon, 1994; Chen et al., 2011). Environmental factors influence and even determine the formation and development of belowground buds in plants (Tomlinson and O’ Connor, 2004; Wu et al., 2020). Therefore, analyzing the size and composition of belowground bud banks and their environmental drivers holds significant importance for elucidating adaptation mechanisms and reproductive strategies of clonal plants in desert ecosystems.

Recent research has increasingly examined the influence of environmental factors on belowground bud banks of plants in arid desert areas (Li et al., 2023). Soil moisture is a critical factor determining the density and composition of belowground bud banks (Carter et al., 2012; Qian et al., 2022), and higher soil moisture levels have been shown to significantly increase bud bank density (Wu et al., 2021a). For example, rhizome buds of *Leymus chinensis* (Trin.) Tzvelev were more sensitive to soil water status than tiller buds (Wang et al., 2008). Soil nutrient availability is another key factor influencing bud bank establishment, and increased nutrient levels can effectively enhance bud bank density (Dalgleish et al., 2008; Yu et al., 2022). Aeolian disturbance can also affect plant belowground bud banks, with moderate disturbance significantly increasing bud bank density. The impact of aeolian disturbance on bud banks is also related to bud type. Root-sprouting buds exhibited greater adaptability to severe wind erosion disturbance, whereas tiller buds were predominant in habitats prone to sand burial disturbance. Rhizome buds were adapted to low levels of disturbance (Ma et al., 2019). Additionally, plant belowground bud bank density is affected by aboveground vegetation (Klimešová and Klimeš, 2007; Zhang et al., 2019). Therefore, at a local scale, the density and composition of plant belowground bud banks may be affected by factors such as soil physical-chemical properties, aeolian disturbance, and aboveground vegetation. However, the response of plant belowground bud demography to environmental changes in desert steppe remains largely unexplored.

Desert steppe is located in the transitional zone between desert and steppe, and the ecosystem in this area is extremely sensitive to global climate change and human activities (Safriel, 2009; Rudgers et al., 2018). Scant precipitation and strong aeolian activities, coupled with frequent anthropogenic disturbances such as overgrazing, lead to vegetation degradation and widespread desertification in the desert steppe zone (Yao et al., 2019). Some studies have shown that most dominant species distributed in the desert steppe zone (such as *Leymus leymus* (Georgi) Tzvelev and *Sophora alopecuroides* L.) are clonal plants with strong vegetative reproduction capabilities (Dong and Alaten, 1999; Yang, 2005; Sui et al., 2011; Luo et al., 2016). These clonal plants play critical roles in desertification prevention and vegetation restoration of degraded areas (Yu et al., 2004, 2008; Zhang et al., 2019). Furthermore, the desert steppe exhibits diverse habitat types, significant spatiotemporal heterogeneity in soil properties (e.g., moisture and nutrients), and pronounced variability in aboveground vegetation characteristics, all of which affect the size and distribution of belowground bud banks of clonal plants (Buxbaum and Vanderbilt, 2007; An et al., 2019). Therefore, studying the size of belowground bud banks and their responses to environmental factors in typical clonal plants is crucial for vegetation restoration and maintenance of ecosystem stability in the desert steppe.

S. alopecuroides, a perennial leguminous herb, is widely distributed in the desert steppe. The species is a typical rhizomatous clonal plant. Due to a thick and leathery seed coat and deep physical dormancy, the species exhibits low germination rates, making clonal propagation the main means of population expansion and persistence (Yang, 2005; Hu et al., 2009). *S. alopecuroides* exhibits excellent tolerance to wind-blown sand, drought, and salinity, and grows well across diverse habitat conditions. Its strong belowground rhizome system can rapidly expand locally, facilitating the expansion of offspring ramets via clonal integration, stabilizing drifting sand, and enhancing vegetation cover, thereby making a major contribution to desertification control and soil erosion mitigation (Zhao et al., 2023). Additionally, this species is a vital medicinal plant resource in the northern desert area of China; however, its wild resources have declined sharply in recent years due to excessive harvesting and grazing (Wang et al., 2020).

In a previous investigation, we found that *S. alopecuroides* was mainly distributed in interdune lowland, flat sandy land, and desert steppe habitats within the desert steppe, with populations exhibiting distinct variation patterns across these three habitats. Furthermore, a previous study documented significant differences in soil texture, moisture, nutrient, and salinity among these habitats (Xu et al., 2008). However, it remains unclear how environmental factors (population characteristics and soil properties) influence the density and distribution patterns of belowground bud banks of *S. alopecuroides*. Therefore, in this study, we measured the density and vertical distribution of various types of rhizome buds, population density (PD), plant height (PH), and soil physical-chemical properties across different habitats, aiming to elucidate the influence of environmental factors on belowground bud bank density of the typical clonal plant *S. alopecuroides* in the desert steppe. This study aimed to answer the following questions: (1) do the density, composition, and distribution pattern of belowground bud banks of *S. alopecuroides* differ among habitat types? and (2) how do environmental factors influence bud bank density? These findings will enhance our understanding of vegetative reproduction of rhizomatous leguminous herbaceous plants and provide a valuable reference for exploring environmental adaptation mechanisms of clonal plants and for the conservation and utilization of wild resources in the desert steppe.

2 Materials and Methods

2.1 Study area

The study area is located in the desert steppe zone of Yanchi County, China (37°35′-38°04′N, 106°57′-107°58′E) at an altitude of 1270-1590 m a.s.l. (Fig. 1 [FIGURE:1]). The area lies in a transitional ecotone between the Loess Plateau and the Ordos Platform, exhibiting a typical continental monsoonal climate in the mid-temperate zone. Annual average temperature was 8.3°C during 1958-2017, with large differences between winter and summer. Average annual precipitation was 297 mm, with most rainfall occurring from July to September, while potential evaporation reaches 2136 mm (Du et al., 2021). Average annual sunshine duration is 2876 h, and average frost-free period is 139 d. The windy season spans from March to May, and average wind velocity is 2.8 m/s. The main vegetation types include desert steppe, psammophytic vegetation, and halophytic vegetation. The main soil types are aeolian sand, sierozem, and saline-alkali soils. *S. alopecuroides* in Yanchi County accounts for more than 50.00% of the total distribution area (Zhang et al., 2006).

2.2 Experimental design

Preliminary field investigations and literature reviews revealed three habitat types of *S. alopecuroides* in the study area: interdune lowland (IL), flat sandy land (FSL), and desert steppe (DS) (Li, 2007; Shao and Li, 2016). A total of 17 populations of *S. alopecuroides* were investigated across the three habitat types, including 6 populations in FSL, 6 populations in DS, and 5 populations in IL (Fig. 1 [FIGURE:1]). At each sampling site, 2 plots with an area of 20 m$×20*mwereestablished.Weestablished*5*quadratswithanareaof*1*m*×$1 m in each plot according to the five-point method (4 in the corners and 1 in the center of the plot). Vegetation cover, PD, and height of *S. alopecuroides* were measured in each quadrat. Vegetation cover was assessed using the quadrat method. PD of *S. alopecuroides* was obtained by counting the number of ramets (Qian et al., 2021). Mean height of *S. alopecuroides* was determined by randomly selecting several ramets within each quadrat and measuring their heights with a ruler under natural conditions.

2.3 Bud bank investigation

All belowground rhizomes of *S. alopecuroides* in each established 1 m$×$1 m quadrat were excavated to a depth of 50 cm. During sampling, we preserved the connection between aboveground stems and belowground rhizomes to facilitate identification of rhizome bud types based on their location. Soil attached to the rhizomes was gently removed. Bud bank samples were then placed in labeled plastic bags and transferred to the laboratory promptly for counting (Kleyer et al., 2008). As preliminary survey results showed that more than 90.00% of rhizome buds of *S. alopecuroides* were distributed within 0–30 cm soil depth in all three habitat types, counts of different rhizome bud types were conducted at 10-cm depth intervals within this range. Only turgid and light-colored buds were counted, while necrotic (decayed or withered) tissues were discarded. Rhizome buds of *S. alopecuroides* were divided into horizontal and vertical rhizome buds following the classification of *Phragmites australis* (Cav.) Trin. ex Steud. bud types (Liu et al., 2014). Horizontal rhizome buds refer to buds situated on the nodes and top of a horizontal rhizome exhibiting an angle $ $90° relative to the rhizome axis, which can develop into a new rhizome and daughter ramet. Vertical rhizome buds refer to buds located on vertical rhizomes (including the tip of vertical rhizome), forming acute angles or aligning linearly with the rhizome axis (Fig. 2 [FIGURE:2]). Vertical rhizome buds are located at the apex of vertical rhizomes, and most develop into new daughter ramets. Similar to the buds of *P. australis*, rhizome buds of *S. alopecuroides* are morphologically identifiable and can be counted directly (Liu et al., 2014). In addition, dry weights of horizontal rhizomes, buds, and roots on horizontal rhizomes were summed to calculate total horizontally oriented biomass (horizontal biomass), and those of vertical rhizomes, buds, and roots on vertical rhizomes were summed to calculate total vertically oriented biomass (vertical biomass) (Liu et al., 2014). The spacer length of rhizomes was measured with a ruler.

2.4 Measurement of soil properties

Soil samples were collected using a soil corer from three quadrats along the diagonal of each plot at a depth of 0–30 cm during the bud bank investigation. After removing stones and root material, we air-dried, crushed, and sieved soil samples for subsequent analysis. Soil particle size fractions were obtained with a laser particle sizer (Mastersizer-3000, Malvern Instruments Ltd., Worcestershire, UK) to determine coarse sand (CS; 0.25–2.00 mm) content. Total nitrogen (TN) content was quantified with an elemental analyzer (Flash 2000 CHNS/O, Thermo Scientific™, Carlsbad, USA). Soil electrical conductivity (EC) was determined with a conductivity meter (MC 5021, INESA Scientific Instrument, Shanghai, China) at a 5:1 (v:w) ratio of deionized water to soil. Soil organic matter (SOM) content was assessed by the potassium dichromate oxidation-titration method (Bao, 2000). In addition, undisturbed soil was collected from two depths (0–10 and 10–30 cm) to measure soil water content (SWC) and bulk density (BD). SWC and BD were measured using the oven-drying method.

2.5 Data analysis

A one-way analysis of variance (ANOVA) was used to assess differences in densities of horizontal, vertical, and total rhizome buds of *S. alopecuroides* across the three habitat types. The same statistical approach was applied to compare soil physical-chemical properties (CS, SOM, EC, BD, SWC, and TN content) among habitats. Prior to analysis, data were log-transformed to conform to the normal distribution assumption of ANOVA. Fisher' s least significant difference (LSD) tests at the 0.05 significance level were used for post hoc comparisons between means. Statistical data are expressed as mean±standard error. Figures presenting data were created using Origin v.2025 software. One-way ANOVA was carried out with SPSS v.27.0 software.

Redundancy analysis (RDA) was employed to assess relationships between belowground bud banks and environmental factors (population characteristics and soil physical-chemical properties). Bud bank density data were log-transformed and standardized prior to analysis. The analysis was used to calculate the explanatory power and relative contribution of individual environmental factors. RDA and graphing were conducted using CANOCO v.5.0 software.

Figure 4

Figure 1: Figure 4

Figure 6

Figure 2: Figure 6

3 Results

3.1 Bud density and composition

Total and horizontal rhizome bud densities of *S. alopecuroides* at the population level showed significant differences among habitat types (Fig. 3 [FIGURE:3]). Total rhizome bud density in IL (175 buds/m^2) was significantly greater than those in FSL (92 buds/m^2) and DS (61 buds/m^2), with a significant difference also observed between the latter two habitats ($P<0.05$). Horizontal rhizome bud density in IL (112 buds/m^2) was significantly greater than those in FSL (45 buds/m^2) and DS (19 buds/m^2), and differed significantly between FSL and DS as well ($P<0.05$). No significant differences were observed in vertical rhizome bud density among the three habitats ($P>0.05$).

Densities of total, horizontal, and vertical rhizome buds of *S. alopecuroides* at the individual level showed similar differences among habitats as those observed at the population level (Fig. 4

). Total rhizome bud density at the individual level in IL (13 buds/individual) was significantly greater than those in FSL (7 buds/individual) and DS (6 buds/individual) ($P<0.05$), whereas no significant difference was observed between FSL and DS ($P>0.05$). Horizontal rhizome bud density at the individual level in IL (9 buds/individual) was significantly greater than those in FSL (4 buds/individual) and DS (2 buds/individual), with no significant difference between FSL and DS ($P>0.05$). Vertical rhizome bud density at the individual level did not differ significantly among the three habitats ($P>0.05$).

We detected differences in rhizome bud composition of *S. alopecuroides* among the three habitats (Fig. 5 [FIGURE:5]). Horizontal rhizome buds constituted the majority (61.80%) of total rhizome buds in IL. The proportion of vertical rhizome buds in total rhizome buds was slightly higher than that of horizontal rhizome buds in FSL. In DS, vertical rhizome buds were the predominant type, accounting for 68.80% of total rhizome buds.

3.2 Vertical distribution of bud bank

Horizontal rhizome buds were primarily concentrated in the 10–30 cm soil depth in IL and FSL, and in the 0–20 cm soil depth in DS. Vertical rhizome buds, on the other hand, were primarily concentrated in the 0–20 cm soil depth across all three habitats (Fig. 6

Figure 7

Figure 3: Figure 7

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We detected differences in the proportion of total rhizome bud density in 0–10, 10–20, and 20–30 cm soil depths among habitats. In DS, about 50.00% of buds were distributed in the 0–10 cm surface soil with a high proportion of vertical rhizome buds. In FSL, about 30.00% of buds were distributed in the 0–10 cm soil depth. However, in IL, more than 80.00% of buds were distributed in the 10–30 cm soil depth, including almost all horizontal rhizome buds (Figs. 6 and 7

).

3.3 Effect of environmental factors on bud bank

We detected differences in population characteristics and soil physical-chemical properties among the three habitats (Table 1). PD did not differ significantly among habitats ($P>0.05$), whereas PH was significantly higher in IL than in FSL and DS ($P<0.05$). CS content and EC in IL were significantly higher than those in FSL and DS ($P<0.05$). CS content in FSL was significantly higher than that in DS, while the trend for EC was opposite. SWC in 0–10 cm and 10–30 cm soil depths in DS were significantly higher than those in IL and FSL, but no significant difference was observed between the latter two habitats. SOM and TN contents in IL and DS were significantly higher than those in FSL, but did not differ between IL and DS. Soil BD did not differ significantly among the three habitats ($P>0.05$).

Environmental factors, including aboveground vegetation and soil properties, together explained 69.50% of the total variation in belowground bud bank density of *S. alopecuroides* across the desert steppe zone. We found that CS content, PD, and SOM content correlated significantly with bud bank density ($P<0.05$). Among these, CS content was the most influential factor, accounting for 38.20% of the variation, followed by PD and SOM content, which explained 10.10% and 9.10%, respectively. Collectively, soil and vegetation properties contributed 83.00% and 17.00%, respectively, to total variation in bud bank density (Fig. 8 [FIGURE:8]; Table 2).

Aboveground vegetation and soil properties also affected densities of different bud types. Horizontal rhizome bud density showed a significantly positive correlation with CS content, whereas vertical rhizome bud density showed a significantly positive correlation with SOM and PD. Additionally, total rhizome bud density exhibited a significantly positive correlation with CS content, PD, and SOM content (Fig. 8 [FIGURE:8]; Table 3).

4 Discussion

4.1 Bud density and composition

In sandy land ecosystems, rhizomatous clonal plants have dense rhizomes and strong vegetative spread, forming a large rhizome network system (Maun, 1998; Yu et al., 2004; Liu et al., 2016). Soil particle size fraction is a critical factor determining rhizome expansion, with higher sand content increasing soil porosity and reducing resistance to rhizome extension (Yu et al., 2008). Our findings revealed that total and horizontal rhizome bud densities in IL and FSL were significantly greater than those in DS. This result can be attributed to the significantly higher CS content in IL and FSL than in DS, which facilitates diffuse rhizome growth and favors formation and development of belowground buds in these habitats. Our results were consistent with Yang (2005), who found that sandy soil was more conducive to rhizome spread growth than clay and sandy-clay soils, and increased bud density, rhizome branching number, and branching intensity of *S. alopecuroides*. We also found that total and horizontal rhizome bud densities of *S. alopecuroides* in IL were significantly greater than those in FSL. In contrast to FSL, IL are usually located in low-lying areas between dunes. Sparse rainfall rarely forms runoff on dune surfaces, and while it infiltrates, it also seeps laterally into IL (Jansen et al., 2001; Bakker et al., 2006; Liu et al., 2007; Wu et al., 2021b). High groundwater level and low surface wind speed result in superior habitat conditions such as high soil nutrients and SWC at 10–30 cm depth in IL (Table 2). Adequate soil water and nutrient conditions can promote growth of plant belowground buds and significantly increase bud bank density (Klimeš and Klimešová, 1999; Qian et al., 2021; Zuo et al., 2023). Therefore, *S. alopecuroides* exhibited greater bud bank density in IL than in FSL.

Rhizomatous clonal plants have the advantage of morphological plasticity, enabling them to produce rhizomes of varying lengths under heterogeneous resources, thereby forming a continuum of clonal configurations from phalanx to guerrilla, and even producing two extreme configurations within the same species (Schmid and Harper, 1985; Ye et al., 2006; Ott and Hartnett, 2015; Zuo et al., 2023). Previous research has shown that the rhizomatous grass *P. australis* exhibited plasticity in horizontal rhizome extension and vertical ramet growth under aeolian disturbance. Specifically, under sand burial conditions, *P. australis* tended to expand horizontally and produce rhizome-based ramets, while under severe wind erosion conditions, the species exhibited a phalanx growth pattern characterized by reduced rhizome length, increased biomass allocation to vertical rhizomes, and a shift toward tiller-derived ramet formation (Liu et al., 2014). In this study, *S. alopecuroides* exhibited the highest proportion of vertical rhizome biomass to total rhizome biomass and the shortest rhizome spacer length in DS, and the lowest corresponding proportion and maximum spacer length in IL, with moderate levels for both traits in FSL (Fig. S1). These results indicated that morphological plasticity existed between horizontal extension and vertical growth of *S. alopecuroides* across the desert steppe zone,

Figure 7

Figure 4: Figure 7

allowing phalanx growth form in DS and guerrilla growth form in IL. Research has demonstrated that the size and composition of belowground bud banks can reflect and even determine clonal growth configuration (Klimešová and Klimeš, 2007; Zhang et al., 2009). Horizontal rhizome buds, serving as reserve resources for horizontally oriented expansion, represent the guerrilla growth form, while vertical rhizome buds, acting as vertically oriented growth potential, represent the phalanx growth form. Therefore, vertical rhizome buds dominated in DS, while horizontal rhizome buds predominated in IL. This distribution pattern of rhizome buds may also be a strategy for *S. alopecuroides* to adapt to the variable environment of the desert steppe transition zone. In IL, horizontal rhizome buds could help *S. alopecuroides* spread laterally to escape stressful microsites and find favorable ones; in DS, vertical rhizome buds are conducive to better use of local resources and outcompeting other species.

4.2 Vertical distribution of bud bank

In this study, more than 80.00% of total rhizome buds in IL were distributed in the 10-30 cm soil depth. By contrast, this depth accounted for lower proportions of total rhizome buds in FSL and DS, with 66.30% and 50.10%, respectively (Fig. 7

). This observed difference in rhizome bud distribution among habitats may be caused by different degrees of desertification impact in the study area. Changes in soil particle size fractions can, to a certain extent, indicate the severity of soil desertification. The higher the CS content in soil, the more severe the soil desertification becomes, and the more frequent wind erosion and sand burial disturbances occur (Su et al., 2004; Xu et al., 2008). Vegetation cover in the study area exceeded 40.00% (Fig. S2), and disturbance from sand burial was greater than that from wind erosion. In this study, IL had the highest CS content, followed by FSL, while DS had the lowest. Therefore, IL had the deepest distribution of belowground buds, followed by FSL, while DS had the shallowest distribution. In addition, frequent human activities such as overgrazing and indiscriminate harvesting by digging in recent decades have severely affected plant growth, making belowground buds easily exposed in shallow soil layers. This impact of human activities may be another reason for the shallow bud distribution observed in DS (Klimešová and Klimeš, 2007; Dalgleish and Hartnett, 2009).

4.3 Factors affecting bud density

Aboveground vegetation and soil characteristics are recognized as the two primary drivers shaping bud bank dynamics (Rusch et al., 2011; Li et al., 2023).

In this study, habitat-specific population traits and soil physical-chemical properties influenced bud bank demography of *S. alopecuroides*. Our results indicated that soil CS, SOM, and PD were the principal factors influencing bud bank size and composition of *S. alopecuroides*. Specifically, horizontal rhizome buds showed greater dependence on soil CS content, whereas vertical rhizome buds were more dependent on SOM content and PD. Similar to rhizomatous grasses, the rhizomes of *S. alopecuroides* grow in both horizontal and vertical directions. Horizontal rhizomes have stronger expansion capacity and are responsible for spreading clones into benign patches to escape adverse ones, while vertical rhizomes primarily function to utilize local resources and maintain population persistence (Marbà and Duarte, 1998; van Kleunen and Fischer, 2001; Zhang et al., 2009). The clonal organ (rhizome, tiller, or root) on which buds are borne serves as an important indicator for characterizing resource acquisition potential of plants (Ott and Hartnett, 2012; Clarke et al., 2013; Klimešová et al., 2018). Buds on horizontal rhizomes are usually situated deeper in the soil and are mainly used to extend rhizomes (Combroux and Bornette, 2004). Soils with higher CS content reduce resistance to rhizome expansion. Thus, horizontal rhizome buds are more adaptive to IL with severe aeolian activities. In contrast, buds on vertical rhizomes are generally situated in the upper soil layer and primarily function in using local resources due to their limited expansion capacity. Vertical rhizome buds show greater sensitivity to nutrient content in surrounding habitats (Passioura, 1988). Thus, vertical rhizome buds are more adaptive to DS with abundant nutrient resources.

Numerous studies have demonstrated that vegetation density is a key factor influencing belowground bud bank density, although this effect varies and depends on specific habitat and bud bank types (Zhang et al., 2019; Qian et al., 2021; Wu et al., 2022; Te et al., 2025). For example, Wu et al. (2020) identified vegetation density as the primary determinant of bud bank dynamics in interdune lowlands of fixed sand dunes, with tiller buds showing stronger correlation with vegetation density. Our study also revealed that, in addition to SOM content, vertical rhizome buds were highly associated with PD.

Furthermore, SWC is the primary factor limiting plant growth and reproduction across the desert steppe zone (Alamusa et al., 2017). However, our study revealed that SWC contributed little to the belowground bud bank of *S. alopecuroides*. This limited contribution may be attributed to high vegetation coverage in the study area, which maintains elevated and relatively uniform soil moisture conditions (Wu et al., 2020). Therefore, SWC does not appear to be a key limiting factor for plant vegetative propagation in the study area. Similar conclusions were reported in analyses of the relationship between plant belowground bud banks and environmental factors in fixed dunes of Horqin Sandy Land in China (Zhang et al., 2019; Wu et al., 2020).

4.4 Limitations and prospects

Although this study characterized the density and vertical distribution of belowground bud banks of *S. alopecuroides* and preliminarily identified key environmental drivers, the results are subject to certain limitations. First, bud bank density is strongly influenced by factors such as precipitation and plant phenology, and therefore exhibits pronounced inter-annual and seasonal variability (Klimešová and Klimeš, 2007; Zhang et al., 2009; Ferraro et al., 2022; He et al., 2025). However, our analysis relied on a single static survey during the peak growing season, which limited our ability to capture dynamic patterns of bud bank gains and losses across seasons and years. Second, the use of RDA allowed us to examine only linear relationships between environmental factors and bud bank density, preventing deeper exploration of potential nonlinear responses and complex regulatory networks. Given these limitations, future work should incorporate continuous, multi-seasonal or multi-year monitoring to quantify how seasonal and inter-annual fluctuations shape bud bank density. In parallel, increasing sample size will improve statistical power needed for advanced analytical approaches such as structural equation modeling (SEM). Based on such datasets, we can use SEM to construct more comprehensive causal pathways linking soil properties and vegetation characteristics, thereby disentangling direct effects of soil properties on bud banks from indirect effects mediated by vegetation characteristics, and ultimately elucidating regulatory mechanisms underlying changes in *S. alopecuroides* bud bank density.

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5 Conclusions

The belowground bud bank of *S. alopecuroides* differed significantly among the three habitats and exhibited habitat-specific differentiation of horizontal and vertical rhizome buds across the desert steppe zone. Specifically, horizontal rhizome buds predominated in IL, where they were positively associated with soil CS content, suggesting adaptation for lateral expansion and resource foraging under frequent wind disturbance. In contrast, vertical rhizome buds were more abundant in DS, where they were positively associated with SOM content and PD, underscoring their role in local resource utilization and competitive persistence. This functional differentiation reflects a key adaptive mechanism supporting species persistence in heterogeneous desert environments. Accordingly, future desertification control and ecosystem management efforts should adopt habitat-specific strategies. In IL, maintaining higher CS content and reducing disturbance would facilitate lateral spread and sand stabilization; in DS, enhancing soil carbon would enlarge bud bank size, thereby strengthening vegetation resilience and stability.

Conflict of interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

Fig. S1 Spacer length (a), biomass (b), and biomass allocation (c) for *Sophora alopecuroides* L. in the three habitats. IL, interdune lowland; FSL, flat sandy land; DS, desert steppe. Lowercase letters indicate significant differences in spacer length, horizontal and vertical biomass, and biomass allocation among habitats at $P<0.05$ level, while uppercase letters indicate significant differences in total biomass (horizontal biomass+vertical biomass) among habitats at $P<0.05$ level. Bars are standard errors.

Fig. S2 Vegetation cover in the three habitats. Bars are standard errors.

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