Soil heterogeneity mediates nutrient feedbacks between the malignant invasive alien species Solanum rostratum and replacement control plants

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Soil heterogeneity mediates nutrient feedbacks between the malignant invasive alien species *Solanum rostratum* and replacement control plants

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Abstract

Background: Plant replacement control is an important ecological approach for managing the invasive weed *Solanum rostratum*, yet its effectiveness is strongly mediated by soil conditions. However, current screening of replacement species often overlooks how soil heterogeneity alters competitive outcomes and plant–soil nutrient feedbacks, limiting the stability and general applicability of this approach. We conducted a two-factor pot experiment using soils collected from typical regions in China where *S. rostratum* is widely distributed. Monocultures and mixtures of *S. rostratum* and six native forage species were established. Plant biomass and chlorophyll content were measured, competitive effects were quantified using the log response ratio (lnRR), and redundancy analysis was used to link plant performance with soil nutrient dynamics.

Results: Mixed planting consistently suppressed *S. rostratum* across all soils (lnRR < 0), although the magnitude of suppression and the most effective replacement species varied markedly among soil types. Soil nutrient variation explained 30.69% of the variation in *S. rostratum* traits. *Leymus chinensis* and *Festuca arundinacea* showed greater competitiveness in soils with higher organic

matter or nitrogen availability, whereas *Medicago sativa* and *Agropyron cristatum* exerted stronger suppression where plant performance was closely associated with changes in nutrient availability. Notably, *M. sativa* maintained relatively stable suppressive effects even under nutrient-poor conditions.

Conclusion: Our results demonstrate that replacement control efficacy is jointly regulated by species-specific competitive ability and soil nutrient feedbacks under heterogeneous soil conditions. These findings highlight the importance of matching replacement species to soil environments to achieve stable and effective ecological control of *S. rostratum*.

Keywords: Invasive alien plant management; Plant replacement control; Soil heterogeneity; Plant-soil feedback; Interspecific competition

1. Introduction

Solanum rostratum, native to Mexico and the Midwestern United States, is a highly aggressive invasive alien plant worldwide. In recent decades, it has rapidly expanded to more than 30 countries and regions across North America, Oceania, Europe, Asia, and Africa [1–3]. This species can invade diverse habitats such as grasslands, riparian zones, abandoned farmlands, and overgrazed pastures, posing serious threats to agricultural production, rangeland livestock systems, biodiversity, and human health. Conventional control approaches, such as mechanical removal and herbicide application, are often inadequate for long-term suppression due to the plant's broad tolerance and high reproductive capacity[4].

Given the limited durability of traditional control measures, more ecologically sound and sustainable management strategies for *S. rostratum* are urgently needed. Plant replacement control has emerged as a promising eco-friendly approach in invasive plant management [5, 6]. Grounded

in interspecific competition and community succession theory, this strategy introduces competitive native species—often with ecological or economic value—to pre-empt resources and suppress the growth and spread of invasive plants, thereby facilitating the recovery of ecosystem structure and function in invaded habitats [7, 8]. Compared with chemical and mechanical methods, replacement control is generally considered more environmentally safe, potentially more sustainable, and relatively cost-effective. Its long-term success hinges on the ability of replacement species to maintain a persistent competitive disadvantage for the invader in resource acquisition [9, 10].

Interspecific plant competition largely involves the acquisition of limiting soil resources, particularly the efficiency and strategies of obtaining and using key nutrients such as nitrogen, phosphorus , and potassium [11]. Nitrogen occurs in multiple inorganic forms in soils, and plant species often differ markedly in their preferences and uptake efficiencies for specific N forms. Such differences can directly shape competitive advantages under particular soil conditions [12, 13]. In addition, available P, available K, and soil organic matter can influence plant growth and competitive intensity by regulating the degree of nutrient limitation, microbial activity, and soil nutrient buffering capacity [14–17]. Therefore, quantifying NH_4^+-N, NO_3^--N, available P, available K, and SOM provides a useful basis to evaluate how invasive and replacement species jointly affect soil nutrient pools and nutrient availability under different competitive contexts.

Plant-soil feedback (PSF)—the process by which plants alter soil properties and nutrient status, thereby affecting plant growth—is a key mechanism regulating interspecific competition and community assembly [18, 19]. Previous studies have shown that invasion by *S. rostratum* can substantially alter SOM, NH_4^+-N, NO_3^--N, and total N, although both the direction and magnitude

of these changes vary among regions [20]. This spatial inconsistency suggests that *S. rostratum* may regulate soil nutrient processes in an environment-dependent manner and may generate differentiated nutrient feedbacks under contrasting soil conditions, thereby reshaping its competitive interactions with native plants. Most studies to date, however, have emphasized competition outcomes in terms of biomass or growth traits, whereas the plant-soil interaction processes underlying replacement control—especially soil nutrient feedback effects—remain less explored. In particular, systematic assessments of how *S. rostratum* and replacement species jointly influence soil nutrient feedbacks under replacement-control scenarios are still limited.

Soil heterogeneity, a fundamental feature of terrestrial ecosystems, arises from variations in nutrient supply, transformation rates, and microbial processes [21, 22], which in turn fundamentally shape plant growth and interspecific competition [23]. In practice, the performance of replacement control is highly dependent on habitat conditions as plants exhibit significant phenotypic plasticity across different soils. Nevertheless, current replacement control programs frequently neglect the capacity of candidate replacement species to cope with soil heterogeneity. Such oversight can result in limited suppressive effects under specific soil conditions, thereby constraining the technique's overall stability and broad applicability. Therefore, systematically evaluating competition between invasive and replacement species, together with their soil nutrient feedbacks under heterogeneous soils, is essential for improving the reliability of replacement control. To capture soil heterogeneity within a controlled experimental framework, we selected eight soils collected from representative regions in China where *S. rostratum* is widely distributed. These soils differ substantially in key properties, including nutrient availability, texture, and organic matter content, thereby providing a robust basis to examine how soil conditions mediate

plant competition and nutrient feedbacks.

In addition, asymmetric competition represents a common mode of interspecific competition, in which unequal resource capture allows dominant individuals to acquire a disproportionate share of resources and exert stronger suppression on subordinate individuals [24, 25]. In replacement control practice, increasing the proportion of replacement plants can intentionally strengthen asymmetric competition, keeping invasive plants persistently disadvantaged in resource acquisition. However, whether different replacement species can establish stable asymmetric competitive advantages under contrasting soil conditions—and whether such advantages are amplified or weakened through shifts in soil nutrient processes—remains insufficiently understood. Under these heterogeneous soil conditions, represented by soils collected from representative regions in China where *S. rostratum* is widely distributed, we established both monoculture and mixed-planting treatments involving *S. rostratum* and six forage species. We measured plant phenotypic traits (chlorophyll content, biomass, and root: shoot ratio) and key soil properties (NH_4^+-N, NO_3^--N, available P, available K, and soil organic matter). To quantify competitive outcomes and associated soil nutrient feedbacks across soil types, we calculated the log response ratio (lnRR) for *S. rostratum* biomass. This metric compares its biomass in mixture to that in monoculture within each soil type, providing a standardized measure of the suppressive or facilitative effects exerted by replacement species.

Specifically, this study aimed to: (1) characterize the variation in *S. rostratum*'s performance and competitive outcomes across heterogeneous soil backgrounds; (2) elucidate how soil physicochemical properties and nutrient composition regulate the competitive ability of replacement species, thereby altering the invader's competitive status through soil nutrient

feedbacks; and (3) compare the suppressive effects of different forage species across multiple soil types to identify broadly applicable and stable replacement candidates under soil heterogeneity. Overall, our findings provide a mechanistic basis for understanding plant-soil nutrient feedbacks associated with *S. rostratum* invasion and for optimizing replacement-control strategies in complex, heterogeneous habitats.

2. Materials and Methods

Plant replacement control is a competition-based ecological approach that aims to suppress invasive plants by introducing native species with ecological or economic value, thereby limiting invader spread through resource pre-emption and space occupation. In this study, replacement species were selected according to the following criteria: Competitive ability. Native species with strong competitive capacity were prioritized. The selected forages exhibit relatively rapid emergence and early growth. In particular, the two legume forages (*Medicago sativa* and *Astragalus adsurgens*) typically emerged in 3 days after sowing, whereas the four grass species emerged in 7 days after sowing. By contrast, *S. rostratum* generally shows slower germination under natural conditions. Early emergence of replacement species can therefore provide rapid site occupation and canopy cover that potentially suppresses *S. rostratum* establishment. Biodiversity and non-invasiveness. Only non-invasive species were selected to minimize ecological risks and avoid negative impacts on native biodiversity. Accordingly, six forage species widely distributed in northern China were used as replacement candidates. Environmental adaptability. Species were selected for their tolerance to local environmental conditions, including soil type and light availability, to increase the likelihood of stable performance in the target habitat.

Replacement control should function as a long term management strategy capable of maintaining

suppression of the target invasive population while providing potential economic value. Based on these criteria, we selected two perennial legumes, *M. sativa* and *A. adsurgens*, and four perennial grasses: *Agropyron cristatum*, *Leymus chinensis*, *Festuca arundinacea*, and *Elymus dahuricus*. Seeds of *Solanum rostratum* were collected in September 2022 from the Yanghe River floodplain, Wanquan District, Zhangjiakou City, Hebei Province, China. The formal identification of this species was performed by Dr. Guoliang Zhang from the Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, based on morphological characteristics following standard taxonomic keys. A voucher specimen was deposited in the Herbarium of the Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Beijing, China, under the accession number *S. rostratum* (Solan-ZJK-20220902).

No specific permission was required for the collection of *S. rostratum* seeds because the collection site was not located in a national park, nature reserve, or restricted area, and *S. rostratum* is an invasive alien plant rather than an endangered or protected species under Chinese wildlife or conservation laws.

Seeds of *Medicago sativa*, commercial cultivar “Chaoren”, a high-yield cultivar adapted to northern China, were purchased in August 2022 from Beijing Jinzhongzi Co., Ltd. Seeds of the remaining forage species, with commercial names identical to their species names, were purchased during the same period from Ningxia Doubaicao Plant Development Co., Ltd.

Experimental soils were collected from Baicheng (Jilin Province), Ürümqi (Xinjiang Uygur Autonomous Region), Tongliao (Inner Mongolia Autonomous Region), Shizuishan (Ningxia Hui Autonomous Region), Chaoyang (Liaoning Province), Zhangjiakou (Hebei Province), and Datong

(Shanxi Province), China. Site information is provided in Table 1. A commercial potting substrate (nutrient soil) was included as a reference control.

At each site, representative plots were selected based on soil type and topography, composite samples were collected using a five-point sampling scheme after removing surface litter, and soils were excavated with a shovel from 20–30 cm depth while keeping sampling depth as consistent as possible among points.

Table 1. Soil collection site information

	Source of soil	Longitude	Latitude	Type of soil
1	Nutritive soil	——	——	——
2	Zhenlai County, Baicheng City, Jilin Province	122˚18'26" N	45˚56'13" E	Chernozems
3	Horqin District, Tongliao City, Inner Mongolia Autonomous Region	122˚25'57" N	43˚32'25" E	Castano-cinnamon soils
4	Saybag District, Urumqi, Xinjiang Uygur Autonomous Region	87˚59'79" N	43˚40'12" E	Castanozems
5	Beipiao County, Beipiao City, Liaoning Province	120˚55'34" N	41˚30'25" E	Cinnamon soils
6	Huai' an County, Zhangjiakou city, HeBei Province	114˚25'43" N	40˚40'48" E	Cinnamon soils
7	Tianzhen County, Datong City, Shanxi Province	113˚53'30" N	40˚42'32" E	Castanozems
8	Dawukou District, Shizuishan City, Ningxia Hui Autonomous Region	106°20'30" N	38°58'6" E	Alluvial soils

2.1 Experimental design

2.1.1 Block arrangement and experimental layout

A two-factor completely randomized block design was used in the pot experiment. For each soil type, seven monoculture treatments were established as controls, including *S. rostratum*, *M. sativa*, *A. adsurgens*, *A. cristatum*, *L. chinensis*, *E. dahuricus*, *and F. arundinacea*. In addition, mixed-planting treatments were set up by growing *S. rostratum* with each of the six forage species at a planting ratio of 1:3 [26]. This mixed-planting setup represents a replacement-control design with a fixed species ratio, rather than a full de Wit replacement series with multiple mixture proportions [27]. Each treatment was replicated three times. In total, 264 pots were established (13 planting treatments × 3 replicates × 8 soil types).

2.1.2 Planting treatments and cultivation management

Seeds of *S. rostratum* were treated with a gibberellic acid (GA_3) solution at 0.083 g mL^{-1} for 24 h [28] prior to sowing. The experiment was conducted in a rooftop greenhouse at the Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, in late July 2022. For mixed plantings, the planting ratio was set to *S. rostratum*: replacement species = 1:3, and the total number of individuals per pot was kept the same in monocultures and mixtures. After emergence, excess seedlings were removed to maintain a total of 24 plants per pot. No additional fertilizer was applied during the growth period. Pots were watered regularly with a fixed amount and weeds were removed manually. Measurements were conducted in mid November 2022 when *S. rostratum* fruits had matured.

2.2 Measurements and calculations

2.2.1 Plant trait measurements

Leaf chlorophyll content. For each plant, two fresh leaves were selected. After gently removing

surface dust, leaf chlorophyll content was measured using a SPAD chlorophyll meter (SPAD-502PLUS, Konica Minolta, Japan).

Biomass. Plants were harvested and separated into aboveground and belowground parts. Roots were carefully removed from the soil and rinsed thoroughly with tap water. Excess water was blotted off with absorbent paper, and fresh mass was recorded. Samples were then placed into labeled paper envelopes and oven-dried at 60 °C to constant weight, after which dry mass was measured.

2.2.2 Soil sampling and chemical analyses

Sample preparation. After plant fresh and dry mass measurements, replicates of each treatment were labeled. Soil from each pot was thoroughly homogenized, and approximately 10 g of soil was placed into a sealed plastic bag with treatment and replicate information.

Analytical methods. Soil physicochemical properties were determined by Beijing Xinbaike Biotechnology Co., Ltd. Ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) were measured using a continuous-flow analyzer (Auto Analyzer 3, SEAL Analytical, Germany) following KCl extraction. Available potassium (AK) was determined using a flame photometer (FP6410, Shanghai Precision & Scientific Instrument Co., Ltd., China) based on flame photometry. Available phosphorus was analyzed using a UV-Vis spectrophotometer (UV-1900i, Shimadzu, Japan): alkaline available P was determined by $NaHCO_3$ extraction followed by the molybdenum-antimony colorimetric method, and acidic available P was determined by double-acid extraction followed by the same colorimetric method. Soil organic matter (SOM) was measured using the potassium dichromate-concentrated sulfuric acid external heating method (Bao, 2000) with a titration system (Titrette, BRAND, Germany).

2.2.3 Derived indices

Leaf chlorophyll content of the invasive plant and the fresh and dry biomass of replacement species were used as key indicators of competitive outcomes. The percentage reduction in chlorophyll content and biomass was calculated as:

$$\text{Chlorophyll reduction}(\%) = \frac{(C_{control} - C_{treatment})}{C_{control}} \times 100\%$$

$$\text{Biomass reduction}(\%) = \frac{(B_{control} - B_{treatment})}{B_{control}} \times 100\%$$

To quantify competitive effects in mixed plantings, the lnRR was calculated as the relative change in biomass of the focal species in mixtures compared with its monoculture baseline within the same soil type. Specifically, the mean monoculture biomass of the corresponding species in each soil type was used as the baseline, and lnRR was calculated for each replicate pot as:

$$lnRR_i = ln(\frac{B_{mix,i}}{\overline{B_{mono}}})$$

where Bmix,i is the dry biomass of the target species in the i-th replicate pot under mixed planting, and $\overline{B_{mono}}$is the mean dry biomass of the same species under monoculture within the same soil type. In this study, lnRR values of *S. rostratum* were calculated for each soil type and mixture treatment, and the replacement species producing the smallest lnRR value (i.e., the strongest suppression) for *S. rostratum* in each soil type was summarized.

2.3 Data analysis

All statistical analyses and data visualization were conducted in R Program (version 4.4.1)[29]. Raw data were first organized and preliminarily checked in Microsoft Excel 2023 and then imported into R for subsequent analyses. To test the effects of planting treatments on *S. rostratum* growth traits (chlorophyll content, root:shoot ratio, and individual dry mass), one-way ANOVA was performed separately within each soil type (functions anova in the stats package). When

assumptions of homogeneity of variance and normality of residuals were satisfied, post hoc comparisons among treatments were conducted using Tukey's HSD test (TukeyHSD in stats). Compact letter displays for significance grouping were generated using the multcomp View package (multcomp Letters4) and annotated on figures and tables. Differences in soil properties (NH_4^+-N, NO_3^--N, available P, available K, and soil organic matter) among planting treatments were also evaluated within each soil type. The blank control (BC) served as the reference treatment, and significance relative to BC was indicated using asterisks based on multiple-comparison results. The significance level was set at $P < 0.05$.

To compare the competitive effects of mixed planting across soil types and species combinations, lnRR values calculated for each replicate pot were imported into R for data processing, summary statistics, and visualization. Data wrangling, grouping, and summarization of lnRR were performed using the dplyr package. By definition, lnRR < 0 indicates suppression under mixed planting relative to the monoculture baseline.

To examine multivariate relationships between plant traits and soil nutrient changes, redundancy analysis (RDA) was conducted with *S. rostratum* dry mass, root:shoot ratio, and chlorophyll content as response variables and changes in soil nutrients (ΔNH_4^+-N, ΔNO_3^--N, ΔAP, ΔAK, and ΔSOM) as explanatory variables. All variables were standardized using Z-score transformation prior to analysis. RDA was implemented using the rda function in the vegan package. Significance of the overall model, constrained axes, and individual explanatory variables was evaluated using Monte Carlo permutation tests (999 permutations; anova.cca). Marginal effects were further assessed to quantify the independent explanatory power of each soil nutrient variable.

To characterize the coupling between plant biomass and soil nutrient dynamics, Pearson

correlation coefficients between plant biomass and nutrient changes (ΔNH_4^+-N, ΔNO_3^--N, ΔAP, ΔAK, and ΔSOM) were calculated within each soil type (functions cor/cor.test in stats) and visualized using correlation heatmaps. Significance levels were indicated using symbols ("·", "*", "**", and "***" corresponding to $P < 0.10$, $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively). Figures were primarily generated using ggplot2 and related R packages.

3. Results

3.1 Growth and competitive responses of *Solanum rostratum* under contrasting soils

3.1.1 Chlorophyll content of *Solanum rostratum*

Leaf chlorophyll content of *S. rostratum* differed significantly among soil types and planting treatments (Fig. 1). Overall, chlorophyll values were consistently higher in *S. rostratum* monocultures than in mixed plantings. Relative to monocultures, mixed planting reduced chlorophyll content by 20.91%-65.25%.

The suppressive effects of replacement species on *S. rostratum* chlorophyll content varied markedly across soils. In soil type 1, *L. chinensis* caused the largest reduction (38.79%). In soil type 2, the strongest suppression was observed in the Festuca treatment (33.30%). In soil type 3, *M. sativa* produced the greatest reduction (84.83%). In soil type 4, A. cristatum and Festuca showed comparable effects, each decreasing chlorophyll content by 49.60%. In soil type 5, *M. sativa* remained the most effective species, reducing chlorophyll by 58.87%. In soil type 6, Festuca and *L. chinensis* reduced chlorophyll content by 56.86% and 44.87%, respectively. In soil type 7, Festuca again showed the strongest effect (43.91%). In soil type 8, both *L. chinensis* and Festuca significantly reduced chlorophyll content, by 54.32% and 42.81%, respectively.

Across treatments, grasses tended to suppress *S. rostratum* chlorophyll more strongly than

legumes, with particularly pronounced effects in mixtures involving *E. dahuricus*, *L. chinensis*, and Festuca ($P < 0.05$). Soil background also influenced chlorophyll content: *S. rostratum* chlorophyll values were generally highest in the more fertile soil type 1 and lowest in soil type 5 across treatments.

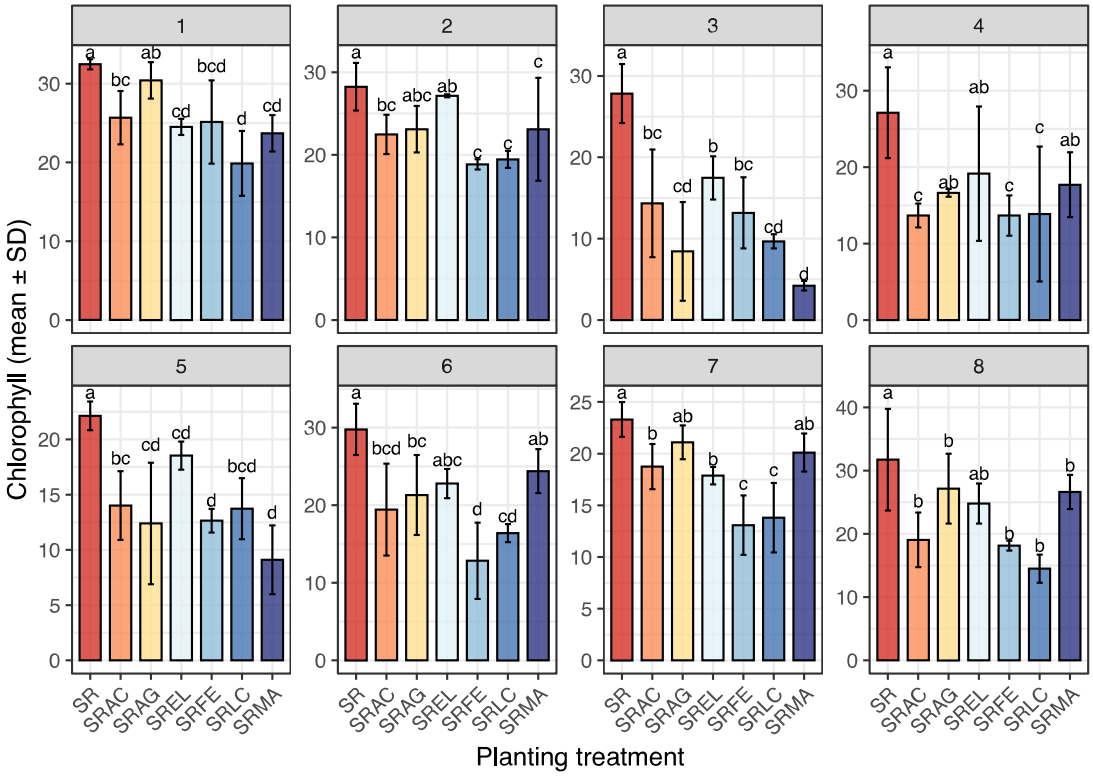


Figure 1. Chlorophyll content of *Solanum rostratum* under different planting treatments across eight soil types

Note: SR, S. rostratum monoculture; SRMA, mixture of S. rostratum with *M. sativa*; SRAG, mixture with *A. adsurgens*; SREL, mixture with *E. dahuricus*; SRLC, mixture with *L. chinensis*; SRFE, mixture with *F. arundinacea*; SRAC, mixture with A. cristatum. Different lowercase letters indicate significant differences among planting treatments within the same soil type ($P < 0.05$).

3.1.2 Biomass responses of *Solanum rostratum* under competition with replacement species across soil types

Based on measurements of fresh and dry biomass (Fig. 2), *S. rostratum* produced relatively high individual biomass in monoculture. In contrast, mixed planting with replacement species significantly reduced *S. rostratum* biomass across soil types. Among the tested replacement species, the treatment involving A. cristatum (SRAC) consistently exerted significant effects on both aboveground biomass and individual biomass of *S. rostratum* across multiple soils ($P < 0.05$). The heatmap (Fig. 3) summarizes suppression patterns among soils and replacement species, with darker colors indicating higher inhibition rates. Most mixed-planting treatments significantly decreased *S. rostratum* biomass, and the strongest suppressive effects were mainly associated with *M. sativa*, *L. chinensis*, A. cristatum, and *F. arundinacea*.

Across soil types, several replacement species achieved very high inhibition rates (>90%). Specifically, *F. arundinacea* in soil type 4 produced the strongest overall suppression, reducing individual biomass of *S. rostratum* by up to 97.26%. *M. sativa* showed consistently high suppression in soil types 2, 3, and 7, with maximum biomass reductions of 94.20% (soil type 2) and 94.25% (soil type 3). *L. chinensis* exhibited strong inhibition in soil types 3, 6, and 8, with biomass reductions reaching 91.95% (soil type 3) and 94.57% (soil type 8). In soil type 6, A. cristatum also produced strong suppression, reducing *S. rostratum* biomass by 92.31%.

Inhibition strength varied among soils. In soil type 1, all replacement species significantly reduced *S. rostratum* biomass, although inhibition rates did not exceed 90%; the most effective treatment reduced biomass by 74.03%, followed by 66.10%. In soil type 5, *S. rostratum* biomass did not differ significantly between monoculture and mixed planting, indicating relatively weak suppression under this soil background. In this soil, inhibition rates for all replacement species remained below 85.00%; the relatively stronger treatments reduced *S. rostratum* biomass by

78.40%, 56.90%, and 54.90%, respectively.

Overall, these results indicate that mixed planting generally suppresses *S. rostratum* biomass, but the magnitude of suppression and the most effective replacement species are strongly soil dependent.

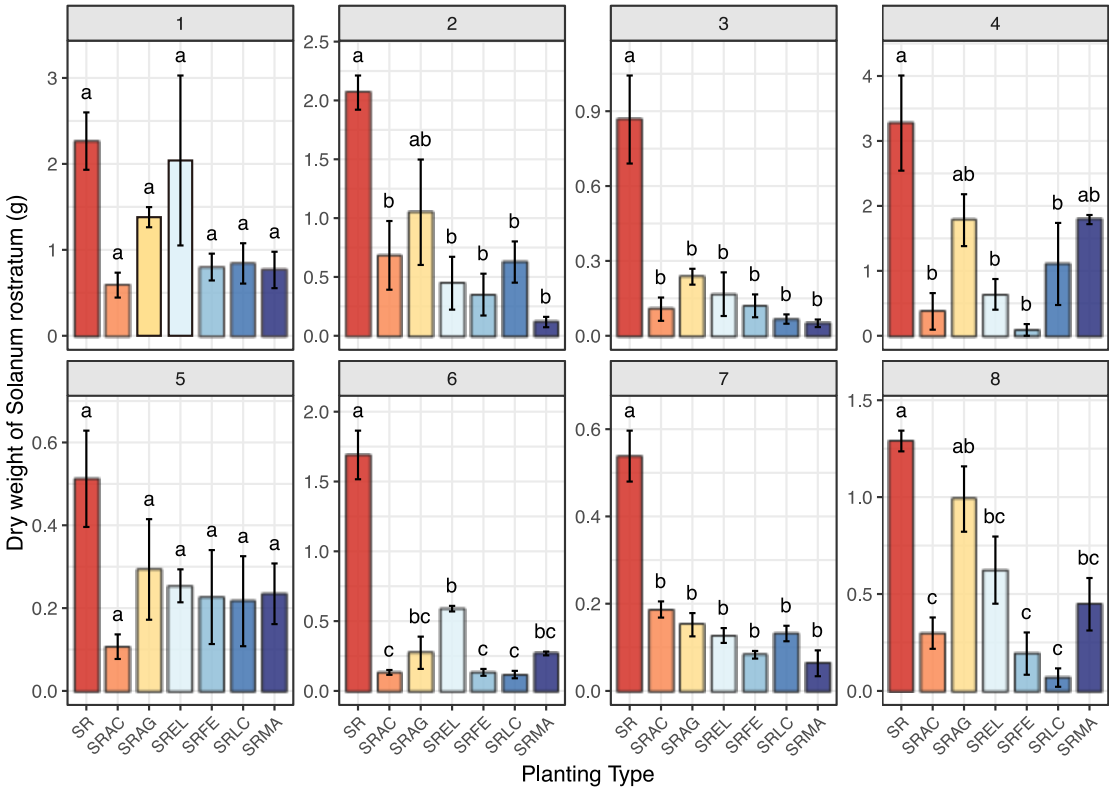


Figure 2. Individual biomass of *Solanum rostratum* and replacement species under monoculture and mixed-planting treatments.

Note: SR, S. rostratum monoculture; SRMA, mixture of S. rostratum with *M. sativa*; SRAG, mixture with *A. adsurgens*; SREL, mixture with *E. dahuricus*; SRLC, mixture with *L. chinensis*; SRFE, mixture with *F. arundinacea*; SRAC, mixture with A. cristatum. Different lowercase letters indicate significant differences among planting treatments within the same soil type ($P < 0.05$).

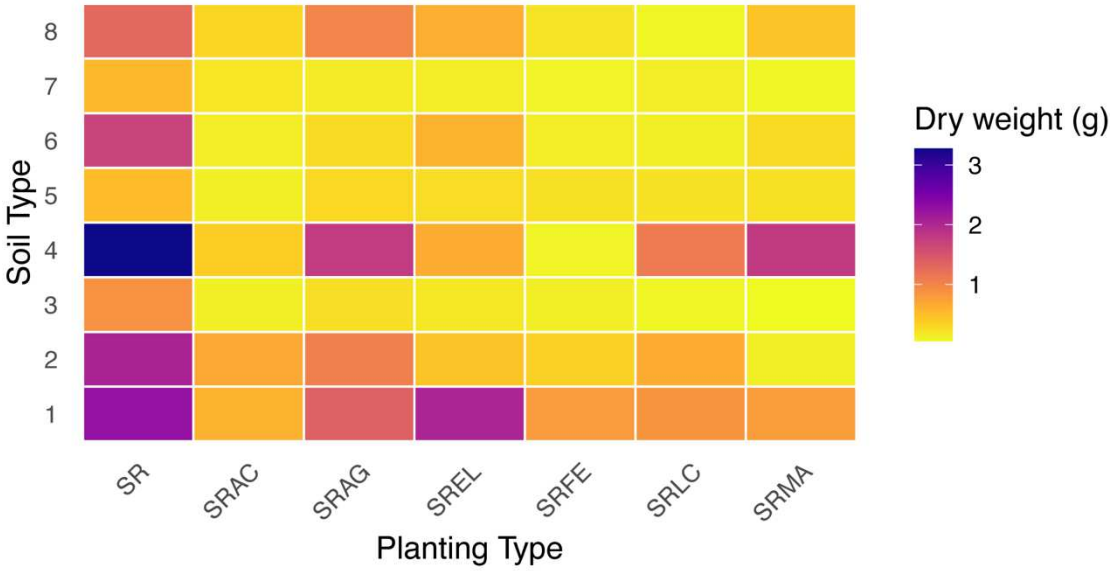


Figure 3. Heatmap of the effects of planting treatments on *Solanum rostratum* biomass across eight soil types.

Note: SR, S. rostratum monoculture; SRMA, mixture of S. rostratum with *M. sativa*; SRAG, mixture with *A. adsurgens*; SREL, mixture with *E. dahuricus*; SRLC, mixture with *L. chinensis*; SRFE, mixture with *F. arundinacea*; SRAC, mixture with A. cristatum. Different lowercase letters indicate significant differences among planting treatments within the same soil type ($P < 0.05$).

3.1.3 Root:shoot biomass allocation of *Solanum rostratum*

The root:shoot ratio (R:S) of *S. rostratum* responded differently to planting treatments across soil types (Fig. 4). In soil types 1-5 and soil type 8, R:S did not differ significantly among planting treatments. Although some numerical variation was observed, the overall allocation pattern remained relatively stable, as indicated by identical significance letters across treatments within each soil type.

In contrast, planting treatments significantly affected R:S in soil types 6 and 7. In soil type 6, the mixture with *A. adsurgens* (SRAG) produced a significantly higher R:S than the other treatments, whereas the mixture with *F. arundinacea* (SRFE) resulted in the lowest R:S. In soil type 7,

mixtures with *A. cristatum* (SRAC) and *E. dahuricus* (SREL) yielded significantly higher R:S than the other treatments, while the mixture with *M. sativa* (SRMA) showed the lowest R:S. Overall, planting treatments significantly altered root-shoot biomass allocation only under specific soil conditions, whereas treatment effects on R:S were weak or absent in most soils.

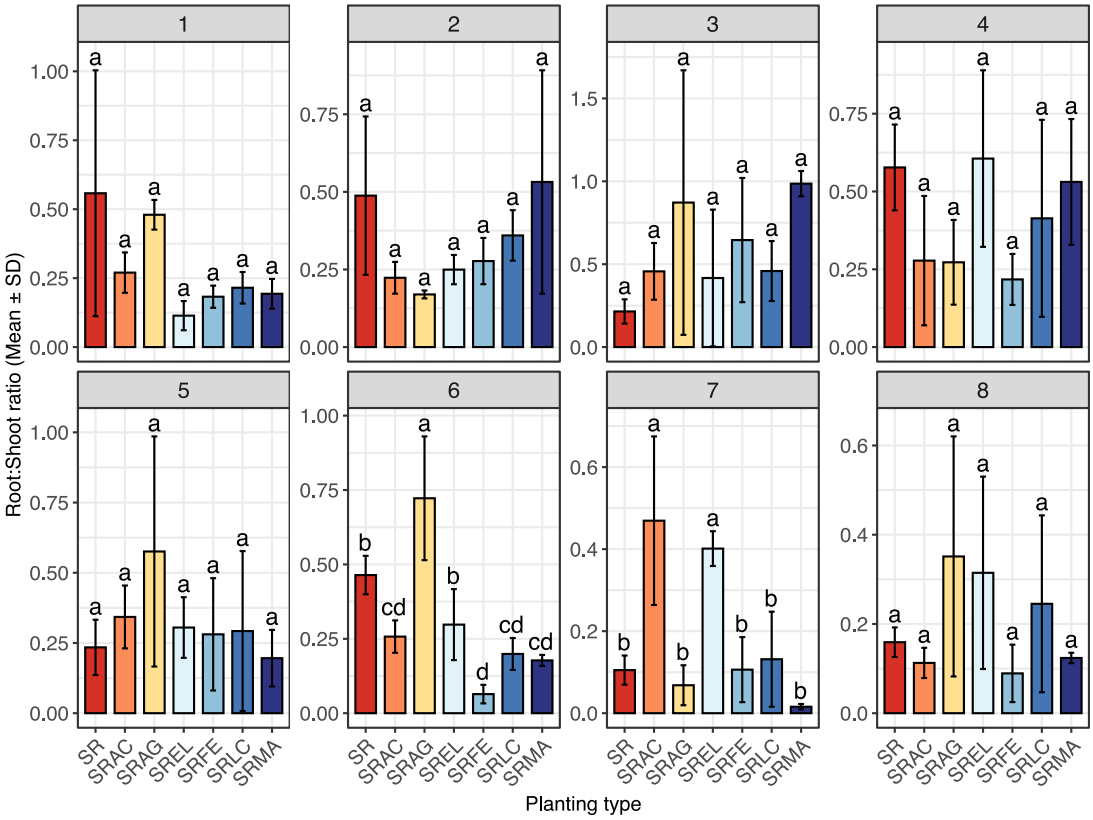


Figure 4. Root:shoot ratio (R:S) of *Solanum rostratum* under different planting treatments across eight soil types.

Note: SR, S. rostratum monoculture; SRMA, mixture with *M. sativa*; SRAG, mixture with *A. adsurgens*; SREL, mixture with *E. dahuricus*; SRLC, mixture with *L. chinensis*; SRFE, mixture with *F. arundinacea*; SRAC, mixture with A. cristatum. Different lowercase letters indicate significant differences among planting treatments within the same soil type ($P < 0.05$).

3.1.4 Log response ratio of *Solanum rostratum* under mixed planting

The lnRR revealed clear differences in the suppressive effects of replacement species on *S.*

rostratum biomass across the eight soil types (Table 2). lnRR values of *S. rostratum* were negative in all soil types, indicating that mixed planting consistently reduced *S. rostratum* biomass relative to the monoculture baseline. However, both the magnitude of suppression and the most effective replacement species varied markedly among soil types.

In soil type 1, A. cristatum produced the strongest suppression, with an lnRR of −1.35 and a 73.98% reduction in biomass. In soil types 2 and 3, *M. sativa* showed the greatest suppressive effect, with lnRR values of −2.87 and −2.85 and biomass reductions exceeding 94% in both soils. In soil type 4, *F. arundinacea* exhibited the strongest suppression and the lowest lnRR across all soils, reaching −3.59 and corresponding to a 97.25% reduction in *S. rostratum* biomass.

Suppression was comparatively weak in soil type 5. Although A. cristatum remained the most effective species in this soil, lnRR was only −0.88 and biomass inhibition was 58.47%, substantially lower than in other soil types. In soil type 6, *L. chinensis* produced the strongest suppression, with an lnRR of −2.67 and a 93.06% biomass reduction. In soil type 7, *M. sativa* again showed the strongest suppression, with an lnRR of −2.14 and an inhibition of 88.23%. In soil type 8, *L. chinensis* was the most suppressive replacement species, with an lnRR of −2.93 and a 94.66% biomass reduction.

Overall, the lnRR results indicate strong soil dependence in replacement control performance. No single replacement species consistently produced the strongest suppression across all soils, suggesting that the effectiveness of replacement control is highly contingent on soil background conditions.

Table 2. Suppressive effects of replacement species on *Solanum rostratum* biomass across eight soil types based on lnRR analysis.

Soil type	Replacement control plants	lnRR	inhibition(%)
1	Agropyron cristatum	-1.346272196	73.97915389
2	Medicago sativa	-2.874371417	94.35483871
3	*M. sativa*	-2.85263143	94.23076923
4	Festuca elata	-3.594263478	97.2519084
5	A. cristatum	-0.878770923	58.47069748
6	Leymus chinensis	-2.668482068	93.06425747
7	*M. sativa*	-2.139918725	88.23355942
8	*L. chinensis*	-2.929558007	94.65793555

Note: lnRR is the log response ratio, calculated using the mean biomass of S. rostratum grown in monoculture within the same soil type as the baseline, and reflects the proportional change in S. rostratum biomass under mixed planting relative to monoculture. Negative lnRR values (lnRR < 0) indicate suppression of S. rostratum in mixtures. For each soil type, the table lists only replacement treatments that significantly suppressed S. rostratum biomass (lnRR < 0, P < 0.05); the treatment with the most negative lnRR was selected to represent the strongest suppression within that soil. Inhibition (%) denotes the percentage reduction in S. rostratum biomass relative to its monoculture.

3.2 Effects of soil nutrient changes on *Solanum rostratum* traits

Redundancy analysis (RDA) was used to examine the multivariate relationships between phenotypic traits of *S. rostratum* (biomass, root-shoot ratio, and chlorophyll content) and changes in soil nutrient variables. The overall RDA model was not statistically significant ($F = 1.59$, $p = 0.125$; Fig. 5), while soil nutrient changes explained 30.69% of the variation in plant traits.

Among the first three constrained axes, RDA1 and RDA2 explained 17.50% and 11.14% of the variation in phenotypic traits, respectively. Permutation tests showed that none of the constrained axes were statistically significant ($p > 0.05$). Marginal effects tests indicated that changes in

available phosphorus (dAP) and soil organic matter (dSOM) showed marginal significance in explaining variation in plant traits (dAP: p = 0.080; dSOM: p = 0.052), whereas changes in nitrate nitrogen, ammonium nitrogen, and available potassium were not significant.

The RDA biplot showed differences in the orientation of phenotypic traits of *S. rostratum* in relation to soil nutrient changes. Biomass was aligned along the positive direction of RDA1 and showed a similar orientation to changes in available phosphorus and nitrate nitrogen. The root-shoot ratio was oriented in a direction similar to that of changes in soil organic matter, while chlorophyll content was mainly distributed along the negative direction of RDA2. Samples from different soil types were dispersed in the RDA ordination space.

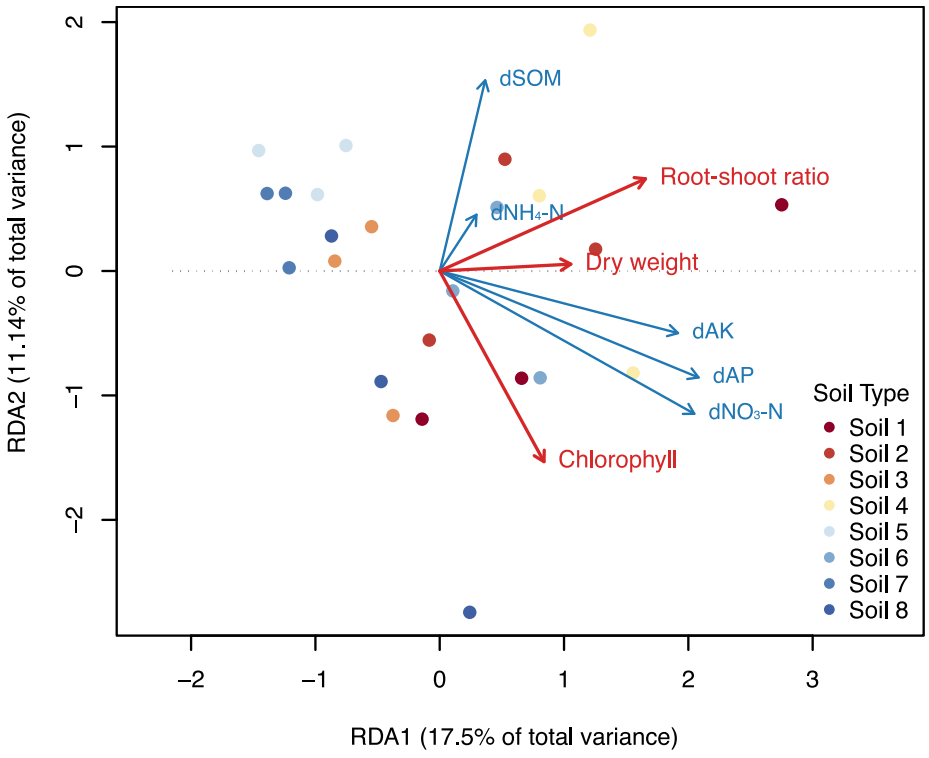


Figure 5. Redundancy analysis (RDA) ordination of *Solanum rostratum* traits and changes in soil properties.

Note: The figure shows an RDA biplot relating plant traits to soil nutrient changes. RDA1 and RDA2 are the first two constrained axes; percentages in parentheses indicate the proportion of trait variation explained by each axis. Red arrows represent plant trait variables, and blue arrows represent soil nutrient variables; arrow length indicates the contribution to the ordination, and angles between arrows reflect correlations among variables. Points represent individual samples, with colors indicating soil types.

3.3 Modulating effects of soil physicochemical heterogeneity on competitive feedbacks between *Solanum rostratum* and replacement grasses

Based on Pearson correlation analyses between plant biomass and changes in soil nutrients across the eight soil backgrounds, both the direction and strength of biomass-nutrient relationships varied markedly among soils. This pronounced heterogeneity indicates that the coupling between soil nutrient feedback and biomass response during competition is strongly dependent on soil background conditions. No single nutrient variable consistently explained biomass variation across all soils; instead, the same nutrient indicator could show either positive or negative correlations depending on soil type. These patterns suggest that initial soil fertility and soil nutrient transformation processes may shift the limiting factors and thereby modify competitive outcomes.

3.2.2 Differences in soil background properties

Across soil types, physicochemical properties differed markedly (Table 3). The eight soils showed pronounced heterogeneity in NH_4^+-N, NO_3^--N, AK, AP, and SOM.

NH_4^+-N varied substantially among soils, with higher concentrations observed in soils 6, 2, and 8, whereas soil 7 had the lowest NH_4^+-N. NO_3^--N showed particularly strong variation: soils 1 and 7 had markedly higher NO_3^--N than the other soils, while soils 2 and 3 remained at comparatively

low levels. For AK and AP, clear gradients were observed, with soils 7 and 1 exhibiting the highest values and soil 5 the lowest. SOM also differed strongly among soils; soils 1 and 8 had substantially higher SOM than the remaining soils, whereas soil 4 had the lowest SOM.

Overall, these soils provided distinctly different nutrient backgrounds in terms of N, P, K, and organic matter, forming a clear basis for evaluating soil-dependent patterns of plant growth and competitive interactions in subsequent analyses.

Table 3. Differences in baseline soil physicochemical properties among the eight soil types.

Soil_Type	NH_4-N	NO_3-N	AK	AP	SOM
1	1.23±0.15c	51.19±1.27a	265.67±24.37ab	17.60±1.06a	262.54±14.00a
2	2.93±0.20a	5.04±0.20cd	200.33±11.89bcd	18.95±1.35a	10.57±0.93cd
3	2.88±0.68ab	2.83±0.39d	207.00±6.24bc	6.05±0.83b	19.33±0.57cd
4	1.46±0.42abc	7.78±0.46bcd	168.67±23.90cde	5.71±0.85b	6.95±0.28d
5	1.23±0.18bc	12.19±1.08b	97.33±5.49e	3.28±0.52b	12.07±0.40cd
6	2.94±0.24a	10.35±0.62bc	169.00±10.41cde	4.78±0.96b	20.91±0.85cd
7	1.15±0.21c	47.84±2.85a	303.67±8.09a	14.68±1.04a	31.50±0.17c
8	2.65±0.29abc	11.31±1.31bc	125.67±18.59de	6.27±1.00b	97.81±0.33b

Note: Data are presented as mean ± standard error (SE) (n = 3). Within each column, different lowercase letters indicate significant differences among soil types (Tukey's HSD test, $P < 0.05$). NH_4^+-N and NO_3^--N denote ammonium-N and nitrate-N, respectively; AK and AP denote available potassium and available phosphorus, respectively; SOM denotes soil organic matter.

3.2.2 Effects of soil physicochemical context on competitive interactions

Pearson correlation analysis showed that biomass-nutrient relationships were highly soil dependent (Fig. 6). The direction and magnitude of correlations between plant biomass and changes in N, P, K, and soil organic matter varied markedly among soil types, and no single

nutrient variable consistently explained plant performance across all soils.

Soil 1. Under the *S. rostratum* monoculture, no significant correlations were detected between its biomass and any soil nutrient-change variables. In mixed plantings, however, *S. rostratum* biomass showed stronger associations with specific nutrients. In particular, when mixed with *F. arundinacea*, *S. rostratum* biomass was highly positively correlated with changes in available phosphorus (ΔAP; $p < 0.01$). In the mixture with A. cristatum, *S. rostratum* biomass was significantly positively correlated with changes in soil organic matter (ΔSOM). These results suggest that, in this soil, P dynamics and SOM changes may play an important role in shaping *S. rostratum* growth under competition.

Soil 2. In both monoculture and mixed treatments, *S. rostratum* biomass did not exhibit consistent significant relationships with most nutrient-change variables, showing only marginal associations with single nutrients in a few mixtures. This indicates that *S. rostratum* growth in this soil may be relatively insensitive to short-term nutrient changes. In contrast, replacement species displayed clearer correlation patterns. *M. sativa* showed relatively rapid responses to changes in NH_4^+-N (ΔNH_4^+-N) and ΔAP, which may contribute to its competitive advantage under this comparatively stable soil background.

Soil 3. In mixed plantings, *S. rostratum* biomass was significantly or marginally correlated with multiple nutrient-change variables. Notably, biomass was often significantly negatively correlated with ΔAP and ΔSOM, suggesting that nutrient depletion or transformation processes may constrain *S. rostratum* growth in this soil. Replacement species exhibited correlation patterns distinct from those of *S. rostratum*. For example, higher biomass of *L. chinensis* was associated with larger changes in available K (ΔAK), indicating a tendency toward increased K availability

459 or enrichment.

460 Soil 4. Correlations between *S. rostratum* biomass and soil nutrient changes were mainly observed
461 in mixed treatments. In some mixtures, *S. rostratum* biomass was significantly associated with
462 changes in ΔNH_4^+-N and ΔNO_3^--N, implying that N dynamics may be an important driver of
463 competitive outcomes in this soil. Replacement species showed more frequent significant
464 correlations with ΔAP and ΔSOM, suggesting that competitive advantage may be linked to
465 regulation of P cycling and SOM-related processes in this soil type.

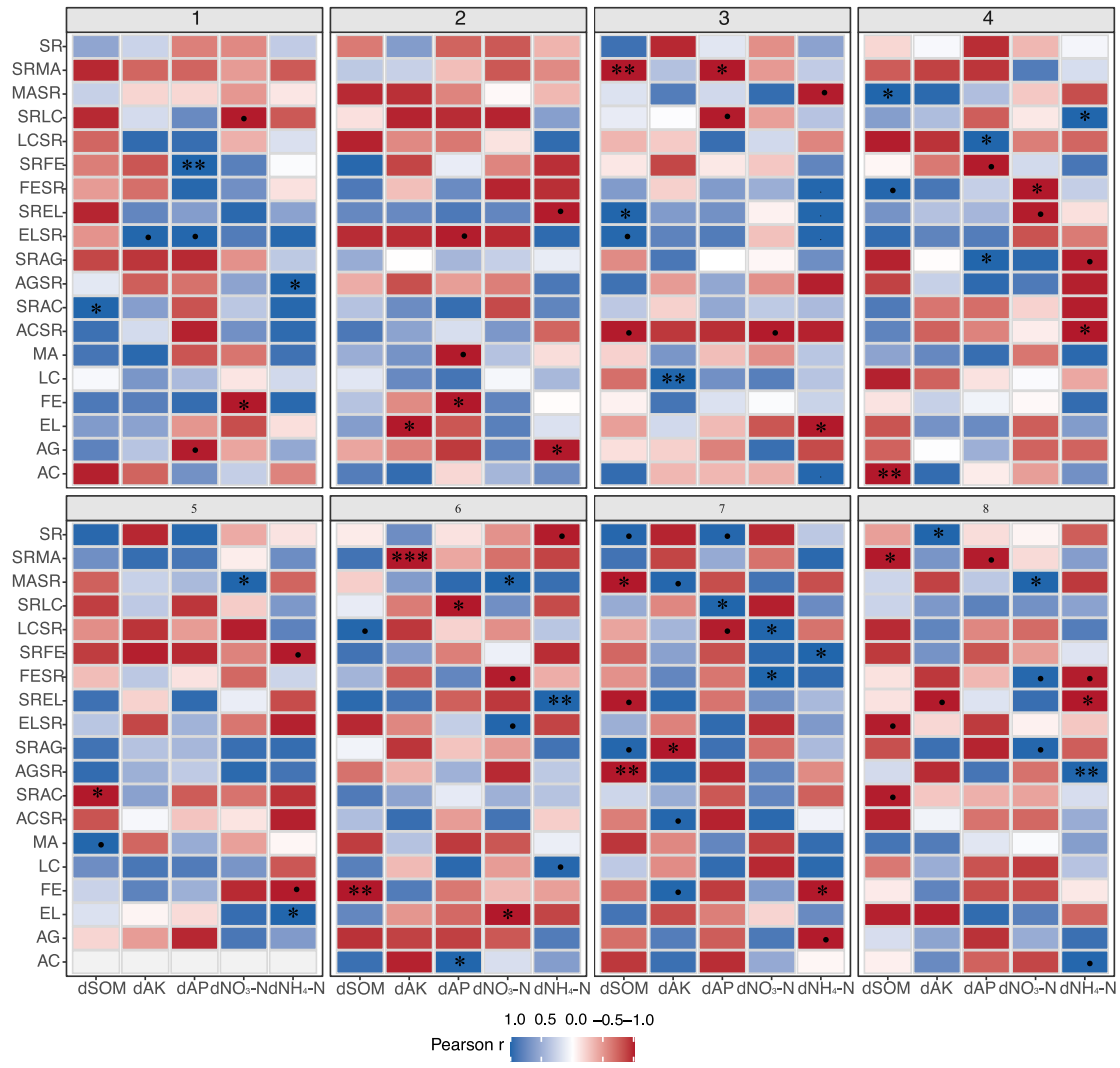
466 Soil 5. Correlations between *S. rostratum* biomass and nutrient-change variables were generally
467 weak and mostly non-significant, consistent with the limited explanatory power of soil nutrient
468 changes for *S. rostratum* growth in this soil. In contrast, replacement species showed relatively
469 stronger associations with ΔSOM, with some treatments reaching significant or marginal
470 significance, indicating that SOM dynamics may be an important factor influencing replacement
471 species performance.

472 Soil 6. In mixed treatments, *S. rostratum* biomass was significantly or highly significantly
473 correlated with ΔNH_4^+-N and ΔAP, suggesting that N and P may jointly regulate *S. rostratum*
474 growth under competition in this soil. Replacement species displayed multiple significant
475 correlations with ΔNO_3^--N and ΔSOM, indicating a stronger dependence on nitrate supply and
476 SOM-related processes.

477 Soil 7. In mixed plantings, *S. rostratum* biomass was significantly correlated with several nutrient-
478 change variables, particularly ΔNO_3^--N and ΔSOM, implying that N transformation and SOM
479 dynamics may substantially affect its competitive performance in this soil. Replacement species
480 also showed strong correlations, but the key nutrient variables differed from those associated with

S. rostratum, further suggesting divergence in nutrient-use pathways between the invasive species and replacement plants.

Soil 8. In mixed treatments, correlations between *S. rostratum* biomass and ΔNH_4^+-N and ΔAP were more prominent, indicating that N and P may be important limiting factors for its growth under this soil background. Replacement species exhibited stronger correlations with ΔNO_3^--N and ΔSOM, suggesting that they may achieve competitive advantage via distinct nutrient pathways. Overall, correlation patterns between plant biomass and soil nutrient changes differed markedly among soil types. *S. rostratum* generally exhibited greater sensitivity to nutrient changes under mixed plantings, whereas replacement species maintained more stable associations with particular nutrient dynamics across multiple soils. These differences indicate that nutrient-mediated plant-soil feedbacks regulate competitive interactions between the invasive plant and replacement species through soil-specific pathways.



493

494 Figure 6. Correlations between biomass of S. rostratum and replacement species and changes in

495 soil physicochemical properties under different planting treatments across eight soil types.

496

Note: SR, biomass of S. rostratum in monoculture; SRMA, biomass of S. rostratum in mixture with *M. sativa*; MASR, biomass of *M. sativa* in mixture with S. rostratum; SRLC, biomass of S. rostratum in mixture with *L. chinensis*; LCSR, biomass of *L. chinensis* in mixture with S. rostratum; SRFE, biomass of S. rostratum in mixture with *F. arundinacea*; FESR, biomass of *F. arundinacea* in mixture with S. rostratum; SREL, biomass of S. rostratum in mixture with *E. dahuricus*; ELSR, biomass of *E. dahuricus* in mixture with S. rostratum; SRAG, biomass of S. rostratum in mixture with *A. adsurgens*; AGSR, biomass of *A. adsurgens* in mixture with S. rostratum; SRAC, biomass of S. rostratum in mixture with A. cristatum; ACSR, biomass of A. cristatum in mixture with S. rostratum; MA, *M. sativa* monoculture; LC, *L. chinensis* monoculture; FE, *F. arundinacea* monoculture; EL, *E. dahuricus* monoculture; AG, *A. adsurgens* monoculture; AC, *A. cristatum* monoculture. Symbols "·", "*", "**", and "***" indicate significance at $P < 0.10$, $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

3.3 Effects of plant competition on soil physicochemical properties

Across the eight soil types, the four planting treatments—blank control, *S. rostratum* monoculture, replacement-species monoculture, and mixed plantings—produced significant and complex effects on soil physicochemical properties.

3.3.1 Changes in soil ammonium nitrogen

Across most soil types, the S. rostratum monoculture and its mixtures with replacement species increased soil NH_4^+-N to varying degrees, and overall NH_4^+-N levels were significantly higher than in the blank control (Fig. 7). However, the magnitude of this effect differed markedly among soil types.

In soil types 2, 6, and 7, NH_4^+-N did not differ significantly between the S. rostratum monoculture and most mixed plantings, yet both were significantly higher than the blank control. In contrast,

monocultures of the replacement species generally did not differ from the blank control, and some grass monocultures showed reduced NH_4^+-N.

By comparison, in soil types 1, 3, 4, and 5, treatment effects on NH_4^+-N were relatively weak. Most plantings did not differ significantly from the blank control, and only a few specific mixtures showed significant changes, indicating a relatively stable NH_4^+-N response to planting in these soils. In soil type 8, NH_4^+-N did not differ significantly among treatments; replacement-species monocultures tended to be slightly lower than the blank control, but the differences were not significant.

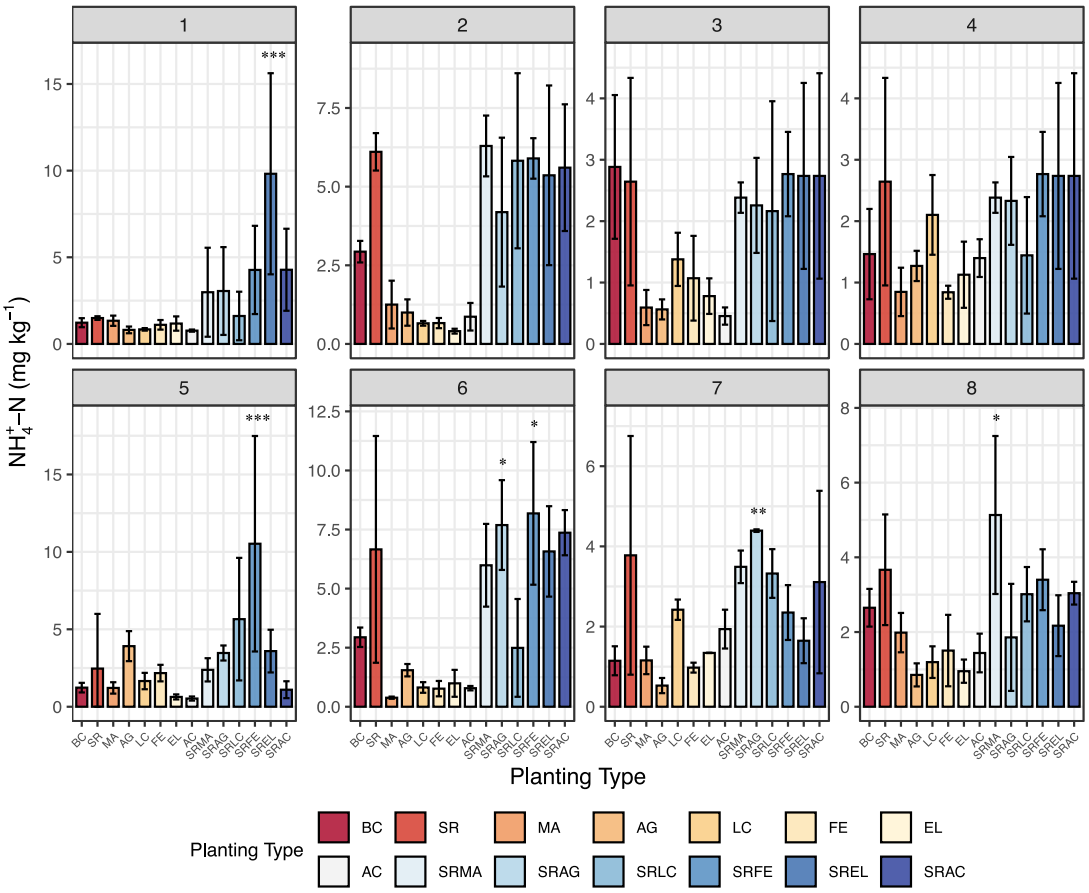


Figure 7. Soil NH_4^+-N under different planting treatments across eight soil types.

Note: Bars represent means and error bars indicate standard errors (SE). Different colors denote planting treatments. BC, blank control; SR, S. rostratum monoculture; MA, AG, LC, FE, and EL denote monocultures of *M. sativa*, *A. adsurgens*, *L. chinensis*, *F. arundinacea*, and *E. dahuricus*, respectively; SRMA, SRAG, SRLC, SRFE, SREL, and SRAC denote mixtures of S. rostratum with *M. sativa*, *A. adsurgens*, *L. chinensis*, *F. arundinacea*, *E. dahuricus*, and *A. cristatum*, respectively. Numbers 1-8 indicate soil types. Asterisks indicate significant differences between a given planting treatment and the blank control (BC) within the same soil type ($P < 0.05$, $P < 0.01$, $P < 0.001$).

3.3.2 Changes in soil nitrate nitrogen

The response of NO_3^--N to planting treatments varied markedly among soil types (Fig. 8). Overall, NO_3^--N declined significantly in some soils but increased in others.

In soil types 4, 5, and 7, most monocultures and mixed plantings significantly reduced NO_3^--N, and the decreases were generally stronger under mixed plantings. This pattern suggests that competition between *S. rostratum* and the replacement species may have accelerated NO_3^--N uptake and/or altered N transformation processes. Notably, in soil type 7, NO_3^--N was significantly lower in all treatments than in the blank control.

In contrast, in soil types 3 and 6, most treatments increased NO_3^--N, particularly monocultures of the replacement species, indicating that under these soil conditions, replacement-species growth may have promoted NO_3^--N accumulation or reduced its loss. In soil types 1, 2, and 8, treatment effects were small and NO_3^--N did not differ significantly from the blank control.

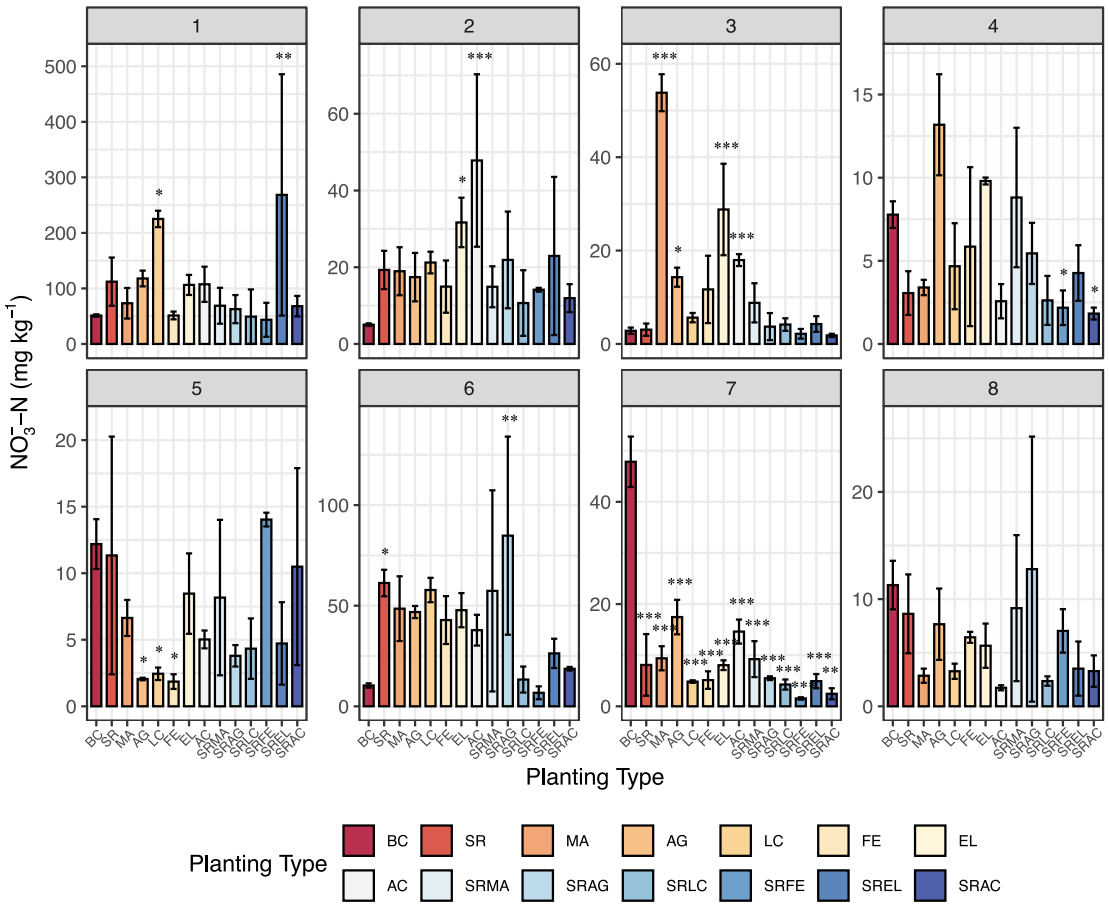


Figure 8. Soil NO_3^--N under different planting treatments across eight soil types

Note: Bars represent means and error bars indicate standard errors (SE). Different colors denote planting treatments. BC, blank control; SR, S. rostratum monoculture; MA, AG, LC, FE, and EL denote monocultures of *M. sativa*, *A. adsurgens*, *L. chinensis*, *F. arundinacea*, and *E. dahuricus*, respectively; SRMA, SRAG, SRLC, SRFE, SREL, and SRAC denote mixtures of S. rostratum with the corresponding replacement species (codes as above; AC denotes *A. cristatum*). Numbers 1-8 indicate soil types. Asterisks indicate significant differences between a given planting treatment and the blank control (BC) within the same soil type ($P < 0.05$, $P < 0.01$, $P < 0.001$).

3.3.3 Changes in soil available potassium

The response of AK to planting treatments showed a broadly consistent pattern across soil types, although the direction of change differed among soils (Fig. 9).

In soil types 3, 4, and 7, AK was significantly lower in all planting treatments than in the blank control, indicating strong depletion of exchangeable K associated with plant growth under these soil conditions.

In soil types 5 and 6, both the *S. rostratum* monoculture and mixed plantings significantly increased AK. The increase was generally greater in mixed plantings than in replacement-species monocultures, suggesting that mixed communities exerted a stronger influence on K cycling in these soils. In soil types 1 and 2, AK did not differ significantly from the blank control in the *S. rostratum* monoculture and in some mixed plantings, whereas replacement-species monocultures more often showed decreases in AK.

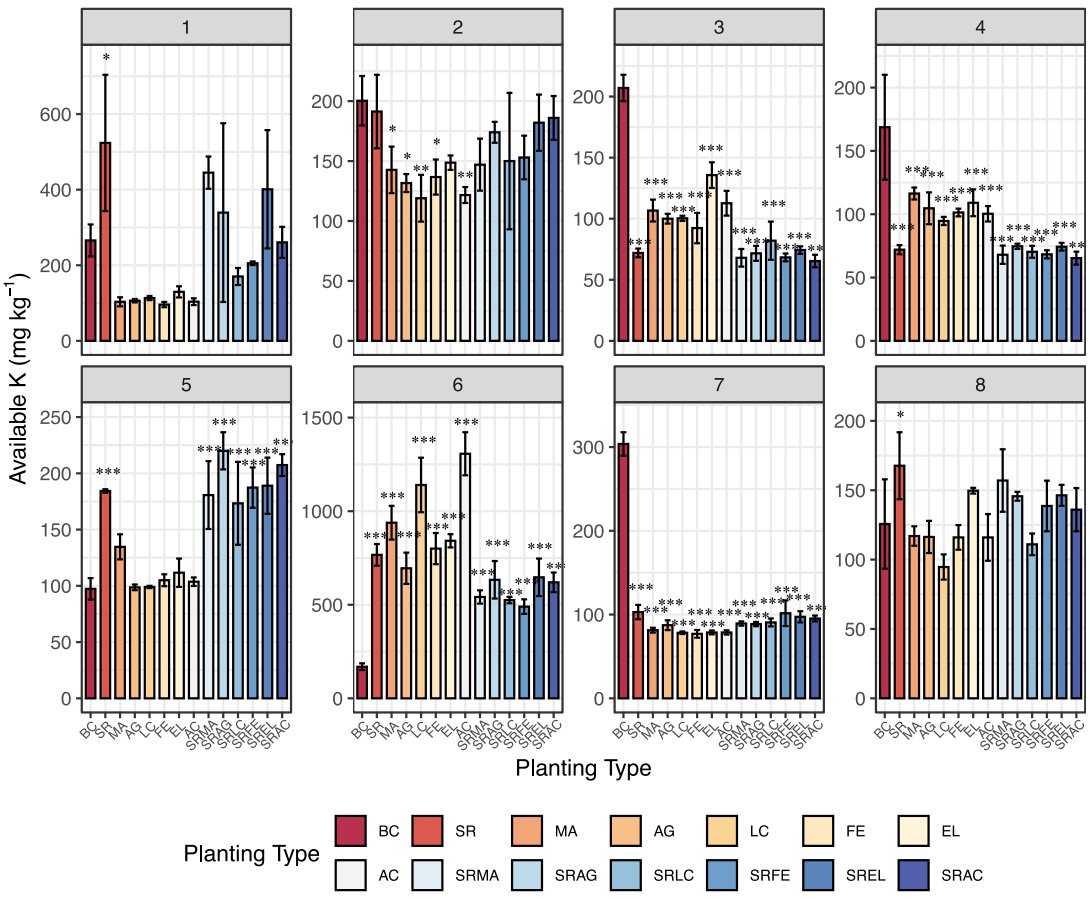


Figure 9. Soil available potassium (AK) under different planting treatments across eight soil types

Note: Bars represent means and error bars indicate standard errors (SE). Different colors denote planting treatments. BC, blank control; SR, S. rostratum monoculture; MA, AG, LC, FE, and EL denote monocultures of *M. sativa*, *A. adsurgens*, *L. chinensis*, *F. arundinacea*, and *E. dahuricus*, respectively; SRMA, SRAG, SRLC, SRFE, SREL, and SRAC denote mixtures of S. rostratum with the corresponding replacement species (codes as above; AC denotes *A. cristatum*). Numbers 1-8 indicate soil types. Asterisks indicate significant differences between a given planting treatment and the blank control (BC) within the same soil type ($P< 0.05$, $P < 0.01$, $P < 0.001$).

3.3.4 Changes in soil available phosphorus

The response of AP to planting treatments was highly soil dependent (Fig. 10). In soil type 1, the *S. rostratum* monoculture and all mixed plantings significantly increased AP, whereas replacement-species monocultures did not differ from the blank control. This indicates that *S. rostratum* promoted the accumulation of plant-available P in this soil.

In soil types 3 and 6, replacement-species monocultures significantly increased AP, while the *S. rostratum* monoculture and mixed plantings did not differ from the blank control. In soil types 2, 4, 5, and 7, most treatments showed no significant differences from the blank control or tended to reduce AP, and differences among planting treatments were generally small.

In soil type 8, AP was significantly higher than the blank control in the *S. rostratum* monoculture and in most mixed plantings, except for mixtures with *L. chinensis*, *F. arundinacea*, and *A. cristatum*, which did not differ significantly from the blank control.

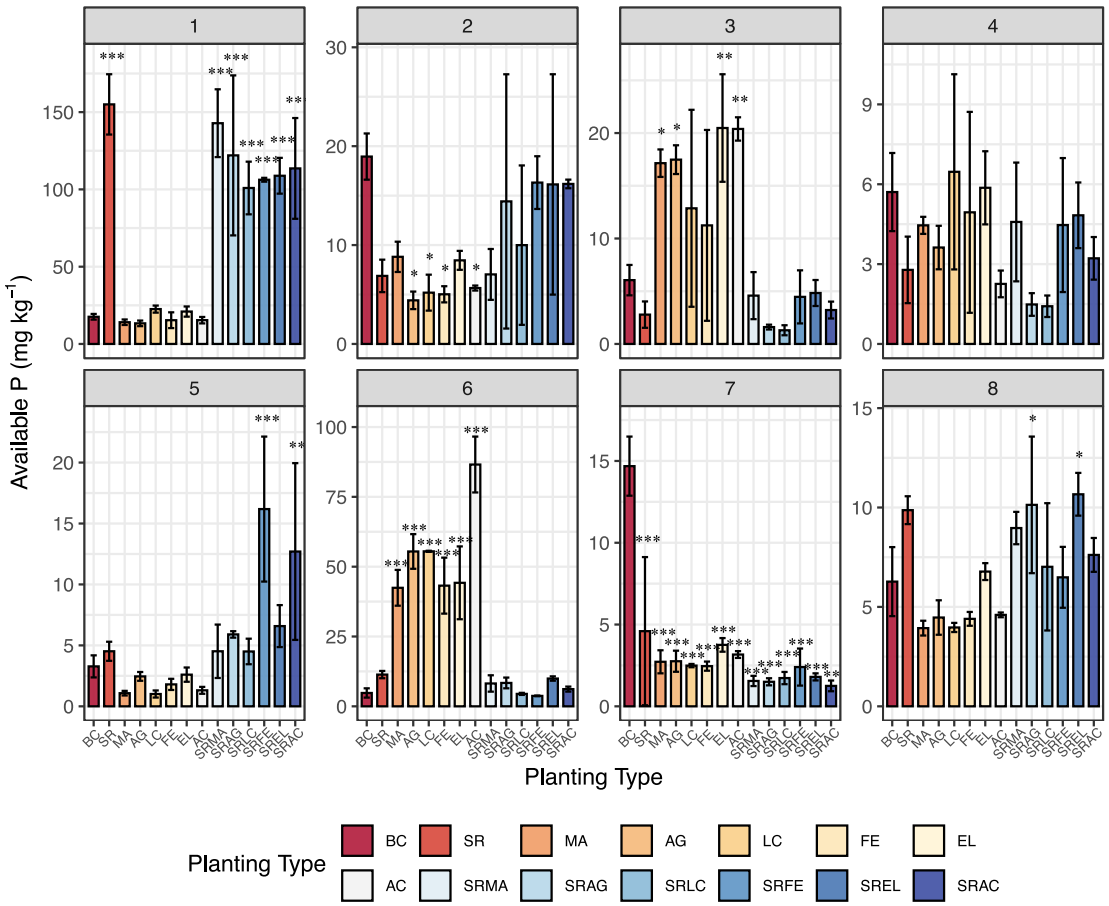


Figure 10. Soil available phosphorus (AP) under different planting treatments across eight soil types.

Note: Bars represent means and error bars indicate standard errors (SE). Different colors denote planting treatments. BC, blank control; SR, S. rostratum monoculture; MA, AG, LC, FE, and EL denote monocultures of *M. sativa*, *A. adsurgens*, *L. chinensis*, *F. arundinacea*, and *E. dahuricus*, respectively; SRMA, SRAG, SRLC, SRFE, SREL, and SRAC denote mixtures of S. rostratum with the corresponding replacement species (codes as above; AC denotes *A. cristatum*). Numbers 1-8 indicate soil types. Asterisks indicate significant differences between a given planting treatment and the blank control (BC) within the same soil type ($P < 0.05$, $P < 0.01$, $P < 0.001$).

3.3.5 Changes in soil organic matter

Soil organic matter showed a relatively consistent response pattern across soil types, although

significant differences were still observed in some soils (Fig. 11). In soil types 3 and 4, most treatments did not differ significantly from the blank control. In soil type 6, the S. rostratum monoculture significantly increased soil organic matter, and its value did not differ significantly from most mixed plantings. In contrast, in soil types 7 and 8, soil organic matter was significantly lower in all planting treatments than in the blank control, suggesting that plant growth accelerated organic matter depletion. In soil type 8, soil organic matter in the mixed plantings was slightly higher than in replacement-species monocultures, but the difference was not significant.

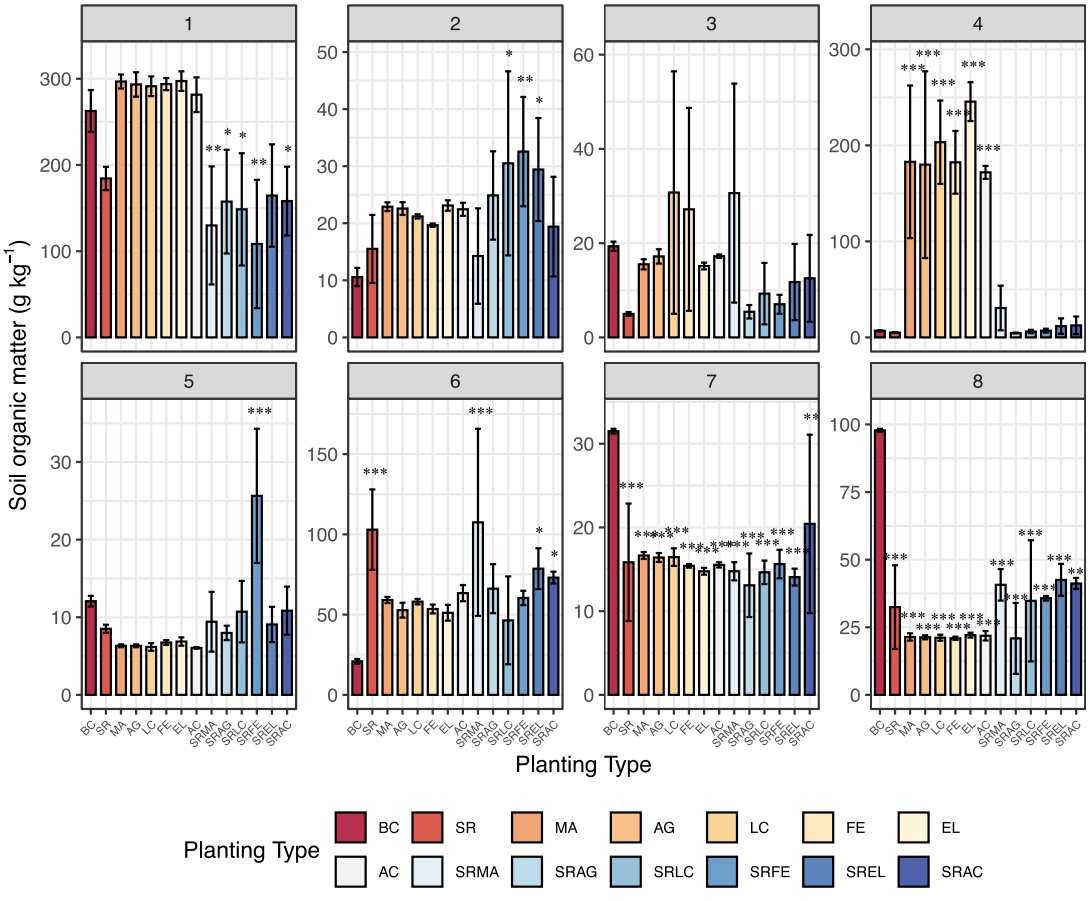


Figure 11. Soil organic matter (SOM) under different planting treatments across eight soil types

Note: Bars represent means and error bars indicate standard errors (SE). Different colors denote planting treatments. BC, blank control; SR, S. rostratum monoculture; MA, AG, LC, FE, and EL denote monocultures of *M. sativa*, *A. adsurgens*, *L. chinensis*, *F. arundinacea*, and *E. dahuricus*, respectively; SRMA, SRAG, SRLC, SRFE, SREL, and SRAC denote mixtures of S. rostratum with the corresponding replacement species (codes as above; AC denotes *A. cristatum*). Numbers 1-8 indicate soil types. Asterisks indicate significant differences between a given planting treatment and the blank control (BC) within the same soil type ($P< 0.05$, $P < 0.01$, $P < 0.001$).

3.4 Integrated evaluation of the suppressive effects of replacement species under heterogeneous soils

Across the eight heterogeneous soil types, mixing *S. rostratum* with each of the six replacement forage species significantly reduced its growth performance. Compared with monoculture, mixed planting generally resulted in lower leaf chlorophyll content and a marked decrease in individual biomass, and the log response ratio (lnRR) of *S. rostratum* biomass was negative in all soil types. These results indicate that the replacement species consistently imposed competitive suppression on *S. rostratum* across contrasting soil backgrounds. However, the magnitude of suppression and the identity of the most effective replacement species were strongly soil dependent, and no single species performed best across all soils.

When considering the strongest suppression within each soil type, *F. arundinacea* showed the greatest inhibitory effect in Soil 4. *M. sativa* was consistently the optimal or near-optimal suppressor in Soils 2, 3, and 7. *L. chinensis* exerted the strongest suppression in Soils 6 and 8. *A. cristatum* provided relatively strong suppression in Soil 1, whereas overall inhibition in Soil 5 was comparatively weak, highlighting that soil background can substantially alter both the magnitude and stability of

635 replacement control. Overall, *M. sativa* maintained relatively stable suppression across multiple soil
636 types, suggesting broad adaptability, whereas *L. chinensis* and *F. arundinacea* tended to achieve strong
637 suppression primarily under specific soil conditions. The generally weaker suppression observed in
638 Soil 5 further suggests that the stability of replacement control may be constrained in low-response soil
639 types.

640 **4. Discussion**

641 **4.1 Role of the logarithmic response ratio in plant-soil feedback analyses**

642 Under research contexts where heterogeneous soil conditions and multiple mixed-planting
643 combinations coexist, a robust metric is required to allow comparable quantification of competition
644 intensity across different soil types and species combinations. Because baseline growth performance
645 differs substantially among soil types and plant species, monoculture biomass often varies widely
646 among treatments. Direct comparisons based solely on absolute biomass under mixed planting can
647 therefore confound environmental background effects with competition effects per se, potentially
648 obscuring the true strength of interspecific interactions [30, 31].

649 The lnRR uses monoculture performance as a reference and expresses biomass changes under mixed
650 planting as a standardized relative effect size. This approach effectively minimizes interference from
651 baseline growth differences among soils and species, thereby enhancing comparability across
652 treatments[32]. Oksanen et al. [33]evaluated several commonly used competition indices, including
653 lnRR, RCI, RNE, and CRCI, using Solidago virgaurea as a model species. Their results showed that
654 lnRR and CRCI produced consistent and largely unbiased estimates of competition effects, regardless
655 of whether calculations were based on pairwise comparisons or pooled data. Although RNE generally
656 performed reasonably well, values derived from averaged pairwise comparisons tended to be

systematically lower than those calculated from pooled data when competition intensity was high. In contrast, RCI was strongly influenced by variability in individual plant performance under pairwise comparisons, frequently generating biased or even aberrant results. Therefore, the study advised against the continued use of RCI as a reliable measure of competition intensity.

Compared with alternative indices, lnRR not only clearly reflects the direction of competitive effects but also provides a quantitative measure of their magnitude, enabling meaningful comparisons of competition outcomes across heterogeneous soil conditions and mixed-planting combinations. In studies of plant-soil feedbacks, lnRR is particularly suitable for revealing how soil environments regulate relative competitive effects through nutrient supply and transformation processes [34, 35]. By standardizing competitive responses across contrasting soil backgrounds, lnRR facilitates the identification of soil-dependent variation in the suppressive capacity of replacement species against invasive plants, thereby providing a robust quantitative basis for the integrated evaluation of replacement control effectiveness.

4.2 Effects of heterogeneous soil backgrounds on the competitive performance of *Solanum rostratum*

4.2.1 *Solanum rostratum*-soil feedback effects

Our results demonstrate that the growth performance and competitive responses of *S. rostratum* vary significantly among soil types, indicating that soil background strongly regulates its response intensity to replacement control species. When *S. rostratum* was grown alone across different soil types, soil ammonium nitrogen consistently increased, whereas nitrate nitrogen, available phosphorus, and available potassium increased in some soils but decreased in others. Soil organic matter declined in most soil types following monoculture cultivation of *S. rostratum*. In soils with relatively high fertility

679 (e.g., soil type 1), *S. rostratum* monocultures exhibited higher chlorophyll content and biomass,
680 suggesting strong capacity for resource acquisition and utilization. In contrast, in soils with lower
681 fertility or constrained nutrient structure (e.g., soil type 5), the growth of *S. rostratum* was markedly
682 limited.
683 Zhao et al. [20]investigated soils from abandoned land, roadsides, farmland, and forest habitats invaded
684 by *S. rostratum* and reported that its effects on soil physicochemical properties differed significantly
685 among habitat types. Similar context-dependent effects have been documented for other invasive
686 species. For example, studies on *Eupatorium adenophorum* have shown contrasting impacts on soil
687 nutrient dynamics: Yu et al. [36]reported increases in soil organic phosphorus, available potassium,
688 total nitrogen, and soil organic carbon following invasion, whereas Wu et al. (2007) [37]observed
689 decreases in alkali-hydrolyzable nitrogen, available phosphorus, and available potassium in invaded
690 sites. Moreover, Sun et al. [38]demonstrated that invasion intensity further modulates these effects,
691 with heavy invasion significantly increasing soil total phosphorus and nitrate concentrations, while
692 moderate invasion led to significant reductions in available phosphorus accompanied by declines in
693 total nitrogen and soil organic matter. These findings collectively indicate that the effects of invasive
694 plants on soil nutrient status are jointly regulated by habitat conditions and invasion intensity.
695 Comparable background dependence has also been reported for *Spartina alterniflora* invasion. Bu
696 Naishun et al. [39]found that *S. alterniflora* invasion increased soil organic carbon content in wetlands
697 of the Yangtze River estuary. Similarly, Sheng et al. [40] reported that invasion by *S. alterniflora* in the
698 Dafeng Milu National Nature Reserve increased soil carbon and nitrogen contents and stocks, while
699 simultaneously reducing soil phosphorus content and stocks. In contrast, Bai et al. (2017)[41] observed
700 a decline in soil organic carbon following *S. alterniflora* invasion in mangrove wetlands along the

eastern coast of Fujian Province. In addition, invasion by stinking chamomile (*Anthemis cotula*) has been shown to significantly alter soil physicochemical properties, with invaded sites exhibiting 10-60% higher levels of organic carbon, total potassium, total nitrogen, total phosphorus, available nitrogen, and available potassium compared with uninvaded sites [42].

Taken together, these studies indicate that invasion by the same plant species can substantially alter soil nutrient status, but the direction and magnitude of these changes are highly dependent on habitat type, invasion intensity, and ecosystem context. This background-dependent soil modification provides an important foundation for understanding how soil conditions mediate the competitive performance of *S. rostratum* across heterogeneous environments.

From an ecological-mechanistic perspective, invasive plant species may gain competitive advantages by altering soil properties or interacting with soil microbial communities [43–45]. In addition, invasive plants may influence resource competition with native species by modifying nutrient supply rates and the relative proportions of nutrient forms through biogeochemical transformation processes [46]. These mechanisms can indirectly regulate the competitive advantage or disadvantage of *S. rostratum* under different soil conditions. In other words, the competitive performance of *S. rostratum* is not solely determined by its intrinsic resource acquisition capacity, but is also likely associated with plant-soil feedback processes and potential self-reinforcing invasion mechanisms that develop under heterogeneous soil backgrounds.

The differentiated responses of soil nutrients to *S. rostratum* indicate that this species does not simply deplete or accumulate a single nutrient, but rather influences soil nutrient transformation pathways, thereby generating complex soil nutrient feedbacks. For example, significant declines in nitrate nitrogen observed in some soils may be associated with enhanced plant uptake or increased microbial

denitrification, whereas increases in nitrate nitrogen in other soils may reflect accelerated mineralization or lower plant uptake efficiency. Previous studies have shown that *S. rostratum* possesses a strong capacity for maintaining internal homeostasis, enabling it to buffer fluctuations in external nutrient supply through physiological regulation and to maintain relatively stable internal elemental ratios, thereby sustaining normal growth and metabolic functions [47]. This physiological characteristic is consistent with the invasion mechanisms inferred from the results of the present study.

4.2.2 Soil physicochemical background drives competitive outcomes through nutrient feedback mechanisms

Invasive plants may adjust their competitive strategies under different resource conditions. For example, the invasive species *Alternanthera philoxeroides* exhibits stronger allelopathic effects under low-nitrogen conditions, whereas the contribution of allelopathy to competition is reduced under high-nitrogen environments, indicating that invasive plants can modify their invasion strategies in response to resource availability [48]. Our results demonstrate that soil physicochemical background strongly influences the competitive outcomes between *S. rostratum* and replacement species. Correlation analyses revealed pronounced differences among soil types in the relationships between plant biomass and changes in soil nutrients, suggesting that soil physicochemical properties do not directly determine competitive success. Instead, they likely shape the direction and intensity of interspecific competition indirectly by regulating nutrient feedback pathways and the identity of limiting factors under different planting treatments. The soil-specific nutrient feedback mechanisms identified here provide important insights into the competitive performance and niche regulation of *S. rostratum* across heterogeneous habitats.

In nutrient-rich soils (e.g. soils 1 and 8), relatively high organic matter content and inorganic nitrogen availability may alleviate single-nutrient limitation, such that competition is no longer dominated by direct exploitation of the same resource. Under these conditions, the biomass of *S. rostratum* and replacement species was associated with different nutrient variables, indicating potential differentiation in resource acquisition and utilization pathways. For instance, *S. rostratum* biomass was primarily correlated with changes in ammonium nitrogen or available phosphorus, whereas replacement grasses such as *L. chinensis* were more closely associated with nitrate nitrogen or soil organic matter. Such differentiation may enable replacement species to establish competitive advantages even under high-resource conditions.

In soils with low initial nitrate nitrogen levels (e.g. soils 4 and 6), soil physicochemical background markedly amplified nutrient limitation effects, resulting in competition characterized by pronounced resource preemption. Correlation results showed that the biomass of most replacement species was significantly associated with changes in nitrate nitrogen or soil organic matter, suggesting that these species were able to effectively utilize or rapidly deplete these limiting resources. In contrast, *S. rostratum* exhibited weaker responses to the same nutrient indicators and was unable to establish stable growth feedbacks. Under these conditions, replacement species suppressed *S. rostratum* growth through efficient occupation of key limiting nutrients, leading to substantial reductions in its biomass.

In soils with rapid turnover of available nutrients (e.g. soils 3 and 7), competitive outcomes were more strongly determined by species' responsiveness to nutrient fluctuations. Correlation analyses indicated that replacement species such as *M. sativa* formed significant positive associations with changes in available potassium or nitrate nitrogen, generating positive feedbacks that promoted their own growth.

765 This suggests that in environments characterized by strong nutrient dynamics, species capable of
766 rapidly responding to and exploiting available nutrients are more likely to gain competitive advantages.
767 Finally, in soils where physicochemical properties explained relatively little variation in plant growth
768 (e.g. soils 2 and 5), correlations between biomass and nutrient changes were generally weak, and
769 competitive outcomes appeared to depend more on intrinsic tolerance and resource-use efficiency. In
770 these soils, although replacement species were less able to establish strong nutrient-driven feedbacks,
771 they were still able to suppress *S. rostratum* through sensitivity to organic matter or specific inorganic
772 nutrients.
773 Soil resource heterogeneity may differentially affect invasive and non-invasive plants by altering root-
774 foraging plasticity and resource acquisition strategies [49]. In the present study, the suppressive effects
775 of replacement grasses on the biomass of *S. rostratum* differed markedly among soil types, indicating
776 that competitive outcomes are strongly soil dependent. Variations in resource availability and the
777 identity of limiting factors appear to be key drivers of this pattern. For example, studies on the invasive
778 species *Centaurea diffusa* in North American grasslands have shown that reductions in resource
779 availability can alter its tolerance to neighbor competition, while exerting relatively limited effects on
780 its competitive impact; moreover, nitrogen and phosphorus limitation do not affect competitive
781 advantage symmetrically, with phosphorus limitation substantially weakening competitive dominance
782 under low-P conditions [50]. This evidence supports the view that differences in limiting factors can
783 fundamentally shape competitive outcomes.
784 When nutrient supply is relatively abundant or nutrient forms are diverse, competition is often no
785 longer strongly constrained by a single resource [51], but instead depends more on interspecific
786 differences in resource acquisition pathways and utilization efficiency [52]. In contrast, under nutrient-

poor conditions or where key nutrient transformation rates are low, competition is more likely to manifest as direct preemption of limiting resources [53], thereby amplifying suppressive effects. However, some studies have shown that certain species, such as *Solidago canadensis*, exhibit relatively low sensitivity of competitive performance to soil origin [54], suggesting that competitive outcomes may also be jointly influenced by species functional traits and resource-use strategies.

Meanwhile, soil nutrients are not static pools. Interactions between plant roots and rhizosphere microorganisms can regulate mineralization, nitrification, and other transformation processes [55, 56], continuously modifying both the quantity and chemical form of nutrients available to plants and thereby further shaping competitive dynamics. In this study, the contrasting correlation patterns between biomass of *S. rostratum* and replacement species and changes in ammonium nitrogen, nitrate nitrogen, and soil organic matter across different soil types provide indirect support for the role of nutrient transformation processes in generating soil background-dependent competitive outcomes.

From an applied perspective, the ranking of suppressive effectiveness among replacement species varied across soils, indicating that replacement control strategies should be tailored to soil conditions rather than relying on a single “optimal” species. Replacement plants that consistently exhibit strong suppressive effects across multiple soil types are more suitable for broad application, whereas species that perform optimally only under specific soil backgrounds may be better suited for targeted management and precision control.

4.3 Feedback effects of competition on heterogeneous soils

4.3.1 Competitive outcomes

Across the eight soil types, mixed planting consistently resulted in lower individual biomass of *S. rostratum*, and lnRR values were negative in all soils, indicating that replacement control plants effectively suppressed the growth of *S. rostratum*. These results support the use of locally dominant species or carefully selected replacement plants to limit the establishment and growth of *S. rostratum* through competitive suppression, representing a feasible control strategy [57]. Moreover, appropriate species selection can substantially enhance restoration outcomes [58].

The reduction in *S. rostratum* biomass under mixed planting likely reflects the combined effects of aboveground and belowground competition. Aboveground, replacement species established rapidly due to higher sowing ratios and may have reduced light availability to *S. rostratum* seedlings through canopy shading [59], thereby constraining growth. Belowground, the strong root proliferation capacity of Poaceae species can enhance soil space occupation [60] and accelerate the depletion of readily available resources, intensifying competition for water and inorganic nutrients. These mechanisms are consistent with general ecological theory, which posits that rapid early growth and effective spatial preemption can generate asymmetric competition and impose disproportionate growth constraints on competitively inferior species.

4.3.2 Competition-mediated regulation of soil nitrogen cycling through changes in nitrogen forms

Previous studies have shown that invasive plants often increase biomass and net primary productivity, enhance nitrogen availability, alter nitrogen fixation rates, and produce litter that decomposes more rapidly than that of co-occurring native species [61]. In the present study, *S. rostratum* monocultures and mixed plantings with replacement species generally increased soil ammonium nitrogen (NH_4^+-N) concentrations across most soil types, with levels significantly higher than those in the blank control,

whereas replacement species grown alone exerted relatively weak effects on NH_4^+-N. This pattern suggests that the growth of *S. rostratum* may promote nitrogen mineralization or modify rhizosphere microbial activity, thereby driving soil nitrogen toward the ammonium form.

Competition has been shown to counteract positive plant-soil feedbacks generated by invasive species [62]. In this study, declines in NH_4^+-N under Poaceae monocultures in some soils may be attributable to their strong nitrogen uptake capacity and preferential use of nitrate nitrogen [63], which could accelerate the depletion of inorganic nitrogen pools.

In contrast, responses of NO_3^--N to planting treatments exhibited stronger soil background dependency. In several soil types, particularly under mixed planting, NO_3^--N concentrations declined significantly, indicating enhanced plant uptake or increased transformation of nitrate under competitive conditions. Conversely, in a few soils, NO_3^--N concentrations increased under replacement species monocultures, potentially due to stimulated rhizosphere nitrification or relatively low plant uptake efficiency. These opposing trends indicate that competition does not influence inorganic nitrogen dynamics uniformly across soils. Instead, under different initial physicochemical conditions, competition may alter the balance between NO_3^--N and NH_4^+-N through distinct uptake and transformation pathways. This finding is consistent with the view that heterogeneous resource backgrounds can modify competitive mechanisms and resource feedback pathways [64].

4.3.3 Effects of competition on available phosphorus and potassium reflect resource-limitation processes

Responses of AK and AP to planting treatments also exhibited pronounced soil heterogeneity. In most soil types, all planting treatments significantly reduced AK concentrations, indicating strong consumption of available potassium by plant growth, with competition likely amplifying the demand

for this resource. In contrast, changes in AP were more species-specific. In some soils, *S. rostratum* monocultures and mixed plantings significantly increased AP concentrations, suggesting that *S. rostratum* may promote phosphorus mobilization through root exudation or microbial mediation. In other soils, however, replacement species grown alone exerted stronger positive effects on AP. These results indicate that different plant species may regulate phosphorus cycling through distinct pathways under competitive conditions, thereby generating differentiated soil nutrient feedbacks.

4.3.4 Effects of plant competition on soil organic matter reflect carbon-nutrient coupling processes

Compared with inorganic nutrients, SOM responded more conservatively to planting treatments overall, although significant differences were still observed in certain soil types. In soil group 6, *S. rostratum* monoculture significantly increased SOM content, which may be associated with higher litter inputs or enhanced root-derived carbon inputs. These patterns suggest that competition influences not only the immediate availability of nutrients but may also indirectly affect long-term soil fertility by altering carbon inputs and decomposition rates, highlighting the coupling between carbon and nutrient cycling processes.

4.4 Implications for the practical application of replacement control strategies

Soil nutrient feedbacks formed during competition between *S. rostratum* and replacement species exhibited pronounced dependence on soil type and competitive context. Certain replacement species were not able to suppress *S. rostratum* through the same mechanisms across all soil types, and their control effectiveness was strongly contingent on specific soil conditions.

In soils characterized by relatively high organic matter and nitrate nitrogen contents or rapid nutrient turnover (e.g., soil groups 1, 7, and 8, and partly soil group 6), replacement plant biomass tended to show significant or marginally significant correlations with changes in nitrate nitrogen or organic matter. Under these conditions, *L. chinensis* and *F. arundinacea* were able to efficiently utilize inorganic nitrogen and organic-matter-related processes, thereby establishing a competitive advantage over *S. rostratum*.

In soils where changes in available phosphorus or potassium represented the primary limiting factors (e.g., soil groups 3 and 7), the biomass of *M. sativa* and *A. cristatum* showed stronger positive correlations with phosphorus or potassium dynamics, indicating higher responsiveness to fluctuations in readily available nutrients. These replacement species were able to establish positive feedbacks under physicochemical conditions characterized by rapid nutrient transformation, resulting in stronger competitive suppression of *S. rostratum*.

By contrast, in soils with generally poor physicochemical properties or where nutrient variation explained little of the variation in plant biomass (e.g., soil groups 2 and 5), correlations between plant biomass and most soil nutrients were weak, and competitive advantages were not driven by a single limiting resource. Under such conditions, *M. sativa* exhibited relatively rapid responses to changes in ammonium nitrogen and available phosphorus, enabling it to gain a competitive advantage in stable but resource-limited environments. In these soils, only replacement species with high stress tolerance or the ability to respond to multiple nutrient changes were able to maintain consistent suppressive effects.

Overall, Pearson correlation analyses indicated that no single replacement species was universally effective across all soil types. The ability of replacement plants to suppress *S. rostratum* in a given soil depended critically on whether they could establish stable positive feedbacks with the dominant

limiting nutrient dynamics in that soil. These findings underscore the importance of explicitly accounting for soil physicochemical heterogeneity when designing replacement control strategies for invasive species.

Therefore, practical management of *S. rostratum* invasion should prioritize soil-specific selection of replacement species rather than relying on a single species or uniform control approach. Matching soil nutrient backgrounds with the functional traits of replacement plants may facilitate the development of soil-plant feedbacks unfavorable to *S. rostratum*, thereby enhancing the long-term stability and effectiveness of replacement control strategies.

5. Conclusions

This study employed a two-factor, completely randomized block pot experiment to investigate the growth responses of *S. rostratum* and six replacement forage species under monoculture and mixed planting across eight contrasting soil types, and to examine the regulatory role of plant-soil nutrient feedback in replacement control effectiveness. The main conclusions are as follows:

Replacement forages generally suppressed *S. rostratum* across all soils, although the degree of suppression was strongly soil-dependent. Mixed planting consistently reduced leaf chlorophyll content and biomass of *S. rostratum*, with negative lnRR values were across all soil types, indicating a uniform inhibitory direction of interspecific competition. In most soils, *L. chinensis*, *M. sativa*, *A. cristatum*, and *F. arundinacea* showed relatively strong suppression, achieving biomass reductions exceeding 90% in certain soils. However, the best-performing replacement species varied among soil types, highlighting pronounced dependence of replacement control on soil context.

The presence of *S. rostratum* altered soil nutrient status, but the direction of change depend on both soil type and competition scenarios. Overall, soil NH_4^+-N tended to increase after *S. rostratum* growth,

whereas soil organic matter generally declined. In contrast, NO_3^--N, available phosphorus, and available potassium exhibited variable patterns across soil types and planting treatments, suggesting that the impacts of *S. rostratum* on nutrient dynamics are contingent on initial soil conditions.

Soil nutrient changes were coupled with trait variation in *S. rostratum*, but this relationship showed limited consistency under soil heterogeneity. Redundancy analysis indicated that changes in soil nutrients explained 30.69% of the variation in *S. rostratum* traits, yet the overall model was not significant. This suggests that under heterogeneous soil backgrounds, the linear "nutrient change-trait response" relationship may be attenuated and likely regulated by soil-specific limiting factors.

Soil physicochemical context likely modulates replacement control by shaping the coupling between nutrient feedback and biomass responses, thereby influencing which replacement species becomes dominant. Integrating correlation patterns with suppression outcomes suggests that in soils with higher organic matter or greater nitrogen availability, *L. chinensis* and *F. arundinacea* were more likely to gain competitive advantages. In soils where biomass responses were more tightly linked to fluctuations in readily available nutrients, *M. sativa* and *A. cristatum* tended to exhibit stronger suppression. In nutrient-poor soils or soils showing generally weak nutrient-biomass coupling, *M. sativa* maintained relatively stable suppression, indicating comparatively high environmental adaptability and application potential.

In summary, while replacement control consistently inhibited *S. rostratum* across diverse soil types, its efficacy and the optimal replacement species varied substantially with soil conditions. These findings highlight the importance of matching replacement species to site-specific soil types and nutrient regimes—potentially mediated through soil nutrient feedback processes—to improve the long-term stability and sustainability of replacement control strategies.

Declaration

Ethical Approval

Not applicable. All methods were carried out in accordance with relevant guidelines and regulations.

Consent for publication

Not applicable.

Availability of data and materials

The data are available from the corresponding author on reasonable request.

Competing 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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Authors' contributions

Z. Y. and Z. G. conceived and conceptualized the research. Y. Z., S. C., and Z. Y. performed the methodology development. Y. Z. and Z. Y. conducted the formal analysis and investigation. Y. Z. prepared the original draft of the manuscript. F. W., S. Z., W. Z., S. C., Z. Y., and Z. G. contributed to writing, reviewing, and editing the manuscript. Z. Y. and Z. G. acquired funding and provided

supervision. All authors contributed critically to the drafts, approved the final version of the manuscript, and agree to be accountable for all aspects of the work.

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