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Mechanisms driving the impact of Wolf Poison (*Stellera chamaejasme*) in grasslands of China

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Abstract

The widespread distribution of wolf poison (*Stellera chamaejasme* L.), spanning from southern Russia to southwestern China and the western Himalayas, contributes to its prevalence as an invasive species in grassland ecosystems. Its extensive range, coupled with its ability to thrive in harsh environments, enables it to rapidly colonize grasslands. Once established, it rapidly spreads and dominates large areas. This process inevitably leads to grassland degradation over time, thereby exerting significant impacts on both ecology and economy. In China, grasslands (26.45 million hectares, 27.5% of land area) face severe degradation, with over 90% impacted by overgrazing and climate change. *S. chamaejasme* infestations exceed 1.4 million hectares in Qinghai, 546,700 in Gansu, and 133,000 in Inner Mongolia, causing annual forage losses of 137.5 million kg and economic damages of 15–20 million yuan in Gansu alone. These impacts threaten ecosystem stability and pastoral livelihoods.Therefore, research on the spread mechanisms of invasive plants is crucial. In this comprehensive description, we investigated the effects of *S. chamaejasme* on plant communities and herbivore interactions. Our research showed how this species successfully invades grasslands and establishes itself as a dominant species. *S. chamaejasme* enhances Its expansion alters soil physicochemical properties, reduces nutrient cycling, and increases pathogenic fungi abundance while enhancing microbial diversity, creating self-favoring soil conditions. With high genetic diversity, robust reproductive capacity, and potent allelopathic effects, it suppresses neighboring vegetation and escapes herbivory due to toxicity, accelerating invasion. These interrelated traits facilitate the rapid invasion and spread of *S. chamaejasme* on grasslands, ultimately leading to its dominance. This trend poses a significant threat to the health and stability of the grassland ecosystem. Future research should delve into the ecological adaptability and allelopathic mechanisms of *S. chamaejasme*, aiming to develop effective management strategies for controlling its spread and promoting grassland recovery and biodiversity conservation.

Keywords: Biological characteristics, Allelopathy, Soil Microbiota, Herbivore selection pressure

Introduction

Wolf poison or bloody-root stellera (*Stellera chamaejasme* L.) belongs to the genus *Stellera* in the family Thymelaeaceae. It is a perennial herbaceous plant (Zhang et al. 2010). According to the “Flora of China,” *S. chamaejasme* thrives in harsh environments, often found at higher altitudes on dry, sunny slopes of mountains and alpine grasslands. The plant forms dense clumps, produces nut-like fruits, and has a long lifespan (Li et al. 2019). Traditionally, *S. chamaejasme* has been used in Chinese medicine. its roots are employed for their bitter and neutral properties, believed to have effects such as antimicrobial, insecticidal, dispersing, diuretic, analgesic, and expectorant properties (Wu et al. 2014; Zhang et al. 2016). However, its marked toxicity induces acute poisoning in grazing animals, potentially leading to fatalities, with specific components, notably the stelleraterpenoids A-M class, exhibiting significant cytotoxic activity (Pan et al. 2021; You et al. 2018). Modern pharmacological studies have further revealed significant pharmacological activities associated with *S. chamaejasme*, including antibacterial and anti-inflammatory effects (Selenge et al. 2023), antiviral properties (Shahrajabianet et al. 2023), antitumor activity (Yu et al. 2022), and potential anticancer properties (Hang et al. 2022).

In grassland ecosystems, *S. chamaejasme* pose a significant challenge. Its robust root system, competitive strength, and high biomass allow it to outcompete other forage grasses for nutrients and space, inhibiting their growth. This negatively impacts grassland productivity and sustainable animal husbandry (Ninan et al. 2013). From 1970 to 2017, invasive plants caused direct global economic losses totaling $100.468 billion (Zhao et al. 2024). In China, (The Third National Land Survey of the State Council, 2021). where grasslands cover approximately 26.45 million hectares (27.5% of the total land area), over 90% of these grasslands have already experienced degradation due to factors like improper grazing and climate change. Specifically, the toxic invasive plant *S. Chamaejasme* has spread across 1.4 million hectares of natural grasslands in Qinghai Province, 546,700 hectares in Gansu Province, 133,000 hectares in Ar Horqin Banner of Inner Mongolia, and 32,300 hectares in Zhaosu County, Ili Prefecture, Xinjiang. Taking Gansu Province as an example, over 466,700 hectares of grassland have been affected by this species, leading to a loss of 137.5 million kilograms of grazing forage and economic damages estimated at 15–20 million yuan (Wang et al. 2015). Its biological characteristics and potent toxicity act as a protective barrier, deterring herbivores from consuming it, thereby granting it a competitive advantage over neighboring plants (He et al. 2019; Li et al. 2019). its allelopathic effects further contribute to its dominance (Song et al. 2023). The phenomenon of *S. chamaejasme* rapidly invading, expanding, and establishing dominance in grassland ecosystems due to its advantageous traits (Fig. 1) had occurred in grasslands in different regions (He et al. 2019; Javed et al. 2019; Wang et al. 2022; You et al. 2018).

The widespread distribution of *S. chamaejasme*, spanning from southern Russia to southwestern China and the western Himalayas, contributes to the prevalence of this phenomenon (Zhang et al. 2010; Zhang et al. 2015). Its impact on grassland ecosystems is severe, not only reducing productivity but also posing economic losses due to acute poisoning in livestock that consume it (Bellard et al. 2016; Murphy et al. 2014). Understanding the mechanisms behind this phenomenon is crucial for effective control measures and the restoration of degraded grasslands, supporting biodiversity conservation. This review aims to conduct a comprehensive description of the impacts of *S. chamaejasme* on plant communities and herbivore interactions, elucidating how this species successfully invades grasslands and becomes a dominant species, thereby providing a scientific foundation for the development of management strategies.

Impacts on Plant Communities

The General Impact of *S. chamaejasme*

S. chamaejasme significantly impacts local plant communities by altering the soil's physicochemical properties, microbial community structure, and enzymatic activity. These changes not only reshape the soil environment but also indirectly affect the growth and distribution of other plants. This ecological interaction is not only beneficial for the growth of *S. chamaejasme*, but also accelerates its expansion, which is one of the reasons why it can successfully invade grasslands (Fig. 2)

Soil Physicochemical Properties

Studies have shown that extracts and plant residues of *S. chamaejasme* have significant impacts on the soil environment. They can reduce electrical conductivity, nitrogen, and available phosphorus while increasing soil pH and total carbon content.

(Zhu et al. 2020). These alterations affect nutrient availability in the soil, subsequently influencing the growth of other plant species. Furthermore, as the *S. chamaejasme* community expands, soil microbes are affected by both nutrient depletion and secondary metabolites, leading to an increase in the content of organic matter, total nitrogen, and nitrate ions. This is conducive to the growth and spread of *S. chamaejasme*, while the levels of ammonium ions and soil pH are reduced. (Zhang et al. 2021). These findings suggest that *S. chamaejasme*, through its released secondary metabolites, not only suppresses other plant growth but also improves soil conditions to suit its own growth requirements. *S. chamaejasme* litter, by regulating soil temperature and moisture, affects seed germination and establishment. In degraded grasslands, seeds that are exposed or shallowly buried may disrupt seedling establishment and population development. (Xia et al. 2021). Furthermore, similar to other invasive plants, *S. chamaejasme*'s expansion disrupts nutrient cycling in rhizosphere soil, leading to reduced soil nutrient content and affecting soil microbial activity (Lu et al. 2019).

Typically, a plant's expansion exacerbates nutrient consumption from the external environment, resulting in soil impoverishment and decreased fertility. However, *S. chamaejasme* research reveals that it can alter soil nutrients through root exudates and litter, enhancing soil biological activity and accelerating nutrient transformation. This contributes to improved soil fertility, creating favorable conditions for *S. chamaejasme* growth and spread (An et al. 2016; Dan et al. 2021). Additionally, *S. chamaejasme*-inhabited soils exhibit higher organic nitrogen and microbial biomass, forming "fertility islands" that enhance its dispersal capacity (Crawford et al. 2017). Increased soil electrical conductivity may also promote *S. chamaejasme* invasion (Zhang et al. 2021).

Soil Microorganisms

Soil enzymes play a crucial role in soil ecosystems, participating in all carbon, nitrogen, and phosphorus cycling processes (Hu et al. 2016). Therefore, studying enzyme activity in the rhizosphere soil of plants is essential for understanding the microbial environment. Research indicates that during its growth and expansion, *S. chamaejasme* significantly influences soil enzymes (An et al. 2016). In the rhizosphere soil of *S. chamaejasme* during different growth seasons, enzyme activities related to sucrose, urease, and phosphatase are notably higher compared to vegetation-free soil. Interestingly, the activities of catalase and peroxidase vary during different growth stages of *S. chamaejasme* (An et al. 2016). Additionally, Cheng et al. (2022) found that secondary metabolites secreted by *S. chamaejasme* roots interact with soil enzymes. Notably, during the initial stages of *S. chamaejasme* coverage, the impact on soil enzyme activity is most pronounced.Rhizosphere bacteria play a vital role in nutrient cycling within soil ecosystems, significantly influencing plant health and soil fertility (Wu et al. 2015). As *S. chamaejasme* expands, it alters rhizosphere soil nutrient availability and bacterial community structure. The active participation of bacterial communities in carbon and nitrogen metabolism promotes plant growth under adverse conditions (Hu et al. 2023). Research reveals that *S. chamaejasme* rhizosphere soil harbors a greater diversity of bacterial and fungal species compared to non-Stellera areas (Dan et al. 2021). Notably, the fungal community structure in rhizosphere soil differs significantly from endophytic fungi (Jin et al. 2015). Nakamura et al. (2023) found distinct differences in fungal and bacterial communities between invasive plant leaves, roots, soil, native, and exotic distributions. This suggests that invasive plants, including *S. chamaejasme*, may influence soil microbiota through root and leaf interactions, potentially favoring their own growth and expansion. Furthermore, Jin et al. (2018) discovered that *S. chamaejasme* rhizosphere and root-associated bacteria include Actinobacteria and Proteobacteria, which can produce hormones like gibberellins and auxins. These bacteria play essential roles in various processes, such as antibiotic production, bioactive compound synthesis, secondary metabolite production, phosphate solubilization, nitrogen fixation, and promoting plant growth (Gan et al. 2017; Sánchez-Gil et al. 2023).

They also exhibit significant biocontrol effects against a range of plant pathogens (Anwar et al. 2016). These interactions favor *S. chamaejasme* growth and expansion. Additionally, Bao et al. (2020) reported that the biomass and diversity index of *S. chamaejasme* patches were higher than those outside the patches. This aligns with Cui et al. (2020) findings that high-density *S. chamaejasme* growth positively influenced microbial composition in rhizosphere soil, resulting in higher microbial diversity. Jin et al. (2024) explored *S. chamaejasme* and its companion grasses (*Stipa purpurea* and *Polygonum viviparum*) and found that *S. chamaejasme* rhizosphere tends to harbor dominant bacterial communities, enhancing microbial diversity and richness. Compared to associated grasses, the fungal community in *S. chamaejasme* rhizosphere significantly decreased. Furthermore, the addition of *S. chamaejasme* litter positively impacted soil nutrient availability, although it had detrimental effects on arbuscular mycorrhizal fungi (AMF) in rhizosphere soil due to changes in nutrient balance and allelopathic compounds (Guo et al. 2022).

In their extensive investigation of microbial communities associated with three invasive weed species in North American grasslands, Gibbons et al. (2017) discovered that invasive species can gain an advantage by altering soil community structure. *S. chamaejasme* has the ability to modify the soil nitrogen-fixing microbial community structure in grasslands, resulting in changes in the relative abundance of rhizobial species (Zhang et al. 2021). Furthermore, research indicates that in soils invaded by *S. chamaejasme*, nitrogen, phosphorus, organic matter, fungal alpha diversity, and arbuscular mycorrhizal fungi (AMF) relative abundance are lower, while pathogenic fungi abundance is higher (He et al. 2019). In plant communities, a high relative abundance of fungal pathogens can negatively impact plant growth. However, *S. chamaejasme* contains flavonoids such as neochamaejasmin B, chamechromone, and isochamaejasmin, which can protect the plant from these pathogens. (Yan et al. 2015). Consequently, in soils with a high incidence of pathogens, *S. chamaejasme* may have a competitive advantage over coexisting species. This phenomenon is reminiscent of Canada thistle [*Cirsium arvense* (L.) Scop.], which influences local plant growth through soil microbiota pathways (such as pathogen accumulation), promoting its own expansion (Verbeek et al. 2019). For dominant plant species, they can gain a competitive growth advantage by modifying the soil microbial composition through increasing pathogen abundance. This alteration specifically inhibits the normal growth of neighboring plants while allowing themselves to remain unaffected due to their protective secondary metabolites that confer resistance against these pathogens., Tang et al. (2023) found that *S. chamaejasme* harbors a diverse endophytic fungal community, with most species exhibiting plant-growth-promoting (PGP) activity. This plays a crucial role in the rapid spread of *S. chamaejasme* in degraded grasslands. Additionally, a comparison of ammonia-oxidizing bacteria (AOB) communities in *S. chamaejasme* and Dahurian wild rye (*Elymus dahuricus* Turcz. Ex Griseb.) soils by Ma et al. (2020) revealed slower soil nitrification in *S. chamaejasme* soils compared to those under *E. dahuricus*. Reduced soil nitrification can lead to conservative nitrogen cycling, potentially conferring greater competitiveness to plants. This may partly explain why *S. chamaejasme* thrives as a dominant species in degraded grasslands.

S. chamaejasme significantly impacts soil ecosystems through secondary metabolites secreted by its roots and leaf litter. These compounds not only alter soil microbial community structure, influencing the growth of specific microorganisms, but also affect soil physicochemical properties such as pH, electrical conductivity, and nutrient content. Consequently, they impact nutrient availability and microbial survival in the soil.

Impacts Through Resource Competition

Environmental Adaptability

S. chamaejasme, a perennial herbaceous plant in the Thymelaeaceae family, as a perennial herbaceous plant possesses a well-developed root system that allows it to thrive even in adverse conditions. The roots can penetrate deep into the soil (with depths ranging from 10 cm for one-year-old plants to 60-100 cm for four-year-old plants), enabling efficient nutrient absorption (Li et al. 2019). Zhang et al. (2024) highlighted that certain root system characteristics, such as a deep root architecture, play a crucial role in crops' effective absorption of water and nutrients under arid conditions. The root system of *S. chamaejasme* aligns with this trait, suggesting that a developed root structure is beneficial for plants to adapt to adverse environments. Additionally, some invasive plants outperform native species in nutrient acquisition through their root systems (Chen et al. 2022). Thus, *S. chamaejasme* 's robust root system not only supports its growth but also facilitates successful establishment and spread in new environments.

S. chamaejasme’s lanceolate leaves are covered by a thick waxy layer, enabling them to withstand prolonged drought. Unlike other plants that wither under extreme dry conditions, *S. chamaejasme* remains lush and vigorous (Lee et al. 2015). The narrow shape of its leaves, combined with the waxy surface, significantly reduces water loss, enhancing its survival in arid environments (Guo et al. 2016). Consequently, *S. chamaejasme* exhibits strong tolerance to adverse conditions, allowing it not only to survive but also to reproduce rapidly and spread. Research suggests that invasive species often display superior drought resistance compared to native plants, contributing to their competitive advantage (Javed et al. 2019; Sun et al. 2022).

As altitude increases, *S. chamaejasme* exhibits correlated changes in flower and leaf size and quantity. This reflects its adaptive strategies during long-term interactions with diverse environments, allowing it to thrive even in unstable growth conditions (Zhang et al. 2014). These traits align with the patterns observed in invasive species within plant communities. Invasive species often maximize light capture and photosynthetic efficiency through larger branches and higher specific leaf area (SLA). They also allocate more nitrogen (N) to photosynthesis-related processes, enhancing their competitive advantage (Dyderski et al. 2019; Musso et al. 2021). *S. chamaejasme*'s resilience after drought further contributes to its success in competitive environments (Zhang et al. 2023).

In the context of ecological adaptation, *S. chamaejasme* exhibits remarkable adaptability in both root characteristics and leaf traits. Furthermore, it demonstrates resilience in adverse environments. These features not only underscore the plant’s high environmental adaptability but also reflect its endurance under challenging conditions.

Consequently, even when soil nutrients are disrupted by external factors such as human activities or climate change, *S. chamaejasme* maintains normal growth, development, and physiological functions. Moreover, this adaptability ensures a competitive advantage for *S. chamaejasme* in resource-limited environments, facilitating its sustained growth and expansion on degraded grasslands. Ultimately, this phenomenon contributes to the occurrence and enhancement of “grassland poisoning” by the *S. chamaejasme* plant

High Reproductive Capacity

S. chamaejasme forms clumps with multiple stems. At the top of each stem, it produces crown-shaped inflorescences. This plant exhibits robust seed production, with mature individuals yielding around 200 seeds per plant (Zhao et al. 2011). This prolific seed production capability facilitates extensive reproduction and rapid spread of *S. chamaejasme* (Li et al. 2019). Notably, these seeds possess remarkable resilience, even when subjected to adverse conditions over several years. The protective features of *S. chamaejasme* seeds contribute to their survival. Their hard, thick seed coat shields them from external pressures such as physical damage, cold, and drought (Li et al. 2019; Wu et al. 2014). Sharma et al. (2022) found that invasive species often exhibit high expansion potential due to their ability to produce abundant, long-lasting viable seeds in the soil.

The species relies on seed dispersal for population expansion. Its dispersal pattern is characterized as "near-mother dispersal" (Li, 1995), where seeds typically fall around the mother plant, forming seed clusters. Subsequently, external forces cause seed displacement within the soil surface, gradually dispersing or homogenizing them. Notably, *S. chamaejasme* lacks long-distance dispersal ability (Luo et al. 2021). All the plant parts in *S. chamaejasme* (root, stem, leaf and flower) are toxic. This toxicity serves as an effective natural defense mechanism, deterring herbivores from consuming it (Zhao et al. 2013). Interestingly, despite its overall toxicity, *S. chamaejasme* still attracts pollinators. Research indicates a mutualistic relationship between *S. chamaejasme* and flower thrips (Thysanoptera), where pollination success is limited by pollinator availability rather than pollen availability (Zhang et al. 2021). Therefore, the pollen dispersal of *S. chamaejasme* relies not only on traditional external forces (wind, water, animal activity) but also benefits from unique biological traits that provide additional pathways for dissemination. As a toxic plant, *S. chamaejasme* faces a lower risk of herbivore consumption, which, to some extent, limits its reproductive opportunities (as animals typically avoid pollinating toxic plants). However, *S. chamaejasme* naturally circumvents this limitation. Its toxicity not only reduces the likelihood of herbivore consumption but also attracts specific pollinators, providing robust support for its reproduction and spread. The clumped growth structure of the stems allows *S. chamaejasme* to dominate spatially, reducing competition with other plants. Additionally, the crown-shaped inflorescences enhance pollination efficiency, significantly increasing the chances of successful pollination (Huang et al. 2014). Despite its seed dispersal mode being "near-mother distribution," this localized dispersal benefits the growth of *S. chamaejasme* seedlings. The soil conditions around the mother plant often support seed germination and seedling growth, promoting healthy seedling development (Peng et al. 2004). Furthermore, mature *S. chamaejasme* plants provide protection to seedlings during their growth (Wang et al. 2022). The species' ability to rapidly produce numerous offspring gives it a competitive advantage, allowing efficient acquisition of critical resources such as light, water, and nutrients. Moreover, its rapid reproductive and dispersal capacity enables it to spread to broader geographical areas within a short time. This not only facilitates rapid colonization of ecological niches and space in new locations but also helps establish stable populations.

High Genetic Diversity

Genetic analysis of the chloroplast genome of *S. chamaejasme* reveals unique adaptive evolutionary features compared to closely related species (Yun et al. 2019). Using amplified fragment length polymorphism (AFLP) markers, researchers have explored the genetic diversity and population structure of *S. chamaejasme*. The results indicate significant genetic differentiation among populations and relatively low gene flow, suggesting that this species is developing distinct genetic traits to adapt to its environment (Zhang et al. 2015). Rana et al. (2024) investigated the effects of Quaternary climate change and glaciation on the genetic diversity of *S. chamaejasme*, emphasizing the role of high altitude and environmental heterogeneity in the development of cryptic species within it. Their research sheds new light on the plant's high genetic diversity and the interplay between this diversity and environmental heterogeneity. This interplay allows the plant to adapt to varied environments and may explain its rapid spread on degraded grasslands. Similarly, another invasive plant, East Asian buttercup (*Ranunculus japonicus*, Thunb), also exhibits high genetic diversity, enabling it to maintain stable populations even under adverse conditions such as increasing altitude and environmental degradation (Yu et al. 2023). Additionally, real-time quantitative polymerase chain reaction (QRT-PCR) analysis of *S. chamaejasme* demonstrates stable gene expression under various abiotic stress and hormone treatments, further explaining its adaptive capacity to environmental changes (Liu et al. 2018).

Studies have also revealed floral color polymorphism in *S. chamaejasme*. High genetic diversity (h(T) = 0.834) and population differentiation (N(ST) = 0.997 and G(ST) = 0.982) indicate restricted gene flow among populations, reflecting significant geographic or environmental isolation. This underscores *S. chamaejasme* 's remarkable adaptability to different environments (Zhang et al. 2010). Recent research further reveals four distinct genetic lineages of *S. chamaejasme* in the Qinghai-Tibet Plateau and northern China, corresponding to different environmental distributions. Highly divergent adaptive evolution genes are widely distributed both within and outside genomic islands, closely associated with local adaptation (Hu et al. 2022). Moreover, studies by Wan et al. (2022) demonstrate that increasing plant genetic diversity decreased the performance of plant antagonists, while increasing the performance of plants and natural enemies of herbivores. Similar findings in the study of seed production in Austrian dragonhead (*Dracocephalum austriacum* L.) by Dostálek et al. (2023) highlight the advantages of high genetic diversity.

Impacts Through Allelopathy

Allelochemicals Of *S. Chamaejasme*

Guo et al. (2015) identified seven allelochemicals in the roots of *S. chamaejasme* (Fig. 3), namely umbelliferone, chamechromone, daphnoretin, isoneochamaejasmin A, neochamaejasmin B, dihydrodaphnodorin B, and 7-methoxylneochaejasmin. Among these, five allelochemicals are found in higher concentrations in the roots and rhizosphere soil (Jin et al. 2022). Research indicates that umbelliferone may be the primary allelochemical in *S. chamaejasme*, and its degradation plays a crucial role in competition with other plants (Guo et al. 2015).

Allelopathy Of *S. Chamaejasme*

Allelopathy is one of the important reasons why *S. chamaejasme* can spread on a large scale on grasslands. This term refers to the ability of plants to inhibit the growth of surrounding plants by releasing specific chemicals (MACÍAS et al. 2023; Wang et al. 2022) into the growth medium. The pathways through which *S. chamaejasme* releases these allelopathic substances mainly include: (1) rainwater leaching (Fernandez et al. 2016); (2) the decomposition of plant residues (Kong et al. 2019); and (3) root exudates (Weston et al. 2013) (Fig. 4). At present, research on the allelopathic effects of *S. chamaejasme* mainly focuses on simulating these release pathways to further explore the specific mechanisms of its allelopathic effects.

S. chamaejasme exhibits allelopathy through its roots, stems, leaves, and pollen. Several studies have simulated the release pathways of allelochemicals from *S. chamaejasme*, revealing that the allelochemicals impact generally increases with the quantity of its root, stem, and leaf material. For instance, Wang et al. (2009) found that Aconitum's allelopathy on sweetclover (*Melilotus suaveolens* Ledeb.) and perennial ryegrass (*Lolium perenne* L). intensified with increasing root, stem, and leaf biomass. Similarly, Wei et al. (2020) observed enhanced allelopathy in lettuce as the concentration of Canada goldenrod (*Solidago canadensis* L.) leaf extracts increased. Notably, *S. chamaejasme*'s allelopathic impact on certain receptor plants exhibits a "low promotion, high inhibition" phenomenon (Liu et al. 2019; Liu et al. 2022). Studies on alfalfa (*Medicago sativa* L.) and Daurian wild rye revealed that the allelopathy of *S.*

chamaejasme displayed this pattern (Li et al. 2022).

Cheng et al. (2017) investigated high-altitude alpine meadow plants on the Qinghai-Tibet Plateau and found that *S. chamaejasme* root extracts generally exhibited stronger allelopathy than stem and leaf extracts. This aligns with the results from Wang et al. (2022) in alpine meadows. However, other studies suggest that *S. chamaejasme* stem and leaf allelopathy may surpass that of the roots. For instance, Liu et al. (2022) discovered that high-concentration *S. chamaejasme* stem leaf infusions had a stronger inhibitory effect on German garlic (*Allium senescens* Thunb.) seed germination and seedling growth compared to root infusions. These differences may be related to varying sensitivities of receptor plants to allelochemicals, resulting in inconsistent responses to the same allelopathic substance. Additionally, Sun et al. (2010) found that *S. chamaejasme* pollen extracts significantly inhibited seed germination and fruit set. Similarly, the pollen of invasive plants like jewelweed can also exhibit allelopathic effects, inhibiting neighboring plant seed germination and growth (Beans et al. 2015). Furthermore, Cheng et al. (2017) observed that *S. chamaejasme*'s allelopathic effects were positively correlated with plant age, suggesting that allelochemical content generally increases with plant age and decreases with organ senescence.

Elymus dahuricus and crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] exhibit some tolerance to *S. chamaejasme* allelopathy, making them suitable grass species for restoring grassland vegetation invaded by *S. chamaejasme* (Liu et al. 2019). This finding highlights differences in allelopathy across different *S. chamaejasme* plant parts and varying tolerance levels among different plant species. Uddin et al. (2020) also observed similar phenomena in interactions between native and invasive plants, suggesting coevolution of tolerance. This implies that the relationship between *S. chamaejasme* and neighboring plants may involve a coexistence pattern rather than unidirectional competition. Furthermore, the intensity of *S. chamaejasme*'s allelopathy depends not only on the source organ (roots, stems, or leaves) but also on the specific allelochemicals type. This also explains why the *S. chamaejasme* can gradually become a "dominant species" from a "companion species" on the grassland, without completely replacing other plants.

Impact of Herbivores on *S. chamaejasme*

Research indicates that herbivore diversity in grassland ecosystems, including grazing livestock, wildlife, insects (Gao et al. 2022; Yue et al. 2021), has multifaceted effects. These herbivores play a role in both promoting the spread of invasive plants and driving grassland degradation, ultimately leading to *S. chamaejasme* becoming a dominant species (Fig. 5). Huang et al. (2012) found that invasive plants, compared to native species, suffer less damage from herbivores. This difference may be attributed to characteristics of their leaf composition, such as lower concentrations of cellulose, hemicellulose, lignin, and carbon, as well as lower leaf density and carbon-to-nitrogen ratio, while maintaining higher nutrient content (Beans et al. 2015). Notably, herbivores do not always choose based on preference when faced with *S. chamaejasme* and other plants. *S. chamaejasme* is toxic throughout its entire plant, and grazing livestock may be poisoned by inhaling its pollen or experiencing allergic dermatitis upon contact. The toxic compounds include neochamaejasmin B, umbelliferone, and chamechromone, making livestock generally avoid consuming fresh *S. chamaejasme* (Gillmeister et al. 2019; You et al. 2018; Yan et al. 2014). However, under extreme hunger conditions in early spring, livestock may accidentally ingest *S. chamaejasme* seedlings and become poisoned. The selective pressure exerted by herbivores on *S. chamaejasme* consumption leads to the depletion of valuable forage grasses, disruption of the reproductive cycle of perennial grasses, and reduced seed bank density (Gao et al. 2022; Li et al. 2018). Meanwhile, the seeds banks of toxic weeds such as *S. chamaejasme* now dominate, making the restoration of degraded grasslands significantly more challenging. (Zhao et al. 2010). Surprisingly, *S. chamaejasme*'s toxicity indirectly benefits its growth and spread by reducing herbivore consumption, resulting in increased organic carbon content in the soil microaggregates around its roots (Zhou et al. 2023). Cheng et al. (2014) discovered that *S. chamaejasme* not only protects itself from herbivore interference but also serves as a biological refuge for neighboring plants, safeguarding plant diversity from excessive grazing by livestock.

The impact of herbivores on *S. chamaejasme* population distribution and expansion is complex. During heavy grazing or overgrazing, *S. chamaejasme* tends to exhibit aggregated distribution patterns, likely due to mutual protection within these clusters, allowing the population to withstand external pressures and stabilize (Zhao et al. 2010). However, as grazing intensity increases, grassland degradation intensifies, and *S. chamaejasme* transitions from a companion species to a dominant one. Consequently, its distribution pattern may shift from aggregated to random or uniform, reflecting adaptive responses and ecological niche expansion (Bao et al. 2019). Early-stage *S. chamaejasme* expansion typically involves aggregated distribution within patches centered around mature individuals, with random or uniform distribution within patches. As the number of mature individuals increases, intraspecific competition becomes dominant (Ren et al. 2013). Grazing activities may accelerate this transition, promoting patch enlargement, fusion, and an overall increase in patch numbers, driving *S. chamaejasme* population spread (Gao et al. 2019; Ren et al. 2013). These findings highlight the intricate interplay between herbivore activity and *S. chamaejasme* population dynamics, crucial for understanding *S. chamaejasme* 's ecological spread in grassland ecosystems.

Conclusion

This article outlines the factors contributing to the successful invasion and subsequent dominance of *S. chamaejasme* in grassland ecosystems. By releasing secondary metabolites, *S. chamaejasme* modifies the soil environment, thereby reinforcing its dominant status. With a robust vitality and an exceptional reproductive capacity, *S. chamaejasme* has secured a competitive edge within these ecosystems. Notably, *S. chamaejasme* exhibits significant allelopathy, secreting allelochemicals through three main pathways that affect the growth and development of surrounding plants. Its strong allelopathic effects on a broad spectrum of plants endow *S. chamaejasme* with formidable invasive and expansion capabilities in novel environments. By inhibiting the growth of neighboring flora, it diminishes the diversity of species within the ecosystem, which in turn aids in its own propagation and strengthens its competitive position. The toxic properties of *S. chamaejasme* also reduce herbivore consumption, easing natural control pressures, and enabling widespread growth and swift expansion, which in turn accelerates its invasion. As a result, the characteristics and behaviors of *S. chamaejasme* present considerable challenges to the health and stability of grassland ecosystems. To address this challenge, future research should focus on several key areas:1. The sequential relationship between invasion and grassland degradation: A systematic investigation is needed to determine whether grassland degradation is a prerequisite for *S. chamaejasme* invasion, or if the invasion itself triggers degradation. 2. Ecological adaptation and allelopathic mechanisms: In-depth exploration of *S. chamaejasme* 's ecological adaptation mechanisms, including its responses to various environmental stressors and the specific pathways and mechanisms of allelopathic substance release. 3. Long-term effects on soilenvironment: Investigate the long-term effects of *S. chamaejasme* on soil physicochemical properties and microbial community structure. Consider changes in soil nutrient cycling, microbial diversity, and enzyme activity. 4. Herbivore-plant interactions: Systematically study the impact of herbivores on *S. chamaejasme* population dynamics and potential effects of *S. chamaejasme* on herbivore behavior. This includes herbivore preferences, seasonal feeding behavior, and their influence on *S. chamaejasme* growth and reproduction. 5. Integrated management strategies: Develop and evaluate comprehensive management strategies for *S. chamaejasme*, including biological control, chemical treatments, and ecological restoration methods. These strategies should consider cost-effectiveness, sustainability, and potential ecosystem impacts. 6. Ecological restoration and biodiversity conservation: Research techniques for restoring grassland ecosystems invaded by *S. chamaejasme* and enhance biodiversity and ecosystem resilience. This involves selecting appropriate native plant species for vegetation reconstruction and assessing the long-term effects of different restoration measures. Through in-depth research on these critical issues, we can more effectively control the spread of *S. chamaejasme*, promote the restoration of degraded grasslands, and protect and maintain the health and stability of the grassland ecosystem

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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.

Data Availability

Data will be made available on request.

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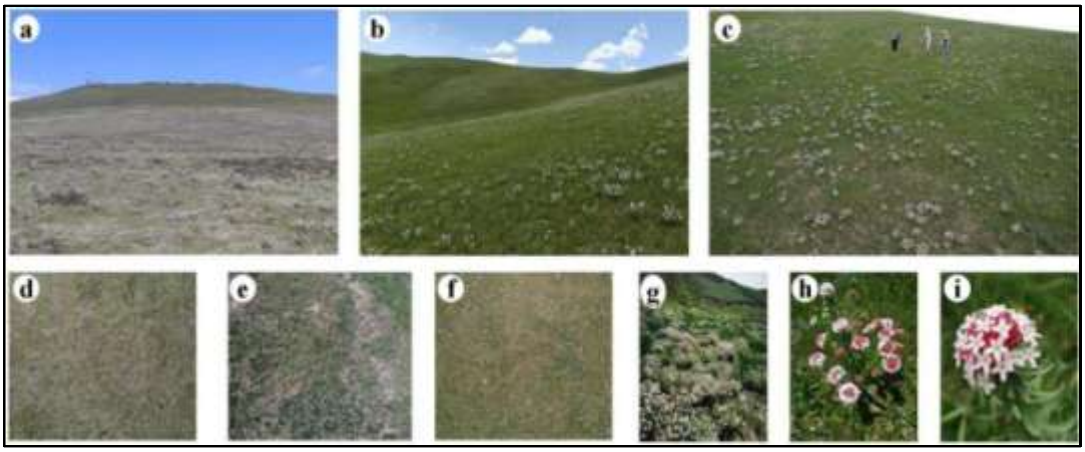

Fig. 1: *S. chamaejasme* invades different grasslands in the Qilian Mountains (a-c habitat: Kang le Grassland, Shan dan Military Horse Farm in Zhangye, City Xi shui Nature Reserve Station; d-f drone image; g-i individual).

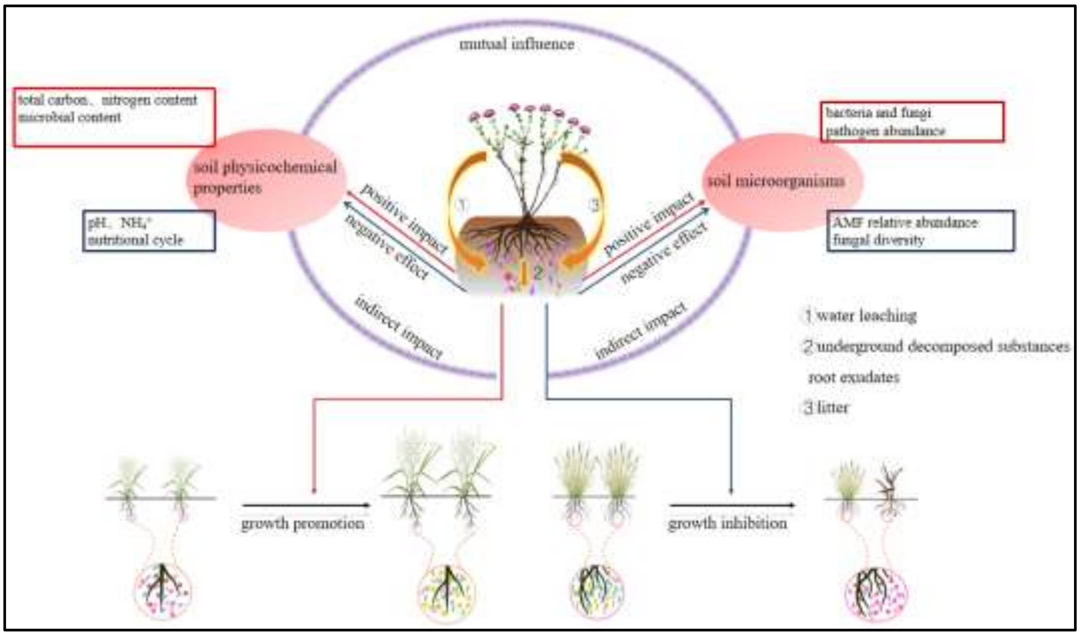

Fig. 2: Mechanisms of *S. chamaejasme* impact on plants through soil factors (AMF; arbuscular mycorrhizal fungi).

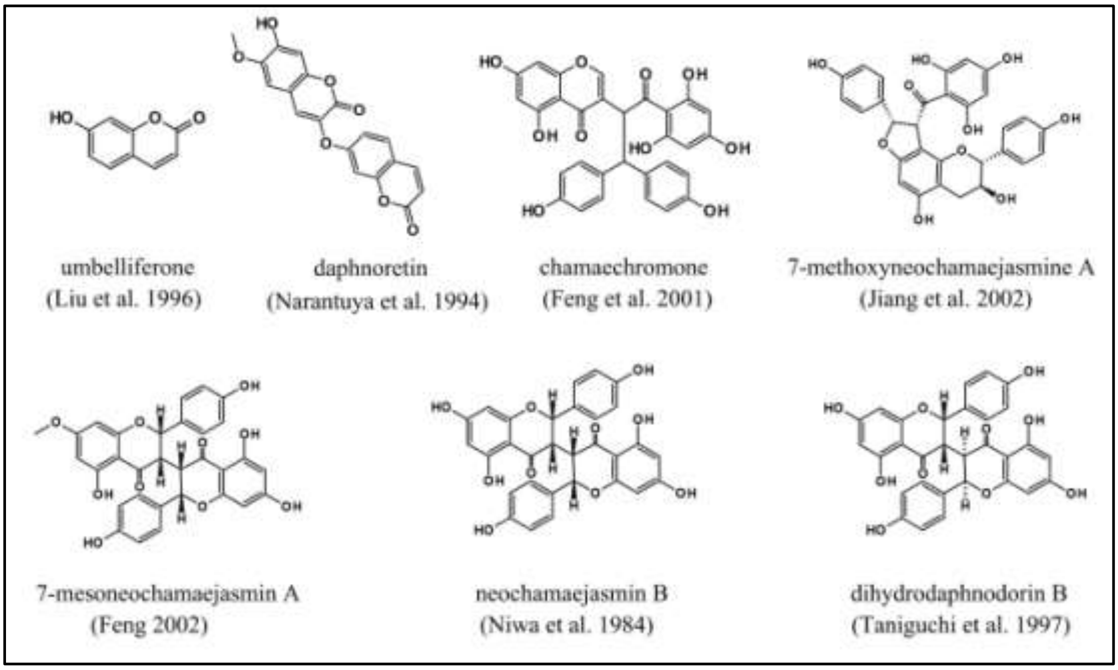

Fig. 3: Main allelochemicals from *S. chamaejasme.*

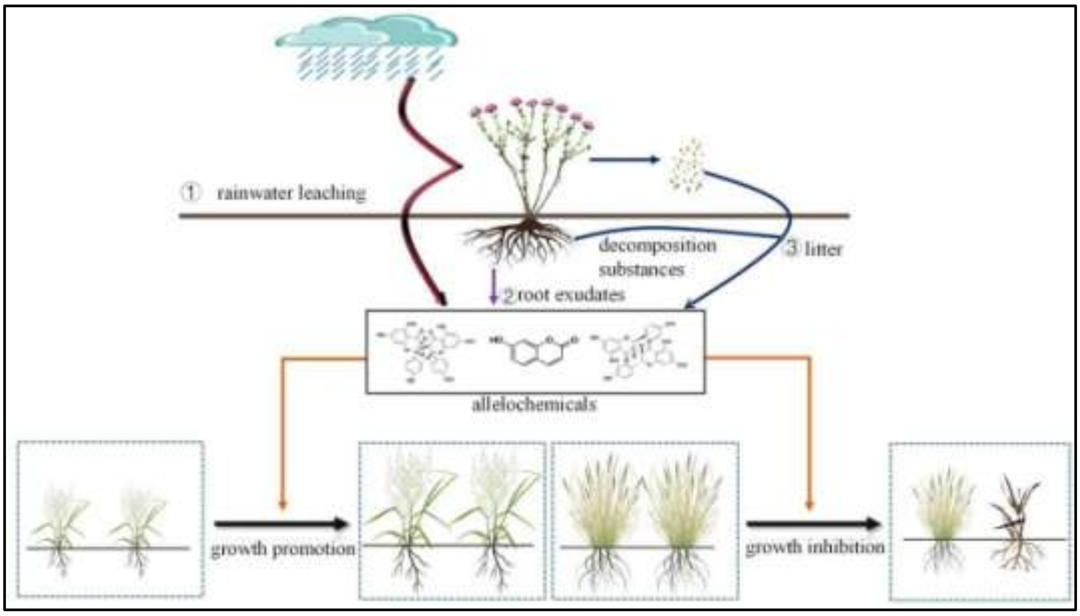

Fig. 4: Release pathways and allelopathy mechanisms of allelochemicals from *S. chamaejasme.*

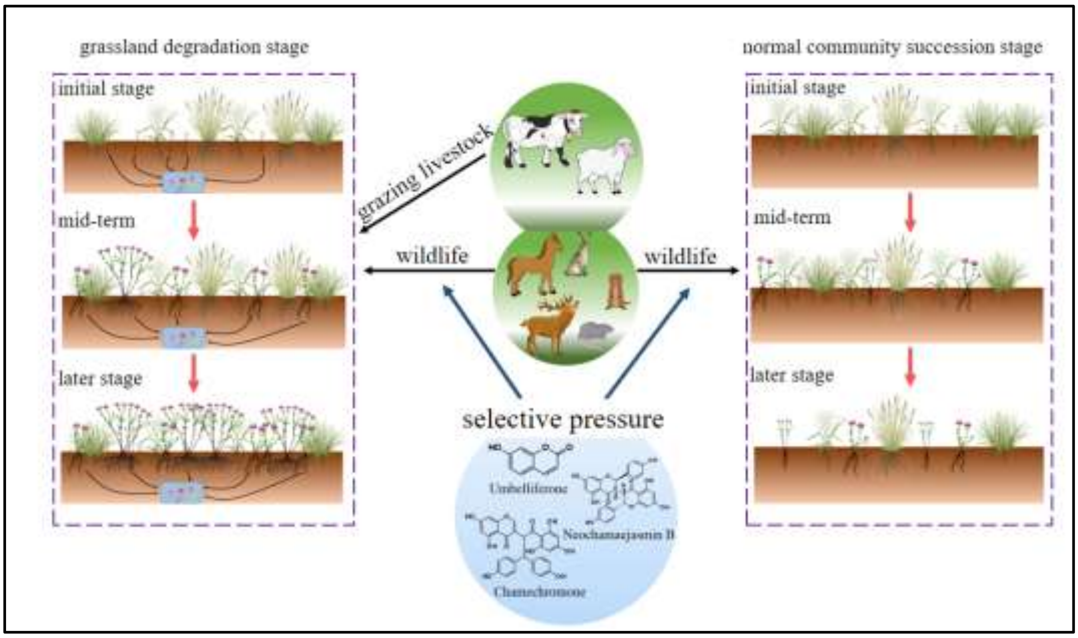

Fig. 5: Dynamic changes in *S. chamaejasme* community succession under herbivore selective pressure.